

SEX-RATIO MANIPULATION IN COLOR-BANDED POPULATIONS OF ZEBRA FINCHES

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Abstract.—Significant correlations were found between attractiveness of leg-band color (determined by preference tests [Burley et al., 1982]) and sex ratio of offspring in two long-term breeding experiments involving zebra finches. In both experiments, birds with attractive band colors produced more same-sex offspring, while birds with unattractive band colors produced more opposite-sex offspring.

The results of these experiments are consistent with those of a previous experiment (Burley, 1981). To explain the earlier results, I hypothesized that parents adjust their allocation to sons and daughters to produce offspring they “expect” to be most attractive. The purpose of such sex-ratio manipulation is to enhance fitness by the production of offspring with superior mate-getting opportunities.

Two alternative hypotheses are presented here. One is that sex ratios change with parental age and/or experience. Evidence does not support this hypothesis. There were no temporal trends in sex ratio independent of band color. A second possibility is that sex ratios reflect differential parental ability to rear sons and daughters. This hypothesis cannot be conclusively tested on the basis of present evidence, but available evidence does not support it. Within color classes, weights of sons and daughters did not differ.

Evidence indicates that parents effect secondary sex-ratio manipulation through the selective rejection of young, usually within six days of hatching. There is no evidence of manipulation prior to egg-laying. The costs associated with brood reduction probably set limits on the extent to which secondary manipulation can be profitably employed.

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It is widely believed that epigamic selection contributes to the evolution of sexual dimorphism (Darwin, 1871; Fisher, 1930; Orians, 1969; Trivers, 1972; Janetos, 1980; O'Donald, 1980; Andersson, 1982; Hamilton and Zuk, 1982; Kirkpatrick, 1982; but see Baker and Parker, 1979). Mating preferences for individuals with an attractive trait lead to enhanced reproductive success (RS) of those individuals, and the trait increases in frequency in the population. It is usually held that females exert mate preferences, but in cases in which males incur substantial parental or mating investment, mate selectivity may be displayed by both sexes (Trivers, 1972; Burley, 1977; Low, 1978).

In sexually dimorphic species with mate choice by both sexes, it may be profitable for individuals (or pairs) to bias offspring production in favor of the sex of the more attractive parent, given the following six conditions. 1) There is heritable variation in the trait(s) conferring attractiveness. 2) Expression of traits is sex-limited. 3) Relative attractiveness affects RS. 4) Preference

for the attractive trait is common to some fraction of the population. In general, the advantages of biasing the sex ratio increase with an increase in the fraction of individuals sharing the same mating preference and decrease as the relative frequency of individuals with attractive traits increases. 5) The mating system is one in which a substantial fraction of the male population is able to obtain a mate(s). (In mating systems in which only a few males mate, all females have access to attractive males, if indeed females control mating, and the selective production of sons would be disadvantageous [Fisher, 1930].) 6) An economical method of sex-ratio manipulation exists.

Previously, I reported findings consistent with the hypothesis that pairs bias offspring production in favor of the sex of the more attractive parent (Burley, 1981) using a captive breeding population of zebra finches (*Poephila guttata*), a sexually dimorphic, typically monogamous estrildid with biparental care of the altricial young (Immelmann, 1962; Goodwin, 1982). This population was founded by never-mated,

wild-type adults, each of which wore one of several colors of plastic leg bands, one band per leg. Males were banded red, orange, or light green; females were banded black, orange, or light blue. Choice experiments conducted earlier, but reported later (Burley et al., 1982), established that females are attracted to red-banded males and are not attracted to green-banded males. Males prefer black-banded females and avoid blue-banded ones. For both sexes, orange-banded individuals are treated like unbanded birds, which have orange legs and are of intermediate attractiveness.

In the breeding population, birds selected their own mates and bred freely for nine months. Nine combinations of parental band phenotypes were possible. The color types of parents were determined by observing activity at nests; however, the individual identity of parents was not determined. Pair bonds with extreme band combinations (attractive males mated to unattractive females and vice versa) tended to produce offspring of the sex of the more attractive parent. The sample size was small, and because individual RS patterns were not determined, results were analyzed only on the basis of parental color type, an approach that was criticized (Immelmann et al., 1982; Thissen and Martin, 1982; but see Burley, 1982a). Experiments reported here answer the principal objections raised by critics.

Between October 1981 and January 1984, I performed two additional breeding experiments, one aim of which was to test for the consistency of sex-ratio trends. Sex-ratio data were collected by retaining surviving offspring until they could be sexed externally (about 8 weeks of age). The data closely approximate secondary sex ratios.

Two alternative explanations for the sex-ratio patterns are considered: 1) offspring sex ratio varies with parental age (e.g., Blank and Nolan, 1983) or reproductive history, and 2) birds of varying attractiveness are differentially able to rear sons and daughters (Trivers and Willard, 1973).

MATERIALS AND METHODS

The two experiments reported here differ from the earlier one in that only one sex was

color-banded. In the Banded Male Experiment (BME), adult males were color-banded red, orange, or light green. In the reciprocal, Banded Female Experiment (BFE), females were banded black, orange, or light blue. Phenotypic combinations of pair bonds were therefore less extreme than in the earlier experiment, because all individuals of the unbanded sex had naturally orange legs of intermediate attractiveness. Each individual also wore a numbered metal band, and parentage was determined by catching birds on the nest as they engaged in parental activities. A fuller account of methods and the rationale for various procedures is presented elsewhere (Burley, 1986a).

Zebra finches with wild-type plumage from outcrossed, domesticated stocks were employed. Males were derived from the same source populations as the birds used in the earlier experiment; these are large ($N > 100$) breeding colonies of wild-type birds, without color bands, maintained in my laboratory. Most of the females were purchased from commercial sources from which I had not previously purchased birds. Females were obtained as subadults to insure they had no prior reproductive history. Subadults of both sexes were isolated into unisexual groups until reaching maturity.

Ninety-six birds (24 of each sex for each experiment) in excellent plumage condition were selected from these unisexual groups. A stratified random design was used in assigning birds to experiments and band colors within experiments. An additional group of birds supplied replacements for subjects that died during the first six months of the experiments.

Experiments were performed in adjacent, nearly identical aviaries containing about 1 m³ of space for each adult bird. (This is less than half the density suggested by Immelmann [1965] as a desirable maximum for this species.) Food and water were continuously available, and all resources needed for reproduction were abundant.

