



# Females manipulate behavior of caring males via prenatal maternal effects

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In species with biparental care, there is sexual conflict as each parent is under selection to minimize its personal effort by shifting as much as possible of the workload over to the other parent. Most theoretical and empirical work on the resolution of this conflict has focused on strategies used by both parents, such as negotiation. However, because females produce the eggs, this might afford females with an ability to manipulate male behavior via maternal effects that alter offspring phenotypes. To test this hypothesis, we manipulated the prenatal conditions (i.e., presence or absence of the male), performed a cross-fostering experiment, and monitored the subsequent effects of prenatal conditions on offspring and parental performance in the burying beetle *Nicrophorus vespilloides*. We found that offspring were smaller at hatching when females laid eggs in presence of a male, suggesting that females invest less in eggs when expecting male assistance. Furthermore, broods laid in the presence of a male gained more weight during parental care, and they did so at the expense of male weight gain. Contrary to our expectations, males cared less for broods laid in the presence of a male. Our results provide experimental evidence that females can alter male behavior during breeding by adjusting maternal effects according to prenatal conditions. However, rather than increasing the male's parental effort, females appeared to suppress the male's food consumption, thereby leaving more food for their brood.

food consumption | manipulation | maternal effects | parental care | sexual conflict

In species where parents cooperate to care for their joint offspring (as long as there is scope for divorce and/or remating following the partner's death), there will be sexual conflict over parental care, with each parent being under selection to minimize its own effort and shift as much as possible of the workload to its partner (1). Previous empirical and theoretical work has focused mainly on three behavioral mechanisms that may mediate the resolution of this conflict (1, 2). First, incomplete compensation, or negotiation, occurs when each parent increases its level of care in response to a reduction in its partner's contribution, but such that it does not fully correspond to its partner's reduction (3). Second, matching occurs when each parent adjusts its level of care to its partner's contribution by matching any increase or reduction in its partner's contribution in the same direction as its partner (4). Third, sealed bid models assume that each parent makes an initial fixed decision about how much care to provide irrespective of its partner's decision (5). There is some support for all three mechanisms from experimental studies on birds and other taxa (6–8); however, a meta-analysis of mate removal and handicapping experiments on birds found the greatest overall support for negotiation (2).

Our current understanding of the resolution of sexual conflict suggest that males and females use the same behavioral strategies for resolving conflict (e.g., negotiation) (9). However, given that females produce the eggs, they might use their control over egg production as a mechanism for biasing conflict resolution in their favor. In many species, females deposit hormones and/or nutrients into the eggs that alter the offspring's behavior or development

(9–11), thereby providing a potential tool for manipulating the behavior of caring males. For example, by producing smaller eggs, females could redirect the costs of parental care from the prenatal period, when they pay the full costs of egg production, toward the postnatal period, when the costs of rearing young are shared with the male (9). Alternatively, females may deposit yolk androgens that modulate offspring begging behavior in a way that alters the male's perception of offspring need, thereby increasing male contributions to care (9–11). Thus, if prenatal maternal effects influence the resolution of sexual conflict over care, this would introduce an asymmetry of power between the two sexes, with the female gaining the upper hand.

At present, we lack conclusive evidence as to whether females can use prenatal maternal effects to manipulate the behavior of caring males (12–16). A main reason for this is that it is difficult to demonstrate female manipulation, owing to several challenges. First, females could manipulate males via several mechanisms, including yolk androgens, other egg components, egg size, and egg coloration (4), and thus existing experimental designs that focus on specific mechanisms risk targeting the wrong mechanism. Second, to demonstrate that prenatal maternal effects alter male behavior, it is essential to separate the effects of prenatal conditions from those of postnatal conditions. Third, there may be a limited time window for maternal manipulation, because maternal effects on offspring behavior often wane as offspring develop (17–19). Fourth, in addition to sexual conflict over parental care, there may be sexual conflict over food consumption from shared resources (20, 21). Finally, to demonstrate

