

Frenemies:

Conflict and cooperation in burying beetle (*Nicrophorus investigator*) parental care

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Abstract

Conflict and cooperation can drive how unrelated individuals interact, while illustrating whether the interests of two individuals converge or diverge. The subsocial, biparental beetle *Nicrophorus investigator* provides an excellent model to study these two interactions because researchers can manipulate aspects of the system and observe ensuing cooperation or conflict. In this experiment, we chose to test what we term the “Happy Couple assumption”, a tendency among scientists to presuppose that there is little conflict in the brood chamber of burying beetles. We found that medium-sized males paired with larger females leave the brood about 45% earlier than both large males paired with large females or medium males with medium females. We also found that injuries occurred in more than 25% of beetle pairs across both treatments and sexes. These findings collectively suggest that not only does conflict exist in burying beetles pairs, but that having a male in the brood chamber can be costly for females.

Introduction

Few naturalists can deny the inherent wonder of burying beetles (genus *Nicrophorus*). These carrion-hungry coleopterans exhibit a provisioning life history rare in their class that can illuminate some of the evolutionary and ecological determinants of cooperation and eusociality (Nowak et al. 2010). While many young mammals and birds enjoy the benefits of provisional parental care, the phenomenon is rare in invertebrates (Eggert et al. 1998), and although fifty families of insects across sixteen orders show some sort of parental care, these species often exhibit rudimentary care strategies, such as protecting mobile young (Trumbo, in prep.). Burying beetles, in contrast, form male-female pairs and cooperatively perform a rainbow of parental tasks including fungi removal,

protection against predators, and larval feeding. Parental care ranges from 9 to 16 days, depending on the species of beetle, carcass size, or temperature, and both males and females are capable of parenting alone (Scott 1998).

Because they provide biparental care, burying beetles present researchers with a dependable model for studying cooperation and conflict between two unrelated individuals (Harrison et al. 2009), and scientists have recognized these behavioral extremes in the beetles for almost a century. In his 1918 account of *Nicrophorus*, the eminent French entomologist Jean-Henri Fabre explained that male burying beetles “are remarkable fathers,” having “nothing of the happy-go-lucky paternal carelessness that is the general rule among insects”. This “exemplary domestic morality” does not last long, however, because Fabre also noticed that the beetles emerge “half-devoured” as “cripples, whose limbs have been amputated at the joints, some higher up, some lower down” (Fabre 1918). While the cooperation aspect of burying beetles has been recognized in contemporary literature, the physical conflict has been extensively overlooked. Researchers describe the adaptations of biparental care often without any mention of how different sexual interests can manifest themselves in the brood chamber. This tendency to assume harmonious cooperation in the brood chamber with little direct conflict –the Happy Couple assumption – faultily buttresses the understanding of male parental care and its duration.

Because of the Happy Couple assumption, researchers have presupposed that the duration of male care honors both male and female interests – that females have little agency in when males “desert”. Females traditionally feed the larval brood until the young fully develop, but males leave the brood first, leaving their mates as sole

caretakers of the larvae (Trumbo 1991). Many researchers have considered the determinants of male care to understand “desertion”, and studies consistently support a single hypothesis – deterring a takeover by competing beetles (Trumbo 2006). Carrion is a “bonanza” resource, or a valuable and unpredictable prize that must be defended from an assortment of organisms (Scott 1998); because of their value, such resources generally select for parental care (Wilson 1971). Therefore, while males (and females) perform behaviors such as brood chamber maintenance, fungi removal, and circling the brood ball (Fetherston et al. 1990), the primary selectionist pressure for male parental behavior has been suggested as warding off inter- and intraspecific competitors (Trumbo 1991). To test this, studies have manipulated aspects of the brood, such as the presence of a female or the size of the carcass, and found that males leave later when the brood is more vulnerable (Trumbo 1991, Suzuki & Nagano 2005). The Happy Couple assumption has confounded these findings, because researchers assume that male desertion honors the interests of both sexes.

