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Sex steroid dependence of carotenoid-based coloration in female zebra finches

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Abstract

Compared to male secondary sexual traits, the effect of testosterone (T) on female ornaments is understudied. In particular, it is unclear whether females experience different costs of T elevation than do males and how this affects the relationship between T and ornamentation in the two sexes. I experimentally and correlationally investigated the effect of T on the color of the carotenoid-based beak in female zebra finches (*Taeniopygia guttata*). Exogenous T administration elevated beak redness, indicative of sex-steroid sensitivity for this ornament. However, unlike in males, the relationship between T and color among unmanipulated birds was inversely U-shaped, with the most colorful females circulating intermediate T levels. This is consistent with the idea that females bear high costs of elevated T levels that weaken color intensity. Likely mechanisms for such an effect include: (1) the need to traffic carotenoids away from the beak to combat the immunosuppressive effects of high T, and (2) the loss of carotenoid stores in the body (e.g. from adipose tissue) due to a T-dependent increase in lipid metabolism (T-implanted females in this study decreased in body mass). Moreover, unlike what occurs in male zebra finches, T did not upregulate levels of plasma lipoproteins (carotenoid transporters) or plasma carotenoids in females; this provides further support that T controls beak-color intensity by different physiological mechanisms in the two sexes, with perhaps more of a localized role of sex-steroids at the beak in females.

Keywords: Androgen; Lipoprotein; Sexual selection; Testosterone; *Taeniopygia guttata*

1. Introduction

Many secondary sexual characteristics in male animals, including antlers, songs, colors, and dances, come under the control of sex steroids like androgens [1]. Solid correlational and experimental evidence exists in support of the notion that males with the highest androgen levels develop the most elaborate features [2]. However, females of some species also display extravagant traits that play a role in mate competition [3], and in these situations the role of sex steroids in governing the development and maintenance of sexual signals is not as well known [4]. Most endocrinological work on female ornaments have been centered on sex-role-reversed species, where female competition and hormone profiles are expected to be male-like [5,6], or on whether or not male-like characters can be induced with androgen treatment in females when they typically show no such traits [7,8]. Only recently have studies considered the importance of physiologically relevant (to females) androgen levels in species where females naturally exhibit some form of ornamentation. In a handful of these studies, androgen (e.g. testosterone, or T) administration clearly can affect traits like aggression [9], courtship [10], song [11–13], and coloration [14,15] in females.

An important thrust of this work on androgens in females, however, is whether females experience higher costs of T elevation than do males and thus generally show lower levels of androgens and sexual-trait expression [16]. In addition to its detrimental effects on survival, immune function, body-mass maintenance, and offspring attentiveness in males [17,18], high T may also delay reproduction or even impair fertility in females [19,20]. If in fact females suffer more from high T, then (unlike in males) those females with elevated T levels may not necessarily be expected to exhibit the most

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elaborate features. This outcome would have important consequences for understanding both the mechanisms and the strength of directional sexual selection on ornamental traits in male and female animals [19,21].

I investigated the relationship between sex steroids and a female ornamental trait in zebra finches (*Taeniopygia guttata*). Adult male zebra finches display a red beak that is derived from the presence of carotenoid pigments [22] and is sexually attractive [23,24]. Females display less intense but variable orange beak coloration (immature birds of both sexes have a black beak). In a previous study, I correlationally and experimentally showed that T levels were positively linked to beak coloration in male finches [25]. I performed the same correlational and experimental study of T and coloration in females here, in order to understand the effects of a forced manipulation (T administration) on coloration, as well as how intact animals naturally balance T and ornamentation (sensu the framework of [26]). Moreover, because I found in my earlier study that T enhanced male beak color by upregulating lipoprotein production [25], which are the transporters that allow efficient accumulation of carotenoids from the diet and delivery to peripheral tissues for coloration, I also monitored lipoprotein status and plasma-carotenoid concentration of females to determine whether T had a similar effect on their pigmentation system.

2. Materials and methods

2.1. Correlational study

I sampled blood and scored beak color from 18 captive, adult, non-breeding, individually housed female zebra finches (see [27] for information on the colony). Approximately 120 μl of blood was sampled from the wing vein of all individuals in the late morning (1000–1200 h). Because all birds were housed in the same room, and because extended periods of time spent bleeding birds in the room might have altered T levels, I randomly bled two birds per day (within 5 min) on nine successive days. Plasma was separated and, except for the fraction immediately assayed for cholesterol, stored at −80 °C for later analyses.

