

Dynamics of House Sparrow Biparental Care: What Contexts Trigger Partial Compensation?

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Abstract

Nest attendance during incubation is characterized by an inequitable division of labor in house sparrows, *Passer domesticus*, with females spending more time at the nest than males. Previous research has shown that if male contributions are reduced experimentally via testosterone (T) implants, females compensate partially for those reductions, consistent with predictions from most models of negotiated biparental care. In this study, we attempted to identify the cues and contexts generating partial compensation, using data from both unmanipulated parents and pairs with T-males. Both males and females of this species sometimes leave the nest before their mate returns to relieve them, and we found that these unrelieved departures by unmanipulated individuals occur when partners are on lengthy recesses. Females compensated partially for long male recesses by marginally extending their bouts; most females also slightly reduced their next recess. By contrast, when males left before their mate returned, they left earlier than when they waited for the female. Neither males nor females adjusted their recess lengths after returning to the nest and discovering that their partner was absent. More pronounced changes in nest attendance of unmanipulated parents occurred in the context of 'visits', when individuals returned to the nest but then left without relieving their mate. Such visits effectively prolonged the bout of the on-duty partner and extended the visitor's recess. Analyses of behavior of T-males and their mates revealed that T-males had significantly longer recesses than control males, and that their mates, in turn, had elevated rates of unrelieved departures. T-males also visited their on-duty mates more often than control males, whereas female visits to T-males were rare. Collectively, the predicted changes in female nest attendance associated with lengthy male recesses and male and female visits account reasonably well for the compensatory response of females paired to T-males. The majority of female compensation was attributable to changes in visit behavior, however, suggesting that much of the negotiation over nest attendance in this species occurs during direct interactions between mates.

Introduction

Biparental care has proven to be an instructive topic for analyzing the degree to which unrelated individ-

uals will cooperate to achieve a common goal. The prevailing view from theoretical models is that the extent of cooperation vs. conflict over parental care is likely to hinge on factors such as the availability

to males of alternative mating options, the effects of reduced care on offspring welfare, and parental opportunities for future reproduction (Parker 1985; Barta et al. 2002; Jones et al. 2002; McNamara et al. 2003; Houston et al. 2005). Recent attention also has focused on how two parents reach their final division of labor and, in particular, whether each parent adjusts its effort level in response to that of its partner. Here, two distinct patterns have emerged (reviewed by Sanz et al. 2000). In some species, experimentally induced changes in one parent's contributions result in no modification of the mate's effort. In contrast, similar studies of other species have found that manipulations of one parent's level of care produce changes in its partner's contributions, indicating that parents somehow assess what their mates are doing and modify their own behavior accordingly.

For the most part, theory predicts that parental care that is adjusted facultatively to partner contributions (i.e. is 'negotiated' behaviorally rather than across evolutionary time) should result in patterns of only partial compensation for a mate's change in effort (Houston & McNamara 1999; McNamara et al. 1999; but see Johnstone & Hinde 2006). Thus, a reduction in effort of x units by one parent is predicted to be countered by an increase in the other parent's contribution by $<x$ units. Empirical studies of biparental negotiation have focused overwhelmingly on testing this prediction, and it has not always been supported: some species show no compensation (as above), and others appear to compensate fully (reviews in Sanz et al. 2000; Johnstone & Hinde 2006). This mismatch between predictions and empirical results has been accompanied by renewed modeling efforts (Jones et al. 2002; Taylor & Day 2004; Johnstone & Hinde 2006).

One revelation from recent models is that the predicted outcomes can hinge on details of the negotiation process (e.g. whether male and female decisions are made simultaneously vs. sequentially: McNamara et al. 2003; Houston et al. 2005) as well as on how parents interpret partner changes in effort (Johnstone & Hinde 2006). We currently lack basic descriptive information on precisely what cues trigger compensatory responses, however. In this study, we attempted to determine how parents respond to putative indications of increases and decreases in partner contributions. We used data on nest attendance by parent house sparrows (*Passer domesticus*) during incubation for this purpose. Although research on this species has shown little evidence that parents respond to modifications of the nestling

provisioning rates of their mates (Hegner & Wingfield 1987; Schwagmeyer et al. 2002, 2005; Mazuc et al. 2003), manipulations of male testosterone (T) levels revealed that females compensate partially for reductions in male incubation contributions: relative to controls, T-treated males reduce their time at the nest by approx. 7 min/h, while their mates increase their nest attendance by approx. 5 min/h (Schwagmeyer et al. 2005).