Two observations have forced us to question the Happy Couple assumption. Firstly, laboratory studies found that when conflict occurs in burying beetles, as with most species, it is typically the larger individual that prevails (Otronen 1988). Secondly, recent fieldwork at the Rocky Mountain Biological Laboratory in Gothic, CO has found large female burying beetles parenting alone by day 5 (Smith, unpublished). Considering that larger individuals prevail in conflicts, this observation would suggest that females may be evicting males and thus, there is a cost to the female for having the male in the brood chamber. Through our experiment, we chose first to test the observation that female size affects the duration of male care and second to test for proximate causes. We

offered two hypotheses for shorter male care in the presence of large females: 1) Males may be deserting the carcass on their own because larger females are more competent; or 2) females are evicting the obsolete males. To test between these hypotheses, we experimentally set up three size pairings – large female-large male (LL), medium female-medium male (MM), and large female-medium male (LM) – and subsequently made predictions (Table 1).

If...	then...
female size affects the duration of male care,	LM males should desert the brood earlier than MM males.
males are deserting the carcass because larger females are competent to parent alone,	LL males and LM males should desert at the same time, while MM males should desert later.
females are evicting smaller males,	LM males should desert earlier than LL and MM males.
there is conflict in the brood chamber,	injuries should be more common in MM and LL treatments.

Table 1. Hypotheses and if-then predictions.

Methods

We collected *Nicrophorus investigator* beetles from tin can chicken traps positioned around the Rocky Mountain Biological Laboratory in Gothic, CO in late June and early July, 2011 in a manner similar to that described by Grossman and Smith (2008). Unlike Grossman and Smith, however, we fastened the cans to aspen trees, measured the pronotums and elytra of the beetles, and kept the organisms in separate male-female containers.

After measuring the pronotal and elytra lengths of the beetles, we assigned male-female pairs to three experimental treatments (N=20 pairs per treatment): large female-large male (LL), medium female-medium male (MM), and large female-medium male (LM). To decide which individuals were assigned to each treatment, we randomly selected 40 large females, 20 large males, 20 medium females, and 40 medium males from our wild-caught collections (Figure 1). We randomly paired individuals in the LM treatment and intentionally paired similarly sized individuals in the LL and MM treatments. We placed the beetles in tin cans with thawed *Mus musculus* specimens, and about 7/8 of each can was filled with sifted soil. We positioned the cans randomly by treatment in a WeatherPort. Although the beetles experienced natural ranges in sunlight and temperature, the setup prevented rainfall. Therefore, we sprinkled the cans with a watering can about every three days, ensuring that the soil and mice remained moist. We placed thirty pairs of beetles (ten of each treatment) in experimental cans on Sunday, July 17, 2011 (trial 1); another batch of thirty started three days later on Wednesday, July 20, 2011 (trial 2).

We checked the cans four to five times each day and noted several observations relating to parental care, such the presence of a male or female, the beetle's location, interactions between beetles, injuries, and the visibility of larvae. If a beetle appeared at or near the surface of the soil in three out of four consecutive checks, we considered it a "desertion"; total parental care ended either when the larvae began dispersal or when both individuals deserted the brood. We disregarded the data from a single LM can because the male deserted (or was evicted) immediately, and the female was unable to lay any

eggs. After removing both the male and female from a can, we removed and weighed the larvae.

We compared the duration of male care and total parental care between treatments and blocks using a one-way ANOVA. When significant ($P < 0.05$), we tested for pairwise differences between means using a Tukey-Kramer HSD post-hoc test. We used SAS JMP v. 9 (SAS Institute, Cary, NC). To test for significant injury distributions, we used a χ^2 test.

