Sex-specific growth rates in zebra finch nestlings: a possible mechanism for sex ratio adjustment

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Wild and captive zebra finches (*Taenopygia guttata*), like several other species, produce a male-biased sex ratio at fledging when food is scarce. This is due to primary sex-ratio adjustment and female-biased nestling mortality. Given that young females fledging at low body masses have been shown to have low fecundity as adults, lower returns to parents from producing female offspring in conditions of restricted food has been raised as a functional explanation (Trivers and Willard's hypothesis of adaptive sexual investment; 1973). However, an alternative, mechanistic hypothesis is that under restricted conditions female chicks are more costly to produce. In consequence, lower returns to parents under these conditions would happen earlier in the life of female offspring rather than later. To test this hypothesis, I hand-reared chicks on a food gradient. In the absence of parent-offspring and sib-sib interactions, final body mass and growth rates for females were lower in conditions of restricted food. For males, final body mass and growth rates did not differ with food condition. Low female growth rates in food-restricted conditions might be one potential mechanism causing female-biased mortality in birds. More importantly, this result is the strongest evidence yet of female offspring experiencing higher marginal fitness benefits from additional food than males and it has implications for primary and secondary sex-ratio adjustment. Also, as this mechanism has been shown in the absence of parent-offspring interactions, significant questions can now be raised as to how parental and offspring behavior interact in their effects on secondary sex-ratio adjustment. *Key words:* hand-rearing, sex allocation theory, sex-biased mortality, sex ratio, sex-specific growth rates, zebra finches. *[Behav Ecol 15:174–180 (2004)]*

Fisher's sex allocation theory (1930) predicts that, at independence, the population sex ratio among offspring should stabilize near equality. This is due to the fact that production costs and reproductive benefits accrued by parents from male and female offspring reach a stable density-dependent equilibrium, i.e. any shift toward one sex would increase the reproductive returns of the less common sex, shifting it back toward equilibrium. At the level of the individual family, Trivers and Willard (1973) predicted that deviations from an equal sex ratio should occur in direct relation to the resources available to parents. These deviations should be a function of net reproductive returns, which in turn depend on male and female offspring having different production costs and reproductive benefits. Thus, at an individual level, when reproductive returns for both male and female offspring are the same, one should expect offspring sex ratio to be equal. Both the existence and adaptiveness of sex-ratio variation at population and individual levels suggest that sexes differ in their production costs and/or reproductive benefits.

In birds, sex-ratio adjustment can occur at laying, or primary sex-ratio adjustment, and during provisioning of the young, or secondary sex-ratio adjustment (Ellegren and Sheldon, 1997; Kilner, 1998). An increasing number of studies in birds have shown evidence for primary sex-ratio adjustment, that is, females laying sex-biased clutches (Appleby et al., 1997; Bradbury and Blakey, 1998; Ellegren et al., 1996; Heinsohn et al., 1997; Kilner, 1998; Komdeur et al., 1997, 2002; Lessells et al., 1996; Nager et al., 1999; Nishiumi, 1998). These studies have shown that females adjust the sex ratio of their clutches to

reflect potential future fitness gains (see Komdeur et al., 1997) and attractiveness or quality of their males (see Burley, 1981, 1986, Ellegren et al., 1996, Kolliker et al., 1999; Svensson and Nilsson, 1996). In several studies, sex-biased mortality of nestlings between hatching and fledging has been shown to further bias secondary sex ratios (see Bradbury and Blakey, 1998; Griffiths, 1992; Grindstaff et al., 2001; Kilner, 1998; Legge et al., 2001; Røskaft and Slagsvold, 1985). Mechanisms for both primary and secondary sex-ratio adjustment in birds remain largely unknown (Emlen, 1997; Hardy, 1997; Krackow, 1995, 1999; Sheldon, 1998), but preovulatory mechanisms have been suggested as the most efficient means of primary sex-ratio adjustment for some species (Komdeur et al., 2002). As females might not be able to perfectly predict their offspring rearing environment 2 weeks in advance, it is also possible that less than optimal sex-ratio adjustment would occur at laying for most species (West and Sheldon, 2002). This, in turn, should provide an opportunity for fine-tuning mechanisms to adjust sex ratio during the nestling period. Understanding mechanisms is critical if the adaptive benefits to sex-ratio adjustment are to be quantified and predictions made about optimal patterns of sex allocation (Krackow, 1995; Oddie, 1998).

