

Biparental care in house sparrows: negotiation or sealed bid?

P. L. Schwagmeyer,^a Douglas W. Mock,^a and Geoffrey A. Parker^b

^aDepartment of Zoology, University of Oklahoma, Norman, OK 73019, USA, and ^bPopulation and Evolutionary Biology Research Group, School of Biological Sciences, University of Liverpool, PO Box 147, Liverpool L69 3BX, UK

We explored the responses of monogamous house sparrow parents to deviations in their mates' contributions to nestling provisioning. Following 1–2 days of baseline measurement of parental food delivery rates, we applied small lead fishing weights to the tail feathers of either male or female parents. Weighting had much greater immediate impact on male parental care than on female care, but the handicapping had little long-term effect on either male or female provisioning behavior. When parental performance of handicapped males was most impaired, their mates did not show significant increases in parental care as compensation, nor did females mated to handicapped males reduce their provisioning as their mates recovered from weighting. Similarly, males mated to handicapped females did not respond to their partners' recovery with declines in their own efforts; paradoxically, these males showed a sustained elevation of provisioning throughout the post-treatment interval, despite no significant reduction in provisioning by weighted females. The apparent insensitivity of both males and females to changes in their mates' parental behavior, and the ineffectiveness of current partner behavior at predicting an individual's provisioning effort, fail to conform to assumptions of biparental care models that require facultative responses to partner deviations in effort. Instead, the remarkable consistency of each individual's behavior supports the notion of "sealed bids" and suggests that variation in nestling provisioning is largely attributable to factors that are independent of the mate's current behavior, such as differences in individual quality. *Key words:* biparental care, evolutionarily stable strategy, house sparrows, monogamy, parental care, *Passer domesticus*. [*Behav Ecol* 13:713–721 (2002)]

Evolutionarily stable biparental care represents a compromise between the genetic interests of mothers and fathers. Except in cases of true monogamy (defined as a pair mating exclusively with each other for life; Parker, 1985), sexual conflict over how much each individual contributes is inescapable. Neither parent gains as much from cooperation as it might by parasitizing its current partner completely, but instead each gains the most it can once its mate's investment is considered. Generally, evolutionarily stable strategy (ESS) models have predicted that for biparental care to be stable, individuals should never respond to a reduction in their partner's effort by raising their own effort enough to make up the difference fully. Thus, if one pair member reduces its effort by a single unit, its partner should respond with an increase of less than 1 unit (Chase, 1980; Houston and Davies, 1985; Parker, 1985). Chase (1980) clearly viewed such adjustments as a bargaining process, whereby each individual responds facultatively to the current workload of its mate with its own best response until ESS expenditure levels are reached (see also Winkler, 1987). Such facultative adjustments could be based either on direct observation of the partner's level of effort or, alternatively, parents could use indirect cues of their partner's effort, such as offspring hunger or condition (Chase, 1980; Houston and Davies, 1985).

Recently, however, McNamara et al. (1999) have pointed out that all these ESS biparental care models are structured such that each parent plays a fixed effort throughout its reproductive life, rather than a level of effort that is adjusted for changes in its partner's expenditure. In these "sealed en-

velope" (Houston and McNamara, 1999) or "sealed bid" models, adjustments in the levels of effort of each sex occur through evolutionary responses (i.e., through invasions by deviant strategies for reproductive effort, rather than through responses during a given episode of breeding). The new model of McNamara et al. (1999), in contrast, allows parents to negotiate—to modify their effort sequentially in direct response to the prior effort of their mate. McNamara et al. (1999) showed that, when biparental negotiation occurs, the general prediction that parents should compensate only partially for reductions in their mate's effort still holds, but the predicted levels of compensatory responses of parents to reductions in their mate's effort are reduced relative to predictions from the earlier sealed bid models.

Whether parents play an expenditure level that is independent of their mates' contributions or respond directly to each other's efforts is an empirical issue that has important implications for theoretical predictions. Certainly, several studies have indicated that, when a mate has been removed completely, widowed birds increase their effort, demonstrating sensitivity to the total absence of a partner (reviewed in Bart and Tornes, 1989; Gowaty, 1996). As pointed out by Wright and Cuthill (1989), however, mate removal experiments do not offer much insight into the dynamics of biparental negotiations over effort levels. As alternatives to mate removal, techniques wherein particular partners are merely handicapped have been used, with an emphasis on testing the prediction that partners of handicapped mates should never react to the handicapped individual's reduction in effort by compensating fully. These studies typically have measured the compensatory response (Wright and Cuthill, 1989) as the post-treatment discrepancy in provisioning at experimental and control nests. Thus far, three patterns have emerged from handicapping experiments (reviewed in Sanz et al., 2000): (1) partial compensation, wherein partners of handicapped birds provision at higher rates than controls, but total feeding rates remain sig-

Address correspondence to P.L. Schwagmeyer. E-mail: pls@ou.edu.

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nificantly lower than at control nests (e.g., Markman et al., 1995); (2) no compensation (i.e., no significant difference between the feeding rates of partners of handicapped birds and control birds; e.g., Slagsvold and Liffeld, 1988, 1990; Saether et al., 1993); and (3) counter to the prediction for any but truly monogamous birds, apparently complete compensation (partners of handicapped birds provision at higher rates than controls, and total provisioning rates at experimental and control nests do not differ significantly; e.g., Wright and Cuthill, 1990a,b). Results showing either partial or complete compensation suggest that parents do, in fact, respond either directly or indirectly to their mate's efforts, whereas the absence of a compensatory response (pattern 2) implies that an individual's parental effort is more or less fixed independently of its partner's contributions.

