

## MECHANISMS OF FACULTATIVE SEX-RATIO VARIATION IN ZEBRA FINCHES (*TAENIOPYGIA GUTTATA*)

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**ABSTRACT.**—The offspring sex ratio at independence in a colony of Zebra Finches (*Taeniopygia guttata*) was significantly male biased. Three possible proximate causes of this bias were examined. (1) The first was that there is a sex-biased laying sequence followed by brood reduction. Males were significantly more likely to hatch from earlier-laid eggs than females, but there was no evidence of increased mortality among late-laid nestlings. (2) The second was that there is sex-biased mortality due to sex-specific growth rates. Male and female offspring had similar rates of mass increase, tarsus growth, and wing-chord growth. (3) The third was that there is sex-biased provisioning by one or both parents, increasing survival probabilities of preferred sex. There was evidence that males fed male-biased broods more frequently than female-biased broods. Fledging age, fledging mass, and the number of days to independence were similar for male and female offspring, suggesting that sex-biased provisioning had no significant biological effect. Although none of the hypotheses adequately explained the observed sex-ratio bias, results from this and other studies suggest that sex-biased laying sequences followed by brood reduction are most likely to cause skewed offspring sex ratios in nature. The implications of a sex-biased laying sequence and of sex-biased provisioning by the male are discussed in reference to the potential evolutionary conflict between males and females over control of offspring sex ratios. Received 5 October 1994, accepted 21 June 1995.

FISHER (1930) PREDICTED that, in dioecious organisms, offspring sex ratios at independence are fixed at unity. Both the existence and adaptiveness of facultative sex-ratio variation have been questioned (Williams 1979, Fiala 1981, Harmsen and Cooke 1983, Clutton-Brock 1986, Breitwisch 1989, Weatherhead and Teather 1991, but see Gowaty 1992). There is evidence that biased sex ratios may be adaptive in some situations: (1) when one sex has high variance in reproductive success (Patterson et al. 1980, Wegge 1980, Blank and Nolan 1983, Bortolotti 1986); (2) when subadults help at the nest (Gowaty and Lennartz 1985, Emlen et al. 1986, Ligon and Ligon 1990, Bednarz and Hayden 1991); (3) when sex differences in dispersal result in competition between parents and the philopatric sex for resources or mates (Hamilton 1967, Clark 1978, Charnov 1982, Gowaty 1993); or (4) when relative attractiveness of adults is variable (Burley 1981).

Sex-ratio variation has received a great deal of attention in the literature, but the causal mechanisms remain poorly understood. In birds, a possible mechanism is meiotic drive, where the female's sex chromosomes segregate non-randomly during egg production. This results in a nonrandom distribution of males and females in the laying sequence (Howe 1977, An-

kney 1982, Ryder 1983, Weatherhead 1985, Bortolotti 1986, Bednarz and Hayden 1991; but see Cooke and Harmsen 1983, Edmunds and Ankney 1987, Leblanc 1987, Ryder and Termaat 1987). Another possible mechanism is sex-specific mortality due to differential energetic costs, especially in sexually dimorphic species (Howe 1976, 1977, Blank and Nolan 1983, Fiala and Congdon 1983, Teather and Weatherhead 1988, 1989, Olsen and Cockburn 1991; but see Dhondt 1970, Newton 1978, Picozzi 1980, Collopy 1986). Two additional, but very costly, mechanisms are selective rejection of young (Burley 1986) or siblicide coupled with a sex-biased laying sequence (Edwards and Collopy 1983, Bortolotti 1986, Edwards et al. 1988).

Another possible mechanism that only recently has received attention in the literature is sex-biased provisioning. Sex-biased provisioning occurs when offspring of one sex receive more food from either or both parents than do offspring of the opposite sex (Stamps 1990). If both parents preferentially feed the same sex, or if one feeds unequally and the other remains egalitarian, the probability of survival of the preferred sex increases. In this paper, I consider sex-biased provisioning to include nestling brooding and material investment in the egg (Howe 1976, Ankney 1982, Ry-

der 1983, Mead et al. 1987; but see Fiala 1981, Bancroft 1984, Weatherhead 1985, Leblanc 1987, Teather 1989).

