Digest: Nature and nurture: influences of parental care and rearing environment on phenotypic plasticity in *Nicrophorus vespilloides*

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Footnote: This article corresponds to Schrader, M., B. J. M. Jarrett, and R. M. Kilner. 2021. Larval environmental conditions influence plasticity in resource use by adults in the burying beetle, Nicrophorus vespilloides. Evolution. https://doi.org/10.1111/evo.14339

Abstract: What conditions favor niche expansion in nature? In the burying beetle *Nicrophorus vespilloides*, Schrader et al. (2021b) found that larvae reared with parental care on larger carcasses were better equipped for resource use than individuals reared without parental care on smaller carcasses. This finding illustrates that developmental plasticity induced by parental care and carcass size has the potential to influence adaptive diversification.

Main Text:

The importance of phenotypic plasticity in evolutionary diversification and the colonization of novel environments is now widely accepted (Narayan 2021). The role of plasticity in evolutionary diversification is often restricted to phenotypic variation in morphology, behavior, or physiology resulting from environmental factors and their interactions (Pfennig et al. 2010). However, the contribution of social factors (i.e. interactions among family members) can also lead to phenotypic variation. Parental effects, for example, present a major source of variation for plasticity because parents can respond rapidly to different environmental cues and produce offspring that are best suited to local environmental conditions (Mateo 2014). Yet, the potential for parentally induced plasticity to drive evolutionary diversification remains an underexplored topic. Burying beetles (genus *Nicrophorus*), which have complex parental care behaviors and rely on carrion to breed (Scott 1998; Royle et al. 2013), present an ideal model system to test this theory.

In this issue, Schrader et al. (2021b) propose that the post-hatching parental care and carcass size that adult beetles receive as larvae determines their ability to use different-sized carcasses later in life. The authors predict that larvae reared on larger carcasses with parental care will perform better as adults due to their larger size. While larger size is generally associated with increased reproductive success and parental performance (Schrader et al. 2016), negative associations with fertilization success (De Nardo et al. 2021; Narayan and Wang 2021) and parental performance (Thomson et al. 2017) also exist.

To test their hypothesis, the authors experimentally manipulated the environment in which larvae developed by varying the size of the breeding carcass (large versus small) and access to post-hatching parental care (full care versus no care), to create four larval environments (Fig. 1). They then measured the performance of adult beetles from these environments on either a large or small carcass (Fig. 1). Here, we reanalyse their data (Schrader et al. 2021a) using One-way ANOVA followed by Tukey's multiple comparisons test to generate a series of pairwise comparisons of larval mass, brood mass, and larvae count for a total of eight different combinations of larval and adult environments (Fig. 2). All analyses were performed in GraphPad Prism version 9.1.

The authors found a strong positive link between post-hatching parental care and rearing carcass size on mean larval mass (Fig. 2A) and brood mass (Fig. 2B). Larvae count was also larger for larvae reared on larger carcasses with parental care compared to larvae that developed on smaller carcasses without parental care (Fig. 2C). Larvae reared on larger carcasses with parental care were on average larger than larvae that developed on smaller carcasses without parental care. This difference was even more pronounced when adults that had been reared as larvae with full care on a large carcass were moved to a smaller sized carcass as adults (Fig. 2). For larvae developed with parental care, performance did not differ amongst adults moved to the same sized carcass, even if the rearing environment was different (Fig. 2). Furthermore, there was no evidence that larvae raised on large carcasses with no care were different from larvae raised on small carcasses with no care. Adults raised as larvae on smaller carcasses with no care had higher average, albeit non-significant, larval mass, brood mass and larvae count on large carcasses (Fig. 2).

