Digit ratio varies with sex, egg order and strength of mate preference in zebra finches

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The steroid environment encountered by developing vertebrates has important organizational effects on physiology and behaviour that persist throughout an organism's lifetime. Optimal allocation of maternal steroids to zygotes may be difficult to achieve because of the sexually antagonistic effects of steroids; thus, for example, a hormone environment beneficial to a developing male may be much less beneficial to a developing female. Research into the important topic of how mothers might adaptively adjust steroid titres experienced by particular young has been constrained by the difficulty of measuring the steroid environment experienced by the embryo at critical times in development. A potential approach to this problem has been suggested by research on variation in digit ratios in humans, where the ratio of the length of the second and fourth digits reflects the steroid environment experienced by the foetus; notably, digit 4 lengthens in response to androgens. In light of the conservative nature of homeobox genes regulating early development in tetrapods, we questioned whether a sex difference in digit ratio exists in a passerine bird, the zebra finch, *Taeniopygia guttata castanotis*, and whether observed variation in the ratio is consistent with the previously reported pattern that androgen allocation to zebra finch egg yolk declines across laying order. We established an aviary population of outbred, wild-type zebra finches, and allowed them to breed freely. Hatchlings were marked to correspond to their egg order, and their digit ratios were measured after birds reached adulthood. We found that digit ratio increased across egg order, which is consistent with a pattern of decreasing androgen allocation. Moreover, digit ratios differed between the sexes. We also investigated whether variation in digit ratio among adult females predicted variation in their performance in mate-choice tests. Digit ratio accounted for almost 50% of the variance in strength of female preference for an attractive male trait: specifically, females with higher (presumably less 'androgenized') ratios had stronger preferences for attractive males. Digit ratio may prove to be an extremely useful tool for addressing a wide range of questions about vertebrate differentiation and behaviour.

Keywords: digit ratio; mate choice; sexual antagonism; zebra finch

1. INTRODUCTION

Exposure to steroid hormones in early life can have significant effects on adult behaviour and reproduction, as has been shown by research on mammals ranging from rodents (vom Saal 1989; Clark & Galef 1998) to humans (Williams *et al*. 2000; Manning 2002). Female Mongolian gerbils (*Meriones unguiculatus*), for example, positioned *in utero* between two androgen-producing male (2M) siblings mature more slowly than females that develop between two females (2F), and 2M males are more preferred as adults than 2F males by oestrous females (Clark & Galef 1998). While effects such as these documented for mammals may represent reproductive constraints, recent research on birds suggests that variable steroid allocation to egg yolk has evolved adaptively to enhance maternal fitness by regulating patterns of intrabrood competition (Schwabl *et al*. 1997; Schwabl & Lipar 2002). In several avian taxa, yolk androgen levels are known to vary with laying order, and these levels influence hatchling performance (Schwabl & Lipar 2002). In species in which androgens increase across the laying order (e.g. black-headed gulls (*Larus ridibundus*) Eising *et al*. 2001; American coot (*Fulica americana*) Reed & Vleck 2001; canary (*Serinus canaria*) Schwabl 1993), the allocation pattern tends to

increase the competitive ability of smaller, late-hatched offspring (but see Sockman & Schwabl 2000). In other species, androgen levels decrease across laying order, which may function to maximize the probability that one or more offspring of a given reproductive attempt survive. This latter pattern may be common in environments with an unpredictable food supply (as in zebra finches (*Taeniopygia guttata castanotis*); Gil *et al*. 1999), as well as among small-brooded species in which siblicide occurs regularly (e.g. Schwabl *et al*. 1997).

Tactical manipulation of yolk steroids may be feasible because an avian egg is well insulated from steroids produced by other embryos in the same clutch by the characteristics of its shell and shell membrane (Burley & Vahedra 1989). A largely unexplored question is the extent to which steroid levels naturally occurring in avian egg yolk have long-term consequences for offspring fitness; this consideration might increase the complexity of yolk steroid allocation tactics. Moreover, since steroid exposure can have important organizing effects in early development, including sexually antagonistic ones (Rice 1996; Clark & Galef 1998), variation in the yolk steroid environment might account for a significant proportion of adult performance variation for traits related to mate acquisition and reproduction.

