

Offspring sex ratio in red-winged blackbirds is dependent on maternal age

(parental age/reproduction/offspring sex/population dynamics)

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ABSTRACT In a marsh-breeding population of red-winged blackbirds, the sex ratio of offspring that survived to leave the nest varied with maternal age. Old mothers produced an excess of male fledglings, middle-aged mothers produced almost equal proportions of males and females, and young mothers produced nearly twice as many females as males. More males than females hatched from the eggs of old mothers, whereas among newly hatched progeny of middle-aged and young mothers the sex ratio did not differ from unity. The hatching rate of eggs of old mothers was unusually low, suggesting that the biased sex ratio of their hatchlings may have been caused by more frequent death of female embryos, although other possibilities can be imagined. Starvation of nestlings after hatching also affected the sex ratio among young that left the nest. When starvation occurred, it fell principally on young produced by the last and next-to-last eggs laid in the clutch. Because old mothers allocated relatively more energy to those eggs than to earlier-laid eggs, whereas young mothers apportioned energy equally to their eggs, few nestlings of old mothers but many nestlings of young mothers starved. Most nestlings that died were male. It followed that the male bias in sex ratio of progeny of old mothers did not change between hatching and nest-leaving, but the ratio among progeny of young mothers shifted after hatching to a strong bias favoring females at nest-leaving.

Even though the age of breeding birds within a population may vary considerably (1-3), little advance has been made toward a comprehensive empirical analysis of the effects of individual age on reproductive performance. Adequate knowledge of how individuals of different ages vary in reproductive output requires long-term field research on single populations, and the difficulty of this requirement has impeded progress. Nevertheless, arriving at a better understanding of age-dependent reproductive processes is of great importance. Age structure is a major element in several key theories pertaining to population biology (4-6), and what few data exist support the view that reproductive performance and age are often related (1, 2, 7).

We searched for and found age-dependent reproductive patterns in a marked population of red-winged blackbirds (*Agelaius phoeniceus*) that had been under continuous study during 10 previous breeding seasons. Redwings, which are widespread throughout North America and have been extensively studied because of their polygynous mating system (8), have several characteristics that rendered them a promising species for this investigation. First, nearly all parental care bestowed directly on the nest and its contents, from building until young leave the nest, is provided by the female. If parental age significantly affects reproductive performance, we postulated that such effects would be most easily detected when a single parent bore most or all of the direct burdens of supplying energy to eggs

and nestlings. Second, the annual survival rate and the fidelity of adults to the breeding site of the previous year are high among redwings (9), so that it is possible to study large samples of birds whose ages and past breeding experience are known. Third, the intense theoretical interest in the general breeding biology of this species has produced a considerable literature for reference and comparison.

In this report we present results that demonstrate parental adjustment of the offspring sex ratio and the dependence of this adjustment on parental age. Specifically, we examine the relationship between age of the female parent and four breeding parameters of importance to female adjustment of the sex ratio: allocation of energy to embryos, sex ratio of offspring at hatching, nestling survivorship, and sex ratio of offspring at nest-leaving.

In his analysis of sex ratio variation, Fisher (10) argued that natural selection will act to maintain the sex ratio at an equilibrium because of the mating advantage that would otherwise accrue to the progeny of individuals producing the minority sex. Whenever the sex ratio of the population deviates from the equilibrium, any genetic disposition to produce the rare sex will be favored by selection and the ratio will eventually return to the equilibrium. The numerical value at the point of equilibrium, according to Fisher, will depend upon the relative expense to the parents of producing and rearing each sex. When males and females are equally costly to rear, the population's sex ratio should be 1:1; when the sexes differ in cost, greater numbers of the less costly sex should be produced.

Notably, Fisher's argument predicts relative values of the sex ratio only at the level of the entire population; it does not speak to the questions of whether and how individual parents within a population having a 1:1 offspring ratio might nevertheless tend to produce more sons or more daughters. Extensions of Fisher's work to account for sex differences in expected fecundity or survivorship (11, 12) have allowed construction of models that predict facultative manipulation of the sex ratio by parents. Whereas data from several vertebrate species (13, 14) have conformed to Fisher's population predictions, attempts to identify instances in which there is variance among parents within a natural population have been largely unsuccessful (15).

