12.

Reproductive Cost and the Sex Ratio in Red-Winged Blackbirds

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The study of the sex ratio occupies a unique place in evolutionary biology. Darwin himself (1871) recognized the sex ratio as an attribute that should be explicable by natural selection, yet after reviewing a wide variety of data, he remained unable to find a selective advantage for one sex ratio over another and explicitly left the problem to future generations to solve. It remained unsolved until 1930, when Fisher (1958) hypothesized that natural selection would adjust the sex ratio so as to equalize parental expenditure in the two sexes. Williams (1966a, p. 21) singled out this hypothesis as a major generalization connecting evolutionary theory and observation and apparently considered the sex ratio to be the major solved problem of evolutionary biology (ibid., p. 272).

Yet, although Fisher's principle has been repeatedly modelled mathematically (Shaw and Mohler, 1953; Bodmer and Edwards, 1960; Kolman, 1960; Mac Arthur, 1965; Verner, 1965; Leigh, 1970; Emlen, 1973; Charnov, 1975) and extended to special cases, including local mate competition (Hamilton, 1967), facultative control (Trivers and Willard, 1973; Werren and Charnov, 1978), and parent-offspring conflict (Trivers, 1974; Trivers and Hare, 1976), it has not received rigorous empirical study. In accounting for the generality of the 1:1 sex ratio and for the independence of the sex ratio from the breeding system, it is consistent with a mass of data, but it is not the only hypothesis that might be so. One might argue that the sex ratio is simply an unmodifiable effect of meiosis (Maynard Smith, 1978). That reasoning, similar to Fisher's accounts for skewed sex ratios in haplodiploid organisms (Hamilton, 1967), gives the genetic aspect of Fisher's principle additional credence, but the aspect of equality of expediture has remained little studied. This inattention is probably largely because few organisms have offspring that clearly receive parental care differentially according to sex and because parental care is difficult to quantify.

In the first part of this paper, I develop a general model of natural selection of the sex ratio, incorporating an operational concept of ''parental expenditure'' (here called reproductive cost). In the second part I report an experimental test of the model in a sexually dimorphic species.

THEORY

A fundamental assumption of life history theory is that natural selection tends to maximize the malthusian parameter or genotypic rate of increase, m (Fisher, 1958). It has been shown (Schaffer, 1974a; Taylor et al., 1974) that a life history that maximizes m also maximizes reproductive value v_x/v_0 at any age x, in the sense that any feasible departure from the optimal life history will decrease both m and v_x/v_0. This result simplifies the modelling of life histories, for it proves to be easier to model the maximization of reproductive value than of m.

Fisher (1958, p. 158) originally pointed out that "the problem of the influence of Natural Selection on the sex-ratio may be most exactly examined by the aid of the concept of reproductive value," and following this lead, the several subsequent approaches to expressing Fisher's principle symbolically (cited above) have all made use of some equivalent of reproductive value. Also like Fisher, nearly all have used some concept of expenditure; still this latter concept remains nebulous. Fisher himself did not carefully define parental expenditure but referred to expenditures of nutriment, time, and activity. But the maximization of reproductive value implies that the effects of such expenditures are subsumed as effects on reproductive value, making it necessary to express expenditure in the same terms as reproductive value.

A useful approach to the problem has been to partition reproductive value at the onset of the breeding season into two components, that accruing to the parent through the expected reproduction of its offspring produced at that time (current reproductive value) and that retained by the parent (residual reproductive value, the present value of all future reproduction (Williams, 1966b; Schaffer, 1974a)). Any event or behavior may be said to be costly to an organism if it decreases either or both of the components of the organism's reproductive value. In particular, any behavior that decreases residual reproductive value while tending to increase current reproductive value may be said to impose a reproductive cost, even if the net effect is to increase total reproductive value. The magnitude of a reproductive cost is the present value of the future reproduction "foregone" (in the sense that the expectation of future reproduction has been reduced) in order to accomplish the increase in current reproductive value. Thus the overall cost of a particular reproductive episode is the present value of all future reproduction foregone in order to reproduce at that time (Hirshfield and Tinkle, 1975). This cost concept is in keeping with the economic concept of opportunity cost, which is that the true cost of any action can be measured by the value of the best alternative that must be foregone when the action is taken (Nicholson, 1972).

I will regard a parent's current reproductive value, C, and its residual reproductive value, R, both measured at the time of conception of offspring, as continuous functions of the numbers of sons, M, and daughters, F, conceived:

$$C = f_1(M,F); R = f_2(M,F).$$

Total reproductive value of the parent is then $V = C + R$. The benefit and cost of producing an offspring will be expressed as the resultant changes in C and R, respectively. I will also use the term "reproductive investment" to mean the incurring of a reproductive cost or the cost incurred.

The model specifically refers to the time of conception because it is only then that a gene influencing the sex ratio can be expressed. Whether or not investment is in any sense "equalized" by the end of parental care is essentially an incidental effect of selection at conception. Note that this restriction reduces such disparate cost factors as differential mortality and "differential demands" to a common basis. Greater demands by one sex on the parent tend to increase that sex's expected cost, while greater mortality of one sex tends to lower its expected cost, owing to the greater probability that the full cost will not be incurred.

