

Conflict over parental care in house sparrows: do females use a negotiation rule?

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How do parents resolve their conflict over parental care? The classical “sealed-bid” model of biparental care suggested that parents use a fixed best effort given the partner’s effort. Alternatively, parents may “negotiate” their actual effort until the efforts of both partners settle down to limiting values, but in this case, the resulting efforts will not be the best responses to one another. Consequently, under the best response scenario, the response of 1 parent to the removal of its mate can be predicted from the response to a reduction in its partner’s effort, whereas the “negotiation” model predicts that such an extrapolation will underestimate the effort of a parent caring alone. We tested this prediction in free-living house sparrows (*Passer domesticus*). We experimentally manipulated the males’ parental care as follows: males’ care in group 1) was reduced by using a capture–handling–release stress protocol, 2) stopped by removing the male, and 3) left as control. In response to these manipulations, control females kept their feeding rate constant, whereas male-stressed-released females showed a moderate increase of feeding rate. When this response was extrapolated to zero male effort, their effort was still significantly lower than the observed effort of male-removed females. These results suggest that females may use the negotiation rule to determine their actual parental effort. *Key words*: biparental care, handicapping, mate removal, *Passer domesticus*, sexual conflict. [*Behav Ecol*]

Social monogamy is the most common mating system in birds (Clutton-Brock 1991), and the necessity of biparental care was proposed as one key factor in the evolution of monogamy (Lack 1968; Reichard 2003). Even when 2 parents are necessary to rear the chicks, there is a conflict of interest between them over the division of labor, with each parent preferring the other to have the greater share of parental workload (Trivers 1972). The classical model of biparental care suggests that biparental care can be an evolutionarily stable strategy if in response to a reduction of the parental care by 1 sex, parents of the other sex provide only partial compensation for the decrease in total care (Houston and Davies 1985). According to this model, the change in the level of parental care occurs in evolutionary time, and the outcome is a “sealed bid,” where individuals of each sex adopt a single fixed level of optimal effort. McNamara et al. (1999) suggested an alternative mechanism by which parents may negotiate the outcome of the parental effort they provide. In this model, individuals adopt a negotiation rule according to which they may respond to the changes in the other’s actual effort until the efforts of both partners settle down to limiting values (McNamara et al. 1999). This model predicts partial compensation if one’s mate reduces its parental effort; however, the evolutionarily stable negotiation rule is less responsive to the changes in the mate’s effort than if the individuals used the best efforts predicted by the solution of Houston and Davies (1985).

Recently, Schwagmeyer et al. (2002) tested the predictions of these models in breeding pairs of house sparrows (*Passer domesticus*) by experimentally handicapping one of the parents. Female parents mated to handicapped males showed

a nonsignificant increase in provisioning behavior, whereas males mated to handicapped females increased considerably their parental care and maintained high levels of provisioning even after their mates recovered from the handicapping. Results of some other studies in the same species seemed to corroborate these results, as females mated to handicapped males also consistently showed only a nonsignificant elevation of their own parental care (Hegner and Wingfield 1987a; Mazuc et al. 2003; Schwagmeyer et al. 2005). Schwagmeyer et al. (2002) concluded that the ineffectiveness of current partner behavior at predicting an individual’s provisioning behavior supports the sealed-bid models of biparental care. However, evidence exists that individuals of other species may readily adjust their parental behavior in response of the partner contributions as predicted by negotiation models (e.g., Wright and Cuthill 1989; Markman et al. 1995; Saino and Moller 1995). It remains therefore unclear why fixed level of parental efforts should have been maintained during the evolution of some species (Schwagmeyer et al. 2002).