Most avian studies investigating parental responses to partner efforts have focused on nestling provisioning (see Sanz et al. 2000), when individuals could potentially assess each others' contributions either indirectly via nestling begging cues (Wright & Cuthill 1990) or directly during overlapping nest visits or foraging sessions (Hinde 2006). However, the number of studies using incubation behavior for experimental research on parental responses to partner efforts is growing (De Ridder et al. 2000; Alonso-Alvarez 2001; Komdeur et al. 2002; Kosztolányi et al. 2003; Van Roo 2004; Magrath et al. 2005). We have previously suggested that in some species, monitoring of partner effort might be relatively easier during biparental incubation than during nestling provisioning, simply because incubating parents are likely to have more information about each other's contributions (Schwagmeyer et al. 2002). In addition to information that egg temperature may provide (e.g. Magrath et al. 2005), the events associated with nest relief offer a discrete set of opportunities for parents to detect and evaluate each other's contributions. Indeed, in some avian species, the two parents must have nearly perfect information about what each has contributed because the eggs are attended virtually continuously. Dearborn (2001) proposed that biparental incubation in such cases could be regarded as an iterated Prisoner's Dilemma. He found that the recess durations of frigate birds (*Fregata minor*) were positively related to the length of their previous bout, a pattern consistent with the possibility that parents that have been left to incubate for longer intervals subsequently retaliate by extending their next recess (Dearborn 2001).

Declines in partner effort in intermittently incubating species may similarly be revealed by unusually long partner recesses or, alternatively, by a returning parent's discovery that its partner is not at the nest. Furthermore, parents could communicate their willingness to increase their own effort by not leaving the nest when relief is offered. In this study, we first used data from unmanipulated pairs to determine: (1) whether the bout durations of individuals are positively correlated with their recess

durations, as in Dearborn's (2001) study; (2) whether departures from the nest before the mate returns are associated with lengthy partner recesses and whether individuals adjust their bout or recess durations when they leave before their mate returns; and (3) whether individuals that return to the nest to find their partner absent then modify the duration of their next recess in response. We then compare recess lengths, likelihood of leaving the nest before the partner returns, and bout durations in control pairs and pairs with T-males to assess their conformity to the patterns of compensation exhibited by unmanipulated females. We also test the hypothesis that situations in which a parent returns to the nest but does not relieve its partner represent offers of relief that have been declined, again using results from unmanipulated pairs as well as comparisons between T-treated and control pairs.

Methods

Behavioral Data

We used data that had been collected during two previous studies for these analyses. Details on the methods used are provided in Bartlett et al. (2005) and Schwagmeyer et al. (2005). Briefly, in one study, 47 unmanipulated pairs were observed during morning hours for an average of 4 h-long samples/pair; no pair was observed during more than one nesting cycle (Bartlett et al. 2005). In the second study, we sampled the nest attendance behavior of 21 control males (C-males) and their mates across 1.3 ± 0.56 SD nesting cycles, for a total of 3.95 h/male (Schwagmeyer et al. 2005). For analyses of the effects of T treatment on behavior, we compared C-males and their mates with data from pairs in which males ($n = 17$) had been implanted with T. Each T-male had been implanted with two 10-mm sections of silastic tubing (i.d. = 1.47 mm; o.d. = 1.96 mm; Dow-Corning, Midland, MI, USA) packed with crystalline testosterone (Sigma-Aldrich, St. Louis, MO, USA) and sealed at the ends; C-males received empty implants. We implanted most T- and C-males after they had paired in the spring but before their mates had begun laying eggs; for those that were implanted after their first breeding cycle had begun, we deferred sampling their behavior until their next breeding cycle to mitigate any effects of capture on their parental behavior (Schwagmeyer et al. 2005).