A population's primary sex ratio will be in selectively stable equilibrium when the total differential of reproductive value with respect to the mean numbers of sons and daughters,

$$\mathrm{d}V = \left(\frac{\partial C}{\partial M} + \frac{\partial R}{\partial M}\right) \mathrm{d}M + \left(\frac{\partial C}{\partial F} + \frac{\partial R}{\partial F}\right) \mathrm{d}F$$

equals zero. If this were not so, then there would be some sex ratio other than the average that would give a selective advantage to those genotypes producing it. Assuming $\mathrm{d}V = 0$ and rearranging,

$$\frac{-\mathrm{d}M}{\mathrm{d}F} = \frac{\dfrac{\partial C}{\partial F} + \dfrac{\partial R}{\partial F}}{\dfrac{\partial C}{\partial M} + \dfrac{\partial R}{\partial M}} \tag{1}$$

This result implies a functional relationship between M and F, the nature of which depends on additional constraining assumptions. In all related previous models, the assumed constraint has been that the total investment is fixed, and that clutch size then varies with the sex ratio (assuming that there is cost dimorphism). In the present context, this is equivalent to fixing R. Assuming this, then by the implicit function theorem,

$$\frac{\partial R / \partial F}{\partial R / \partial M} = \frac{-\mathrm{d}M}{\mathrm{d}F},$$

and by substituting into (1) and rearranging, the sex ratio is found to be stable when

$$\frac{-\mathrm{d}M}{\mathrm{d}F} = \frac{\partial R / \partial F}{\partial R / \partial M} = \frac{\partial C / \partial F}{\partial C / \partial M}. \tag{2}$$

From this it may be seen that a more general way of stating Fisher's principle is that the population sex ratio will be stable when the ratio of marginal costs of the two sexes equals the ratio of their marginal values.

A complementary model that has not been previously examined but which may be more appropriate for many organisms (e.g., birds) is that in which the clutch size is fixed, and cost varies according to the sex ratio. In this case, $\mathrm{d}M = -\mathrm{d}F$ and therefore, at equilibrium

$$\frac{\partial C}{\partial F} + \frac{\partial R}{\partial F} = \frac{\partial C}{\partial M} + \frac{\partial R}{\partial M}.$$

Both models give the same sex ratio for the globally optimal clutch size because at that point $\partial C / \partial F = -\partial R / \partial F$ and $\partial C / \partial M = -\partial R / \partial M$. However, the two cases predict different paths toward equilibrium from non-equilibrial states. In general, the stable sex ratio is nearer 50 per cent under clutch size constraint than under investment constraint for smaller-than-optimal clutch size and further from 50 per cent for greater-than-optimal clutch size.

It remains to determine the functional relationships between value and cost, respectively, and clutch composition. Although the contrary assumption is commonly made (it is implicit in Fisher's principle), both functions cannot be linear. If they were, the optimal clutch size would in all instances be either zero or infinite. (But the stable sex ratio would be independent of investment. This allows the success of linear models such as those of Fisher and of Bodmer and Edwards (1960) and others.) For the purposes of modelling sex ratio optimization, it has proven instructive to consider the implications of assuming current reproductive value to be a linear function of clutch composition, i.e., that each offspring in a population makes the same contribution to its parents' current reproductive value as any offspring of the same sex regardless of the number or sexes of its siblings.

This assumption has been analyzed by Shaw and Mohler (1953), whose argument may be briefly summarized as follows. Consider a population in which the mean individual sex proportion (probability that a given offspring will be male) is p. Since the collective amount of reproduction by males must exactly equal that by females, each sex has half the cohort's collective reproductive value. Then, if the population produces n clutches, each averaging M males and F females, collective reproductive value equals $n(M + F)$, and

$$\text{mean reproductive value per son} = \frac{n(M+F)}{2nM} = \frac{1}{2p}$$

$$\text{mean reproductive value per daughter} = \frac{n(M+F)}{2nF} = \frac{1}{2(1-p)} .$$

If the population contains a small subpopulation in which the mean individual sex proportion is p', then the expected reproductive value of one of its offspring is $V = \frac{1}{2}(p'/p + (1-p')/(1-p))$.

By finding dV/dp' and equating it to zero, the stable sex proportion (ignoring cost) is found to be one half. That the second derivative is zero shows that the equilibrium is not at a maximum of V (in fact the function has neither maximum nor minimum) but at a line toward which the population is drawn as individuals are selected for higher values of V and along which there is no variance of fitness between sex proportions. Thus, a population has an equilibrial but not an optimal sex ratio; an individual may have an optimal sex ratio but only if the population sex ratio is not at equilibrium. The equilibrial nature of the stable sex ratio is best appreciated graphically (Figure 12–1).

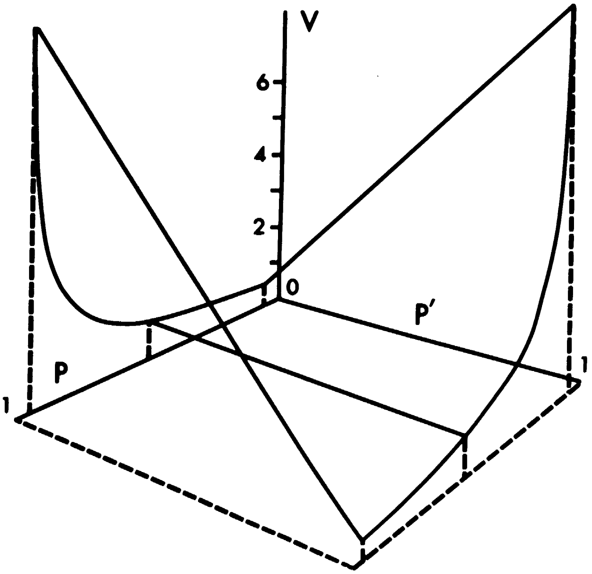

Figure 12–1. The function $V = \frac{1}{2}(p'/p + (1-p')/(1-p))$. Note that when $p < \frac{1}{2}$, the optimal p' is 1, when $p > \frac{1}{2}$, the optimal p' is 0, and when $p = \frac{1}{2}$, all values of p' are equally fit.

