ORIGINAL ARTICLE

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Yolk androgen deposition as a compensatory strategy

Abstract The deposition of androgens into the yolks of eggs can have long-lasting effects on the growth and development of young birds. It has been proposed that female birds and reptiles deposit yolk androgens according to the differential allocation hypothesis (DAH), which posits the allocation of more resources to offspring sired by more attractive, higher-quality males. We examined deposition patterns of yolk androgens in relation to mate attractiveness in the house finch *Carpodacus mexicanus*. Contrary to the predictions of the DAH, female house finches deposited significantly more androgens into eggs sired by less attractive males. We propose that, rather than serving as resources, androgens are used as mediators in a compensatory distribution strategy, enabling females to improve the quality of young produced with less attractive males.

Keywords Differential allocation hypothesis · Egg · Testosterone · Maternal investment

Introduction

Discussions of maternal investment often focus on patterns of resource allocation to offspring. Many behavioral measures of maternal investment, such as incubation, provisioning, and protection of offspring, have been well characterized. Female birds and reptiles also have the ability, however, to invest in offspring before they hatch, through the deposition of physiologically relevant substances, such as carotenoids (Surai et al. 2001; Dierenfeld et al. 2002), antibodies (Saino et al. 2003), and hormones (Schwabl 1997; Lovern and Wade 2001) into eggs. Yolk androgens have specifically become the subject of much discussion, and the effects of androgens on offspring as well as the adaptive significance associated with deposition patterns of yolk androgens remain unclear.

Androgens are mediators that, when deposited into eggs by female birds and reptiles, can have potent effects on offspring growth and survival. For example, *in-ovo* injections of androgens into the yolks of canary (*Serinus canaria*) and black-headed gull (*Larus ridibundus*) eggs increased begging behavior and growth rates of chicks (Schwabl 1996b; Eising and Groothuis 2003) and decreased the chance of starvation during a drought year in European starling chicks (*Sturnus vulgaris*) (Pilz et al. 2004). In addition, yolk testosterone levels were positively correlated with growth of the hatching muscle in red-winged blackbirds (*Agelaius phoeniceus*) (Lipar and Ketterson 2000). On the other hand, injections of androgens into eggs were associated with decreases in T-cell immunity (Groothuis et al. 2005; Navara et al. 2005) as well as increases in offspring mortality (Sockman and Schwabl 2000; Navara et al. 2005). Because many of the measured effects of yolk androgens appear positive, however, androgens have been frequently described as resources that, when allocated to eggs, benefit offspring and increase reproductive success.

Previous research has shown that the strategies of androgen deposition in yolk differ according to environmental and social contexts. For example, females of some avian species deposit more androgens into eggs laid later in the clutch, potentially negating the offspring size gradient caused by hatching asynchrony (Schwabl 1993; Lipar et al. 1995; French et al. 2001; Royle et al. 2001; Sockman et al. 2001; Groothuis and Schwabl 2002). In addition, androgen concentrations in eggs have been found to vary according to mate quality; female zebra finches (*Taeniopygia guttata*) deposited more yolk androgens into eggs sired by males

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wearing 'more attractive' red legbands than those sired by males wearing 'less attractive' green legbands (Gil et al. 1999), and female canaries deposited more yolk androgens into eggs after being exposed to 'more attractive' songs (Gil et al. 2004; Tanvez et al. 2004). These latter studies, in which androgens appear to be allocated as a resource with more androgens going to offspring of higher value, have caused researchers to describe yolk androgen distribution in the framework of the differential allocation hypothesis (DAH)—the preferential allocation of resources to offspring sired by more attractive, higher-quality males (Burley 1988). On the other hand, female collared flycatchers (*Ficedula albicollis*) deposit more androgens into eggs sired by younger males (Michl et al. 2005). Because older males may provide more direct benefits and may be of better genetic quality, female flycatchers may instead use yolk androgens in a compensatory strategy to counterbalance the potential detriments associated with a young and, thus, lower-quality father (Michl et al. 2005).

The DAH has three underlying assumptions: (1) attractive males must provide a greater opportunity for production of high-quality young than unattractive males, making the offspring of the former males worthy of greater investment, (2) differential resource investment (in this case, yolk androgens) must be costly to the female in terms of future reproductive effort, and (3) the resource must be beneficial to the offspring of the current reproductive attempt (Sheldon 2000). A compensatory strategy, on the other hand, would also have three underlying assumptions. The first two assumptions are similar to the DAH in that (1) attractive males must provide a greater opportunity for production of high-quality young than unattractive males (e.g., providing more direct benefits or better genes) and (2) the differential deposition of the mediator in question (in this case, yolk androgens) must be costly to the female or the offspring in terms of reproductive success. The third assumption, however, differs from the DAH in that (3) the deposition of the mediator must in some way mitigate the disadvantages experienced by an offspring sired by a lower-quality male. Thus, the mediator need not be a resource that is always beneficial to offspring, but exposure to such a mediator must provide certain benefits to offspring that are lacking as a result of the current breeding situation.

