Original Article

Alternative matings and the opportunity costs of paternal care in house sparrows

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Among avian species with biparental care, male alternative reproductive opportunities can occur in the form of either extrapair fertilizations or additional social mates. We manipulated testosterone (T) levels in male house sparrows to assess whether participation in parental care detracts from male success in securing alternative matings; we also compared the annual reproductive success of males that engaged in normal levels of care with the success of males that displayed increased mating effort at the expense of parental care. Our results showed that the incidence of polygyny among high-T/low-parenting males was elevated relative to control males, but that success in obtaining extrapair mates was independent of hormonal treatment. Thus, male parental care seems to carry an opportunity cost in terms of reduced acquisition of additional social mates. Despite this cost, between-treatment comparisons of the estimated number of fledglings sired annually suggest that, in this species, the value of male contributions to care is sufficiently high to favor the reductions in T that facilitate normal male parenting. *Key words:* extrapair fertilizations, opportunity costs, parental care, polygyny, testosterone. *[Behav Ecol]*

INTRODUCTION

Fundamental to theoretical treatments of parental care evolution—and to many sexual selection and mating systems models—is the assumption that parental care is costly, specifically, that a trade-off exists between providing care and engaging in alternative current or future reproductive activities. The ways in which parental care is envisioned as costly vary, but in some models, providing care and seeking additional mates are viewed as mutually exclusive, such that the main cost of care is the number of extra offspring that could be produced during the parental care period if care was not pro vided (Maynard Smith 1977 ; Werren et al. 1980). The reproductive cycle is envisioned as divisible between "time-in," when the individual is available for mating, and "time-out," when it is engaged in parenting, replenishing gametes, etc., and is not available for mating (Clutton-Brock and Parker 1992; Kvarnemo and Ahnesjo 1996; Parker and Simmons 1996; Reynolds 1996; Kokko and Jennions 2008). The realized opportunity costs of parenting will then be a function of 1) the degree to which engagement in care renders the individual unready for mating (i.e., represents at least a partial time-out from the mating pool) and 2) the availability of mating partners while in time-out (as influenced, e.g., by local breeding synchrony).

Among females of diverse taxa, providing care to one brood often is incompatible with concurrent initiation of a second brood. In mammals, for example, pregnancy is incompatible

with conception. In such cases, female investment in one brood automatically represents time-out from the population's mating pool. But gauging the extent to which male parenting similarly precludes successful pursuit of available mating opportunities can be problematic, and in some taxa, the assumed trade-off between male parental effort and mating effort does not apply (Reynolds and Jones 1999; Stiver and Alonzo, 2009).

One fruitful approach to determine whether male parental care represents time-out from the mating pool and to estimate the opportunity costs of male parenting consists of manipulating the hormonal mechanism(s) that regulate male mating competition, mate attraction, and parental care. Among avian species, testosterone (T) has been hypothesized to mediate the trade-off between male mating effort and parental effort (Wingfield et al 1990; Ketterson and Nolan 1994). Maintaining T at concentrations approximating the naturally occurring peak level in males has often, but not always, been shown to impair male parental care (Lynn 2008; Stiver and Alonzo 2009). Thus, for many avian species, high T levels seem to be incompatible with normal male parenting. It is less clear to what extent low T levels, which appear to be necessary for males to initiate and maintain parental care, detract from male abilities to capitalize on alternative mating opportunities. Although several studies have found that T-treated males exhibit increased aggression or elevated rates of vocal display (Lynn 2008; Stiver and Alonzo 2009), the impact of these phenotypic changes on male success in acquiring additional social and extrapair mates has seldom been quantified. In the most thorough study of the effects of T on avian male reproduction, Ketterson and colleagues showed that male dark-eyed juncos (*Junco hyemalis*) maintained on high T concentrations throughout

the breeding season sired more offspring via extrapair fertilization (EPF) than control (C) males (Raouf et al. 1997; Reed et al. 2006).

