Negotiation between parents: does the timing of mate loss affect female compensation in *Nicrophorus vespilloides*?

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Summary

Facultative adjustments in care are usually interpreted as a form of negotiation between the parents over how much care each should provide. Previous research on the burying beetle, *Nicrophorus vespilloides*, shows that males but not females appear to adjust their levels of care following negotiation. However, the importance of negotiation is likely to decrease over the course of a breeding attempt, and thus the timing of mate removal might affect the degree to which females adjust their levels of care. We therefore performed an experimental study where we removed *N. vespilloides* males at different intervals; before the female was provided the resources needed for breeding, 24 h after receiving resources, at the time of larval hatching, or after the parental care period. We monitored the effects on levels of female care of the offspring when parental care is at its highest. We found that the timing of male removal had a significant effect on the time females spent maintaining the carcass, but not on the time females spent providing food for the offspring or processing carrion. Our findings suggest that, in *N. vespilloides*, female decisions about how much care to provide involves negotiation, although the importance of negotiation decreases towards the end of breeding attempts.

Introduction

In many species in which both males and females provide care, parents have been found to adjust their levels of care facultatively following the

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experimental removal or handicapping of their mate (Wright & Cuthill, 1989, 1990a,b; Markman et al., 1995, 1996; Saino & Møller, 1995; Smiseth & Amundsen, 2000; Hunt & Simmons, 2002). However, there is variation in whether or how much parents respond and models suggest that a major cause behind this variation is the process by which parents make decisions about how much care to provide (Houston et al., 2005). Whenever this decision process involves negotiation between parents, the degree to which a parent responds facultatively to a reduction in its mate's care is expected to change over time as the breeding attempt progresses.

Burying beetles (*Nicrophorus* spp.) provide a good model for tests of theories of biparental care. In addition to directly provisioning food to the offspring, the most spectacular aspect of parenting in burying beetles, males provide care prior to larval hatching by assisting in the burial and preparation of the carcass for breeding (Eggert & Müller, 1997; Scott, 1998). Preparing the carcass involves considerable work, removing hair or feathers from the carcass, rolling it into a ball, burying it, and treating the carcass with secretions to prevent fungal and bacterial growth. Males are also often involved in other post-hatching care by preventing fungal and bacterial growth on the carcass, and defending the carcass against predators and competitors. Males tend to spend less time provisioning food for the larvae than females but are more involved in maintenance of the carcass and guarding of the brood (Fetherston et al., 1990; Smiseth & Moore, 2004; Smiseth et al., 2005).

Recent studies on *N. orbicollis* (Rauter & Moore, 2004) and *N. vespilloides* (Smiseth & Moore, 2004; Smiseth et al., 2005) show that male and female burying beetles respond differentially to loss of a mate. Males adjust their care following the experimental removal of their mate that previously provided care, while females generally show no response. However these results are seemingly inconsistent with earlier studies of parental adjustment in burying beetles. In studies where the male was removed well before or soon after larval hatching, unassisted females spent more time provisioning food for the larvae than assisted females (*N. vespilloides*, Jenkins et al., 2000; *N. orbicollis*, Fetherston et al., 1994). There are other differences between these studies and those of our laboratory (Smiseth et al., 2005), but one possible explanation for the difference is that timing of male removal influences the degree to which female parents adjust their levels of parental care in burying beetles. Such flexibility by females would suggest that negotiation depends on the value of male assistance.

The aim of our study was to test the prediction that the timing of male removal affects the degree that female parents show facultative adjustments in their levels of parental care in *N. vespilloides*. We measured female care behaviours after experimentally removing males at times that coincide with specific stages in the breeding cycle: (1) immediately before the female was provided with a mouse carcass, (2) 24 h after the pair was provided with a mouse carcass, (3) at the time of larval hatching and (4) where the male was allowed to desert the brood naturally. Thus, females provided both pre- and post-hatching care without male help in treatment (1), males provided some pre-hatching care in preparing the carcass in treatment (2), males fully participated in pre-hatching care but no post-hatching care in (3), and males were able to provide care in all contexts in (4). We predicted that the degree to which female parents show facultative adjustments in their levels of parental care would decrease over time, reflecting that negotiation between parents would be less important towards the end of the breeding attempt when male help was less valuable.