The current method used to assay yolk steroids for studies on hatchling performance is to remove a small amount of yolk with a needle inserted through the shell and

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239

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albumin (Schwabl 1993). This technique's accuracy has been called into question by the finding that steroid concentrations differ substantially between layers of yolk (Lipar *et al.* 1999*b*). As an alternative, we considered the possibility that an indicator of prenatal steroid exposure in humans, the relative lengths of the second and fourth digit, or the '2D : 4D ratio' (McFadden & Schubel 2002; Manning 2002), may reflect early steroid exposure in an avian species, the zebra finch. In humans, evidence suggests that developing digits differ in their sensitivity to the effects of steroids: digit 2 lengthens in response to increased oestrogen, whereas digit 4 responds to increased androgen levels. Males and females differ in the distribution of 2D : 4D ratios of the right hand, with males typically having lower ratios than females (Manning 2002). This pattern is established by week 13 of gestation (Garn *et al.* 1975), and persists into adulthood (Manning *et al.* 1998). While the occurrence of sexually dimorphic digit ratios was first documented for humans over a century ago (Baker 1888), only recently has a similar pattern been shown for the right hind limb of another mammal, the laboratory mouse (*Mus domesticus*; Brown *et al.* 2002). The rationale for expecting a similar pattern in such a distantly related taxon as passerines is that the early ontogeny of tetrapod digits is under the control of homeobox genes (Peichel *et al.* 1997), which are highly conserved across vertebrate taxa (Kondo *et al.* 1997). Moreover, pentadactyly is an ancient tetrapod trait (Laurin *et al.* 2000). Thus, the 2D : 4D ratio may provide a window onto the early hormone environment experienced by a wide range of extant vertebrates (Manning 2002).

To explore this possibility, and one of its possible implications for adult reproductive performance, we measured the homologous digits in the right foot of a passerine (Romer 1955; King & McLelland 1984), the zebra finch, a species that breeds freely in captivity (Zann 1996). Because yolk androgens have been reported to decline across egg order (of unsexed eggs) in this species (Gil *et al.* 1999), we began by examining the relationship between egg order and digit ratio. Next, we asked whether 2D : 4D ratio predicts mate-choice behaviour of adult females. We selected this assay because choice of a mate is a critical determinant of female fitness in sexual eukaryotes (Andersson 1994). Thus, the possibility that early steroid exposure has organizing effects on mate preference has important implications for understanding the intraspecific variation in mate choice and its consequences for sexual selection.

We predicted that, if egg steroid levels influenced adult female mate-choice behaviour, females exposed to higher levels of androgens would have weaker, or 'defeminized' (Adkins Regan 1998), mate preferences. To investigate this possibility, we capitalized on a previous finding from this laboratory that female zebra finches are attracted to males wearing red leg bands and have a mating aversion to males wearing green leg bands. In several mate-choice experiments (Burley *et al.* 1982; Burley 1986*b*, 1988), females averaged about twice as much time affiliating with males with red bands as they did with males with green bands; there was, however, considerable variability between individual females. We question whether this variation reflects a female's egg order and/or her digit ratio.

2. MATERIAL AND METHODS

(a) *Breeding procedures*

Birds were bred in three large (90 m³) outdoor aviaries at standard densities; each flight contained 30 pairs of outcrossed, wild-type adult zebra finches. Commercial finch seed, cuttlebone and other resources needed for reproduction were available *ad libitum*. Offspring were removed from their natal aviaries at 50–55 days of age and housed unisexually in cages in view of adults of both sexes until they reached adulthood (90–100 days). At that time, birds from flight A were measured for digit ratio; females from flight B were assigned as test subjects in the mate-choice experiment; and males from flight C were assigned as stimulus subjects in the choice experiment. Birds from flights B and C had no contact prior to the beginning of the mate-choice experiment.

(b) *Egg order and digit ratio*

Eggs in flight A were individually marked in the order in which they were laid and the young were marked upon hatching. Prints of the right foot were collected from 103 offspring after birds reached an age of 110 days. (Passerine legs reach full adult size at or before fledging; e.g. Alatalo & Lundberg (1986).) Toe prints of live birds were made by gently pressing the very flexible toes of the foot alternately on an art-quality stamp pad and an acid-free paper. The right foot was selected for printing in preference to the left because preliminary results suggested greater sex differences in the 2D : 4D ratio of the right foot; this pattern is consistent with those reported for humans (McFadden & Schubel 2002; Manning 2002).

Between 5 and 14 prints were made for each bird. The two that appeared to the scorer to be most complete and not smudged, and with toes in straight positions, were measured under bright illumination using electronic callipers. When two measurements of the same digit differed by more than 0.2 mm, they were repeated as a check against measurement error. In a few cases, all prints collected on a single day for a given bird were judged to be substandard, and prints were taken again at a later time.