We combined data from Bartlett et al. (2005) and C-males and their mates in analyses of 'unmanipu-

lated pairs' for a total sample of 70 pairs. Data collection for Bartlett et al. (2005) occurred during 2000–2001 at a site located on university-owned property on the outskirts of Norman, Oklahoma (35.25°N, 97.47°W, elevation = 349.9 m); data for Schwagmeyer et al. (2005) were collected during 2001–2003 at a second site approx. 5 km away. Monthly average temperatures in this area range from 15.3°C to 24.9°C during April–June, when most data were collected. Pairs at both study sites used nestboxes for breeding, and the nest attendance behaviors recorded during sampling (times of arrival to, entry into, exit from, and departure from the nestbox) were similar for the two studies. In both studies, we observed parental activities at the nest from a parked vehicle equipped with a window-mounted spotting scope. Sampling of behavior during Bartlett et al. (2005) began slightly earlier in the cycle (usually on the day the 4th egg was due to appear) than the onset of sampling in Schwagmeyer et al. (2005) (on either the 4th or 5th day after the last egg in the clutch had appeared). To eliminate the variation in either male and/or female behavior at the nest arising from male mate-guarding or female egg-laying, we analyzed only data collected one or more days after clutch completion. We also excluded data from one pair in which the female refused to enter the nestbox during the last sample; the clutch eventually was deserted. The mean cumulative time spent at the nest by females in the two studies did not differ significantly ($t_{60} = 0.18$, $p = 0.856$). There was also no significant difference in the total minutes per hour spent at the nest by C-males and males from the Bartlett et al. (2005) study ($t_{64} = 0.67$, $p = 0.506$). A mixed model (random effects of individual and day nested within individual) additionally revealed no significant difference in the cumulative minutes per hour females were at the nestbox at the two study sites ($F_{1,63.5} = 0.06$, $p = 0.808$), as well as no significant effect of year ($F_{3,76.2} = 1.30$, $p = 0.281$), or day of the cycle ($F_{1,64.5} = 1.94$, $p = 0.166$). The parallel model for males likewise showed no significant effects of study site ($F_{1,64.5} = 1.35$, $p = 0.249$), year ($F_{3,52.4} = 0.74$, $p = 0.534$), or day since clutch completion ($F_{1,121} = 2.21$, $p = 0.139$).

The combined datasets were recoded for this study to allow within-individual comparisons of male and female reactions to each other's contributions and to divide time within each sample according to which parent appeared to be responsible for remaining at the nest. We focused on nest attendance, rather than incubation *per se*, as our measure of an individual's contributions; we have no precise estimates of how

much males, in particular, actually contribute to effective incubation of the eggs (Bartlett et al. 2005). We partitioned nest attendance for each individual into 'bouts'. Often only a single parent was present at the nest and remained there continuously until relieved by its partner, in which case the duration of its 'bout' was defined simply in terms of its arrival and departure times. In some cases, a parent left the nest during a bout but returned after only a brief absence (e.g. it simply flew down to the ground below, where it presumably remained capable of detecting potential intruders at the nest). We considered these interrupted periods at the nest to constitute a single bout if the bird was gone for ≤ 3 min (unless its partner had arrived in the interim); otherwise, if the bird left for >3 min and then returned (and its partner was still absent), we scored it as having begun a new bout. During nest reliefs, an arriving parent was credited for beginning a bout even if its partner had not yet departed; similarly, a departing parent was credited for continuing its bout until it left the nest, even if its partner had already arrived. However, an incoming parent that arrived at the nest and then left briefly (e.g. to allow the partner to exit) before returning was not considered to have begun its bout until the second arrival. Outgoing parents also sometimes left the nest after the partner's arrival, but then returned (e.g. to interact with the partner), and we excluded from their bout duration the time spent at the nest after the return. Beyond these arrivals and departures occurring in the context of nest relief, both parents were present at the nest during 'visits', where an individual returned to the nest but then did not relieve the partner. A parent was considered to have 'visited' its partner when its arrival and departure both occurred within the partner's bout. If both parents arrived simultaneously, whichever one departed earlier was considered to have visited (and the other to have begun a bout); if one arrived while its partner was in a bout but they left simultaneously, the later-arriving bird was regarded as the visitor. Furthermore, to exclude from visits returns to the nest occurring in the context of nest relief, the visitor's arrival had to have occurred >3 min after the end of its previous bout or its departure occurred >3 min from initiation of its next bout. Neither bouts nor visits had any minimum duration and, because we focused on nest attendance rather than incubation, we did not require parents to spend any minimum duration of time inside the nestbox (as opposed to being on the entry perch or roof) during bouts. In defining whether one parent was present vs.

absent when the other arrived or departed, we allowed a 3-min 'grace period' because arriving parents sometimes perched near the nestbox prior to landing on it, and parents sometimes seemed to depart upon detection of their mate's approach rather than waiting until the mate actually arrived. Thus, a partner was considered 'present' if it had been at the nest within 3 min of the arrival of the focal individual, and 'absent' if it had not, and a parent was considered to have left the nest before the return of the partner if its departure occurred more than 3 min before the arrival of its mate. 'Recesses' were defined simply as the interval between successive bouts of an individual. Events that were ongoing at the time the sample began or ended (such that we did not have accurate information on when a bird had arrived, ultimately departed, or had departed for a previous recess) were omitted from calculations of bout and recess durations.

