Are species differences in maternal effects arising from maternal care adaptive?

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Abstract

Parental care benefits offspring through maternal effects influencing their development, growth and survival. However, although parental care in general is likely the result of adaptive evolution, it does not follow that specific differences in the maternal effects that arise from care are also adaptive. Here, we used an interspecific cross-fostering design in the burying beetle species *Nicrophorus orbicollis* and *N. vespilloides*, both of which have elaborate parental care involving direct feeding of regurgitated food to offspring, to test whether maternal effects are optimized within a species and therefore adaptive. Using a full-factorial design, we first demonstrated that *N. orbicollis* care for offspring longer regardless of recipient species. We then examined offspring development and mass in offspring reared by hetero- or conspecific parents. As expected, there were species-specific direct effects independent of the maternal effects, as *N. orbicollis* larvae were larger and took longer to develop than *N. vespilloides* regardless of caregiver. We also found significant differences in maternal effects: *N. vespilloides* maternal care caused more rapid development of offspring of either species. Contrary to expectations if maternal effects were species-specific, there were no significant interactions between caretaker and recipient species for either development time or mass, suggesting that these maternal effects are general rather than optimized within species. We suggest that rather than coadaptation between parents and offspring performance, the species differences in maternal effects may be correlated with direct effects, and that their evolution is driven by selection on those direct effects.

Keywords

burying beetle; coadaptation; coleoptera; life-history; *Nicrophorus*; parental care

Introduction

Maternal (paternal, parental) effects arise when the traits of the mother (father, parent) exert a causal influence on the traits of an offspring, independent of the offspring's genotype (Wolf & Wade, 2009). These effects, once considered a statistical nuisance in measurements of inheritance (Falconer & Mackay, 1996), are now considered fundamentally important to understanding evolution, but yet the evolutionary consequences of maternal effects are often nonintuitive (Kirkpatrick & Lande, 1989; Cheverud & Moore, 1994; Mousseau & Fox,

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1998; Wade, 1998). Maternal effects are expected to be adaptive, evolving to allow organisms to ameliorate uncertain or inhospitable environments (Badyaev & Uller, 2009; Duckworth, 2009). However, the evolutionary trajectories involved in maternal effects are unusual. As traits expressed in one generation that influence the fitness of the next generation, maternal effects influence adaptive evolution through genetic changes in the parent rather than in the offspring but create a selective environment on the offspring (Kirkpatrick & Lande, 1989; Badyaev & Uller, 2009). By evolving adaptive maternal effects, mothers can adjust how they influence offspring to fit immediate circumstances and environmental variability. Implicit in this is the expectation that maternal effects are species-specific; that is, that maternal effects adaptively evolve to fit the specific ecology of the species studied.

Current understanding of adaptive maternal effects comes largely from work on the ability of parents to adjust offspring traits in response to variable environments. The evidence presented often consists of a common garden-type experiment, wherein offspring fitness is measured when the maternal effect is dissociated from its characteristic environment (e.g. Fox *et al.*, 1997). However, maternal effects may still be adaptations even if they are not environmentally responsive. To assess whether this type of maternal effect is adaptive, the maternal environment needs to be dissociated from the offspring experiencing that environment. Post-zygotic–post-natal maternal effects (Wade, 1998) arising from parental care are especially amenable to this type of study, as opposed to prezygotic or prenatal maternal effects such as egg provisioning, where the maternal trait is physically linked to the offspring. Parental care is one of the traits expected to result in strong maternal effects (Cheverud & Moore, 1994) and is expected to evolve to allow species to exploit competitive environments, counter environmental adversity and defend resources (Tallamy, 1984; Tallamy & Wood, 1986; Royle *et al.*, 2012). Parental care has costs (Royle *et al.*, 2012) typically in terms of energy, exposure to predation and lost reproductive opportunities. Thus, although there is variation within a species, parental care is expected to be a species-specific adaptation (Dulac *et al.*, 2014) responsive to the particular abiotic and social environment of a species (Royle *et al.*, 2014). However, it is important to separate the evolution of parenting from the effects of parenting (maternal effects), as these are traits expressed in different generations and subject to different selection pressures (Cheverud & Moore, 1994). Thus, although parenting and maternal effects are linked, they are not necessarily simultaneously optimized (Marshall & Uller, 2007).