The scorer lacked information on egg order and, in many cases, the sex of the bird being scored. The average of the two measurements for each digit was used in calculating digit ratios. The correlations between pairs of measurements were high ($r > 0.90$ for both second and fourth digits).

Fresh egg mass (which is positively correlated with egg order; V. S. Foster, unpublished data) and nestling mass at day 15 (asymptotic mass; Price & Burley 1994) were also obtained for 90 of these offspring. The 2D : 4D ratios of the female test subjects from population B were obtained using the identical procedure.

(c) *Mate preferences*

Stimulus and test birds were all young, wild-type adults with no previous reproductive experience. Stimulus sets consisted of two males from population C matched for bill colour and general body size; each male was employed in only one of the eight stimulus sets used. In any given trial, one male in a stimulus set wore a matched set of red leg bands, while the other male wore a set of green bands. Fifteen females from population B were employed as test subjects. Test females were selected that possessed bill colours within the range preferred by males (Burley & Coopersmith 1987) and that had excellent physical and plumage condition. After a period of familiarization with the test

apparatus, females were tested twice each with three of the stimulus sets (for a total of six trials). Each trial lasted 30 min, during which the female's activity was continuously monitored. At the end of each trial, time spent by the test female in the proximity of each stimulus male was tallied. Between two trials involving the same stimulus set, the colour bands on males' legs were exchanged. Each female's performance over all six trials was then summed, and from this we calculated the average percentage of social time spent with red-banded males. This procedure was used to minimize the effects of idiosyncratic preferences for, or aversions to, specific individual males (Jennions & Petrie 1997) on the females' preference scores. Additional details of the testing procedure are presented elsewhere (Burley 1986b; Burley & Symanski 1998).

(d) Statistical analyses

All analyses were performed using SYSTAT 7.0. Log-normal transformation of the 2D : 4D ratio was unnecessary, as no digit ratio exceeded 1.0.

3. RESULTS

To ascertain whether digit ratio varied with egg order and/or other relevant variables, we performed a multiple linear regression on data from birds in flight A, with the 2D : 4D ratio as the dependent variable, and sex, egg order, egg mass, day 15 mass and laid clutch size as independent variables. The resulting model was highly significant (adjusted $r^2 = 0.212$, $p < 0.001$); however, egg mass ($p = 0.676$) and day 15 mass ($p = 0.672$) did not contribute significantly to it. Because inclusion of these variables reduced the sample size of the analysis (see § 2), we removed them and repeated the regression procedure. When the regression was run with these variables deleted, the resulting model remained highly significant (adjusted $r^2 = 0.259$, $p < 0.001$). Significant contributors to this result included sex (partial $r = -0.045$, $p < 0.001$) and egg order (partial $r = 0.015$, $p < 0.001$); clutch size did not contribute significantly ($p = 0.338$).

Separate regression analyses performed for males and females showed similar effects, with digit ratio increasing across egg order (figure 1: males—adjusted $r^2 = 0.101$, $n = 47$; $p = 0.017$; females—adjusted $r^2 = 0.204$, $n = 56$, $p < 0.001$). Overall, female digit ratio was lower (mean + s.e. = 0.84 + 0.01) than that of males (mean + s.e. = 0.89 + 0.01).

To determine whether these results were influenced by the variation in length of the second or fourth digits, or by both, we performed separate regressions on these variables. In males, digit 2 (mean + s.e. = 6.13 + 0.04 mm) did not vary with egg order (adjusted $r^2 = 0.00$, $p = 0.902$; figure 2a). In females, digit 2 (mean + s.e. = 5.98 + 0.05 mm) increased with egg order (adjusted $r^2 = 0.064$, $p = 0.034$; figure 2b). Digit 4 decreased with egg order in both sexes (figure 3: males, mean + s.e. = 6.93 + 0.06 mm, adjusted $r^2 = 0.076$, $p = 0.034$; females, mean + s.e. = 7.08 + 0.06, adjusted $r^2 = 0.056$, $p = 0.043$).

