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No evidence for differential maternal allocation to offspring in the house sparrow (*Passer domesticus*)

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We tested the differential maternal allocation hypothesis in a population of house sparrows. We experimentally altered the attractiveness of males by treating them with implants filled with crystalline testosterone (T) or left empty (C). We subsequently monitored maternal investment as a function of male hormonal treatment and the size of the black patch of feathers on the throat (i.e., the badge), a sexually selected trait. The differential allocation hypothesis predicts that females should adjust their investment with respect to the benefits they receive by mating with an attractive male. Given that both circulating levels of T and badge size are condition-dependent traits, we expected that females mated with T males and/or with large-badged males should invest more into current reproduction. Contrary to this prediction, we found no evidence that suggested differential maternal allocation in this population of house sparrows. Female investment in yolk T, yolk mass, clutch size, chick brooding, and feeding was not affected by male hormonal treatment or by male badge size. As expected, T males invested less into chick brooding and feeding. More surprisingly, females did not compensate the reduced paternal contribution to chick feeding. As a consequence, the breeding success of T pairs was largely reduced compared with that of C pairs. The absence of differential allocation in a system in which it could have an adaptive role raises the question about the possible constraints or overriding factors operating on patterns of reproductive investment in this species. *Key words:* badge size, reproductive investment, sexual selection, testosterone. *[Behav Ecol 14:340–346 (2003)]*

Sexual selection arises as a result of the variance in mating success being nonrandomly related to display characters of the chosen sex (Andersson, 1994). Females, usually being the choosy sex, could benefit from mating with males harboring exaggerated ornaments for two reasons. The direct benefit hypothesis suggests that females mated with the most attractive males will acquire direct benefits such as nest sites, good territories, nuptial gifts, or increased male parental care, while avoiding contagious diseases or parasites (Andersson, 1994). The good genes hypothesis posits that only males of high genetic quality will be able to develop and maintain highly exaggerated sexual displays. In this case, females benefit indirectly from their mate choice when mating with the most attractive males, as such males will transmit genes for sexual attractiveness (Fisher, 1930) or viability (Møller and Alatalo, 1999) to their progeny.

However, the evolution of female preference does not only have profound repercussions for the evolution of male sexual displays. Theory on the evolution of life-history traits predicts that reproductive investment should depend on the potential gain in terms of fitness benefits (Stearns, 1992). Thus, if offspring fathered by attractive males are likely to be high-quality individuals, females are expected to show high reproductive investment when mated with attractive males. This hypothesis has been called the differential allocation hypothesis (DAH), and it predicts that females that invest in reproduction according to the attractiveness of their mate may gain a selective advantage (Burley, 1986). Observational and experimental evidence provides support for the DAH (for review, see Sheldon, 2000). Most of the tests concerning differential investment in reproduction have focused on obvious components of parental investment, such as clutch size (Petrie and Williams, 1993) and feeding rates of dependent young (de Lope and Møller, 1993). Recent studies suggest that other forms of differential allocation could also occur. For example, female mallard ducks laid larger eggs when mated with the most attractive males, and variance in egg size was correlated with hatchling body size (Cunningham and Russell, 2000). In addition, another study found that females could modulate their hormonal investment in the eggs according to male attractiveness (Gil et al., 1999). Maternal androgens transferred to the egg have been shown to affect several traits associated with offspring quality, such as begging behavior and growth rate (Eising et al., 2001; Lipar and Ketterson, 2000; Schwabl, 1996b; also see Sockman and Schwabl, 2000).

Only experimental manipulations allow one to discriminate between the DAH and alternative explanations. A study system is required in which either mate attractiveness can be manipulated (Burley, 1988; de Lope and Møller, 1993) or mates can be assigned experimentally (Reyer et al., 1999). Furthermore, behavioral characters, as well as morphological ones, may be important in assessing mate quality. It may be very difficult to determine which of these characters are used in the decision to differentially allocate resources, as they often share the same physiological mechanisms. For example, testosterone (T) affects the expression of sexual behaviors—such as song rate (Enstrom et al., 1997; Stoehr and Hill, 2000), mate guarding (Møller, 1987; Moore, 1984; Saino and Møller, 1995), or territorial defense (Gwinner and Gwinner, 1994; Wingfield, 1984; Wingfield et al., 1987)—and the development of many secondary sexual characters, including plumage (Buchanan et al., 2001; Evans et al., 2000; Gonzalez et al., 2001; Kimball and Ligon, 1999).