Burying beetles (*Nicrophorus spp.*) present an ideal system for experimentally examining the evolution of maternal effects and parental care. Beetles in the genus *Nicrophorus* provide extensive and elaborate parental care for their young, which are reared on vertebrate carcasses (Pukowski, 1933; Eggert & Müller, 1997; Scott, 1998). Adults process a carcass into a brood ball, partially digesting and manipulating the carrion, and upon hatching directly feed begging larvae regurgitated food. Highly developed parental care behaviour is conserved across the genus. Parental care (typically maternal care) has strong influences on offspring mass (Smiseth *et al.*, 2003; Smiseth & Moore, 2004), development (Eggert *et al.*, 1998; Meierhofer *et al.*, 1999; Rauter & Moore, 2002a,b; Lock *et al.*, 2004, 2007), which are offspring performance traits closely related to fitness (Lock *et al.*, 2004), as well as survival

(Trumbo, 1992; Eggert *et al.*, 1998; Lock *et al.*, 2004). There is, however, substantial variation among species in body size, habitat usage, duration of development, duration of care and other life-history characters (Eggert & Müller, 1997; Scott, 1998). Both males and females can provide care (Eggert & Müller, 1997; Walling *et al.*, 2008), although most offspring receive only maternal care (A. J. Moore, unpub. data), and the addition of paternal care to maternal care does not seem to matter to offspring fitness (Bartlett, 1988; Scott, 1989; Trumbo, 1991; Müller *et al.*, 1998). The extensive and easily observed parental care of *Nicrophorus* makes it an extremely useful system for examining maternal effects (Rauter & Moore, 2002a,b; Lock *et al.*, 2004, 2007) and paternal effects (Head *et al.*, 2012), not the least because they are easily cross-fostered because burying beetles use timing rather than kin recognition to direct their parental care (i.e. temporal kin recognition; Müller & Eggert, 1990; Eggert & Müller, 2000; Oldekop *et al.*, 2007). This allows us to use an interspecific cross-fostering design to measure maternal effects in two burying beetle species, *N. orbicollis* and *N. vespilloides*.

We used both *N. vespilloides* and *N. orbicollis* in a full-factorial design, with both species acting as caregiver parents and recipient offspring. These two species differ substantially in size and mass (Scott, 1998), with *N. orbicollis* weighing on average more than twice as much as *N. vespilloides*. Furthermore, they differ behaviourally in that *N. orbicollis* larvae require feeding from birth (Trumbo, 1992) whereas *N. vespilloides* can survive without parental care (Eggert *et al.*, 1998). They are also distantly related within the genus, with an estimated divergence time of over 85 million years (Sikes & Venables, 2013). We tested two hypotheses. First, we predicted that maternal care would differ between species. Given that parental care is clearly adaptive in burying beetles (Eggert & Müller, 1997; Scott, 1998), we next predicted that these differences would reflect adaptive divergence in maternal effects. That is, our second hypothesis was that if maternal effects were optimized to provide maximum benefit for a given species, and not just general benefits of care, then we should see a significant interaction between caregiver and recipient species for offspring performance traits. We found that although there were highly significant differences in care between the species, these do not necessarily result in optimal maternal effects within a species, as we found no coadaptation between levels of care and maternal effect on development or mass. This suggests that species differences may be more related to life-history differences than adaptation of maternal effects.