We examined the idea that yolk androgens are resources deposited according to the DAH or mediators deposited according to a compensatory strategy in a wild population of house finches. Female house finches often begin incubating before the last egg is laid, resulting in offspring that hatch asynchronously. As a result, house finch nestlings hatching from eggs in the fifth clutch position have been shown to be significantly smaller and significantly less likely to survive (Dervan 2001). Male house finches express carotenoid-based plumage coloration ranging from bright red to drab yellow, with females showing a mating preference for males with redder, more saturated plumage (Hill 1990, 1991). In this species, redder males provision at a higher rate, providing direct benefits to females and their offspring (Hill 1991). Male color has also

been positively correlated with breeding success (McGraw et al. 2001) and over-winter survival (Hill 1991), and it has been shown that brighter red males pair with older, more attractive females (Hill 1993a). Because female house finches paired with more attractive males gain more direct (Hill 1991) and, perhaps, indirect benefits (Hill and Farmer 2005) than females paired to less attractive males, we predicted that, if yolk androgens are deposited according to the DAH, females paired to more attractive males would deposit more androgens into their eggs. If yolk androgens are deposited according to a compensatory strategy, we alternatively predict that females will deposit more androgens into eggs sired by less attractive males. In addition, due to the level of hatching asynchrony exhibited in this species, we predicted that female house finches would deposit more androgens into eggs laid later in the clutch.

Materials and methods

Male color and female condition

We monitored a nesting population of house finches in Lee County, AL, USA. The field site contained approximately 150 nest boxes within a 64-km^2 area, most of which were occupied by nesting house finches. House finches are extremely non-territorial; however, all nests were located at least 10 m from one another, minimizing breeding density. We examined the allocation patterns of yolk androgens at each nest in relation to the color of the attending male as well as in relation to female condition. Nesting male and female house finches were captured using either potter traps specially altered to enclose the nest or basket traps surrounding feeders throughout the study site.

For males, three color measurements were taken from each of three locations on the body, including the head, breast, and rump, using a Colortron reflectance spectrophotometer (Hill 1998). This device measures three separate aspects of color: hue, saturation, and brightness. All measurements of separate body parts were averaged to provide an overall average measurement for each color variable. The three color variables that make up plumage coloration are often highly correlated with one another, so the average values for the three male colour variables were analyzed using a principal components analysis. The first component explained 46% with an eigenvalue of 1.39, the second component explained 33% of the variance with an eigenvalue of 0.98, and the third explained 21% of the variance, with an eigenvalue of 0.64. PC1 had a strong positive loading from hue (0.83) and brightness (0.60) and a strong negative loading from saturation (−0.70), and, thus, we used this component for our assessment of "attractiveness". The Colortron measures hue as position on a color wheel where scarlet is arbitrarily assigned a value of zero and yellow is assigned a value around 20, so male house finches with higher saturation but lower hue scores are more ornamented. For our comparisons, we divided males into two groups—above the median and

below the median. There was a natural break in the distribution of the principal component values at the median value, which occurred at zero. Males with a PC1 score below zero will hereafter be referred to as "more attractive" males, and males with a PC1 score above zero, which means they were less ornamented, will hereafter be referred to as "less attractive".

Female tarsus length was measured using manual dial calipers (accuracy=0.01 mm) and mass was measured using a digital scale (accuracy=0.05 g). The residuals of mass-to-tarsus-length ratio were calculated as a measure of condition in these females. Despite suggestions by Green (2001) that mass-to-tarsus-length ratio is a generator of spurious results, we feel that a measurement that incorporates both skeletal size and mass of the animal generates an excellent estimation of individual avian condition, and the residuals of these measurements provide a clean method of separating the effects of condition from the effects of body size (Reist 1985).