These findings demonstrated the importance of plasticity induced by parental effects in driving shifts in future resource use as adults, as evidenced by carrion niche expansion from small to large carcasses. This intraspecific variation also mirrors the evolutionary diversification patterns in carrion use with respect to dependence in parental care within the genus *Nicrophorus* (Jarrett et al. 2017). Importantly, it is also because of this that wider ecological conditions need to be integrated in future studies to fully understand how often, and to what extent, developmental plasticity is relevant in shaping carcass use plasticity in natural populations. Competition for carcasses within and between *Nicrophorus* species is ubiquitous, and can vary in space and time, leading to divergent selection for plasticity among populations. For example, while plastic responses to breeding on larger carcasses can be adaptive in the context of intraspecific competition, it might not necessarily be favored, especially when larger carcasses are routinely occupied by larger, more competitive interspecific rivals (Sun et al. 2020). Hence, individuals can adjust their behaviors in resource use in an adaptive manner in response to heterogenous environments. Understanding community structure, resource availability, and parental effects will provide further insights into the causes and consequences of developmental plasticity and its evolutionary processes under varying environmental conditions (Uller 2008).

More broadly, this study by Schrader et al. (2021b) demonstrates that parental care not only influences offspring reproductive success, but can also generate phenotypic variation that may fuel subsequent adaptive diversification. These results also reinforce the findings of previous studies that early-life environmental conditions affect population growth rates by generating cohort differences in individual fitness and resource use (Hopwood et al. 2014; Maenpaa and Smiseth 2020). Two main non-mutually exclusive hypotheses could also explain the pattern of results seen in this study: (1) the silver spoon hypothesis, where individuals born in optimal conditions have a higher fitness as adults across a range of environments (Grafen 1988); and (2) the “environmental matching” or “predictive adaptive response” (PAR) hypothesis, where fitness is highest when the adult environmental conditions match early-life environmental conditions (Gluckman and Hanson 2004). Consideration of evolutionary life-history theory in future studies may generate valuable insights in understanding the contribution of parentally induced plasticity to adaptive diversification.

References

De Nardo, A. N., J. Roy, S. H. Sbilordo, and S. Lüpold. 2021. Condition-dependent interaction between mating success and competitive fertilization success in *Drosophila melanogaster**. Evolution 75:2014-2026.

Gluckman, P. D. and M. A. Hanson. 2004. Maternal constraint of fetal growth and its consequences. Semin Fetal Neonatal Med 9:419-425.

Grafen, A. 1988. On the uses of data on lifetime reproductive success. Reproductive success:454-485.

Hopwood, P. E., A. J. Moore, and N. J. Royle. 2014. Effects of resource variation during early life and adult social environment on contest outcomes in burying beetles: a context-dependent silver spoon strategy? Proc Biol Sci 281:20133102.

Jarrett, B. J., M. Schrader, D. Rebar, T. M. Houslay, and R. M. Kilner. 2017. Cooperative interactions within the family enhance the capacity for evolutionary change in body size. Nat Ecol Evol 1:0178.

Maenpaa, M. I. and P. T. Smiseth. 2020. Resource allocation is determined by both parents and offspring in a burying beetle. J Evol Biol 33:1567-1578.

Mateo, J. M. 2014. Development, maternal effects, and behavioral plasticity. Integr Comp Biol 54:841-849.

Narayan, V. P. 2021. Digest: On the contribution of phenotypic plasticity to adaptation in desert environments. Evolution 75:1585-1586.

Narayan, V. P. and Y. Wang. 2021. Digest: Does size matter? Condition-dependent sexual selection in *Drosophila melanogaster*. Evolution 75:2135-2136.

Pfennig, D. W., M. A. Wund, E. C. Snell-Rood, T. Cruickshank, C. D. Schlichting, and A. P. Moczek. 2010. Phenotypic plasticity's impacts on diversification and speciation. Trends Ecol Evol 25:459-467.

Royle, N. J., P. E. Hopwood, and M. L. Head. 2013. Burying beetles. Curr Biol 23:R907-909.

Schrader, M., R. M. Crosby, A. R. Hesketh, B. J. Jarrett, and R. M. Kilner. 2016. A limit on the extent to which increased egg size can compensate for a poor postnatal environment revealed experimentally in the burying beetle, *Nicrophorus vespilloides*. Ecol Evol 6:329-336.

Schrader, M., B. Jarrett, and R. Kilner. 2021a. Data for: Larval environmental conditions influence plasticity in resource use by adults in the burying beetle, *Nicrophorus vespilloides*. Dryad Dataset.