Results

The duration of male care differed significantly between blocks and treatments. Overall, males in the LL and MM treatment remained with the brood 43% and 49% longer than those in the LM treatment, respectively (Figure 2). Males in the first block remained with the brood 41% longer than those in the second block, though there was no effect of both block and treatment (Figure 3). Injuries were distributed similarly across treatments (LL, LM, MM), sexes (M, F), and sexes within treatments (LL-M, LL-F, etc.) (Figure 4).

We used brood weight, brood size, and average larval weight as proxies for fitness; none of these measures differed significantly between treatments. The duration of female care also compared similarly across the size pairings.

Discussion

Our experiment elucidated two important factors concerning burying beetle parental care. Firstly, conflict exists in the brood chamber. We documented injuries in 17 out of 60 cans and wounds ranged from damaged antennae to legless individuals unable to turn themselves right-side-up like momentumless tortoises. Unlike our predictions,

however, injuries were not solely restricted to LL and MM pairings, but were documented across all treatments and sexes. This was an odd finding because, as natural history recurrently depicts, individuals should avoid physical combat if a costly injury is likely. We suggest that future research investigate the determinants of injury in the brood chamber and thus, the costs and benefits of intersexual conflict.

Our second finding not only stems from the first, but may also explain it: female and male interests concerning the duration of male care differ considerably. We found a significant difference in male desertion time between the LM treatment and the remaining two pairings, showing that not only do large females parent alone for longer, but they are also evicting males. We also found a significant difference in duration of male care in block 1 and block 2, though this does not influence our findings and probably resulted from warmer or moister days in the beginning of the experiment. Overall, these findings suggest that there is a cost to females for having a male in the brood chamber for an extended duration of time. The duration of male care not only depends on the vulnerability of the carcass, as many experimenters have suggested (Trumbo 1991), but also the degree conflict or cooperation between the two mates. We hypothesize that large males paired with smaller females remain with the brood the longest, small males with large females desert early, and similarly sized mates dwell in a happy medium. Other studies have found that males stay the longest when females are absent (Suzuki & Nagano 2009), but this may simply result from a relaxation of a conflicting pressure (the female), as it is a form of compensation (Harrison et al. 2009). In other words, we are proposing that the relative size between males and females determines, and facilitates, cooperation in burying beetle biparental care.

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Figures

Figure 1. Average sizes for males and females across treatments. Size is the product of elytra length and pronotum width.

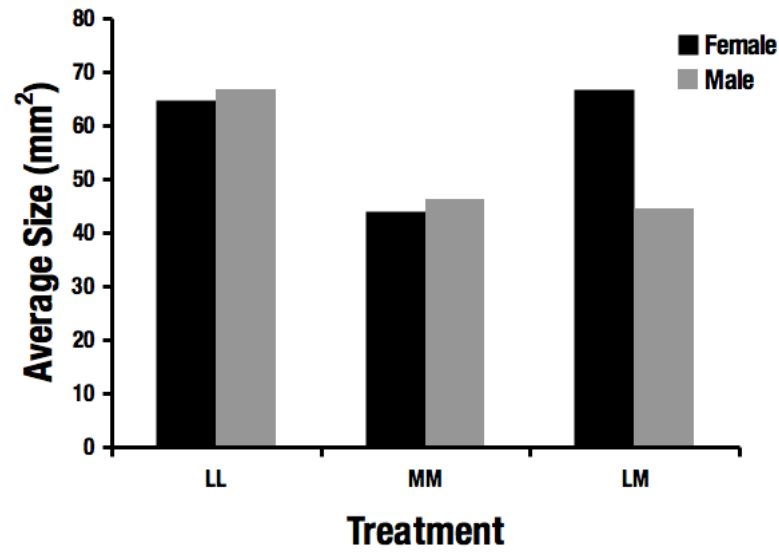


Figure 2. Duration of male care by treatment ($F_{2,58}=4.4307$, $p=0.0166$).