## Significance

In biparental species, sexual conflict arises as each parent attempts to minimize its personal effort. Most work has focused on how this conflict is resolved through symmetrical decisions between parents. We investigated whether females can influence male decisions by altering the offspring's phenotype via the eggs. We manipulated the prenatal presence of the male, performed a cross-fostering experiment, and monitored the subsequent effects on offspring and parent performance. Offspring laid in presence of a male were smaller at hatching. In addition, males lost more weight when with larvae laid in presence of a male. Our results show that females can manipulate male behavior, suggesting that prenatal maternal effects can play an important role in the resolution of sexual conflict between parents.

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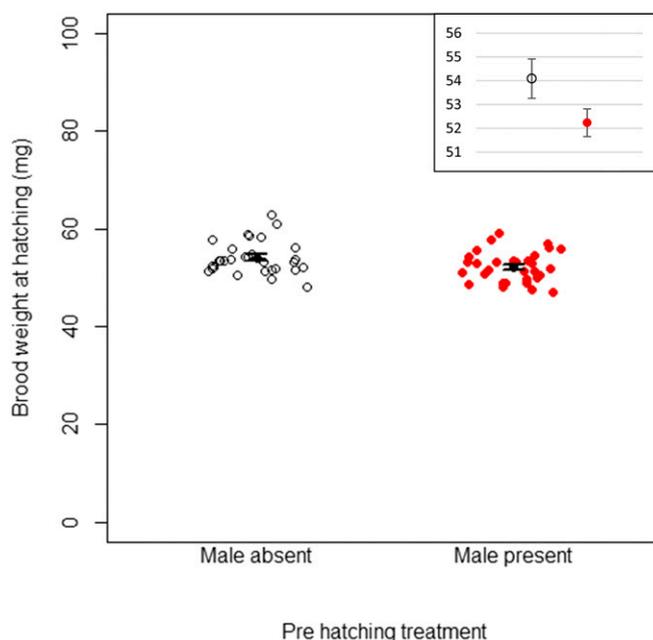
female manipulation, it is crucial to document fitness benefits to females and/or offspring and fitness costs to males (4).

Here we report an experiment on the burying beetle *Nicrophorus vespilloides*, an insect exhibiting facultative biparental care (22). This species is ideal for studying female manipulation of male behavior because it allows us to address all five challenges listed above. First, we used a new experimental approach in which we targeted prenatal environmental conditions expected to influence female decisions on maternal effects and then monitored downstream consequences for offspring size at hatching, male and female care, and male, female, and offspring fitness (9). Here we targeted a prenatal environmental condition that is essential for female manipulation of males: the presence or absence of the male during egg laying. Second, we conducted a cross-fostering experiment to separate prenatal and postnatal effects by giving each pair of beetles an experimental brood of newly hatched larvae derived from one of our two treatment groups. In one treatment, larvae derived from eggs laid when the male was present during egg laying, whereas in the other treatment, larvae derived from eggs laid when the male was absent during egg laying. Third, we recorded parental behaviors over 3 consecutive days, covering the full duration of parental care from hatching until nutritional independence (23). Fourth, we investigated sexual conflict over both parental care and food consumption from a resource shared by both parents and their offspring (i.e., a small vertebrate carcass). To this end, we recorded the body mass of males and females before and after breeding. Finally, we monitored subsequent effects on post-breeding survival of males and females as well as offspring growth and survival across different life stages.

## Results

We found evidence for a prenatal maternal effect on offspring size at hatching owing to the presence or absence of the male during laying. Females that laid eggs in the presence of a male partner produced larvae that were 3.4% lighter at hatching compared with larvae from females who laid eggs in the absence of a male (estimated mean  $\pm$  SE,  $1.85 \pm 0.826$  mg;  $F_{1,59} = 5.02$ ;  $P = 0.0289$ ) (Fig. 1 and Table S1). There was no difference in the number of eggs laid by females in the presence or absence of a male partner ( $F_{1,142} = 0.431$ ;  $P = 0.512$ ). Thus, our result provides evidence of an anticipatory maternal effect, whereby females reduce their prenatal investment in offspring when anticipating help from a male partner (24, 25).