Each nest was inspected every day between 1100 and 1300 hrs, and the numbers of eggs and nestlings were recorded. Birds that hatched within the previous 24 hours were individually marked on their posterior down feathers. At 11 days, young were given

numbered leg bands. For the first 10 months of the BFE and the first 11 months of the BME, all nestlings were weighed every other day. Offspring were removed from the aviary 2 to 5 weeks post-fledging and were kept in cages until their sex could be determined by plumage traits. A few offspring with white plumage (caused by recessive alleles) could not be sexed by plumage and were sexed by behavior (as adults).

Parentage was ascertained by catching adults on the nest as they engaged in parental activities. In less than one percent of all nesting attempts, trios attended nests. When this occurred, it was assumed that the two same-sex attendees contributed equally to parentage.

Experiments were initiated by releasing individuals of the color-banded sex into the aviary shortly after they were banded. A week later, opposite-sex individuals were added. Potential nest sites were made available after an additional week. Experiments were terminated by destroying all clutches started after a certain date. The BME lasted 22 months, the BFE 15 months. After the first 10 months of the BFE, color bands were removed and the birds were allowed to breed for 5 more months. Color bands were left on males for the entire duration of the BME.

In reporting results of statistical analyses, I employ two-tailed probabilities throughout. Since I had clear *a priori* expectations regarding the direction of sex-ratio trends, the use of two-tailed probabilities is a conservative measure of significance.

Goodman and Kruskal's test (Ghent, 1976) was employed to analyze the correlation between attractiveness as determined by band color and sex ratio of offspring. For the BME, analysis is based on the sex ratio produced by each individual male during the experiment. For the BFE, I made separate calculations for the first 10 months and for the entire 15-month interval. Sex ratios are presented as the number of sons in a cohort divided by the total number of offspring in that cohort.

RESULTS

In the BME, 320 sons and 247 daughters were produced by 26 males (aggregate sex ratio = 56.44% male). The correlation be-

tween attractiveness of male band color and sex ratio of offspring is significant and in the expected direction, with red-banded males having the most male-biased sex ratio ($\gamma = 0.452$, $P = 0.021$; Fig. 1A). RS varied considerably among males (Burley, 1986a). Since the correlation analysis is based on individual male RS, it could be affected by small progeny sizes, which tend to produce more extreme sex ratios. If cohorts of five or fewer offspring (Fig. 1A) are deleted from analysis, the correlation between attractiveness and sex ratio rises to 0.554. Hence the correlation does not result from extreme sex ratios produced by males with small progenies.

I also examined the number of males of each color type that produced sex ratios above and below the population mean. Eight of nine red-banded males, two of eight orange-banded males, and two of nine green-banded males produced progeny sex ratios above the population mean of 56.44% male; the remaining males produced ratios below the mean. This result is significant (Fisher 2×3 Exact Test, $P = 0.01$; Ghent, 1972).

During the first 10 months of the BFE, 31 females produced 150 sons and 131 daughters, for an overall sex ratio of 53.38%. The sex-ratio trend is in the expected direction (black-banded females have the most female-biased sex ratio), but the correlation coefficient is not significant by a two-tailed test ($\gamma = -0.340$, $P = 0.059$; Fig. 1B). During the full 15-month span, color-banded females produced a total of 215 sons and 203 daughters, for an overall ratio of 51.44%. The sex-ratio trend is significant ($\gamma = -0.356$, $P = 0.042$; Fig. 1C). Deletion of data for small cohorts increases the correlation ($\gamma = -0.413$). Two of 10 black-banded females, 6 of 11 orange-banded females, and 8 of 11 blue-banded females produced progeny sex ratios above the population mean; the remaining females produced ratios below the mean (Fisher 2×3 Exact Test, $P = 0.07$).

At an aggregate level, the overall differences in sex ratios in the present experiments are not significant (Table 1). A probable reason for this result is discussed below.