The male and female reproductive values derived above may be substituted for $\partial C / \partial M$ and $\partial C / \partial F$ in equation (1), giving

$$\frac{-\mathrm{d}M}{\mathrm{d}F} = \frac{\dfrac{M+F}{2F} + \dfrac{\partial R}{\partial F}}{\dfrac{M+F}{2M} + \dfrac{\partial R}{\partial M}}$$

Making the same substitution into (2) shows the equilibrial sex ratio under investment constraint to be given by

$$\frac{-\mathrm{d}M}{\mathrm{d}F} = \frac{\partial R / \partial F}{\partial R / \partial M} = \frac{\partial C / \partial F}{\partial C / \partial M} = \frac{M}{F}\,.$$

Specification of the form of the cost function is a more difficult task. But note that with the assumptions of fixed R and linear C, an expression ($-\mathrm{d}M/\mathrm{d}F = M/F$) for the equilibrial sex ratio exists that contains only M and F and neither R nor C. This has the important consequence that in an empirical study of investment with respect to sex ratio it is, in principle, sufficient to measure investment on an ordinal scale, i.e., all that is needed is to know what different family compositions have the same cost, so that $\mathrm{d}M/\mathrm{d}F$ may be calculated (Figure 12–2). Unfortunately, the empirical difficulties of distinguishing small differences between adjacent isocosts may lead to considerable imprecision in the estimate of the slope of the isocosts.

The above conclusion that $M/F = -\mathrm{d}M/\mathrm{d}F$ is formally identical to that reached by Mac Arthur (1965), but the underlying model is different in an important way. Mac Arthur's

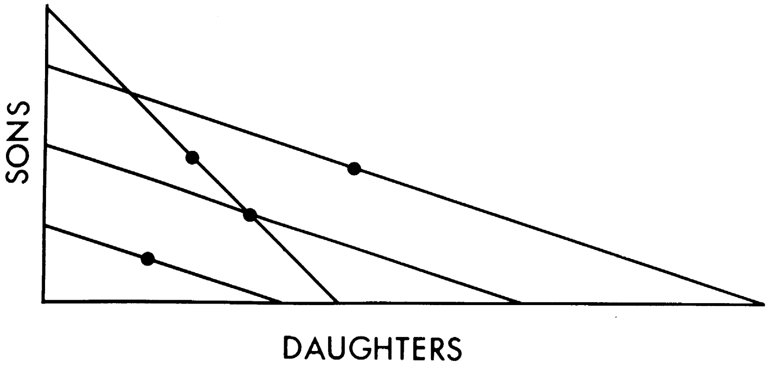

Figure 12–2. Hypothetical cost and value functions. The cost of any particular combination of sons and daughters could be shown in a third dimension, depicted here by three representative contour lines or isocosts. Since the isocosts have a slope $\mathrm{d}M/\mathrm{d}F = -1/3$, the stable sex ratio is 1 male to 3 females. The reproductive values of the family compositions can be depicted by isovalues, of which one representative is shown here, crossing the isocosts. The slope of the isovalues is the negative of the ratio of males to females; the mean sex ratio occurs at the midpoints of the isovalues. Selection will adjust the sex ratio so that the isovalues are coincident with the isocosts.

model is restricted to discrete generations and thus does not actually incorporate anything corresponding to reproductive cost as I have defined it; rather it simply divides all family compositions into those that are "permitted" by a given genotype and those that are not. The identity of our conclusions rests on the similarity of the boundary of the set of permitted family compositions to an isocost. This similarity breaks down in the case of clutch size constraint, to which Mac Arthur's model does not extend because of its lack of recognition of a tradeoff between present and future reproduction. The clutch size constraint model seems more realistic, as fixing investment, given sexual dimorphism, requires exacting control over the sex of offspring, which is apparently unknown among diploids with genetic sex determination. But this model lacks the analytic tractability of the investment constraint model, and because both give the same optimal mean family composition, the latter serves as a first approximation. A possible inadequacy of it will be discussed below.

FIELD STUDY

A test of the theory requires a study organism with young that are decidedly sexually dimorphic during the period of parental care. Relatively few species meet this requirement; some of the most promising are certain raptorial birds and icterids. I studied one of the latter, the red-winged blackbird, *Agelaius phoeniceus*, because it can be found in abundance, and a great deal is already known about its breeding biology, including the sexual dimorphism of nestlings, which has been documented in four previous studies (Williams, 1940; Haigh, 1968; Holcomb and Twiest, 1970; Laux, 1970).