We found evidence that females use maternal effects to manipulate the behavior of caring males, but maternal effects influenced male food consumption rather than male care. There was no evidence that males increased the amount of care that they provided in response to prenatal maternal effects. Males did not adjust their direct care at 1 h after hatching ( $Z = 0.0716$ ;  $P = 0.943$ ) (Table S2), but in contrast to what we predicted, males provided less direct care at 25 h after hatching when caring for a foster brood derived from eggs laid in the presence of a male (estimate,  $1.02 \pm 0.477$  scans of care per observation session;  $Z = 2.15$ ;  $P = 0.0319$ ) (Fig. 2A and Table S2). We found that males gained less or lost more weight when caring for a foster brood derived from eggs laid in the presence of a male (estimate,  $0.0127 \pm 6.02e^{-04}$  g;  $F_{1,57} = 4.44$ ;  $P = 0.0394$ ) (Fig. 2B and Table S1). Males that provided more care at 25 h after hatching also gained more weight, suggesting that spending more time caring for larvae provided them with better access to the food resource (Fig. 2C) (lm, estimated,  $1.58e^{-3} \pm 6.72e^{-4}$  g per caring event;  $F_{1,58} = 5.53$ ;  $P = 0.0222$ ). Finally, male weight gain decreased as the initial brood weight increased (estimate,  $-2.67 \pm 0.925$  g/mg;  $F_{1,57} = 8.32$ ;  $P = 0.00552$ ) (Fig. 2D and Table S1), indicating that males also adjust the amount of carrion they eat based on the larvae's size. Our findings suggest that maternal effects provide females with a means to manipulate the behavior of