Materials and methods

We collected *N. orbicollis* from Whitehall Forest, Athens GA in the spring of 2013. These individuals were used to start an outbred colony maintained under temperature and light control (21 °C; 14: 10 light : dark) for five generations before the start of this experiment. Individuals were kept in isolated, plastic boxes (9 cm diameter, 4 cm deep; Eco Products, Boulder, CO, USA) half-filled with soil and fed two decapitated mealworms (*Tenebrio*) twice a week.

Nicrophorus vespilloides used in the experiment were taken from a population originating from Cornwall, UK (Head *et al.*, 2012) and maintained at the University of Georgia

(Cunningham *et al*., 2014). All experimental trials were performed at 21 °C under a 14:10 light cycle as described above for *N. orbicollis*.

All individuals in the experiment were at least 14 days old post-eclosion and were bred in plastic boxes (17.2 × 12.7 × 6.4 cm; Pioneer Plastics, Dixon, KY, USA) filled with approximately 2 cm of soil. Each plastic box contained a thawed mouse weighing between 22 and 26 g (RodentPro, Evansville, IN, USA). All individuals were weighed and measured before breeding. *Nicrophorus orbicollis* takes significantly longer to produce hatched offspring than does *N. vespilloides*. Therefore, we bred *N. orbicollis* pairs about 48 hours before breeding *N. vespilloides* pairs. After pairing, each box was checked twice daily for eggs. Timing of egg appearance was used to determine the parents to be switched. Intraspecific switches (controls) were made between mothers whose eggs appeared at the same time. Interspecific switches were made between *N. orbicollis* mothers that laid eggs 16–24 h before the corresponding *N. vespilloides* mother, to account for longer hatching time in the former.

We transferred both the mother and the carcass she prepared into a box containing foster eggs to control for prenatal maternal effects. At this point, we also removed the male to avoid possible post-hatching paternal effects. The removal of males does not affect either female behaviour or offspring fitness (Smiseth *et al.*, 2005). Before transferring, the mouse was checked, and any larvae that had hatched and crawled onto the mouse before we switched parents were removed. These larvae would have been very newly arrived and we never observed any receiving parental care from their biological parents before they were removed. Such early larvae typically die and do not receive any care (Eggert & Müller, 2000).

After switching caretakers, we checked pairs twice daily (morning and afternoon) to determine duration of parental care and timing of dispersal of offspring (Head *et al.*, 2012). We considered a mother to have abandoned the brood when we did not observe her on the carcass for two consecutive observations (Benowitz *et al.*, 2013). At dispersal, we removed the mother, counted the number of offspring per brood, and weighed each larva individually to 0.1 mg using an electronic balance (Mettler-Toledo, Columbus, OH, USA). Thus, we measured two offspring traits: duration of development on the resource and mass at dispersal. These traits influence fitness (Lock *et al.*, 2004) as the only feeding that occurs is during the development on the carcass, so mass at dispersal reflects the final size that can be attained (although mass can change after adult emergence as adults can and do feed). We analysed these traits using a Model 1 two-way ANOVA with SAS type III sums of squares, with the fixed effects being recipient species, caregiver species and their interaction. Mouse mass was used as a covariate in all analyses. However, as it was never a statistically significant effect (a common result when variation in mass of mouse is kept to a minimum; Moore, pers. obs.), we do not report any statistics for mouse mass or discuss it further. Our first test was for influences on parental care, measured as duration of maternal care. We then examined how caregiver species, recipient species or their interaction influenced average larvae mass, development time (hatching to dispersal from the carcass) and number of larvae dispersed. We used JMP (v11.0.0; SAS Institute, Cary, NC, USA) for all statistical analyses.

Results

The duration of care depended only on maternal traits; that is, which species was caring (Fig. 1). *Nicrophorus orbicollis* mothers remained present on the carcass longer than *N. vespilloides* mothers ($F_{1,131} = 7.687$, P = 0.006). However, duration of maternal care was neither affected by offspring species ($F_{1,131} = 2.032$, $P = 0.156$) nor by the interaction between caregiver and offspring species ($F_{1,131} = 1.555$, $P = 0.215$).