One goal of our study was to determine how house sparrows, *Passer domesticus*, of each sex respond to changes in their mates' parenting contributions. A second goal was to examine simultaneously how handicapping, which presumably increases the costs of provisioning young, affects the level of care provided by the handicapped partner. A variety of sealed bid models have predicted that parents should reduce their effort when faced with either increases in the unit costs of care or declines in the expected number of offspring produced per unit effort (Chase, 1980; Houston and Davies, 1985; Winkler, 1987). Handicapping experiments have, indeed, typically yielded reductions in the handicapped parent's provisioning rate (reviewed by Sanz et al., 2000), although these have not always been statistically significant (e.g., Wright and Cuthill, 1990b; Sanz et al., 2000). Sanz et al. (2000) suggested that three optimal responses to being handicapped exist: a decrease in effort, no change, or even an increase in effort. In the latter two responses, individuals sacrifice personal survival in exchange for maintaining or increasing their parental care, and according to the Sanz et al. (2000) model, which of the three responses is favored can hinge on how sharply parental survival decreases with total effort expended.

We used the tail-weighting technique developed by Wright and Cuthill (1989) to examine the effects of handicapping on the responses of burdened individuals of both sexes and on the responses of their partners. We used a repeated-measures design, which allowed us to assess how much handicapped individuals modified their effort relative to their previous effort; similarly, the reactions of their partners could be analyzed in terms of changes across time in their own and their mates' delivery rates to take into account individual variation in baseline levels of provisioning effort.

MATERIALS AND METHODS

We conducted the study across five field seasons, 1995–1999, at two study sites on the outskirts of Norman, Oklahoma, USA. Pairs of house sparrows at these sites produce up to four broods per year; they routinely begin laying in late March and typically end breeding in mid- to late July. We censused nest-boxes twice weekly from mid-March through early August to determine clutch size and anticipated hatching date, brood size, and fledging success. As the anticipated day of hatching approached, we further resolved the actual hatch date by daily or alternate-day visits to nests.

Following the method of Wright and Cuthill (1989), our handicapping procedure consisted of attaching small, lead, split-shot fishing weights, totaling an average of 5–7% of typical adult mass, to the base of tail feathers. The technique is believed to act primarily by disrupting balance (Wright and Cuthill, 1989). In 1995 we used two weights per bird that totaled 1.6 g; however, we found that some birds recaptured within a few days after attaching the weights had either lost

one or both of the feathers to which the weights were attached or had lost the weights. We omitted data from such birds and subsequently verified retention of weights by (1) applying weights that had been painted with nail polish so that they were detectable at a distance when viewed with a spotting scope; (2) detecting abnormal skewing of weighted tail feathers; and (3) for 4/20 weighted females and 6/24 weighted males, recapturing the bird. To reduce further the impact of any single weight being lost, we applied four smaller (0.5 g) weights during 1996–1999. Birds that lost more than one of the four weights were excluded from analyses.

We used pairs with either four-egg or five-egg clutches for treatments. Within each clutch-size category, we assigned treatments to particular nests (MW = male weighted, FW = female weighted, C = control) according to a sequence established at the outset of each field season. We omitted from analyses data from pairs that lost their broods before day 8 of the nestling period due to predation, nest takeover, or inclement weather; such losses typically occurred early in the nesting cycle before treatment. We also omitted data from pairs in which either or both parents disappeared (in apparent association with capture or not) before day 8 of the nestling period (two C pairs; one MW pair, one MW female; two FW males) or in which the male was simultaneously polygynous (one MW male). Toward the end of each season, when new breeding attempts became less frequent, we attempted to equalize sample sizes across treatments by treating additional nests in whichever category had suffered the greatest losses; the exception to this occurred in 1995, our initial year, when we observed additional C nests in an effort to equalize sample sizes for simultaneously ongoing measurements of parental energetic expenditures. From 1996 to 1999, seasonal sequences of treatment were established so that each began with the treatment that had the lowest sample size to date. Across the 5 years, the numbers of pairs per treatment totaled 24 MW, 20 FW, and 27 C (1995: 5 MW, 1 FW, 6 C; 1996: 4 MW, 5 FW, 5 C; 1997: 6 MW, 5 FW, 5 C; 1998: 3 MW, 3 FW, 5 C; 1999: 6 MW, 6 FW, 6 C). With the exception of two birds of each sex that we failed to capture, both members of each pair were color-banded for identification, and none of the banded birds served as subjects more than once during the 5-year study. Mean \pm SD clutch sizes were 4.63 ± 0.49 at C nests, 4.65 ± 0.49 at FW nests, and 4.54 ± 0.51 at MW nests. The mean Julian date of hatching was 160 ± 27.3 for broods at C nests, 153 ± 19.6 at FW nests, and 155 ± 24.8 at MW nests.

We observed parental feeding of nestlings for 1–3 h per day at each nest, with behavioral sampling beginning on the 3rd or 4th day after the day hatching had begun (day 0) and continuing through the 10th day. The daily scheduling of samples was based on a preliminary study indicating which hours of the day provided data on parental food delivery rates that reliably predicted both between-nest differences in parental behavior and within-nest changes across days in parental food delivery rates (Schwagmeyer and Mock, 1997). During each hour's sample, we recorded the time (to the nearest second) at which a parent arrived at or departed from the nest, its sex, and the size of prey delivered. We gauged prey size relative to the width of the parent's bill and categorized prey as $< \sim 0.6$ cm (S = small), ~ 1 cm (M = medium), $\geq \sim 2$ cm or larger (L = large, usually large orthoptera or large lepidopteran larvae), or none, seed, or bread. (Seed and bread were provided for trapping; see below.) We also recorded whether the parent entered the nestbox to remove fecal sacs or feed the young (versus feeding from the perch), and the approximate distance it flew as it departed (categorized as $\leq \sim 10$ m of the nest, ~ 15 – 30 m from the nest, or $> \sim 30$ m from the nest). Interobserver agreement averaged 94.6% (range = 88.2–100%) for total number of parental visits per hour, and 97.9%

(range = 92.9–100) for sex of the visiting parent (both $n = 6$ pairs of observers).