Zebra finches have been extensively studied in captivity and in the wild, and several lines of evidence suggest that deviations in sex ratio occur in relation to food available to parents. Zebra finches' broods often exhibit a male-biased sex ratio in the wild (Burley, 1981; Burley et al., 1989; Zann, 1996) and in the laboratory when raised under conditions of low food availability (Bradbury and Blakey, 1998; de Kogel, 1997; Kilner, 1998). This sex-ratio bias starts with the primary sex ratio, that is, adult females fed on low-quality diet lay significantly more male than female eggs (Bradbury and Blakey, 1998; Kilner, 1998). The sex bias is carried on to the nestling stage, and because of reduced female survival, the

Table 1

Nest of origin of zebra finch chicks hand-reared in the three food levels

Low food level		Medium food level		High food level	
Female	Male	Female	Male	Female	Male
1a	4a	1a	4a	3a	4a
11a	10a	13a	11a	13a	5a
14a	11b	1b	14a	14a	12b
5b	8c	5c	5b	1b	13c
8c	12c	11c		11b	14c
10c		12c		10c	8c
13c		14c		7d	
		7d		8d	
		8d			

Each entry corresponds to a single chick, numbers representing a nest-box and letters representing a breeding attempt.

brood becomes more male biased if kept on the low-quality diet (Bradbury and Blakey, 1998; Kilner, 1998). These studies have shown that sex ratio is a function of the quantity of resources available to parents (probably dependent on the adult female condition) and hint that female chicks may benefit more than males from additional resources.

The sex-ratio bias in zebra finches has been addressed by Kilner (1998), who suggested the data supported Trivers and Willard's (1973) hypothesis and reflected differences in net reproductive benefits between sons and daughters. According to Kilner (1998), zebra finch parents should invest less in daughters in conditions of restricted food because there is evidence that females shows reduced fecundity as adults if they fledge at low body mass. So, when zebra finch parents have few resources available, they should bias their offspring sex ratio toward males, which are the sex with lower variance in reproductive success, but when resources levels are higher, they should bias it toward females, the sex with higher variance. Although functional explanations are important, it is obvious that secondary sex-ratio adjustment involves reduced survival in female chicks and offers the unique opportunity of investigating the mechanisms producing such sex-biased mortality. Understanding these mechanisms might reveal important sex-specific characteristics of nestlings that could help explain sex-ratio adjustment at both secondary and primary level. For instance, female chicks might be more likely to die when food is scarce, because they need more food than do males for growth or because they obtain (or are given) less food than are males. Thus, two hypotheses could explain why female chicks experience reduced survival in the nest: either (1) female chicks need more food for growth than do males (but obtain or receive the same amount) or (2) females obtain or receive less food than do males. In the present study, I investigated hypothesis 1, that under restricted conditions female chicks require more food for growth than do males chicks; that is, female chicks are more costly to produce than are male chicks. If that is the case, growth rates for sons and daughters would be different under conditions of restricted food availability, providing one possible mechanism for female-biased mortality.

To test this hypothesis, I hand-reared (to remove any confounding sibling-sibling and parent-offspring interaction) a similar number of female and male chicks on a food gradient ranging from low to high food availability. I predicted that if females need more food than do males, they would grow more slowly than do males when in the low

food range and they should also show an increase in growth rate with food availability.