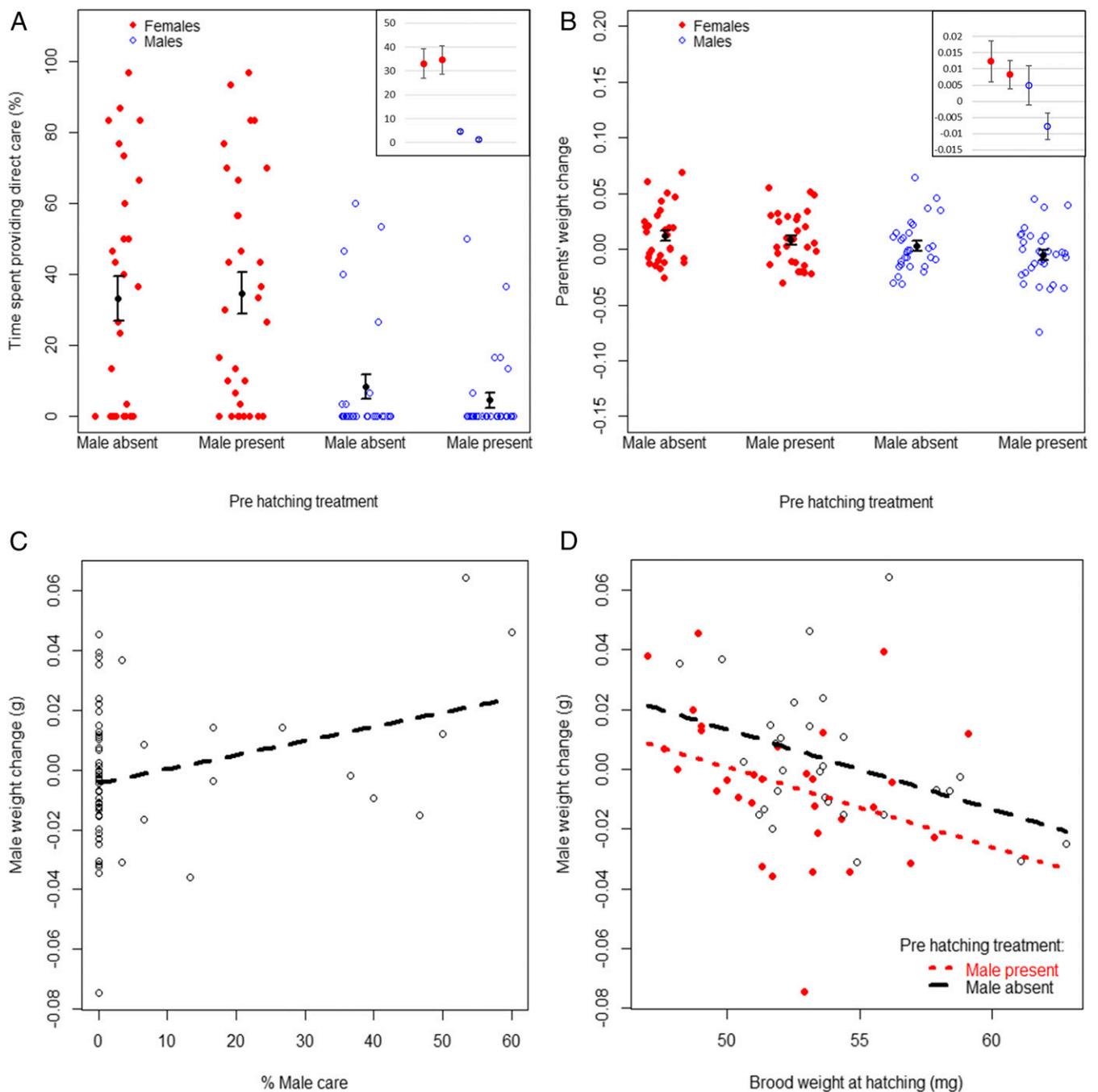


**Fig. 1.** Maternal effect of the presence of the male before hatching on brood weight at hatching. Raw data and associated mean  $\pm$  SE values are shown for brood weight of larvae laid in absence of a male (black open circles;  $n = 30$ ) and brood weight of larvae laid in presence of a male (red filled circles;  $n = 31$ ). (Inset) Predicted mean  $\pm$  SE values from the final model. Each experimental brood comprised 20 larvae mixed from different donor pairs of the same pre-hatching treatment that were not the larvae's foster parents. We weighed the 20 larvae together before placing them on the carcass as a measure of prenatal maternal investment.

caring males by suppressing male food consumption from the shared resource.

We found no evidence that maternal effects influenced the behavior of caring females. There were no effects of prenatal maternal effect on female direct care at 25 h or 49 h after hatching ( $Z = 0.626$ ;  $P = 0.531$  and  $Z = -0.365$ ;  $P = 0.715$ , respectively) (Fig. 2A and Table S2). As predicted under the hypothesis of female manipulation, females tended to provide less care at 1 h after hatching for larvae laid in presence of a male, but this effect was marginally nonsignificant ( $Z = 1.93$ ;  $P = 0.0539$ ) (Table S2). In contrast to what we found for males, prenatal maternal effects did not affect female weight gain ( $F_{1,58} = 0.437$ ;  $P = 0.511$ ) (Fig. 2B and Table S1). Thus, these results confirm that the prenatal maternal effect affected male behavior, but had no impact on the female's own behavior.

