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Larval environmental conditions influence plasticity in resource use by adults in the burying beetle, *Nicrophorus vespilloides*

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Recent studies have shown that intraspecific patterns of phenotypic plasticity can mirror patterns of evolutionary diversification among species. This appears to be the case in *Nicrophorus* beetles. Within species, body size is positively correlated with the size of carrion used to provision larvae and parental performance. Likewise, among species, variation in body size influences whether species exploit smaller or larger carrion and the extent to which larvae depend on parental care. However, it is unclear whether developmental plasticity in response to carcass size, parental care, or both underlie transitions to new carcass niches. We examined this by testing whether variation in the conditions experienced by *Nicrophorus vespilloides* larvae influenced their ability to breed efficiently upon differently sized carcasses as adults. We found that the conditions experienced by larvae during development played a critical role in determining their ability to use large carcasses effectively as adults. Specifically, individuals that developed with parental care and on large carcasses were best able to convert the resources on a large carcass into offspring when breeding themselves. Our results suggest that parentally induced plasticity can be important in the initial stages of niche expansion.

KEY WORDS: **Burying beetle, diversification, parental care, parental effects, phenotypic plasticity.**

Biologists have long been interested in both the causes and consequences of phenotypic plasticity. Much of this research has focused on adaptive plasticity, specifically the ecological conditions that favor adaptive plasticity, the costs and constraints that might limit adaptive plasticity, and the genetic control of phenotypic plasticity (Via et al. 1995). More recently, there has been renewed interest in the idea that phenotypic plasticity shapes the direction of evolutionary diversification (Price et al. 2003; West-Ebberhard 2003; Pfennig et al. 2010). Theories concerning the potential link between phenotypic plasticity and evolutionary diversification were first put forward over a century ago by Baldwin, who suggested that phenotypic plasticity may allow populations to persist in novel environments long enough for adaptive evolution to occur (Baldwin 1896). More recent ideas, such as genetic assimilation and the flexible stem hypothesis, similarly propose that phenotypic plasticity facilitates and dictates the path of adaptive diversification (Waddington 1953; West-Ebberhard 2003). According to these hypotheses, ancestral patterns of phenotypic plasticity will channel evolutionary changes in response to new environmental selection pressures with subsequent evolution changing the shape of ancestral reaction norms (Waddington 1953; West-Ebberhard 2003; Crispo 2007).

Recent empirical studies have examined the role of plasticity in evolutionary diversification by asking whether patterns of plasticity within species mirror patterns of evolutionary diversification among species (Pfennig et al. 2010; Levis and Pfennig 2016). For example, in threespine stickleback, diet-induced plasticity in head morphology matches the ecotypic divergence between benthic and limnetic forms that has repeatedly evolved during the postglacial radiation of this species (Wund et al. 2008). Studies of spade-foot toads (*Spea bombifrons* and *Spea*

multiplicata) have also indicated that developmental plasticity can be an important driver of character displacement (Pfennig and Murphy 2000; Pfennig and Pfennig 2010). Both of these species exhibit a resource-use polyphenism in which individuals can develop as either a small "omnivore" morph or a "large" carnivore morph. In allopatry, both species produce both morphs. In sympatry, *S. multiplicata* produces primarily omnivores and *S. bombifrons* produces primarily carnivores, which presumably reduces resource competition (Pfennig and Martin 2009). In theory, environmentally induced changes such as these may become canalized resulting in population divergence and potentially speciation (Pfennig et al. 2010; Pfennig and Pfennig 2010).

Studies examining the role of plasticity in evolutionary diversification often focus on abiotic factors or ecological interactions as factors that induce phenotypic variation (see examples in Pfennig et al. 2010). However, interactions among family members (e.g., between parents and offspring or dependent siblings) can also be an important source of phenotypic variation. For example, the duration or quality of parental care that an individual receives can generate continuous variation in body size, which may impact offspring fitness (Eggert et al. 1998; Schrader et al. 2018). Variation in parental care can also generate discrete morphological variation (i.e., a polyphenism) in some species. For example, in the beetle *Onthophagus taurus* variation in the quality and quantity of parental provisioning generates variation in body size, which in turn determines whether males develop horns (Moczek 1998). There is also evidence that variation in access to parental care generates behavioral variation among individuals. For example, in both threespine stickleback and lizards, access to parental care influences the development of antipredator behaviors in offspring (McGhee and Bell 2014; Munch et al. 2018). Although the impact of parental care on the development and expression of phenotypes has been extensively studied, we still know very little about whether parentally induced plasticity has the potential to drive evolutionary diversification.