An intriguing result of the BME was that four of the red-banded males became

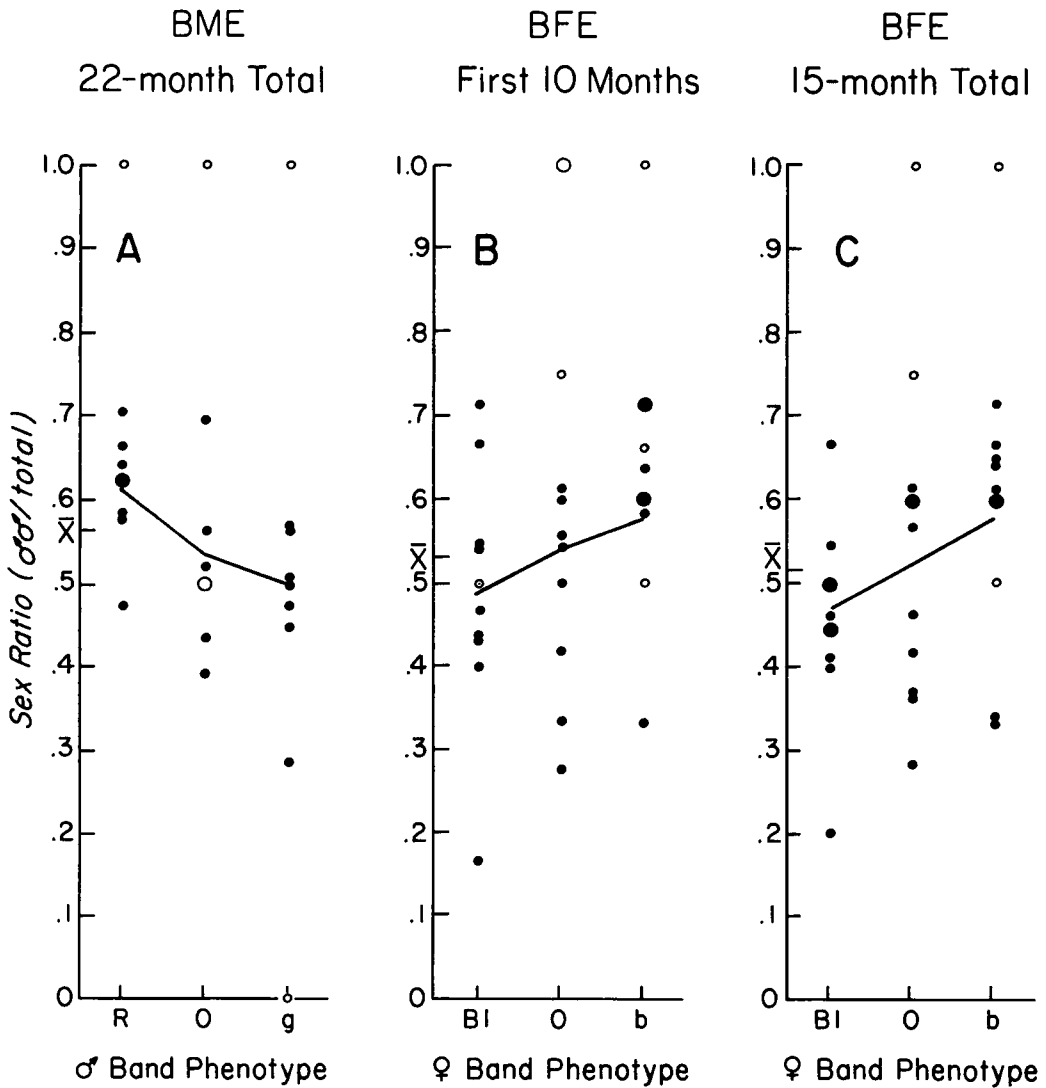


FIG. 1. Sex ratios of individual progeny cohorts in the Banded Male Experiment (BME) and Banded Female Experiment (BFE). Small circles are ratios for single cohorts; large circles represent two cohorts with an identical sex ratio. Open circles represent ratios based on cohorts of five or fewer offspring. Lines connect mean sex ratios for each color class. A: BME, full experimental interval. R = red-banded, O = orange-banded, and g = green-banded males. B: BFE, first 10 months. Bl = black-banded, O = orange-banded, b = blue-banded females. C: BFE, full experimental interval.

successful simultaneous polygynists. Polygynous red-banded males produced a somewhat higher sex ratio than monogamous red-banded males (Table 1B). The significance of polygyny in this typically monogamous species is discussed elsewhere (Burley, 1986a).

Alternative Hypotheses

If sex ratio varies with age and if band color has a systematic effect on survivorship, then the observed patterns might result from differential lifespans of color-banded birds. In fact, band color does appear to affect survivorship (Burley, 1985a, 1986a).

TABLE 1. Aggregate sex ratios produced in experiments with color-banded zebra finches. A. Banded Male Experiment: $X^2 = 5.569$, 2 *d.f.*, $P < 0.10$. * Two males, 722 red and 730 green, shared two clutches from which 5 offspring (4 males, 1 female) were produced. B. Banded Male Experiment: polygynous versus monogamous red-banded males, $X^2 = 0.723$, 1 *d.f.*, $P > 0.30$. C. Banded Female Experiment: $X^2 = 3.709$, 2 *d.f.*, $P < 0.25$. Data for entire 15-month interval.

	Number of		Sex ratio (% sons)
	Sons	Daughters	
A. Red-banded males	169	106.5*	61.3
Orange-banded males	76	66	53.5
Green-banded males	75	74.5*	50.2
B. Polygynous,			
Red-banded males	106	61.5	63.3
Monogamous,			
Red-banded males	63	45	58.3
C. Black-banded females	79	91	46.5
Orange-banded females	72	66	52.2
Blue-banded females	64	46	58.2

In both experiments, unattractive birds (blue-banded females, green-banded males) experienced the highest rates of mortality, and attractive birds (black-banded females, red-banded males) the lowest. These findings, however, make it very unlikely that an age- or experience-related effect can explain sex-ratio patterns reported here, because opposite trends are needed to account for observed patterns. The high sex ratios produced by attractive males could result from their longer lifespans if sex ratio increases over time, but the low sex ratios produced by attractive females necessitate a declining sex ratio.

Nevertheless, to explore the possible impact of differential mortality on sex ratios, I have plotted aggregate sex ratios produced by various color types as a function of time. (Because birds were of fairly uniform age at the beginning of the experiments and all were reproductively inexperienced, it is not possible to separate effects of age and experience.) For the BFE, the experiment is partitioned into three 5-month intervals (Fig. 2); the 22-month span of the BME is partitioned into four, 5.5-month intervals (Fig. 3). There is no indication of systematic changes in the sex ratio that are independent of band color. Instead, the results for the

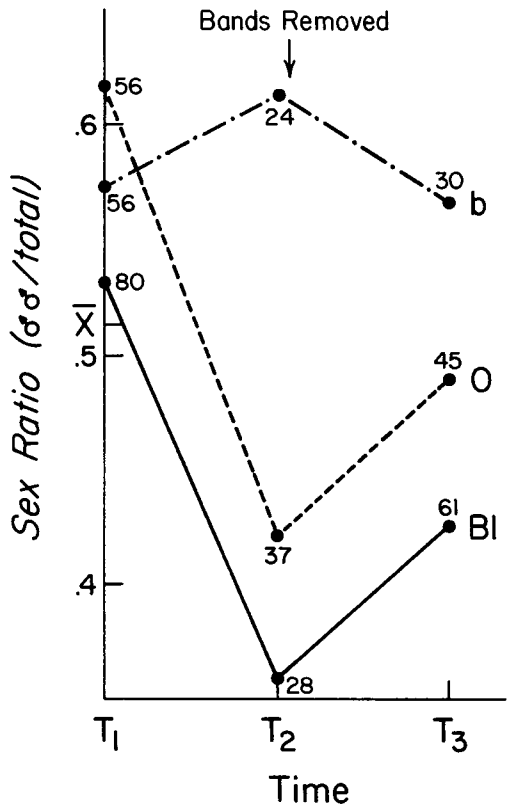


FIG. 2. Aggregate sex ratios by color type in the Banded Female Experiment. BI = black-banded, O = orange-banded, b = blue-banded females. Numbers at each point represent the number of offspring from which each sex ratio was calculated. T₁: the first 5 months; T₂: the second 5 months; T₃: the final third of the experiment. Not all females were present in the experiment from its initiation, and some data are not included in this illustration.

