Offspring overcome poor parenting by being better parents

Ahva L. Potticary*, Christopher B. Cunningham, and Allen J. Moore

Department of Entomology, University of Georgia, Athens, Georgia, 30602 USA

***Corresponding Author:**

Ahva L. Potticary

120 Cedar Street

Biological Sciences West #360

Athens, GA 30602

ORCID identifier:

Ahva L. Potticary: 0000-0002-1157-5315

Christopher B. Cunningham: 0000-0003-3965-2076

Allen J. Moore: 0000-0002-1498-3322

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ABSTRACT

The evolutionary repercussions of parental effects are often discussed as fixed effects on offspring phenotype that can even have negative influences on offspring fitness if parental and offspring environments do not match. Yet individuals are not passive recipients and may mitigate the persistence of parental effects through their own behavior. Here we test how the burying beetle *Nicrophorus orbicollis*, a species with highly developed parental care, responds to poor parenting. We manipulated the duration of parental care received and measured both offspring and grandoffspring traits of males and females. As expected, reducing parental care negatively impacted key traits that influence fitness, including offspring development time and body size. However, offspring that received reduced care increased uniparental care when they became parents and, in addition, shifted the type of parenting behavior to more direct feeding of offspring. Parents that had received full care as larvae invested more time maintaining the food resource, a form of indirect parental care. As a result, both the number and mass of offspring were unaffected by the different developmental experience of their parent. Our results show that flexible parental care can overcome poor parental environments and limit negative parental effects to a single generation.

IMPACT SUMMARY

Parental care is one of the most visible means by which parents influence the development of their offspring and is expected to evolve to buffer offspring from challenging environments. Yet, variation in parental care itself can have negative effects on offspring that cascades across generations. How can offspring overcome these poor developmental environments? Here we test the hypothesis that organisms can compensate for their own poor developmental environments by changing their parental care behavior in the burying beetle *Nicrophorus orbicollis*. Specifically, we asked whether receiving poor parenting begets poor parenting. We manipulated the amount of parental care provided by burying beetles, an insect that feeds its offspring regurgitated food. Reduced parental care resulted in smaller offspring that developed more slowly in early developmental stages. However, when these offspring reached adulthood, they modified their own parental care so that the grandoffspring were unaffected by the negative conditions experienced by the previous generation. We suggest that these result show that parental care not only serves as a buffer within-generation but can also compensate for poor natal environments across generations.

64 *Introduction*

65

66 Organisms inhabit challenging environments that require accommodation of or buffering against
67 environmental variation. Which response prevails depends on both an organism's experience of the
68 current environment and the environments experienced by ancestors. Parental effects are particularly
69 clear examples of this, as all parents influence the development of their offspring (Roach and Wulff
70 1987; Mousseau and Fox 1998; Molinier et al. 2006; Marshall and Uller 2007; Royle et al. 2012),
71 ranging from short-term impacts on offspring to effects that persist for multiple generations (Cheverud
72 and Moore 1994; Molinier et al. 2006; Yin et al. 2019). As environments can change rapidly or
73 unpredictably, parental effects on offspring development can range from positive (Badyaev et al. 2006;
74 Galloway and Etterson 2007; Dantzer et al. 2013; Duckworth et al. 2015) to negative (Gluckman et al.
75 2005; Sheriff and Love 2013; Potticary and Duckworth 2018) depending on how well offspring
76 phenotypes match prevailing conditions (Bernardo 1996; Bateson et al. 2014). Consequently, the
77 evolutionary repercussions of parental effects are often viewed as fixed effects on offspring phenotype,
78 but this is an assumption that should be tested (Badyaev and Uller 2009).

79 Individuals are not passive recipients of the environment, and the persistence of a parental effect
80 depends on the interactions between offspring and their environment in later life (Cheverud and Moore
81 1994; Bernardo 1996; Francis et al. 2002), which can be directly mediated by individual behavior. One
82 of the most recognizable parental effects that can impact offspring development is parental care
83 behavior, and variation in parental care behavior can produce transgenerational effects (Rossiter 1996;
84 Champagne 2008). Adaptive parental effects are broadly expected to evolve to help offspring overcome
85 challenging environments through modification of offspring phenotypes or buffering (Wilson 1975;
86 Mousseau and Fox 1998; Badyaev and Uller 2009). In the former, parents prepare offspring to face a
87 future environment (Mousseau and Dingle 1991; Dantzer et al. 2013; Potticary and Duckworth 2020)

88 and are thought to evolve when parental experience is predictive of the environment that will be
89 experienced by offspring (Bateson et al. 2014; Burgess and Marshall 2014). Alternatively, parents may
90 buffer offspring from the environment they experienced by changing how they provision offspring
91 with resources, showing experience-dependent parental care.