The first of two goals of this research was to determine whether a similar opportunity cost of male parenting—or of the lower T that accompanies parenting—exists in house sparrows, *Passer domesticus*, a multibrooded passerine that is mainly socially monogamous, but in which both EPFs (Wetton et al. 1995; Whitekiller et al. 2000; Stewart et al. 2006; Ockendon et al. 2009) and occasional polygyny occur (Veiga 1990; Griffith et al. 1999). We implanted males with exogenous T, which induced an increase in male aggressiveness and advertisement calling (Schwagmeyer et al. 2005; see also Hegner and Wingfield 1987), while simultaneously reducing male contributions to incubation and nestling feeding (Schwagmeyer et al. 2005; see also Hegner and Wingfield 1987; Mazuc et al. 2003). In this study, we test the prediction that the heightened mating effort displayed by T-treated males enhances their success in acquiring additional social and/or extrapair mates. One feature of male house sparrows that is potentially relevant to this prediction is their hormonal profile, which differs from that of some multibrooded monogamous species (Wingfield and Farner 1978; Wingfield 1984a; Ketterson and Nolan 1992; Logan and Wingfield 1995), in that T levels normally show multiple peaks during the breeding season. Thus, T levels decline while males participate in incubation, are low during the first two-thirds of the nestling period, but then rise again, when nestlings are about 10 days old and remain high throughout laying of the next clutch (Hegner and Wingfield 1986). As a consequence, a male house sparrow that tends three broods per season typically spends many days (roughly one out of three) in a high-T state. This may diminish any differences between T- and C-males in their success in acquiring extrapair or polygynous matings, depending on how often alternative mating opportunities become available when C-males periodically return to a high-T state.

A second goal of this study was to assess the value to males of providing parental care at normal levels relative to the potential opportunity costs of doing so. Based on Hegner and Wingfield's (1987) work, we anticipated that C-males would produce more fledglings per breeding attempt with their social mates than T-males; our question was whether the enhanced offspring production by parental males across the breeding season would compensate for any relative deficiencies they might have in siring offspring via EPFs or polygynous pairings. To address this, we compared the estimated number of fledged young sired annually by T- and C-males.

METHODS

We conducted this study during 2001–2003 on a large tract of university-owned land located on the south side of Norman, OK. The study was preceded by preliminary work in 2000, when we refined our implant techniques and color-banded nearly all adult nestbox residents on the study area. All nestlings that survived to day 11 posthatch on the study area had been banded since 1994. Nestboxes at the site were mounted on utility poles that were located along streets and driveways. We inspected nestboxes twice weekly to establish the dates when clutches were initiated and to determine clutch and brood sizes; we supplemented this routine census of nest contents with additional visits to nests as the anticipated date of hatching approached. Resident adults were determined to be either unbanded or they were identified based on their color-band combinations during laying or early incubation, and color-band combinations were resolved independently by at least two observers. We rechecked the identity of adult residents when we found additional eggs in a nest after a clutch had apparently been completed (assuming that eggs are laid at one egg per day on consecutive days). We typically waited until the nestling provisioning stage of the cycle to capture, band, and collect blood samples from any unbanded adult residents.

Our methods for selecting the males used in this experiment, our implant procedures, and the effects of T implants on T plasma concentrations were described in Schwagmeyer et al. (2005). Briefly, T-males received T-filled silastic implants, whereas C-males received empty implants. We implanted a total of 60 males (30 C-males, 30 T-males) across the 3 years of the study; no male received implants in more than 1 year. In each year, we began capturing and implanting males in March, before the onset of breeding. Assignment to treatment (T vs. C) was alternated between males captured successively, except when doing so would have interfered with our efforts to avoid spatial clustering of males from the same treatment and to have roughly equal age distributions in the two treatments. We tracked the presence/absence of implanted males on the study site by their breeding activities with social mates, their appearance at their nests during behavioral sampling of incubation and nestling feeding behavior, and by regularly identifying any males observed calling at unoccupied nestboxes. In late April and May, we attempted to recapture males to obtain blood samples for hormonal analyses and to verify that males had retained their implants; we replaced any implants that had been lost, and subsequently defined the effective date the male entered treatment as the date of replacement. A few males in each treatment were implanted after breeding had begun in an attempt to compensate for disappearances of implanted males. Five of 30 C-males disappeared very soon (within 12 days) after having been implanted and 6 of 30 T-males did so, as well. The sample of T-males was further reduced because we excluded data from three T-males who had lost their implants by the time we recaptured them late in the season to remove the implants. Implant retention rates improved across the years of the study, reaching ≥90% for 2002 and 2003; however, in 2001, the rate was only about 70%, and we additionally omitted from analyses data from two 2001 T-males because they disappeared before we could confirm that they had retained their implants. The mean masses of T- and C-males did not differ (T-males = 28.8±1.10 standard deviation [SD] g; C-males = 28.9±1.52 SD g; t_{42} = 0.39, P = 0.744). However, as a consequence of implant losses and male disappearances, the age distributions in the two treatments were not as similar as we would have liked: 7 of the 25 C-males were at least 2 years old, whereas only two of the 19 T-males were known to be older males. In both treatments, the majority of males (15/19 T-males; 15/25 C-males) were of unknown age (i.e., they had been unbanded before they were implanted); two T-males and three C-males were known yearlings. Because most dispersal by male house sparrows is thought to occur before their first breeding attempt (Fleischer et al. 1984; Anderson 2006), we pooled known yearlings with males of unknown age into a single category of "minimum age 1." For analyses of male nesting success, parentage losses, and mating status (polygynous vs. monogamous), we excluded data for any breeding attempts for which the first egg of the clutch had been laid before the date the male was implanted. Similarly, we excluded data for any extrapair young (EPY), the male was determined to have sired when the first egg of the extrapair clutch had been laid before the male was implanted. We classified males as polygynous if they were simultaneously the resident male at two or more nests where laying, incubation, or nestling provisioning were occurring. At the time we captured a male for treatment, we usually had no way to predict

