



Interspecific interactions explain variation in the duration of paternal care in the burying beetle



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Why is there so much variation within species in the extent to which males contribute to offspring care? Answers to this question commonly focus on intraspecific sources of variation in the relative costs and benefits of supplying paternal investment. With experiments in the laboratory on the burying beetle, *Nicrophorus vespilloides*, and its phoretic mite *Poecilochirus carabi*, we investigated whether interactions with a second species might also account for intraspecific variation in the extent of paternal care, and whether this variation is due to adaptation or constraint. In our first experiment we bred beetles in the presence or absence of phoretic mites, using a breeding box that mimicked natural conditions by allowing parents to leave the breeding attempt at a time of their choosing. We found that males abandoned their brood sooner when breeding alongside mites than when breeding in their absence. Female patterns of care were unchanged by the mites. Nevertheless, in this experiment, no correlates of beetle fitness were affected by the presence of the mites during reproduction (neither paternal life span after reproduction nor brood size or average larval mass). In a second experiment, we again bred beetles with or without mites but this time we prevented parents from abandoning the brood. This time we found that both parents and the brood suffered fitness costs when breeding alongside mites, compared with families breeding in the absence of mites. We conclude that males adaptively reduce their contributions to care when mites are present, so as to defend their offspring's fitness and their own residual fitness. Interspecific interactions thus account for intraspecific variation in the duration of paternal care. © 2015 The Authors. Published on behalf of The Association for the Study of Animal Behaviour by Elsevier Ltd. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

The extent to which males care for their young varies considerably within species, commonly to a greater extent than is typically seen among females (e.g. Sheldon, 2002) and for a range of reasons that are not mutually exclusive. For example, some of this variation has been attributed to individual variation in the optimal level of paternal care (e.g. Møller & Birkhead, 1993; Balshine-Earn, Neat, Reid, & Taborsky, 1998; Neff, 2003; Manica, 2004; Velando, Drummond, & Torres, 2006; Ward, Cotter, & Kilner, 2009). In species in which either sex can successfully raise offspring single-handedly, or in which there is biparental care, variation in paternal care has additionally been explained by interactions with the mother of their offspring. Males may increase their level of care if raising offspring with a female of very high quality (Johnstone & Hinde, 2006; Moreno & Osorno, 2003), because the benefits to be gained are correspondingly greater. Or they may contribute less investment if paired with a high-quality female, because she can

more easily bear the greater costs of providing more care (Lessells & McNamara, 2011). Sexual conflict between parents over the division of the costs associated with parental care can further explain patterns of paternal care (Bennett & Owens, 2002). If males win this conflict, they may force the female to bear greater fitness costs as a result of providing care, and so contribute relatively little parental care themselves (Van Dijk, Szentirmai, Komdeur, & Székely, 2007). However, if females gain the upper hand, males may take the greater share of the fitness costs associated with parental care and contribute to a far greater extent than the female (Lessells, 2012).

Here we consider whether interactions with other species might also influence the extent of paternal care. Interspecific interactions can strongly impact the reproductive success of fathers and their young. They can reduce the size of the brood (Clotfelter & Yasukawa, 1999; Hillegass, Waterman, & Roth, 2010), increase the success of individual offspring by increasing individual size (Fredensborg & Poulin, 2006; Shostak, 2009) and/or reduce (Watson, 2013) or increase the life span of fathers (Hurd, Warr, & Polwart, 2001). Moreover, interspecific interactions are already known to change paternal contributions to offspring care (Smith, 1980; Dewsbury, 1985; Zeh & Smith, 1985; Smith & Wootton, 1995; Tallamy, 2001;

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Haley & Müller, 2002; Requena, Buzatto, Munguía-Steyer, & Machado, 2009; Grayson, Glassey, & Forbes, 2013). For example, heavily parasitized upland bully males, *Gobiomorphus breviceps*, spend more time fanning their eggs than males that are more lightly infected (Hamilton & Poulin, 1995), while male spotless starlings, *Sturnus unicolor*, adjust their paternal effort in response to the extent of egg spotting, a trait induced by an ectoparasite carried by females (Avilés, Pérez-Contreras, Navarro, & Soler, 2009). However, in most instances it is not known how these changes in paternal behaviour influence the fitness of males. Therefore it is not clear whether changes in the male's contributions to care are imposed by constraints (the male and his offspring could have greater fitness, were it not for costs imposed by a second species) or whether they are adaptive (the change in male behaviour induced by a second species serves to maintain or even enhance the male's fitness and the fitness of his young). We addressed this shortcoming by investigating interactions between the burying beetle, *Nicrophorus vespilloides*, and a phoretic mite commonly associated with it (*Poecilochirus carabi*, Mesostigmata, Parasitidae).