Egg collection and yolk androgen analysis

After the appearance of the first egg, we used visual assessments to determine the date of incubation onset. Previous experiments using nest temperature measurements showed that visual assessments consistently and accurately estimated the day of incubation onset (Badyaev et al. 2003). All eggs were retrieved after 36 h of incubation, before the development of embryonic gonadal tissue (K. Navara, unpublished data), and frozen at −20°C. In cases where incubation began before the last egg was laid, each egg within the nest was collected after 36 h of its incubation onset, resulting in a similar incubation time for all eggs. Because previous studies have shown that concentrations of yolk androgens decrease after the onset of incubation (Elf and Fivizzani 2002; Rutstein et al. 2005), we were careful to collect all eggs after the same period of incubation, thus eliminating variation resulting from the period of incubation itself. We were able to obtain full data, including yolk androgen concentrations, male color, and female condition, on 15 nests. In two cases, we captured only the male parent. Finally, clutch sizes often vary among individuals and among nest attempts, resulting in unequal sample sizes among clutch positions in our analyses.

The albumin, yolk, and small embryo were separated by thawing. Embryos in collected eggs were of comparable sizes at this stage of development. The yolks were homogenized and 20–40 mg of the homogenate was diluted in 1 ml of water for the analysis. Yolk testosterone (T), androstenedione (A4), and dihydrotestosterone (DHT) were separated by celite column chromatography according to methods described by Schwabl (1993). T and A_4 were quantified using a standard competitive binding radioimmunoassay, using a specific antibody (Endocrine Science, USA) according to methods outlined in Mendonça et al. (1996). DHT was quantified using a commercial ^{125}I-labeled radioimmunoassay kit from Diagnostics Systems Laboratories (Webster, TX, USA). Interassay variation was 20% for A_4, 3% for T, and 14% for DHT and intra-assay variation was 6% for A_4 and 4% for T. Assay lower detection limits were 20 pg/ml for A_4 and T and 25 pg/ml for DHT. Because all androgen concentrations were highly correlated with one another (A_4–T $r=0.653$, $p<0.001$; A_4–DHT $r=0.442$, $p<0.001$; T–DHT $r=0.593$, $p<0.001$) and, in most cases, all androgens showed similar patterns when analyzed separately, we used the sum of all three androgens in our analyses.

Statistical analyses

The relationship between yolk androgens and male attractiveness was tested using a nested analysis of variance (ANOVA), using male ID as the nested variable within treatment group. This allowed the inclusion of potentially important within-clutch variation while preventing the replication that may occur using eggs within the same nest and sired by the same males as independent samples. All nests included in these analyses were sired by individual pairs of birds that were not repeated in the analyses.

Total yolk androgens were examined in relation to female condition using the residuals of the regression of female mass-to-tarsus-length ratio, and comparisons were made using a simple regression. A variation in total yolk androgen content in relation to the month in which the eggs were laid was analyzed using an ANOVA. Clutch averages of total yolk androgens were used in these analyses to avoid using the same females in duplicate analyses.

The patterns of yolk androgen content across clutch positions were analyzed in relation to male attractiveness using a two-way ANOVA. In addition, we conducted a linear regression to examine the within-clutch patterns of yolk androgen content and split those analyses based on male attractiveness. Using an F test, we tested for equality of the slopes for the two regression lines created for attractive vs unattractive males (Sokal and Rohlf 1995). Finally, the relationship between yolk androgens and male attractiveness was analyzed in each individual clutch position using unpaired t tests. While the use of a repeated-measures ANOVA to analyze yolk androgen content in relation to clutch position would be preferable, we were not able to utilize such analyses because clutch size was not constant for these birds. Statistical analyses were conducted using JMP software (SAS Institute, 1993).

Results

House finch females deposited significantly higher concentrations of total yolk androgens overall into eggs sired by less attractive males ($F_{19,52}=4.53$, $p<0.001$) (Fig. 1). Unpaired t tests showed that this pattern of increased yolk androgens in eggs sired by unattractive males persisted across all laying positions (egg #1 $t=1674$, $p<0.001$; egg #2 $t=1.794$, $p=0.055$; egg #3 $t=2.449$, $p=0.05$; egg #4 $t=2.175$, $p=0.025$; egg #5 $t=2.064$, $p=0.03$) (Fig. 2). Average yolk androgen content did not vary with female condition

(R^2=0.107, p=0.23) (Fig. 3) or according to the month in which the eggs were laid ($F_{2,30}$=0.656, p=0.56) (Fig. 4). In addition, the number of days between the appearance of the first egg and the onset of incubation was statistically similar between females mated to attractive and unattractive males ($F_{1,12}$=2.031, p=0.18).