We usually began attempting to ground-trap females that were to be weighted, males that were to be weighted, or either parent of C pairs between the afternoons of days 4 and 5 after hatching. We were able to capture about half of the birds that were to be weighted (and about half of C parents) in either walk-in ground traps or mistnets; when we failed to do so, we resorted to using a remote-controlled trap (Mock et al., 1999) to capture them in their nestboxes so that weighting was accomplished no later than day 6 after hatching. The modal time of capture and weighting at both MW and FW nests was the afternoon of day 5. Accordingly, days 3–5 after hatching were considered pretreatment for C parents, and from day 6 on were considered as post-treatment. We omitted from analyses any behavioral samples in which recently captured parents had not returned to the nest vicinity. Pretreatment sampling per nest averaged 4.95 ± 1.05 h at FW nests, 5.50 ± 1.67 at MW nests, and 5.89 ± 1.15 at C nests; post-treatment sampling per nest averaged 9.95 ± 2.89 , 9.83 ± 2.46 , and 8.67 ± 1.44 h at FW, MW, and C nests, respectively.

Control parents, as well as partners of weighted individuals, received the same handling (body mass measurement, banding for subsequent identification) as weighted parents, except that they did not have weights applied. A subset of 20–30% of the individuals of each sex in each treatment also received upon capture an injection of doubly-labeled water for energy analyses, and these birds were then trapped at the nest subsequently (usually 48 h after injection) for blood sampling. Because we feared that capturing the birds twice in their nests would increase desertion risk (and because individuals seldom enter a ground trap if they have been ground-trapped previously), we allowed weighted birds simply to shed their weights when they molted. Also, to avoid desertion, the subset of birds used for energetic analyses was restricted to individuals that initially had been captured in ground-traps or mistnets (with two exceptions: one 1996 C male, one 1995 C female).

In 1997–99, we weighed nestlings to the nearest 0.1 g on the afternoons of days 5, 7, and 9. Nestlings in all years were banded and weighed on day 11 after hatching. Once nestlings had been banded, we observed their nests at least once every 2 days to determine whether the chicks were still visible at the nest entrance and/or parents were continuing to provision. We excluded from fledging date analyses records from nests that we inadvertently failed to check on at least alternate days.

Means are reported with standard deviations, and all significance values are based on two-tailed tests. For comparisons of continuously distributed behavioral variables among groups across time, we first calculated pre- and post-treatment means per sample hour at each nest, and then converted these to mean differences across time (post-treatment minus pretreatment) at each nest. One-way ANOVAs (GLM; SAS version 6.12) were then used to test for significant differences among the three groups, and Dunnett's tests were used to evaluate the overlap in 95% CI between FW or MW nests with C nests. Sex differences in response to weighting were analyzed via ANCOVA (SAS GLM). We used logistic regression to analyze brood reduction events. For analyses of the sources of individual variation in parental care at particular stages of the nesting cycle, we used multiple linear regression (SAS REG) with a stepwise selection procedure. Preliminary analyses were used to evaluate the impact on response variables of uncontrolled factors such as original clutch size, julian date, and brood size; these were included in final models as appropriate.

RESULTS

Long-term effects of the manipulation

The results of ANOVAs comparing the three groups in the changes in behavior that occurred across the entire pre- and

post-treatment intervals are shown in Table 1. As indicated by the overall F values, the manipulation created few persistent differences among the three groups. Briefly, we found little indication that the handicapping of females produced any sustained impairment of their provisioning behavior, their foraging behavior, or their nest attendance; similarly, the decline in parental care by weighted males was relatively slight, producing a nonsignificant decrease in provisioning rate (relative to controls), coupled with a significant reduction in the proportion of large prey that they delivered. At MW nests, the slight decline in deliveries by males was offset by a nonsignificant increase in female deliveries; at FW nests, males dramatically increased their provisioning, despite no overall decrease by their handicapped mates. Chicks at FW nests consequently experienced significantly greater gains across time in food delivery rates than chicks at C nests.

As shown in Table 2, mean nestling mass on day 11 after hatching was similar among the three groups, as were the mean gains in mass by chicks from days 5 to 7 and from days 7 to 9 (Figure 1). Overall, only chicks at MW nests showed any possible growth impairment, and this was restricted to the interval between days 9 and 11 after hatching, when chick mass was reaching an asymptote (Figure 1).

Brood reduction and subsequent differences in brood size clearly could influence nestling growth patterns, and post-treatment mortality before day 11 of the nestling period occurred in approximately 32% of the nests in this study (22 of 68, after eliminating data from two C nests that sustained partial predation, plus 1 FW nest where the male disappeared between days 9 and 10 after hatching). Neither FW nor MW nests differed significantly from C nests in the occurrence of chick loss, either before day 11 or before fledging (Table 3). Nor were there any significant differences among groups in the number of days elapsing before fledging or in the interbrood interval or subsequent clutch size of females that bred again that season (Table 2).

Short-term responses to manipulation and predictors of partner responses

In contrast to the rather minimal effects of the experimental manipulation on the behavior of weighted individuals revealed by simple pre- and post-treatment comparisons, more dramatic changes in behavior occurred across the days immediately before weighting (second half of the pretreatment period = late pre-W) and the day after weighting (early post-W; Figure 2A,B). The delivery rates of weighted males fell by an average of about 40%, which differed significantly from C male behavior (Figure 2B). Weighted females showed a much smaller, nonsignificant reduction (from late pre-W to early post-W) in total food deliveries (Figure 2A). The decline in weighted female provisioning rate was more exaggerated if seed and bread items were eliminated from the tally of food deliveries, but it still remained relatively slight (mean hourly reduction by FW females = 1.18 ± 3.83 ; mean increase by C females = 1.16 ± 3.24 ; FW vs. C, $p < .05$).