BFE suggest that experience may facilitate sex-ratio manipulation; as might be expected, there appears to be a convergence of sex ratios following color band removal. (The inference that convergence of sex ratios resulted from band removal must be made guardedly.) Results of the BME are less clear-cut, especially since green-banded males produced an aggregate sex ratio above the population mean during the third time interval but not during the other three intervals. Clutch-by-clutch analyses show greater fluctuations resulting from fewer data at each point; again no trend is evident. In a third breeding experiment in which nei-

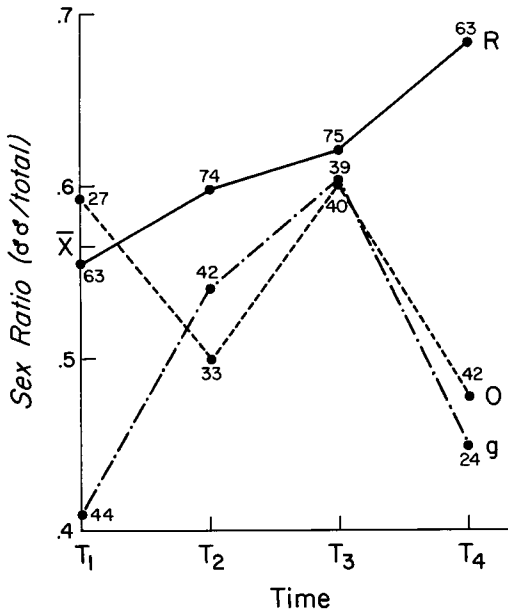


FIG. 3. Aggregate sex ratios by color type in the Banded Male Experiment. R = red-banded, O = orange-banded, g = green-banded males. Numbers at each point represent the number of offspring from which each sex ratio was calculated. The 22-month experiment is divided into four, 5.5-month intervals. Not all males were present in the experiment from its initiation, and some data are not included in this illustration.

ther sex was color-banded, there were no temporal trends in sex ratio over a 10-month interval (Burley, unpubl.).

An alternative possibility is that sex-ratio patterns result from differences in ability to rear sons and daughters. While data are insufficient to exclude this possibility, I do not think it very likely for reasons developed below (see Discussion).

The Timing of Manipulation

In principle, sex ratios could be manipulated either prior to egg-laying (primary manipulation) and/or at some later stage (secondary manipulation). Primary manipulation involves either selective fertilization and/or differential destruction of gametes or zygotes. In birds, females are the heterogametic sex, and females might possibly influence the sex ratio at conception by differential production of male and female ova. Secondary manipulation most likely involves selective sex-biased brood reduction after hatching.

If primary manipulation occurs, then the above-noted sex ratio trends should be evident in data for "perfect" clutches, those in which all eggs hatched and all offspring survived to sexing age. However, since only a fraction of clutches were perfect, such trends are not proof of primary manipulation; perfect clutches could represent cases in which parents were satisfied with the brood composition produced through chance. Seventy-six offspring (representing 21 clutches) from the BME and 54 offspring (12 clutches) from the BFE derived from perfect clutches. Because of small sample sizes, I performed chi-square analyses in these comparisons and those that follow below. There is no evidence of primary manipulation (Table 2). This is by no means a conclusive demonstration that zebra finches are incapable of primary manipulation, but it does suggest that primary manipulation was not the means by which sex ratio was altered in these experiments.

To test for secondary manipulation, one would ideally determine the sex of offspring that die. Unfortunately, I have been unable to determine the sex of offspring that die within a few days of hatching, which is a period of high mortality. Analysis is restricted to an examination of sex ratios among surviving young.

Parent birds are likely to use visual or auditory cues to recognize sex of offspring, probably detecting sex after hatching. To look for evidence of secondary manipulation, I compiled data on sex ratios of clutches with brood losses prior to fledging, but in which all eggs are known or suspected to have hatched. Cases of suspected hatching involve clutches in which one or more eggs "disappeared" when they were scheduled to hatch. (Hatchlings weigh about 0.5 g and desiccate quickly upon death. Even when dead hatchlings were recovered, it was not always possible to be certain of their nest of origin.) These clutches are included because each nest was inspected only once a day, and hatching can occur at any hour. Parents do not evict eggs that fail to hatch on schedule; eggs that fail to hatch remain in the nest until the brood fledges unless they are broken by nestlings. Clutches in which one or more eggs failed to hatch, and

TABLE 2. Distribution of sons and daughters in various types of clutches. BME: Banded Male Experiment, BFE: Banded Female Experiment. Perfect clutches (those in which all eggs hatched and survived to sexing age), BME: $X^2 = 0.229$, 2 *d.f.*, $P > 0.75$; BFE: $X^2 = 1.493$, 2 *d.f.*, $P > 0.25$. Clutches which sustained pre-fledging brood losses and in which all eggs are known or suspected to have hatched, BME: $X^2 = 8.548$, 2 *d.f.*, $P < 0.025$; BFE: $X^2 = 7.900$, 2 *d.f.*, $P < 0.025$. Clutches with post-fledging brood losses and in which all eggs are known or suspected to have hatched, BME: $X^2 = 4.667$, 2 *d.f.*, $P < 0.10$; BFE: $X^2 = 1.523$, 2 *d.f.*, $P > 0.25$. R = red-banded, O = orange banded, g = green-banded, Bl = black-banded, and b = blue-banded.

	BME			BFE		
	R	O	g	Bl	O	b
Perfect clutches						
Number of sons	22	8	12	8	11	5
Number of daughters	17	8	9	12	9	9
Sex ratio (% sons)	56.4	50.0	57.1	40.0	55.0	35.7
Clutches with pre-fledging brood losses						
Number of sons	40	13	20	17	14	24
Number of daughters	16	17	22	27	14	10
Sex ratio (% sons)	71.4	43.3	47.6	38.7	50.0	70.6
Clutches with post-fledging brood losses						
Number of sons	23	13	12	10	10	9
Number of daughters	11	8	17	10	7	5
Sex ratio (% sons)	67.6	61.9	41.4	50.0	58.8	64.3

those in which one or more young died after fledging, are excluded here to minimize the possible impact on the data of other forces of mortality (see below).

In both experiments, sex-ratio trends for clutches with pre-fledge brood losses are stronger than, and in the same direction as, the overall trends (compare Table 2 with Table 1), and for both experiments results are significant (BME: 41 clutches, $X^2 = 8.548$, $P < 0.025$; BFE: 37 clutches, $X^2 = 7.900$, $P < 0.025$; Table 2). In both experiments most losses (80% or more) occurred before offspring were 6 days old; young usually fledge at 18 to 20 days. These results indicate that sex-ratio manipulation is performed after hatching and imply that parent zebra finches can detect offspring sex within days of hatching.

For comparison, I compiled data for clutches in which brood losses occurred only between fledging and the end of parental care (two weeks post-fledging). Again, only clutches in which all eggs hatched are included. If, as the results of the previous analysis suggest, parents are able to determine the sex of offspring early, one would not expect a strong sex-ratio pattern for clutches with exclusively late brood losses, because the cost of brood reduction increases as off-

spring age (Maynard Smith, 1980). Among such broods, significant sex-ratio trends did not occur in either experiment (27 clutches in BME, 18 clutches in BFE; Table 2). In the BME, however, a nonsignificant trend in the same direction as previous patterns is evident ($P < 0.10$).