Statistical Analyses

We used SAS version 8.1 and 9.1 (SAS Institute Inc., Cary, NC, USA) for analyses. In evaluating how individuals of each sex reacted to potential cues of partner reductions in effort, we relied on paired t-tests for cases where the events of interest were dichotomously distributed (e.g. we derived the difference between the mean bout durations of each individual when it was and was not relieved by its partner, then determined whether the mean of these differed significantly from zero). In analyzing changes in the behavior of individuals as a function of continuously distributed variables, we followed the approach of Dearborn (2001) and calculated a regression for each individual for which we had at least three data points to determine the slope of the relationship. We then used a t-test to determine whether these slopes, averaged across individuals, differed significantly from zero. When the focus was on the behavior of males or females, the individual was considered the unit of analysis; in tests examining the variation within and across pairs, we used the pair as the unit of analysis. Sample sizes based on the number of individuals differ from those based on the number of pairs because some individuals paired with different partners during the course of the studies; moreover, in examining the variation within individuals, sample sizes were necessarily restricted to the number of individuals for which we had data representing both conditions (for dichotomously distributed events) or multiple levels of the independent variable (for continuously distributed predictors). Means are

given ± 1 SD, all statistical tests are two-tailed, and we relied on non-parametric analyses when variables were not normally distributed.

Results

Bout Duration and Recess Duration

To determine if parents that have undergone lengthier bouts subsequently extend their next recess in possible ‘retaliation’ (Dearborn 2001), we analyzed recess durations as a function of the individual’s previous bout length. Female bout duration was not related significantly to subsequent recess duration ($\bar{x} \pm SD$ slope = -0.08 ± 0.647 min; 5.2 ± 2.14 cycles/female; t-test: $t_{44} = -0.84$, $p = 0.403$). The same analysis for unmanipulated males (5.1 ± 2.47 cycles/male) also yielded a negative slope (-1.40 ± 9.961 min), which, again, did not differ significantly from zero (t-test: $t_{47} = -0.97$, $p = 0.336$). Similarly, the duration of female bouts was not a function of the length of the previous recess ($\bar{x} \pm SD$ slope = -0.15 ± 1.19 min; 5.1 ± 2.10 cycles/female; t-test: $t_{46} = -0.91$, $p = 0.366$); the same was true for males ($\bar{x} \pm SD$ slope = -0.01 ± 0.358 min; 5.1 ± 2.15 cycles/male; t-test: $t_{48} = -0.10$, $p = 0.919$).

Potential Indirect Cues of Reduced Partner Effort: Lengthy Recesses

The sexes differed in the relative frequency with which they left the nest before their mate arrived; males were much more likely to do so than females (Table 1, $\bar{x} \pm SD$ difference = $14.4 \pm 32.67\%$, paired t-test: $t_{69} = 3.68$, $p = 0.0005$). To assess whether these unrelieved departures were responses to

Table 1: Descriptive statistics for male and female behaviors (unmanipulated pairs)

| | Male | | Female | |
|---|------------------|----|------------------|----|
| | $\bar{x} \pm SD$ | n | $\bar{x} \pm SD$ | n |
| Recess length (minutes) ^a | 13.8 \pm 5.53 | 64 | 12.0 \pm 5.10 | 62 |
| Bout length (minutes) ^b | 7.6 \pm 4.83 | 66 | 12.9 \pm 4.93 | 60 |
| Minutes at nest per hour | 16.1 \pm 8.77 | 70 | 31.2 \pm 8.25 | 70 |
| Unrelieved departures (proportion of bouts) | 0.39 \pm 0.266 | 70 | 0.24 \pm 0.239 | 70 |
| Visits per hour | 1.01 \pm 1.004 | 70 | 0.25 \pm 0.488 | 70 |

^aRecess lengths are based on 5.0 ± 2.64 samples/male and 6.1 ± 2.95 samples/female.

^bBout lengths are based on 6.5 ± 4.83 samples/male and 5.9 ± 3.08 samples/female.