Our results show the presence of significant variation among parents in the production of sons and daughters within a natural population of redwings despite the fact that the offspring sex ratio at the population level did not differ from unity. A shift from production of more daughters to production of more sons was related to maternal age and had two primary causes. A pre-hatching mechanism caused the eggs of old mothers to produce a disproportionate number of males; this was not the case with young mothers. Further, maternal age-dependent variations in

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the pattern of allocation of energy to embryos within the clutch influenced nestling starvation and, as a result of this starvation, the sex ratio of the survivors that left the nest. Nestlings of young mothers starved more often than did those of old mothers, and the sex of starved nestlings was usually male.

METHODS

This investigation was conducted in a marsh of approximately 2.5 hectares ($2.5 \times 10^4 \text{ m}^2$) adjoining Yellowwood Lake, Brown County, Indiana. Every year about 23 males establish breeding territories at this site and mate with 1 to 10 females each. Redwings exhibit extreme sexual size dimorphism, and this appears early in life. Adult male body mass [$\bar{x} = 67.5 \pm 0.85$ (SEM) g, $n = 75$] averages approximately 38% greater than adult female body mass ($\bar{x} = 42.0 \pm 0.39$ g, $n = 30$); at nest-leaving, males ($\bar{x} = 35.74 \pm 0.45$ g, $n = 65$) are 25% larger than females ($\bar{x} = 26.71 \pm 0.25$ g, $n = 80$) on the average (16).

Study of this population began in 1969 (9, 17, 18). During a continuous banding program thereafter, nearly all breeding individuals were marked with unique combinations of color-coded bands. In the years reported on here, 1978 and 1979, 85% of all successfully breeding females were identifiable at sight. We classified these as young (1 to 2 years old), middle-aged (3 to 4 years old), or old (at least 5 years old). Age was determined by one of two criteria. First, minimal ages of many were revealed by the records of the banding program ($n = 35$). Second, for females that had not previously bred at the marsh we estimated age on the basis of knowledge of age-dependent variation in plumage ($n = 68$); we had derived this knowledge from studying plumage changes in a series of banded individuals over several years. Wing epaulets (marginal coverts) of females range from dull brown in yearlings to bright crimson in old birds, and the size of the area of brighter coloration increases with age. We therefore matched every female's wing epaulets with 1 of 12 ranked photographs showing epaulets of different color and size, and assigned each individual a rank. In 1978 and 1979, among banded females of known minimum age, a significant positive correlation existed between minimal age (1 to 10 years) and epaulet rank (Spearman rank correlation coefficient, $r_s = 0.55$, $n = 15$, $P < 0.005$). [In 1982 the method was applied to the epaulets of 48 females with known minimal ages of 1 to 7 years, breeding at the site we studied; $r_s = 0.67$, $P < 0.001$ (James Hengeveld, personal communication).] Accordingly, on the basis of ranks of their epaulets we placed our previously unbanded females in one of the three age classes described above.

We made or performed the following additional observations or operations: Clutch size varied between two and five; clutches of four made up 57% and clutches of three, 35%. Clutch size did not differ with maternal age. Each egg, on the morning it was laid, was measured (length and width) and weighed to 0.1 g with a 10-g Pesola balance; its numerical sequence in the clutch was marked on its shell. Egg mass was converted to energy units by using a table that we derived from direct calorimetry of freshly laid redwing eggs collected from marshes near the study area. This calorimetry analysis revealed a significant and positive relationship between energy content and mass (least squares regression, $r^2 = 0.82$, $n = 19$, $P < 0.01$; $y = 4.73487x + 4.18429$, in which y = energy content in kilojoules and x = egg wet weight in grams).

Nests were visited every other day until it was time for their eggs to hatch, after which they were inspected every few hours during daylight until hatching was completed. Hatchlings were associated with the eggs from which they emerged and were marked for subsequent individual recognition; 77% of all hatchlings could be assigned to the eggs that produced them.

Time intervals between successive hatchings of eggs within the clutch were recorded.

Body mass of each offspring was determined to 0.1 g within 1 hr of its hatching. Just after the last egg in a clutch hatched, that hatchling was weighed for the first time, and all its earlier-hatched nest mates were weighed, these for the second time. Thereafter, all siblings were weighed every day or every other day, until they starved or left the nest. Nestlings that starved showed a characteristic decline in growth rate and exhibited a substantial decline in body mass in the few hours preceding death; in no case did all members of a brood starve. Predation was the only other known cause of nestling mortality during this study and was characterized by the disappearance of the full brood between two of our visits to the nest. The incidence of nest predation did not vary with maternal age.