The size dimorphism is prima facie evidence for cost dimorphism but, in view of the importance of cost dimorphism to the model, a major objective of this study was to document it more thoroughly. Doing so was especially necessary because cost is properly measured in terms of parental reproductive value rather than physiological requirements of offspring. The two quantities are not necessarily proportional; however, the former can be measured much less precisely than the latter, and effects on parental reproductive value, especially those that depend on the sex of offspring, will certainly be related at least qualitatively to offspring requirements. Therefore, I attempted to estimate isocost slope, dM/dF, using both more precise, but perhaps less accurate, physiological comparisons, and more accurate, but perhaps less precise, comparisons of assumed correlates of residual reproductive value. This approach at least permits testing of the null hypothesis that the sexes are equally costly and provides rough estimates of the expected sex ratio for comparison with the actual sex ratio, the second main objective of the study.

Methods. The study was conducted from 1974 to 1978, principally in four marshes in or near the E. S. George Reserve, Livingston Co., Michigan, and ranging in size from 2.3–6.8 ha. During the breeding season, these marshes were searched thoroughly to find as many nests as possible, which were then followed until they became inactive. Most nests were found before egg-laying was complete and nearly all before hatching. Once young hatched, they were individually marked by clipping one toenail or, at later ages, plucking one primary feather. Nestlings were regularly weighed to the nearest 0.1 gm with a 50 gm Pesola spring balance and a tared mesh bag. I attempted to concentrate on weighings on days 0, 2, 5, and 8 after hatching, but strict adherence to this schedule was not feasible.

During the first three years of the study, the sex of nestlings was determined by weight on or after day 8. Near the end of the third year, I developed a laparotomy technique (Fiala, 1979) for sexing very young nestlings, and in 1977 and 1978, 545 nestlings were sexed in this manner at an average age of 2.27 days.

In 1975 and 1976, I hand-raised a total of 28 nestlings from late-season nests for varying lengths of time. The birds were fed a homogeneous diet, and the food for each was kept separately and replenished in weighed units so that total food consumption of each individual could be measured. The diet was the nestling softbill mix of Lanyon (1979), except that in the first year only half the amount of turkey starter mash was used. In 1976 the daily fecal production of some of the nestlings was collected. Both food and feces were analyzed by bomb calorimetry.

In 1977 the total metabolism of five male and six female nestlings was measured under field conditions using doubly-labelled water (Mullen, 1973). Usually one bird of each sex in a brood of four was labelled on day 5 or 7. Samples of cloacal fluid were then collected in capillary tubes at 12-hour intervals for up to 36 hours (Fiala and Congdon, in prep.).

Early sexing by laparotomy permitted brood manipulations involving the sex composition as well as size of broods. Such manipulations were usually done the day or the day after the birds involved were laparotomized. To observe the success of enlarged unisexual broods, in 1977 I assembled five broods of five males each and five broods of five females; and in 1978, 11 broods of five males, seven broods of five females, and two broods of six females, all in nests with an original clutch of four eggs. To compare feeding frequencies between family compositions, in 1977 I assembled 16 unisexual broods of two to five young in nests with original clutches of three to four eggs and including some of the broods mentioned above. These broods were watched for one-hour intervals, and the number of feeding trips by the parents recorded. One brood in which a male died during the period of observation was counted as both a brood of five and of four. Also, one opposite-sex pair of broods of three and one opposite-sex pair of broods of four were each nearly synchronous, and about halfway through the respective observation periods I interchanged the two broods so that the feeding frequencies of the same broods could be compared between two "mothers." These five broods counted twice gave a total of 21 mother-brood combinations.

Most statistical calculations were made using the Michigan Interactive Data Analysis System or other programs supported by the University of Michigan Statistical Research Laboratory.

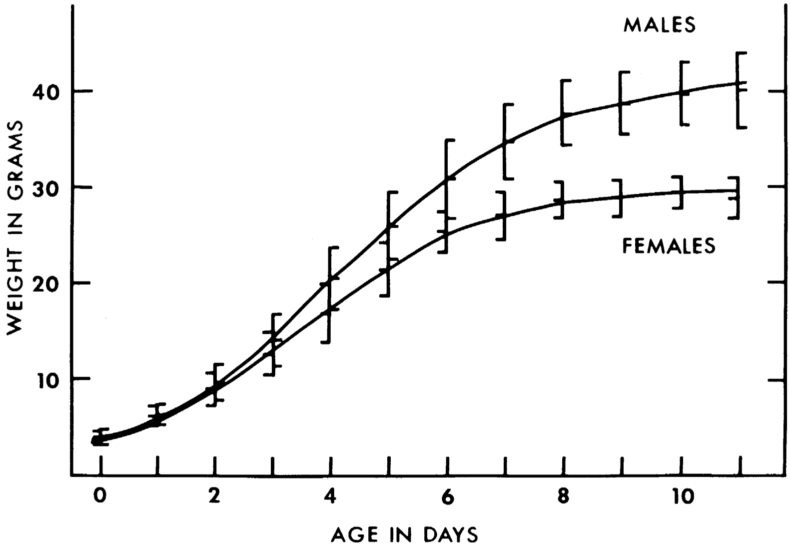

Figure 12–3. Growth of nestling red-wings. Vertical bars show one standard deviation on either side of the mean. Sample sizes range from 79 to 353. The logistic curves were fitted by least squares regression.