Table 2: Comparisons of behaviors when parents left the nest before their partner returned (top) and arrived at an unattended nest (bottom)

| | Unrelieved departure ($\bar{x} \pm SD$) | Relieved departure ($\bar{x} \pm SD$) | Paired t | p |
|----------------------|---|---|-----------------|--------|
| Mate’s recess | | | | |
| Female | 18.7 \pm 8.42 | 13.3 \pm 4.36 | $t_{18} = 2.82$ | 0.012 |
| Male | 15.5 \pm 6.93 | 9.7 \pm 5.22 | $t_{45} = 5.21$ | <0.001 |
| Bout length | | | | |
| Female | 14.4 \pm 9.55 | 11.9 \pm 5.05 | $t_{40} = 1.85$ | 0.071 |
| Male | 5.4 \pm 3.44 | 8.0 \pm 4.61 | $t_{55} = 4.06$ | <0.001 |
| Next recess | | | | |
| Female | 10.0 \pm 7.50 | 10.6 \pm 3.98 | $t_{34} = 0.42$ | 0.680 |
| Male | 11.9 \pm 6.09 | 12.9 \pm 5.07 | $t_{43} = 0.84$ | 0.407 |
| | Mate present ($\bar{x} \pm SD$) | Mate absent ($\bar{x} \pm SD$) | Paired t | p |
| Next recess | | | | |
| Female | 10.1 \pm 4.08 | 10.9 \pm 7.39 | $t_{33} = 0.66$ | 0.515 |
| Male | 12.1 \pm 5.01 | 14.4 \pm 7.27 | $t_{39} = 2.33$ | 0.114 |

All durations are measured in minutes.

lengthy partner recesses, we compared the lengths of the partner’s recesses in cases where the focal individual left before the partner returned vs. waited for the partner. We also compared the bout durations and subsequent recesses of focal individuals when they were vs. were not relieved by their mate.

The mates of females that left before being relieved had been on significantly longer recesses than their recesses when the female waited (Table 2). Females tended to extend their bouts by approx. 2.5 min when leaving before their mate arrived, although this extension did not differ significantly from zero (Table 2). Most females subsequently took shorter recesses after unrelieved departures (sign test: $M = 7.5$, $n = 35$, $p = 0.017$) than they did when the male had relieved them; the differences in recess duration were very small, however, and not significantly different from zero (Table 2).

Similar analyses for males (Table 2) also showed that unrelieved male departures were associated with extended partner recesses. In contrast to females, though, when males left before the female returned, they left significantly earlier than when they waited for their mate. Males appeared not to modify how long they remained away from the nest after unrelieved departures (Table 2). In sum, lengthy partner recesses are associated with unrelieved departures for unmanipulated individuals of both sexes. When females left before their mate

returned, they tended to extend their bouts a little, and most then took slightly shorter recesses. When males left before their mate returned, they did so earlier than when they waited for their partners.

Potential Indirect Cues of Reduced Partner Effort: Arriving Parent Responses to Absent Partners

Parents that return to the nest to find their partner absent could conceivably shorten their next recess in response, thereby pre-emptively reducing the time the nest is left untended. We compared within individuals the duration of the next recess individuals took after returning to the nest and finding their mate present vs. absent (Table 2), and found that neither males nor females modified significantly their recess length after having arrived to find the nest unattended, although males tended to take longer recesses under that circumstance.

Effects of Testosterone on Recess Lengths and Unrelieved Departures

As previously reported (Schwagmeyer et al. 2005), T-implants substantially reduced male contributions to nest attendance on a minutes per hour basis, while their mates significantly increased their minutes per hour at the nest. As shown in Table 3, females paired to T-males shortened their recesses and had marginally longer bouts than females paired to C-males, while T-male declines in nest attendance occurred via both reduced bout durations (which were not associated with any change in frequency of leaving the nest before their mate returned: Table 3) and prolonged recesses. If unrelieved departures by females are a response to their mate's failure to return to the nest in a timely manner, we expected that their incidence would be elevated among T-females. Females paired to T-males left the nest before their mate returned about as frequently as their mates, and significantly more often than C-females (Table 3).