whether he would become polygynous because often either the male and/or a female he was observed interacting with were unbanded and because (banded) individuals frequently were seen at more than one nestbox before breeding began. Consequently, we did not attempt to consider male mating status when assigning males to treatment. However, two T-males were already polygynous when we implanted them. One of these males retained one of his two original mates postimplant and also paired with two additional females during the remainder of the season; the overlap among his postimplant breeding attempts was such that we considered him to be polygynous. The other T-male retained only one of his two mates postimplant and attracted no other social mates, so we classified him as socially monogamous.

Our final sample of T- and C-males comprised slightly less than half (from 40–45%) of the males that eventually bred at least once on the study site each year; thus, T-males were always in a minority. T- and C-males collectively were involved in a total of 117 breeding attempts postimplant. To assess the effects of treatment on male success over the entire breeding season, we needed to account for variation in both implant dates and dates when males disappeared or had their implants removed. Measuring success as a rate based simply on the number of days each male had been in treatment would be problematic because breeding opportunities are not distributed uniformly across days. As an alternative, we measured success in relation to the estimated number of breeding females available to each male. The maximum value for any male consisted of the total number of broods scored for paternal exclusions (see Parentage analyses) in each year (n = 64, 63, and 88 for 2001, 2002, 2003, respectively). From this, we subtracted broods that had clutch initiation dates before the date the male had been implanted, as well as broods that had clutch initiation dates occurring after the male was last seen on the study area or, for T-males, after the date we removed implants. This measure (hereafter, "female availability") also allowed statistical adjustment for yearly differences in male reproductive opportunities; it averaged 56.9 (±17.58 SD) female breeding events for C-males and 55.0 (±18.07 SD) for T-males (t_{42} = 0.34, P = 0.732).

Parentage analyses

We collected blood samples (~100 μL) from the brachial veins of adults and all 11-day-old nestlings that had been reared in nestboxes; samples were transferred into lysis buffer (Longmire et al. 1988) and refrigerated. At nests of T- and C- males, we also opportunistically salvaged dead nestlings and eggs that had been deserted. Parentage exclusion analyses were based on multilocus minisatellite DNA fingerprinting following procedures described in Mauck et al. (1995). Parentage analyses were conducted by individuals who were blind to hormonal treatment. We followed the same criteria for exclusion as described in Edly-Wright et al. (2007). Generally, males were excluded if their band-sharing values with the nestling were <0.53 and they left two or more offspring bands unaccounted for when considered with the dam. Some exclusions were made with only one unattributable band if band-sharing values were below 0.25. Any young excluded during this preliminary round were typed at two microsatellite loci (Pdoμ3 and Pdoμ6; Neumann and Wetton 1996) and compared against the genotypes at the same two loci of all males implanted that season. The reduced number of males that matched at both microsatellite loci was then run by multilocus minisatellite fingerprinting with the offspring and dam, further excluding all mismatches except the one that matched at minisatellite loci based on the same exclusion criteria as above. We scored a total of 752 samples from 215