Cholesterol (mg/dl) was used as a proxy for lipoprotein concentrations (see [28] for justification) and was determined from fresh plasma using a commercially available kit (Polymedco, Inc. CHO-200 total cholesterol assay, Cortlandt Manor, NY). This assay employs heat-induced enzymatic hydrolysis and oxidation to form a colorful indicator of cholesterol that can be quantified with an absorbance spectrophotometer. In a new Eppendorf tube, I added 1 ml of cholesterol reagent to 10 μl plasma, vortexed the tube for 3 s, and incubated at 37 °C for 5 min. I then removed the tube from the water bath and transferred the contents to a clean cuvette to determine the absorbance of the solution at $\lambda = 500$ nm with an absorbance spectrophotometer (Bausch and Lomb Spectronic 1001). Total cholesterol concentration of samples was determined by comparison to external cholesterol standards provided by Polymedco, Inc. In pilot tests, this procedure was found to be highly repeatable ($R_i = 0.99$, $F_{9,10} = 189.2$, $P < 0.0001$).

Radioimmunoassay (sensu [29]) was used to determine plasma T titers from 50 μl thawed plasma in 14 females (insufficient plasma was available for three females). Plasma was incubated with ca. 1000 cpm of tritiated testosterone (NEN, Boston, MA) for 1 h before extraction with diethyl ether. Samples were then evaporated to dryness under a stream of nitrogen, resuspended in phosphate buffer, equilibrated at room temperature for 1 h, and then incubated in duplicate with tritiated testosterone and a testosterone antibody (Endocrine Sciences, Casablanca, CA) for 4 h at room temperature. Assay sensitivity was 10 pg/ml, intra-assay variation averaged 11%, and average percent recovery was 75%. The testosterone antibody used cross-reacts (44%) with dihydrotestosterone, thus making the assay technically a total androgen assay [29].

Following my previous studies (e.g. [30]), plasma-carotenoid concentration was determined using high-performance liquid chromatography and beak hue was scored at the time of blood sampling with a hand-held Colortron™ II reflectance spectrophotometer (Light Source Inc., San Rafael, CA). Note that, because hue is based on a 360° color wheel, the Colortron assigns lower hue scores to redder birds.

2.2. Experimental study

Seventeen non-breeding, adult, individually housed female zebra finches were used for this study (same birds as above). Ten randomly chosen females were implanted with an empty 10 mm Silastic capsule (control group) and seven were implanted with capsules packed full with crystalline testosterone propionate (Sigma Chemical Co., St. Louis, MO). I chose an implant of this size based on previous work in this species [31,32]. All implants were sealed at both ends with 1 mm Silastic adhesive. Each bird was first given a 50 μl injection of Lidocaine™ to numb the site of implantation, which was in the left flank region, just above the hip and below the wing. I inserted implants subcutaneously, as far posterior as possible, and sealed the skin with surgical glue. Birds were returned to housing cages within 30 min. Just prior to capsule implantation, I scored beak hue and drew blood from all birds to determine pre-treatment hormone, cholesterol, and carotenoid levels (as above).

Implants were left in for 8 weeks, at which time I again scored beak color and sampled blood for cholesterol, carotenoid, and T analyses. Upon removing the implants, I found that 50–90% of T had dissolved from the capsules; in no case were any of the T-filled capsules empty. I also measured body mass for all females before and after the experiment.

3. Results

3.1. Correlational study

I found no significant linear relationship between blood T titers and beak hue ($r = 0.02$, $P = 0.95$), plasma-carotenoid