The sex of each nestling was determined by laparotomy (incision of the rib cage) on the fifth or sixth day after hatching. An otoscope with a magnifying ocular and a tapered plastic viewing tip was used to inspect the gonad. Statistical tests of experimental and control nestlings and fledglings have shown that this procedure has no effect on nestling growth or survival (16).

Results reported here derive from clutches produced by 103 females. We focus on 4-egg clutches, the modal size, and note the results from 3-egg clutches only when they differ. In χ^2 tests in which $df = 1$, Yates' correction has been made.

RESULTS

Energy Content of Eggs. The relationship between an egg's number in the laying sequence of the clutch and its energy content relative to that of the other eggs in its clutch varied with maternal age (Fig. 1A) in four-egg clutches. Energy content of eggs of old mothers increased significantly [one-way analysis of variance (ANOVA), $P < 0.01$] with laying sequence; the mean mass of the first egg in broods of four was significantly different from mean mass of all other eggs in the laying sequence (Student-Newman-Keuls test, $P < 0.05$). In contrast, middle-aged and young females allocated equal amounts of energy (one-way ANOVA, $P > 0.05$; Student-Newman-Keuls test, $P > 0.05$, in each case) to all eggs in the clutch (Fig. 1A). In three-egg clutches, distributions of energy were similar to those just described, but differences among age classes were not significant.

Old females began to lay approximately 16 days earlier in the season than young females, on the average, but the age-related difference in allocation of energy to eggs was invariant throughout the season; that is, the age-specific differences in allocation patterns were independent of possible environmental differences associated with date of laying. In one test for a relationship between date of laying and allocation patterns, we calculated for all clutches the proportional difference between the masses of first and third eggs [$\arcsin(\text{first egg}/\text{third egg})$] and used this as an index of variation in egg size with egg number. The first and third eggs were chosen because the difference between them represented the largest size change (if any) with laying sequence over the smallest number of eggs. Within each age class, this index value was independent of breeding date (least squares regression, young females $r^2 = 0.08$, $n = 16$, $P > 0.30$; middle-aged females, $r^2 = 0.2$, $n = 16$, $P > 0.30$; old females, $r^2 = 0.2$, $n = 22$, $P > 0.30$). Other analyses of allocation patterns (e.g., comparisons restricted to periods during which females of all ages were laying) also reached the same negative result (16). Data for three-egg clutches were insufficient for statistical comparison.

Hatching Asynchrony, Hatching Order, Hatching Rate, and Sex Ratio of Hatchlings. In pooled three-egg ($n = 28$) and four-egg ($n = 74$) clutches, the interval between hatching of the first

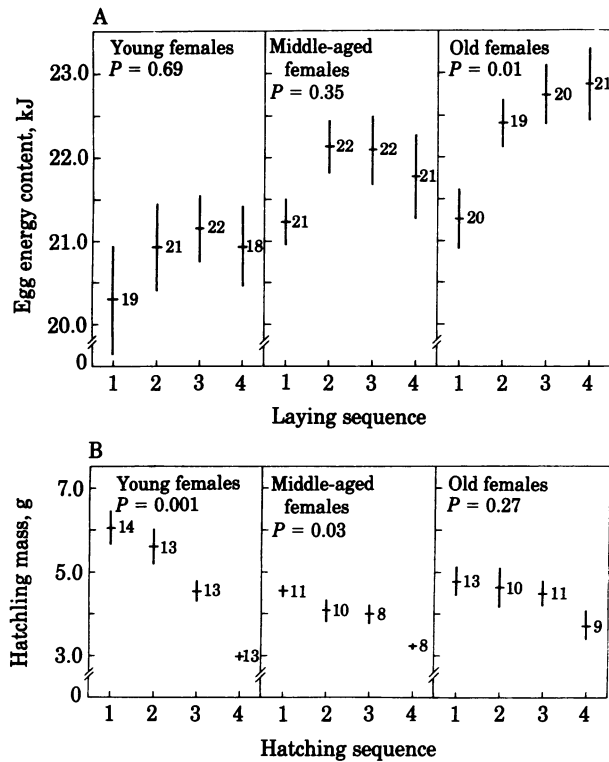


FIG. 1. (A) Variation in egg energy content in clutches of four as a function of position in the laying sequence and according to female age class. Energy contents of eggs were determined as described in the text. (B) Variation in mass of members of broods of four as a function of position in the hatching sequence and according to female age class. Brood members were weighed just after the last egg hatched. Data are presented as mean \pm SEM; sample size is shown beside each mean; and a one-way ANOVA was performed for data within each age class.

and last eggs of the clutch ranged from 0 to 48 hr, with a mean \pm SEM of 17.9 ± 1.2 hr. In four-egg clutches the mean of this measure of hatching asynchrony was 64% greater than in three-egg clutches. There was a slight trend toward reduced asynchrony with increasing maternal age (one-way ANOVA, $F_{(2,54)} = 2.18, 0.25 > P > 0.10$) in four-egg clutches; data for three-egg clutches were insufficient for this comparison. Eggs nearly always hatched in the order laid and invariably did so when asynchrony of hatching was considerable. In four-egg clutches in which both laying and hatching sequence were known for all eggs, eggs hatched in the order laid in 31 of 34 nests. In clutches of three, the comparable figures were 16 of 20 nests.