broods for paternal exclusion (64 broods in 2001, 63 in 2002, and 88 in 2003), which excluded samples from one brood of five chicks where we failed to obtain a blood sample from the resident male, and approximately, eight samples that had dried or had degraded DNA. The resident male was excluded as sire of 49/227 (21.6%) offspring in 2001, 57/229 (24.9%) in 2002, and 57/296 (19.2%) in 2003. A mean of 5.6±4.39 SD putative offspring of T-males were scored for paternal exclusion; C-male parentage was scored for an average of 7.2±4.96 SD offspring (t_{42} = 1.06, P = 0.2940). Parentage exclusion results for T- and C-males indicated most EPY present in their broods were a result of EPF, although conspecific brood parasitism was detected in two broods from a polygynous C-male.

Statistical analyses

We used SAS v. 9.2 (SAS Institute, Cary, NC) for statistical analyses. We relied often on mixed models (either linear or generalized linear), and when we did so, denominator degrees of freedom used in testing fixed effects were calculated using the Kenward–Roger method. On a priori grounds, we expected that the unequal representation of older males in the two treatments was likely to affect estimates of male extrapair paternity (Wetton et al. 1995), but less likely to affect other measures of male reproduction. Nevertheless, for all analyses, we ran preliminary models that included minimum age as a fixed effect. Nonsignificant main effects of minimum age and nonsignificant first-order interactions were eliminated from final models.

To compare the incidence of polygyny by C- and T-males, we applied a generalized linear mixed model (logit link function) with a random effect of year. The dependent variable was the ratio of the number of postimplant breeding attempts in which the male was polygynous to his total number of postimplant breeding attempts that season. We assessed the impact of polygyny on the total number of fledglings T- and C-males produced via their social mates with a general linear mixed model (random effect of year); female availability (defined above) was included as a continuous covariate. Paternity losses from EPF in relation to male treatment and mating status (monogamously vs. polygynously paired during the breeding attempt) were evaluated with a generalized linear mixed model (logit link function), which included a random effect of male identity; the dependent variable was the number of embryos or nestlings that were identified as having been sired via EPF relative to the number of embryos and nestlings from that breeding attempt that were scored for exclusion. We also used a generalized linear mixed model (log link function, random effect of year) to examine the effects of treatment on male extrapair mating success. The dependent variable was the number of females with which each male had sired extrapair offspring (range = 0–5). The minimum age of males (2 vs. 1 y.o.), treatment, and the interaction between minimum age and treatment were the fixed effects.

To examine the effects of T treatment on the average outcome of male nesting attempts, we used a linear mixed model MANOVA (multivariate analysis of variance) to compare success at three stages of the nesting cycle: clutch size, number of hatchlings, and number of fledglings. We had two within-subject factors to accommodate: repeated measurements across stages of each breeding attempt and repeated breeding attempts by the same male (117 breeding attempts by 44 males). We used the unstructured covariance option for repeated measurements across stages, and the compound symmetry option for repeated breeding attempts by the same individuals. We also used MANOVA to analyze the effects of treatment on the cumulative postimplant reproductive success of males, as assessed by four dependent variables that

were measured on comparable scales: total number of eggs laid by the male's social mate(s), total number of hatchlings, total number of fledglings produced, and the total estimated number of fledged young each male had sired during the season. To calculate this last measure, we multiplied the number of fledglings the male produced with his social mate(s) on each breeding attempt by the proportion of those that he had sired (based on the number of offspring in that brood that he was not excluded from siring divided by total number scored for exclusion). We then summed fledglings sired across all breeding attempts and then added any EPY he sired that successfully fledged. The fixed effects in the model were treatment, male minimum age, and the interaction of treatment and minimum age. Female availability was included as a continuous covariate; thus, this model adjusts for both variation among males in time in treatment and yearly variation in female availability.