A fundamental question concerns the rules that parents use when responding to their partners’ effort (McNamara et al. 2003). One possibility is that individuals use a best response rule, that is, after the negotiation phase the effort of each parent is the best, given the effort of the partner. In this case, the pair of efforts would agree with the prediction of the Houston–Davies solution, even though the Houston–Davies model is not based on real-time responding (McNamara et al. 2003). Another possibility is that individuals use a negotiation rule of McNamara et al. (1999), and hence the efforts are not the best responses to one another. One possible way to discriminate between these outcomes is to compare the parents’ response to an experimental decrease in the partner effort with the response to the absence of the partner (McNamara et al. 2003). Due to sexual conflict over care, a parent using the negotiation rule as described in McNamara et al. (1999) will provide less effort when its mate is present but its contribution is zero than if the partner is absent (e.g., because it was

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killed by a predator). For a parent adopting the Houston-Davies rule (i.e., providing the best level of parental effort given its partner effort), a “lazy” partner putting in no effort and a dead partner would be the same in terms of the focal parent’s own behavior. In other words, the response to the removal of the partner can be predicted from the response to a decrease in the partner’s effort (McNamara et al. 2003). Coupling the results of handicapping experiments with those of mate-removal experiments may therefore give further insights to the understanding of the evolution of biparental care.

In this paper, we tested these predictions by combining the effects of temporary mate removal and experimentally induced decrease of parental effort on the partners’ effort in a free-living population of house sparrows (*P. domesticus*). The house sparrow is an important model species of biparental care (e.g., Hegner and Wingfield 1987b; Schwagmeyer et al. 2002; Václav and Hoi 2002; Mazuc et al. 2003; Schwagmeyer and Mock 2003; Nakagawa et al. 2007) for which several handicapping experiments have been done in various populations, including the population used in this study (Mazuc et al. 2003).

Male parents were captured in their nest during the chick-provisioning period and were either taken into captivity for 48 h or restrained for 30 min to induce a stress response and released thereafter. We show that, on returning to their nest, released males reduced significantly their provisioning effort in response to the capture and handling stress. We observed the behavior of the females in the 2 days after male capture. Specifically, we asked whether 1) females responded at all to the decrease of their partner’s effort in the male-removed and the male-released groups and whether 2) their response in the male-removed group could be predicted from the response of the females in the male-released group.

MATERIALS AND METHODS

Study species and population

The study was carried out between March and July 2006 on a free-living population of house sparrows that breed in nest-boxes in Chizé (46°08′50″N, 0°25′29″W), France (Chastel et al. 2003). A large proportion of the adults used in this study were captured either in previous years or during the prebreeding period using mist nets and marked with a unique metal ring and color combination. Nest-boxes were monitored daily to determine laying dates, clutch sizes, hatching dates, and the number of hatchlings.

Experimental protocol

Nests were randomly assigned to one of the following experimental groups. In male-removed nests, the male parent was captured and taken into captivity ($N = 21$ nests). In male-released nests, the male parent was captured, restrained for 30 min, but released after measurements were taken ($N = 22$ nests). In a third group, 8 nests were randomly chosen from the available nests ($N = 41$); in these control nests, the male parent was not captured, but the nest was subjected to the same disturbance as in the 2 other groups, that is, the nest-box was taken down and the chicks were ringed and measured. This group contained fewer individuals than the other 2 groups because the focus of our study was to compare the male-removed and the male-released groups; the control group was used only to test whether the manipulation was effective.

These manipulations were carried out on day 7 after hatching (day 0). In male-removed and male-released nests, the male parent was captured in the nest-box while feeding their chicks. Males in the removed group were removed from the nest for

48 h and were housed in individual cages (30 × 40 × 50 cm high) where food and water were provided ad libitum. Food consisted of a mixture of seeds and a protein-rich cat food that were regularly provided on the study site for other captive animals and which was often consumed by house sparrows to feed their chicks and themselves. Cages were placed indoor at ambient temperature and natural lighting conditions, and they were invisible and inaccessible for other sparrows.

Males in the male-released group were subjected to a standardized capture–handling–restraint or, in other words, a stress protocol (Wingfield 1994; Lendvai et al. 2007). Immediately after the capture, a small blood sample (50–100 µl) was collected from the males, and then they were placed in cloth bags while the chicks were measured and weighed. A subsequent blood sample was collected from 30 min after the first bleeding. After taking the second blood sample, males were released. All males returned to their nest and resumed parental activities.

