

RESEARCH PAPERS

To Compensate or Not? Caring Parents Respond Differentially to Mate Removal and Mate Handicapping in the Burying Beetle, *Nicrophorus quadripunctatus*

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Abstract

Game theoretical models predict that when one parent reduces its care, the mate should adjust its care facultatively to compensate partially. To test these models, mate-removal and mate-handicapping techniques have been used. However, there have been few experimental studies comparing results from mate removal and mate handicapping, and there has been no study on insects employing handicapping. Male and female burying beetles both maintain the nest and regurgitate to young. We examined how burying beetle parents adjust their level of care when their mates are removed or handicapped. Males increased their frequency of provisioning significantly after female removal, whereas females showed no response to male removal. However, neither sex showed a response to the handicapping of its partner, although handicapped mates decreased the frequency of their care. This result showed that burying beetle parents respond differentially to mate removal and handicapping, and suggests that parents do not respond to a change in the behavior of their mates.

Introduction

The main benefit of biparental care is an increase in the number of offspring that can be reared (Clutton-Brock 1991). In systems with biparental care, an individual's optimal investment will depend, in part, on the amount of investment provided by the cooperating partner (Trivers 1972). In species showing biparental care, parents have been found to adjust their levels of care facultatively (Westneat & Sargent 1996). Because sexual conflict over the amount and division of care exists in biparental care (Houston et al. 2005), the optimal investment of two parents is likely to reflect the outcome of a contest played between the sexes over behavioral and evolutionary time (Westneat & Sargent 1996).

The way that each parent responds to the presence and effort of its partner will affect the parenting

system and the success of the brood. Game theory has been the main theoretical tool for investigating the evolutionary stability of biparental care (Houston & McNamara 1999). In the 'negotiation model', parents modify their effort sequentially in direct response to the prior effort of their mate. The negotiation model predicts that parents should partially compensate for a reduction in their mate's effort (Houston & McNamara 1999).

There have been many studies of biparental systems to investigate behavioral dynamics between the sexes, and the negotiation model has been tested empirically because it makes predictions about facultative adjustments between caring parents. Empirical results, however, varied from full (Sanz et al. 2000), partial (Wright & Cuthill 1989), to no compensation (Schwagmeyer et al. 2002). These studies have been mostly of birds employing mate-removal (Smiseth &

Amundsen 2000) or mate handicapping techniques (Wright & Cuthill 1989; Sanz et al. 2000). Mate removal experiments do not offer much insight into the dynamics of biparental negotiations over effort levels (Wright & Cuthill 1989), but handicapping experiments can alter parental effort of one member, so the response of the other member can be measured. Although theory predicts that after mate removal the remaining parent should not respond the same as a parent after its mate is handicapped (McNamara et al. 2003), there have been few experimental studies comparing the results of mate removal and mate handicapping.

Biparental care is found in a number of insects, including dung beetles (Hunt & Simmons 2002), pas-salid beetles (Schuster & Schuter 1997) and tenebrioid beetles (Heg & Rasa 2004). Burying beetles (*Nicrophorus* spp.) provide a particularly good model for empirical tests of biparental care theory. The complex biparental care of burying beetles (Silphidae: *Nicrophorus*) is well known and has received considerable attention (reviewed in Eggert & Müller 1997; Scott 1998). *Nicrophorus* exploit small vertebrate carrion as food for their young. Typically a male–female pair prepares a carcass by burying it, removing hair, and rounding it into a ball. Eggs are laid in the soil adjacent to the carrion ball. After hatching, larvae crawl to the carrion ball where they are fed by parental regurgitations. Males, but not females, adjust their care following the experimental removal of a mate that previously provided care (Rauter & Moore 2004; Smiseth & Moore 2004a; Smiseth et al. 2005).

Mate compensation studies of burying beetles have been conducted by both removal experiments (Trumbo 1991; Fetherston et al. 1994; Rauter & Moore 2004; Smiseth et al. 2005) and comparison among families (Smiseth & Moore 2004a,b). However, there has been no study of a subsocial insect employing handicapping. The aim of our study is to determine how burying beetle parents adjust their level of investment relative to their partner's contribution by comparing the behavioral responses to mate removal and mate handicapping.