RESULTS

Success in mate acquisition and fertilization

Nine of 19 T-males versus 5 of 25 C-males became polygynous at least once during the breeding season. From 29–67% of T-males were polygynous each year, whereas all cases of C-male polygyny occurred in 2003, when five of the nine C-males became polygynous. Only a minority of T- (3/9) and C- (1/5) males that became polygynous during any given season were polygynous on all of their breeding attempts that year; consequently, we evaluated the effects of treatment on the proportion of each male's breeding attempts that occurred under polygynous circumstances. Proportion of polygynous breeding attempts was elevated by T-treatment ($F_{1,39} = 9.21$, $P = 0.004$) and by greater female availability ($F_{1,31.6} = 8.99$, $P = 0.005$). Female availability additionally interacted with treatment ($F_{1,39} = 6.84$, $P = 0.013$): the proportion of polygynous breeding attempts rose more sharply with increased female availability among C-males than among T-males. There was also a positive effect of male mass on frequency of polygynous breeding attempts ($F_{1,39} = 6.93$, $P = 0.012$). We confirmed this last result by a simple comparison of the mass of T-males that became polygynous at some point during the season with the mass of T-males that remained socially monogamous: the 9 polygynous T-males were on average 1g heavier ($\bar{x} = 29.3 \pm 1.27$ SD) than the 10 monogamous T-males ($\bar{x} = 28.3 \pm 0.57$ SD; $t_{10.8} = 2.39$, $P = 0.036$).

Becoming polygynous during the breeding season was advantageous to males in terms of the total number of fledglings they produced via social mates (main effect of mating system: $F_{1,39} = 7.78$, $P = 0.008$). Fledgling production was marginally reduced by T-treatment ($F_{1,40} = 3.67$, $P = 0.063$) and positively influenced by female availability ($F_{1,40} = 5.64$, $P = 0.022$). However, polygynous pairings elevated the incidence of parentage loss through EPFs: analysis of variation in parentage losses across individual breeding attempts revealed that males that were polygynously paired during a breeding attempt had a greater proportion of EPY in their broods than monogamously paired males ($F_{1,82} = 4.63$, $P = 0.034$), with no significant effect of T-treatment ($F_{1,27.2} = 1.83$, $P = 0.188$). Neither time in treatment (number of days between implant date and clutch initiation date) nor the interaction between treatment and time in treatment had significant effects on the proportion of EPY present in broods (time in treatment: $F_{1,81} = 1.47$, $P = 0.229$; interaction: $F_{1,79} = 0.15$, $P = 0.702$).

The enhanced success of T-males in attracting social mates did not extend to success in acquiring extrapair mates: 9 of the 25 C-males sired EPY (6/7 ≥ 2 y.o. C-males; 3/15 C-males of unknown age; 0/3 1 y.o. C-males) versus 4 of the 19 T-males (2/2 ≥ 2 y.o. T-males; 2/15 T-males of unknown age;

0/2 yearling T-males). As shown in Table 1, the mean number of EPY sired was higher for C-males than for T-males. We found no significant effect of T-treatment ($F_{1,41} = 1.40$, $P = 0.244$) on the number of females by which the male sired EPY, but a strong advantage for minimum age 2 males ($F_{1,41} = 11.61$, $P = 0.002$).

Nesting success with social mates

T-treatment had no impact on the mass of nestlings that survived to day 11 posthatch (Table 1; $t_{36} = 0.56$, $P = 0.576$). We used MANOVA to evaluate the effects of treatment on clutch size, number of hatchlings, and number of fledglings per breeding attempt (Table 1). Not surprisingly, measures of nesting success declined across successive stages of the cycle, from eggs through fledglings ($F_{2,56.6} = 109.83$, $P < 0.0001$). The effect of T-treatment on the linear combination of the three measures was negative ($F_{1,57.3} = 4.30$, $P = 0.043$), with no significant interaction between stage of the cycle and treatment ($F_{2,56.6} = 1.17$, $P = 0.317$).

Cumulative reproductive success

We examined seasonally cumulative measures of male reproduction (Figure 1) in terms of T-treatment, male minimum age, and their interaction; female availability was included as a covariate. MANOVA showed significant effects of both treatment (Pillai's Trace = 0.253, $P = 0.029$) and age (Pillai's Trace = 0.417, $P = 0.0005$) on the combined measures; the parameter estimates from univariate analyses indicated C-males and ≥ 2 y.o. males were consistently favored across the four measures. However, there was also a significant interaction between male minimum age and treatment (Pillai's Trace = 0.337, $P = 0.004$), which represented a negative effect on reproduction by ≥ 2 y.o. C-males. Planned comparisons of the effects of treatment within minimum age classes indicated that T-treatment in minimum age 1 males resulted in a marginally reduced number of fledglings produced via social mates for the season ($P = 0.059$) and a significant reduction in the estimated number of fledglings sired annually ($P = 0.012$); by contrast, the two older T-males (both polygynous) outperformed older C-males (1/7 polygynous) on all measures (eggs: $P = 0.0003$; hatchlings: $P = 0.017$; fledglings: $P = 0.007$; estimated fledglings sired: $P = 0.022$).