We observed the behavior of the parents both before and after day 7. We carried out observation that lasted 1 h, we aimed at collecting 2 observations both before and after day 7, and we refer to these periods as pre- and postmanipulation periods, respectively. Whenever it was possible, the observations in each period were carried out once early in the morning and once during midday on 2 consecutive days (i.e., days 6 and 7 for pre-manipulation and days 8 and 9 for postmanipulation). The daily scheduling of observations was based on the recommendations of Schwagmeyer and Mock (1997) to choose the hours that best predicted daily food delivery rates. During the observations, we recorded the number of feedings, as it is the most frequent and probably the most energy-demanding parental activity. For each nest, in day 9, after the observations ended, we released the captive male. After being released from captivity, all but 1 male returned to their nest and resumed parental activities. The one that did not return to his nest occupied a new nest-box and was seen singing on it.

Feeding rates were defined as the number of food deliveries per hour per chick. We calculated the mean feeding rates of the 2 observations for both the pre- and postmanipulation period.

Data processing and statistical analysis

Behavior of the parents were analyzed by fitting general linear models in the R computing environment (R Development Core Team 2008). Assumptions of the models were checked by graphical diagnostic tools (Faraway 2006). Model selection was undertaken in a stepwise backward manner by removing nonsignificant terms beginning with the interactions with the largest P value in each step. In Results, we give the final models. Interaction terms were nonsignificant unless otherwise reported.

The effects of the manipulations on male feeding rate were analyzed in a linear mixed model, with per capita feeding rates of males (i.e., feedings per hour per chick) as a response variable. Initial models contained observation period (i.e., before or after manipulation), Julian date (date of capture: from 17 May to 13 July), brood size (2–6 eggs, mean ± standard error [SE]: 3.84 ± 0.16 eggs), and the type of the manipulation as fixed effects and their interactions. The model also contained nest identity as a random factor. By doing so, for each individual, the premanipulation behavior was used as its own “control,” and our main interest was to test whether the change in the behavior from the pre- to the postmanipulation behavior was affected by the manipulation, which is given by the observation period × manipulation type interaction term. Note that for removed males, observations for the postmanipulation period were by definition zero.

To test the response of females whose partners received different manipulations, we used the same linear mixed model design as for the males described above, but the response variable was the per capita feeding rate of the female parents. We also analyzed the total feeding rate using the same linear mixed model design and the total (i.e., male + female) feeding rate as response variable.

Finally, as proposed by McNamara et al. (2003), to investigate whether the females behaved in accordance with the negotiation rule or the best response rule, we analyzed if the effect of removing the male can be predicted from the response of the female to the experimentally induced reduction in the male effort. First, for each male-released pair, we obtained the extrapolated female effort to zero male effort, that is, the expected feeding rate of the female if her partner did not contribute to the feeding, based on the observed response of the female to the experimentally induced reduction of her partner feeding rate. This extrapolation was done by fitting a linear model to each male-released pair's data and obtaining the intercept of the linear regression (Figure 1). Second, we compared these extrapolated efforts of male-released females with the actual observed feeding rates of the male-removed females in a linear model, where we controlled for the date and brood size. Note that this procedure is very conservative because extrapolation tends to seriously inflate the variance of the extrapolated values. This makes it more difficult to detect any significant differences.