Schrader, M., B. J. M. Jarrett, and R. M. Kilner. 2021b. Larval environmental conditions influence plasticity in resource use by adults in the burying beetle, *Nicrophorus vespilloides*. Evolution. https://doi.org/10.1111/evo.14339

Scott, M. P. 1998. The ecology and behavior of burying beetles. Annu Rev Entomol 43:595-618.

Sun, S. J., A. M. Catherall, S. Pascoal, B. J. M. Jarrett, S. E. Miller, M. J. Sheehan, and R. M. Kilner. 2020. Rapid local adaptation linked with phenotypic plasticity. Evol Lett 4:345-359.

Thomson, C. E., F. Bayer, N. Crouch, S. Farrell, E. Heap, E. Mittell, M. Zurita-Cassinello, and J. D. Hadfield. 2017. Selection on parental performance opposes selection for larger body mass in a wild population of blue tits. Evolution 71:716-732.

Uller, T. 2008. Developmental plasticity and the evolution of parental effects. Trends Ecol Evol 23:432-438.

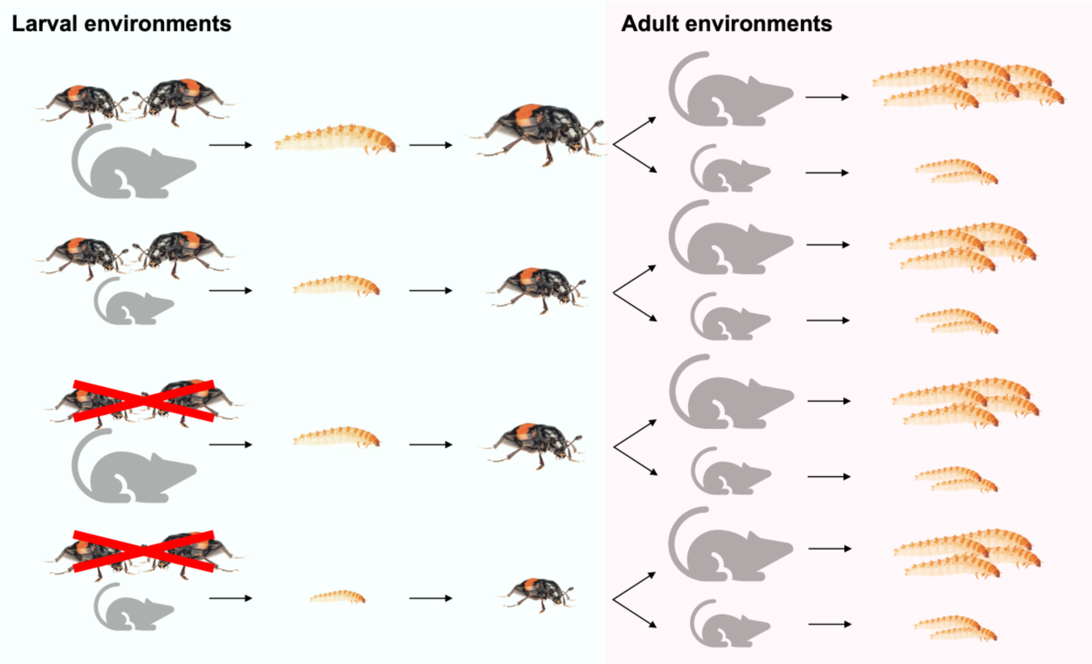

Figure 1. Graphical illustration of the experimental design used by Schrader et al. (2021b) to test if developmental plasticity induced during larval environments (i.e., presence of parental care and carcass size) facilitates a shift in resource use (small or large carcasses) as adults. The number and size of beetles, larvae, and mice presented here were for illustrative purposes only. Photo credit: Dr. Tom Houslay.