We began by setting up *N. vespilloides* pairs to breed in the laboratory, with and without *P. carabi*, and determined the duration of paternal care in each scenario (experiment 1). After finding that mites did indeed affect the duration of paternal care of the burying beetle, we tested whether these changes were due to adaptation or constraint, by forcing males to remain with their brood for longer than they stayed in the first experiment, again staging breeding events with and without mites (experiment 2). We predicted that if the change in male care induced by mites was adaptive then components of fitness should be smaller in males and their offspring when males bred alongside mites and were forced to remain with the brood until the end of the breeding event than when males were allowed to leave. However, if the duration of care induced by mites was the result of a constraint then mites should consistently reduce components of fitness in the burying beetle, irrespective of the extent of paternal care.

METHODS

Ethical Note

We gently collected larvae in their dispersal stage from breeding boxes and we placed them in eclosion boxes with moist soil. We gently removed adults at eclosion from these boxes and housed them in small transparent plastic containers filled with moist soil. We provided them with adequate food twice a week until they reached sexual maturation. After each experimental breeding event we returned experimental individuals to our standard laboratory housing conditions. During our experiments we handled our beetles with care and they were not harmed at any stage. None of the beetles that we used showed any signs of stress before, after or during the experiments.

Study Species

Burying beetles (*Nicrophorus* spp.) use the body of a small dead vertebrate as a resource for reproduction. Together, the two parents remove the fur or feathers, roll the flesh into a ball, smear it with antimicrobials and inter it in a shallow grave (Scott, 1998). During this process of carcass preparation the female lays her eggs in the soil nearby. After hatching, the larvae crawl to the carcass where they take up residence in a specially prepared crater on the ball of flesh. There, they solicit food from their attendant parents, which also defend the offspring and carcass from potential rivals (Scott, 1998). *Nicrophorus vespilloides* males typically stay with the brood for a few days after hatching (Pukowski, 1933), before flying off in

search of new mating opportunities, although there can be considerable variation in the timing of the male's departure (Scott, 1998). After the male leaves, the female remains with the brood until approximately 1 week after pairing, at which point the larvae disperse from the scant remains of the carcass to pupate in the soil. Females then depart to find new carrion for reproduction (Pukowski, 1933; Scott, 1998).

Natural populations of burying beetles interact with several species of phoretic mites (Wilson & Knollenberg, 1987). The *P. carabi* species complex comprises several species that are morphologically similar (Müller & Schwarz, 1990; Brown & Wilson, 1992). We focused on the *P. carabi* complex because they are the most common mites we find on naturally caught burying beetles at our field sites (most of the mites found on *N. vespilloides* beetles in nature are *P. carabi* sensu stricto; Schwarz, Starrach, & Koulianos, 1998). These mites are readily apparent as the deutonymphs (the phoretic stage) are large, very mobile and aggregate on the beetle's head and thorax. They use the burying beetle as a means of transport between opportunities for reproduction on carrion. Once a beetle has located a carcass, the mites alight, moult into sexually mature adults and breed. Their life cycle closely matches the duration of parental care and the majority of the next generation of deutonymphs leaves the carcass on the departing parents (Schwarz & Müller, 1992). Experimental studies have revealed a somewhat complex relationship between *P. carabi* and the burying beetle. Some studies suggest that *P. carabi* is beneficial to the burying beetle because the mites help defend the carcass breeding resource from rival species by piercing blowfly eggs, particularly when the carcass is buried shallowly (Springett, 1968; Wilson, 1983; Wilson & Knollenberg, 1987). Furthermore, experiments examining the relationship between the congeneric burying beetle *Nicrophorus orbicollis* and *P. carabi* suggest that mites can provide long-term fitness benefits for burying beetles, although not if the mites are at very high densities (Wilson & Knollenberg, 1987). However, phoretic mites can reduce burying beetle reproductive success, by eating their eggs (Beninger, 1993; Blackman & Evans, 1994). Furthermore, *P. carabi* can reduce components of male and brood fitness, depending on their density on the carcass (De Gasperin & Kilner, in press; De Gasperin Quintero, 2015). Nevertheless, the effect of *P. carabi* on the duration of male care is not yet known.

General Stock Maintenance

The beetle colony

All the beetles used in these experiments came from a stock population initially founded in 2005. Every year new field beetles are brought into the colony between April and September, and bred with our population colony to avoid inbreeding. Before introducing field beetles we removed any mites on them (see below), and thus kept our burying beetle colony separate from our mite colony. All beetles were kept in small plastic containers (12 × 8 cm and 2 cm high) filled with moist soil and fed twice a week with small pieces of minced beef. The colony was maintained in a laboratory at 20 °C and on a 16:8 h light:dark cycle. Adult beetles bred when they were 2–3 weeks old in plastic breeding boxes (17 × 12 cm and 6 cm high) filled two-thirds with moist soil with a mouse carcass. Note that these general methods mean that all the beetles used in the experiments described here developed as larvae in an environment without mites.

The mite colony

Deutonymphs of the *P. carabi* species complex were harvested from field-caught *N. vespilloides* by anaesthetizing the burying beetle with CO₂, and using a brush and tweezers to remove and count the mites. We did not identify individual mites further down

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