Burying beetles (genus *Nicrophorus*) provide an intriguing system to examine the role of parentally induced phenotypic plasticity in adaptive diversification. Beetles in this genus rely on carrion to breed and exhibit complex parental care behaviors (Scott 1998; Royle et al. 2013). Parents first prepare and defend a vertebrate carcass that is the sole source of energy for the developing brood. Carcass preparation involves rolling the carcass into a ball and coating the surface with antimicrobial exudates. After hatching, parents directly feed begging larvae with predigested carrion. Variation in carcass size and access to parental care both influence the development of adult phenotypes. For example, in *Nicrophorus vespilloides* larvae that develop on a large carcass can attain a greater mass than larvae that develop on a small carcass (Smiseth et al. 2014). Furthermore, larvae that receive posthatching parental care are larger at dispersal than larvae that do not receive posthatching care (Eggert et al. 1998). The effects of carcass size and parental care on larval body mass are likely to have important fitness consequences because larval mass at dispersal determines adult body size, which has also been linked to increased competitive ability and more effective parental care (Otronen 1988; Steiger 2013). Variation in adult size has also been linked to niche breadth in *N. vespilloides*, with large adults preferring to use large carcasses (Hopwood et al. 2016). Intriguingly, these patterns of plasticity within *N. vespilloides* broadly mirror variation in parental care and carcass niche among *Nicrophorus* species. For example, large-bodied *Nicrophorus* species are able to exploit large carrion and tend to exhibit obligate parental care, whereas small-bodied *Nicrophorus* species exploit smaller carrion and tend to display facultative posthatching parental care (Scott 1998; Capodeanu-Nägler et al. 2016; Jarrett et al. 2017).

Based upon these patterns, we suggest a mechanism through which *Nicrophorus* beetles may have initially adapted to new carrion niches. Specifically, we hypothesize that developmental plasticity in body size, induced by variation in the care that an individual receives during development and the carcass that they feed on as a larva, influences their ability to exploit carcasses of different sizes as adults. Such plasticity can potentially facilitate a shift in the carrion niche, a process that appears to have occurred in natural populations (Sun et al. 2020). Our hypothesis predicts that larvae that are reared with parental care on a large carcass will be best able to exploit large carcasses as adults, in part because these developmental conditions allow them to attain a larger body size, which in females is associated with both increased fecundity and parental performance (Steiger 2013; Schrader et al. 2016). Here, we test this hypothesis by experimentally manipulating the environment in which larvae develop and then testing whether this environment influences the performance of these individuals when they are given either a small or large carcass to breed upon as an adult.

Methods

Our experiment focused on the burying beetle, *N. vespilloides*, which is a medium- to small-sized species (mean pronotum width = 4.8 mm [Jarrett et al. 2017]) that displays facultative posthatching parental care (Eggert et al. 1998; Scott 1998; Schrader et al. 2015; Capodeanu-Nägler et al. 2016). All of the beetles used in this experiment were part of a laboratory population that was maintained without inbreeding and was supplemented annually with wild beetles collected from Bryon's Pool, Cambridgeshire, UK. Our experiment involved manipulating the environment that individuals experienced as larvae (hereafter the larval environment) and the size of the carcass they bred on as an adult (hereafter the adult environment; Fig. 1).