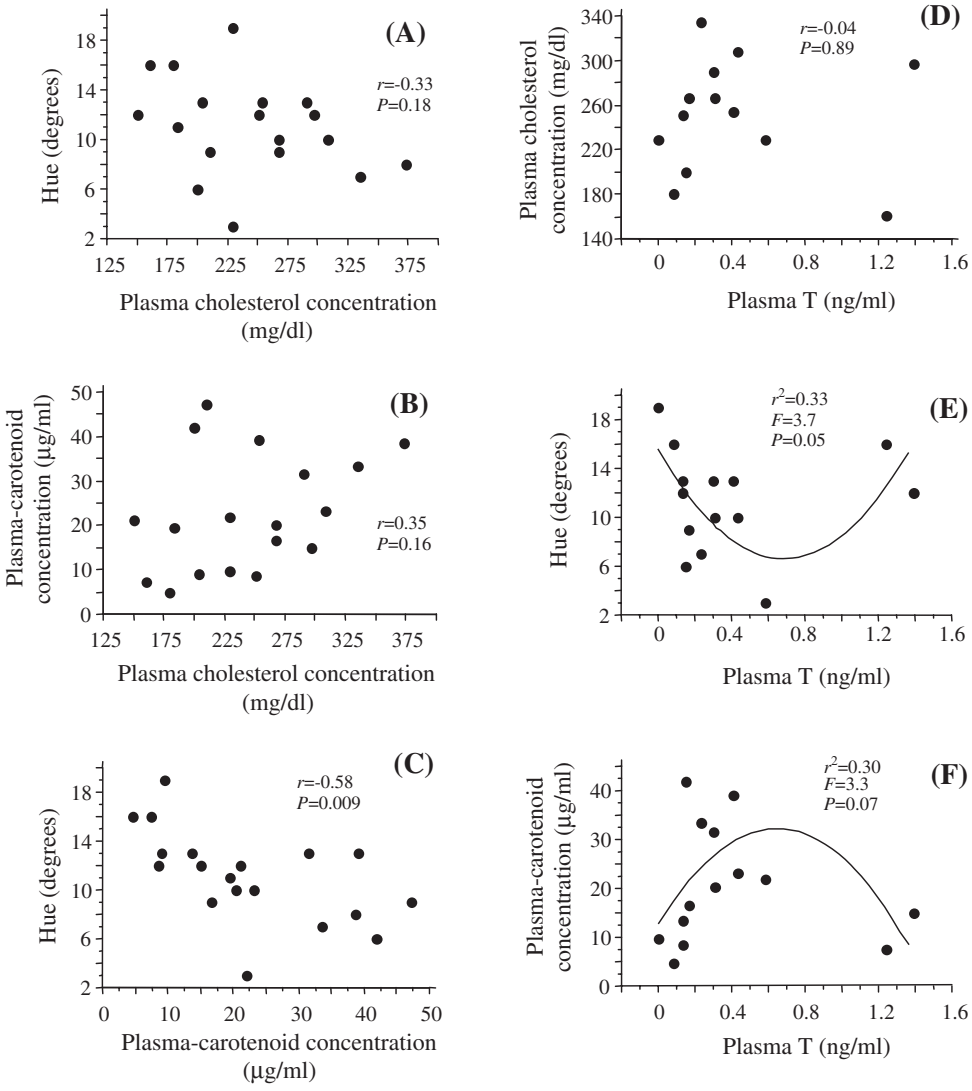

Fig. 1. Correlations between beak color and concentrations of cholesterol, T, and carotenoids in plasma in unmanipulated, adult, non-breeding, captive female zebra finches. Polynomial functions did not provide better fits in panels A, B, and D (all $P>0.3$) but fit equally as well ($r^2=0.45$, $F=6.5$, $P=0.009$) as did a linear equation in C.

concentration ($r=-0.14$, $P=0.64$), or plasma-cholesterol concentration (Fig. 1). Cholesterol levels also were not correlated with either plasma-carotenoid concentration or beak hue, but as in previous studies (e.g. [27]), beak hue was correlated with plasma-carotenoid accumulation (Fig. 1).

However, the relationship between T and beak color was significant when a second-order polynomial function was fit to the data, with the brightest females circulating intermediate levels of T (Fig. 1E). Note, however, that this pattern is largely driven by the two females that circulated the highest T levels but displayed drab beaks; when these points are omitted, there is a significant linear and negative relationship between T and hue ($r=-0.61$, $p=0.03$). The curve comparing T and plasma-carotenoid concentration was similarly shaped (with T levels lowest in females having the highest and lowest amounts of blood carotenoids) and approached statistical significance (Fig. 1F).