RESULTS

Premanipulation feeding rate of the females was influenced by both the date and the brood size, with a significant interaction, indicating that per capita feeding rate decreased with the brood size, but this effect was rather small early in the date and became more pronounced as the date progressed (date:

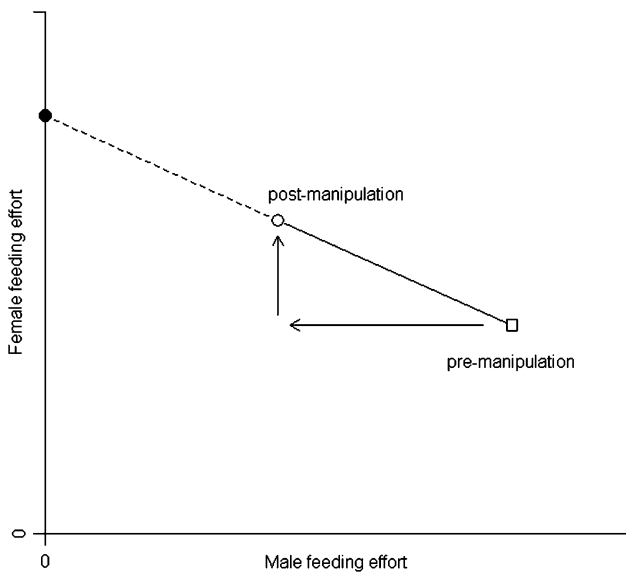


Figure 1
Calculating the female response extrapolated to zero male effort. The open square and the open circle denote the male and female behavior in the pre- and the postmanipulation period, respectively. The solid line represents the response function, that is, the observed change of the female effort (vertical arrow) in response of the experimentally induced reduction in her partner's effort (horizontal arrow). The dashed line gives the linear extrapolation of the response function, where the filled circle represents the extrapolated female response (the intercept of the linear regression).

Table 1
The effects of the manipulations on the feeding rate of male house sparrows in a linear mixed model

Effects	β	SE	<i>P</i>
(Intercept)	4.90	0.71	<0.001
Observation period	-1.54	0.80	0.060
Brood size	-0.59	0.16	0.001
Manipulation (male released)	0.75	0.53	0.162
Manipulation (male removed)	-0.38	0.52	0.463
Observation period \times brood size	0.48	0.18	0.010
Observation period \times manipulation (male released)	-1.38	0.59	0.025
Observation period \times manipulation (male removed)	-2.59	0.58	<0.001

The table shows the parameter estimates (β), their SEs, and the corresponding significance (*P* value).

$F_{1,45} = 16.72$, $P < 0.001$; brood size: $F_{1,45} = 19.86$, $P < 0.001$; date \times brood size interaction: $F_{1,45} = 7.71$, $P = 0.008$). Therefore, in all further analyses, we controlled for the date and brood size. In the above model, the type of manipulation was not significant ($F_{2,45} = 1.62$, $P = 0.209$), that is, the premanipulation feeding rate did not differ between the experimental groups.

The effect of stress protocol on male feeding effort

Overall, feeding rate of males changed from the pre- to the postmanipulation period ($F_{1,47} = 47.95$, $P < 0.001$), and this change was larger in small broods (observation period \times brood size interaction: $F_{1,47} = 11.13$, $P = 0.002$; Table 1). Moreover, the change in feeding rate was different between the manipulation groups ($F_{1,47} = 10.63$, $P < 0.001$; Figure 2, Table 1). In response to the capture and handling stress, the

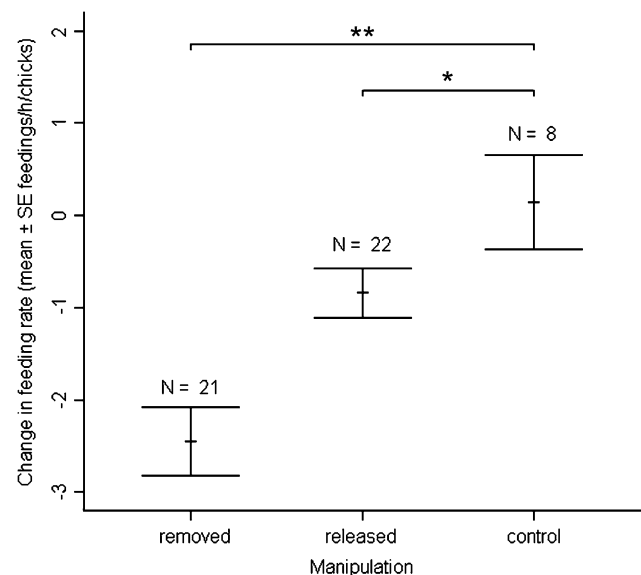


Figure 2
Mean \pm SE change in the feeding rate of the males from the premanipulation period to the postmanipulation period. Asterisks denote significant differences between the groups ($*P < 0.05$, $**P < 0.005$, obtained from a linear mixed model—see Table 1). Sample sizes are given above the error bars.