Direct Interactions among Mates: The Role of Partner Visits

Unmanipulated males visited females 0.39 ± 0.501 times/female bout ($n = 60$ females, 5.9 ± 3.08 bouts/female). Analyses of female bout durations as a function of male visits showed that, in the absence of any male visit, female bouts lasted 10.5 ± 4.54 min, with an average increase of 5.5 ± 6.32 min/male visit (6.6 ± 3.07 bouts/female;

Table 3: Differences in nest attendance behavior of T- and C-males and their mates

| | T ($\bar{x} \pm SD$) | C ($\bar{x} \pm SD$) | Test | |
|--|------------------------|------------------------|------------------|-------|
| | | | Statistic | p |
| Recess length ^a | | | | |
| Male | 18.9 ± 6.20 | 13.2 ± 5.31 | $z = 3.05$ | 0.002 |
| Female | 9.4 ± 4.14 | 12.0 ± 5.84 | $z = 2.17$ | 0.030 |
| Bout length ^b | | | | |
| Male | 5.0 ± 6.30 | 7.9 ± 5.22 | $z = 2.52$ | 0.012 |
| Female | 14.5 ± 6.38 | 11.8 ± 5.07 | $z = 1.72$ | 0.084 |
| Unrelieved departures (proportion bouts) | | | | |
| Male | 0.42 ± 0.249 | 0.40 ± 0.265 | $t_{36} = -0.25$ | 0.800 |
| Female | 0.42 ± 0.267 | 0.26 ± 0.211 | $t_{41} = -2.17$ | 0.036 |
| Visits paid/partner bout | | | | |
| Male | 0.61 ± 0.512 | 0.27 ± 0.235 | $z = 2.63$ | 0.009 |
| Female | 0.01 ± 0.048 | 0.14 ± 0.207 | $z = 3.12$ | 0.004 |

$n = 21$ C-males, 22 females paired to C-males, 17 T-males, 21 females paired to T-males.

^aRecess lengths are based on 6.0 ± 3.50 samples/C-male, 7.1 ± 3.51 samples for the mates of C-males, 4.5 ± 2.65 samples/T-male, and 6.3 ± 3.33 samples for females paired to T-males. Mean T-male recess duration is probably an underestimate.

^bBout lengths are based on 8.5 ± 4.51 samples/C-male, 6.6 ± 3.61 samples for the mates of C-males, 7.4 ± 4.03 samples/T-male, and 5.8 ± 3.36 samples for females paired to T-males.

t-test for mean slope: $t_{40} = 5.54$, $p = 0.0001$). From focal male data, this increase in female bout duration allowed males that visited at least once to extend their recesses by an average of 8.9 ± 9.13 min relative to recesses in which they did not visit (paired t-test: $t_{35} = 5.86$, $p < 0.0001$). There was no apparent effect of male visits on female recesses: females that were not visited by their mates during a bout later took a recess averaging 10.7 ± 4.69 min, and the change in recess time with each additional male visit averaged -0.7 ± 5.52 min (5.6 ± 2.33 recesses/female; t-test for mean slope: $t_{30} = -0.74$, $p = 0.4625$).

Unmanipulated males received visits from their partners at a mean frequency of 0.10 ± 0.203 visits/male bout ($n = 66$ males, 7.6 ± 4.83 samples/male). Analysis of how long males remained at the nest as a function of the number of times they were visited by their mates showed that, on average, males with no visits remained for 8.1 ± 4.00 min, with each female visit adding an additional 9.2 ± 5.09 min to the male's bout ($n = 21$ males, 8.2 ± 4.33 bouts/male). Thus, a single visit by a female to her mate more than doubled how long he remained at the nest (t-test for mean slope: $t_{20} = 8.31$, $p < 0.0001$). From the focal female data, this extended female recesses by a mean of 12.3 ± 8.95 min (paired t-test: $t_{30} = 5.83$,

$p < 0.001$). Additionally, visited males reduced their next recess: male recesses after bouts lacking visits averaged 12.1 ± 3.23 min, and males shortened their next recess by 3.0 ± 4.67 min/female visit (6.1 ± 3.53 recesses/male; t-test for mean slope: $t_{16} = -2.69$, $p = 0.0162$).

Visits: Coercion or Generosity?