Methods

Experimental procedures

We randomly selected pairs of non-sibling and outbred two-week old virgin males and females for use in the experiment (see Smiseth & Moore, 2002 for details of rearing and maintenance of stocks). Pairs were placed in 17×12 cm and 6 cm plastic box filled with about 2 cm of moist soil and the next day we provided the beetles with a previously frozen mouse carcass, the mean size (± SD) of which was 21.1 ± 4.0 g ($N = 60$). We experimentally removed the male at the four different intervals as indicated above.

Behavioural observations

We monitored the effects of male removal on the behaviour of females when larvae were 48 h old and measured the three parental behaviours that make up most of the time budget of caring females (Smiseth & Moore, 2004): (1) ‘provisioning larvae’, (2) ‘processing carrion’, and (3) ‘carcass maintenance’ (see Smiseth & Moore, 2002, 2004 for detailed descriptions). Males and females sometimes also ‘guard’ — stand on top of the carcass without processing carrion. We did not include this category because the relevance in a laboratory study is not clear given there is nothing to guard against and we saw low levels of guarding in our study. Larvae and the female were not disturbed prior to observations, and lids were removed carefully for over an hour to allow the beetles to acclimate. We recorded all occurrences of the parental behaviours that occurred during the period of a sample using instantaneous scan sampling (see Smiseth & Moore, 2002, 2004). All observations were conducted under red light. After the observation session we counted and weighed the larvae to obtain data on brood size and the approximate age of the larvae.

Statistical analyses

We used ANOVA if data were normally distributed or a Kruskal-Wallis test for behavioural variables that were not normally distributed to test for the effect of timing of male removal. We estimated the statistical power given the effect size for all non-significant results. All statistical tests were performed using SYSTAT 10.0. All tests were two-tailed, and the significance level was set at $p < 0.05$. We experimentally minimised or eliminated variation in size of the carcass, brood size and larval age. There were no differences among treatment groups associated with variation in carcass size ($F_{3,121} = 0.30$, $p = 0.76$) or brood size ($F_{3,121} = 2.12$, $p = 0.10$). We controlled for larval age by conducting all of our observations at the same age.

Results

The timing of male removal had a statistically significant effect on the time spent maintaining the carcass by caring females (Kruskal-Wallis test: $H = 8.26$, $N_{\text{o-h}} = 32$, $N_{\text{24-h}} = 31$, $N_{\text{hatching}} = 31$, $N_{\text{control}} = 31$, $p = 0.041$). As predicted, females spent more time maintaining the carcass when the male was removed earlier rather than later in the breeding cycle and spent the least time maintaining the carcass in the control group where the male was left with the female (Figure 1a). There were no significant effects of the timing of male removal on the time spent processing carrion (Figure 1b; Kruskal-Wallis test: $H = 3.70$, $N_{\text{o-h}} = 32$, $N_{\text{24-h}} = 31$, $N_{\text{hatching}} = 31$, $N_{\text{control}} = 31$, $p = 0.30$). The power of our test was 0.4 with an effect size = 0.2. A sample size of 268 would be required to achieve a power of 0.8.