METHODS

Maintenance of stock

Fourteen breeding pairs of zebra finches were kept in an outside aviary (with a shed for shelter) from May–October. They were fed ad libitum on foreign finch mix and twice a day on egg biscuit food (John E. Haith) and once a day on sprouted seeds and fresh fruit. Aviary dimensions allowed for 1 m^3 per pair, and nest-boxes and nesting material were available in excess. When chicks were removed from the nest for hand-rearing, one or two of their younger siblings were left in the nest. This allowed experimental chicks to be more successful at competing with sibs (who often had been raised by parents singly or in pairs) when they were returned to their natal nest after the hand-rearing period.

Hand-rearing

Food levels were determined by using Skagen's (1988) estimates for daily mean seed requirements for zebra finch nestlings aged 1–14 days. Low, medium, and high food levels were chosen as 83%, 110%, and 137% of a chick's daily food requirement estimates for each chick age. The seed mixture used by Skagen (1988) had a protein content of 14%, whereas the low energy hand-rearing food (Birdcare Company) used in the present study had a protein content of 22%. As high-protein diets have been shown to increase growth rates (Boag, 1987), the mass of food given to birds in this experiment was adjusted to the appropriate protein content as follows:

$$M_{Si} = 14/22 M_{Mi},$$

where M_{Si} is the mass of food per chick age in Skagen's study, and M_{Mi} is the mass of food per chick age in the present study. It is important to point out that the food levels differed only in the quantity of food but not in the quality of food given.

The hand-rearing food powder was mixed with cooled boiled water according to the manufacturer's instructions and fed to chicks in a 1-ml syringe. As directed by the manufacturer, the ratio of powder to water was changed as the chicks grew older, and Potent Brew and Calcivet (Birdcare Company) were added to the food at the specified rate (one drop per feed and one drop per day at day 5 and day 8, respectively). The chicks were removed from the nest at 5 or 6 days old. Their body mass was measured on a precision balance (day 5 body mass; Oertling, model TP35, 100 g capacity, 0.01 g precision), and their tarsi (tarsometatarsus) were measured by using calipers (day 5 tarsus). They were then hand-reared on a medium food level for a day. Early next day they were randomly assigned to one of the three food levels, but care was taken to ensure that no full siblings were assigned to the same group and that over the whole period a similar number of chicks was assigned to each group (see Table 1). During hand-rearing, chicks were kept in a box resembling their nest-box, sitting singly on paper tissue-covered Petri dishes on a heat mat (Habistat Vivarium Heat Mat, Euro Rep) at a thermostatically controlled temperature of 21°C. A maximum of six chicks were hand-reared at any given time. Overall a total of 39 nestlings were hand-reared: 12 in the low, 13 in the medium, and 14 in the high food levels. The food was mixed early in the morning, and the amount needed for each chick was set up in individually marked syringes. All chicks consumed all food allocated to them on that day. Syringes were stored flat so that the powder remained in suspension. Chicks were fed every hour from 0600–2000h. All equipment was immersed in

sterilizing solution overnight to avoid bacterial infections. At 2000 h every day, chicks were weighed on the precision balance, and their tarsus length (tarsometatarsus) measured by using a pair of calipers. Chicks were hand-reared from 5 to 10 or 11 days old (i.e., before body mass reached an asymptote), after which their eyes began to open. At the end of the hand-rearing period, a sample of blood (approximately 30 µl) was taken from the brachial vein and mixed with an equal volume of 95% ethanol. The chicks were color-ringed before being put back in their original nests. If the nestling died before fledging, the carcass was frozen and a small piece of liver or muscle used for the DNA sexing. The DNA sexing was performed in the next 3–5 days in the Avian Molecular laboratory in Stirling using the technique described by Griffiths et al. (1998). As DNA sexing was performed after the hand-rearing, female and male chicks were assigned to their food levels blind. In the low food level there were seven females and five males, in medium, nine females and four males, and in high, eight females and six males. The sex of surviving fledglings was confirmed at their first molt. DNA sexing gave the same sex as sexing by plumage characters in every case.