Both direct and maternal effects influenced development time (Fig. 2). *Nicrophorus vespilloides* offspring developed faster than *N. orbicollis* offspring regardless of the species that provided maternal care ($F_{1,131} = 22.415$, $P < 0.0001$). Broods raised by *N. vespilloides* parents developed faster than those raised by *N. orbicollis* ($F_{1,131} = 12.607$, $P = 0.0005$). However, there was no statistically significant interaction between caregiver and offspring species on development time ($F_{1,131} = 0.343$, $P = 0.559$).

Offspring mass was determined almost entirely by direct effects (Fig. 3).Regardless of parent, *N. orbicollis* larvae were much larger than *N. vespilloides* larvae ($F_{1,127} = 307.777$, $P < 0.0001$), and there was no statistically significant effect of caregiver species ($F_{1,127} = 2.297$, $P = 0.132$). The interaction was again not statistically significant ($F_{1,126} = 1.896$, $P = 0.1709$).

Discussion

A trait can be considered an adaptation if its function is tied to the selective forces that led to its evolution (Gould & Lewontin, 1979) or in the words of Williams (1966, p. 9) '… the machinery involved was fashioned by the selection for the goal attributed to it.' Useful (or good) and adaptive are not equivalent (Williams, 1966). Maternal effects are common and important in phenotypic evolution and therefore have been suggested to be selected and adaptive (Mousseau & Fox, 1998). Parenting is an especially important source of environmental influences on offspring. If species differences in maternal effects arsing from parenting are adaptive, we predicted that parenting differences between species would reflect optimization for within-species performance and a coadaptation between offspring performance and parenting. That is, the maximum benefit should occur when there is a match between caretaker and recipient species. To test this, we used cross-fostering across species; if our hypothesis was correct, we expected significant interactions between the caregiver and recipient species on offspring performance. As expected, the effects of parenting were strong and important, but contrary to our prediction we found little evidence for species-specific optimization of maternal effects. In *N. vespilloides* and *N. orbicollis*, the lack of coadaptation between care and development and mass suggests that species differences in maternal effects on these traits are not adaptations, even if parental care itself is adaptive.

In a study that used a similar design to address how differences in social interactions contribute to species differences, Linksvayer (2007) examined worker (subsocial) care in ants to test for coevolution between brood genotype (direct effects) and worker genotype (social effects). He measured offspring performance in three reciprocally cross-fostered ant

species and found both direct genetic effects and an effect of social environment, resulting in significant interactions between offspring and worker species and indicating a complex relationship between giving and receiving of care. As in our study, direct genetic effects predominated and the direct-by-indirect covariance could contribute to species differences. Interestingly, this was only true when including the most divergent species (*Temnothorax longispinosus*), which has much larger workers that were larger regardless of the foster sibs. For the two more closely related species (*T. ambiguus* and *T. curvispinosus*), there was only an interaction effect. As Linksvayer (pers. comm.) suggests to us, perhaps more closely related *Nicrophorus* spp. would also show the expected interaction effect.

Coadaptation is only one possible outcome when there are parent-offspring interactions. Following Kölliker *et al*. (2005) who modelled coadaptation between parental provisioning and offspring solicitation, we suggest that the existence, sign and extent of the species differences in coadaptation between direct and maternal effects for each trait may reflect the nature of phenotypic control – is the extent of parenting determined by the parent, offspring or both? For example, we found that the species of caregiver did not affect the mass of the offspring. Given reduced parental care can result in smaller offspring in *Nicrophorus*, we expected to observe smaller *N. orbicollis* when raised by *N. vespilloides* as the latter spend less time parenting. The fact that we did not observe this may reflect the ability of offspring to influence maternal behaviour. Burying beetle parents respond to offspring begging by increasing provisioning (Smiseth & Moore, 2002, 2008; Lock *et al.*, 2004) and offspring appear to control food allocation (Smiseth *et al*., 2003), although parents influence sibling competition (Smiseth *et al.*, 2007a,b). Anecdotally, we observed that *N. orbicollis* larvae beg much more aggressively, which could manipulate parents of either species to provide the requisite feeding for normal growth. Another possibility for why caregiver species did not affect offspring mass is that burying beetle larvae can partially compensate for differences in parental care through self-feeding (Smiseth *et al.*, 2003, 2006; Smiseth & Moore, 2004). Thus, as long as they receive some food during a critical period of growth, they may be able to reach their optimal weight without additional parental help. If this was the case, we might expect to see costs in later life-history stages for individuals raised by the wrong species. However, maternal effects tend to act most strongly early in development (Cheverud & Moore, 1994).