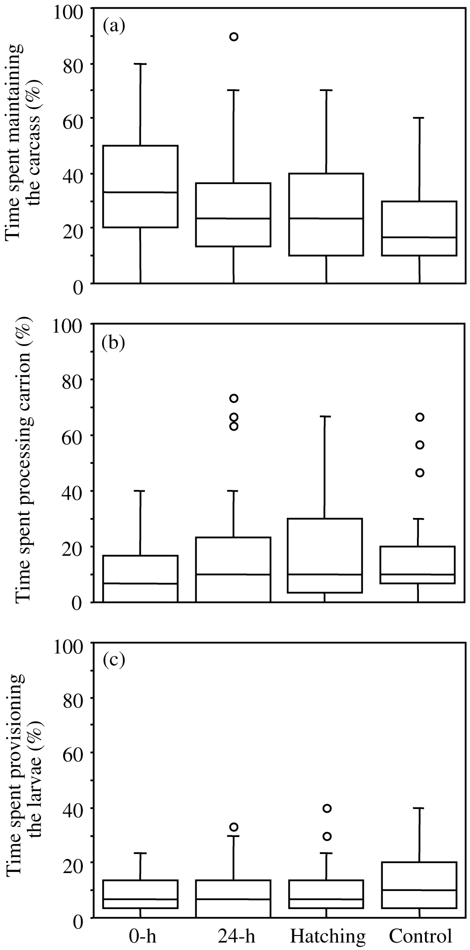

Figure 1. Box plots for the effect of the timing of male removal on the behaviour of caring female *N. vespilloides* parents on day 2 after hatching. The male was experimentally removed after pairing but before the female was provided with a mouse carcass (o-h), 24 h after the pair was provided with a mouse carcass (24-h), and at the time of larval hatching (hatching) or after it deserted the brood naturally after providing direct care to the offspring (control). We then examined the effects of male removal on: (a) Time spent maintaining the carcass and the crypt (b) Time spent processing carrion. (c) Time spent provisioning the larvae. Because the data are not normally distributed, we have presented box plots where the horizontal lines show the 10th, 25th, 50th (median), 75th and 90th percentiles. Data outside this range are plotted as open circles.

Likewise, there were no significant effects of timing of male removal on time spent provisioning food for the larvae by caring female (Figure 1c; Kruskal-Wallis test: $H = 3.77$, $N_{\text{o-h}} = 32$, $N_{\text{24-h}} = 31$, $N_{\text{hatching}} = 31$, $N_{\text{control}} = 31$, $p = 0.29$). The power of this test was 0.45 with an effect size = 0.21. A sample size of 244 would be required to achieve a power of 0.8. There was virtually no difference among the treatment groups in the average weight of larvae after care (ANOVA $F_{3,121} = 0.03$, $p = 0.99$), further supporting no difference in female allocation of resources to offspring in response to loss of a mate.

Discussion

Our results suggest that the timing of male removal can affect the degree to which *N. vespilloides* female parents show facultative adjustments in their parental behaviour. Visual inspection of Figure 1 suggests that compensation by females for the loss of male care only occurred when the male had been removed very early in the breeding cycle. Presumably this reflects that the importance of parental negotiation over care decreases over time. We did not measure guarding, but it is likely that this behaviour has similar value before and after larvae hatch. Defence is very important because intra- and inter-specific competition for carcasses is known to be intense in nature (Scott, 1989, 1990, 1994; Scott & Gladstein, 1993). Burying beetle reproduction cannot occur without a carcass, and the scarcity and value of this resource may have driven the evolution of male care (Scott, 1990; Scott & Gladstein, 1993).

The extent that a parent should show facultative adjustments in its care following a reduction in the amount provided by its mate depends critically on the process by which parents make decisions about how much care to provide (Houston et al., 2005). Whenever parents negotiate, the degree to which a parent responds facultatively is predicted to change over time as the importance of male assistance and therefore parental negotiation decreases towards the end of a breeding attempt. In burying beetles, as in some birds (Bart & Tornes, 1989) the importance of male assistance decreases towards the end of a breeding attempt. Male burying beetles provide considerable amounts of care prior to hatching, including participating in the burial and preparation of the carcass, which are likely to be energetically expensive (Eggert & Müller, 1997; Scott, 1998). The assistance of males in pre-hatching care may be of additional importance because females have to lay eggs during this time, which occurs away from the carcass. After larvae hatch there may be less for males to do. Male assistance in providing food for the offspring appears to be redundant in burying beetles because single females have been found to be as competent at providing food as females with male assistance (Barlett, 1988; Müller et al., 1998; Jenkins et al., 2000; Smiseth et al., 2005). This may reflect that males tend to be considerably less involved in direct care for the offspring than females (Fetherston et al., 1990; Smiseth & Moore, 2004; Smiseth et al., 2005).

Facultative adjustments in the parental behaviour of females following a reduction in or the loss of male care may be complex. Our study provides some evidence for parental negotiation as modelled by McNamara et al. (1999), although female *N. vespilloides* parents only seem to partially compensate for male removal when the male is removed early in a breeding attempt. Thus, our study highlights the need to consider temporal changes in the importance of male assistance in care and corresponding temporal changes in the importance of the negotiation process when testing and developing the models for the evolution of biparental care.

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