Next, we queried whether a female's egg order and/or the digit ratio of her right foot influenced her relative preference for males with red bands. The 2D : 4D ratio was the only significant contributor to the resulting model (adjusted $r^2 = 0.472$, $p = 0.009$). With digit ratio included
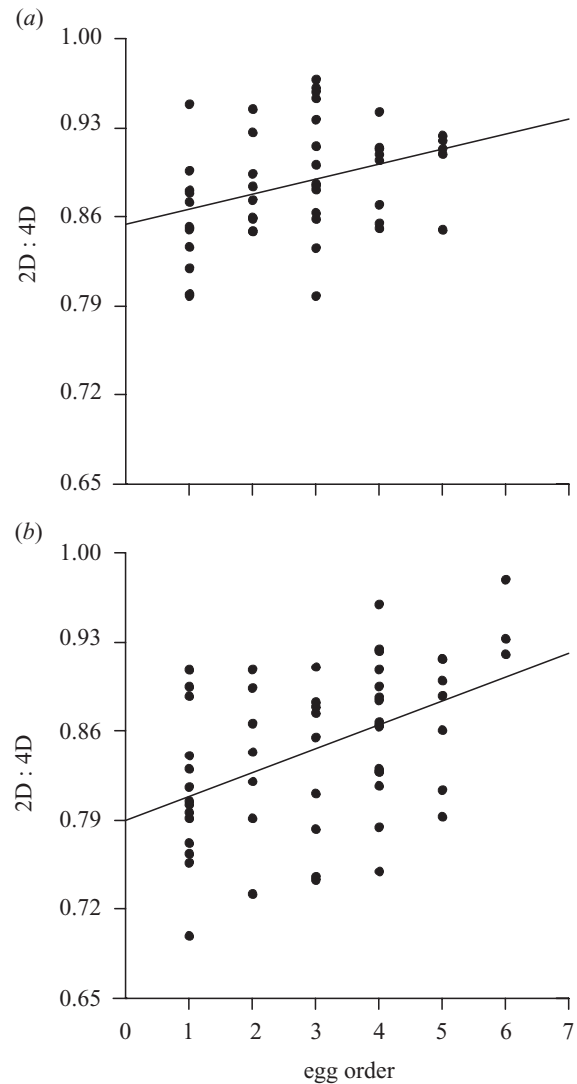

Figure 1. Digit (2D : 4D) ratio as a function of egg order within clutches. (a) Male digit ratio (mean + s.e. = 0.89 + 0.01; $n = 47$) increases across egg order (adjusted $r^2 = 0.101$, partial $r = 0.012$, $p = 0.017$). (b) Female digit ratio (mean + s.e. = 0.84 + 0.01; $n = 56$) increases across egg order (adjusted $r^2 = 0.204$, partial $r = 0.019$, $p = 0.001$).

as the sole independent variable, nearly half the variation in female performance was accounted for (adjusted $r^2 = 0.497$, $p = 0.002$; figure 4). A separate analysis included the lengths of the second and fourth digits rather than their ratio. The amount of variation in the data explained by these variables considered separately was somewhat lower (adjusted $r^2 = 0.440$, $p = 0.012$) than that explained by their ratio, and the direction of influence on preference score differed between variables (second digit, partial $r = 0.237$, $p = 0.009$; fourth digit, partial $r = -0.172$, $p = 0.020$).

4. DISCUSSION

Results suggest that measurements of digit ratio variation may provide very useful approximations of the early hormone environment experienced by birds. The finding that digit 4 is longer in birds produced from early eggs of zebra finches, which have higher yolk androgen levels, is consistent with the sensitivity of human fourth digits to
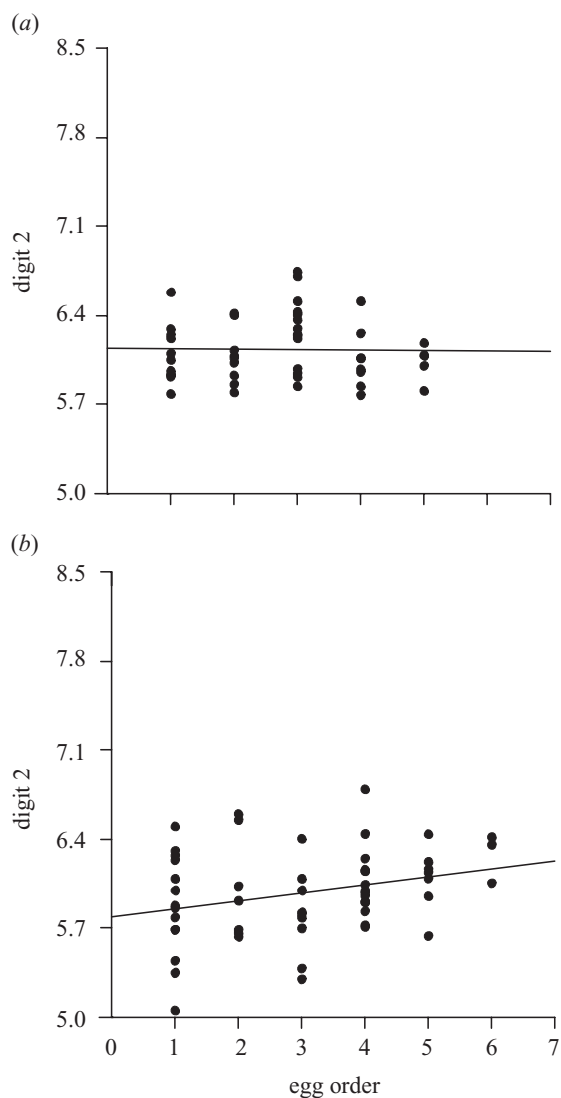
Figure 2. Relationship between length of digit 2 and egg order. (*a*) In males, digit 2 (mean + s.e. = 6.13 + 0.04 mm) does not vary significantly with egg order (adjusted $r^2 = 0.0$, $p = 0.902$). (*b*) In females, digit 2 (mean + s.e. = 5.98 + 0.05 mm) increases with egg order (adjusted $r^2 = 0.064$, $p = 0.034$).