Further support for the importance of the direct–indirect genetic covariance comes from the other performance trait we measured, development time, where we found a different pattern. Regardless of offspring species, broods cared for by *N. vespilloides* mothers dispersed earlier than those that received care from *N. orbicollis*. This indicates the presence of a positive maternal effect in burying beetles; in other words, for development time, maternal effects are correlated with direct genetic effects (Lande & Price, 1989). To the extent that this covariance reflects genetic variation in the two traits, this should enhance the evolution of this trait (Kirkpatrick & Lande, 1989) and could reflect strong selection in *N. vespilloides* for broods to leave the carcass as early as possible because it is an inferior competitor (Scott, 1998), resulting in phenotypic change in both parent and offspring phenotypes. However, the maternal effect appears to have evolved independently from the offspring trait, as development time is not affected by any mother–offspring interactions.

A possible explanation for the lack of coadaptation in maternal effects is that there is an absence of species differences in ecology or the costs and benefits of care. This seems unlikely as the ecology and behaviour between the species are strikingly different, suggesting that they can and do differ on many axes. In nature, *N. orbicollis* typically exploit larger carcasses (> 30 g) whereas *N. vespilloides* use smaller (< 20 g) resources, although there is overlap in the carcass size that these species will exploit and no evidence for a preference (Scott, 1998). We found differences in carcass processing, which may be related to differences in typical resource size between these species. *Nicrophorus orbicollis* parents formed the mouse into almost perfect spheres, whereas *N. vespilloides* parents may not have been able to completely process the larger carcasses used in this study (Trumbo, 1992). These species also differ in burial depth (*N. orbicollis* buries the mouse about 10 cm underground, whereas *N. vespilloides* does not completely bury the mouse, but rather uses a shallow depression; Eggert & Müller, 1997; K. M. Benowitz pers. obs.). Moreover, given *N. orbicollis* is a North American species and *N. vespilloides* is found in Europe, offspring may be adapted to different fauna. The microbiota associated with different species appears to be more influenced by environment than phylogenetic relationship among burying beetle species (Kaltenpoth & Steiger, 2014). It does not appear, however, that transfer of symbionts by parents is important in burying beetles (Eggert *et al.*, 1998). Perhaps most importantly, *N. orbicollis* mothers remain with their broods longer than *N. vespilloides* mothers. This difference in duration of care is potentially a necessary consequence of the increased development time and mass in *N. orbicollis*, as females may need to remain longer on the carcass to protect and feed their offspring.