Table 12–1. Logistic regressions of weight on age.*

Sex	*a*	*b*	*c*	*n'*	*ems"*
Males	41.4 ± .218	9.85 ± .265	.564 ± .00805	2042	9.25
Females	30.5 ± .137	7.34 ± .156	.577 ± .00748	2033	4.17

* Weight at age x, $W(x) = a/(1 + be^{-cx})$. Coefficients shown ± 1 asymptotic standard deviation.
' Number of weighings.
" Error mean square.

Estimation of cost dimorphism. The sexes are not significantly different in weight on days 0 and 1 after hatching, but males are significantly heavier at all later ages (Figure 12–3); by day 8 there is virtually no overlap. The growth data were well fit by logistic functions obtained by least squares regression (Tables 12–1, 12–2). There are apparently no statistical tests for comparisons of non-linear regressions, but support-plane confidence intervals can be calculated for individual parameters (Conway et al., 1970). Of the three logistic parameters, there is a clear sexual difference in a, the upper asymptote, and in b, which is equal to the weight to be gained after hatching divided by hatching weight; but there is no clear difference in c, a measure of the rapidity with which the asymptote is attained though there is some suggestion that females tend to have a higher c. Thus the growth curve for each sex has the same shape, but that for females is lower for any given position on the curve and, in addition, is shifted to the left relative to the male curve.

This leftward displacement reflects the fact that in hatching at essentially the same weight as males, females hatch at a higher percentage of their asymptotic weight. This head start is maintained through the nestling period; females give the impression of gaining coordination and alertness more rapidly than do males and tend to fledge slightly sooner (Holcomb and Twiest, 1970). I cannot report fledging ages because my handling of older nestlings tended to precipitate fledging, but one observation conveys the sexual difference: Of birds still in the nest or near enough to be captured and weighed on days 10 or 11, the proportion of males was significantly higher than at younger ages ($X^2 = 25.1$, 1 d.f., $p < .00001$).

The hand-raising experiments were done to investigate the possibility that the sexual differences in growth arise from differences in efficiency rather than food intake. Substantial retardation of growth relative to that of wild nestlings as well as considerable individual variation, rendered the analysis of the growth patterns of the hand-raised birds rather fruitless. However, the wet weight of daily food consumption was found to be a quadratic function of morning body weight in each sex (Figure 12–4). The regression for males is food $= -2.43 + .823$ wt $- .00848$ wt^2 ($r^2 = .56$, $p < .0001$, $n = 149$); for females, food $= -1.75 + .776$ wt $- .0101$ wt^2 ($r^2 = .37$, $p < .0001$, $n = 206$). Neither intercept is significantly different from zero. Analysis of covariance of food consumption with weight and its square showed the regression coefficients to be significantly different between the sexes ($p < .0005$), i.e., for a given weight males consume more food than do females.

The food used in the first year contained 37.12 ± .55 per cent dry matter, with 5.297 ± .112 kcal/gm dry weight. The second year's mix was 46.21 ± .64 per cent dry, with 5.107 ± .103 kcal/gm dry weight. Curiously, a two-way analysis of covariance of the feeding data with food consumption converted to calories showed the same sex effect each year but also a significant difference between years; i.e., more calories were consumed on the richer diet. The biological significance of this is not clear. Possibly the birds' hunger was regulated by mass consumed rather than by energy, but it is also possible that an unconscious preconception of the birds' requirements biased my perception of their hunger (I did not know which diet had the higher energy content at the time).

Table 12–2. Logistic regressions of weight on age in broods of four.*

Sex Ratio ♂♂	♀♀	Male Regressions *a*	*b*	*c*	n	ems	Female Regressions *a*	*b*	*c*	n	ems
0	4						30.9 ± .650	8.20 ± .942	.614 ± .0403	109	6.35
1	3	42.3 ± 1.55	9.28 ± 1.29	.532 ± .0447	80	12.6	30.1 ± .484	6.81 ± .392	.542 ± .0221	219	3.94
2	2	42.3 ± .700	10.1 ± .806	.562 ± .0255	170	7.71	30.9 ± .523	7.12 ± .569	.567 ± .0292	158	5.02
3	1	40.1 ± .680	10.5 ± .985	.611 ± .0285	202	10.4	30.0 ± .776	8.21 ± 1.25	.623 ± .0512	65	5.48
4	0	42.1 ± .652	9.85 ± 1.11	.609 ± .0332	54	4.37					

* see footnotes to Table 1.

The linear regression of caloric value of daily fecal production on daily food consumption has an intercept not significantly different from zero, so it was recalculated to pass through the origin. The resulting regression equation is fecal calories = .261 food calories ($r^2 = .407$, $p < .0001$, $n = 14$). There is no significant difference in the regressions (and hence in digestive efficiency) between sexes (analysis of covariance, $p < .4$).

Because the growth of the hand-raised birds was different from that of wild nestlings and because of the possibility of bias in the way they were fed, I used doubly-labelled water to measure metabolic rate directly in the next year. The measured rates of CO_2 production were not significantly different between sexes; assuming the same respiratory quotient in both sexes, the rates of O_2 consumption are likewise not significantly different.