Other Forms of Sex-Biased Investment

The above results indicate that zebra finches manipulate the sex ratio by withholding parental resources from recently hatched offspring. Zebra finches could make qualitative as well as quantitative investment decisions. For example, parents could allocate different types or quantities of food to offspring of the two sexes. To explore this possibility, I examined the weights of offspring just prior to fledging, as well as peak weights prior to fledging. Results were analyzed by nested analyses of variance in which offspring sex and brood size were nested within parental band color. Monogamous and polygynous red-banded males were considered as separate "band" categories in the BME.

In the BME, analyses of both fledging and peak weights showed significant overall trends (fledging weights: $F = 3.58$, 20 *d.f.*, $P < 0.0001$; peak weights: $F = 3.58$, 20 *d.f.*,

TABLE 3. Weights at fledging and peak weights prior to fledging for offspring in the Banded Male Experiment (BME) and Banded Female Experiment (BFE). Weights are expressed in grams \pm 1 SE. R = red-banded, O = orange-banded, g = green-banded, Bl = black-banded, and b = blue-banded.

Paternal band color/mating type	\bar{x} weight of sons (<i>N</i>)	\bar{x} weight of daughters (<i>N</i>)
Fledging weights (BME)		
R monogamous	9.67 \pm 0.17 (23)	10.11 \pm 0.25 (17)
R polygynous	9.79 \pm 0.19 (31)	9.37 \pm 0.23 (19)
O monogamous	9.30 \pm 0.21 (25)	9.47 \pm 0.20 (21)
g monogamous	9.37 \pm 0.24 (24)	9.29 \pm 0.16 (28)
Peak weights prior to fledging (BME)		
R monogamous	9.75 \pm 0.15 (23)	10.29 \pm 0.21 (17)
R polygynous	9.83 \pm 0.19 (31)	9.38 \pm 0.52 (19)
O monogamous	9.42 \pm 0.22 (25)	9.49 \pm 0.20 (21)
g monogamous	9.55 \pm 0.19 (24)	9.47 \pm 0.16 (28)
Maternal band color		
Fledging weights (BFE)		
Bl	9.92 \pm 0.12 (53)	9.65 \pm 0.17 (49)
O	9.89 \pm 0.15 (46)	9.49 \pm 0.16 (37)
b	9.80 \pm 0.11 (40)	9.88 \pm 0.13 (33)
Peak weights prior to fledging (BFE)		
Bl	10.16 \pm 0.14 (53)	9.94 \pm 0.14 (49)
O	10.04 \pm 0.15 (46)	9.73 \pm 0.15 (37)
b	9.86 \pm 0.10 (41)	10.03 \pm 0.13 (33)

$P < 0.0001$; Table 3). Offspring weight varied with paternal band color/mating type (fledging weights: $F = 3.39$, 3 *d.f.*, $P = 0.02$; peak weights: $F = 3.48$, 3 *d.f.*, $P = 0.02$). Offspring weight did not vary with sex (fledging weights: $F = 1.38$, 4 *d.f.*, $P = 0.24$; peak weights: $F = 1.40$, 4 *d.f.*, $P = 0.24$), but did vary with clutch size (fledging weights: $F = 4.30$, 13 *d.f.*, $P = 0.0001$; peak weights: $F = 4.29$, 13 *d.f.*, $P = 0.0001$). Duncan's Multiple Range Test was employed to determine the location of significant differences among band-color/mating-type groups. Monogamous red-banded males' offspring were significantly heavier than those of orange- and green-banded males ($P < 0.05$), but the weights of offspring of polygynous red-banded males did not differ significantly from either extreme. Similar results are obtained if all red-banded males are treated as one category; in this case the offspring of red-banded males are found to be heavier than those of the other two categories.

In the BFE, there were no significant trends (overall fledging weights: $F = 1.48$, 20 *d.f.*, $P = 0.09$; peak weights: $F = 1.30$,

20 *d.f.*, $P = 0.18$; Table 3). Offspring weight did not vary with maternal band color (fledging weights: $F = 0.36$, 2 *d.f.*, $P = 0.70$; peak weights: $F = 0.57$, 2 *d.f.*, $P = 0.57$), sex (fledging weight: $F = 2.03$, 3 *d.f.*, $P = 0.11$; peak weights: $F = 1.71$, 3 *d.f.*, $P = 0.16$), or brood size (fledging weight: $F = 1.52$, 15 *d.f.*, $P = 0.10$; peak weights: $F = 1.31$, 15 *d.f.*, $P = 0.19$).

In sum, for both experiments, there is no evidence of differential quantitative allocation to surviving sons and daughters as a function of parental band color. An intriguing finding in the BME, that offspring weight varied with parental band color/mating pattern, did not hold in the BFE, in which the color classes produced offspring of uniformly high weight.

Limits to Manipulation

There are at least two costs associated with the practice of secondary manipulation through brood reduction shortly after hatching; the actual wasted investment in the rejected offspring, and the lowered RS that results from brood reduction. The relative importance of these costs depends on

the nature of future reproductive opportunities. Since zebra finches are opportunistic breeders that may often face uncertain future mating opportunities, lowered immediate RS may be an important factor ultimately limiting the degree to which the sex ratio can be profitably manipulated.

Perhaps parents "intending" to practice secondary manipulation lower the cost by increasing clutch size (the number of eggs laid per clutch) in anticipation of subsequent brood reduction. If this were the case, one would predict that attractive and unattractive birds would have larger clutches than birds of intermediate attractiveness. In both experiments, however, there is no clear association between band color and clutch size (Burley, 1986a). There is, however, an association with brood size (see below). Hence, zebra finches do not appear to adjust clutch size facultatively. Perhaps clutch size cannot be manipulated, or perhaps all females lay the largest clutches feasible when food is abundant.