Our work suggests that direct genetic effects in response to these selection pressures associated with differences in ecology and life-history may have a stronger influence on species differences than maternal effects and that any evolution of maternal effects would reflect indirect selection and a correlated response. The ultimate causes of species differences are likely ecological pressures and subsequent life-history trade-offs. Maternal effects may have evolved to influence life-history trade-offs in *N. vespilloides* (Steiger, 2013), but such a relationship is less clear for *N. orbicollis*. Based on general species differences, it appears that size trades off with development time and offspring number in burying beetles (Bartlett & Ashworth, 1988; Trumbo, 1990; Smiseth *et al.*, 2014). However, these trade-offs are less stringent in broods raised by *N. vespilloides*, as they are able to speed up development and raise more larvae without a cost to body size at dispersal. Why one species should be more efficient in raising offspring is not clear. This may be due to the fact that the carcasses used in this experiment were large enough to relax trade-offs in the smaller *N. vespilloides*, but not *N. orbicollis* as the size-number trade-off is only seen on small carcasses with *N. vespilloides* (Smiseth *et al*, 2014), but is seen across all carcass sizes in *N. orbicollis* (Trumbo, 1990). Another potential explanation is that *N. vespilloides* mothers suffer a direct cost to future reproductive potential by expending more energy during care (Wade, 1998), despite a shorter time on the carcass. Thus, if *N. orbicollis* reproduce multiple times, they may not be less efficient parents over their lifetime.

It is clear that species differences in maternal effects are widespread and that maternal effects can be adaptive (Mousseau & Fox, 1998). Parenting is also adaptive (Royle *et al*,

2012). However, our results show that it does not necessarily follow that the differences between species in maternal effects arising from care reflect differences in direct selection on specific aspects of parental care. It seems more likely that the species differences can reflect a correlated response to other traits, especially given a covariance between direct and maternal genetic effects is expected to be ubiquitous (Cheverud & Moore, 1994; Wilson & Réale, 2007), reflecting selection arising from differences in the species' life-history.