Within each sex, substantial individual differences in the immediate response to being handicapped occurred. As shown in Figure 3, some individuals actually increased their per-chick delivery rates after weighting, whereas others reduced their deliveries. Responses to weighting were contingent on variation in provisioning rates before weighting: For both sexes, the previous days' delivery rate of an individual was strongly predictive of its rate the day after weighting (Figure 3). ANCOVA revealed that preweighting provisioning levels had parallel effects within each sex on responses to handicapping, but weighted males reduced their provisioning significantly more sharply than weighted females (Figure 3).

Table 1

Post- versus pretreatment mean \pm SD changes in delivery rates, type of food delivered (proportion of deliveries of seed or bread; proportion of deliveries with large prey), distance flown upon departing from nest (proportion far trips \geq 30 m), nest attendance (min/h at nest, visits with no prey), and nest entry behavior (proportion visits with nest entry), by group and parental sex

Variable	FW change	MW change	C change	<i>F</i> (df)	<i>p</i>
Total female feeds/h	+3.20 \pm 5.10	+3.16 \pm 2.97	+1.68 \pm 2.52	1.47 (2,68)	.2369
Total male feeds/h	+3.66 \pm 5.04*	-0.18 \pm 4.77	+0.22 \pm 2.93	5.30 (2,68)	.0073
Feeds per chick					
Female	+0.99 \pm 1.66	+1.17 \pm 1.15	+0.68 \pm 0.70	1.14 (2,68)	.3256
Male	+1.09 \pm 1.49*	+0.06 \pm 1.18	+0.18 \pm 0.67	5.43 (2,68)	.0065
Total parental feeds/h	+6.86 \pm 6.49*	+2.97 \pm 5.96	+1.91 \pm 4.18	4.91 (2,68)	.0102
Total feeds per chick	+2.09 \pm 2.09*	+1.23 \pm 1.50	+0.86 \pm 0.87	3.88 (2,68)	.0254
% Female feeds	-0.34 \pm 14.10	+14.11 \pm 16.03	+5.62 \pm 10.76	6.26 (2,68)	.0032
Proportion seed, bread					
Male	+0.02 \pm 0.15	-0.01 \pm 0.09	+0.01 \pm 0.12	0.56 (2,65)	.5728
Female	+0.05 \pm 0.09	+0.04 \pm 0.08	+0.01 \pm 0.09	1.21 (2,67)	.3039
Proportion large prey					
Male	-0.01 \pm 0.12	-0.06 \pm 0.15*	+0.03 \pm 0.12	3.04 (2,65)	.0548
Female ^a	+0.01 \pm 0.09	+0.05 \pm 0.12	+0.07 \pm 0.14	0.86 (2,66)	.4289
Proportion far trips					
Male	-0.04 \pm 0.17	-0.05 \pm 0.25	-0.06 \pm 0.29	0.04 (2,64)	.9622
Female	-0.06 \pm 0.17	+0.00 \pm 0.18	-0.01 \pm 0.21	0.72 (2,64)	.4909
Time at nest (min/h)					
Male	-4.02 \pm 3.36	-5.46 \pm 5.03	-4.05 \pm 3.25	1.03 (2,68)	.3634
Female	-7.95 \pm 6.19	-5.96 \pm 6.52	-6.17 \pm 3.86	0.83 (2,68)	.4408
Visits with no prey					
Female	+0.01 \pm 0.37	-0.27 \pm 0.83*	+0.17 \pm 0.55	3.20 (2,68)	.0472
Male	+0.00 \pm 0.37	-0.09 \pm 0.41	-0.08 \pm 0.50	0.29 (2,68)	.7471
Proportion with nest entry					
Female	-0.39 \pm 0.24	-0.29 \pm 0.24	-0.28 \pm 0.24	1.43 (2,67)	.2471
Male	-0.47 \pm 0.19	-0.41 \pm 0.27	-0.37 \pm 0.26	1.08 (2,67)	.3462

F and *p* values refer to differences among the three groups. FW, weighted female; MW, weighted male; C, control.

^a *F* test represents contribution of group after adjustment for Julian hatch date as a covariate.

* Cases in which changes across time at either FW or MW nests differed significantly from C levels based on Dunnett's tests.

Despite the significant reduction in delivery rates of handicapped males on the day after weighting, we found no significant compensatory increase by their mates (Figure 2A). Similarly, the increase in deliveries by FW males on the day after their mates were handicapped did not differ significantly from the change in behavior of C males on comparable days (Figure 2b). As a more sensitive analysis of how responsive parents were to their mates' behavior during this interval, we combined the data from partners of handicapped individuals and same-sex C partners and used multiple regression to determine the best predictors of the provisioning behavior of these birds during early post-W (i.e., the day after weighting

for FW males and MW females; day 6 after hatching for C males and females). In contrast to the previous ANOVA approach, this allows each bird's behavior to be evaluated relative to the behavior of its own mate. We used as potential predictor variables (1) the individual's own mean per-chick delivery rate during late pre-W; (2) their mate's mean per-chick delivery rate during late pre-W; and (3) their mate's current (early post-W) per-chick delivery rate. The first variable allows individual variation in previous provisioning rate to be taken into account; the third variable is expected to be negatively related to the mate's provisioning rate if parents respond to the current behavior of their partner, with a slope

Table 2

Mean \pm SD chick mass at day 11, days from hatching to fledging, interclutch interval (date on which first egg of next clutch was laid minus hatch date of previous brood), and subsequent clutch size, by group

Variable	FW	MW	C	<i>F</i> (df)	<i>p</i>
Mean mass, day 11 (g) ^a	23.26 \pm 2.85	22.76 \pm 1.76	22.79 \pm 3.21	0.41 (2,67)	.6685
Days to fledge ^a	15.41 \pm 1.28	15.72 \pm 2.11	15.46 \pm 1.76	0.23 (2,57)	.7981
Interclutch interval	27.25 \pm 5.52	26.00 \pm 3.32	27.25 \pm 3.02	0.26 (2,24)	.7762
Next clutch size	4.12 \pm 0.64	4.57 \pm 0.98	4.17 \pm 0.72	0.78 (2,24)	.4687

FW, female weighted; MW, male weighted; C, control.