Considering only eggs that were present in the nest when hatching began, the percentage that hatched varied according to maternal age, as follows: old females 74.5% (105 of 141), middle-aged females 84% (127 of 151), and young females 93% (104 of 112) ($\chi^2 = 15.23, df = 2, P < 0.001$). Estimated energy contents of eggs that failed to hatch were not different from those of eggs that hatched. Mean energy content per egg of old females [$\bar{y} = 22.32 \pm 0.19$ (SEM) kJ] was slightly greater (one-way ANOVA, $F_{(2,242)} = 3.09, P < 0.05$) than that of females of the other age classes (young females, $\bar{y} = 20.48 \pm 0.27$ kJ; middle-aged females, $\bar{y} = 21.82 \pm$ kJ). No seasonal trends in frequency of egg death were detectable, and no association was found between egg death and the presumed paternity of the eggs. Therefore, the data suggest a negative correlation between hatching success and maternal age, independent of the factors just mentioned.

For each maternal age class we estimated the sex ratio at hatching by adding the numbers of starved nestlings whose sex

we determined by dissection to the numbers of nestlings that survived to leave the nest. Starved nestlings that we could not recover for sexing (see below) were not counted. This procedure assumes (i) that the sex ratio among starved offspring that we were unable to recover and include in our estimates was the same as the ratio among starved and surviving young whose sex we ascertained, and (ii) that the entire broods that were taken by predators before we could sex them were not taken for reasons associated with their sex ratio (cf. ref. 13).

The sex ratio at hatching of offspring of young mothers was not significantly different from unity, although females were in a majority (36 males to 52 females, $\chi^2 = 2.56, df = 1, P > 0.10$). For middle-aged females, the ratio was 54 males to 66 females ($\chi^2 = 1.01, df = 1, P > 0.20$). In broods of old females the ratio was 55 males to 34 females ($\chi^2 = 4.49, df = 1, P < 0.05$). The difference among age classes is significant ($\chi^2 = 8.90, df = 2, P < 0.02$).

The sex ratio at hatching (hatched males/hatched females) declined with breeding date (arcsin transformations of percent males, $r^2 = 0.42, P < 0.05$). Again, in an effort to determine whether the maternal age-dependent ratios reported above differed merely as a function of date of laying (see above and refs. 13 and 14), we compared for each maternal class the sex ratio among offspring produced during the first half of the breeding season with the ratio among those produced during the second half (Table 1). For each age class, the difference was nonsignificant, indicating an effect of maternal age on hatching sex ratio, independent of breeding date.

Nestling Body Mass and Probability of Starvation, According to Hatching Sequence. When broods of four were weighed just after the fourth egg hatched (Fig. 1B), the relationship between a nestling's place in the hatching sequence and its body mass varied according to the age of its mother. In nests of young female parents, nestling body mass at this time declined significantly with hatching sequence (one-way ANOVA, $F_{(3,49)} = 13.75, P < 0.001$); the fourth nestling to hatch averaged 34.2% less in mass than its most recently hatched sibling [$\bar{x} = 2.98 \pm 0.10$ (SEM) g vs. $\bar{x} = 4.53 \pm 0.40$ g] and 50.7% less than the first nestling to hatch ($\bar{x} = 2.98 \pm 0.10$ g; vs. $\bar{x} = 5.99 \pm 0.40$ g). For nestlings of middle-aged females, the decline was significant though less extreme (one-way ANOVA, $F_{(3,33)} = 5.87, P < 0.01$); the fourth nestling to hatch averaged 29% less in body mass than the first nestling to hatch ($\bar{x} = 3.23 \pm 0.06$ g vs. $\bar{x} = 4.53 \pm 0.15$ g). In contrast to both these results, nestlings in broods of old females did not differ significantly in mass immediately after the last egg hatched (one-way ANOVA, $F_{(3,39)} = 1.39, P < 0.25$). For three-egg clutches, trends were similar