Acknowledgments

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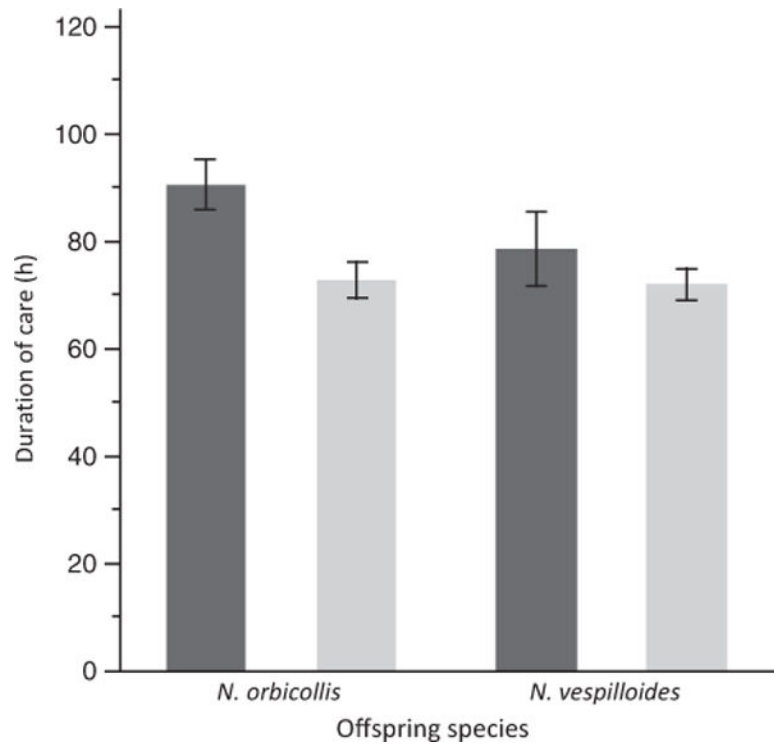**Fig. 1.**
Mean (± SE) duration of maternal care measured from larval hatching to carcass abandonment. Dark grey bars indicate *Nicrophorus orbicollis* caretakers; light grey bars indicate *N. vespilloides* caretakers.
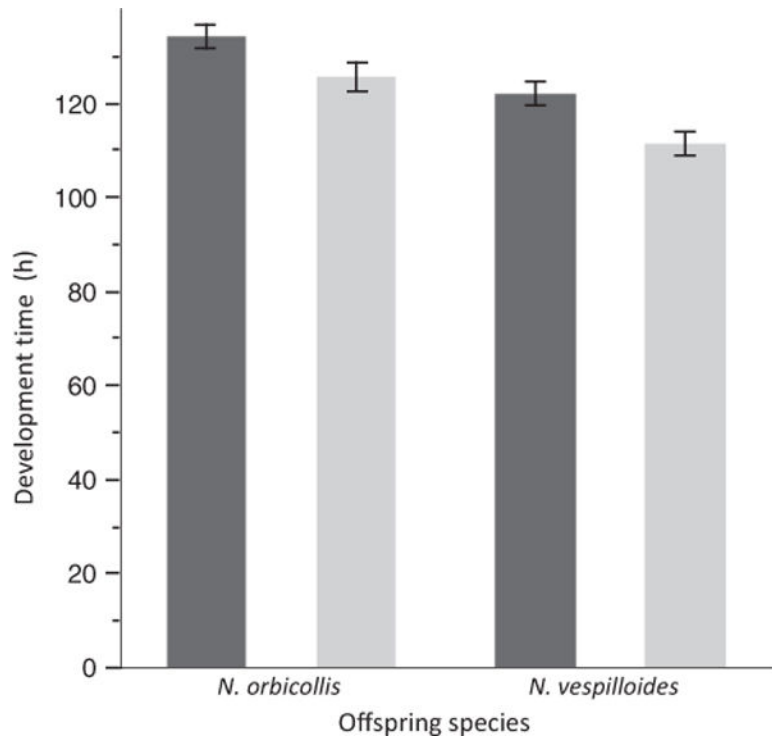
Fig. 2.
Mean (± SE) development time of larval broods, measured from hatching to dispersal from the carcass. Dark grey bars indicate *Nicrophorus orbicollis* caretakers; light grey bars indicate *N. vespilloides* caretakers.
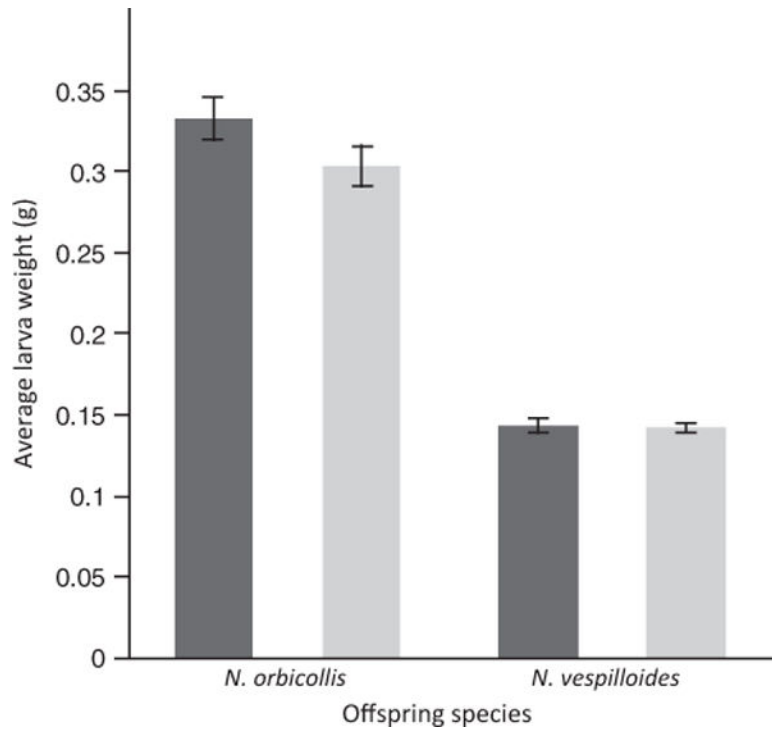
Fig. 3.
Mean (± SE) of larval weight at dispersal. Average larval weight of each dispersing brood was calculated. Dark grey bars indicate *Nicrophorus orbicollis* caretakers; light grey bars indicate *N. vespilloides* caretakers.