3.2. Experimental study

Pre-treatment T levels averaged 0.40±0.11 ng/ml (mean± S.E.), and implants elevated these levels by 118% to 0.87± 0.19 ng/ml in T-implanted birds. Before the experiment, treatment groups did not differ in body mass, beak color, or concentrations of carotenoids, cholesterol, and T in plasma (analyses of variance (ANOVAs), all $P>0.3$). Treatment groups also did not differ in these variables when post-experimental levels were compared (ANOVAs, all $P>0.15$), with the exception of body mass, which was significantly lower in T-implanted compared to control birds at the end of the study ($F_{1,15}=4.63$, $P=0.049$). However, T-implants induced significant changes in beak color, body mass, and cholesterol after 8 weeks. Beaks in T-implanted females became redder than those of control females (Fig. 2A), although all were still less red than those of males [25]. Plasma-carotenoid concentration, however, did not change accordingly (Fig. 2B), unlike what I

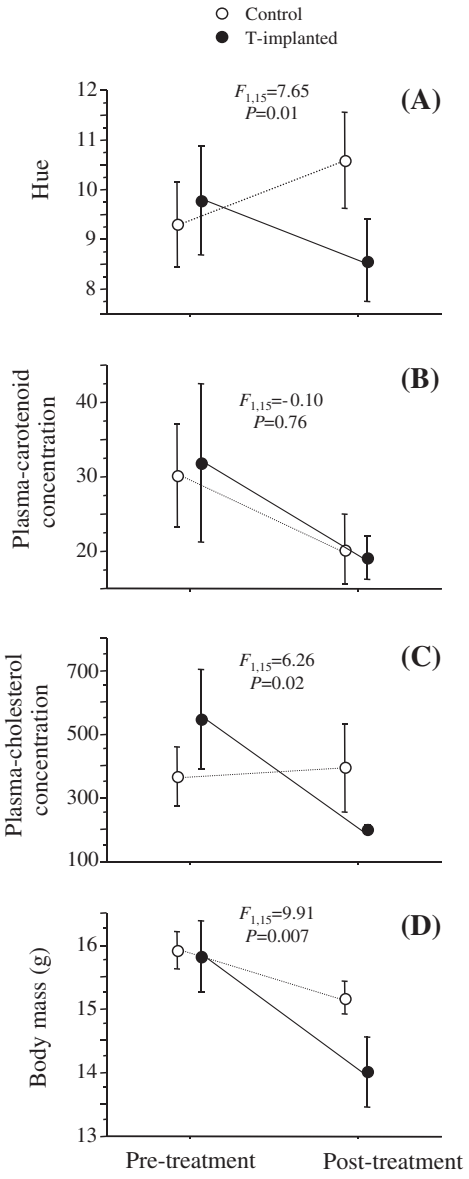

Fig. 2. Effects of experimental T implantation on (A) beak hue, (B) plasma-carotenoid concentration, (C) plasma-cholesterol concentration, and (D) body mass in female zebra finches. Both pre- and post-treatment data are shown for control and T-implanted females, and analyses of variance (ANOVAs) were run to determine whether pre- to post-treatment changes in values differed between treatment groups.

found in my previous study of T-implanted male zebra finches [25]. Interestingly, cholesterol levels declined significantly (by 64%) in T-implanted females (Fig. 2C), whereas they increased in T-implanted males [25]. Last, T-implanted females lost significantly more body mass (11%) than did controls (Fig. 2D).

4. Discussion

Here, I provide correlational and experimental evidence in support of the idea that carotenoid-derived beak color in female zebra finches, like in males [25], is sex-steroid-dependent. This study adds to the growing body of literature showing that, although T levels and sexual-ornament expression are typically lower in females than in males, when females develop ornamental features they, like in males, can also come under the activational control of sex steroids.

Despite the fact that T had a directional experimental effect on female beak pigmentation, T was nonlinearly related to coloration in unmanipulated females. That is, beak color increased with T up to a point and then declined in females that circulated high T levels. Admittedly, this was driven largely by two females that had much higher T levels than the rest; however, these were not unreasonably high levels for adult female zebra finches [33]. Moreover, this bell-shaped curve is what is predicted if females experience higher costs of T that do males—the so-called 'antagonistic selection hypothesis' [19]. I offer two possible mechanisms by which T may be polynomially related to female coloration:

(1) T is known to have immunocompromising effects in birds [34–36]. A rise in T in females may call for resource mobilization to fight infections, and carotenoids are known to be important immunomodulatory molecules (e.g. in zebra finches; [24,30]). By using carotenoids to combat T-induced immunosuppression (as suggested by [37]), females with naturally high T levels may be diverting carotenoids away from the beak and thus fading in beak color;
(2) T significantly decreased body mass and cholesterol stores in females, unlike what occurred in my previous studies of males, where body mass was stable and cholesterol levels increased in T-implanted birds [25]. T traditionally increases lipid metabolism in animals [18,38], and adipose tissue is thought of as a major storage depot for carotenoids in birds [39]. So, even if carotenoids are not playing an immunoenhancing role, females with high T may simply have fewer fat stores from which to draw carotenoids, or fewer lipoproteins with which to circulate carotenoids, for beak pigmentation.

