

# Forum

## Yolk androgen deposition as a female tactic to manipulate paternal contribution

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The differential allocation hypothesis (DAH) predicts that females should invest more in reproduction when mated with an attractive male (Burley 1988; Sheldon 2000); and, according to this hypothesis, females mated with attractive males frequently invest more resources in eggs (Cunningham and Russell 2000; Saino et al. 2002; Rutstein et al. 2004). In zebra finches (*Taeniopygia guttata*) and barn swallows (*Hirundo rustica*), females deposit more androgens (testosterone, 5 $\alpha$ -dihydrotestosterone, androstenedione) in eggs when mated with attractive males (Gil et al. 1999; Gil, Ninni, et al. 2006). Similarly, canary (*Serinus canaria*) females deposit more androgens when exposed to attractive male songs (Gil et al. 2004). Because some studies have shown that yolk androgens improve nestling growth and survival (Schwabl 1993; Eising et al. 2001; Pilz et al. 2004), it has been suggested that this pattern is consistent with the DAH. However, other studies have shown that yolk androgens may have detrimental effects on nestling growth and survival, especially reducing the immune capacity (Sockman and Schwabl 2000; Gil 2003; Groothuis, Eising, et al. 2005; Müller, Groothuis, Kasprzik, et al. 2005). Therefore, it is unclear whether this pattern is consistent with the DAH.

On the other hand, recent studies (Michl et al. 2005; Navara et al. 2006a) have shown that females of other species (collared flycatcher, *Ficedula albicollis*, and house finches, *Carpodacus mexicanus*) deposit more androgens when mated with unattractive males, thereby contradicting the DAH. These studies suggested that yolk androgen deposition may act as a compensatory strategy (the compensatory strategy hypothesis, CSH) employed by females mated with males of low parental quality. The CSH might also explain results found in the barn swallow (Gil, Ninni, et al. 2006) and the zebra finch (von Engelhardt et al. 2006), as in these species attractive males invest less in parental care. However, yolk androgens may be detrimental for nestlings in some situations (Sockman and Schwabl 2000; Groothuis, Eising, et al. 2005; Müller, Groothuis, Kasprzik, et al. 2005), and thus, this hypothesis hardly explains such behavior, as yolk androgens do not always compensate for low parental care.

It has also been proposed that yolk androgen deposition may act as a female mechanism to manipulate paternal contribution (here, the manipulating androgens hypothesis, MAH) (Michl et al. 2005; also Gil, Ninni, et al. 2006; von Engelhardt et al. 2006). Yolk androgens increase nestling begging behavior in some species (Schwabl 1996; Eising and Groothuis 2003; von Engelhardt et al. 2006), and begging may increase male contribution to the feeding rate more than the female contribution (Ottosson et al. 1997). Therefore, it may be feasible that, by increasing androgen deposition, females manipulate male contribution throughout nestling begging. The premises for this hypothesis are as follows:

1. Female birds may strategically vary the quantity of androgens that they deposit in egg yolk. Empirical evidence suggests that this is probable. In an experiment with the lesser black-backed gull (*Larus fuscus*), food-supplemented females had more androgens in plasma, but deposited less androgens in eggs, than control females (Verboven et al. 2003). Similarly, plasma androgens in the mothers were unrelated with yolk androgens in the house sparrow (*Passer domesticus*) and the eastern bluebird (*Sialia sialis*) (Mazuc, Bonneaud, et al. 2003; Navara et al. 2006). These findings strongly suggest that androgen deposition is not simply the result of a passive transmission from female plasma.
  2. Yolk androgens increase the begging behavior of nestlings. Empirical studies suggest that yolk androgens favor begging in canaries, black-headed gulls (*Larus ridibundus*), and female zebra finches (Schwabl 1996; Eising and Groothuis 2003; von Engelhardt et al. 2006). However, starling (*Sturnus vulgaris*), yellow-legged gull (*Larus michahellis*), and male zebra finch chicks from eggs supplemented with testosterone do not beg more fiercely (Pilz et al. 2004; Boncoraglio et al. 2006; von Engelhardt et al. 2006). Therefore, the effect of yolk androgens on nestling begging cannot be generalized, but the MAH is possible only in species where yolk androgens affect begging.
  3. Females cannot maximize the androgen deposition because their production is costly for female or yolk androgens are costly for nestlings. Although evidence for production costs are unclear (Gilbert et al. 2005; Gil, Marzal, et al. 2006), there is clear support for the contention that androgens imply a trade-off between growth and immune capacity in nestlings and excessive yolk androgens may be detrimental for nestlings (Sockman and Schwabl 2000; Groothuis, Eising, et al. 2005; Müller, Groothuis, Kasprzik, et al. 2005; Navara et al. 2005). Some studies have shown negative effects of yolk androgens on male chicks only (Müller, Groothuis, Eising, and Dijkstra. 2005; Saino et al. 2006). Other costs are also possible (Gil 2003).
  4. Male parents are more responsive to the begging behavior of nestlings than are female parents. The parental feeding rate is determined, in part, by the begging behavior of the brood (Kilner and Johnstone 1997). In many bird species, males contribute less than females to the feeding rate (e.g., Moreno-Rueda 2004); therefore, males have a broader scope to respond to the brood begging by increasing their feeding rate than females have. For the hypothesis to be feasible, males should respond more strongly than females to the chick begging. This result has been shown, for example, in the superb fairy-wren (*Malurus cyaneus*) and the pied flycatcher (*Ficedula hypoleuca*), where males, but not females, increased feeding rate when exposed to playbacks of begging (Ottosson et al. 1997; MacGregor and Cockburn 2002). Similarly, in the great tit (*Parus major*), males, but not females, increased the feeding rate in response to an elevated nestling begging provoked by ectoparasites (Christe et al. 1996).
- Yolk androgens appear to modulate the relative allocation of resources delivered to the immune system and to the growth of nestlings (Navara et al. 2006b). On these premises,

when females mate with low-parental quality male, they may use androgen deposition to alter the investment in begging by the chicks, increasing male feeding rate, at a cost of nestling immune suppression. This strategy would benefit the female when this cost is balanced by an increase in paternal feeding rate, which would increase the consumption of antioxidants by nestlings, improving the immune function (Blount et al. 2003). When females mate with high-parental quality males, an increase in feeding rate would be probably lower, as these males already feed at high rates. This could explain why some studies have failed to find a positive effect of androgens on nestling growth.