Table 1. Sex ratio of offspring produced in the first and second halves of the breeding season, according to maternal age class

Maternal age class	Half of breeding season	Sex ratio			
		Hatching		Nest-leaving	
		No. of males	No. of females	No. of males	No. of females
Young	First	8	14	7	13
	Second	25	47	21	37
Middle-aged	First	32	33	32	33
	Second	22	32	21	33
Old	First	39	26	39	26
	Second	16	8	15	8

For each age class the sex ratio is given at time of hatching and time of nest-leaving. In no age class were differences in numbers of male and female offspring in the first and second halves of the season significant, either at hatching or at nest-leaving (contingency table analyses, $P > 0.1$ in all cases).

to those in four-egg clutches but were not significantly different.

Twenty-six cases of starvation were observed in the nests under consideration. The probability that a nestling would starve was related to (i) the age of its mother, (ii) its position in the laying (therefore hatching) sequence, (iii) its sex, and possibly (iv) the number of its nest mates. Starvation was highest by far among offspring of young females. Among 28 broods of young females in which at least one nestling left the nest, 19 experienced at least one case of starvation. Just prior to the first death in these 19 nests, 9 broods consisted of four nestlings, 6 of three nestlings, and 2 each of two and five nestlings. By comparison, in 33 broods of old and 41 broods of middle-aged females, only three and four offspring starved, respectively.

With respect to the relationship between starvation and hatching sequence in broods of young mothers whose last-laid egg hatched, 12 of 18 nestlings (67%) from that egg starved. Of 19 nestlings that hatched from the penultimate egg, 9 (47%) starved. By comparison, of the 40 nestlings that hatched from the last or penultimate egg in nests of old and middle-aged parents combined, 5 (12.5%) starved. Hence, a nestling's place in the hatching sequence principally affected its probability of survival when its mother was young.

An offspring's sex strongly influenced its chances of starving. We determined the sex of 17 nestlings that starved; the remainder were removed from the nest by the female before we were able to recover and dissect them. Of the 17 examined, 15 were male ($\chi^2 = 8.47$, $df = 1$, $P < 0.001$). Among eggs that hatched, there was no indication that position in the laying sequence was associated with sex of the embryo nor any indication that eggs from which males and females hatched differed in their energy context.

Finally, probability of starvation of nestlings may have been affected by brood size at hatching. Because fewer eggs of old mothers hatched, mean brood size of that age class was 3.02 ± 0.16 (SEM) ($n = 34$), as compared to 3.00 ± 0.13 ($n = 39$) for middle-aged mothers and 3.54 ± 0.16 ($n = 26$) for young mothers. In a one-way ANOVA ($F_{(2,96)} = 3.66$, $P < 0.05$), young mothers differed significantly from middle-aged and old mothers (Student-Newman-Keuls test, $P < 0.05$). Thus, young mothers, having larger broods to feed, may have been less able to meet the energy demands of all their nestlings, even though most of these nestlings were female (cf. ref. 13).

Sex Ratio of Fledglings. The sex ratio at nest-leaving varied significantly with maternal age (Table 2). Young mothers produced nearly twice as many female as male fledglings ($\chi^2 = 5.56$, $df = 1$, $P < 0.05$); middle-aged mothers produced statistically indistinguishable numbers of male and female fledglings ($\chi^2 = 1.21$, $df = 1$, $P > 0.20$); and old mothers produced significantly more males ($\chi^2 = 4.10$, $df = 1$, $P < 0.05$). This difference was independent of date (Table 1).

The sex ratio of all offspring to leave the nests of all females breeding at this site did not differ from unity (175 males:201 females, $\chi^2 = 1.66$, $P > 0.4$).

Table 2. Number of male and female offspring surviving to leave the nest, according to maternal age class

Maternal age class	No. of surviving males	No. of surviving females	χ^2 value
Young ($n = 31$)	28	50	5.65*
Middle-aged ($n = 41$)	53	66	1.21
Old ($n = 31$)	54	34	4.10*

Number of female parents in each age class is shown in parentheses. * $P < 0.05$.