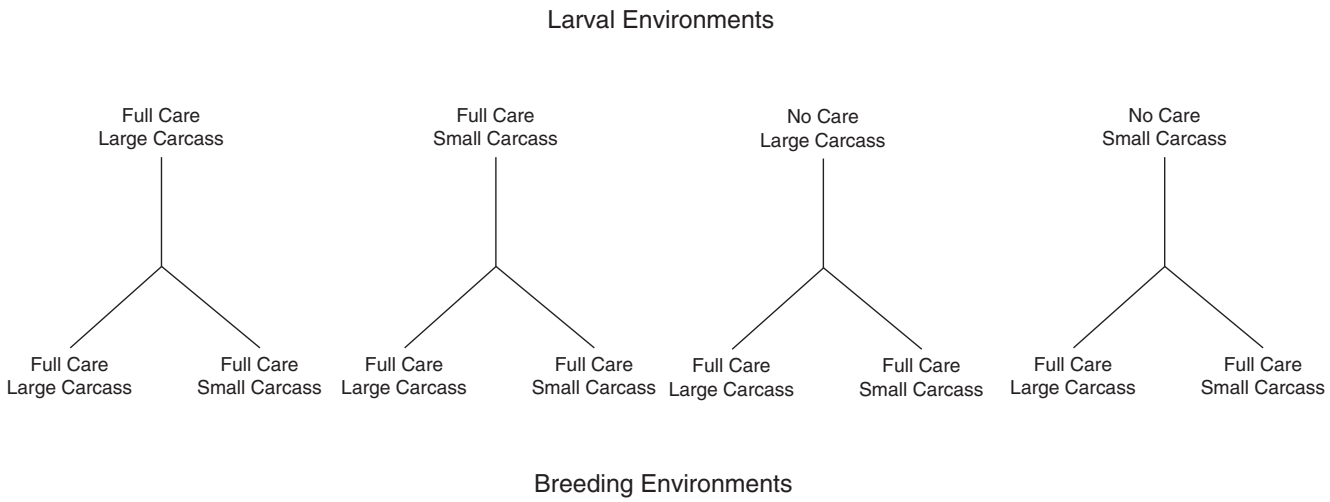

Figure 1. An overview of the experimental design. Beetles were reared as larvae in one of four larval environments: Full Care/Large Carcass, Full Care/Small Carcass, No Care/Large Carcass, No Care/Small Carcass. Larvae from each treatment were bred as adults in one of two breeding environments: Large Carcass or Small Carcass. We allowed adults in all of these treatments to provide parental care. Sample sizes are in Table 1.

We manipulated the larval environment by varying the size of the breeding carcass they developed on and their access to posthatching parental care. We bred pairs of beetles on either small or large carcasses (mean mass ± SD: small carcasses = 10.05 ± 2.02 g, large carcasses = 22.41 ± 2.08 g; difference between means, $t = 22.67$, $P < 0.0001$), with or without posthatching parental care (hereafter Full Care and No Care treatments). This resulted in four larval environments: Full Care/Large Carcass (FL), Full Care/Small Carcass (FS), No Care/Large Carcass (NL), and No Care/Small Carcass (NS). We initially set up 35 replicates of each of the No Care treatments (NS and NL) and 15 replicates of each of the Full Care treatments (FS and FL). The contrasting sample sizes were intentional and designed to anticipate a greater number of breeding failures in the treatments without parental care (Schrader et al. 2017).

All pairs were bred in plastic boxes (28.5 × 13.5 × 12 cm) containing a thawed mouse carcass and a thin layer of moist soil. In the Full Care treatments, we allowed both parents to remain with the brood for the entire larval period and therefore to interact with their larvae during this time. In the No Care treatments, we removed both parents 53 h after pairing. Removing parents at this time does not influence carcass preparation or egg laying, but eliminates all posthatching parental care (Schrader et al. 2015; Jarrett et al. 2017; Schrader et al. 2017). Upon larval dispersal (8 days after pairing), we counted the number of dispersing larvae (brood size) and measured the mass of the entire brood (brood mass). We then placed the dispersed larvae from each successful family into a 5 × 5 × 2 cm "eclosion box." These boxes were subdivided into 25 cells (1 × 1 × 2 cm) and we placed one larva within each cell (Schrader et al. 2015). This generated 10 FL families, 12 FS families, 26 NL families, and 11 NS families (and a total of 1092 larvae).

Upon eclosion (∼17 days after dispersal), we placed each individual beetle in its own plastic box containing damp soil and a small amount of organic minced beef. Individuals were kept in these boxes and fed twice per week. When the beetles were 14 days old, we photographed a sample of adults from each family and measured their body size (pronotum width, in mm) from the images (Jarrett et al. 2017). This sample included 444 adults in total (with an average of 7.5 adults per family) and was used to estimate the mean adult body size for each family. We then randomly selected photographed adults that had been exposed to each experimental larval environment to form breeding pairs. Individuals were assigned to pairs randomly, with the only condition that they had experienced the same larval environment and were not siblings. Each pair was then bred on either a small or large carcass (mean mass ± SD: small carcasses = 10.93 ± 1.77; large carcasses = 19.26 g ± 1.79; difference between means, $t = 30.17$, $P < 2.2 \times 10^{-16}$). Breeding conditions were the same as those described above, but all adults were allowed to remain with their offspring throughout larval development. This resulted in eight different combinations of larval and adult environments in all, and in each treatment $N = 22$ pairs (see Fig. 1). Upon larval dispersal (8 days after pairing), we counted the number of dispersing larvae in each brood. Breeding attempts that produced at least one dispersing larva were considered to be successful. For each successful brood, we weighed the entire brood and used this to calculate the average larval mass (brood mass/brood size).