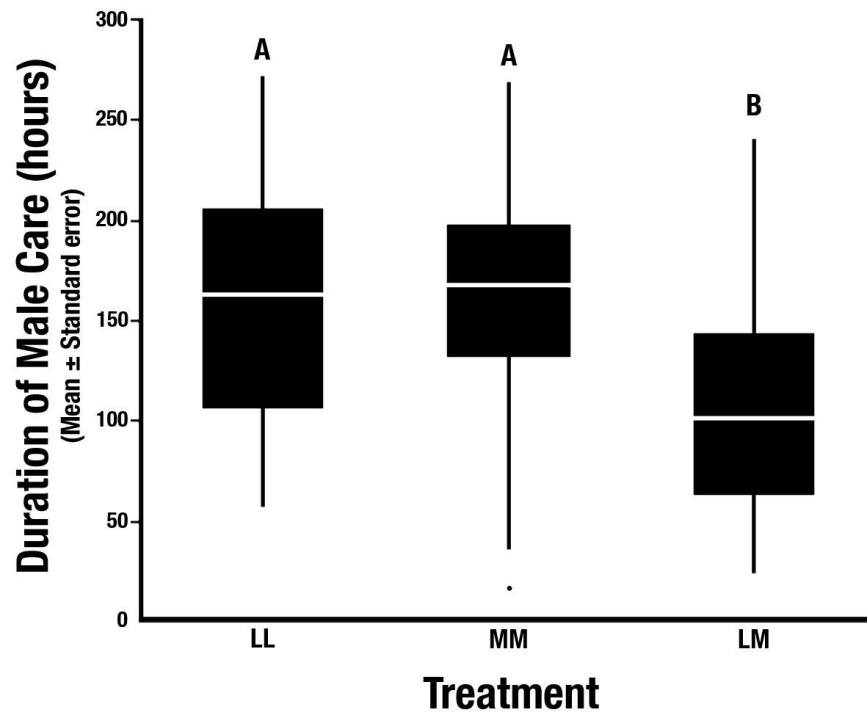


Figure 3. Duration of male care by block ($F_{1,58}=9.6570$, $p=0.0030$).

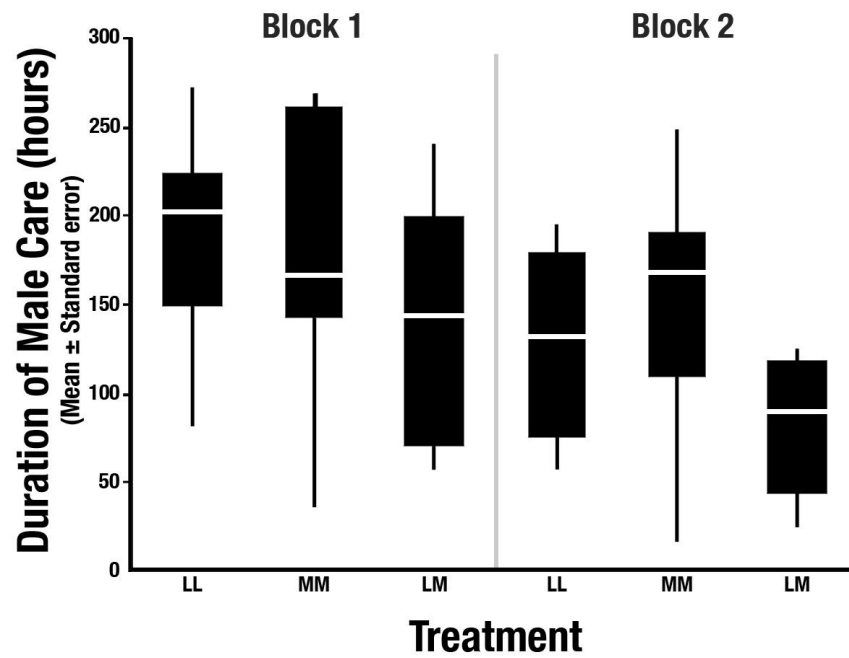


Figure 4. Distribution of injuries across treatments.