We found evidence of immediate fitness consequences of prenatal maternal effects mediated through the change in male behavior. Foster broods derived from eggs laid in the presence of a male were heavier at dispersal (i.e., the end of the parental care period) compared with foster broods derived from eggs laid in the absence of a male (estimate,  $-0.333 \pm 0.144$  g;  $F_{1,57} = 5.35$ ;  $P = 0.0243$ ) (Fig. 3 and Table S1). There were no significant effects of prenatal maternal effects on either the number of dispersing larvae or average larval weight ( $F_{1,58} = 2.04$ ;  $P = 0.158$  and  $F_{1,57} = 2.69$ ;  $P = 0.106$ , respectively) (Table S1), suggesting that the greater brood weight when eggs were laid in the absence of a male was related to a relatively small increase in both number of offspring and average larval weight. We also found that broods that were heavier at dispersal were heavier at hatching (estimate,  $50.3 \pm 22.1$  g/mg;  $F_{1,57} = 5.16$ ;  $P = 0.0269$ ) (Fig. 3 and Table S1). Keeping in mind that foster broods derived from eggs laid in the presence of a male were lighter at hatching, this suggests that the maternal effects on postnatal brood weight were strong

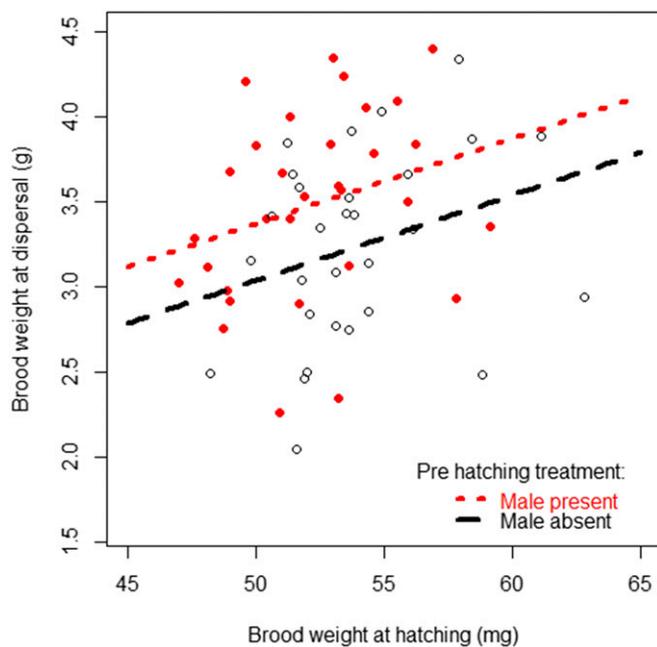


**Fig. 2.** Prenatal maternal effects on parental care and weight change. (A and B) Raw data and associated mean  $\pm$  SE values for the time that females and males spent providing direct care at 25 h after hatching (A), and weight change in females and males from mating to larval dispersal (B) when caring for larvae laid in the absence of a male ( $n = 29$ ) or in presence of a male ( $n = 31$ ). (Insets) Predicted mean  $\pm$  SE values from the final models. (C) Male care at 25 h after hatching was positively associated with male weight change. The dashed lines depict the regression line from the model. (D) Brood weight at hatching and larvae laid in presence of a male have negative effects on male weight change. The dashed lines depict the regression lines from the final model for each pre-hatching treatment.

enough to override the initial differences in weight at hatching, which were in the opposite direction from those at dispersal.

We then added male weight gain to the model on brood mass to examine whether the maternal effects on male weight change explained why broods derived from eggs laid in the presence of a male were heavier at dispersal. We found that male weight change had a highly significant effect on brood weight (estimate,  $-9.93 \pm 2.81$ ;  $F_{1,58} = 12.5$ ;  $P = 0.000810$ ) (Table S3), and when we included male weight change, the effect of treatment

was no longer significant ( $F_{1,57} = 1.62$ ;  $P = 0.208$ ) (Table S3). There was also a significant effect of female weight change on brood weight (estimate,  $-7.58 \pm 2.75$ ;  $F_{1,56} = 7.62$ ;  $P = 0.00779$ ), but in contrast to what we found for males, the effect of treatment was still significant when female weight gain was added (estimate,  $-0.306 \pm 0.138$  g;  $F_{1,56} = 5.01$ ;  $P = 0.0291$ ) (Table S3). Thus, our results suggest that the beneficial effects of prenatal maternal effects on offspring growth were mediated through the reduction in male food consumption from the shared resource.