ANALYSES

Previous studies have suggested that adult body size can influence the quality of parental care in *N. vespilloides* (Steiger 2013). Thus, our first analyses focused on how the larval environment influenced mean larval mass at dispersal and how this translated into variation in adult body size. We first examined the effects of carcass size, parental care, and their interaction on mean larval mass at dispersal using a two-way ANOVA (with type III sums of squares). Here (and in subsequent analyses), we treated carcass size as a discrete factor with two levels (small and large). We did this because the means of the two groups were different, their ranges did not overlap, and there was little variation in mass within each group compared to the differences between each group. In this analysis, the carcass size by parental care interaction was not significant ($F_{1,55} = 0.97$, $P = 0.34$) so it was removed from the final model. We next tested whether mean larval mass at dispersal predicted mean adult body size (pronotum width) using a linear regression on family means. Finally, we examined the effects of carcass size, parental care, and their interaction on mean pronotum width using a two-way ANOVA (with type III sums of squares). In this analysis, the carcass size by parental care interaction was not significant ($F_{1,55} = 0.24$, $P = 0.63$) so it was removed from the final model.

We next examined the effects of the larval environment (care $_{larva}$, carcass $_{larva}$) and the adult environment (carcass $_{adult}$) on two measures of breeding performance: brood size at dispersal and mean larval mass. For successful broods, we analyzed both measures of breeding performance using linear mixed models. These models included both larval environmental conditions (care $_{larva}$ and carcass $_{larva}$) and the parental environment (carcass $_{adult}$) as fixed effects and the maternal and paternal family as random effects. As above, we treated carcass size as a discrete factor with two levels (small and large). Although brood size at dispersal is a count, diagnostic plots indicated that a model with a Gaussian distribution provided a better fit than a model with a Poisson distribution. We initially included the random effects and all interactions involving the fixed effects in each model, and then removed nonsignificant ($P > 0.05$) random effects and interactions involving the fixed effects. In *Results*, we present the reduced models. All analyses were performed in R (R Core Team 2016).

Results

THE IMPACT OF THE LARVAL ENVIRONMENT ON THE DEVELOPMENT OF BODY SIZE

Parental care and carcass size had significant effects on mean larval mass at dispersal. Larvae that developed with parental care were ∼11% larger on average than larvae that developed without care, and larvae that developed on large carcasses were ∼20% larger on average than larvae that developed on small carcasses (Fig. 2A; effect of carcass, $F_{1,56} = 17.55$, $P = 9.90 \times 10^{-5}$; effect of care, $F_{1,56} = 9.67$, $P = 0.0029$). Differences among families in mean larval mass translated into differences in adult body size (Fig. 2B; linear regression of mean pronotum width on mean larval mass: $F_{1,57} = 111.2$, $P = 5.41 \times 10^{-15}$, $r^2 = 0.66$). As a consequence, larvae that developed with care were ∼8% larger as adults than those that developed without care ($F_{1,56} = 26.37$; $P = 3.68 \times 10^{-6}$; Fig. 2C), and larvae that developed on large carcasses were ∼2% larger as adults than those that developed on small carcasses ($F_{1,56} = 6.56$; $P = 0.013$; Fig. 2C).

THE IMPACT OF THE LARVAL ENVIRONMENT AND ADULT BREEDING CONDITIONS ON PARENTAL PERFORMANCE

We measured the parental performance of individuals that had experienced different larval environments using brood size at dispersal and the mean mass of dispersing larvae. Brood size at dispersal was influenced by the size of the breeding carcass and the care environment that individuals had experienced as larvae (Fig. 3A; Tables 1 and 2). Specifically, we found that brood size at dispersal was greater for adults that were given large carcasses to breed on, rather than small carcasses. This difference was most pronounced when the parents had been reared as larvae with full care on a large carcass (Fig. 3A; Tables 1 and 2). Mean larval mass was also influenced by the size of the breeding carcass, with parents breeding on large carcasses producing larger offspring than parents breeding on small carcasses (Fig. 3B; Tables 1 and 2). However, there was no evidence that mean larval mass was influenced by the care environment that the parents had experienced as larvae (Fig. 3B; Tables 1 and 2).