Experimental tests of the hypothesis that cost dimorphism exists took the form of asking whether different family compositions within a brood size could be considered to lie on the same isocost. The relevance to the model of such tests depends on the validity of the model's assumption that the reproductive value of an offspring is independent of the sex of its siblings, at least in normal clutch sizes, i.e., that any sexual differences in offspring requirements are reflected only in the mothers' residual reproductive value and not in the offsprings' own fitness. To test this assumption, nestlings' weights were grouped by brood composition and logistic growth curves were calculated for each group by least squares regression. The results for broods of four are shown in Table 12–2 and indicate that there is apparently no effect of sex ratio on growth. Thus, for example, an individual of either sex is no worse off if its three nestmates are brothers than if they are sisters. Similarly, stratifying the data by brood size, regardless of family composition, shows no apparent effect of brood size on the sex-specific regressions. Interpretation of this absence of a sibling effect on growth as an absence of an effect on offspring fitness requires the assumption that offspring fitness is dependent on body weight. There is support for this assumption in that, of 20 males individually marked as nestlings and recaptured in a subsequent year, 16 were above

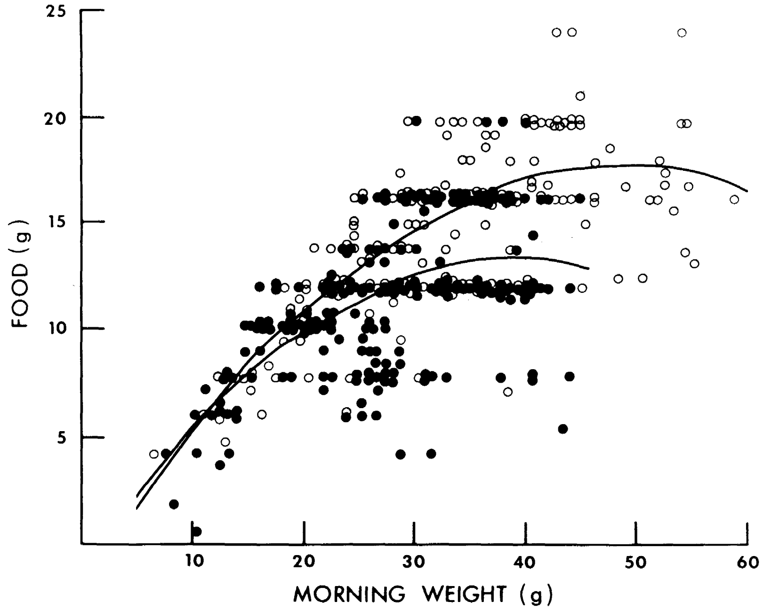

Figure 12–4. Hand-raised nestlings' daily food consumption (grams wet weight) as a function of body weight at the beginning of the day. Open circles: males. Solid circles: females.

the mean weight for their age when last weighed and only three were below ($X^2 = 8.89$, 1 d.f., $p < 0.005$). (The hatching date of the remaining male was not accurately known. Too few females were recaptured for a similar comparison.)

Because the growth pattern did not vary with sex ratio in normal-sized broods, parents apparently respond to normal variation in offspring demands by providing the appropriate amount of food. There is evidence that this parental adaptability does not fully extend to enlarged broods, which presumably place the parents under greater stress than it is optimal for them to incur. In much of their range, redwings have only two common clutch sizes, three and four (196 and 391, respectively, of 640 clutches in this study; cf. Crawford, 1977; Francis, 1975; Robertson, 1973), and reproductive success of both naturally large and experimentally enlarged broods appears to be reduced (Francis, 1975; Robertson, 1973). In the present study, natural clutches of five in which all eggs hatched accounted for a disproportionate number of presumed starvation deaths (Table 12–3). I attempted to exploit the possibility that response to enlarged broods would not be entirely adequate for the nestlings' needs by assembling enlarged unisexual broods. Under the null hypothesis that males and females are equally costly, the success of enlarged all-female broods should be equally reduced as that of enlarged all-male broods, but under the hypothesis that cost is related to physiological requirements, male broods of five could be expected to have more severely lowered success than female broods of five which have about the same biomass as a normal-sized brood of four males.

In 1977, one of the enlarged all-female broods was predated before any results could be observed. In the other four broods of five females, all young grew well and fledged, except for one individual late in the season. On the other hand, only one of the five broods of five males had all young survive, the single exception being a brood that the "father" helped feed. In three other broods, one male died, and in the last brood, also a late-season nest, two males died. These data suggested greater difficulty in raising males, especially because starvation deaths are rare (Tables 12–3,12–4), but they are too few to be significant.

In the following year's repeat of the experiment, 10 of the 20 nests were predated, but 14 survived until at least day 8. Unlike the previous year, there were no starvation deaths in any of these nests (Table 12–3). Furthermore, in neither sex were growth curves significantly different from those of control birds that had also been laparotomized but not placed in enlarged broods.

A second experiment was designed to compare the relative effects of sex and number of offspring on feeding frequency. Although feeding frequency is an imprecise measure of offspring requirements because of variation in the amount of food delivered each trip (Royama, 1966), it may be a more satisfactory measure of parental stress and, hence, investment than is the rate of food delivery. In any case, feeding frequency has usually been found to

Table 12–3. Presumed starvation mortality.

	Starved'	Not Starved"
Natural broods of 5	5	40
Experimental broods		
of 5: 1977	6	39
of 5 or 6: 1978	0	102
All other broods	48	1,287
Total	59	1,468

' Found dead in nest or vanished from nest.

" Fledged or hatched but predated.

Table 12–4. Fate of eggs in completed clutches.