Ethical note

The food levels in the present study were chosen to generate possible differences in the body mass and tarsus growth rate and were not intended to affect chick health and survival. Thus, this experiment was not designed to cause mortality but to determine a possible mechanism for the reduced survival of female chicks reported in other studies. Before the experiment, I decided to intervene if chicks fell below the quartile level for body mass for their age (Skagen, 1988: Figures 1 and 2). However, during the experiment, this circumstance did not arise as chick body mass never fell below that level. After being returned to their nests, survival to independence of hand-reared chicks was not different for males and females ($\chi^2 = 1.612$, df = 1, $p = .204$). However, for the low food group only, hand-reared females were less likely to survive to independence than were males ($G = 3.89$, df = 1, $p < .05$).

As blood sampling for DNA sexing is now considered part of normal animal husbandry by the UK Home Office, this project did not require a UK Home Office license. However, the project was approved by the Stirling University Ethics Committee, and the blood sampling was done under the Stirling University veterinarian's supervision as determined by the Ethics Committee following UK Home Office guidance.

Statistical analyses

As breeding birds were kept in an outside aviary for 5 months, an effect of date was likely; therefore, date at the beginning of hand-rearing was included as a covariate in the analysis. Growth rate was analyzed in two ways: (1) using final body mass and final tarsus length as response variables controlling for the initial measurement of both variables (day 5 body mass and day 5 tarsus length as covariates), and (2) using growth rates calculated from the daily measurements as the slope of a simple regression, since during this period growth is linear (Skagen, 1988).

An ANCOVA with sex and food levels as categorical variables and initial measurements (both tarsus and body mass) and date as continuous variables was run for both final body mass and final tarsus length. As initial tarsus length did not significantly explain any additional variance of final body mass, and initial body mass had no significant effect on final tarsus length, they were subsequently removed from those particular models. The final ANCOVA model for both final body mass and final tarsus length therefore included sex and food levels as categorical variables and initial measurement for each variable of interest and date as continuous variables.
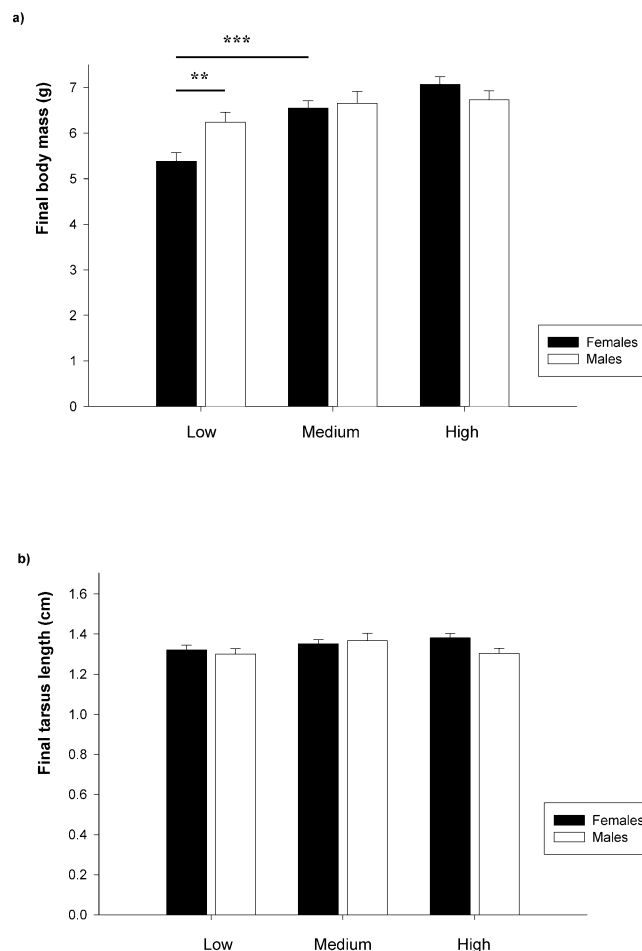

Figure 1
Final body mass (a, in grams) and final tarsus length (b, in centimeters) for male and female zebra finch chicks hand-reared on low, medium, and high food levels (83%, 110%, and 137% of predicted need, see Methods). Significance levels for multiple comparison Tukey tests (Table 2) are shown above the horizontal bars (***$p < .01$; **$p < .05$).