Few instances of sex-biased provisioning have been reported (see reviews in Stamps 1990, Gowaty and Droge 1991). This lack of information is due largely to difficulties in identifying nestling birds by sex. Yasukawa et al. (1990) found in Red-winged Blackbirds (*Agelaius phoeniceus*) that both parents fed male-biased broods more frequently than female-biased broods. Stamps et al. (1987) observed male Budgerigars (*Melopsittacus undulatus*) feeding female-biased broods more frequently than male-biased broods. In Eastern Bluebirds (*Sialia sialis*), Gowaty and Droge (1991) observed a similar bias by fathers in favor of female-biased broods. Individual female bluebird nestlings also received more feedings from their fathers than did individual males (Droge et al. 1991).

Droge et al. (1991) found that feeding patterns in Eastern Bluebirds were unrelated to the offsprings' energetic demands, while studies on many sexually dimorphic species show significantly different male and female growth rates, but no apparent feeding biases (*Accipiter nisus*, Newton 1978; *Quiscalus quiscula*, Howe 1979; *Agelaius phoeniceus*, Fiala 1981; *Corvus frugilegus*, Roskaf and Slagsvold 1985; *Aquila chrysaetos*, Collopy 1986; *Quiscalus mexicanus*, Teather and Weatherhead 1988; see review in Gowaty and Droge 1991). The functional importance of sex-biased provisioning remains unclear, as no study to date has been able to link it to differential energetic demands or survival due to sexual dimorphism.

In this study, I examined potential causal mechanisms of facultative sex-ratio variation in a colony of Zebra Finches (*Taeniopygia guttata*), a species known to have biased sex ratios in the wild and the laboratory (Burley 1981, 1986, Burley et al. 1989). From the literature I developed the following hypotheses: (1) the brood-reduction hypothesis predicts that the sex of Zebra Finch offspring varies nonrandomly with laying and hatching order, and that posthatching survival also varies nonrandomly in such a way as to produce a biased sex ratio at independence; (2) the sex-specific growth hypothesis predicts that, despite sexual monomorphism, male and female Zebra Finches differ in growth rate in some way that influences their survival and, therefore, the sex ratio at independence; (3) the sex-biased provisioning hypothesis predicts that adult male and/or female Zebra Finches invest

in their offspring nonrandomly with respect to offspring sex, and that this difference in investment affects offspring survival and produces a biased sex ratio.

#### METHODS

Zebra Finches are monogamous estrildid finches. They are sexually monomorphic, sexually dichromatic, and typically reach sexual maturity and attain adult plumage within 90 days of fledging. Zebra Finches are primarily granivorous and breed opportunistically in response to seasonal rainfall (Immelmann 1965, Zann and Straw 1984). Both sexes participate in nest building and defense, incubation of eggs, brooding of young, and feeding of nestlings and fledglings (Immelmann 1965, Skagen 1988).

I randomly selected 15 adult female and 15 adult male finches from a breeding colony at the University of Wisconsin, Madison. Ten pairs had wild-type plumage and five pairs were leucistic (i.e. had white plumage). I assigned five pairs to each of three aviaries (leucistic pairs were isolated to one aviary). Aviaries were approximately 18 m<sup>3</sup> in volume, temperatures were set at 22°–25°C, humidity was kept at 50%, and rooms were on a 14:10 h light:dark cycle. All aviaries contained numerous branches and perches, five open basket nests, and *ad libitum* nesting material (shredded string). I allowed the birds 7 to 10 days to habituate to aviaries and to begin forming pair bonds before introducing nesting material. Food (Kellogg's Cage Bird Food and Kellogg's Nestling Bird Food), oyster-shell grit, vitamin supplements, cuttlebones, and water were provided *ad libitum*. Data were collected between June and December 1992. Results from wild-type and leucistic pairs were not significantly different and were analyzed together.

*Egg data.*—I checked nests daily for eggs between 0700 and 0900 CST. Newly laid eggs were weighed to nearest 0.01 g (Ohaus Brainweigh electronic balance), and length and breadth were measured to nearest 0.01 mm with dial calipers. Egg volume (*V*) was calculated according to the formula:

$$V = 0.51L(B)^2, \quad (1)$$

where *L* is the length, *B* is the widest breadth, and 0.51 is an experimentally determined and tested constant (Hoyt 1979). Eggs within a clutch were marked sequentially with nontoxic felt-tipped pens and returned to the nest. Infertile eggs also were marked and included in the laying sequence because no *a priori* distinction could be made between fertile and infertile eggs.