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Table 1

Principal component analysis (PCA) of the four morphological measurements (wing length, tarsus length, head-bill length, sternum length) for male and female house sparrows

Sex	PCA axis	Eigen values	Proportion of variance explained
Males ($n = 74$)	Axis 1	1.73	0.433
	Axis 2	0.89	0.222
	Axis 3	0.73	0.183
	Axis 4	0.65	0.162
Females ($n = 52$)	Axis 1	1.82	0.454
	Axis 2	0.97	0.243
	Axis 3	0.73	0.182
	Axis 4	0.48	0.121

In the present study, we wished to investigate whether male ornaments, or male sexual behaviors that share the same hormonal basis, are used as cues for differential maternal allocation into reproduction. The study was conducted on house sparrows (*Passer domesticus*) because previous studies have shown that (1) a male plumage ornament (the patch of black feathers on the throat and the chest, hereafter called a badge) is under intrasexual and intersexual selection (Griffith et al., 1999a,b; Møller, 1988; Veiga, 1993); (2) the size of the badge and the expression of sexual behaviors are correlated and controlled by androgens (Buchanan et al., 2001, Evans et al., 2000; Gonzalez et al., 2001); and (3) unknown environmental effects have been evoked as a major cause of resemblance between fathers and sons with respect to the sexually selected badge size (Griffith et al., 1999a).

To disrupt any natural covariance between badge size and the expression of sexual behaviors, we treated male sparrows with subcutaneous T implants and looked at the effect of treatment and badge size on female reproductive investment. We assessed female investment in terms of egg "quality" (hormonal and energetic investment in the eggs), quantity (clutch size), and nestling rearing (brooding and feeding). As the experimental manipulation of male attractiveness was performed before pair-bond formation, we also checked whether there was assortative mating with respect to individual quality.

METHODS

Manipulation of T levels in a naturally breeding population

The experiment was conducted during the breeding season of 2000 (March–June) in a natural population of house sparrows in the Centre d'Etudes Biologiques de Chizé (CEBC), Deux Sèvres (46°09′ N, 0°24′ W), France. In March, 74 males and 52 females were caught by using mist nests before pair formation.

Birds were ringed with a numbered aluminium band along with a unique combination of color bands. For each individual, we measured wing length (to nearest 1 mm), tarsus length (to nearest 0.1 mm), sternum length (to nearest 0.1 mm), head-bill length (to nearest 0.1 mm), and body mass (to nearest 0.1 g). For males, we also measured the maximum length and width of the badge by flattening it against a ruler (to nearest 1 mm). Badge area (hereafter, badge size) was calculated from the regression equation: badge area (mm^2) = 166.67 + 0.45 × badge length (mm) × badge breadth (mm) (Møller, 1987). To compute a body condition index, we performed a principal component analysis (PCA) on the four morphological measurements of the 74 males and 52 females (Table 1). For both sexes, body mass was significantly correlated only with the first axis of the PCA (PC1: males, $r = .443$, $p < .0001$; females, $r = .675$, $p < .0001$). The residuals from these regressions were used as an index of body condition. Badge size was not related to any PCA axis (axis 1: $r = .16$, $p = .17$; axis 2: $r = .03$, $p = .82$; axis 3: $r = -.04$, $p = .74$; axis 4: $r = -.18$, $p = .12$). Similarly, it was not significantly correlated with body condition ($r = .17$, $p = .15$).

Males were randomly assigned to two groups. One group of males ($n = 36$) was given a subcutaneous implant of T. The second group ($n = 38$) was given an empty implant (C). All implants were 20-mm lengths of Silastic tubing (inner diameter, 1.47 mm; outer diameter, 1.96 mm; Dow Corning) packed with crystalline T (Sigma Chemical) or left empty (for the choice of implant size in house sparrows, see Hegner and Wingfield, 1987). The implants were inserted under the skin between the shoulder and the neck. Twelve males (7 C and 5 T) were recaptured after completion of the first breeding attempt, and T males had empty implants, indicating that they had released their contents. As males were randomly assigned to either T or C groups, there was no difference in badge size between treatments (mean ± SE: T males, 364.81 ± 7.55 mm^2; C males, 366.30 ± 6.11 mm^2; one-way ANOVA: $F_{1,72} = 0.02$, $p = .881$).