This model has the advantage that pair-wise comparisons (multiple comparison Tukey test; Zar, 1984) can be performed on the combinations of interest of sex and food levels (results in Table 2).

For the analysis on growth rates (body mass and tarsus length), two separate ANCOVAs were run with food levels and date as continuous variables and sex as a categorical variable. Food levels were entered as a continuous variable because levels are points in a numerically ordered gradient (Sokal and Rohlf, 1981). The ANCOVA model for each of the response variables (body mass growth rate and tarsus growth rate) was date, food levels, sex, and the interaction between these two last variables. Date had no significant effect on either body mass growth rate or tarsus growth rate, and so, it was subsequently dropped from the model. The final model for both variables, body mass growth rate and tarsus growth rate, included only food level as a covariate, sex, and the interaction between sex and food level.

RESULTS

Final body mass

There was a significant interaction between sex and food level, showing that males and females differ in their final body mass

Table 2

Multiple comparison Tukey test (unequal sample sizes) on differences between mean final body mass (grams) of female and male zebra finch chicks reared at different food levels

Comparison	Difference between group means	SE	q	p
Sex within food level				
Low food	0.854	0.199	4.293	<.05
Medium food	0.110	0.204	0.539	NS
High food	0.335	0.183	1.831	NS
Food level within sex				
Female				
Low versus medium	1.167	0.171	6.810	<.01
Medium versus high	0.518	0.193	2.680	NS
Male				
Low versus medium	0.423	0.279	1.510	NS
Medium versus high	0.073	0.219	0.330	NS

Critical value for q for 33 degrees of freedom was estimated by using harmonic interpolation ($q_{0.05,33,6} = 4.280$; from table B.5 in Zar, 1984).

within food levels when initial body mass and date are controlled for (sex × food level: $F_{1,31} = 4.53$, $p = .02$). This result is explained by the fact that females attained lower body masses than did males in the low food level, but a similar final body mass in the other two groups (Figure 1a). As anticipated, food level had a significant effect on final body mass (food level: $F_{2,31} = 16.83$, $p = .00$), but there was no overall significant effect of sex on final body mass (sex: $F_{1,31} = 1.51$, $p = .23$). Initial body mass (day 5 body mass) and date both had a significant effect on the final body mass (day 5 body mass, i.e., body mass at age 5: $F_{1,31} = 92.11$, $p = .00$; date day 5, i.e., Julian date at age 5: $F_{1,31} = 7.84$, $p = .01$). Pair-wise comparisons (Tukey test; Table 2) confirmed that males and females differed in their final body mass within the low food level only. Also, final body mass of female chicks raised on low and medium food levels were significantly different. These two results, when taken together, demonstrate that females raised in the low food level attained lower body masses than both their male counterparts and females in the medium food level.

Final tarsus length

The results for the ANCOVA showed final tarsus length was not affected by food level (food level: $F_{2,30} = 1.69$, $p = .20$) (Figure 1b) and that females and males' final tarsus lengths were not significantly different (sex: $F_{1,30} = 1.59$, $p = .22$). In addition, there was no significant interaction of sex and food level, suggesting that females and males' skeletal growth (measured as tarsus length) varied with food level in the same way (sex × food level: $F_{2,30} = 1.60$, $p = .22$). As expected, initial tarsus length and date of initial measurement both had a significant effect on final tarsus length (day 5 tarsus: $F_{1,30} = 37.68$, $p = .00$; date day 5: $F_{1,30} = 7.65$, $p = 0.01$).

