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Digest: Nature and nurture

Citation for published version:

Sun, SJ, Narayan, VP, Wang, Y & Wasana, N 2022, 'Digest: Nature and nurture: Influences of parental care and rearing environment on phenotypic plasticity in *Nicrophorus vespilloides*', *Evolution: International Journal of Organic Evolution*, vol. 76, no. 3, pp. 681-684. <https://doi.org/10.1111/evo.14433>

Digital Object Identifier (DOI):

[10.1111/evo.14433](https://doi.org/10.1111/evo.14433)

Link:

[Link to publication record in Edinburgh Research Explorer](#)

Document Version:

Peer reviewed version

Published In:

Evolution: International Journal of Organic Evolution

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

3
4 **Abstract:** What conditions favor niche expansion in nature? In the burying beetle
5 *Nicrophorus vespilloides*, Schrader et al. (2021b) found that larvae reared with parental care
6 on larger carcasses were better equipped for resource use than individuals reared without
7 parental care on smaller carcasses. This finding illustrates that developmental plasticity
8 induced by parental care and carcass size has the potential to influence adaptive
9 diversification.

10
11 **Main Text:**

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

24
25 In this issue, Schrader et al. (2021b) propose that the post-hatching parental care and carcass
26 size that adult beetles receive as larvae determines their ability to use different-sized
27 carcasses later in life. The authors predict that larvae reared on larger carcasses with parental
28 care will perform better as adults due to their larger size. While larger size is generally
29 associated with increased reproductive success and parental performance (Schrader et al.
30 2016), negative associations with fertilization success (De Nardo et al. 2021; Narayan and
31 Wang 2021) and parental performance (Thomson et al. 2017) also exist.

32 To test their hypothesis, the authors experimentally manipulated the environment in which
33 larvae developed by varying the size of the breeding carcass (large versus small) and access

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

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

54 These findings demonstrated the importance of plasticity induced by parental effects in
55 driving shifts in future resource use as adults, as evidenced by carrion niche expansion from
56 small to large carcasses. This intraspecific variation also mirrors the evolutionary
57 diversification patterns in carrion use with respect to dependence in parental care within the
58 genus *Nicrophorus* (Jarrett et al. 2017). Importantly, it is also because of this that wider
59 ecological conditions need to be integrated in future studies to fully understand how often,
60 and to what extent, developmental plasticity is relevant in shaping carcass use plasticity in
61 natural populations. Competition for carcasses within and between *Nicrophorus* species is
62 ubiquitous, and can vary in space and time, leading to divergent selection for plasticity
63 among populations. For example, while plastic responses to breeding on larger carcasses can
64 be adaptive in the context of intraspecific competition, it might not necessarily be favored,
65 especially when larger carcasses are routinely occupied by larger, more competitive

66 interspecific rivals (Sun et al. 2020). Hence, individuals can adjust their behaviors in resource
67 use in an adaptive manner in response to heterogenous environments. Understanding
68 community structure, resource availability, and parental effects will provide further insights
69 into the causes and consequences of developmental plasticity and its evolutionary processes
70 under varying environmental conditions (Uller 2008).