Egg collection and behavioral observations

Only first reproductive attempts were considered here. Nest-boxes were checked daily for egg laying. We marked the first egg in 32 clutches fathered by testosterone ($n = 20$) and control ($n = 12$) males. The eggs were then collected before the start of incubation. We also collected nine complete clutches of unmanipulated males with known laying order to assess whether interclutch variation in testosterone content exceeded intraclutch variation. Eggs were stored at −20°C until androgen analyses.

Behavioral observations lasted 2 h between 0800 and 1200 h. Time spent brooding and feeding rates were assessed when nestlings were 5 (T = 13 pairs, C = 11 pairs) and 10 days old (T = 10 pairs, C = 10 pairs). Parents were assumed to be brooding when they stayed for longer than 30 s in the nest-box (maximum time required to transfer the food and to remove fecal sacs; Chastel and Kersten, 2002). However, brooding activity was likely finished when nestlings were 10 days old, as chicks are able to thermoregulate at this stage. Thus, we only considered brooding during the early stage of rearing in the statistical analyses. Feeding rates of adults were recorded by measuring the number of visits per hour and per nestling (the number of nestlings was checked at the end of each observation).

Testosterone assays in eggs

Yolk concentrations of testosterone were determined by radioimmunoassays at the CEBC (CNRS). Within 3 months of collection, frozen eggs were thawed, and the yolk and albumen were separated. Each yolk was weighed, and 25 mg was homogenized in 1 ml of distilled water by vortexing, with glass beads. Testosterone extraction consisted of adding 3 ml of diethyl ether, vortexing for 1 min, and centrifuging for 5 min (4°C, 2000 rpm). The ether phase was decanted after snap-freezing the tube in an alcohol bath at −30°C, and evaporated under a stream of nitrogen. The dried extract was redissolved in 1 ml of phosphate buffer. Tritiated testosterone (1000 cpm) (Amersham Pharmacia Biotech Europe, Orsay, France) was added to the samples for the calculation of extraction recovery. This extraction technique is a standard method used for plasma samples (Mauget et al., 1994), and is

Table 2

ANCOVA with yolk testosterone concentration of the first laid egg as the dependent variable, hormonal treatment as a factor, and badge size, laying date, and *z*-transformed squared laying date as covariates

Dependent variable	Source	$F_{1,23}$	Parameter estimate (± SE)	p
Yolk testosterone (log 10 of pg/mg)	Hormonal treatment	0.09	−0.054 (±0.185)	.773
	Badge size	3.63	−0.005 (±0.003)	.070
	Laying date	8.23	0.044 (±0.015)	.008
	Laying date squared	8.07	−0.003 (±0.001)	.009

Interactions were all nonsignificant ($p > .1$).

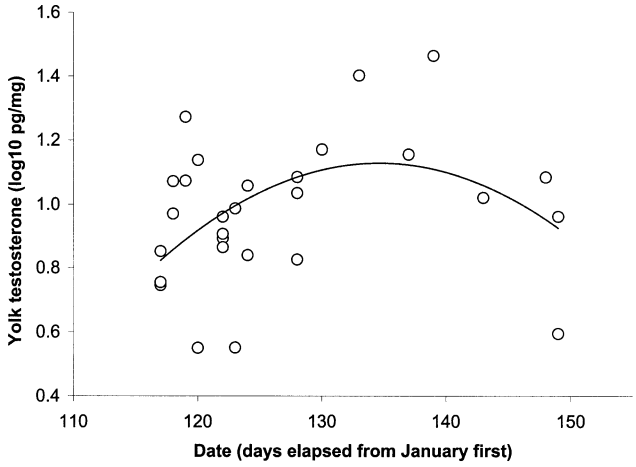

Figure 1
Quadratic relationship between yolk testosterone and laying date in house sparrows.

simpler and faster that Schwabl's standard extraction for avian egg yolks (Schwabl, 1993). The Schwabl method is used for extraction of whole yolk. However, as we only required extracting a small portion of the yolk to assay the concentration, the more laborious Schwabl method was not necessary. The determination of testosterone concentration follows standard radioimmunoassay techniques. Testosterone was quantified by using duplicates in a single assay. Duplicate aliquots of the extracts, redissolved in 0.01 M phosphate-buffered saline (ph 7.4) containing 0.1% bovine albumin (PBS-BSA), were incubated overnight at 4°C with approximately 6000 cpm of ^{3}H-T and a specific antibody. The antibody was kindly provided by Dr. G. Picaper (Médecine Nucléaire, CHU, La Source, France). Bound and free fractions were separated by adsorption with dextran-coated charcoal and centrifuged. Aliquots of the bound fractions were counted with a Packard 1600 liquid scintillator counter. Recovery values of all samples were greater than 90%. The intraassay variation was 7% for the first egg samples and 9% for the complete clutch samples.