Discussion

Recent studies have shown that intraspecific patterns of phenotypic plasticity in resource use can map onto patterns of evolutionary diversification among species (Pfennig et al. 2010). This appears to be the case in *Nicrophorus* beetles where associations between body size, the carrion niche, and parental performance appear to be similar within species and among species (Scott 1998; Hopwood et al. 2016; Jarrett et al. 2017). The carrion niche is one axis of ecological variation within the genus *Nicrophorus* (Hopwood et al. 2016), but little is known about whether developmental plasticity can facilitate a shift from breeding on small carcasses to breeding on large carcasses. We addressed this issue experimentally by examining the effects of the natal resource and parental care on the ability of individuals to exploit differently sized carcasses as adults. Our results suggest that conditions experienced by larvae during development play a critical role in determining their ability to exploit larger carrion as adults.

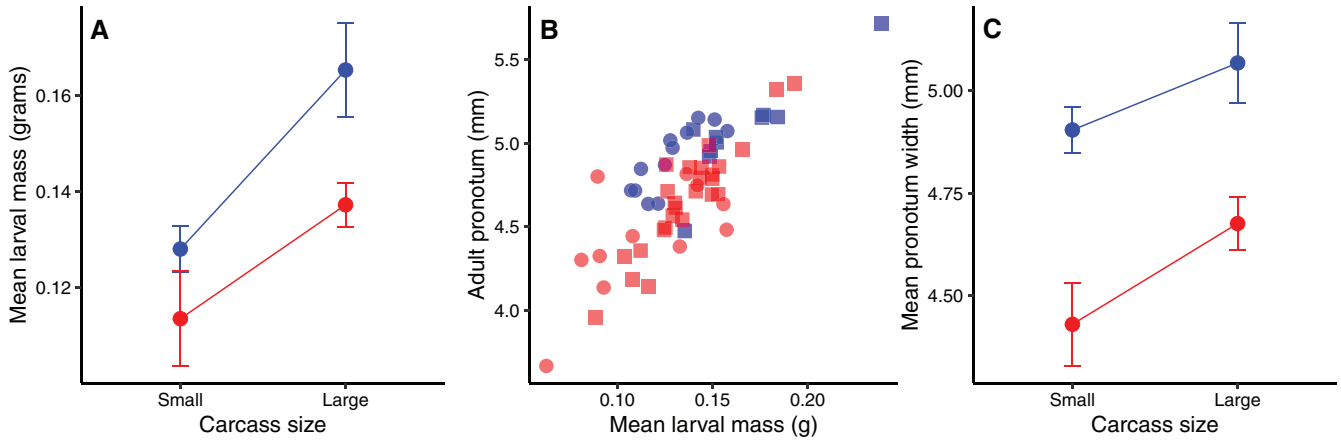

Figure 2. The impact of larval environmental conditions on the development of adult body size. The left panel (A) shows the effects of parental care and carcass size on larval mass at dispersal (mean ± SE), the middle panel (B) shows the relationship between mean larval mass at dispersal and mean adult pronotum width (with each symbol representing a different brood), and the right panel (C) shows the ultimate effects of parental care and carcass size on adult pronotum width (mean ± SE). In each panel, broods developing with or without parental care are shown with blue and red symbols, respectively. In panels (A) and (C), carcass size is indicated on the *x*-axis. In panel (B), different carcass size treatments are indicated by different symbols (circles for small carcasses and squares for large carcasses).