^a *F* test for significant effect of group after adjustment for covariate of Julian hatchdate.

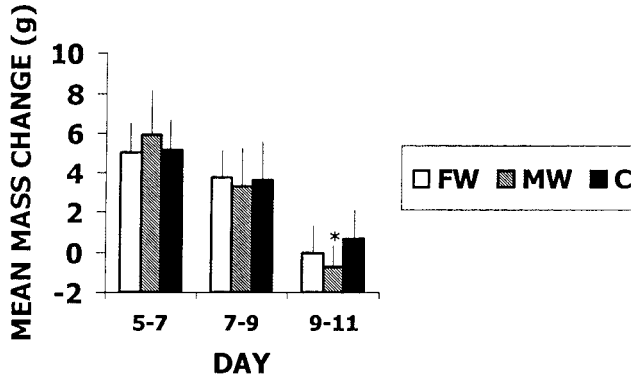


Figure 1

Mean gains or losses in mass of offspring at female-weighted (FW), male-weighted (MW), and control (C) nests across successive intervals. Bars represent SDs. ANOVAs showed no significant difference among groups for growth between days 5 and 7 after hatching ($F = 0.68$, $df = 2, 27$) or between days 7 and 9 ($F = 0.13$, $df = 2, 30$), but a significant difference between days 9 and 11 ($F = 3.38$, $df = 2, 31$, $p = .047$; MW vs. C: $p < .05$).

equal to the average reduction in effort per partner unit of effort; and the second variable might be expected also to show such a negative relationship if parents react mainly to the prior, rather than current, behavior of their mates.

The only significant predictor of the behavior of MW females plus C females at the early post-W stage was the females' own earlier per-chick delivery rate ($F = 37.52$, $df = 1, 49$, $p = .0001$; model $r^2 = .43$). Once that variable entered the model, female delivery rates tended to be negatively related to the current provisioning behavior of their mates, hinting at possible negotiation. However, the relationship was not significant ($F = 3.33$, $p = .07$) and explained little variation (4%) in female provisioning. Retrospective power analyses showed that power at the observed effect size was relatively weak (0.43), although our power for detecting an effect that was at least one-fourth as strong as that observed for the earlier behavior of each female (i.e., accounting for one-fourth the sum of squares explained by the female's own earlier behavior) was reasonable (0.89). Among C males plus males paired to weighted females, the only significant predictor of early post-W per-chick food delivery rates was each male's own late pre-W delivery rate ($F = 34.83$, $df = 1, 45$, $p = .0001$; model $r^2 = .44$). Once that variable was included in the model, the current delivery rates of their mates showed no significant effect on male provisioning ($F = 0.24$, $p = .625$). Thus, the extent of impairment of handicapped birds immediately after weighting had no strong impact on their partners' provisioning level.

Experimentally handicapped parents recovered quickly. Relative to their provisioning behavior the day after treatment, weighted parents of both sexes significantly increased their delivery rates across the remainder of the post-treatment interval (late post-W). Weighted females increased their deliv-

eries by roughly 40%, far exceeding changes in C female behavior (Figure 2A). Similarly, weighted males increased their feeding rate by more than 70%, compared to a slight decline by C males (Figure 2B). This recovery of handicapped birds between early post-W and late post-W was not accompanied by a slackening of their partners' efforts (Figure 2A,B). As above, we used multiple regression to determine how closely the behavior of unweighted birds of each sex during late post-W tracked that of their mates. We compared mate's and self's per-chick delivery rates during the entire pretreatment period; mate's and self's per-chick delivery rates during early post-W; and mate's current (late post-W) delivery rates as potential predictors. As above, the only significant predictor of what FW males plus C males did during the late post-W "recovery" phase of handicapped birds was what they had done earlier: per-chick delivery rates during early post-W accounted for 51.6% of the variation in late post-W delivery rates ($F = 47.95$, $df = 1, 45$, $p = .0001$). The counterpart analyses for MW females plus C females revealed two variables as strong predictors of late post-W delivery rates: the females' own per-chick delivery rates during early post-W ($F = 16.83$, $df = 1, 49$, $p = .0002$) was positively related to their later behavior and, once that variable had entered the model, the pretreatment delivery rates of their mates also were positively related to what females did ($F = 12.62$, $p = .0009$).

Overall sensitivity to mates' current and prior efforts

Finally, we asked how well, among all unweighted individuals, the provisioning level of the partner during the entire post-treatment period (early post-W plus late post-W) predicted the provisioning behavior of the focal parent during that interval; perhaps pair members evaluate each other's efforts over a longer time scale. The possible predictors we considered were (1) behavior of the individual during the entire pretreatment interval; (2) behavior of the individual's partner before treatment; and (3) partner's behavior during the entire post-treatment period. As before, the first variable allows individual variation in food delivery rate to be taken into account; once that has been done, the second and third variables test whether there is a negative relationship between the prior or current efforts of partners.