Statistical analyses

The effect of hormonal treatment and badge size on female and male investment in reproduction was assessed by using ANCOVA models. In each model, we included body condition, laying date, and *z*-transformed squared laying date as covariates. The squared term was added to account for any nonlinear relationship between date and components of female investment in reproduction. However, as body condition was missing for a few unmarked females, we also ran models without female body condition. For all analyses, we started with the full model with all interactions and dropped in a step-by-step fashion all nonsignificant terms (significance level for model elimination at $p > .05$). Hormonal treatment and male badge size were, however, always left in the final model. Normality and homoscedasticity of residuals were checked for each model. Differences in sample sizes among statistical analyses reflect missing values. All analyses were performed with SAS release 6.12 (SAS Institute, 1996).

RESULTS

Assortative mating

We found no evidence suggesting assortative mating, at least with respect to the descriptors of individual quality we measured. Female body condition was not correlated with male body condition (Pearson correlation coefficient: $r = .164$, $p = .433$, $n = 25$) or with male badge size ($r = -.083$, $p = .694$, $n = 25$). Likewise, female body condition did not differ between male hormonal groups (one-way ANOVA: $F_{1,23} = 2.77$, $p = .109$). Similar results were obtained by using PCA axis 1 and axis 2, and body mass instead of body condition (data not shown).

Investment in eggs

Females mated with T or with large-badged males did not lay more eggs than did females mated with C or small-badged males (ANCOVA: hormonal treatment, $F_{1,29} = 0.44$, $p = .515$; badge size, $F_{1,29} = 0.89$, $p = .353$). Yolk mass of the first egg did not differ between hormonal treatments, and it did not correlate with male badge size (ANCOVA: hormonal treatment, $F_{1,25} = 1.12$, $p = .3$; badge size, $F_{1,25} = 0.67$, $p = .422$). Yolk mass was also not correlated with clutch size, suggesting that females did not trade egg number against egg volume ($r = .051$, $p = .797$, $n = 28$). Similar to yolk mass, females did not invest more testosterone in eggs when mated with T or large-badged males (Table 2). However, both laying date and squared laying date explained a significant fraction of the variation in yolk testosterone (Table 2). Early and late laid eggs contained significantly less testosterone than did eggs laid in the middle of the breeding season (Figure 1).

The validity of using only first laid eggs for analyses was confirmed by the analysis of nine complete clutches with known laying order. Both yolk testosterone concentration and yolk mass were significantly less variable within clutches than among clutches (one-way ANOVA: testosterone concentration, $F_{8,35} = 5.79$, $p < .0001$; yolk mass, $F_{8,32} = 7.37$, $p < .0001$). Female identity explained 57% and 65% of variation for testosterone concentration and yolk mass, respectively. Laying order also significantly affected the amount of yolk testosterone and yolk mass (nested ANCOVA: yolk T, $F_{9,26} = 3.21$, $p = .0096$; yolk mass, $F_{9,23} = 7.37$, $p = .0398$). Testosterone concentrations in the yolk increased with the laying order (Figure 2A), whereas yolk mass decreased with laying order (Figure 2B).

Investment in nestlings

Female investment in brooding was not affected by the hormonal treatment of their mate or by male badge size; brooding was, however, negatively correlated with laying date