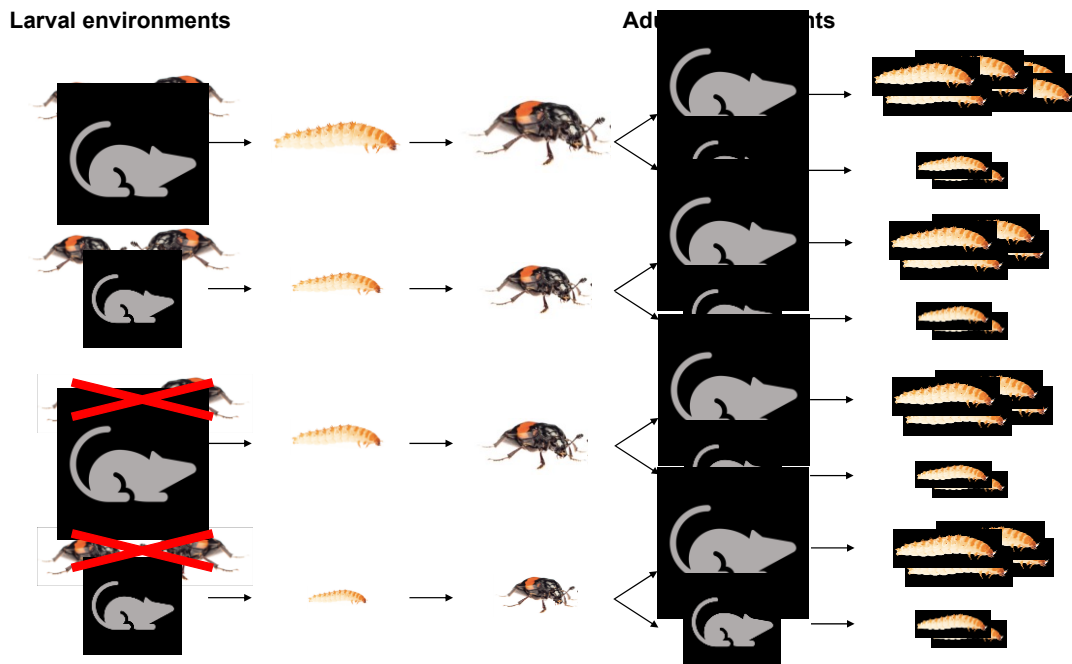
71 More broadly, this study by Schrader et al. (2021b) demonstrates that parental care not only
72 influences offspring reproductive success, but can also generate phenotypic variation that
73 may fuel subsequent adaptive diversification. These results also reinforce the findings of
74 previous studies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

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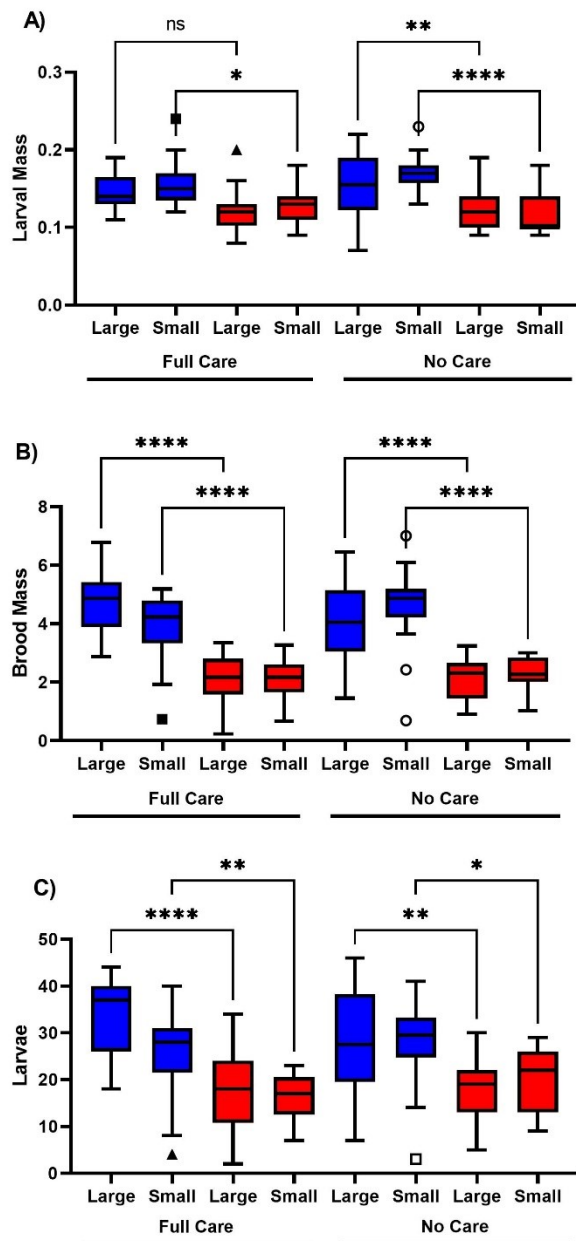
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Figure 1. Graphical illustration of the experimental design used by Schrader et al. (2021b) to test if developmental plasticity induced during larval environments (i.e., presence of parental care and carcass size) facilitates a shift in resource use (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.



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

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