**Fig. 3.** Effect of brood weight at hatching and prenatal condition (i.e., presence or absence of a male during laying) on brood weight at dispersal. Raw data are shown ( $n = 60$ ). The dashed lines represent the regression lines from the final model for each pre-hatching treatment.

Finally, we examined long-term fitness consequences of prenatal maternal effects by assessing offspring survival until eclosion as an adult, adult size, and life span after eclosion. We found a nonsignificant trend toward better survival from dispersal to eclosion in offspring laid in the presence of a male (lm, eclosion rate;  $F_{1,57} = 3.80$ ,  $P = 0.0561$ ), but a longer life span after eclosion in offspring laid in the absence of a male (hazard coefficient,  $-0.632 \pm 0.250$ ;  $\chi^2 = 6.39$ ;  $P = 0.0114$ ) (Table S4 and Fig. S1). The longer adult life span of offspring laid in the absence of a male may be caused by selective disappearance if weaker offspring have higher mortality in the period before eclosion. There was a nonsignificant trend for males (but not females) to die sooner after caring for larvae derived from eggs laid in the presence of a male ( $Z_{1,57} = 1.83$ ;  $P = 0.0670$ ) (Table S4 and Fig. S2).

## Discussion

Our results provide experimental evidence that females can manipulate the behavior of caring males through prenatal maternal effects, and that females appear to suppress male food consumption from a resource that is shared by the two parents and their offspring. We found that females respond to the presence of a male during egg laying by producing larvae that are lighter at hatching, suggesting that females redirect the costs of parental care from the prenatal period, when they pay the full costs of egg production, toward the postnatal period, when the costs of care are shared with the male. We also found that males gained less weight when caring for broods derived from eggs laid in the presence of a male, that such broods gained more weight during parental care, and that the greater weight gain of these broods came at the expense of the male's weight gain. These findings suggest that the female's suppression of the male's food consumption was beneficial to the offspring, increasing their access to the shared resource. Our results indicate that female manipulation of male behavior was targeted toward sexual conflict over food consumption rather than conflict over parental care.

Previous work on sexual conflict between caring parents has focused mainly on conflict over parental care (1, 2). Our present

results suggest that sexual conflict over food consumption from shared resources may be more important than traditionally recognized. This suggestion is also consistent with theoretical predictions and previous empirical work on *N. vespilloides*. Although explicit models of maternal effects as a tool for female manipulation of male behavior are lacking, they could be interpreted as a form of Stackelberg competition in which one parent (here the female) makes the initial decision about how much to contribute and then the second parent responds by determining its contribution (26). In this game theory model, the individual making the initial decision is expected to gain the upper hand (26). Thus, if sexual conflict is primarily over care, then we should expect females to provide less care than males. This prediction is not supported in our system, where females provide more care than males (27, 28); however, if sexual conflict occurs over food consumption from a shared resource, then females would be expected to consume more than males. This prediction is supported by our finding that females gained more weight during breeding than males (paired  $t$  test:  $t_{59} = 3.37$ ,  $P = 0.00131$ ). Sexual conflict over consumption may be particularly important in our study species, given that it breeds on carcasses of small vertebrates that serve as food for both parents and developing larvae (20, 21); however, such conflict may be important in other systems as well, such as birds, where the two parents find food for themselves and their offspring within a shared territory.