feeding rate of released males dropped by an average of 25%, and this change was significant compared with control males ($P = 0.025$) in a linear mixed model, controlling for brood size effects (Figure 2, Table 1).

The response of females to the decrease in their partner's effort

The change in the feeding rate from the pre- to the postmanipulation period was different between the 3 experimental groups ($F_{1,48} = 7.7$, $P = 0.001$; Figure 3, Table 2). Parameter estimates showed that this change was close to and not significantly different from zero in control females ($P = 0.923$). During the same period, females in male-released nests increased slightly and nonsignificantly their feeding rate ($P = 0.390$). Mate-removed females, however, responded more strongly to the absence of their mates, and this change was highly significant ($P = 0.002$). Total parental effort (i.e., male + female) did not change between the pre- and postmanipulation period ($F_{1,47} = 0.09$, $P = 0.760$).

Finally, we analyzed whether the response of the male-removed females can be predicted from the response of the male-released females. Extrapolating the feeding rate of the male-released females to a hypothetical zero postmanipulation male effort yielded lower values than the actual feeding rate of the male-removed females ($F_{1,41} = 8.90$, $P = 0.005$; Figure 4). Our extrapolated values were similar to the actual feeding rates of females whose partners provided no feeding effort while present, as found by Mazuc et al. (2003) (see Discussion for details).

DISCUSSION

We investigated the response of female house sparrows to 2 types of experimental reduction in their partner's contribution. We found that females whose mate had been removed increased their feeding rate significantly more than females whose mate was present but decreased his parental contribution. The response of male-removed females was still significantly higher

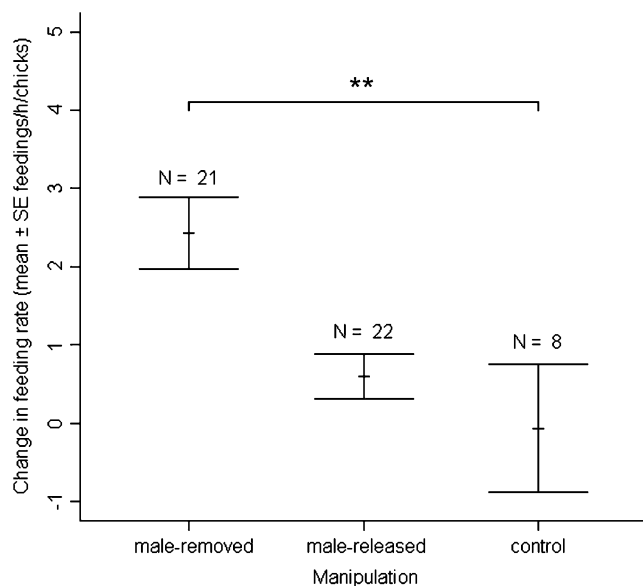


Figure 3
Mean \pm SE change in the feeding rate of the females from the premanipulation period to the postmanipulation period. Asterisks denote significant difference between the groups (** $P < 0.005$, obtained from a linear mixed model—see Table 2). Sample sizes are given above the error bars.

Table 2
The effects of the manipulations on the feeding rate of female house sparrows in a linear mixed model

Effects	β	SE	P
(Intercept)	-1.25	2.63	0.638
Observation period	-0.06	0.65	0.923
Date	0.09	0.03	0.005
Brood size	1.01	0.61	0.106
Manipulation (male released)	0.00	0.66	0.999
Manipulation (male removed)	-0.05	0.65	0.936
Date \times brood size	-0.02	0.01	0.006
Observation period \times manipulation (male released)	0.66	0.76	0.390
Observation period \times manipulation (male removed)	2.50	0.77	0.002

The table shows the parameter estimates (β), their SEs, and the corresponding significance (P value).

than the expected response of male-released females if their mate had provided zero effort. These results support the predictions of McNamara et al. (2003) and suggest that female house sparrows may use a negotiation rule to adjust their level of parental effort to the actual effort of their partners.