*Nestling observations and measurements.*—Upon hatching, I gave each nestling a unique marking on their legs and feet with a nontoxic pen. Marks were reapplied as needed. Nestlings were weighed daily (between 0700 and 0900) to the nearest 0.01 g, and tarsus and wing-chord lengths were measured to the

nearest 0.01 mm with dial calipers. Daily measurements were continued until the young fledged. At 10 to 12 days of age, I fitted nestlings with colored leg bands, and marking with pens was discontinued. Leg-band colors were assigned following Burley's (1985) recommendations.

I began observing brooding and nestling feeding when all eggs hatched (or when remaining eggs failed to hatch after 48 h) and continued until all young fledged. All pairs with nestlings were observed from behind tinted observation windows for 20 min each day between 0700 and 1000, when feeding rates were highest (unpubl. data). Time spent brooding (estimated to within 10 s) and number of feedings (to entire brood per min) were recorded for both parents.

*Fledgling observations.*—Fledged broods were observed for 20 min each day between 0700 and 1000, and the number of feedings (per fledgling and per brood) was recorded for both parents. Observations continued until fledglings reached independence (see below). Several weeks after independence, fledglings molted and began to show adult plumage. Sex of leucistic fledglings was initially determined by bill color, and later confirmed by behavioral observations. Thus, I did not know sex of individual fledglings until after all feeding observations were completed.

*Definitions and statistical analysis.*—Egg rank is the order (ascending) in which an egg was laid within a clutch, including infertile or otherwise unhatched eggs. As Zebra Finches lay eggs asynchronously at approximately 24-h intervals, laying order also reflects hatching order. Successful eggs produced a nestling that survived to independence. I considered a fledgling independent if neither parent was observed feeding it for three consecutive observation days. Unsuccessful eggs produced nestlings that died before reaching independence (excluding eggs that did not hatch). Infertile eggs or those that did not hatch were not included as successful or unsuccessful.

Three indices of parental investment—brooding nestlings, feeding nestlings, and feeding fledglings—were recorded. Rates of brooding and feeding were obtained by dividing the total time spent brooding or the total number of feedings by the total number of observation hours. I defined a feeding as the insertion of the parent's bill into the gape of its offspring, the regurgitation of food, and the bill's subsequent retraction.

The sex ratio is the proportion of males within a brood. Three nestling and fledgling variables—fledging age, fledging mass, and days to independence—were recorded. Fledging age and fledging mass were recorded on the day a given nestling was last seen in the nest. Fledging age was determined as number of days posthatching. I defined days to independence as the number of days postfledging on which I saw a given fledgling fed by either parent.

Statistical tests were performed using SYSTAT (Wilkinson 1990). Binomial tests, *t*-tests, Mann-Whitney *U*-tests, and Spearman rank correlations (two-

tailed, where appropriate) were performed according to Siegel (1956) and Snedecor and Cochran (1989). Because some pairs had more than one brood during the period of study, I analyzed parental investment to first and second broods separately to avoid problems with nonindependence. Differences were considered significant at the 0.05 probability level. Means are given  $\pm 1$  SD.

## RESULTS

Including unhatched eggs, the mean clutch size for this population was  $6.4 \pm 1.73$  ( $n = 35$  broods). Twenty-one clutches produced successful eggs, of which 19 were used in the analysis below because the whole-brood sex ratio was known. The mean brood size of these 19 broods was  $2.5 \pm 1.36$ . Of these broods, 11 were first broods, 6 were second broods, and 2 were third broods. An additional 14 clutches were used to collect data on unsuccessful eggs, and were not used in the remainder of the study. Sample sizes vary slightly among the analyses due to the availability of data from each pair and each brood.