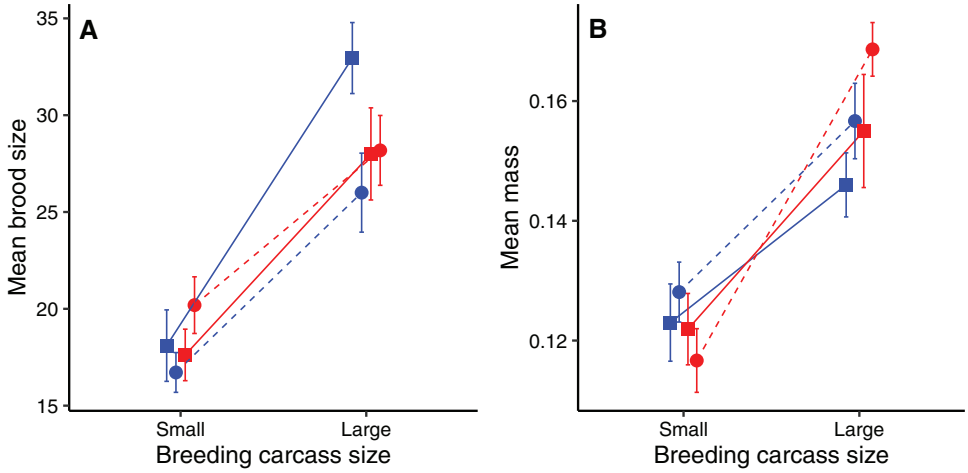

Figure 3. The impact of the larval and adult environments on two measures of parental performance: brood size at dispersal (A) and mean larval mass (B). In each panel, the adult environment (small or large breeding carcass) is on the *x*-axis and the different symbols and colors denote the larval environment: individuals developed as larvae with or without care (blue and red symbols, respectively) and on a small (circles with dashed lines) or large (squares with solid lines) carcass. Symbols represent means (mean ± SE).

Table 1. Summary data for brood size at dispersal and mean larval mass for all treatment combinations. Larval environments are as follows: No Care/Small Carcass (NS), No Care/Large Carcass (NL), Full Care/Small Carcass (FS), Full Care/Large Carcass (FL). For each variable, we present the mean, standard deviation, and sample size.

Adult	Small carcass				Large carcass			
Larval environment	NS ($n = 21$)	NL ($n = 21$)	FS ($n = 21$)	FL ($n = 20$)	NS ($n = 22$)	NL ($n = 20$)	FS ($n = 21$)	FL ($n = 20$)
Brood size	20.19 (6.71)	17.62 (6.09)	16.71 (4.70)	18.10 (8.19)	28.18 (8.46)	28 (10.64)	26 (9.35)	32.95 (8.20)
Mean larval mass (g)	0.116 (0.024)	0.122 (0.027)	0.129 (0.022)	0.123 (0.029)	0.169 (0.021)	0.154 (0.042)	0.16 (0.029)	0.146 (.024)

Table 2. The effects of the larval and adult breeding environments on brood size at dispersal and mean larval mass. Maternal and paternal family were initially included as random effects in each model. These random effects were not significant in either model (brood size at dispersal: female family, $P = 0.67$; male family, $P = 0.18$; mean larval mass: female family, $P = 1.0$; male family, $P = 0.80$) and were removed during model reduction.

	Brood size at dispersal		Mean larval mass	
Factor	$F_{1, 161}$	P	$F_{1, 162}$	P
Carcass $_{adult}$	72.14	$\mathbf{1.27 \times 10^{-14}}$	61.63	$\mathbf{5.38 \times 10^{-13}}$
Care $_{larva}$	0.0012	0.97	0.25	0.62
Carcass $_{larva}$	1.29	0.26	1.95	0.16
Carcass $_{larva}$ × Care $_{larva}$	4.91	**0.028**		

***P* values < 0.05 are shown in bold.**

Specifically, individuals that developed with parental care and on large carcasses had greatest reproductive success on large carcasses as adults.

We found that larvae that developed with care were larger than those that developed without care and that larvae that developed on large carcasses were larger than those that developed on small carcasses. These effects of parental care and carcass size on larval phenotype are consistent with the results of previous studies of *N. vespilloides* (Eggert et al. 1998; Smiseth et al. 2014; Hopwood et al. 2016). However, our experiment went one step further and examined how individuals that had experienced different environments as larvae responded, as parents, to variation in the size of the breeding carcass. On small carcasses, parents had similar reproductive success regardless of the environment that they had experienced during development as larvae. This suggests that small carcasses limited the expression of developmentally induced variation in parental performance. In contrast, the ability of parents to use all the resources on a large carcass for reproduction depended on the environment that the parents had experienced as larvae. Specifically, parents that had developed as larvae on large carcasses with posthatching care (FL) were able to produce ∼18% more offspring on large carcasses than parents that had developed on smaller carrion. Thus, the relationship between brood size and carcass size was steeper when individuals had been reared as larvae with full care and on a large carcass. The pattern of plasticity that we induced experimentally is remarkably similar to recently described population-level differences in plasticity that are associated with divergence in the carrion niche (Sun et al. 2020).