Table 1

Mean offspring mass at day 11 posthatch, number of eggs, hatchlings, fledglings, and proportion of offspring sired per breeding attempt for C and T males, plus mean number (#) of EPY sired

	Control			Testosterone		
	$\bar{x}$	SD	N	$\bar{x}$	SD	n
Mass (day 11)	23.9	2.42	21	24.2	2.08	17
Clutch size	4.75	0.606	25	4.52	0.569	19
Hatchlings	3.14	1.760	25	2.75	1.543	19
Fledglings	2.52	1.529	25	1.90	1.369	19
Proportion Sired	0.87	0.194	21	0.70	0.360	17
# EPY sired	0.84	1.573	25	0.32	0.749	19

Sample sizes are number of males, with means for clutch size, hatchlings, fledglings based on 1–6 breeding attempts per male, including attempts that failed. Means for mass include only data from broods where at least one chick survived to day 11 posthatch. Means for proportion offspring sired via social mates are based on the number of embryos or nestlings that the male was excluded from siring divided by the number of embryos or nestlings that were scored. Treatment effects on all variables except mass were assessed via MANOVAs and reported in the text; treatment effects on nestling mass also are reported in the text.
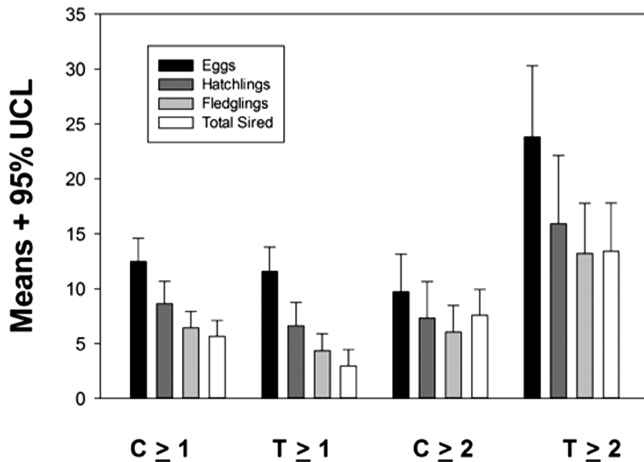
Figure 1
Least square mean + 95% upper confidence limit number of eggs, hatchlings, fledglings, and estimated number of sired fledglings produced annually by minimum age 1 and 2 T- and C-males. Sample sizes: 17 T-males ≥ 1 y.o.; 18 C-males ≥ 1 y.o.; 2 T-males ≥ 2 y.o.; and 7 C-males ≥ 2 y.o.

DISCUSSION

Our manipulation revealed that when plasma T concentrations decline as male house sparrows provide their normal level of parental care, the males incur an opportunity cost in the form of a reduced likelihood of reproducing simultaneously with multiple social mates. We know of only two other mainly monogamous passerines in which T-treatment has been shown to elevate the incidence of polygynous breeding: white-crowned sparrows, *Zonotrichia leucophrys pugetensis*, and song sparrows, *Melospiza melodia* (Wingfield 1984b). Yet in studies of other socially monogamous or facultatively polygynous species, T-treated males increase investment in sexual advertisement (Silverin 1980; Dittami et al. 1991; Ketterson et al.1992; De Ridder et al. 2000) and/or defend multiple nesting sites (Silverin 1980; De Ridder et al. 2000), but fail to attract additional social mates. Some authors have suggested that this failure was attributable to a scarcity of receptive females (Silverin 1980; De Ridder et al. 2000). In such species, then, male parental care presumably carries no opportunity cost of decreased likelihood of polygyny because females typically are not available for mating during parental care periods.