In contrast, male zebra finches would not be expected to suffer as high of costs as females, because: (1) T increases circulating carotenoid levels in males (via lipoprotein upregulation [25]; see more below), which should buffer, if not boost, health; or (2) T does not seem to impose the same metabolic costs in males, since T-implanted males did not lose body mass [25].

If T is costly at high levels in females, why did I fail to find depressed color in T-implanted females? One potential explanation is that, since I only used a single experimental dose of T, I could not detect subtle, perhaps nonlinear changes in coloration with increasing T. Another is that the T treatment was simply too short to sufficiently influence immunity, endogenous carotenoid stores, or other parameters that govern beak-pigment accumulation over time. Future studies should calculate more comprehensive dose–response curves for T and coloration and consider how long-term T elevation may influence the aforementioned parameters (e.g. fat stores, lipoprotein transporters, health) to potentially drain carotenoid pools from the body.

In light of the proposed mechanistic link between T and coloration, it is interesting to consider the functional (sexual selection) consequences of such a steroid-dependent trait. In most species, we see directional selection for the most colorful males or females, either through intrasexual competition or intersexual choice (reviewed in [40]). However, zebra finches are unusual, in that males show mating preferences for females exhibiting intermediate levels of coloration [23]. Results from my study indicate that these are females that have sufficient T (of value for courting, competing for food and mates [41], and perhaps allocating sufficient amounts to developing offspring via egg yolk) but not such high, potentially costly levels, which are known to directly inhibit fecundity in this species [20]. This is suggestive of an unusual adaptive optimum for a sexual trait that is not necessarily the most exaggerated, but instead is under stabilizing selection and balances the costs and benefits of both natural and sexual selection.

Carotenoid-based coloration in female moorhens (*Gallinula chloropus*; [15] and European starlings (*Sturnus vulgaris*; [12]) is also responsive to androgen titers. It is noteworthy that these traits are bare regions of the integument (the shield in moorhens, the beak in finches and starlings), and that carotenoid-based plumages in birds (even in males) are rarely androgen dependent, and if anything their expression is inhibited by T (e.g. [42]). Bare parts, often displayed throughout the breeding season or year, require constant tissue growth, pigment deposition, and presumably androgen action. Colorful feathers, in contrast, largely grow at a time of year (the autumn molt) when androgen titers are at their annual low [43]. In fact, experimentally elevated T levels delay molt in species that grow their feathers in autumn (e.g. [12]). Thus, if carotenoid-based feather coloration is to be influenced, at least positively, by T in birds, we might expect this to occur only in species that develop their carotenoid-based plumage in spring (e.g. in American goldfinches, *Carduelis tristis*), when T levels are typically at their highest.

Ultimately, I found that T did not modulate beak coloration in female zebra finches as it did in males, where lipoprotein upregulation by T allowed males to accumulate more carotenoids in the blood and thus the beak [25]. The fact that there were not higher carotenoid levels in blood in T-implanted females suggests that the mechanism for increased pigmentation occurred more downstream, likely at the beak itself. Peripheral sites like the follicles of colorful feather tracts [6] and the beak in zebra finches (A. Arnold, personal communication) are rich in androgen receptors, so in females these targets may play a more important role in the likelihood with which beak carotenoids are taken up into the tissue from the blood (e.g. via carotenoid-binding proteins [44]) or with which blood-circulated yellow carotenoid precursors are enzymatically transformed into red beak carotenoids [45]. In fact, it may not even be T itself that is the bioactive molecule in this system, since I did not use reductase or aromatase inhibitors (or estrogen-receptor blockers) in my study to rule out the role that the T metabolites dihydrotestosterone or estrogen may have played in controlling beak color. This is a common drawback of most studies on sex steroids and ornamental traits, and we must adopt these more sophisticated experimental methods if we are to improve our understanding of how T per se influences the expression of sexual signals in male and female animals.

