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Offspring are predisposed to beg more towards females in the burying beetle *Nicrophorus vespilloides*

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In species with biparental care, begging offspring may preferentially associate with or beg more towards one of their parents. Such preferences may reflect that the benefits of begging vary with the parent's sex given that females and males often differ in the amount of care they provide and/or in their responsiveness to begging levels. Alternatively, they may reflect the outcome of sexual conflict over care as females may deposit compounds into eggs tha talter offspring begging behaviour such that it increases male contributions towards care. For example, females might use male presence during egg laying as a cue for whether they might receive male assistance in care. Here, we studied offspring begging behaviour towards male and female parents in the burying beetle *Nicrophorus vespilloides* by manipulating male presence or absence during egg laying and providing larvae with a simultaneous choice between an unfamiliar female and male adult beetle. We then recorded begging behaviour of (1) naïve newly hatched larvae that had no prior experience of a parent and (2) larvae after 24 h of care by foster parents. Larvae showed a clear preference for associating with and begging towards females both when naïve and after 24 h of care. We found no evidence for prenatal maternal effects on larval begging behaviour. Our study reveals that offspring are predisposed to preferentially beg towards females independently of prior experiences with parents and highlights the importance of considering responses of begging offspring to parental attributes, such as the parent's sex, for our understanding of family conflicts.

In many birds and mammals, as well as some insects, offspring have evolved conspicuous begging displays that serve as mechanisms for resolving parent–offspring conflict by signalling the offspring's need or condition to the parents (Godfray, 1991; Kilner & Johnstone, 1997). In species where both parents care for their offspring, offspring might preferentially beg towards and/or associate with one of the parents. There are two main explanations for why offspring might evolve such preferences. The first is that such preferences evolve in response to differences in the parents' behaviour towards offspring. For example, females and males may differ in the amount or the type of care they provide (Kokko & Jennions, 2012), how they allocate care to different-sized offspring (Lessells, 2002) and/or how they respond to offspring begging (reviewed in Müller, Lessells, Korsten, & Engelhardt, 2007). Previous studies on birds and insects provide mixed evidence for such offspring preferences and whether they are associated with sex differences in parental behaviour (Roulin & Bersier, 2007). For example, in great tits, *Parus major*, where females allocate more food to food-deprived nestlings than males, food-deprived nestlings position themselves near the female's feeding position (Kölliker, Richner, Werner, & Heeb, 1998). In contrast, in blue tits, *Cyanistes caeruleus*, food-deprived nestlings move towards the male's feeding position, presumably because males allocate more food to those nestlings (Dickens, Berridge, & Hartley, 2008). Finally, in the burying beetle *Nicrophorus quadripunctatus*, where females provision most of the food, larvae beg more towards females (Suzuki, 2015). Although there is some evidence of offspring preferences for one parent over the other, little is known about the mechanisms involved. For example, it is unknown whether such preferences simply reflect that offspring learn which parent provides more care, or whether offspring have innate preferences for parents of one sex and identify it via sexually dimorphic sensory cues.

The second explanation is that offspring preferences for one parent reflect the outcome of sexual conflict over parental care. Recent work suggests that females might manipulate the amount of care provided by their male partner through prenatal maternal

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effects (Moreno-Rueda, 2007; Müller et al., 2007; Paquet & Smiseth, 2015). In birds, females control the deposition of hormones and other compounds in the egg yolk that influence the offspring's begging behaviour (Müller et al., 2007; Smiseth, Scott, & Andrews, 2011). Thus, females might extract more care from their male partner by depositing yolk hormones that specifically alter those components of the offspring's begging behaviour to which males are most responsive (Moreno-Rueda, 2007; Müller et al., 2007). For example, in yellow-legged gulls, *Larus michahellis*, males are more responsive to one component of begging (i.e. chatter calls) than females, and experimentally elevated levels of yolk testosterone specifically stimulate this component of begging (Noguera, Kim, & Velando, 2013). Thus, there is now a need for more experimental work investigating (1) offspring preferences for begging towards and associating with male and female parents, (2) whether such preferences are innate or based on familiarity with the two parents, and (3) whether females use prenatal maternal effects to alter such preferences to their advantage.