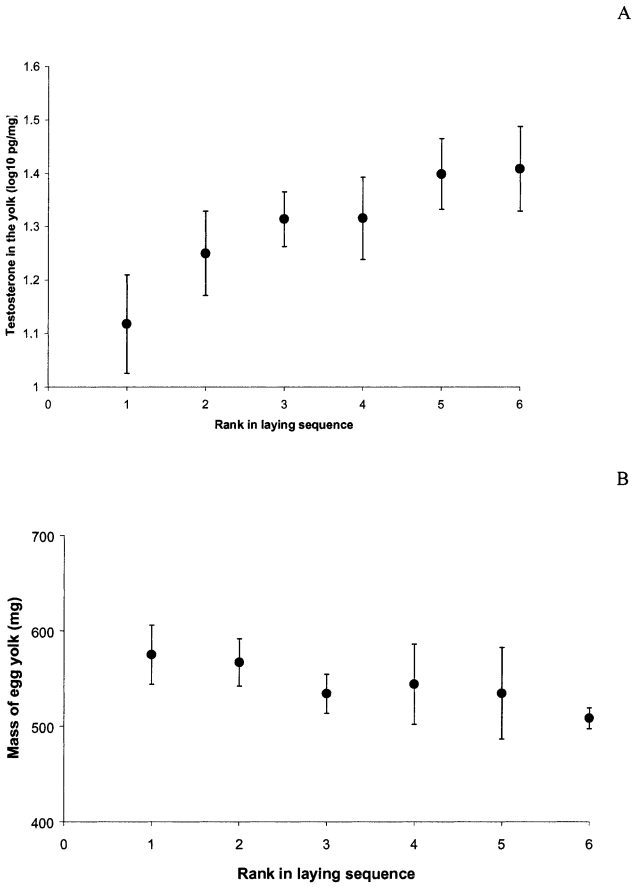

Figure 2
Relationship between laying order and testosterone concentration in the yolk (A) and yolk mass (B).

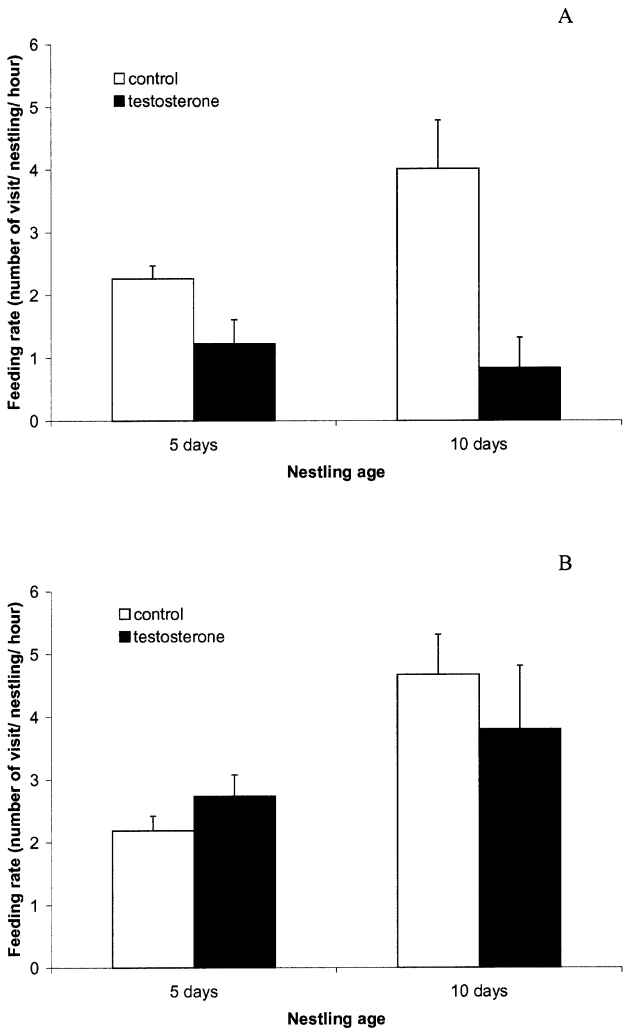

Figure 3
Effect of hormone implants on the feeding rate of male (A) and female (B) house sparrows when nestlings were 5 and 10 days old (± SE).

(ANCOVA: hormonal treatment, $F_{1,20} = 0.03$, $p = .871$; badge size, $F_{1,20} = 0.01$, $p = .961$; laying date, $F_{1,20} = 12.29$, $p = .002$). Males that were implanted with testosterone spent less time brooding than did control males (mean ± SE: T males, 151.6 ± 83.3 s/h, C males, 556.6 ± 134.2 s/h), whereas badge size was not significantly correlated with the brooding activity of males (ANCOVA: hormonal treatment, $F_{1,21} = 5.05$, $p = .036$; badge size, $F_{1,21} = 0.53$, $p = .476$). Male and female brooding activities were not significantly correlated ($r = .123$, $p = .568$, $n = 24$).