Total yolk androgens increased significantly with clutch order ($F_{4,70}$=2.680, p=0.04). Post hoc analyses using a Fisher test indicate that, overall, eggs in the fifth clutch position contained significantly higher levels of total yolk androgens than in the first clutch position (p=0.004) and second clutch position (p=0.03). When clutches of males differing in attractiveness were analyzed separately, the same pattern remained for eggs sired by less attractive males, with eggs in the fifth clutch position containing significantly more total yolk androgens than those in the first (p=0.02). In eggs sired by more attractive males, however, there was no difference in total yolk androgens among eggs in any of the clutch positions (Fig. 2) (p=0.30). In addition, the slopes of the regression lines of within-clutch patterns of yolk androgens were significantly different between eggs sired by attractive and unattractive males ($F_{1,73}$=150.04, p<0.001). As a result, offspring sired by less attractive males and hatching from eggs in the fifth clutch position received the highest levels of yolk androgens.

Discussion

Contrary to the predictions of the DAH, house finch females deposited more yolk androgens into eggs sired by less attractive males. In addition, females deposited more androgens into eggs laid later in the clutch, but only when paired with less attractive males. This suggests that yolk androgens are not resources deposited by female house

Fig. 2 Mean contents per milligram of total yolk androgens, defined as the sum of testosterone, androstenedione, and dihydrotestosterone (error bars show standard errors) in eggs of different clutch positions. Numbers located inside the bars indicate the number of eggs in each clutch position and sired by males in each attractiveness group

finches according to the DAH. Alternate factors that may have influenced these patterns could include the occurrence of extra pair copulations (EPCs), seasonal effects, or limitations associated with female quality. Less than 9% of house finch offspring, however, result from EPCs, and the number of extra-pair young in a nest is not related to the color, age, or condition of the social male at that nest (Hill et al. 1994). In addition, while males of higher quality tend to pair earlier in the reproductive season (Hill 2002), yolk androgen content did not vary by the month in which the eggs were laid, suggesting that the observed pattern is not due to a seasonal effect (Fig. 3). Female quality could potentially affect allocation strategies of yolk androgens, and previous research has shown that more attractive male house finches tend to mate with older, more attractive females. We found no link, however, between female condition and average yolk androgen content of a clutch.
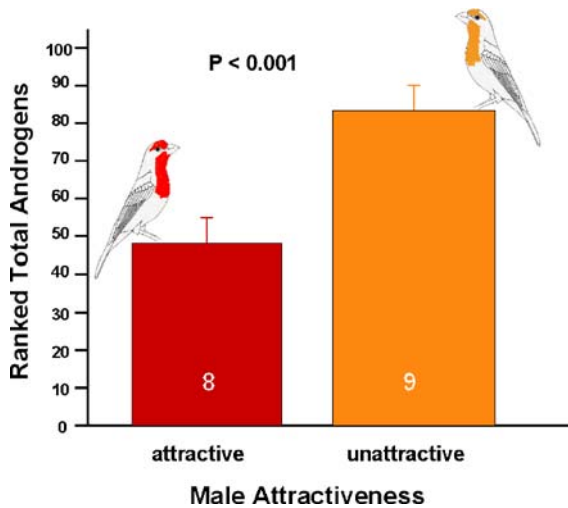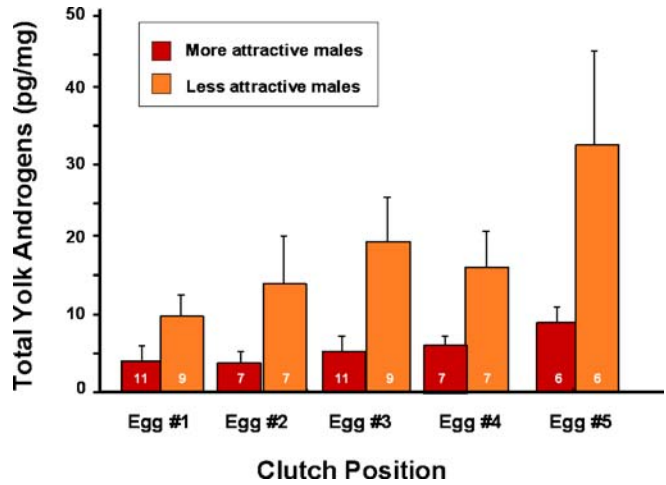