The power for the interaction term in this ANCOVA was estimated as being 39.0%; the effect size, as 0.32 (Cohen 1988).

Body mass growth

A significant interaction between sex and food levels ($F_{1,35} = 5.56$, $p = 0.02$) showed that males and females differed in
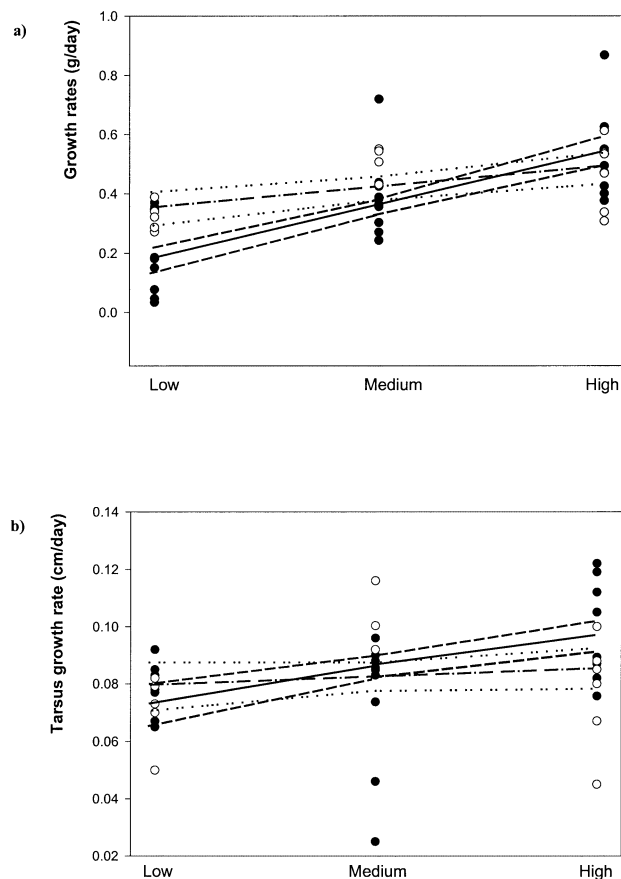

Figure 2
Growth rate (a, grams per day) and tarsus growth rate (b, centimeters per day) for male (open symbols) and female (solid symbols) zebra finch chicks hand-reared on low, medium, and high food levels (83%, 110%, and 137% of predicted need, see Methods). Regression lines for each sex (dashed line indicates males; solid line, females) and standard errors (dotted lines indicate males; dashed lines, females) are also shown to highlight differences within food levels.

their growth rate (grams per day) within food levels. This result is explained by the fact that females showed an increase in growth rate with an increase in food levels, whereas males did not (Figure 2a). As anticipated, food level had a significant effect on body mass growth rates ($F_{1,35} = 23.73$, $p = .00$). In addition, body mass growth rates were on average significantly lower for females than for males (mean rates: females = 0.37 ± 0.03, males = 0.43 ± 0.03; $F_{1,35} = 6.61$, $p = .01$). Therefore, females differed from males in the way they allocated food to growth, and this difference was primarily evident at low food levels.

Tarsus growth rate

Tarsus growth rate (millimeters per day) was transformed (squared) to normalize residuals (Anderson-Darling Normality test: $A^2 = 0.25$, $p = .73$). The results for the ANCOVA showed tarsus growth rate significantly increased with food level ($F_{1,34} = 4.27$, $p = .04$) (Figure 2b), but females and males' tarsi grew at similar rates ($F_{1,34} = 1.21$, $p = .28$) and there was no significant interaction of sex and food level ($F_{1,34} = 1.57$, $p = .22$), suggesting that females and males skeletal growth (measured as tarsus growth rate) varied with food level in the same way. The power for the interaction term in this ANCOVA was estimated as being 90.0% (effect size = 0.502)

demonstrating that the null hypothesis of no effect can be accepted in this instance (Cohen, 1988).