Treatment with testosterone entailed a significant decrease in the male's contribution to the feeding of 5-day-old nestlings (ANCOVA: hormonal treatment, $F_{1,21} = 4.76$, $p = .041$, badge size, $F_{1,21} = 1.70$, $p = .206$) (Figure 3). This difference was even more pronounced when nestlings were 10 days old (ANCOVA: hormonal treatment, $F_{1,17} = 11.23$, $p = .004$, badge size, $F_{1,17} = 3.78$, $p = .069$) (Figure 3). At both ages, badge size was not a good predictor of male feeding effort. Female feeding rate was not correlated with the male's hormonal treatment or badge size for either age (5 days old, ANCOVA: hormonal treatment, $F_{1,21} = 1.36$, $p = .256$, badge size, $F_{1,21} = 0.22$, $p = .647$; 10 days old, ANCOVA: hormonal treatment, $F_{1,17} = 0.97$, $p = .339$, badge size, $F_{1,17} = 0.76$, $p = .394$) (Figure 3). Male and female feeding rates were not correlated when nestlings were 5 days old ($r = -.159$, $p = .458$, $n = 24$) (Figure 4A). Feeding rates were positively correlated at age 10 ($r = .452$, $p = .045$, $n = 20$), although this was essentially owing to two C pairs (Figure 4B).

Reproductive success

After first egg removal, 69% of the remaining eggs hatched. Two terms were marginally significantly correlated with hatchling number, the concentration of testosterone in the yolk of first laid egg, and the interaction between hormonal treatment and badge size (ANCOVA: hormonal treatment, $F_{1,23} = 3.92$, $p = .060$; badge size, $F_{1,23} = 0.01$, $p = .964$; yolk T, $F_{1,23} = 4.32$, $p = .049$; hormonal treatment × badge size, $F_{1,23} = 4.32$, $p = .049$). Yolk testosterone was negatively correlated with hatchling number ($r = -.392$, $p = .039$, $n = 28$) (Figure 5).

T clutches produced on average three times fewer fledglings than did C clutches (mean ± SE: T clutches, 0.70 ± 0.24, $n = 20$; C clutches, 2.19 ± 0.40, $n = 11$), whereas badge size was not correlated with the number of fledglings (ANCOVA: hormonal treatment, $F_{1,28} = 10.93$, $p = .003$, badge size, $F_{1,28} = 0.01$, $p = .907$).

DISCUSSION

In agreement with previous results (Hegner and Wingfield, 1987), the manipulation of circulating levels of testosterone

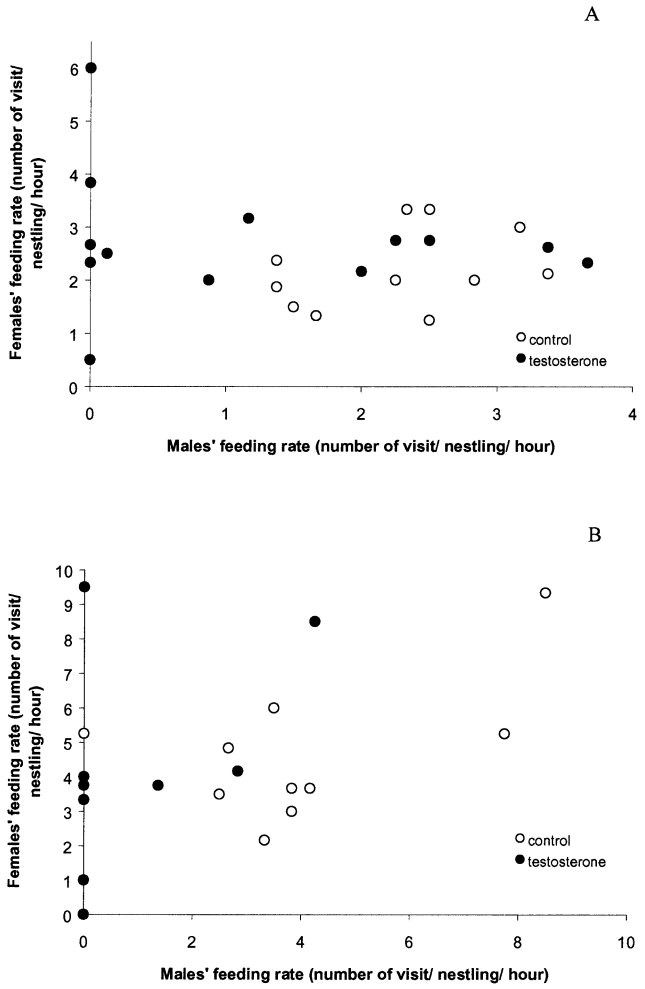

Figure 4
Correlation between male and female feeding rate in house sparrows when nestlings were 5 days old (A) and 10 days old (B).