Fig. 1 Mean contents per milligram of yolk of total yolk androgens, defined as the sum of testosterone, androstenedione, and dihydrotestosterone (error bars show standard errors) in eggs sired by less attractive male house finches vs eggs sired by more attractive male house finches. Numbers located inside the bars indicate the number of males analyzed in each attractiveness group
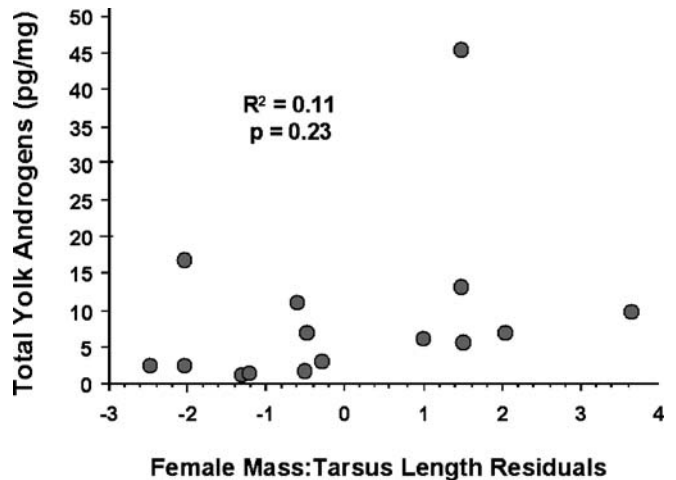

Fig. 3 Female condition, as defined by the residuals of mass-to-tarsus-length ratios, analyzed according to average clutch total yolk androgens using a simple regression
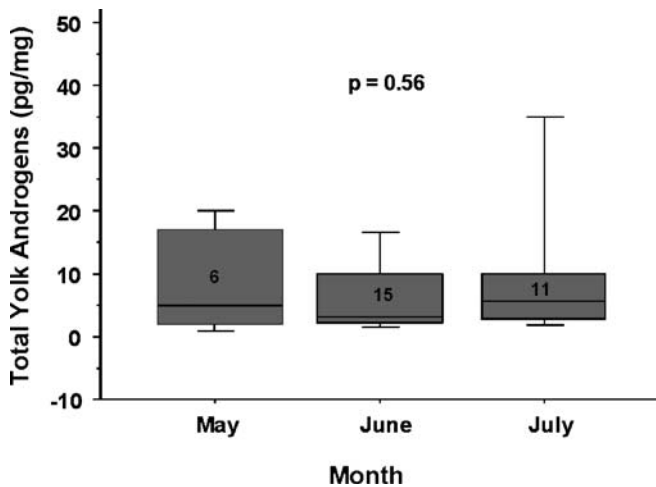
Fig. 4 Mean contents per milligram of total yolk androgens, defined as the sum of testosterone, androstenedione, and dihydrotestosterone (*error bars* show standard errors) in eggs laid in May, June, and July. *Numbers* located inside the boxes indicate the number of clutches (used for clutch average yolk androgen analyses) in each month of the breeding season

(Fig. 4). Thus, our observations suggest that females altered their patterns of androgen deposition according to the color of their social mates.

The patterns of yolk androgen deposition in house finches do not follow the DAH for several possible reasons: First, there is still no definitive evidence that the deposition of yolk androgens is adaptive. Thus, from a non-adaptive standpoint, yolk androgen content may simply reflect steroid concentrations in females as a result of other physiological processes. In addition, because male color and female quality are often correlated in house finches (Hill 1993b), it is impossible to completely separate the effects of female condition from male color when examining a potential deposition strategy. Thus, perhaps the observed patterns of yolk androgen deposition are not related to male quality at all but result from the physical quality of the female. If this were true, however, we would expect females mated to more attractive males to be of better quality and, thus, to deposit more androgens into eggs than females mated to unattractive males, the opposite of what we found in this study. We suggest, instead, that the deposition of yolk androgens in this species may not meet assumptions 1–3 (above) of the DAH and that female house finches distribute yolk androgens according to an entirely different strategic model.

Attractive male house finches provide more food to females and offspring, so the first assumption of the DAH, that attractive males contribute in some way to the current reproductive effort, is met (Hill 1991). The second assumption, (i.e., that producing and transferring androgens to the yolk by females is costly) has yet to be shown in this or other species. Although it has been shown, in general, that high levels of plasma androgens can have detrimental physiological effects (Olsen and Kovacs 1996; Klukowski et al. 1997) and that, at the time of follicular development in the canary, plasma androgens are posi-

tively correlated with yolk androgen levels (Schwabl 1996a), there has been no direct demonstration of a cost to the mother associated with the allocation of yolk androgens. If testosterone levels required for the deposition of yolk androgens were costly to females, we would predict that females in better condition would be better able to withstand any costs associated with depositing higher levels of androgens into eggs. Pilz et al. (2003b) showed that yolk androgen concentration in European starling eggs correlated to age and clutch size but not to female body condition. In the house finch, female condition similarly did not relate to yolk androgen content (Fig. 4), challenging the idea that females incur a cost related to the deposition of yolk androgens.