The pronounced effect of T on the incidence of polygyny in this study provides support for Pinxten et al.'s (2003) suggestion that, although male T levels may increase with exposure to a receptive female, there exists a threshold concentration of T required for males to respond to such females by engaging in mate attraction efforts. This offers a means of defining at a mechanistic level the concept of males being in time-out from the mating pool when they are parenting; perhaps, the reduced T levels that usually characterize such males are simply below this threshold. Our results also showed, however, that the incidence of polygyny among C-males rose relatively sharply with increased female availability. Exposure of breeding males to receptive females is known to increase plasma T in several passerines (Goymann 2009). Consequently, increased female availability could trigger C-male mate attraction behaviors by either: 1) amplifying C-male exposure to prospective mates when the males are in low-T states, such that T levels rise above the threshold necessary to initiate mate attraction behaviors; or 2) by raising the chance that C-males encounter available females when they are in a high-T state. Regardless, the effect

of female availability on C-male polygyny suggests that house sparrow males usually do not invest the considerable time and effort required to defend an additional breeding site and attract another social mate unless their chance of success is fairly high.

Female availability, however, is just one variable that can influence whether males that attempt to attract an additional social mate will be successful; as outlined by Emlen and Oring (1977), resources required for breeding must also be obtainable, and males must be able to defend those resources from other males. Our study site had at least some unoccupied nestboxes in each season of this study, and their availability may well have elevated male prospects for becoming polygynous. Nevertheless, males still had to compete to defend these nesting resources, and the importance of male competitive abilities was underscored by our finding that the frequency of polygyny increased with male body mass. This effect of male mass on polygyny additionally offers an explanation for why not all T-males in our study managed to become polygynous.

Although polygynous males breed with social mates at a rate at least double that of socially monogamous males, the impact of polygyny on male house sparrow reproductive success can be diminished by breeding failures stemming from female–female competition (Veiga 1990). Nevertheless, in both Veiga's (1990) study of house sparrows and in this study, males that became polygynous produced more fledglings per breeding season than males that remained socially monogamous. One further factor that can erode male gains from acquiring multiple social mates is increased loss of paternity; within facultatively polygynous passerines, polygynous males often suffer higher parentage losses than monogamous males (Vedder et al. 2011). This was, indeed, the case in this study; males that were polygynously paired during a breeding attempt had a higher proportion of their nestlings sired by EPF than males that were socially monogamous during the attempt. Once mating system was taken into account, we found no significant effect of T-treatment on parentage losses via EPF.

T-treatment also has no effect on parentage losses of male dark-eyed juncos (Reed et al. 2006). Conversely, higher parentage losses by T-males occur in blue tits, *Cyanistes caerulens* (Foerster and Kempenaers 2005). Foerster and Kempenaers (2005) had monitored mate-guarding and sexual behavior of pairs containing either T- or C-males and had found no differences that could account for this effect. They consequently suggested that spermatogenesis might be compromised by long-term T-treatment because of negative feedback from T on gonadotropin production (Foerster and Kempenaers 2004). In captive house sparrows, for example, exogenous T can have a dose-dependent effect on the testes; testicular atrophy occurred after males had been maintained for about 7 weeks on low dosages of T, whereas higher dosages, including those that produce unphysiologically elevated plasma T concentrations, preserved testes function (Turek et al. 1976). Foerster and Kempenaers's (2004) explanation was also consistent with their finding that blue tit T-males that bred relatively soon after they had been implanted had lower parentage losses than males whose implants had been in place for a lengthier interval before clutch initiation, whereas no effect of time in treatment on parentage losses was observed among C-males. We checked for the existence of similar relationships between time in treatment and paternity and did not detect any. One potentially relevant feature of Foerster and Kempenaers's (2004) study is that they intentionally created T levels in T-male blue tits that were substantially higher than the peak concentrations of blue tit C-males, whereas the implants we used, as well as those used in the dark-eyed junco work (Ketterson and Nolan 1992), produced T concentrations that were very similar to naturally occurring peak levels.