For both sexes, then, partner visits are associated with extension of the on-duty parent's bout and hence lengthening of the visiting partner's recess. The sexes differ in frequencies of visitation: males visit females about four times more often than females visit males (Table 1). Within pairs, there was a strong male bias in visit rates (paired t-test: $t_{69} = 4.93$, $p < 0.0001$), and across pairs, male and female visit rates were negatively correlated (Pearson correlation: $r = -0.29$, $p = 0.0165$, $n = 70$ pairs). Given that visits basically consist of returns to the nest without subsequent assumption of responsibility, there are two possible interpretations of them. One is that visits represent offers of relief to the on-duty parent, which are then declined; the other possibility is that visitors are verifying the partner's presence at the nest (or are accompanying their partner to the nest), but not offering relief. If visits are offers of relief, then their timing relative to the visitor's previous bout should be very similar to the average length of recesses that are not extended by visits. For females, this appears to be the case: on average, females arrived at the nest for visits 10.7 ± 6.66 min after their previous bout, which did not differ significantly from their mean recess length when they had not visited the nest ($\bar{x} \pm SD$ difference = 0.5 ± 8.21 min, paired t-test: $t_{17} = 0.24$, $p = 0.8115$). For males, however, the interval between bout termination and arrival for a visit averaged 2.3 ± 8.03 min shorter than recesses lacking visits. Although this difference was not significant (paired t-test: $t_{35} = 1.73$, $p = 0.0931$), the majority of males (28/36, 77.8%) returned for visits earlier than they returned for bouts (sign test: $M = 10$, $p = 0.0012$, $n = 36$).

Effects of Testosterone on Visits

We compared the visit behavior at nests of T- and C-males as an additional means of assessing whether visits do or do not represent offers of relief. If male visits are offers of relief, we expected T-males to visit less than C-males; on the other hand, if male visits are verification (and perhaps enforcement) of part-

ner presence, we predicted that T-males would visit more frequently than C-males. For females, we assumed that if visits represent offers of relief, T-males would seldom turn those down, such that female visits to T-males should occur more rarely than visits to C-males.

Female visits were more common in pairs with C-males than in pairs with T-males (Table 3). Only 2 of 21 females paired to T-males ever visited them during our sampling, whereas 12 of 22 females with C-male partners visited them at least once. When female visit rates were calculated in terms of their opportunity for occurrence (the number of times per hour females returned to the nest and the male was present), female visits to T-males remained significantly rarer, occurring on $3.5 \pm 10.92\%$ of opportunities vs. $12.7 \pm 13.43\%$ for the mates of C-males (median two-sample test: $z = 2.78$, $n_C = 21$, $n_T = 20$, $p = 0.0055$). A different pattern emerged for male visits: T-males visited about twice as frequently as C-males (Table 3).

Sources of Partial Compensation

To evaluate how well visits by both sexes and female departures without relief can collectively predict female compensatory responses, we used female bout and recess durations from pairs with C-males as a baseline and computed predicted deviations from those for females paired to T-males. Among unmanipulated females, a male visit increased female bouts by 5.5 min. T-males averaged 0.34 visits/female bout higher than C-male visits, leading to an expected shift upward of 1.9 min in the bout lengths of females paired to T-males. Females with T-males as mates visited them less often (0.13 times/male bout less frequently than females paired to C-males); given that unmanipulated female recesses were extended by an average of 12.3 min/female visit, the predicted decline in recess durations of females with T-male partners is 1.6 min. Finally, females paired to T-males left the nest before their mate returned in an increased proportion of their bouts (0.16 more than the mates of C-males). When unmanipulated females left in these circumstances, their bouts lasted 2.5 min longer, for a predicted increase in the bouts of females paired to T-males of 0.4 min (but see below). In sum, females with T-males as mates were expected to reduce their recesses by 1.6 min (vs. observed decrease of 2.6 min) and increase their bouts by 2.3 min (observed = 2.7). Extrapolating from bout and recess durations to estimated minutes per hour at the nest, females paired to

C-males tended the nest for approx. 29.7 min/h [=11.8/(12.0 + 11.8)* 60 min/h]. The predicted increase in nest attendance by the mates of T-males was approx. 4.8 min/h higher (14.1/(10.4 + 14.1)* 60 min/h = 34.5 min/h), which is relatively close to the 5.5 min/h observed increase (Schwagmeyer et al. 2005).

Discussion

House sparrow parents sharing the task of nest attendance during incubation obviously do not coordinate their efforts perfectly with their partners: individuals of both sexes sometimes leave the nest before their mate returns, with females being less likely than males to do so. Unrelieved departures from the nest by both sexes are associated with one potential cue to decreased partner contributions, namely, lengthy partner recesses. Females appear to compensate partially for long male recesses by marginally extending their bouts; most females also shorten their next recess, but only slightly. The existence of a causal relationship between lengthy male recesses and the likelihood that females will leave before their mate returns is supported by results from experimental manipulation of male T: both T-male recesses and the rate of their partners' unrelieved departures were significantly increased relative to controls.