This does not mean, however, that the offspring do not incur a cost as a result of exposure to high levels of yolk androgens. Although yolk androgens have been shown to advantageously alter growth and developmental patterns, their effects are not universally beneficial. For example, injections of androgens into American kestrel (*Falco sparverius*) eggs resulted in offspring that hatched later and had a higher mortality rate (Sockman and Schwabl 2000). In addition, in the eastern bluebird (*Sialia sialis*), in-ovo androgen injections had both a stimulatory effect on offspring growth while exerting a suppressive effect on immune function at the same time (Navara et al. 2005). These studies suggest that yolk androgens are not simply beneficial resources but are mediators that can have a multitude of effects on offspring quality, perhaps providing a set of costs along with the benefits previously observed. The documented immunological costs experienced by offspring, as well as other costs that have yet to be identified, associated with exposure to high yolk androgen levels potentially satisfy the second assumption of both the DAH and the compensatory deposition strategy. Because yolk androgens are not simply beneficial resources, however, the third assumption of the DAH, that the investment is a beneficial resource to offspring, is not satisfied. The stimulatory effects of androgens on growth of avian offspring may instead help to mitigate the lack of direct benefits received from males of lower quality and, while those benefits come with an immunological cost, they satisfy the third assumption of the compensatory deposition strategy. Thus, while the deposition of yolk androgens by female house finches does not satisfy the assumptions of the DAH, all three assumptions associated with a compensatory strategy are satisfied, suggesting that female house finches deposit yolk androgens in a compensatory manner.

Our observation that within-clutch patterns of yolk androgens only existed in clutches sired by unattractive males can also be explained by a compensatory deposition strategy. Because attractive male house finches provide more food to offspring (Hill 1991), it is likely that size gradients resulting from hatching asynchrony would be more pronounced in broods sired by less attractive males and receiving less food than in broods sired by attractive males and receiving more food. In fact, male provisioning behavior has been shown to have direct effects on offspring

recruitment in house finches (Badyaev and Hill 2002). Pilz et al. (2004) showed, in European starling chicks (*S. vulgaris*), that injections of yolk androgens decreased the chance of starvation during a drought year but had no detectable effects during a year in which water and food was abundant. Only house finch nestlings that are sired by an unattractive male and receive a suboptimal amount of food through the nestling period perhaps require compensation through exposure to yolk androgens, while nestlings sired by an attractive male and receiving more than enough food can overcome the size gradients associated with hatching asynchrony without any assistance. This idea has yet to be tested in this or any species.

Despite the uncertainties concerning the effects of yolk androgen deposition, we continue to see striking within- and among-clutch patterns of yolk androgen content that lend support to the idea that yolk androgens play an important role in offspring development. It is less likely, however, that yolk androgens are "costly resources" that are traded off between reproductive attempts than that they are utilized as modulators to alter the growth and development of the offspring in a more immediate sense. Many asynchronously hatching species, including the house finch, deposit more androgens into eggs laid later in the clutch, a distribution pattern of yolk androgens consistent with the idea of counterbalancing the effects of hatching asynchrony (Schwabl 1993; Lipar et al. 1995; French et al. 2001; Royle et al. 2001; Sockman et al. 2001; Groothuis and Schwabl 2002). In addition, females of many species deposit more yolk androgens when breeding under more crowded conditions (Schwabl 1997; Whittingham and Schwabl 2001; Groothuis and Schwabl 2002; Pilz et al. 2003a), a strategy that could potentially prepare offspring for the impending competitive environment resulting in areas where conditions are more crowded. In the house finch, the role of yolk androgens appears to be consistently compensatory, with females depositing more androgens into eggs sired by less attractive males and into later laid eggs, but only in clutches sired by less attractive males. The observed allocation pattern targets those offspring that are smaller at hatch and exist in a nest where the male provisions less, a compensatory form of hormone distribution that may help to negate both the size gradient caused by hatching asynchrony as well as the consequences associated with the lower quality and/or the lack of direct benefits received from a less attractive male.

In most cases of sexual selection by female choice, there exists a spectrum of males based on the quality of the sexually selected trait. The DAH predicts that females mated to less attractive males would 'cut their losses' and save their investment potential for future reproductive attempts (Sheldon 2000). We propose that females might attempt to alter the condition of lower-quality offspring to salvage an otherwise unsuccessful breeding attempt. This compensatory strategy would require that the overall effect of the observed allocation pattern is beneficial in terms of current reproductive success and that the observed investment strategy is not costly to the female in terms of future reproductive success. Differential patterns of investment

may instead persist due to a range of costs incurred by some offspring as a result of the allocation strategy. Whether or not yolk androgen allocation meets those assumptions is still unclear. It is possible, however, that the compensatory allocation hypothesis is an alternative strategy of investment adopted by females of some species when distributing yolk androgens.