In this study, we experimentally induced a reduction in male feeding rate by a capture–restraint protocol. Conventional handicapping experiments use feather clipping or attach weights to the tail feathers, which beside affecting energy consumption also alter the birds' appearance; therefore, it is often impossible to disentangle whether the partners of the handicapped birds respond to the change in the perceived quality or/and to the change in the contribution of their mates. By using the capture–restraint protocol, the birds' physical appearance was not affected, but we induced a physiological stress response (Wingfield 1994), which adversely affects the parental behavior. Male sparrows subjected to this protocol

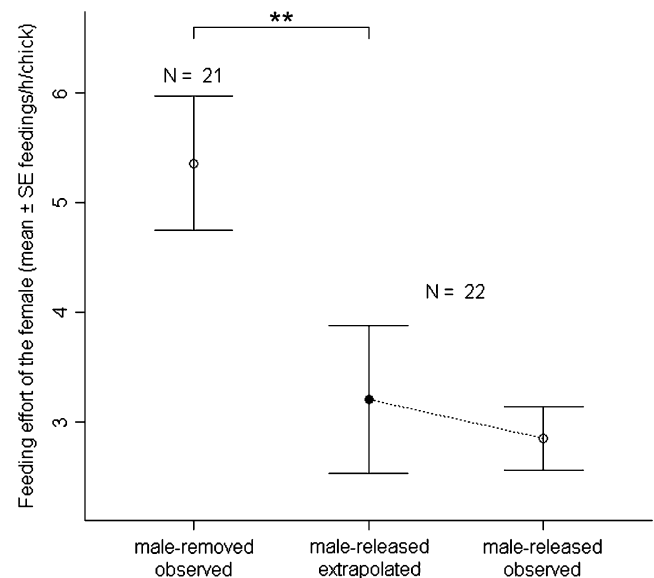


Figure 4
Mean \pm SE for the feeding rate of the females in the postmanipulation period. The open circles show the observed feeding rates, and the filled circle denotes the female effort extrapolated to a zero male effort. Asterisks denote a significant difference between the groups (** $P < 0.005$, obtained from a linear model). Sample sizes are given above the error bars.

showed a marked increase in the circulating level of corticosterone, and the magnitude of this stress response predicted their postmanipulation behavior (Lendvai ÁZ and Chastel O, unpublished data). On the other hand, one may argue that the capture–restraint protocol could have potentially influenced female behavior directly in an unexpected way: for example, the temporary removal of the males may have stressed the females, either because of the physical disappearance of their partner or because of the alarming behavior of the returning partner. This was not case in our study: after the observations, females were also captured, and their baseline corticosterone levels did not differ between the control and male-released groups (Lendvai ÁZ and Chastel O, unpublished data, see also Lendvai and Chastel 2008).

Despite the significant decrease of their mates' feeding rate, females showed only a slight and nonsignificant increase in their feeding rates. This result is consistent with at least 3 recent handicapping experiments. Schwagmeyer et al. (2002) induced a decrease in male feeding effort by using fishing weights attached to the parents. Immediately after the weighting, the feeding rate of the males fell by about 40%, but their mates showed only a moderate and nonsignificant increase in their own feeding rate. Two other recent studies used testosterone implants to induce a reduction in male contributions. Feeding rate of testosterone-implanted males in Mazuc et al. (2003) was about half of the control males' at day 5 after hatching, and their mates showed about 20% higher feeding rates than females of control males, but this difference was not statistically significant. Schwagmeyer et al. (2005) found similar results: testosterone-implanted males fed their chicks almost 3 times less than control males, but their mates showed a nonsignificant, average 25% elevation of feeding rates relative to the mates of control males. Although the direct comparisons between these studies are hampered by the differences in the geographical locations of the study populations, in the age of the brood when the observations were collected, and the methodology used, these studies corroborate the results of the present study, namely, that when the male parent is present, but decreases his parental effort, the females show only slight compensation for this shortfall.