The mean egg mass of fertile eggs ( $n = 82$ ) was  $0.96 \pm 0.098$  g; the mean egg volume was  $0.92 \pm 0.096$  cm<sup>3</sup>. Figure 1 summarizes the relationships of egg mass and volume relative to offspring sex and survivorship. Eggs that hatched male offspring had similar masses ( $\bar{x} = 1.01 \pm 0.082$  g,  $n = 31$ ) to those that yielded female offspring ( $\bar{x} = 1.01 \pm 0.092$  g,  $n = 13$ ;  $t = 0.244$ ,  $df = 42$ ,  $P > 0.05$ ). Egg volumes also were similar between sexes of offspring (males,  $\bar{x} = 0.96 \pm 0.072$  cm<sup>3</sup>,  $n = 31$ ; females,  $\bar{x} = 0.96 \pm 0.084$  cm<sup>3</sup>,  $n = 13$ ;  $t = 0.264$ ,  $df = 42$ ,  $P > 0.05$ ). Successful eggs were significantly heavier ( $\bar{x} = 1.01 \pm 0.084$  g,  $n = 48$ ) than unsuccessful eggs ( $\bar{x} = 0.96 \pm 0.079$  g,  $n = 34$ ;  $t = 2.85$ ,  $df = 80$ ,  $P < 0.01$ ). Volumes of successful eggs ( $\bar{x} = 0.95 \pm 0.074$  cm<sup>3</sup>,  $n = 48$ ) were not significantly different from those of unsuccessful eggs ( $\bar{x} = 0.92 \pm 0.104$  cm<sup>3</sup>,  $n = 34$ ;  $t = 1.56$ ,  $df = 80$ ,  $P > 0.05$ ).

Males were significantly more likely to hatch from eggs laid earlier within a clutch than were females (Mann-Whitney  $U = 102.5$ ,  $z = -2.81$ ,  $P = 0.003$ ). Egg ranks of nestlings that survived to sexing age were  $3.74 \pm 1.77$  ( $n = 31$ ) for males and  $5.29 \pm 1.16$  ( $n = 13$ ) for females (Fig. 2). There was no evidence of brood reduction due to mortality of late-hatching females. Unsuccessful eggs were not significantly different in mean rank ( $4.03 \pm 1.74$ ,  $n = 34$ ) from successful

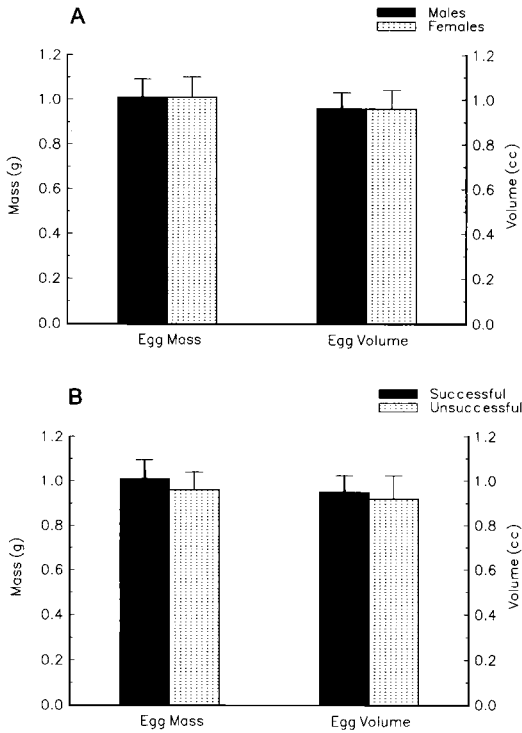


Fig. 1. Mean mass and volume of eggs that: (A) produced males ( $n = 31$ ) versus females ( $n = 13$ ); and (B) successful ( $n = 48$ ) versus unsuccessful ( $n = 34$ ). Male and female differences not significant. Successful eggs were significantly heavier ( $P < 0.01$ ) than unsuccessful eggs. Whiskers represent standard deviations.

eggs ( $4.17 \pm 1.82$ ,  $n = 48$ ; Mann-Whitney  $U = 796.5$ ,  $z = 0.373$ ,  $P = 0.36$ ).

Stepwise multiple regressions (Wilkinson 1990) were used to determine the importance of nestling sex as a factor affecting growth rate of three morphological characters. Nestling sex did not explain a significant proportion of the variation in the rates of increase of mass ( $F = 0.144$ ,  $P = 0.704$ ), tarsus length ( $F = 0.527$ ,  $P = 0.468$ ), or wing-chord length ( $F = 0.443$ ,  $P = 0.506$ ).