For C males combined with FW males, only each male's own per-chick delivery rate before treatment significantly predicted his later behavior ($F = 36.09$, $df = 1, 45$, $p = .0001$, model $r^2 = .445$). After accounting for the effects of the males' earlier behavior, the current provisioning of the males' partners was the next best predictor, but its effect was far from significant ($F = 0.30$, $p = .588$). Thus, as above, the best predictor of what a male did late was simply what he had done early. Among females (MW as well as C females), per-chick food delivery rates during the entire post-treatment interval were best predicted by the individual's own earlier parental behavior ($F = 19.36$, $df = 1, 49$, $p = .0001$). In contrast to males, however, female behavior was, again, also influenced significantly by their partners' efforts, specifically the pretreatment

Table 3

Mean \pm SD numbers of chicks lost post-treatment, by group, and results of logistic regression analyses, adjusted for both pretreatment brood size at each nest and Julian date

Variable	FW	MW	C	Wald χ^2		p	
				FW-C	MW-C	FW-C	MW-C
Losses to day 11	0.26 \pm 0.56	0.50 \pm 0.59	0.40 \pm 0.87	0.61	0.13	.435	.723
Losses to fledging	0.47 \pm 0.77	0.59 \pm 0.59	0.60 \pm 1.08	0.37	0.06	.544	.812

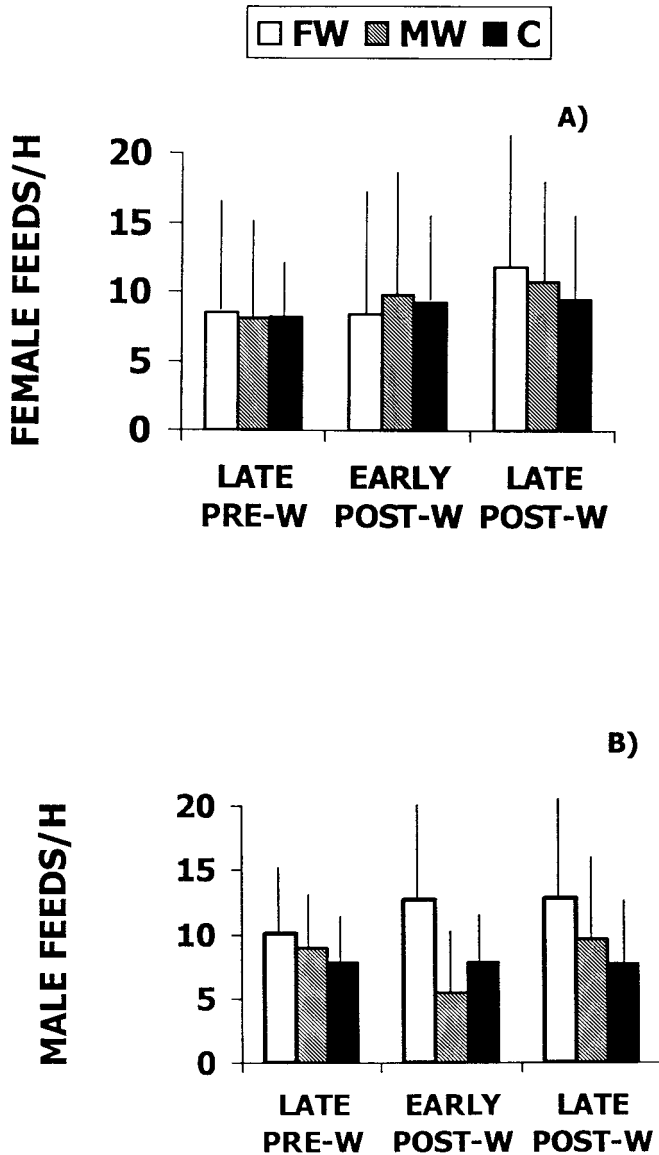


Figure 2
Mean (\pm SD) hourly delivery rates for (A) female and (B) male parents on the day(s) just before treatment (late pre-W, mean = 3.10 ± 1.04 h observation/nest), the day after weighting of females (FW) and males (MW; early post-W, mean = 2.32 ± 0.73 h observation/nest), and the remainder of the post-treatment period (late post-W, mean = 5.49 ± 1.36 h observation/nest). ANOVAs were used to examine differences among the three treatments in changes in delivery rates relative to the immediately preceding interval (overall F), and Dunnett's tests were used to compare differences between FW and control (C) and MW and C treatments in changes across time. (A) Female changes in delivery rates from late pre-W to early post-W: overall $F = 1.20$, $df = 2, 68$, $p = .31$; from early post-W to late post-W: overall $F = 4.93$, $df = 2, 68$, $p = .01$; FW vs. control, $p < .05$. (B) Male changes in delivery rates from late pre-W to early post-W: overall $F = 12.37$, $df = 2, 68$, $p = .0001$; MW vs. control, $p < .05$; from early post-W to late post-W: overall $F = 5.51$, $df = 2, 68$, $p = .006$; MW vs. control, $p < .05$.

delivery rates of their mates ($F = 8.18$, $df = 1, 48$, $p = .0062$). The relationship between early provisioning by males and their mates' subsequent behavior was positive ($y = 0.35 + 0.80$ feeds/chick early by female + 0.46 feeds/chick early by mate).

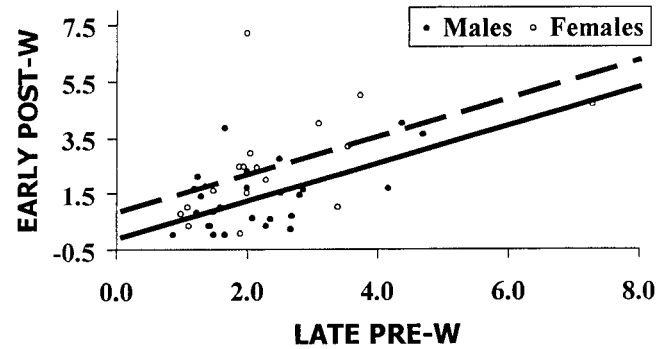


Figure 3
Relationships between preweighting delivery rates (late pre-W, feeds/chick) and weighted individual's delivery rates the day after weighting (early post-W). Regression results for weighted males (solid line): $F = 8.40$, $df = 1, 22$, $p = .0083$; $y = -0.03 + 0.63$ feeds/chick late pre-W; for weighted females (dashed line): $F = 6.71$, $df = 1, 18$, $p = .018$, $y = 0.82 + 0.65$ feeds/chick late pre-W. ANCOVA results for sex differences in the slope of the relationship between late pre-W and early post-W behavior: $F = 0.00$, $df = 1, 40$, $p = .954$; for sex differences in the intercepts: $t = 2.27$, $df = 42$, $p = .028$.