92 Here we test the hypothesis that organisms can compensate for their own poor developmental
93 environments by changing their parental care behavior in the burying beetle *Nicrophorus orbicollis*.
94 Specifically, we examine how *N. orbicollis* as parents overcome poor parenting received as larvae. We
95 investigated this by manipulating the duration of parental care that mixed foster broods received to
96 produce larvae that experience reduced (six hours) or full parental care (approximately seven days).
97 Burying beetles require small animal carcasses to breed and show complex parental care behavior
98 (Robertson 1993; Eggert and Müller 1997; Scott 1998a). Parental care is not a single behavior, but a
99 category describing a suite of behaviors (Royle et al. 2012). In *Nicrophorus*, parents bury and defend
100 carcasses, which in part acts to ensure that the carcass is available for longer (Robertson 1993; Trumbo
101 and Sikes 2021), eliminate bacterial and fungal consumers to avoid putrefaction (Arce et al. 2012;
102 Haberer et al. 2014), create cavities with predigested carrion "soup" to support offspring self-feeding
103 (Eggert and Müller 1997; Capodeanu-Nägler et al. 2018; Duarte et al. 2021), and directly transfer food
104 to larvae through regurgitation of pre-digested carrion (Eggert et al. 1998). Larvae do not feed after
105 they leave the carcass until they metamorphose into adults, and thus adult body size is largely
106 determined by the efficiency of resource acquisition during the larval period on carcass. Body size is a
107 key fitness trait for *Nicrophorus*, as larger beetles are more effective competitors for carcasses (Otronen
108 1988; Robertson 1993). Thus, parental care creates a direct link between a larva's developmental
109 experience and competitive ability upon reaching adulthood, and the outcome of this effect will depend
110 on the ecological context offspring experience in later life.

111 Our study was designed to ask if poor parenting begets poor parenting. We found that, in *N.*
112 *orbicollis*, it does not; parents behaviorally compensated for their own poor rearing environment,

113 showing experience-dependent parental care and an adaptive parental effect ensuring that the influence
114 of poor parenting on development does not persist. This suggests that parental care behavior may not
115 only buffer offspring development within a generation but may also act as a buffer that mitigates the
116 legacy of environments past.
117

118 *Materials and Methods*

119

120 **INSECT COLONY AND HUSBANDRY**

121

122 We used *Nicrophorus orbicollis* from an outbred colony maintained at the University of Georgia that
123 is regularly supplemented with wild-caught beetles from Whitehall Forest in Athens, GA, USA. All
124 beetles were maintained in an incubator (Percival, model no. I4-66VL, Perry, IA) at 22 ± 0.1°C on a
125 14:10 hour light:dark cycle that simulated summer breeding conditions. We bred all individuals used
126 here in the laboratory to ensure that parentage, age, and to standardize rearing conditions. We housed
127 beetles individually at larval dispersal in 9-cm-diameter by 4-cm-deep circular compostable deli
128 containers (EP-RDP5, Eco-Products) filled with ~2.5 cm of organic potting soil. Larvae had no further
129 social interactions with other burying beetles until they were randomly allocated into treatments. We
130 defined individuals as age Day 1 on the day of eclosion to adulthood. Beetles were fed *ad libitum*
131 organic ground beef twice a week following adult eclosion.
132

133 **EFFECT OF REMOVING PARENTAL CARE ON OFFSPRING DEVELOPMENT**

134

135 We manipulated the duration of parental care to determine the effect of parental care on offspring traits
136 related to fitness and their expression of care once they attained adulthood. We randomly mated focal