Here we investigated offspring preferences for associating with and begging towards male and female parents, and whether females can alter such preferences through prenatal maternal effects, in the burying beetle *Nicrophorus vespilloides.* This species is an excellent system for addressing these issues because the larvae beg for food from the parents (Smiseth, Darwell, & Moore, 2003), and females spend more time provisioning food than males (Smiseth & Moore, 2004). Furthermore, correlational evidence suggests that only males adjust their food provisioning in response to begging levels (Smiseth & Moore, 2004). Recent work indicates that larvae do not beg differently towards males and females (Mäenpää, Andrews, Collette, Leigh, & Smiseth, 2015). However, this previous experiment was based on a sequential choice design, in which larvae were presented with a single male or female beetle. Such designs may be associated with a lower probability of detecting preferences than simultaneous choice designs where individuals can choose between both options (Dougherty & Shuker, 2014). Finally, recent work suggests that females manipulate the behaviour of caring males through prenatal maternal effects as broods laid in the presence of a male gained more weight after hatching and did so at the expense of the male's weight gain (Paquet & Smiseth, 2017). However, the mechanism involved remains unknown and it is currently unclear whether females manipulate male behaviour by altering offspring begging behaviour.

The first aim of our study was to investigate whether larvae associate more with and beg more towards male or female parents. To control for potential differences in the behaviour of male and female parents, we used an established experimental set-up where larvae are presented with a dead adult (Mäenpää et al., 2015; Smiseth & Parker, 2008). Here, we modified this set-up by providing larvae with a simultaneous choice between male and female adults. We expected larvae to preferentially associate with females given that they provision more food than males (Smiseth & Moore, 2004). However, we expected larval begging rates to be higher towards males given that previous work suggests that only males adjust their food provisioning to begging levels (Smiseth & Moore, 2004). We also investigated whether such preferences were innate and expressed at the time of hatching or whether larvae learned them over time. To this end, we monitored begging of (1) naïve newly hatched larvae that had no prior experience with either parent and (2) larvae after 24 h of care by foster parents. The second aim of this study was to investigate whether females alter larval begging rates and preferences for begging towards males or females via prenatal maternal effects. To do so, we targeted a prenatal environmental condition that is critical for female manipulation of males; that is, the presence or absence of the male partner during egg laying (Paquet & Smiseth, 2017). We then tested whether larvae hatching from eggs laid in the presence or absence of a male begged at different rates and whether they differed in their behaviour towards males and females. Given evidence that only males respond to begging levels (Smiseth & Moore, 2004), we expected females laying eggs in the presence of a male to use the maternal effect in a way that increases offspring begging. Additionally, if females manipulate offspring preference towards males, we expected larvae to show a stronger preference for males when they hatched from eggs laid in the presence of the male. We expected such effects to be particularly strong early after hatching as maternal effects on offspring behaviour often wane as offspring develop (Barnett, Clairardin, Thompson, & Sakaluk, 2011; Paquet, Covas, & Doutrelant, 2015; Schwabl, 1996).

METHODS

Study Population and Animal Husbandry

All beetles used in this experiment were from an outbred laboratory population maintained at the University of Edinburgh. The beetles used in this study descended from beetles collected in the wild in Edinburgh, U.K. and Warmond, The Netherlands. The beetles were housed individually in transparent plastic containers (124 × 82 mm and 22 mm high) containing moist soil and were kept at 21 ± 2 °C under a 16:8 h light:dark cycle (Sieber, Paquet, & Smiseth, 2017). Nonbreeding adults were fed raw organic beef twice a week.

Cross-fostering Procedure

For all treatments, we used the same initial procedures to generate foster broods and foster parents for our experiment. We generated foster broods by randomly selecting pairs of 10–21-day-old nonsibling males and females that would act as donor parents. The pairs were first placed in a plastic container (110 × 110 mm and 30 mm high) with approximately 10 mm deep moist soil for 24 h to allow all experimental females to be fertilized by the male. We manipulated the presence and absence of the male at egg laying to allow us to test for prenatal maternal effects of the presence of the male on offspring begging behaviour. To this end, we placed either both parents (initial $N = 66$) or only the female (initial $N = 63$) in a larger plastic container (170 × 120 mm and 60 mm high) filled with a 10–20 mm layer of soil. We provided the beetles with a previously frozen mouse (20–27 g, supplied from Livefoods Direct Ltd, Sheffield, U.K.) to stimulate the onset of egg laying in the soil near the carcass. We removed all donor parents and their prepared carcass in the interval between the end of egg laying and the start of hatching (65–67 h after providing the carcass). The eggs from both treatments were left to develop in their original box without parents and were later used to generate experimental foster broods (see below). We set up foster parents ($N = 126$) in parallel with generating foster broods following the same procedure as described above for the foster broods where both male and females were present at egg laying. The only exception was that we moved the foster parents and their prepared carcass (this was done in the interval between the end of egg laying and the start of hatching) to a new box with fresh soil so that they could later receive foster broods of experimental larvae (see below). We kept the eggs of the foster parents in the initial box to gain information on the time of hatching. We did this to ensure that we only provided broods to foster parents whose own eggs had hatched in order to avoid filial cannibalism (Bartlett, 1987).

We used the experimental larvae hatching from eggs laid by the donor parents to generate experimental foster broods that differed with respect to whether they hatched from eggs laid in the