The indirect effect of lengthy male recesses on female bout and recess durations contributes little to the predicted difference in the nest attendance of females paired to T- vs. C-males, however. Indeed, if we omit the predicted extension of female bout durations associated with lengthy T-male recesses, the effect is trivial, reducing the expected difference in female minutes per hour at T- and C-male nests by only 0.4 min. The differences between T- and C-female nest attendance are also not likely to stem from female reactions when they return to the nest and discover their partner is absent: unmanipulated females did not significantly modify the length of their next recess in that circumstance.

Instead, the factors generating the majority of the predicted discrepancy in nest attendance of females paired to T- vs. C-males were differences in visit rates of T- and C- pairs. In unmanipulated pairs, male visits occurred relatively often and were associated with extensions of both male recesses (by nearly 9 min) and female bouts (by approx. 5.5 min). Most males returned to the nest earlier for visits than for bouts, and T-treatment doubled the

rate of male visits. Some male visits occur simply when males return to the nest to add nesting material; this seems unlikely to account for the observed difference in T- and C-male visit rates, however, because T-males delivered nesting material at non-significantly lower frequencies per hour than C-males (Schwagmeyer et al. 2005). In sum, these results offer little support for the hypothesis that visiting males are communicating their willingness to relieve their partner.

Female visits, on the other hand, actually do seem to represent offers of relief that are declined by males. Female visits were associated with a prolonging of male bouts by approx. 9 min, increases in female recesses of approx. 12 min, and a significant reduction in the length of a visited male's next recess. The timing of female returns to the nest for visits was very similar to that of female returns for bouts. Moreover, female visits were virtually non-existent among T-treated pairs. These features of female visits and male contributions after visits imply that the males that permit female visits are those that are most committed to nest attendance: female visits, by definition, cannot occur unless the male remains at the nest after his mate arrives. In other species, male behavior during incubation has been linked to perceived opportunities to acquire additional social mates or extrapair fertilizations (see Smith 1995; Magrath & Elgar 1997; Komdeur et al. 2002). Alternative factors that may influence male behavior during incubation include their own and their mate's condition (Gorman & Nager 2003; Lislevand & Byrkjedal 2004; see also Barta et al. 2002; Houston et al. 2005), clutch size (e.g. Komdeur et al. 2002; Larsen et al. 2003), and the duration of the relationship. It would be interesting to know the impact of these factors on within-pair behavioral dynamics. Similarly, female contributions may change according to ambient temperature (and did so for females paired to C-males: Schwagmeyer et al. 2005), and it would be useful to examine how temperature affects a female's responsiveness to her mate's contributions. The limited nature of our sampling precluded us from doing so.

Taken together, our findings indicate that the bulk of the partial compensation of females for the reduced nest attendance of T-males resulted from changes in the nature and frequency of interactions between mates, rather than female responses to indirect cues of male declines in effort. We had previously noted that exogenous T altered one aspect of the relationship between mates: T-males were more likely to behave aggressively toward their mates

than C-males (Schwagmeyer et al. 2005). This raises the possibility that there may be some element of coercion occurring during male visits and, consequently, that the outcomes of negotiations over house sparrow nest attendance may hinge on the relative dominance of pair members.

Finally, although it is clear that the nest attendance behavior of male house sparrows is influenced by interactions with their mates, we found no indication that males compensate either when they arrive at the nest and find that their mate is gone or when their mate takes a lengthy recess. In the first situation, unmanipulated males tend to extend their next recess; in the second circumstance, males reduce their bouts, and they could not possibly be reacting directly to the females' prolonged recess because they do not experience it. One possible explanation for the reduced bout lengths of males when their mates are on lengthy recesses is that females increase their recesses as a reaction to some environmental factor (e.g. ambient temperature: Conway & Martin 2000), and males abbreviate their bouts in response to the same environmental cue. Experimental manipulations clearly would be helpful in interpreting male behavior. When Dearborn (2001), for example, provided incubating great frigate birds with supplemental food during lengthy shifts, they subsequently took relatively shorter recesses than they typically would, supporting the hypothesis that recess length is chiefly driven by the need to regain lost body mass rather than a retaliatory response to having been left on an extended shift. Supplemental feeding had less effect on males than on females, though, and Dearborn (2001) left open the possibility that some element of retaliation may underlie male responses. For house sparrows, we would be especially interested in knowing whether males confronted with reduced female nest attendance would respond by increasing their own efforts, or whether they would simply boost their visits to their partner.

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