Methods

We trapped *Nicrophorus quadripunctatus* in the field by baiting with rotten meat. Similar-sized *N. quadripunctatus* beetles (pronotal width 4.5–5.0 mm) were selected for experiments. A pair of *N. quadripunctatus* and 15 g of chicken meat were introduced into a polyethylene container (15 × 15 × 9 cm) that was half filled with soil. All containers were kept at 20°C

in constant darkness. We checked these daily, and about 24 h after hatched larvae reached the carcass, soil covering the carcass was removed, and containers were randomly assigned to a treatment. Beetles were removed, handicapped or disturbed as appropriate at this time. Because the experiments were conducted when larvae were about 24 h old, when parental care is most intense (Fetherston et al. 1990), especially for females, we expected that handicapping would reduce the level of care.

Details of Handicapping Methods

We manipulated parental behavior by attaching a small metal weight (about 0.2 g) with aronalpha® to the pronotum of either the male or female (Fig. 1). This weight is about 40% of the wet weight of *N. quadripunctatus* for the size range used in this experiment (Suzuki, unpublished data). Handicapped beetles can walk, but their speed is significantly slower than beetles that are not handicapped (handicapped: 0.46 ± 0.33 , non-handicapped: 2.12 ± 1.77 m/min, $\bar{x} \pm SD$, $n = 21$, $p < 0.001$, $U = 456.0$, U-test, Suzuki, unpublished data). They can open their wing but cannot fly because of the weight. However, handicapped females can copulate normally with males, and can deposit fertile eggs (Suzuki, unpublished data). The weight can be removed after the experiments and these beetles are intact and can reproduce normally.

Behavioral Difference Between Mate Removal and Handicapping

Removal treatment (male removal: $n = 15$, female removal: $n = 15$): We manipulated absence or presence of a mate by removing one parent.



Fig. 1: Appearance of a handicapped beetle.

Handicapping treatment (male handicap: $n = 15$, female handicap: $n = 16$): We manipulated parental behavior by handicapping either the male or female, leaving the other parent unmanipulated. If the weight became dislodged from the beetle before the observation period was finished, the trial was excluded from the analysis.

Control treatment ($n = 18$): Neither parent was removed or handicapped.

Four to eight hours after removing or handicapping one parent, we recorded parental behavior. All observations were conducted under dim light. Using instantaneous sampling, we recorded parental behavior every 30 s for 1 h. We scored the following parental care behaviors.

1. *Provisioning the brood*: parent regurgitates to larvae through mouth-to-mouth contact.
2. *Carrion maintenance*: parent treats the outside of the carrion with mouthparts, or its abdomen. Previous studies (e.g. Rauter & Moore 2004; Smiseth et al. 2005) distinguished 'processing carrion' and 'carrion maintenance', but we combined these two in this category as we could not distinguish these behaviors.

Statistical Analysis

We first tested for sex differences in parental care (carrion maintenance and provisioning) by conducting Wilcoxon rank tests in the control broods. We next examined the extent of behavioral adjustments among treatments in either sex using ANOVA. For pair-wise comparisons in experiments among treatment groups, we used the Tukey–Kramer method.

Results

Time allocated to carrion maintenance was not different between the male and female parent in control trials ($Z = 1.38$, $p = 0.16$). Single males and single females after mate removal also allocated similar time as controls to carrion maintenance. Only in handicapped trials, there was a significant decrease in the time allocated to carrion maintenance by the handicapped parent (Fig. 2, male: $F = 4.85$, $d.f. = 3$, $p < 0.001$; female: $F = 12.06$, $d.f. = 3$, $p < 0.001$, one-way ANOVA). This indicated that handicapped beetles reduce their effort in carrion maintenance.

In control trials females provisioned at a significantly higher rate than males ($Z = 3.73$, $p < 0.001$). In mate-removal trials, single females allocated similar time, and, in contrast, single males allocated more time than controls to provisioning the brood.