Correlations between brood sex ratio and measures of parental investment are shown in Table 1. Brood sex ratios had no effect on parental investment to first broods. In second broods, however, female brooding was significantly negatively correlated with sex ratio ( $r_s = -0.926$ ,  $P < 0.05$ ,  $n = 6$ ), and male nestling feeding was positively correlated with sex ratio ( $r_s = 0.926$ ,  $P < 0.05$ ,  $n = 6$ ). Brood-size effects cannot explain this feeding bias, as male nestling feeding rate was not significantly correlated with brood size ( $r_s = 0.098$ ,  $P > 0.05$ ,  $n = 6$ ). Brood sex ratio was unrelated to fledgling feeding rates in second broods. Measurements of feeding to individual fledglings indicated that the proportion of feedings given by the father did not differ between male fledglings ( $\bar{x} = 0.58 \pm 0.265$ ,  $n = 30$ ) and female fledglings ( $\bar{x} = 0.61 \pm 0.231$ ,  $n = 14$ ;  $t = 0.43$ ,  $df = 42$ ,  $P > 0.05$ ). Thus, during the fledgling stage, there was no evidence of sex-biased provisioning at either the brood or the individual level.

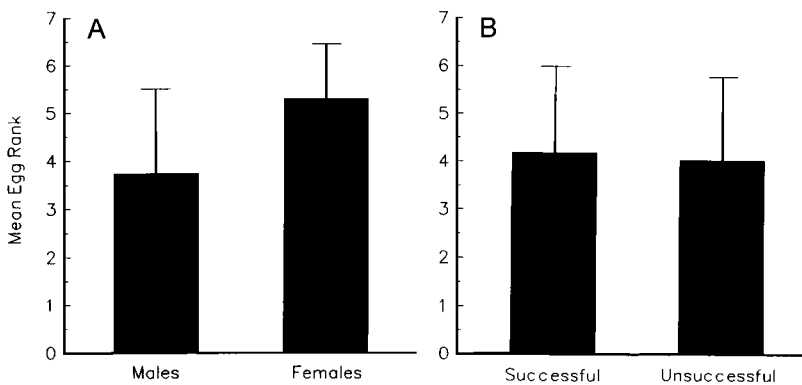


Fig. 2. Mean egg ranks i.e. order laid within brood, including unhatched eggs that: (A) produced males ( $n = 31$ ) versus females ( $n = 13$ ); and (B) were successful ( $n = 48$ ) versus unsuccessful ( $n = 34$ ). Male eggs had significantly lower ranks than female eggs ( $P < 0.003$ ). Differences between successful and unsuccessful eggs not significant. Whiskers represent standard deviations.

There were no significant differences between male and female offspring in fledging age (males,  $\bar{x} = 15.9 \pm 2.34$  days,  $n = 35$ ; females,  $\bar{x} = 15.7 \pm 2.32$  days,  $n = 15$ ;  $t = 0.37$ ,  $df = 48$ ,  $P > 0.05$ ), fledging mass (males,  $\bar{x} = 9.54 \pm 0.781$  g,  $n = 35$ ; females,  $\bar{x} = 9.81 \pm 0.693$  g,  $n = 15$ ;  $t = 1.24$ ,  $df = 48$ ,  $P > 0.05$ ), or mean number of days to independence (males,  $\bar{x} = 6.7 \pm 0.999$  days,  $n = 35$ ; females,  $\bar{x} = 6.7 \pm 3.15$  days,  $n = 15$ ;  $t = 0.28$ ,  $df = 48$ ,  $P > 0.05$ ).

The overall sex ratio at independence was significantly biased in favor of males (binomial test,  $z = -2.69$ ,  $P = 0.004$ ). The 19 broods included in the analysis produced 35 males and 15 females (2.33 males : 1 female). The sex ratios of individual broods were not significantly correlated with brood sizes ( $r_s = 0.20$ ).

The sex of nestlings that died before attaining adult plumage could not be determined reliably by laparotomy due to dessication, decomposition, and underdevelopment of gonads. Broods in which the sex ratio was unknown were not included in the analysis. Thirty-four nestlings died in my study. Most deaths occurred as part of whole- or partial-brood losses within 72 h of hatching ( $n = 20$ , 58.8%). Postfledging mortality was extremely low ( $n = 2$ , 5.9%).