DISCUSSION

Variation in egg mass according to the egg's sequence in the clutch has been described in other bird species (e.g., refs. 1, 14, and 19), but variation limited to particular maternal age classes has not previously been reported. Because of the importance we attach to the effect of this variation on the sex ratio of offspring that survived to leave the nest, we emphasize that seasonal differences (if any) in factors influencing egg size cannot account for our data. The findings of a bias toward males in the hatchlings and fledglings of old female parents also have no reported parallel in natural-breeding avian populations. Among other vertebrates, no data parallel the trends we have described. Long-term study of red deer (11) indicates no variation in sex of offspring with maternal age. Records from some human populations (20, 21) illustrate little or no effect of maternal age on the sex ratio once other factors (principally birth order and paternal age) are taken into account. Indeed, where variation in sex ratio occurs with age of the human mother, deviations from unity are so small, in light of sample sizes exceeding 100,000, that meaningful generalizations concerning the significance of the variation are difficult to derive.

We attribute the maternal age-specific variation in sex ratio at the time of nest-leaving to (i) the mechanism(s) that skewed the sex ratio in favor of males among hatchlings of old mothers, and (ii) the considerable incidence of nestling starvation in broods of young mothers, with most of this mortality impinging on males. Intermediate were middle-aged mothers whose offspring sex ratio was neither unbalanced at hatching nor altered thereafter by any substantial mortality of nestlings.

Causes of the male-biased sex ratio at hatching in clutches of old females could, in theory, include nonrandom segregation of sex chromosomes resulting in an unbalanced sex ratio of ovulated gametes (among birds, the female is heterogametic), differential mortality of female offspring after ovulation, or some combination of these. If the data derived from this 2-year study can be extrapolated, and if they reflect adaptive variation in the sex of offspring produced over the course of an individual's life, the heavy mortality of embryos of old mothers seems a costly way to manipulate the offspring sex ratio. But it is noteworthy that the rate of hatching failure (25%) in eggs of this age class was unusually high for a passerine bird (5–15% are common extremes; see refs. 1 and 22) and, taken together with the other results reported here, this rate seems suggestive of disproportionate deaths among female embryos.

As for the mechanism (i.e., nestling starvation) that accounts for the second cause of age-specific variation in offspring sex ratio at nest-leaving, we propose an interaction of the following two factors: (i) At the moment offspring from the last and next-to-last eggs of young female parents hatched, they were at a considerable disadvantage to their siblings because of their smaller body mass, despite the fact that all the eggs of young mothers received equal energy. The disadvantage arose out of the asynchrony of hatching of eggs within the clutch. The effect of this asynchrony was that offspring from early-hatched eggs had received considerable food and therefore had developed greater body mass by the time late-hatching siblings emerged. Hence, when mothers—in most cases young mothers—were unable to deliver food sufficient for the entire brood, late hatchlings were more likely to suffer in competition with their larger siblings. (ii) Male redwing nestlings attain a much greater body mass than female nestlings during the same interval of development, and therefore they require more energy (cf. ref. 23). The combined effect of these two factors was, we suggest, that when offspring hatching from eggs laid last or next-to-last in clutches of young mothers were male, they faced a high risk

of receiving insufficient food to meet their greater energy requirements. In sharp distinction, males produced by the late-hatching eggs of old mothers and, to a lesser extent, of middle-aged mothers did not confront this same risk because they did not suffer a comparable disadvantage despite asynchronous hatching. These late-hatched nestlings of older parents had received compensation for the effects of a delayed start on growth, relative to their siblings, by the fact that their eggs had been more heavily provisioned; when they hatched they were already as large as their nest mates (Fig. 1B). The disparity in starvation rates of nestlings of young and of old mothers reflects, at least in part, the effectiveness of this energetic compensation for the late start produced by hatching asynchrony.

The importance of this study lies in its identification of the presence of significant variation in production of sons and daughters by parents of different ages and of factors that were responsible for the variation. This interesting age-associated shift would have been concealed if only the fledgling population as a whole had been considered, because at that level the sex ratio did not differ significantly from unity. Thus, the absence of deviation from theoretically predicted sex ratios in a population (24) may lead to inaccurate conclusions regarding the lability of individual manipulation of offspring sex. Equally, the identification of variation in offspring sex ratio at the population level (13, 14) provides no information about how individual parental investment influences the numbers of each sex produced or about the parental attributes and environmental factors that affect this investment.

We have demonstrated that an age-dependent pattern of investment of energy in embryos and a mechanism causing the production of more sons at the hatching of eggs of old mothers are two factors influencing the offspring sex ratio. Further investigation of these factors and of other parental attributes should clarify the subjects of (i) proximate control of the sex of offspring in this species, as well as (ii) the consequences of variation in offspring sex for parental reproductive success. The

redwing offers an excellent natural system for long-term observational and experimental study of these matters.

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