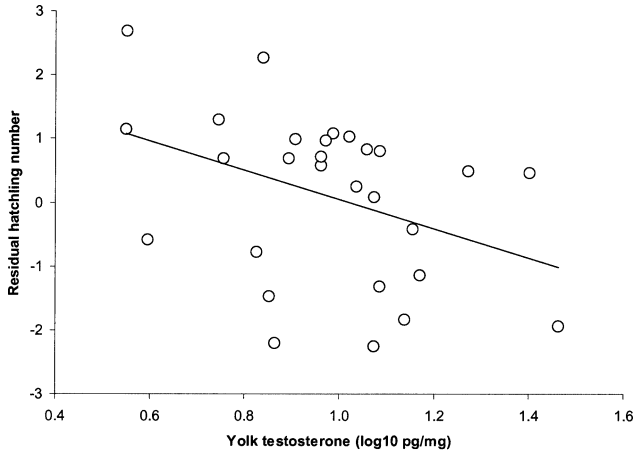

Figure 5
Relationship between yolk testosterone concentration in the first egg of the clutch and residual hatchling number (residuals from the ANCOVA model with hormonal treatment, badge size, and their interaction).

clearly affected several components of male parental behavior in house sparrows. T males showed a lower contribution to brooding and feeding activities than did C males. Surprisingly, however, females did not seem to compensate for the decrease in male investment. Furthermore, badge size and treatment were not related to any component of female reproductive investment, both before (egg quality and quantity) and after egg laying (chick brooding and feeding). Consequently, hormonal treatment resulted in a drop in the reproductive output of T pairs, whereas badge size did not affect the outcome of reproduction. Overall, these results offer no support for the female DAH. Interestingly, we observed a negative relationship between the testosterone concentration in the first egg and the hatching probability of remaining eggs. In a context in which effects of yolk testosterone on embryonic development remain unclear (Eising et al., 2001; Sockman and Schwabl, 2000), this result opens the question of whether variation of testosterone levels in eggs is adaptive in this species.

Although we did not assess testosterone levels after the insertion of implants, several lines of evidence let us think that the manipulation was effective. In particular, we used same-sized implants as Hegner and Wingfield (1987). They found that 20-mm-long implants raised mean testosterone level of male house sparrows to 10. 6 ng/ml (± 0.5 SD) compared with 3.7 ng/ml (± 0.3 SD) for control males. The range of behavioral modifications observed in our study, as well as the recapture of testosterone males with empty implants, suggest that we successfully increased testosterone levels.

One possible caveat of this study is that the manipulation of male attractiveness occurred before pair-bond formation. Usually, experimental tests of the DAH have been performed either by manipulating male traits after pair-bond formation or by assigning males of different attractiveness to females under controlled conditions (for review, see Sheldon, 2000). Studies in natural populations of birds have mainly focused on the manipulation of male traits after mating (see de Lope and Møller, 1993). Although this design has the advantage of controlling for the effect of assortative mating with respect to individual quality, it can produce unnatural conditions, particularly for male morphological traits that are static and are not expected to vary between mate choice and egg laying. Our decision to manipulate male behavior before pair-formation could be criticized because it could have led to assortative-mating, high-quality females (likely to invest more in reproduction) having preferential access to large-badged and/or T males. However, we found no evidence suggesting assortative mating: Females in good body condition were not paired with large-badged or T males, and laying dates (another measure of individual quality) did not differ between hormonal treatments or with badge size (Mazuc J, unpublished data). Furthermore, female body condition was always controlled for in statistical analyses.

Experimental designs that handicap males and therefore reduce male feeding effort have been criticized on the basis that females could simply compensate for the decrease in paternal contribution (Witte, 1995). Given that testosterone manipulation entails a decrease in male reproductive investment, an increase in female parental effort could reflect compensation rather than differential investment based on the perceived quality of the male. However, females paired with T males did not show increased effort during nestling rearing.

This last result might appear surprising in the light of previous theoretical and empirical work. In species with biparental care, theoretical models predict that partial compensation should be the evolutionary stable strategy; parents are then expected to respond to reduction in care by their mates by increasing their own effort (Houston and Davies, 1985). Experimental work has provided supportive evidence for this

prediction. Female starlings (*Sturnus vulgaris*) mated with handicapped males (weights attached to their tails) showed an increased feeding rate of nestlings that partially compensated the reduced paternal contribution to feeding (Wright and Cuthill, 1989). Similarly, in the house sparrow, reduced feeding rate of T-implanted males resulted in partial compensation of females (Hegner and Wingfield, 1987). Recently, however, these results have been challenged by other findings that failed to show female compensation to reduced paternal care. Male yellow-legged gulls (*Larus cachinnans*) implanted with testosterone were found to spend less time incubating the clutch compared with that of control males. However, females mated with T males did not spend more time incubating than did C females (Alonso-Alvarez 2001). Similarly, male super fairy-wrens (*Malurus cyaneus*) exhibited a dramatic suppression of nestling provisioning when treated with testosterone, but females did not compensate at all for their mate's underperformance in feeding (Peters et al. 2002). To know whether these discrepancies reflect differences in cues used by females to assess paternal effort or differences in local environmental factors likely to affect costs and benefits of current versus future breeding attempts, definitely requires further experimental and theoretical work.