The premise of the compensatory distribution hypothesis is flexible and allows for the contradictory patterns and effects found in relation to the deposition of yolk androgens. For example, in some asynchronously hatching species, yolk androgen concentrations are higher in later laid eggs (Schwabl 1993), while in other species, androgen levels are higher in eggs laid earlier in the clutch (Gil et al. 1999). In the offspring of some species, yolk androgens exhibit beneficial effects (Schwabl 1996b; Lipar and Ketterson 2000), while in others, they evoke clearly detrimental effects (Sockman and Schwabl 2000; Navara et al. 2005). These data suggest that the basis behind the deposition of yolk androgens is not simple and that females do not always use these mediators in a one-directional way. It is instead likely that the optimal patterns of yolk androgen deposition are determined by a mixture of plastic environmental, social, and physiological circumstances and that distribution patterns may differ according to a variety of adaptive allocation strategies adopted by different species. A more comprehensive examination of the costs and benefits associated with the strategies of yolk androgen distribution must be completed before we can understand the adaptive significance of this potentially powerful maternal effect.

References

Badyaev AL, Hill GE (2002) Paternal care as a conditional strategy: distinct reproductive tactics associated with elaboration of plumage ornamentation in the house finch. Behav Ecol 13:591–597

Badyaev AL, Hill GE, Beck ML (2003) Interaction between maternal effects: onset of incubation and offspring sex in two populations of a passerine bird. Oecologia 135:386–390

Burley N (1988) The differential-allocation hypothesis: an experimental test. Am Nat 132:611–628

Dervan A (2001) The effects of hatch order and sex on nestling growth in the house finch. Department of Biological Sciences. Auburn University, Auburn, AL

Dierenfeld E, Norkus E, Carroll K, Ferguson G (2002) Carotenoids, vitamin A, and vitamin E concentrations during egg development in panther chameleons (*Furcifer pardalis*). Zoo Biol 21:295–303

Eising C, Groothuis TGG (2003) Yolk androgens and begging behaviour in black-headed gull chicks: an experimental field study. Anim Behav 66:1027–1064

Elf PK, Fivizzani AJ (2002) Changes in sex steroid levels in the yolks of the leghorn chicken, *Gallus domesticus*, during embryonic development. J Exp Zool 293:594–600

French JB Jr, Nisbet ICT, Schwabl H (2001) Maternal steroids and contaminants in common tern eggs: a mechanism of endocrine disruption? Comp Biochem Physiol 128:91–98

Gil D, Graves J, Hazon N, Wells A (1999) Male attractiveness and differential testosterone investment in zebra finch eggs. Science 286:126–128

Gil D, Leboucher G, Lacroix A, Cue R, Kreutzer M (2004) Female canaries produce eggs with greater amounts of testosterone when exposed to attractive male song. Horm Behav 45:64–70

Green AJ (2001) Mass/length residuals: measures of body condition or generators of spurious results? Ecology 82:1473–1483

Groothuis TG, Eising C, Dijkstra C, Müller W (2005) Balancing between costs and benefits of maternal hormone deposition in avian eggs. Biol Lett 1:78–81

Groothuis TG, Schwabl H (2002) Determinants of within- and among-clutch variation in levels of maternal hormones in black-headed gull eggs. Funct Ecol 16:281–289

Hill GE (1990) Female house finches prefer colourful males: sexual selection for a condition-dependent trait. Anim Behav 40:563–572

Hill GE (1991) Plumage coloration is a sexually selected indicator of male quality. Nature 350:337–339

Hill GE (1993a) Male mate choice and the evolution of female plumage coloration in the house finch. Evolution 47:1515–1525

Hill GE (1993b) Male mate choice and the evolution of female plumage coloration in the house finch. Can J Zool 71:619–627

Hill GE (1998) An easy, inexpensive method to quantify plumage coloration. J Field Ornithol 69:353–363

Hill GE (2002) A red bird in a brown bag. Oxford Univ. Press, New York

Hill GE, Farmer KL (2005) Carotenoid-based plumage coloration predicts resistance to a novel parasite in the house finch. Naturwissenschaften 92:30–34

Hill GE, Montgomerie R, Roeder C, Boag P (1994) Sexual selection and cuckoldry in a monogamous songbird: implications for theories of sexual selection. Behav Ecol Sociobiol 35:193–200

Klukowski LA, Cawthorn JM, Ketterson ED, Nolan V Jr (1997) Effects of experimental elevated testosterone on plasma corticosterone and corticosteroid-binding globulin in dark-eyed juncos (*Junco hyemalis*). Gen Comp Endocrinol 108:141–151