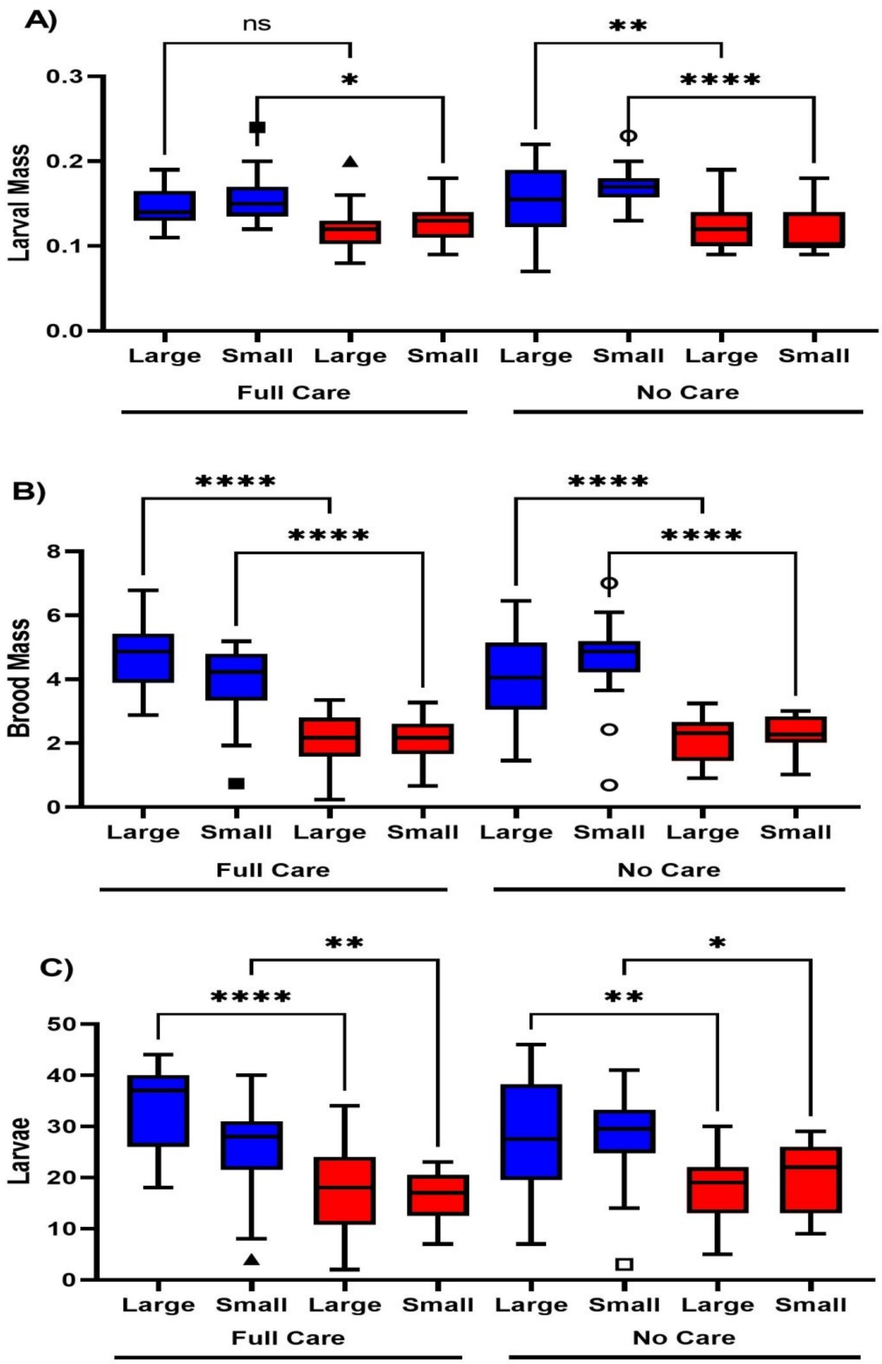

Figure 2. Graphical representation of the patterns described by Schrader et al. (2021b) that illustrates the effects of parental care and carcass size rearing on A) larval mass, B) brood mass, and C) larvae count for all eight different combinations of larval and adult environments. The larval environment is on the x-axis: Parental Care (full care versus no care) and Carcass size (small versus large). Color denotes the adult environment of large or small breeding carcass (blue and red bars, respectively). Bars represent means and error bars represent the SE of the mean. Asterisks indicate the statistical significance of differences between groups: ns P > 0.05; *P ≤ 0.05; **P ≤ 0.01; ***P ≤ 0.001; **** P ≤ 0.0001.