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References

[1] Nelson RJ. An introduction to behavioral endocrinology. 3rd edition. Sunderland (MA): Sinaeur Associates Inc; 2005.
[2] Adkins-Regan E. Hormones and animal social behavior. Princeton (NJ): Princeton University Press; 2005.
[3] Amundsen T. Why are female birds ornamented? Trends Ecol Evol 2000;15:149–55.
[4] Kimball RT, Ligon JD. Evolution of avian plumage dichromatism from a proximate perspective. Am Nat 1999;154:182–93.
[5] Johns JE. Testosterone-induced nuptial feathers in phalaropes. Condor 1964;66:449–55.
[6] Schlinger BA, Fivizzani AJ, Callard GV. Aromatase, 5α- and 5β-reductase in brain, pituitary and skin of the sex-role reversed Wilson's phalarope. J Endocrinol 1989;122:573–81.
[7] Witschi E. Sex and secondary sexual characters. In: Marshall AJ, editor. Biology and comparative physiology of birds. New York: Academic Press; 1961. p. 115–68.
[8] Lank DB, Coupe M, Wynne-Edwards KE. Testosterone-induced male traits in female ruffs (*Philomachus pugnax*): autosomal inheritance and gender differentiation. Proc R Soc Lond B Biol Sci 1999;266:2473–8.
[9] Searcy WA. Do female red-winged blackbirds limit their own breeding densities? Ecology 1988;69:85–95.
[10] Nespor AA, Lukazewicz MJ, Dooling RJ, Ball GF. Testosterone induction of male-like vocalizations in female budgerigars (*Melopsittacus undulatus*). Horm Behav 1996;30:162–9.
[11] Hausberger M, Henry L, Richard MA. Testosterone-induced singing in female European starlings (*Sturnus vulgaris*). Ethology 1995;99: 193–208.
[12] De Ridder E, Pinxten R, Mees V, Eens M. Short- and long-term effects of male-like concentrations of testosterone on female European starlings. Auk 2002;119:487–97.
[13] Langmore NE, Cockrem JF, Candy EJ. Competition for male reproductive investment elevates testosterone levels in female dunnocks, *Prunella modularis*. Proc R Soc Lond B Biol Sci 2002;269:2473–8.
[14] Rand MS. Hormonal control of polymorphic and sexually dimorphic coloration in the lizard *Sceloporus undulatus erythrocheilus*. Gen Comp Endocrinol 1992;88:461–8.
[15] Eens M, Van Duyse E, Berghman L, Pinxten R. Shield characteristics are testosterone-dependent in both male and female moorhens. Horm Behav 2000;37:126–34.