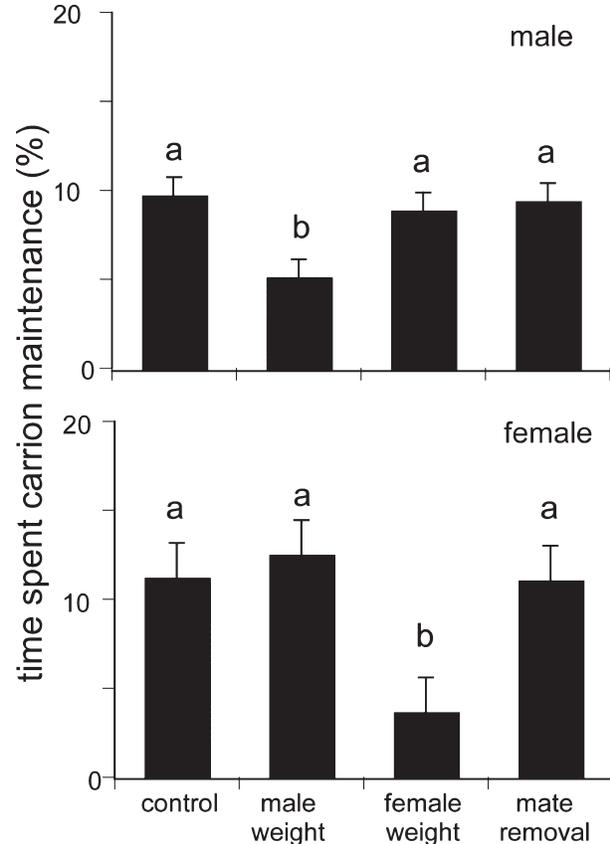


Fig. 2: Effects of handicapping and mate removal on time spent on carrion maintenance (%). Data are presented as $\bar{X} \pm SE$. The same letters above the bars on each graph indicate that they are not significantly different (Tukey–Kramer method, $p < 0.05$).

When a weight was attached to the mate, provisioning times of the unmanipulated partner were not different from those of the controls for either sex (Fig. 3, male: $p > 0.05$; female: $p > 0.05$; overall model: male: $F = 43.24$, $d.f. = 3$, $p < 0.001$; female: $F = 53.48$, $d.f. = 3$, $p < 0.001$, one-way ANOVA). Total provisioning of male and female when the female is handicapped (17.5 ± 1.4), is less than that of male's even when the female was removed ($p = 0.003$, $t = 4.16$, t -test).

Discussion

One of our aims was to compare the effect of removal or handicapping of mates in burying beetles. There have been many studies of birds to test whether parents adjusted their care in response to removal or handicapping of their mate. In contrast, there have been no studies using handicapping in insects. Handicapped burying beetles decreased the

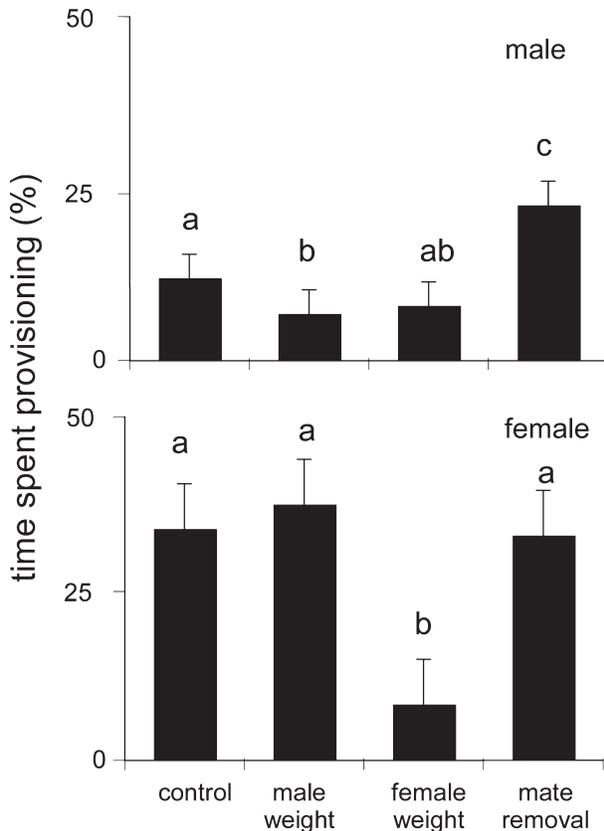


Fig. 3: Effects of handicapping and mate removal on time spent provisioning larvae (%). Data are presented as $\bar{X} \pm SE$. The same letters above the bars on each graph indicate that they are not significantly different (Tukey–Kramer method, $p < 0.05$).

frequency of provisioning and carrion maintenance (Figs 2 and 3). In previous studies the removal of a mate had no effect on the time spent in carrion maintenance (Rauter & Moore 2004; Smiseth et al. 2005); the decrease by the handicapped beetle in our study indicates that our handicapping method does decrease the level of parental care.