The finding that clutch size is not increased to compensate for secondary reductions strengthens the conclusion that decreased short-term RS is a potentially important cost of sex-ratio manipulation. It follows that the profitability of manipulation falls if other factors limit brood size (e.g., Lack, 1954; Ricklefs, 1965, 1968; O'Conner, 1978; Clark and Wilson, 1981 and references therein). One such possible factor is hatch failure. To explore this possibility, I compiled sex-ratio data for clutches in which one or more eggs failed to hatch (due to accidental cracking or breakage, infertility of eggs, or embryo mortality). Eggs were designated as having failed to hatch if they were still in the nest 18 days after the last egg of a clutch was laid. (Eggs usually hatch in 12 to 14 days). Also included are clutches in which one or more eggs disappeared or were found broken less than 11 days after the first egg was laid (before the onset of hatching). Females sometimes laid a second clutch before or shortly after a previous clutch hatched. When they did so, they usually laid in a separate nest. Instances in which females laid a second clutch in the same nest before the previous one hatched are excluded because I am unable to assign

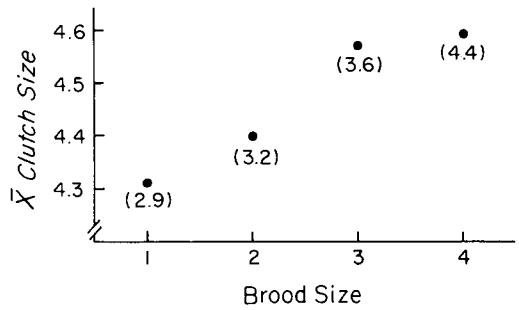


FIG. 4. Relationships among final brood size, clutch size, and number of hatchlings in the Banded Male Experiment. Brood size is the number of offspring surviving two weeks post-fledging. The mean number of known hatchlings is presented in brackets for each brood size. The number of known hatchlings underrepresents somewhat the actual number of hatchlings.

individual eggs to particular clutches. For clutches in which one or more eggs failed to hatch, there is no relationship between band color and sex ratio of offspring in the BME (64 clutches: $X^2 = 0.614$, 2 d.f., $P > 0.50$). Sample sizes in the BFE were too small for analysis, because blue-banded females tended to lay successive, overlapping clutches in the same nest, so that hatch failure could not be ascertained.

Other constraints on brood size that might limit the profitability of secondary sex-ratio manipulation include accidental brood losses and impaired health or viability of some young. Since the cause of any individual offspring's death is not known, it is not possible to directly test the hypothesis that parental tendency to effect secondary sex-ratio manipulation is limited by these competing considerations. However, a comparison of sex ratios produced in broods of various sizes offers some evidence.

In both experiments, clutch size increased with increasing brood size, but throughout the typical brood-size range (one to four young surviving to the end of parental care), differences in clutch size are smaller than corresponding differences in brood size. Figure 4 presents results for the BME; trends in the BFE were similar. The same generalization holds for a comparison of brood sizes and the number of hatchlings (Fig. 4). The significance of this is that the opportunity for secondary manipulation should

TABLE 4. Sex ratios as a function of final brood size. "Final brood size" is the number of offspring surviving to the age at which sexing was possible based on plumage. Cases in which two color-banded birds shared a nesting attempt are excluded. Final brood sizes larger than 4 did occur, but are not included. R = red-banded, O = orange-banded, g = green-banded, Bl = black-banded, and b = blue-banded.

Final brood size	Banded Male Experiment Paternal band color			χ^2	Banded Female Experiment Maternal band color			χ^2
	R	O	g		Bl	O	b	
	$\delta:\varnothing$	$\delta:\varnothing$	$\delta:\varnothing$		$\delta:\varnothing$	$\delta:\varnothing$	$\delta:\varnothing$	
4	56:28	18:26	15:21	11.174 ^a	24:20	11:5	20:12	1.130
3	43:38	29:16	20:16	1.546	16:19 ^b	20:22	17:16	0.237
2	30:18	23:19	10:14	2.816	16:26	16:16	9:7	1.928
1	11:6	5:4	8:10	1.456	5:7	7:6	8:4	1.510

^a $P < 0.005$.

^b The sex of one bird was not determined.

have been greater in small broods (which sustained, on average, more brood reduction) than in large broods. Therefore, if parents were willing to reduce brood size to any degree necessary to influence the sex ratio, the most skewed sex ratios should be found in the smallest broods. If, on the other hand, parents have an optimal brood size larger than the minimal size of one, there should either be no relationship between brood size and departure from Mendelian sex ratios, or the greatest discrepancies should be found in brood sizes greater than one.

My sample sizes were generally too small to analyze distributions within each brood size for conformity to binomial expectations (Williams, 1979). Therefore, I used chi-square analyses of the aggregate sex ratios produced by each color class for brood sizes one through four. (Brood sizes larger than this were too rare to be analyzed.) In the BME, the greatest and only statistically significant departure from randomness occurred at the largest brood size; in the BFE, significant deviations were not found for any brood size (Table 4). These results support the conclusion that other factors beside sex composition are important, i.e., that finches are not willing to reduce broods to any size necessary to manipulate the sex ratio.

To further explore the nature of interactions between band color, brood size, and sex ratio, I used three-dimensional contingency analyses (Sokal and Rohlf, 1969; Fienberg, 1977; Waldbauer and Ghent, 1984) on the data in Table 4. In both experiments there were significant interactions between band color and sex ratio

(BME: $G^2 = 6.64$, 2 *d.f.*, $P < 0.05$; BFE: $G^2 = 6.22$, 2 *d.f.*, $P < 0.05$); this result is consistent with the results of Goodman and Kruskal's test and the Fisher Exact Test (see above). In the BFE, the interaction between brood size and band color was also significant ($G^2 = 13.63$, 6 *d.f.*, $P < 0.05$); this interaction was not significant in the BME ($G^2 = 11.22$, 6 *d.f.*, $P < 0.10$). For both experiments the model that best describes the data recognizes significant interactions between brood size and band color as well as between sex ratio and band color. However, brood size and sex ratio are independent.

DISCUSSION

In both experiments sex-ratio trends are consistent with those found previously (Burley, 1981) and are concordant with the hypothesis that parents manipulate their progeny to selectively produce offspring of the sex of the more attractive partner. The trend is more pronounced in the BME, a result that may be explained by the longer duration of the experiment and the greater number of offspring produced. The sex ratios produced were not as extreme as some in an earlier experiment in which red-banded males mated to blue-banded females produced 81.81% male offspring (based on 11 offspring) and green-banded males mated to black-banded females produced 11.11% male offspring (based on nine offspring). This result is not surprising, since the maximum disparity in attractiveness between mates in the present experiments is less than in the first experiment.