DISCUSSION

In an experiment in which zebra finch chicks were reared in the absence of parent-offspring and sib-sib interactions, final body mass and growth rates for female and male chicks differed according to conditions. In restricted food conditions, female chicks showed a lower final body mass and lower growth rates compared with levels for their male counterparts and also compared with levels for females being raised on higher levels of food. As final tarsus length (controlled for initial measurement) and tarsus growth rates were not different between the two sexes, it is also clear that females were not trading-off body mass growth with skeletal growth. Higher mortality rates for female chicks in conditions of restricted food that have been found both in laboratory and field studies (Bradbury and Blakey, 1998; Burley, 1981; Burley et al., 1989; de Kogel, 1997; Kilner 1998), are consistent with this finding. Even though all these studies reported lower female survival in the nest in the zebra finch, no particular mechanism had been found (Clotfelter, 1996; de Kogel, 1997). The sex-specific growth rate found in this study could be a mechanism responsible for the reduced female survival shown in these studies when conditions deteriorate.

In zebra finches, growth rates of nestlings and fledging body mass are strongly related to adult body mass (Boag, 1987; Skagen, 1988). Fecundity, attractiveness to mates, and mortality all correlate with fledging weight, but the relationships differ between the sexes. There is evidence that females pay higher fitness costs than do males by being underweight as adults (low fecundity; Haywood and Perrins, 1992). For males the evidence is unclear: being a light adult does not affect body size or primary sexual traits (testes mass, number of stored sperm, sperm function, velocity, and morphology; Birkhead et al., 1999). However, being raised in enlarged broods reduces attractiveness for males (song rate and beak color; de Kogel and Prijs, 1996). Finally, mortality rates are correlated with fledging body mass. Females reared in experimentally enlarged broods leave the nest at lower body masses and are more likely to die after independence than are males reared in the same way (de Kogel, 1997). In short, the amount of resources received in the nest by offspring will have a profound impact on their reproductive success, but this impact is higher for females than for males.

The results in the present study have shown that females fed on medium and high food levels showed higher growth rates than those fed on low food levels, but food levels did not affect growth rates in males. This study has also shown that the lower growth rates reported could result in sex-biased mortality (survival to independence) after chicks were returned to their nests and experienced good conditions after the hand-rearing. In addition, within the experimental period this study has shown that female low growth rates result in low final body mass. If this low body mass is likely to persist until fledging as shown in other studies (see Boag, 1987; Skagen, 1988), it will certainly result in lower female fecundity (see Haywood and Perrins, 1992) and/or mortality (see de Kogel, 1997). The sex-specific growth rates found in the present study suggest that resources received in the nest will affect female chicks to a greater degree. This means female chicks experience higher marginal benefits from additional resources than do male chicks when conditions are good. However, it also means that female chicks are more likely to fledge at low body mass and show reduced survival when conditions deteriorate. So, resources in the nest have a more profound impact on female offspring fitness than on

male offspring. The results in this study show a convincing sex difference in the marginal benefits of additional parental resources. Also, it can be said then that fitness benefits are accrued not just later in life, as Kilner (1998) suggested, but in early life during growth. Thus, mothers with access to additional food should benefit most by producing daughters rather than sons. In a recent study, the proportion of male eggs laid by female zebra finches was reduced when food improved dramatically (after the first egg was laid), showing that female zebra finches respond quickly to availability of resources by laying more eggs of the sex, yielding higher marginal benefits (Rutkowska and Cichón, 2002).

My results also suggest that raising female chicks under restricted conditions must be more costly to parents. This has considerable relevance to the question of how parental and offspring behavior interact in their effects on sex ratio. It is now crucial that studies concentrate on the possible consequences of sex-specific production costs and how this might affect the behavioral interactions of parents and offspring. It is particularly important to investigate whether sex-specific growth rates are enough to produce the sex-biased mortality shown in the wild and in the laboratory. Studies should concentrate on whether sex-specific growth rates alone can produce enough of a size difference to enhance male access to resources or whether parental favoritism could also be playing a role in selecting male chicks when conditions deteriorate.