Lipar JL, Ketterson ED (2000) Maternally derived yolk testosterone enhances the development of the hatching muscle in red-winged blackbird *Agelaius phoeniceus*. Proc R Soc Lond Ser B 267:2005–2010

Lipar JL, Ketterson ED, Nolan V Jr (1995) Steroid hormones in the yolk of red-winged blackbird eggs. Poult Avian Biol Rev 6:329

Lovern MB, Wade J (2001) Maternal plasma and egg yolk testosterone concentrations during embryonic development in green anoles (*Anolis carolinensis*). Gen Comp Endocrinol 124:226–235

McGraw KJ, Stoehr AM, Nolan PM, Hill GE (2001) Plumage redness predicts breeding onset and reproductive success in the house finch: a validation of Darwin's theory. J Avian Biol 32:90–94

Mendonça MT, Chernetsky SD, Nester KE, Gardner GL (1996) Effects on gonadal sex steroids on sexual behavior in the big brown bat *Eptesicus fuscus*, upon arousal from hibernation. Horm Behav 30:153–161

Michl G, Török J, Péczely P, Garamszegi LZ, Schwabl H (2005) Female collared flycatchers adjust yolk testosterone to male age, but not to attractiveness. Behav Ecol 16:383–388

Navara KJ, Hill GE, Mendonça MT (2005) Variable effects of yolk androgens on growth, survival, and immunity in eastern bluebird nestlings. Physiol Biochem Zool 78:570–578

Olsen NJ, Kovacs WJ (1996) Gonadal steroids and immunity. Endocr Rev 17:369–384

Pilz KM, Smith HG, Sandell MI (2003a) Interfemale variation in egg yolk androgen allocation in the European starling: do high-quality females invest more? Anim Behav 65:841–850

Pilz KM, Smith HG, Sandell MI, Schwabl H (2003b) Inter-female variation in egg yolk androgen allocation in the European starling: do high quality females invest more? Anim Behav 65:841–850

Pilz KM, Quiroga M, Schwabl H, Adkins-Regan E (2004) European starling chicks benefit from high yolk testosterone levels during a drought year. Horm Behav 46:179–192

Reist JD (1985) An empirical evaluation of several univariate methods that adjust for size variation in morphometric data. Can J Zool 63:1429–1439

Royle NJ, Surai PF, Hartley IR (2001) Maternally derived androgens and antioxidants in bird eggs: complimentary but opposing effects? Behav Ecol 12:381–385

Rutstein AN, Gilbert L, Slater PJB, Graves JA (2005) Sex-specific patterns of yolk androgen allocation depend on maternal diet in the zebra finch. Behav Ecol 16:62–69

Saino N, Romano M, Ferrari R, Martinelli R, Møller AP (2003) Maternal antibodies but not carotenoids in barn swallow eggs covary with embryo sex. J Evol Biol 16:516

Schwabl H (1993) Yolk is a source of maternal testosterone for developing birds. Proc Natl Acad Sci U S A 90:11446–11450

Schwabl H (1996a) Environment modifies the testosterone levels of a female bird and its eggs. J Exp Zool 276:157–163

Schwabl H (1996b) Maternal testosterone in the avian egg enhances postnatal growth. Comp Biochem Physiol A 114:271–276

Schwabl H (1997) The contents of maternal testosterone in the house sparrow *Passer dimesticus* eggs vary with breeding conditions. Naturwissenschaften 1984:1–3

Sheldon BC (2000) Differential allocation: tests, mechanisms and implications. Trends Ecol Evol 15:397–402

Sockman KW, Schwabl H (2000) Yolk androgens reduce offspring survival. Proc R Soc Lond Ser B 267:1451–1456

Sockman KW, Schwabl H, Sharp PJ (2001) Regulation of yolk-androgen concentrations by plasma prolactin in the American kestrel. Horm Behav 40:462–471

Sokal R, Rohlf J (1995) Biometry, 3rd edn. Freeman, New York, NY

Surai PF, Speake BK, Wood NAR, Blount JD, Bortolotti GR, Sparks NHC (2001) Carotenoid discrimination by the avian embryo: a lesson from wild birds. Comp Biochem Physiol B 128(4):743–750

Tanvez A, Béguin N, Chastel O, Lacroix A, Leboucher G (2004) Sexually attractive phrases increase yolk androgens deposition in canaries (*Serinus canaria*). Gen Comp Endocrinol 138:113–120

Whittingham L, Schwabl H (2001) Maternal testosterone in tree swallow eggs varies with female aggression. Anim Behav 62