Figure 3. Relationship between length of digit 4 and egg order. (*a*) In males, the fourth digit (mean + s.e. = 6.93 + 0.06 mm) decreases with egg order ($r^2 = 0.076$, partial $r = -0.097$, $p = 0.034$). (*b*) In females, the fourth digit (mean + s.e. = 7.08 + 0.06 mm) decreases with egg order (adjusted $r^2 = 0.056$, partial $r = -0.080$, $p = 0.043$).

androgen levels. Unfortunately, although small amounts of oestrogen have been detected in zebra finch yolk (Schwabl 1993), patterns of egg order variation have not yet been established for this steroid. Since the second digit of females increases with egg order, we predict that oestrogen will be found to increase across egg order in zebra finches. The lack of egg order variation in length of digit 2 among males suggests the possibility that the sexes have evolved differential sensitivity to steroids from an early developmental stage (Schwabl 1993), or possibly that mothers are able to adjust hormone levels depending upon egg sex (birds display female heterogamety).

The digit ratios reported here tended to be lower in female finches than males; this is the opposite of the pattern reported for mouse hind limbs (Brown *et al.* 2002) and that established for human fingers (Manning 2002). Nevertheless, the lower female toe ratio in finches is consistent with recent trends reported for human toes (McFadden & Schubel 2002), and the general inverse
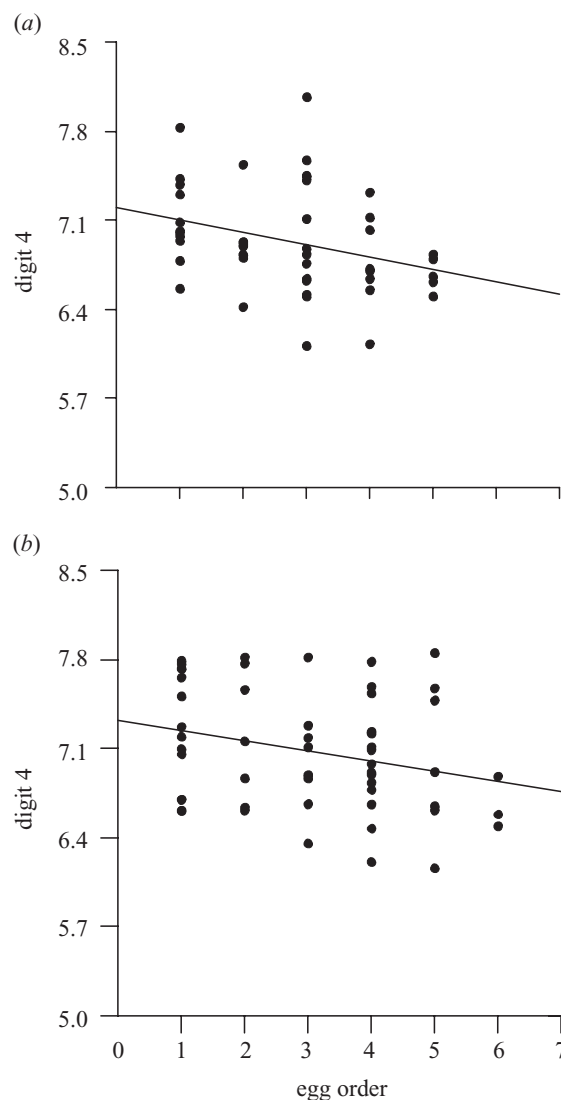
relationship between prenatal androgen exposure and 2D : 4D ratio reported for humans does appear to be upheld. The finding that egg mass does not influence the 2D : 4D ratio is consistent with a previous finding for this species that steroid allocation is not correlated with egg yolk mass (Schwabl 1993). The finding that day 15 mass does not predict adult digit ratio suggests that the 2D : 4D ratio is not complicated by body size considerations. Considerable variation in digit ratio occurs for each egg order (figure 1); this allows us to separate possible effects of egg order, *per se*, from those reflecting digit ratio, and suggests that females may show substantial individual variability in yolk steroid allocation, as has been reported for another passerine, the red-winged blackbird *Agelaius phoeniceus* (Lipar *et al.* 1999*a*).