DISCUSSION

The goals of our study were twofold: (1) to determine how parent house sparrows respond to changes in their mates' contributions to parental care and (2) to evaluate how handicapped birds respond to the presumably increased costs of care associated with handicapping. With respect to (1), our results collectively showed that, contrary to the perspective that parents respond facultatively to changes in the effort levels of their mates, the provisioning behavior of both male and female parent house sparrows was relatively insensitive to their mates' current efforts. Instead, parents of both sexes showed a remarkable consistency across time in their delivery rates. Females, but not males, were also found to provision at levels that were affected by the prior efforts of their mates, but the relationship was positive, and thus counter to predictions from negotiation models. With respect to (2), we found that the immediate responses of handicapped males and females to the handicapping were very different, with males displaying a much greater impairment. Because the magnitude of such handicapping effects could easily influence our ability to detect responses by their partners (e.g., Sanz et al., 2000), we first discuss the effects of handicapping on handicapped birds, and then consider partner responses in terms of both negotiation and sealed bid models.

When changes in behavior occurring across the pre- and post-treatment intervals were evaluated (Table 1), between-group comparisons indicated that weighted males sustained a modest (and nonsignificant) impairment of their total delivery rates and a significant decline only in the proportion of large prey they delivered. Handicapped females showed sufficient recovery of parental function that their overall increase across time in provisioning was even slightly higher than that of control females. Our experimental manipulation apparently caused few long-lasting changes in either the behavior of handicapped individuals or the welfare of their broods.

In contrast, the effects of the manipulation on handicapped birds were more pronounced when scrutinized over shorter time scales. Compared to their behavior on the day(s) immediately before weighting, birds of both sexes reduced their total food deliveries once they had resumed provisioning. For both male and female house sparrows, responses to receiving weights were proportional to previous food delivery rates: par-

ents that had been provisioning at relatively high levels (presumably for reasons of competence, prey abundance, and/or brood quality) continued to do so after weighting relative to weighted birds that had provisioned at lower levels before treatment. Handicapped males showed a more dramatic short-term reduction in delivery rates than handicapped females: Males showed a statistically significant decline in provisioning rate, with females showing a significant effect only if seed and bread items were discounted. This sex difference parallels that discovered by Sanz et al. (2000) in great tits (*Parus major*), where feather clipping had more profound effects on male than on female delivery rates. In starlings (*Sturnus vulgaris*), however, males and females appear to respond similarly to weighting (Wright and Cuthill, 1989; 1990a,b). Theoretically, sex differences in response to increased costs of provisioning could stem from several factors that might vary between the sexes, including the relationship between increased parental effort and survival (Sanz et al., 2000; Slagsvold and Lifjeld, 1990), the availability of nonparental reproductive alternatives, and the compensatory response of the mate (Chase, 1980; Winkler, 1987).

In house sparrows, it seems unlikely that handicapped females reduced their provisioning less than handicapped males because their mates were providing meager levels of compensation. Indeed, the reactions of males whose partners were handicapped is the most paradoxical result of this study. The provisioning rates of FW males showed a significantly higher increase from pre- to post-treatment than C males (Table 1). Within the post-treatment interval (Figure 2B), FW males showed a nonsignificant elevation of deliveries at the time when their mates were most impaired (late pre-W to early post-W) and then, remarkably, they sustained that elevated rate (early post-W to late post-W), despite the subsequent recovery of their partners.

Previous handicapping studies typically have relied on between-group analyses of behavior after treatment, and based on those standards, the results in Table 1 would imply that the behavior of FW males constituted overcompensation, given that both total male and total parental delivery rates increased significantly more post-treatment at FW nests than at C nests. Patterns of either apparently complete or overcompensation, where the effect size of compensatory responses is equal to or greater than the effect size of handicapping, have been observed in previous studies (e.g., Ketterson et al., 1992; Sanz et al., 2000; Wright and Cuthill, 1990a,b). The pattern has interesting implications for the rules mediating parental provisioning behavior. First, assuming current models are correct in their assumptions, the pattern could be produced if handicapped birds shift their diet to lower quality prey, and their partners either observe that directly and adjust their reaction accordingly or base their compensatory response on feedback from malnourished chicks. Handicapped males in this study did, indeed, reduce the proportion of large prey they delivered (see also Wright and Cuthill, 1990a), and although we found no similar diet shift in weighted females, the females' immediate post-treatment reaction to handicapping was certainly more pronounced when artificial food sources (seed and bread) were eliminated from the tally. Still, if the partners of handicapped females were responding either directly or indirectly to their mates' contributions, one would expect that their provisioning behavior would have reflected the changes in those contributions that occurred immediately after weighting and, especially, as their mates recovered and substantially increased their delivery rates—even if diet quality had shifted. We did not find this to be the case for FW males.

Second, it seems realistic to suppose that, regardless of whether individuals are assumed to use offspring begging lev-

els to estimate what their partners are contributing (see Wright and Cuthill, 1990a; Wright and Dingemanse, 1999) or direct observations of partners, any such estimates are likely to have some error. Kedar et al. (2000), for example, have shown that the begging levels of nestling house sparrows may reflect not just current hunger, but also the level of begging that was required to obtain food on previous days. This could readily introduce a source of error in parental estimates of the extent to which changes (or lack of changes) in begging are attributable to a change in its mate's provisioning, and it would be useful to know just how reliably cues from offspring track moderate reductions or increases in a partner's effort. A pattern of complete compensation or overcompensation certainly could arise if parents respond inversely to their mates' efforts but for some reason chronically underestimate those efforts. As above, however, this also would be predicted to yield a negative relationship between the efforts of partners if they are engaged in negotiation, which we failed to find.