Previous studies suggest two explanations for the increased reproductive potential of FL adults on large carcasses. First, it may be that FL females simply have a higher potential fecundity (due to their larger size) than females that had experienced alternative environments (i.e., NL, NS, and FS females). No studies have explicitly examined the impact of natal carcass size and access to parental care on adult egg production in *N. vespilloides*. However, there is evidence that the duration of care experienced by a female during development impacts her adult body size, which in turn influences her fecundity (Steiger 2013; Schrader et al. 2016; Bladon et al. 2020). Second, there is evidence in *N. vespilloides* that the quality of posthatching parental care varies with female body size, with larger females producing heavier larvae than smaller females (Steiger 2013). Thus, larvae that develop on large carcasses with full care may become better parents as adults simply because they attain a larger body size. These two mechanisms are not mutually exclusive, but they make predictions that could be tested in future work. For example, the first potential mechanism predicts that females reared on large carcasses with full parental care should produce larger clutches than females reared in alternative environments. The second hypothesis predicts that larvae will have higher survival when they are raised by parents that had developed on a large carcass with full posthatching care. Testing this prediction will requirecross-fostering experiments in which brood size is standardized, similar to those of Steiger (2013).

Animals with extensive parental care often have young that are incapable of developing without that care. Such extreme dependence on parental care is presumably the outcome of coevolution between traits expressed in parents (e.g., parental attendance) and traits expressed in offspring (e.g., developmental dependence on care and altriciality). The conditions that initiate this coevolutionary process and determine its outcome are still poorly understood (Hale and Travis 2012; Capodeanu-Nägler et al. 2016; Capodeanu-Nägler et al. 2018); however, changes in the developmental environment of offspring are likely to play a key role (Hale and Travis 2012). Our results suggest that a shift from developing on small carcasses to developing on large carcasses might be an initial step in the evolution of obligate parental care in some species of *Nicrophorus*. For example, although all adults had increased fecundity on large carcasses, those with the highest fecundity had themselves developed on a large carcass with parental care. Thus, the move to a larger carrion niche could

reinforce selection for posthatching parental care. Increased selection on parenting might in turn increase dependence on care via a positive genetic correlation between parental provisioning and offspring begging (Lock et al. 2004). In contrast, the environment that individuals experienced as larvae had no effect on their ability to use a small carcass. This may weaken selection on parental care when carcasses tend to be small. This hypothesis predicts that carcass niche and larval dependence on parental care will covary within the genus: *Nicrophorus* species that exploit larger carrion will display obligate parental care, whereas those that exploit smaller carrion will display facultative care. Consistent with this hypothesis, Jarrett et al. (2017) found that large-bodied *Nicrophorus* (which tend to exploit larger carcasses) were more likely to have obligate parental care than small-bodied species (which tend to exploit smaller carcasses). Further testing of this hypothesis will require integrating life history data (e.g., whether care is facultative or obligate) (Capodeanu-Nägler et al. 2016; Capodeanu-Nägler et al. 2018), estimates of body size (Jarrett et al. 2017), and descriptions of carcass niche breadth (Hopwood et al. 2016; Sun et al. 2020) with a phylogeny of the genus. Although there is a well-resolved phylogeny of the genus (Sikes and Venables 2013), life history data, estimates of body size, and carcass niche data are available for only a handful of species (e.g., Jarrett et al. 2017).

Finally, our results add to a growing body of literature demonstrating that parental care can generate phenotypic variation that may fuel subsequent adaptive diversification. In some species, parental care plays a key role in the establishment of mating behaviors through facilitating sexual imprinting, which might lead to population differentiation and speciation (Sorenson et al. 2003; Balakrishnan et al. 2009; Kozak et al. 2011; Verzijden et al. 2012; Gilman and Kozak 2015; Grant and Rosemary Grant 2018; Yang et al. 2019; Jamie et al. 2020). In other cases, the early environment created by parents influences the development of morphology and behavior, which may enable ecological divergence (West-Ebberhard 2003; Snell-Rood et al. 2016; Schrader et al. 2018; Stein and Bell 2019). How frequently such plasticity becomes canalized and what conditions facilitate canalization are still largely unanswered questions. Addressing these issues will be essential for determining whether and how parentally induced plasticity contributes to adaptive diversification in nature.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA ARCHIVING

Data are available on Dryad: https://doi.org/10.5061/dryad.mgqnk9906.

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