Alternative Hypotheses

To evaluate the hypothesis that sex ratio patterns result from differential ability to rear sons and daughters, it is first necessary to consider whether one or both sexes manipulate the sex ratio. Since parent zebra finches of both sexes participate in all parental activities except egg-laying, and since manipulation appears to be effected after hatching (see Results), there is no compelling reason to expect that manipulation occurs in response to the physical capacity of only one sex. The hypothesis that manipulation occurs in response to the condition or parenting ability of both sexes (the parental condition hypothesis) requires an explanation of why, for example, green-banded males should be more "adept" at rearing daughters while blue-banded females should be more successful with sons. This possibility would seem to require that males and females selectively forage for different food types to bring to offspring and that male and female offspring have different nutritional requirements. Moreover, in order for band color to affect quality of food obtained for offspring, it seems necessary to invoke a band-color effect on intrasexual competitive ability and to suppose that certain types of food are limited in supply. I have no data on the nutritional needs of male and female offspring, but in my aviaries adults of both sexes feed offspring of both sexes. They do so through regurgitation of crop contents and may feed several offspring (including both sexes) after a foraging bout. These experiments were designed to minimize intrasexual competition and, thus far, no effects of band color on competitive ability have been found (Burley, unpubl.). Since food was provided ad lib, and vitamins and minerals were supplied amply, it is not clear what resources might have been sufficiently limiting to provide a basis for competition.

If the sex ratio is manipulated in response to the condition of only one parent, it is probably the mother, since female zebra finches incur, on average, somewhat more than half the parental investment per offspring (based on time-budget estimates [Burley, unpubl.]). There is no sexual size dimorphism (by weight), so it is not clear

how maternal condition might affect offspring survival or reproductive potential. Since secondary and tertiary sex ratios are routinely slightly male-biased in my laboratory (Burley, 1985a), and since females appear somewhat more "delicate," I will assume for the purpose of argument that females are the more vulnerable sex. This leads to the expectation that females in good condition should produce daughters, those in poor condition, sons.

How could a female's band color or that of her mate affect her physical condition? I have hypothesized that, in species with biparental care, individuals adjust their parental investment based on their own mate-getting ability vis-à-vis that of their mate or potential mate (the differential allocation hypothesis, Burley, 1986a). Both circumstantial (Burley, 1986a) and direct observational data (Burley, unpubl.) support this hypothesis for birds in the BME and BFE. That is, the fraction of the total parental workload varied with band color (or mate's band color) for both sexes. There is also evidence that relative parental expenditure affected the condition of both sexes (Burley, 1985a, 1986a, unpubl.).

The correlation between relative parental expenditure of females and sex ratio of offspring is superficially consistent with the maternal condition hypothesis: blue-banded females and mates of red-banded males have high expenditures and male-biased sex ratios, while black-banded females and mates of green-banded males have lower expenditures and female-biased sex ratios. A serious problem with this argument, however, is that the condition of females in all groups declined over time as a result of the experimental treatment of permitting continuous breeding for 15 to 22 months. For all birds, peak condition probably occurred at or near the beginning of the experiment when they were released into the aviary as never-mated adults (Burley, unpubl.). Accordingly, if females in good condition produce daughters and those in poor condition, sons, there should have been an overall low (female-biased) sex ratio at the beginning of the experiments. This should have been followed by a general trend toward increasing sex ratio by all groups, though blue-banded

females and mates of red-banded males should have displayed a more rapid increase in sex ratio than other females. The actual temporal trends (Figs. 2, 3) show no suggestion of this pattern. A second problem with this argument is that there is no good reason to suppose that male condition does not influence offspring in a manner similar to that of females. The trends in male condition offset those of the females, since males with low expenditures (red-banded males and mates of blue-banded females) were mated to females with high expenditures, while males with high expenditure (green-banded males and mates of black-banded females) were mated to females with low expenditure.

The failure of the maternal condition hypothesis to account for sex-ratio trends does not depend on the assumption that females are the more vulnerable sex. If males are more vulnerable, females in good condition should produce sons. There is no concise logical framework for expecting that blue-banded females and mates of red-banded males would sustain superior condition throughout the experiment and, in fact, empirical evidence suggests otherwise. Finally the temporal trends predicted by this hypothesis (a declining sex ratio, with steeper slopes for black-banded females and mates of green-banded males) did not occur.

In sum, there is insufficient evidence for a conclusive rejection of the condition hypothesis, but available evidence and logical considerations make both versions of it (parental condition and maternal condition) unlikely. Evidence does not support the age/experience hypothesis.

Recognition of Offspring Sex

Research by R. Balda and J. Balda (unpubl.) reveals the probable means by which parents recognize the sex of offspring. The begging calls of dependent zebra finches are complex, containing at least 22 distinguishable call notes. The frequency with which some of these calls are given varies between the sexes. Discriminant function analysis of begging calls indicates that sex-specificity of signaling increases with offspring age. Between hatching and five days of age such analysis correctly predicts sex in 74% of

cases; for young six to 10 days of age, the success rate is 87%; and for young 11 to 15 days of age, the method predicts sex 100% of the time (R. Balda, pers. observ.). Interestingly, the expression of these calls follows the course predicted by parent-offspring conflict theory (Trivers, 1974) if parents use them to make brood-reduction decisions based on offspring sex. That is, as an offspring ages, the risks of revealing its sex to its parents should diminish as the cost to the parent of brood reduction increases.

Limits to Manipulation

Brood reduction is an expensive mechanism of sex-ratio manipulation that must limit its practice. It is important to consider how the costs of brood reduction could possibly be offset enough to make manipulation profitable at all. One possibility is that the costs of rearing offspring increase nonlinearly with increasing brood size. When this occurs, optimal brood size is lower than maximal brood size as long as future reproductive opportunities are likely. Furthermore, if different phases of offspring development are differentially taxing on parental abilities, it may be adaptive to stagger successive clutches so that they are overlapping, with the least overlap occurring during the period in which offspring are most demanding of parental resources (Burley, 1980). It seems likely that greater degrees of overlap are possible with smaller clutches.

If it is true that large clutches are disproportionately expensive, the practice of brood reduction by zebra finches may have been stimulated by at least three aspects of the experimental environment: the abundance of food, the relative constancy of conditions, and the abundance of nest sites. Given an unchanging bountiful environment, future opportunities for reproduction were likely and risks associated with brood reduction may have been worth taking. Given an abundance of suitable nest sites, birds may have been able to recoup some of the costs of brood reduction by overlapping successive clutches, a practice engaged in at least occasionally by a majority of birds. I would expect to find less brood reduction when nest sites are less available.

Although brood reduction is a common passerine practice, its role among free-living zebra finches is not known. We do know that zebra finches are found in a wide variety of habitats (Keast, 1958; Immelmann, 1962). At different times and places, food, water, or nesting sites may limit their ability to survive and reproduce (Finlayson, 1932; Frith and Tilt, 1959; Immelmann, 1962, 1965). The sexes could vary in their responses to environmental stresses, which might cause local imbalances in tertiary sex ratios (making sex-ratio compensation potentially profitable [Burley, 1982*b*]) or lead to differential survivorship of sons and daughters under various environmental conditions. Temporal variation in population recruitment could affect male and female fitness differently (Werren and Taylor, 1984).