## DISCUSSION

*Brood-reduction hypothesis.*—For brood reduction to result in facultative sex-ratio variation, both offspring sex and survival probabilities must vary nonrandomly with laying order (and, subsequently, hatching order). In this study, males were significantly more likely than females to come from earlier-laid eggs, but there was no evidence of differential mortality of late-laid eggs that produced females. The latter result is not consistent with those of many studies (Ricklefs 1965, Parsons 1975, Bryant 1978a, b, Moss 1979, Clark and Wilson 1981), including work done on the same Zebra Finch colony (Skagen 1988), which demonstrated that late-hatched nestlings are prone to starvation. Skagen (1988) observed brood reduction even during times of food abundance, conditions similar to those in my study. This suggests that differential mortality of late-laid nestlings may normally occur, but did not occur in my study or was missed due to a Type II statistical error.

That males hatched from earlier-laid eggs than females is significant for two reasons. My study is among the first to find nonrandom sex allo-

TABLE 1. Correlations between brood sex ratios and absolute or relative measures of parental investment (Spearman rank correlations;  $n = 11$  for first broods,  $n = 6$  for second broods).

	First brood	Second brood
<b>Brooding</b>		
Male	0.116	0.154
Female	-0.235	-0.926*
<b>Nestling feeding</b>		
Male	0.405	0.926*
Female	-0.125	-0.062
<b>Fledgling feeding</b>		
Male	0.099	0.062
Female	0.130	0.278

\*,  $P < 0.05$ .

cation in laying sequence in a passerine species (*Quiscalus quiscula*, Howe 1977; *Agelaius phoeniceus*, Fiala 1981, Weatherhead 1985), and agrees with Ankney (1982) and Ryder (1983), who found males were laid earlier in the clutches of Snow Geese (*Chen caerulescens*) and Ring-billed Gulls (*Larus delawarensis*), respectively. Secondly, it suggests that in nature, where brood reduction is more likely to occur than in captivity, this is a likely mechanism of sex-ratio manipulation.

*Sex-specific growth hypothesis.*—For sex-specific growth to result in differential mortality, the sexes must be measurably different in the growth rates of at least one morphological character. Males and females had similar rates of increase of mass, tarsus length, and wing-chord length. Females fledged at slightly higher masses than did males, but this is likely an adaptation for breeding rather than a residual effect of nestling growth (Skagen 1988). In sexually dimorphic Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*), males increase more rapidly in mass than females, but females make up their competitive disadvantage by accelerating plumage development (Richter 1983). As a result, there is little sex-biased mortality and fledgling sex ratios are near unity. This is not true for Zebra Finches, where males and females gain mass and grow primaries (wing chord) at similar rates.

*Sex-biased provisioning hypothesis.*—Although males were significantly more likely to hatch from earlier-laid eggs, there was no evidence that these eggs differed in mass or volume and, thus, nutrient reserves from those hatching fe-

males. This finding is consistent with those of some studies (Fiala 1981, Bancroft 1984, Leblanc 1987, Teather 1989), but not others (Howe 1976, Ankney 1982, Ryder 1983, Mead et al. 1987).

Although there was evidence of sex-biased provisioning to second broods in both brooding (females brooded male-biased broods less) and nestling feeding (males fed male-biased broods more), the significance of these behaviors is unclear. There was no measurable effect of this feeding bias that would promote male survival: male and female offspring fledged at similar ages, similar masses, and were dependent for similar lengths of time. The observation that sex-biased provisioning occurred during the nestling stage and not during the fledgling stage is consistent with Horsfall's (1984) hypothesis that it functions in facultative brood reduction. If males bias their investment in order to influence survival and adjust the offspring sex ratio, they should do so early in the nesting cycle so as not to waste reproductive effort. Given that mortality during the fledgling stage was rare (5.9% of all mortality), it is unlikely that this is the case.

Brood division has been cited as a possible mechanism by which sex-biased provisioning can occur (Harper 1985, but see Kopachena and Falls 1991). Harper found in European Robins (*Erithacus rubecula*) that parents specialized in feeding opposite-sexed nestlings. Although there is evidence of brood division in this population of Zebra Finches, there is no evidence that divided broods differ in sex ratio from undivided broods, or that brood division results in biased feeding of either sex (unpubl. data).