Although our study provides evidence for female manipulation of male behavior, it leaves the question of what mechanisms are responsible unanswered. To be effective, such mechanisms must influence the offspring's phenotype, thereby altering the male's behavior in a way that increases the female's or the offspring's fitness at the expense of the male's fitness. Our results reveal that egg size (measured as larval weight at hatching) is not the mechanism responsible for female manipulation of male behavior. Although females reduced egg size in response to the male's presence, we found that males gained more weight when caring for lighter larvae. Thus, the effect of egg size on male weight change was in the opposite direction of the effect due to prenatal conditions. Nevertheless, this result demonstrates that females respond to the presence of the male by adjusting offspring size at hatching, suggesting that females might adjust other maternal effect mechanisms as well. One potential such mechanism is the deposition of maternal hormones in the eggs (9, 10). There is good evidence that female birds deposit testosterone into the eggs, and that maternal testosterone stimulates nestling begging and growth, although whether this provides a mechanism for female manipulation of male behavior is debatable (10–12). Insects have a different hormonal system than vertebrates, but there is evidence that females deposit juvenile hormones or ecdysone into the eggs (29, 30). Potentially, these maternal hormones might influence larval behavior or development, thereby altering male behavior. Males also might respond to the prenatal maternal effect indirectly, by responding to the female's response to the offspring phenotype; however, we found no evidence to support this suggestion, as females did not respond to prenatal maternal effects in this study.

Our findings raise a key question: why should males allow themselves to be manipulated by females? After all, if females use maternal effects to enhance their own or their offspring's fitness at the expense of male fitness, then we should expect males to be under selection to evolve a counterstrategy to such manipulation (11). In a recent study, we distinguished between deception, where maternal effects somehow bias the male's behavior away from his own optimum, and incentivization, where maternal effects somehow alter the cost/benefit function of male behavior (9). It is unlikely that deception would be evolutionarily stable, because males should simply evolve to ignore manipulating maternal effects. In contrast, incentivization might be evolutionarily stable, because maternal effects alter the benefits and/or costs of male behaviors, inducing a change in the males'

optimal behavior (9, 31). For example, by depositing hormones into eggs, females might alter the offspring's physiology and growth trajectory, thereby incentivizing males to consume less food for themselves to achieve their cost/benefit optimum.

## Conclusion

Until now, most theoretical and empirical work on the resolution of sexual conflict has assumed symmetry of power between males and females, with the same mechanisms of conflict resolution applying to both parents (3–5). This study adds to our understanding of sexual conflict between caring parents by showing that maternal effects provide females with a greater power over their partner's behavior, which in turn allows them to manipulate male behavior. Therefore, we urge future work to consider the potential importance of prenatal maternal effects in the resolution of sexual conflict between parents.

## Methods

**General Procedure.** We used virgin beetles from an outbred laboratory population maintained at the University of Edinburgh. Beetles were housed individually in clear plastic boxes (124 × 82 × 22 mm) containing moist soil, kept at 21 ± 2 °C under constant lighting, and fed small pieces of organic beef twice a week. The beetles were aged 13–24 d posteclosion at the start of the experiment.

**Cross-Fostering Procedure.** We weighed males and females at the beginning of the experiments to record their prebreeding mass. We then placed each pair into a plastic box (110 × 110 × 30 mm) with 10 mm of moist soil for approximately 24 h to allow all experimental females to be fertilized by a male. We randomly placed either both parents ( $n = 72$ ) or females only ( $n = 72$ ) in a larger box (170 × 120 × 60 mm) filled with a 10- to 20-mm layer of soil and provided with a freshly defrosted mouse (21.4–23.7 g, supplied from Livefoods Direct). In the interval between the end of egg laying and the start of hatching (62–63 h after providing the carcass), we moved the parents and their prepared carcass to a new box with fresh soil. Females breeding alone and their prepared carcass were discarded from the rest of the experiment, and only boxes with both parents were used as foster parents. At this stage, we counted the number of eggs visible at the bottom of the box as an estimation of clutch size (32). The eggs from both treatments were left to develop in the original box.