Unhatched:	Predated	520
	Hatching failure	138
	Other	133
Hatched:	Predated	522
	Collected	119
	Died or vanished	59
	Other	44
	Fledged	818
		2,353

Table 12–5. Hourly feeding frequencies at experimental nests.

Sex		Brood size			
		2	3	4	5
Male:	Mean		12.5	14.2	11.3
	SD		.69	.74	.92
	Hours		41	31	12
	Nests		5	5	2
Female:	Mean	12.9	12.6	13.8	10.5
	SD	1.25	1.51	1.37	.94
	Hours	9	7	11	20
	Nests	2	2	2	3

increase with brood size (see Klomp, 1970 for a review) and thus a comparable increase with sex ratio should be expected.

Most feedings were by females, but males fed during most observations at three nests containing five males, five females, and three males, respectively; and rarely at three other nests. Most observations were made after nestlings were at least five days old, and age did not contribute significantly to the variation.

Within brood size-sex combinations, there were significant differences in feeding rate between nests (two-level nested ANOVA). These differences and unequal sample sizes from different nests preclude a complete analysis of variance. A two-way ANOVA of mean feeding frequencies at each mother–brood combination (excluding the broods of two females because there were no broods of two males) showed neither brood size nor sex to be a significant factor (Table 12–5).

The estimates of $-\mathrm{d}M/\mathrm{d}F$ that follow from these results fall into two groups, those based on metabolic requirements of the young and those based on observable effects of the young on their parents. The simplest estimate, the ratio of the asymptotic weight of females to that of males, is .737. Even if metabolic requirements vary with the .724 power of weight, as found by Lasiewski and Dawson (1967) in between-species comparisons of standard metabolic rate, the estimate increases only to .802. Alternatively, an index of food consumption by each sex at each age can be obtained from the regressions of food consumption on weight in hand-raised birds and the regressions of weight on age in wild birds, and an index of total requirements for each sex can be obtained by summing the daily indices. The ratio of these sums is .776. The sex ratios expected from these relative cost estimates are 42.4, 44.5, and 43.7 per cent males, respectively. The apparent lack of effect of sex of offspring on parental behavior, on the other hand, provides no basis for rejecting the null hypothesis that the sexes are equally costly, i.e., that $-\mathrm{d}M/\mathrm{d}F = 1$. From this hypothesis, the stable sex ratio is expected to be 1:1.

Table 12–6. Sex ratios of nestling redwings.

	Males	Females	% Males	X^2
Williams (1940)	57	62	47.9	
Haigh (1968)	206	225	47.8	
Holcomb & Twiest (1970)	50	68	42.4	
Laux (1970)	162	166	49.4	
Knos & Stickley (1974)	35	38	48.0	
Subtotal	510	559	47.7	2.25
This study: 1974	77	93	45.3	
1975	69	61	53.1	
1976	145	151	49.0	
1977	113	132	46.1	
1978	164	198	45.3	
Subtotal	568	635	47.2	3.73 $p < .054$
Grand total	1078	1194	47.4	5.92 $p < .02$

Mean sex ratio. Previous to the present study, five investigators had published sex ratios of nestling redwings (Table 12–6), all based on nestlings sexed by weight or tarsal length late in the nestling period. All the reported sex ratios are very similar, and all show fewer males than females. However, the proportions are not significantly different from 50 per cent.

In four of the five years of my study, the sex ratio was likewise biased in favor of females (Table 12–6); there is some reason to discount the single exception because there is a small seasonal decrease in the sex ratio (Fiala, in prep.), and I did not sample through to the end of the season in 1975. The overall sex ratio is as near significance at the 5 per cent level as is possible without being significant; if a single male had been a female instead, the male proportion would be significantly different from 50 per cent. The combined sex ratio of all the studies is significantly less than 50 per cent (Table 12–6).

These are not direct measurements of either the primary or secondary sex ratio. The first three years' data are based almost entirely on birds that survived to day 8 or later. The last two years' data are largely based on birds sexed by laparotomy at an average age of just over 2 days. (This incidentally makes them a more nearly complete sample of the population, and it is noteworthy that these two samples together do contain significantly less than 50 per cent males ($X^2 = 4.63$, 1 d.f., $p < 0.05$).) Whether or not these sex ratios represent the primary or secondary sex ratios depends on whether or not differential mortality occurred before sexing. Note (Table 12–4) that very nearly all the post-hatching mortality is the result of predation. There is no reason to suppose that this might affect the sexes differentially because the whole brood is virtually always taken at once. Furthermore, of those few birds that were assumed to have starved, there is no apparent sex bias (Table 12–7). Therefore, I conclude that my data are representative of the sex ratio at hatching. It is impossible to estimate the primary sex ratio (Fiala, 1980) because the rate of hatching failure is high (Table 12–4) and no method of sexing an egg is known. In order for the primary sex ratio to have been exactly 50 per cent, it would have been necessary for male egg hatching failure to exceed that of female eggs by about three or four to one, but a much less dramatic bias could have been sufficient to account for the statistical significance of the observed sex ratio.

Discussion. Although the growth and physiological data provide compelling evidence for sexual dimorphism in offspring requirements, the data on the effect on the parents of this dimorphism are at best ambivalent. From the theoretical model it is known that the marginal

Table 12–7. Sex of presumed starvation mortalities.