Sex-biased provisioning cannot account for the observed sex-ratio deviation in this population of Zebra Finches. It may, however, be an important phenomenon in other bird and mammal species, especially those with biparental care, where males can employ sex-biased provisioning in response to female heterogamety (Gowaty and Droge 1991). Support for this idea comes from examining mammalian systems, where sex roles are reversed from those in birds. In mammals, males are the heterogametic sex, and sex-biased provisioning by females has been reported by several authors, primarily in ungulates and pinnipeds (Clutton-Brock et al. 1981, 1982, Lee and Moss 1986, Trillmich 1986, Anderson and Fedak 1987, Wolff 1988, Byers and Moodie 1990). The widespread distribution of biparental investment in birds, especially in

those species where male investment is not essential (Gowaty 1983, Bart and Tornes 1989), may be due in part to this escalated evolutionary sex-ratio conflict (Gowaty and Droge 1991).

In what situations would conflict exist between the sexes? Where variance in reproductive success of one sex is high, or where there are helpers at the nest, both parents should agree on which sex is most beneficial to produce. Where relative attractiveness of parents differs, parents will agree only if they agree on which sex is more attractive. Possible conflict can arise, however, in situations where both parents want to produce more of the offspring that is least likely to compete with them in the future, whether it be for food, territories, or mates (local-resource-competition and local-mate-competition models; Hamilton 1967, Clark 1978, Charnov 1982, Gowaty 1993).

*Is sex-ratio variation adaptive?*—None of the three mechanisms investigated explains the observed sex-ratio bias in this population of Zebra Finches. At least three other possible explanations are consistent with the data, but were not addressed in my study.

(1) The first is that, as the heterogametic sex, females are subject to greater mortality from deleterious sex-linked traits (Breitwisch 1989). Evidence of differential mortality of female embryos is difficult to obtain, and beyond the scope of this paper.

(2) The second is that selective rejection of female offspring (Burley 1986) could produce a male-biased sex ratio, though at the cost of significant loss of reproductive effort. However, rejection behavior would be selected against unless parents can accurately determine offspring sex and, even then, discriminating against females must have some demonstrable adaptive value. Unpublished data by Balda and Balda (cited in Burley 1986) suggest that Zebra Finch nestlings emit sex-specific begging calls, and that the accuracy with which nestling sex can be determined by human observers increases with nestling age. If parents use begging calls to selectively identify and reject females, there should be intense selection pressure on females to imitate males.

(3) The third is that feedings to males and females could have differed in some qualitative aspect. Variation in mass delivered or in caloric and nutrient content could have positively influenced male survivorship. Differences in feeding quality may be particularly important

in wild populations, where food is more nutritionally and temporally variable.

Male-biased adult sex ratios have been reported for many sexually monomorphic and dimorphic passerines, due primarily to increased female mortality from the physiological stresses and predation pressures of egg production and extended parental care (Trivers 1972, Breitwisch 1989). This explanation does not satisfactorily address the existence of male-biased sex ratios at independence as is demonstrated here. Perhaps sex ratios at independence are male-biased and offset high male mortality in adults from sexual dichromatism and increased male conspicuousness to predators. In his original treatment of sexual selection, Darwin (1871) predicted that highly ornamented and colored males would be subject to higher predation, but this hypothesis has had little empirical endorsement.

The male-biased sex ratio also may be explained by the large parental investment provided by male Zebra Finches. In this population, males and females incubated eggs, brooded nestlings, and fed fledglings for similar lengths of time (unpubl. data). Except for the physiological costs of egg laying, males and females are under similar energetic constraints. Therefore, males are subject to many of the same sources of mortality as females are, particularly predation on the nest.

Although the brood-reduction hypothesis did not account for the biased sex ratio of this population, the finding that the sexes are laid non-randomly within a clutch suggests that brood reduction may explain biases in wild populations. In both nature and in the laboratory, Zebra Finches incubate their eggs so that nestlings hatch asynchronously at approximately 24-h intervals (Skagen 1988). Hatching asynchrony allows for adaptive, efficient brood reduction in response to rapid changes in resource availability (Lack 1954, Ricklefs 1965, Lack 1968, Howe 1976, Clark and Wilson 1981, Richter 1983). Therefore, male-biased secondary sex ratios in wild Zebra Finches (Burley et al. 1989) may not be inherently adaptive, but rather a result of environmental unpredictability.

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