Larvae hatching from eggs left in the original containers were used to generate experimental foster broods. As soon as possible after their own larvae began to hatch, we provided pairs of breeding beetles with experimental foster broods that differed with respect to whether they hatched from eggs laid in the presence or the absence of a male. Each experimental brood comprised 20 larvae from at least two different donor pairs that were not the larvae's foster parents. We gave caring parents 20 larvae to match the mean brood size in this species (33). We weighed the larvae before placing them on the carcass as a measure of prenatal maternal investment (34). From the 72 potential receiver pairs, we excluded 5 pairs because their own eggs failed to hatch and 6 other pairs because we did not obtain enough larvae to set up foster broods. Thus, we set up a total of 61 experimental pairs. One experimental pair was subsequently excluded from further analyses because one of the parents died during the period of parental care. Because we had no prior expectation of effect size, we aimed for a large and predefined sample size of 30 successful pairs per treatment. The total sample size in the experiment was  $n = 60$ , including 31 pairs raising broods laid in the presence of a male and 29 pairs raising broods laid in the absence of a male.

**Behavioral Observations.** To cover the entire period of parental care (23), we conducted three observations on each pair. We first conducted behavioral observations of parents at 1 h (± 15 min) after generating the experimental

brood, which is when maternal effects are likely to be most pronounced (32, 35). We then conducted observations after 25 h ± 15 min, which corresponds to the peak in parental care and offspring begging (23). Finally, we conducted observations after 49 h ± 15 min, which is just before larvae become nutritionally independent (23). We used instantaneous sampling, scoring behaviors every 1 min for 30 min in accordance with established protocols (33). We scored the number of scans each parent spent providing direct care, defined as regurgitation of food to the larvae, manipulation of carrion, or regurgitation of carrion within the crater (36, 37).

**Offspring and Parental Fitness.** Parents were left undisturbed until the larvae dispersed from the carcass at 8–10 d after pairing, at which point we recorded the number of larvae and weighed the brood. Parents were weighed, placed in individual boxes, and checked for survival twice a week as we fed them small pieces of organic beef. We obtained measures of life span for 57 females (excluding 3 females that escaped from their boxes) and 60 males. We placed the dispersed larvae in a box (170 × 120 × 60 mm) filled with soil to allow them to pupate and eclose as adults. We then recorded the number and sex of the eclosed offspring. We randomly selected one male and one female offspring from each brood, kept them in individual boxes, and fed them twice a week to record their life span. The number of eclosed beetles was not available for one brood (eclosed beetles were accidentally discarded before being counted after selection of one male and one female). After death, we measured the pronotum width of adult parents and offspring using a Mitutoyo Absolute Digimatic caliper. To minimize observer bias, all observations and measurements were done blinded with respect to the treatment by allocating a two-letter code to each experimental pair.

**Statistical Analyses.** All statistical analyses were conducted using R (38). We used linear models (lm function in stats) except for the behavioral data, where we used generalized linear models for zero-inflated negative binomial distributions (glmmadmb function in glmmADMB), and for offspring adult size, where we used linear mixed models (lme function in nlme), given that we measured one male and one female per brood. For survival analyses, we used survival models (survreg and coxph functions in the survival package). Because parametric tests (when an appropriate distribution is available) are statistically more powerful and give more accurate estimates than semiparametric and nonparametric tests (39), we first attempted to fit the different available survival distributions to our data and selected the best distribution (log-logistic for parent survival) based on an Akaike information criterion (AIC) comparison, and confirmed graphically that the model fitted our data (Fig. S2). Given the nonnormal distribution of offspring survival (Fig. S1), we used semiparametric Cox proportional hazard regression models because the effect of the treatment met the assumption of proportional hazards ( $\chi^2 = 0.622$ ;  $P = 0.430$ ). For all analyses, we included the effect of treatment (presence or absence of a male partner before hatching), as well as a small set of pertinent explanatory variables, in the full models (SI Materials and Methods). We then applied a backward-stepwise procedure to remove nonsignificant variables. Statistics of the nonsignificant variables presented in the tables were obtained by sequentially reintroducing each of them into the minimal model (40).

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