An additional limitation to the form of sex-ratio manipulation found here is that other factors besides attractiveness of parents may influence the sex ratio (Burley, 1982*b*; Charnov, 1982; Silk, 1983). For example, seasonal fluctuation in sex-ratio production has been found for several passerines (Howe, 1977; Fiala, 1981; Weatherhead, 1983); this could result from different environmental conditions favoring son versus daughter production (Oksanen, 1981). If the sexes are not equally expensive to produce, then parental condition (which may or may not be independent of stage in the breeding season) may influence offspring sex. This hypothesis is usually framed in terms of polygynous species in which males are thought to be the more expensive sex (Trivers and Willard, 1973; Clutton-Brock et al., 1984; Meikle et al., 1984). There is no evidence that one sex is more expensive to produce in zebra finches, but this possibility cannot be excluded; studies on birds have so far failed to show a clear relationship between food delivery rates and sexual dimorphism at fledging (Newton, 1978; Bancroft, 1983; Richter, 1983). Effects of brood size and/or hatching order have also been suggested (Howe, 1976; Fiala, 1981; Ankney, 1982; Ryder, 1983; but see Cooke and Harmsen, 1983).

Interestingly, in the only other studies which have purported to investigate sex ra-

tio as a function of (male) attractiveness, different sex-ratio trends have been found. Patterson and Emlen (1980) found for the yellow-headed blackbird (*Xanthocephalus xanthocephalus*) that males with large harems produced sex ratios no different than those with small harems. There was a tendency, however, for the primary brood to have a higher sex ratio than later broods, which might be explained by the fact that male yellow-headed blackbirds help to care for young of only the primary nest. Weatherhead (1983) used harem size and female density on territories as indices of male attractiveness in the red-winged blackbird (*Agelaius phoeniceus*). He found no relationship between male attractiveness and sex ratio, but he did find significant seasonal effects. In neither of these studies was male attractiveness actually determined by measuring female preference. Harem size may reflect differences in the quality of male territories rather than (or in addition to) the personal qualities of males (Searcy, 1979; Lenington, 1980; Yasukawa et al., 1980).

A final limitation to successful secondary manipulation is the ability of parents to recognize the sex of offspring. Of course, a hatchling that signals "maleness" in a situation in which males are favored should benefit over a sib that does not indicate its sex. Assuming that offspring cannot determine which sex is to be favored in a given situation, however, a hatchling that signals ambiguously would seem more likely to survive than one that signals "maleness" in a brood in which females are favored or one signaling "femaleness" in a brood in which males are favored. For selection to favor sex advertisement by offspring requires that the net benefit from accurate advertisement of sex on average outweighs the net benefit from ambiguous signaling. The costs of signaling ambiguously depend in part on the rationale for manipulation. If, for example, the sexes require somewhat different resources for optimal development, then an offspring that signals ambiguously might have lower fitness than a same-sex sibling that advertises its sex, assuming both survive. There is also the kin-selected cost which results if an ambiguous signaler of the unfavored sex receives investment that

could more profitably be applied to a sib. This cost, however, would have to be very large before it could be expected to influence offspring behavior.

The Evolution of Begging Calls and Manipulation

In attempting to build a scenario for the evolution of facultative secondary sex-ratio manipulation based on begging calls, it is tempting to suppose that offspring identify their sex as a result of selection placed on them by parents. That is, parents "want" to manipulate the sex ratio and so have favored offspring that identify their sex. It is more parsimonious to invoke the opposite order of events: begging calls evolved with some sex-identifying component, and parents capitalized upon this cue to manipulate the sex ratio. It is not necessary to suppose that the sex cue was initially functional in any way. It could have originated, for example, through the different effects of male and female sex hormones on neural differentiation (Gurney and Konishi, 1980; Pohl-Apel and Sossinka, 1984). If so, we might expect corresponding sex differences in the calls of adults. As in most estrildid finches (Goodwin, 1982), only male zebra finches sing the courtship song, but adults of both sexes make other calls. Among adult zebra finches and certain congeners, the structure of the "distance call" differs between the sexes (Zann, 1975, 1984). This call, which may function in sex and individual recognition, develops ontogenetically from begging calls (Zann, 1985). If sex differences in the structure of begging calls bear some resemblance to the differences in adult calls, then no special origin for the ability to discriminate between the begging calls of males and females is necessary. Assuming that parent zebra finches have a general capacity for opportunistic brood reduction (a trait that is probably widespread among altricial birds), all that may have been required for the evolution of facultative sex-ratio manipulation is a circumstance that makes it profitable and an appropriate parental response to that situation. Once parents began to manipulate the sex ratio, selection on offspring would have influenced whether the

sex-identifying elements of begging calls became more or less ambiguous.

Conditions for Sex-Ratio Manipulation

It is important to evaluate the extent to which zebra finches meet the six necessary conditions for sex-ratio manipulation based on parental attractiveness (see Introduction). Profitable manipulation requires that attractive traits are 1) heritable and, for sexually dimorphic species, have 2) sex-limited expression. Zebra finches react to color bands both as if they are heritable and have sex-limited expression. Sex-limited expression is well developed in these finches and in many other sexually dimorphic organisms; presumably it is a trait that evolves readily (Rice, 1984). Unfortunately, we have no knowledge of the current or past heritabilities of naturally occurring traits that zebra finches find attractive in opposite-sex conspecifics. Therefore, we cannot evaluate how often finches in nature have had the opportunity to vary sex ratio as a function of parental attractiveness. Novel traits arising through mutation, however, should have substantial heritabilities, and there is no reason to expect finches to discern the non-genetic basis of the novel phenotypes used in these experiments. 3) Attractiveness must affect reproductive success. In both the BME and BFE attractive individuals had greater RS than unattractive ones (Burley, 1986a). 4) The preference for the attractive trait must be common to some fraction of the population. I have demonstrated this repeatedly (Burley et al., 1982; Burley, 1985b, 1986b). 5) The mating system must be one in which a substantial fraction of the male population mates. This requirement is easily met by zebra finches. Their typical mating system is monogamy. 6) There must be an economical means of sex-ratio manipulation. In these experiments, sex-ratio manipulation occurred through brood reduction shortly after hatching. Brood reduction does have costs and must set limits to the extent to which the sex ratio can be profitably manipulated. The spontaneity with which zebra finches responded to this novel situation leads me to expect that brood reduction and secondary sex-ratio manipulation will be found to be facultative tactics employed by

zebra finches under a possibly wide range of environmental and social conditions.

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