The only study to have investigated a related consequence of these possible interactions was the study conducted by Oddie (2000). Her study concentrated on the effect of the interaction between sex and size within broods of great tits, *Parus major*, a species in which males are a fraction larger than females (3.5–4% skeletal size) and which also shows female-biased sex ratios when conditions deteriorate. Oddie (2000) was able to show that being slightly larger enhanced competitive ability of male great tit offspring in poor rearing environments. My results also suggest that sex-specific growth rates should help males in competitive interactions by initiating sex-specific size differences. Right from the beginning, even if males could not obtain more food, they could still grow larger than could females on the amount obtained. In a natural brood, this would probably lead to an escalating size asymmetry and greater male success. It is possible that higher growth rates in males might explain why the size effect in Oddie's study became more obvious as the nestling period progressed.

What could be responsible for this sex-specific growth rate? One possible explanation is that females are spending energy elsewhere. Sex-specific metabolic rates are a possibility, and the results obtained here would suggest that female chicks might have higher metabolic costs than do males at low levels of food availability. It would be important to evaluate how females are allocating energy in these conditions.

Another possibility is that even though the result is this study is independent of parental effects, maternal effects at the egg stage played an important role, particularly if maternal effects were responsible for the more efficient way in which males in the low food group converted food to growth and also if maternal effects were likely to be more evident in food-restricted conditions. So far, studies of maternal effects at the egg stage in birds have not taken into account the sex of the eggs or embryos (Gil et al., 1999; Whittingham and Schwabl, 2002; but see Rutkowska and Cichón, 2002), making it difficult to ascertain whether there could be any difference. There is evidence, however, that eggs with male embryos are larger than are eggs with female embryos in house sparrows (Cordero et al., 2000), the larger size possibly giving male embryos a better start. For zebra

finches, there is very recent evidence of no sexual size dimorphism in eggs, but subsequent male hatchlings were slightly heavier than were female hatchlings after a diet improvement (Rutkowska and Cichón, 2002). Although egg size was not investigated in the present study, all analyses controlled for initial measurements and differences in size per se can be ruled out as the cause of the differences in final body mass and growth rates. Yet, it remains possible, in this study and others (Petrie et al., 2001; Whittingham and Schwabl, 2002), that male eggs contained more of some substance (e.g., testosterone), giving males higher growth rates when in low food conditions. If that is shown to be the case for male eggs or embryos, then studies on the effect of physiological differences between the sexes, that is, the effect of androgens on early growth of male and female nestlings, would be crucial. Maternal control of primary sex ratio adjustment and maternal effects and their consequences for sex-ratio adjustment and sex-specific growth rates during the nestling phase deserve further investigation.

Clearly, a bias in fledging sex ratio can occur within the same species due to a combination of sex ratio at laying (Bradbury and Blakey, 1998; Kilner, 1998), which has received a great deal of attention recently, and postlaying sex-biased mortality, the importance of which has been largely ignored. The present study has shown that investigating sex-biased mortality during the nestling stage can enhance our understanding of the mechanisms underpinning the adaptive benefits to sex-ratio adjustment. Sex-biased mortality possibly involves a differential effect of egg quality on male and female offspring (see Cunningham and Russel, 2000; Gil et al., 1999; Petrie et al., 2001; Rutkowska and Cichón, 2002) and differential effects of sex and size composition of broods on fledging sex ratio (see Oddie, 2000). The results in this study suggest that sex-specific growth rates could be the mechanism through which egg quality and the effect of sex and size composition in broods take form and determine differential mortality of one sex. It is crucial now that we evaluate the consequences of such a mechanism for the question of how parental and offspring behavior interact in their effects on sex ratio.

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