#### **EVIDENCES FOR DAH AND MAH: ANDROGEN DEPOSITION ACCORDING TO MALE ATTRACTIVENESS**

Females seek direct benefits (e.g., parental care) or indirect benefits ("good" genes) from their mates (Andersson 1994). However, the relationship between male attractiveness and male parental quality vary greatly among species (Møller and Thornhill 1998). For the MAH to be correct, females should invest more androgens in eggs when mated with males with low parental quality, attractive in some species and unattractive in others. Moreover, in species in which this occurs, yolk androgens should improve nestling begging behavior and begging should affect males more than females. However, for the DAH to be correct, females should invest in yolk androgens when mated with attractive males, independent of their parental quality. The limited results in the literature are consistent with the scenario for the MAH.

#### **Females investing more androgens when paired with attractive males**

Both zebra finch and barn swallow females invest more androgens in eggs when mated with attractive males (Gil et al. 1999; Gil, Ninni, et al. 2006), which invest less in parental care (Burley 1988; de Lope and Møller 1993). Moreover, yolk androgens increase begging at least in female chicks in the zebra finch (von Engelhardt et al. 2006). For the barn swallow, Saino et al. (2006) failed to find any effect of yolk androgens on nestling begging, but they measured begging in 10-day-old nestlings, and perhaps the effect of yolk androgens was lost at this age. Canary females also deposit more androgens in eggs when exposed to attractive male songs (Gil et al. 2004), and yolk androgens increase begging in this species (Schwabl 1996), but it is not known whether males with more attractive songs invest less in parental care, as predicted by the MAH. In general, results for these species are consistent with both the DAH and the MAH.

#### **Females not investing more androgens when paired with attractive males**

Female collared flycatcher seems not to deposit more androgens when paired with attractive males but do so when mated with 1-year-old males (Michl et al. 2005). Frequently, young males are less willing to invest in parental care (Clutton-Brock 1991; McNamara and Houston 1996). In the similar species the pied flycatcher, androgens increase begging in nestlings (Goodship and Buchanan 2006) and males are more responsive to begging than are females (Ottoosson et al. 1997), all these results being strongly consistent with the MAH. Female house finches deposit more androgens when paired with unattractive (duller colored) males (Navara et al. 2006a). In this species, attractive (colorful) males are better parents (Hill 1991); therefore, the result of Navara et al. (2006a) also sup-

ports the MAH, but not the DAH. However, it is unknown whether yolk androgens increase nestling begging in this species. Lastly, female house sparrows do not deposit more androgens in eggs sired by attractive males (with a bigger badge; Mazuc, Chastel, and Sorci 2003). This is also according to the MAH, as the relationship between male badge size and paternal care is complex in this species. For example, in an Austrian population, males with midsize badge feed more than males with a small or a big badge (Václav and Hoi 2002).

All together, these results are inconsistent with the DAH but consistent with the MAH. Unfortunately, a crucial prediction of the MAH is that males should respond more strongly to begging than females do, and there is no test available concerning this for the 6 species studied.

#### **FINAL CONSIDERATIONS**

Sexual conflict is widespread in nature, and it prompts each member of the pair to manipulate the other into increasing parental investment (Chapman et al. 2003; Houston et al. 2005). Yolk androgen deposition is directly under maternal control, and androgens increase nestling begging in some species, which in turn may increase paternal contribution of feeding with a lower effect on mother's behavior. Therefore, female birds may use androgen deposition as a strategy to manipulate males. Because androgens are immune suppressive for nestlings, this strategy should pay more for females when they are mated with low-parental quality males, which have a broader scope to increase the feeding rate. As the relationship between male parental quality and male attractiveness varies across species, the response of females to male attractiveness also should vary. Findings reported in literature are strongly consistent with this hypothesis (MAH), but not with the DAH, which predicts that females should invest more androgens when paired with attractive males, this not always being supported (Mazuc, Chastel, and Sorci 2003; Michl et al. 2005; Navara et al. 2006a). Of course, the MAH does not preclude other functions of yolk androgens, for example, in the regulation of brood asymmetries (Schwabl et al. 1997) or in the modification of future offspring phenotype (Dufty et al. 2002; Groothuis, Müller, et al. 2005).

If this hypothesis is demonstrated to be correct, it might have noteworthy implications in the evolution of biparental care and nestling begging behavior, as well as in the resolution of the parent-offspring conflict, and an arms race between males and females is probable. Moreover, the MAH could explain why female lesser black-backed gulls deposit less androgens in eggs when food is abundant (Verboven et al. 2003). When food is abundant, the aid of males is less necessary (Dunn and Robertson 1992), and thus, females would not need to manipulate males, saving the costs of androgens.

In conclusion, the MAH satisfactorily explains why female birds choose to vary or not vary yolk androgen deposition according to male attractiveness, a question not explained by the DAH. However, data come only from 6 species, and future studies, especially testing whether males are more responsiveness to begging than females in these species, may shed more light on the function of yolk androgens in the social relations in bird families.

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