The 2D : 4D ratio varied with female mate preference as predicted based on egg androgen levels, suggesting that early exposure to steroids irreversibly affects brain organization in ways that influence subsequent preferences
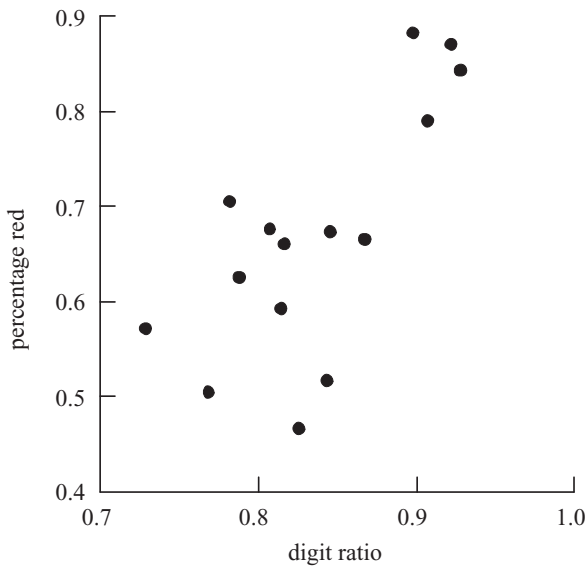
Figure 4. Relationship between 2D : 4D ratio of test females' right feet and their relative preference for red-banded males ('percentage red': mean + s.e. = 0.67 + 0.03).

(Adkins Regan 1998). An alternative hypothesis is that mating decisions of adult females vary dynamically with their own mating quality (Burley 1977); if this is true, we expect that male zebra finches will be found to be most attracted to females with high digit ratios, and that females with such ratios will have superior fecundity. These two possibilities are not mutually exclusive, as social experience may mediate early organizational effects in adult organisms (Breedlove *et al.* 1999).

The 2D : 4D ratio accounts for a surprisingly large proportion of the observed variation in the mate preferences of female zebra finches. This raises the important possibility that the strength of consensus of female mate preferences, a key determinant in the intensity of sexual selection operating on males (Andersson 1994), is constrained by developmental processes that have sexually antagonistic effects. Finally, these results, along with findings that female zebra finches mated to males with red bands increase their androgen allocation to eggs (Gil *et al.* 1999) and that pairs containing red-banded males rear more sons (Burley 1986*a*), suggest that birds may have evolved to adjust steroid allocation based on the sex ratio composition of broods favoured by particular circumstances (Trivers & Willard 1973; Komdeur *et al.* 1997).

Our results suggest that examination of digit ratio variation may be a very useful tool in future research. Combined with greater understanding of levels of variation in all types of steroids occurring in egg yolk, measurement of digit ratios in living vertebrates may be useful in understanding taxon differences in the organizational effects of steroids (Arnold & Schlinger 1993; Wade 1999), as well as the intergenerational consequences of variable hormone environments in early development (Birkhead *et al.* 2000). By varying the timing of experimental injections of physiological doses of steroids into egg yolks, for example, the possible variation in digit ratios may reveal age-specific yolk steroid use patterns by embryos (Lipar *et al.* 1999*b*). Insights into these areas could facilitate the discovery of the roles of steroids in vertebrate ontogeny from the comp-

lementary perspectives of evolutionary adaptation and constraint (Ketterson & Nolan 1999).

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