In contrast to its influence on acquisition of social mates, T-treatment in male house sparrows did not affect extrapair mating success. Instead, our results showed simply that older males achieve more EPFs, consistent with Wetton et al.'s (1995) findings for an unmanipulated British population of house sparrows. Male success in obtaining EPFs is similarly related to male age, but not to T level, in blue tits (Foerster and Kempenaers 2004), whereas in dark-eyed juncos, both increased age and exogenous T enhance male EPF success (Raouf et al. 1997; Reed et al. 2006). We can think of two hypotheses that might account for the lack of difference between T- and C-male house sparrows in EPF success. First, T may not enhance the specific traits that improve male house sparrow success in extrapair mating. In other words, the particular components of mating effort that are useful in attracting social mates may be largely independent of those that are useful in obtaining EPFs, and T-males either may not increase their investment in pursuing EPFs, or their efforts may be ineffective. This would be a lot easier to evaluate if more were known about the behavioral traits that predict male house sparrows' success in securing EPFs. Second, T-male house sparrows may be competing for EPFs with males that also are in a high-T state (i.e., the naturally occurring resurgence of male T levels, coupled with breeding synchrony, may result in most EPF opportunities coinciding with intervals in which the majority of males are in a high-T state). This hypothesis is supported by Wetton et al.'s (1995) analyses of EPFs in British house sparrows. They examined the timing at which extrapair sires were likely to have secured EPFs relative to the stage of the sires' own nesting cycles and concluded that approximately half of the EPF events probably occurred during the fertile period of the extrapair sire's social mate, when T levels are high. Another appealing feature of this hypothesis is that it could explain why extrapair mating success was enhanced by T-treatment in multibrooded dark-eyed juncos, but not in house sparrows; in contrast to male house sparrows, the hormonal profile of male dark-eyed juncos is not characterized by periodic returns to peak levels of T during the breeding season (Ketterson and Nolan 1992). Foerster and Kempenaers (2004) also invoked species differences in the synchrony and frequency of breeding in explaining why maintaining male dark-eyed juncos at peak T levels throughout the season promoted EPF success, but increasing T levels of male blue-tits beyond the average peak did not.

Our comparisons of mate acquisition by T- and C-males thus imply that when house sparrow males undergo reductions in plasma T levels that permit normal participation in parental care, they do so at the expense of acquiring multiple social mates, but not extrapair mates. Relative to T-males, the additional parental care they provide enhances various measures of nesting success. On the other hand, the accelerated mating rate of polygynous males confers advantages in production of fledglings, which is offset partially by reduced parentage. Once these assorted influences on male reproduction are considered, comparisons of the estimated number of fledglings T- and C-males sire annually show that, for most males in our samples (yearlings plus males of unknown age), C-males significantly out-reproduce T-males, due largely to T-male deficiencies in producing offspring with their social mates. Conversely, among older individuals, T-males appear to be favored, but we do not have much confidence in this finding given how few older T-males we had in our final sample.

However, the reproductive disadvantage of the majority of T-males seems sufficient to conclude that, in this relatively short-lived species (Anderson 2006), selection is unlikely to favor a male phenotype that maintains persistently high T levels throughout the breeding season, especially if there also exists any survival cost of doing so. This differs from the results for dark-eyed juncos, where the superiority of T-males in gaining EPFs more than compensates for their reduced within-season survival and the impaired growth of their nestlings (Reed et al. 2006). We suspect that the dissimilarity of outcomes for the two species derives chiefly from species differences in the impact of T on male parental care and the relative value of male parental care. Although T-treatment does not totally eliminate male parental care in either species, it reduces the rate at which male house sparrows provision nestlings to about half or less that of C-males (Hegner and Wingfield 1987; Mazuc et al. 2003; Schwagmeyer et al. 2005). By contrast, the effect of T-treatment on male dark-eyed junco provisioning is less profound (Ketterson et al. 1992), and dark-eyed junco females paired to T-males compensate at least partially for the reduced provisioning of their mates (Ketterson et al. 1992).

Generally, T levels of male birds that are participating in parental care are assumed sufficient for maintenance of sexual behavior and fertilization (Moore 1983; Moore and Kranz 1983; Wingfield et al. 1990). In terms of their abilities to copulate and fertilize eggs, then, males engaged in parenting could be viewed as in time-in. As Ketterson and Nolan (1994) pointed out, however, the physiological state that characterizes avian male parental care and the activity regimes that correspond to that state may be incompatible with effective pursuit of alternative mating options. Our results support this view: parental care by male house sparrows appears to place them in at least a partial time-out with respect to acquisition of additional social mates, such that they do not participate fully in the mating pool.

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