In contrast, male-removed females showed a substantial increase in their feeding rate when their mate was in captivity. Most importantly, however, the increased effort of male-removed females was not only higher than that of the mate-released females but also significantly higher than the extrapolated response of mate-released females to zero male effort. Therefore, the response of females was higher if their mate was absent than it would be if he had been present but had provided zero effort. In our study, we used an extrapolated (i.e., predicted) female response to a hypothetical zero male effort, although all males in our study provided some effort. The extrapolation assumes that the response function of the females is linear (McNamara et al. 2003). Would the response of females have been different if their mate had been actually present but if he had provided zero effort? In the study of Mazuc et al. (2003), in the same population, at day 10 after hatching (i.e., chicks that were on average 1.5 days older than chicks in our study), two-third of the testosterone-implanted males and 1 control male were present but did not feed the chicks (Figure 4b in Mazuc et al. 2003). The feeding rate of their mates was 3.84 ± 1.17 (SE) feedings per chick per hour ($N = 7$), which fell within the 95% confidence intervals of our extrapolated values (1.79–4.60). Therefore, even if the shape of response function of the females is not exactly known, we are confident that the predicted female care for zero male effort reported in our study shows realistic values.

Whittingham et al. (1994) published one of the handful of studies that used both handicapping and mate removal to test the response of females to the reduction of their mate's effort.

Similar to our study, they found that females whose partner had been handicapped increased slightly and nonsignificantly their feeding effort, whereas females whose mate had been removed increased dramatically their parental effort. These results are consistent with our study and suggest that parents may adjust their behavior to their partner's effort depending on the context. When the partner is present, but reduces its effort, its mate will not provide the best effort given this situation; however, when the partner is removed, the effort of the remaining parent should be the best effort (McNamara et al. 2003).

These results show that female house sparrows respond to their mate's effort as it has been shown in several other species (e.g., Wright and Cuthill 1990; Whittingham et al. 1994; Markman et al. 1995; Sanz et al. 2000). The finding that females' response is greater when the male is removed than the predicted response when he reduces his effort to zero suggests that females may use a negotiation rule. Whether males in this species also use a negotiation rule remains unknown, although recent evidence suggests that males may differ in their responsiveness. Schwagmeyer and Mock (2003) and Nakagawa et al. (2007) also found that repeatability of parental care is higher in males than in females. High between- and within-year repeatability of male effort is more consistent with the sealed-bid model of parental care because in the negotiation model, the negotiated parental effort may vary in function of several factors (condition of the parent, partner contribution, etc.), whereas according to the sealed-bid model, the parents make a single decision independently from their partner, and the changes in effort occur in evolutionary time. Alternatively, an extension of the negotiation game may also predict different responses and different repeatabilities of parental effort for the sexes. Johnstone and Hinde (2006) incorporated uncertainty regarding brood "value" or brood "need" into the negotiation framework of McNamara et al. (1999, 2003). They showed that when there is informational asymmetry about brood value between the sexes, so that the female is better informed than the male (e.g., because of maternal hormones deposited in the eggs, about which the male has no information), the female is predicted to be more responsive than the male and to have lower repeatability of individual effort across broods. Further experiments combining female handicapping and female removal are necessary to understand the response rules of males.

Taken together, we provide an experimental test of the predictions of McNamara et al. (2003) to contrast the negotiation and the best response rules, and we show that female house sparrows behave in accordance with the predictions of the negotiation model. This result suggests that sexual conflict has been an important source of selection in this species. What type of response rule males use and why their remarkable individual consistency in parental behavior has been evolved remain to be answered.

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