	Males	Females	Unknown
Vanished nestlings	6	9	24
Dead nestlings	10	8	2
	16	17	26

rate of transformation of the sexes, $-dM/dF$, rather than absolute costs, determines the stable sex ratio, at least under investment constraint, so that inability to distinguish slight differences does not rule out the possibility that they exist and have an important effect on the sex ratio. Nevertheless, the difference in the amount of dimorphism implied by the two kinds of data is puzzling.

It is possible that the experiments on the parents gave the less accurate assessment of cost dimorphism. Much of the lack of significant differences in effects on the experimental mothers may be because actual effects on future reproduction could not be directly observed. The females who successfully raised broods of five males might, contrary to my expectation, have done so exclusively at the cost of reduced survival probability, rather than a combination of the latter and reduced offspring survivorship. Likewise, the small variation in feeding frequency between sexes or number of offspring might have been accomplished in part by a decrease in the mother's own food consumption.

Conversely, it is likely that physiological dimorphism exceeds reproductive cost dimorphism. The slightly greater precocity of females can have a bearing on this in two ways. First, it may slightly reduce the difference in food requirements. Still greater precocity of the smaller sex has been observed in the sparrowhawk, *Accipiter nisus,* with the net results being an apparent absence of a difference in food intake (Newton, 1978) and no effect on the sex ratio (Newton and Marquiss, 1979). Second, because of high mortality (Young, 1963; Table 12-4), at conception, the expected length of parental care probably extends only to several days beyond hatching, when, because of the advancement of female growth, the full degree of sexual dimorphism is not yet established. This would tend to reduce the disparity in expected costs at conception, but the importance of the reduction is difficult to evaluate, because even though the probability of requiring the full amount of parental care is small, the amount required in the later stages probably sufficiently outweighs that received earlier to make a substantial contribution to the expectation at conception. Growth resumes after fledging; the exact pattern of this later growth is unknown, but fledging weight in both sexes is roughly only two thirds of adult weight, and observation of hand-raised birds suggests that most of the additional weight is gained during the post-fledging period of parental care.

Depending on how it is given, male parental care could be expected to influence differentially maternal reproductive costs. From the mother's point of view, if her mate's assistance is given unpredictably or at least independently of the sex of her nestlings, then his expected contribution is simply another resource, with no differential effect on cost or sex ratio. However, if the mother is more likely to obtain assistance by producing sons, then the disparity in the costs of the two sexes is reduced for the mother, and the optimal proportion of sons is raised. Although the father would be, in effect, manipulated into investing excessively in sons, if their fitness would be unduly low under the mother's care alone, then the marginal value of helping them may be sufficiently great to justify it.

Time constraints did not permit study of the male role, but males were observed feeding at both male and female broods in the 1977 feeding frequency experiment. In the 1978 brood enlargement experiment, males were observed making at least some contribution at several (probably a greater than expected proportion) enlarged broods of either sex. Thus, males may preferentially feed large broods, but there is no clear evidence of a sex preference. A non-significant trend toward higher male proportion in male-assisted broods has been observed in another population (C. B. Patterson, pers. comm.), and a significantly higher male proportion in primary nests, which are consistently male-assisted, has been observed in the yellow-headed blackbird, *Xanthocephalus xanthocephalus* (C. B. Patterson, pers. comm.).

There can be little doubt that there is some degree of cost dimorphism of the sexes, and that the marginal rate of transformation of the sexes lies between the physiologically-based estimates of about .75 and the null hypothesis of 1. The observed male proportion of 47.2 per cent does lie about halfway between the proportions predicted from these two dimorphism estimates. But although the deviation from 50 per cent is in the predicted direction, it is suspiciously small, given the uncertainty of the true degree of dimorphism, and the conclusion that it is adaptive, not merely fortuitous, can be accepted only with reservations.

It is possible that cost dimorphism is as extreme as implied by the physiological data but that the model used to predict the sex ratio is not applicable. The intermediacy of the sex ratio suggests parent–offspring conflict in the determination of sex (Trivers, 1974) as an intriguing, if not very parsimonious, alternative hypothesis, but such conflict seems unlikely with female heterogamety, as the mother never produces a genotype different from her own that does not already have its sex determined.

Finally, environmental uncertainty of breeding success has been shown in theory to reduce optimal brood size relative to the optimum for mean conditions (Schaffer, 1974b), and the clutch size constraint model suggests that such a reduction might increase the stable sex ratio. For example, the discrepancy between the incidence of brood reduction in natural and artificial broods of five suggests that the reason for the rarity of broods of five may not lie in the inability of parents to raise them but in the uncertainty of the last-hatched young's becoming established in competition with its older siblings. If so, it could be advantageous for the mother who is capable of raising five young to invest in a more certain brood of four, but with an increased sex ratio.

SUMMARY

A theoretical model predicts that a population's sex ratio will equilibrate so that the ratio of the marginal costs of the two sexes equals the ratio of their marginal values. From this it follows that the equilibrial sex ratio can be predicted from the marginal rate of transformation of the sexes, $-dM/dF$. In principle, this can be measured, but empirical problems make imprecision likely.

Male and female nestling red-winged blackbirds were shown to have markedly different metabolic requirements, but experiments designed to test whether or not $dM/dF = -1$ gave ambivalent results. The sex ratio was found to be significantly biased at hatching. The results are interpreted as a qualitative but not quantitative verification of theory.

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