Both sexes of *N. quadripunctatus* provision food and maintain the carcass, although food provisioning by males is performed at lower rate than by females. Subjects of prior studies of biparental care in birds generally have similar male and female food-provisioning rates (Sanz et al. 2000; Schwagmeyer et al. 2002). Usually, biparental care is thought to be evolutionary stable when one sex compensates partially for changes in care by the other parent (Houston & Davies 1985; Ratnieks 1996), or when one sex cannot rear offspring on its own (Maynard Smith 1982). In contrast, biparental care in *Nicrophorus* does not increase the brood size or brood mass (Scott & Gladstein 1993; Trumbo & Fernandez 1995; Sakaluk

et al. 1998; Jenkins et al. 2000; Smiseth et al. 2005; Trumbo 2006, 2007), males can compensate for a missing partner, and either sex can rear a brood on its own without partner (Fetherston et al. 1994; Rauter & Moore 2004). Though previous models suggest that lack of full compensation or the necessity of biparental effort is needed to the evolution of biparental care, the case of *Nicrophorus* does not follow model predictions.

Males of *N. quadripunctatus* adjusted their rate of provisioning after removal of their partners, whereas females did not. Adjustment of male provisioning has also been reported for *N. orbicollis* (Fetherston et al. 1994; Rauter & Moore 2004) and *N. vespilloides* (Smiseth et al. 2005). Female burying beetles sometimes adjust provisioning (Fetherston et al. 1994) but sometimes not (Rauter & Moore 2004; Smiseth et al. 2005), and these adjustments are affected by the timing of male removal (Smiseth et al. 2006). Although males adjusted their provisioning in response to mate loss in this experiment, neither males nor females responded to the handicapping of its partner even though handicapping clearly altered rates of provisioning and carcass maintenance.

Theoretical models of biparental care can be divided into ‘sealed envelope’ and ‘negotiation’ models (Houston & McNamara 1999). The former model assumes that each parent makes an independent decision, and the latter model assumes that parents negotiate to modify their effort in direct response to the prior effort of their mate. Smiseth et al. (2005) assumed that provisioning behavior by *N. vespilloides* males is consistent with predictions of the negotiation model. As larval begging provides a reliable signal of nestling hunger (Smiseth & Moore 2004a,b), parents are provided with a feedback mechanism to increase care when their partners reduce care (Rauter & Moore 1999). The results of the handicapping treatments, however, contradict this assumption. If the negotiation model were to apply to biparental care of *N. quadripunctatus*, then some compensation of provisioning should have been observed in response to handicapping.

It is possible that negotiation is incomplete when one parent is handicapped. The negotiation model assumes that parental effort affects current reproductive success, and parental effort is decided on the basis of the response to the effort of the mate (Houston et al. 2005). In the case of *N. quadripunctatus*, the parent would have the opportunity for confirming the current parental effort of the handicapped mate. However, neither sex responded to the reduction of parental effort by the

handicapped mate even though the male did respond by increasing care to removal of his mate. If males assessed the hunger of the larvae, they should regurgitate more to larvae when females were handicapped and providing less care. If males assessed the behavior of their partner, they should compensate for the reduction of the care of their partner. Our results showed that males assess neither. Then, the apparent difference in the response to mate removal and mate handicapping in burying beetles is that beetles can assess only the presence or absence of their mate, not the level of care being provided by their partner although this hypothesis needs further investigation.

There have been few studies comparing the effect of mate removal and handicapping. Our study shows that *N. quadripunctatus* reacted differently to mate removal and handicapping and contradicted some predictions of the negotiation model. It is possible that the stimulus determining compensation of care in burying beetle is not current behavior of the mate, but other stimuli.

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