Differential allocation can be seen as a particular form of maternal effect, and as such, it can have strong evolutionary repercussions on the rate and direction of the evolution of secondary sexual traits (Qvarnström and Price, 2001). This idea is based on the findings that the expression of sexually selected traits is affected by the environmental condition experienced by offspring (Hunt and Simmons, 2000). If females invest more in offspring fathered by attractive males, their sons could inherit the paternal attractiveness by means of maternal allocation, resulting in a resemblance between father and sons independent of shared genes. In agreement with this view, a recent study showed that the size of a sexually selected trait, the badge of black feathers, was environmentally inherited in a population of house sparrows (Griffith et al., 1999a). Resemblance between foster fathers and sons could arise (1) if females mated with large-badged males allocate more to nestling feeding (differential maternal allocation), (2) if large-badged males invest more into nestling feeding (direct benefit of mate choice), and (3) if condition experienced in the nest affects the size of badge when adult (Griffith, 2000). To our knowledge, this study provides the first test of the first two hypotheses, with our findings providing little support for them. The absence of differential maternal allocation, as well as the lack of relationship between male badge size and nestling feeding effort, might therefore indirectly indicate that environmental factors responsible for the foster father/son resemblance in badge size reported by Griffith et al. (1999a) imply other forms of parental effects, perhaps linked to nest and territory quality.

Patterns of differential allocation could vary among populations of the same species for adaptive or nonadaptive reasons. As predicted by theory, optimal patterns of maternal allocation to offspring depend on the expected fitness return (Stearns, 1972). A female mated with an attractive male should invest more in reproduction if her offspring will inherit attractiveness or quality (Burley, 1986). For cavity nesting species, the availability of suitable nesting sites can be an important limiting factor. In our study population, males face intense competition to acquire a nest-box because natural cavities are particularly scarce. In a previous study, we showed that both circulating levels of testosterone and badge size are significant predictors of the probability to acquire a nest-box (Mazuc J, unpublished data). As both testosterone levels and badge size have been shown to be condition dependent (Duckworth et al., 2001; Griffith, 2000), we should have expected variable levels of maternal investment into offspring depending on both paternal traits.

On the other hand, one factor that could affect patterns of differential allocation has been neglected in studies of the DAH. The DAH is based on the assumption that females adopt an allocation rule in line with the quality of their mate. However, in the past decade there has been overwhelming evidence showing that females actually engage in extrapair copulations and fertilizations (Petrie and Kempenaers, 1998). Could this multipaternity affect optimal patterns of allocation? Would be adaptive for females to adjust their investment into reproduction as a function of their social mate quality when males of potentially different quality sire offspring? The answer to these questions might likely depend on the type of benefits (direct or indirect) a female gains by mating with attractive males. If females are looking for good genes, then we believe that multipaternity is likely to inflate the variance around the relationship between maternal investment and male attractiveness, making harder to detect any differential allocation.

Surprisingly, we found that yolk testosterone had a negative effect on hatching probability. Although this result is based on the correlation between yolk testosterone of the first laid egg and the hatching probability of the remaining eggs, we are confident that it reflects a real cost because interclutch variation in yolk testosterone was found to be much higher than intraclutch variation in an independent sample of complete clutches. This result calls into questions the adaptive function of testosterone in yolk; a function generally assumed from recent studies that have revealed increased growth rate (Eising et al., 2001; Schwabl, 1996b), begging vigor (Lipar and Ketterson, 2000), and aggression (Schwabl, 1993) in nestlings from eggs with higher maternal androgen concentrations. However, results concerning embryonic development remain unclear as both positive (Eising et al., 2001) and negative (Sockman and Schwabl, 2000) effects of yolk testosterone have been found. As yolk steroid hormones are correlated with the hormone levels of the mother (Schwabl, 1996a), further studies concerning the impact of environmental or social disturbance on circulating level of androgens in females during laying period would be of interest.

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