[16] Staub NL, De Beer M. The role of androgens in female vertebrates. Gen Comp Endocrinol 1997;108:1–24.
[17] Ketterson ED, Nolan Jr V, Casto JM, Buerkle CA, Clotfelter E, Grindstaff JL, et al. Testosterone, phenotype and fitness: a research program in evolutionary behavioral endocrinology. In: Chaturvedi C, editor. Avian endocrinology. New Delhi, India: Narosa Publishing; 2001. p. 19–38.
[18] Wingfield JC, Lynn SE, Soma KK. Avoiding the 'costs' of testosterone: ecological bases of hormone–behavior interactions. Brain Behav Evol 2001;57:239–51.
[19] Clotfelter ED, O'Neal DM, Gaudioso JM, Casto JM, Parker-Renga IM, Snajdr EA, et al. Consequences of elevating plasma testosterone in females of a socially monogamous songbird: evidence of constraints on male evolution? Horm Behav 2004;46:171–8.
[20] Rutkowska J, Cichon M, Puerta M, Gil D. Negative effects of elevated testosterone on female fecundity in zebra finches. Horm Behav 2005;47:585–91.
[21] Ketterson ED, Nolan Jr V, Sandell M. Testosterone in females: mediator of adaptive traits, constraint on sexual dimorphism, or both? Am Nat 2005;166:S85–98.
[22] McGraw KJ, Adkins-Regan E, Parker RS. Anhydrolutein in the zebra finch: a new, metabolically derived carotenoid in birds. Comp Biochem Physiol B 2002;132:811–8.
[23] Burley N, Coopersmith CB. Bill color preferences of zebra finches. Ethology 1987;76:133–51.
[24] Blount JD, Metcalfe NB, Birkhead TR, Surai PF. Carotenoid modulation of immune function and sexual attractiveness in zebra finches. Science 2003;300:125–7.
[25] McGraw KJ, Correa SM, Adkins-Regan E. Testosterone upregulates lipoprotein status to control sexual attractiveness in a colorful songbird. Behav Ecol Sociobiol in press.
[26] Peters A. Testosterone treatment is immunosuppressive in superb fairy-wrens, yet free-living males with high testosterone are more immuno-competent. Proc R Soc Lond B Biol Sci 2000;267:883–9.
[27] McGraw KJ, Gregory AJ, Parker RS, Adkins-Regan E. Diet, plasma carotenoids, and sexual coloration in the zebra finch (*Taeniopygia guttata*). Auk 2003;120:400–10.
[28] McGraw KJ, Parker RS. A novel, lipoprotein-mediated mechanism controlling sexual attractiveness in a colorful songbird. Physiol Behav 2006;87:103–8.
[29] Stoehr AM, Hill GE. Testosterone and the allocation of reproductive effort in male house finches (*Carpodacus mexicanus*). Behav Ecol Sociobiol 2000;48:407–11.
[30] McGraw KJ, Ardia DR. Carotenoids, immunocompetence, and the information content of sexual colors: an experimental test. Am Nat 2003;162:704–12.
[31] Bottjer SW, Hewer SJ. Castration and antisteroid treatment impair vocal learning in male zebra finches. J Neurobiol 1992;23:337–53.
[32] Balthazart J, Absil P, Flasse V, Ball GF. Effects of the aromatase inhibitor R76713 on sexual-differentiation of brain and behavior in zebra finches. Behaviour 1994;131:225–60.
[33] Adkins-Regan E, Abdelnabi M, Mobarak M, Ottinger MA. Sex steroid levels in developing and adult male and female zebra finches (*Poephila guttata*). Gen Comp Endocrinol 1990;78:93–109.
[34] Duffy DL, Bentley GE, Drazen DL, Ball GF. Effects of testosterone on cell-mediated and humoral immunity in non-breeding adult European starlings. Behav Ecol 2000;11:654–62.
[35] Casto JM, Nolan Jr V, Ketterson ED. Steroid hormones and immune function: experimental studies in wild and captive dark-eyed juncos (*Junco hyemalis*). Am Nat 2001;157:408–20.
[36] Roberts ML, Buchanan KL, Evans MR. Testing the immunocompetence handicap hypothesis: a review of the evidence. Anim Behav 2004;68:227–39.
[37] McGraw KJ, Ardia DR. Sex differences in carotenoid status and immune performance in zebra finches. Evol Ecol Res 2005;7:251–62.
[38] Buchanan KL, Evans MR, Goldsmith AR, Bryant DM, Rowe LV. Testosterone influences basal metabolic rate in male house sparrows: a new cost of dominance signaling? Proc R Soc Lond B Biol Sci 2001;268:1337–44.
[39] Negro JJ, Figuerola J, Garrido J, Green AJ. Fat stores in birds: an overlooked sink for carotenoid pigments? Funct Ecol 2001;15:297–303.
[40] Hill GE, McGraw KJ. Bird coloration. Volume II. Function and evolution. Cambridge (MA): Harvard University Press; 2006.
[41] Arnold AP. The effects of castration and androgen replacement on song, courtship, and aggression in zebra finches (*Poephila guttata*). J Exp Zool 1975;191:309–26.
[42] Stoehr AM, Hill GE. The effects of elevated testosterone on plumage hue in male House Finches. J Avian Biol 2001;32:153–8.
[43] Wingfield JC. Interrelationships of androgens, aggression, and mating systems. In: Wada M, Ishii S, Scanes CG, editors. Endocrinology of birds: molecular to behavioral. Tokyo: Springer-Verlag; 1990. p. 187–205.
[44] Yemelyanov AY, Katz NB, Bernstein PS. Ligand-binding characterization of xanthophylls carotenoids to solubilized membrane proteins derived from human retina. Exp Eye Res 2001;72:381–92.
[45] McGraw KJ. Colorful songbirds metabolize carotenoids at the integument. J Avian Biol 2004;35:471–6.