Third, partners of handicapped birds could show complete or exaggerated compensation that is not actually a response to changes in the provisioning behavior of their mates but is instead a response to some alternative effect of the experimental manipulation. Artificial handicapping (whether by weighting or feather clipping) undoubtedly creates changes in the birds' appearances, and, although control treatments require capture, handling, and banding of the birds, they obviously do not produce the same magnitude of change in appearance as experimental treatments. We may never know how such effects are interpreted by the birds, or why males, in particular, might be more sensitive to such changes in their partners than females. It seems clear, though, that the prolonged elevation of the provisioning rates of FW males was not triggered in response to their mates' current delivery rates.

We also found little indication that females mated to handicapped males were responsive to the changes across time that occurred in the provisioning behavior of their mates. When faced with sharp drops in their partners' food delivery immediately after treatment, females exhibited a nonsignificant increase in their own provisioning rate. The females then encountered an equally marked increase in their partners' food deliveries, yet their own provisioning behavior did not decline. These results are similar to those obtained by Hegner and Wingfield (1987), who used flutamide and testosterone implants to increase or decrease, respectively, the feeding rates of male house sparrows. At brood ages 11–14 days, when their treatment groups differed most in male provisioning, female feeding rates did not differ significantly. The fact that female house sparrows routinely encounter a reduction in the relative investment of their mates as broods age (Hegner and Wingfield, 1986; Veiga, 1990) may be relevant to their apparent insensitivity to their partners' contributions at this time.

Collectively, the results fail to support the hypothesis that parents of this species adjust their efforts in response to modifications of their mates' efforts in a way that is consistent with current negotiation models. Between-group comparisons showed that males mated to handicapped females achieved significantly higher increases in food delivery rates from pre- to post-treatment than control males, despite no significant reduction in their mates' efforts; at a shorter time scale, these males did not reduce their contributions even as their mates recovered from weighting. MW females showed a similar insensitivity to changes in their partners' efforts: These females failed to increase their efforts significantly at the point when their mates were most impaired and failed to reduce their efforts as their mates recovered. Furthermore, the regression analyses, which allow quantitative estimates of the magnitude and slope of the relationship between partner provisioning

efforts, showed no indication that variation in the provisioning behavior of either males or females at particular stages of the nesting cycle was strongly influenced by their own mates' current contributions. A relatively strong female sensitivity to prior efforts of the mate was revealed, but the positive slope of that relationship is opposite to that predicted from negotiation models. The effect is intriguing because it suggests the existence of a positive feedback mechanism between early male efforts and subsequent female investment, such that males investing more heavily at early stages are, in effect, rewarded later on. Because females increase their provisioning rates as their broods age, the effect could conceivably be produced by a simple relationship between early male investment and the subsequent early maturity of the brood; female responsiveness in that case could be accounted for by sealed bid behavior that is adjusted according to developmental stage of the young. On the other hand, given that the females' sensitivity was limited to the pretreatment (i.e., unmanipulated) efforts of their mates, it may just reflect the strong positive correlation between delivery rates of paired individuals, which could stem from either sealed bids or negotiation (see below).

As an alternative to direct or indirect responses to changes in their mates' efforts, the regression analyses uniformly showed that, when judged relative to other parents of the same sex, an individual's provisioning behavior remains remarkably consistent across time; even the behavior of weighted individuals was predictable in terms of their prior effort levels. This consistency is, in fact, what one would expect if parents commit at the outset of the nestling stage to an effort level that is essentially fixed by individual quality and then subsequently adjust that according to offspring age, reproductive value, and so on.

Biparental care involving effort levels that are largely independent of the mates' efforts (fitting the implicit sealed bid assumption of the earlier ESS models) may be more common than is generally recognized: An insensitivity to changes in partner contributions has been found now in several handicapping studies (e.g., Lozano and Lemon, 1996; Sanz et al., 2000; Slagsvold and Lifjeld, 1988, 1990). This is not to say that a negotiation phase between partners never occurs. What appears as a sustained commitment to an effort level at one stage of the nesting cycle could be the product of earlier negotiations between pair members. For house sparrows, incubation might be a likely phase for parental bargaining (and for evaluation of evidence for inverse responses to partner effort) because each partner has fairly accurate information about what the other is contributing. An incubating parent usually does not leave the nest until its partner has arrived, and even in those few cases where one might do so, egg temperature may still provide an incoming parent with some reliable cues about how long its mate has left the eggs unattended. Alternatively, Houston and Davies (1985) suggested that much of the negotiation may occur during courtship. Negotiation during courtship could account for the strongly positive correlation between the provisioning rates of mates in this species, which is robust to removal of the effects of time of season (Vultura, 1998) and cannot be explained on the basis of the sharing of a common feeding territory because this species does not defend feeding territories. In contrast, the positive correlation between provisioning rates of partners need not involve negotiation during pairing or early stages of parenting but could equally well be the outcome of mutual mate assessment based on partner condition, with each pair member subsequently contributing a sealed-bid effort level that corresponds to its condition (see Lessells, 2002).

Though the earlier ESS models were sometimes couched or interpreted incorrectly in terms of effort adjustments in real-time negotiation (see McNamara et al., 1999), their pre-

dictions still stand for parental strategies that are largely explicable as individual commitments to condition-dependent effort levels, with adjustments in the division of labor achieved across evolutionary time. Evidence is increasing that the biological relevance of sealed bid models may be extensive. Precisely why insensitivity to partner contributions (sealed bid behavior) has not been replaced by real-time adjustments (negotiation) in more species remains unclear.

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