137 virgins at Day 13-19 by placing an unrelated male and female in a small plastic container and observed
138 them to ensure that mating occurred. The pair was then moved to a plastic breeding box filled with
139 approximately two cm of potting soil moistened with distilled water and containing a freshly thawed
140 mouse 20.8 ± 0.6 g SD (max = 22.2, min = 20.0; Rodent Pro, Inglefield, IN, U.S.A.). There was no
141 difference in the size of the mouse provided between treatments (20.9 g in full care treatment, 20.8 g
142 in reduced care treatment; $F_{1,34} = 0.153$, $P = 0.698$). We then returned breeding boxes to the incubator
143 and kept them on a darkened shelf to simulate underground breeding conditions. We checked breeding
144 boxes for eggs every twenty-four hours. Once eggs we observed eggs, we moved the female and brood
145 ball to a new breeding box filled with approximately two cm of moistened potting soil, while the male
146 was removed. We left eggs in the original breeding box with a small piece of ground beef. Once 90
147 hours had elapsed since egg laying, we checked the breeding box containing the eggs every hour to
148 determine when larvae had hatched and crawled to the beef. After we observed the focal females'
149 larvae hatch, we provided the focal female with an unrelated, mixed brood of 10 larvae. Burying beetles
150 identify their offspring temporally and eat any larvae that arrive too early on the carcass (Oldekop et
151 al. 2007), and thus we only provided females with larvae after her own larvae had hatched. For the full
152 duration parental care treatment, we allowed females to associate with larvae until at least 2 of the
153 larvae had dispersed from the breeding carcass (~7 - 8 days). For the reduced duration parental care
154 treatment, we allowed females to associate with larvae for 6 hours and then the female was removed.
155 We checked experimental treatments daily to determine larval dispersal date, subsequently, larval
156 survival.

157 We measured several offspring traits related to fitness (Lock et al. 2004), including mass at
158 dispersal, duration of developmental periods, and adult size. We measured larval mass at dispersal to
159 the nearest 0.1 mg. We also measured the duration of development on the carcass (from hatch until
160 dispersal), which is when parental care and all larval growth occurs; the number of days of development
161 from larval dispersal to pupation; the number of days as pupae (from pupation to adult eclosion), and

total duration of development (from larval hatch until adult eclosion). When the larvae left the carcass (dispersal), we placed larvae into individual containers with ~2 cm of moistened soil. We checked treatments daily to determine the number of surviving larvae, length of larval period, pupation date, and adult ecolsion date. We measured the pronotum length of full and reduced care offspring on Day 14 – 16 post-eclosion with calipers to the nearest 0.01 mm.

EFFECT OF VARIATION IN PARENTAL CARE ENVIRONMENT ON SUBSEQUENT GENERATIONS

At Day 14 – 16 following eclosion, adult beetles that received full or reduced care as offspring were provided with an unrelated, virgin mate from our stock colony and a 19.6 - 21.2 g thawed mouse carcass (mean = 20.6 g). These were placed into breeding container with ~2 cm of moistened soil. As variation of parental care may manifest as variation in investment across the breeding cycle, breeding boxes were fitted with an escape chamber to allow focal beetles to desert the breeding attempt. Breeding boxes were checked daily for eggs. Beetles that escaped into the escape chamber prior to egg laying were replaced in the breeding box. Beetles that escaped after egg-laying and remained in the escape chamber for over 15 minutes were counted as deserters and removed. Once larvae were observed, the non-focal partner was removed, and the focal male or female was left in a uniparental context to care for the offspring. If the focal beetle deserted the breeding attempt prior to larval hatch, no further monitoring was conducted on that breeding attempt.

As rates of parental provisioning may be affected by the number of larvae (Rauter and Moore 2004), we measured parental care using both behavioral measures and larval traits associated with fitness. Behavioral observations were conducted twenty-four hours after larva were first observed on the carcass for each focal individual to quantify parental care. We moved breeding boxes into an observation room, and we gave the focal beetle at least 30 minutes to acclimate prior to observation. All observations were conducted under red lights to ensure no light effects on individual care behavior,

187 as *N. orbicollis* are nocturnal (Wilson et al. 1984). In each behavioral observation, we recorded both
188 direct and indirect parental care behaviors for 15 minutes (Walling et al. 2008). Direct care is defined
189 as when the male or female fed larvae. Indirect care is defined as activities related to carcass cleaning
190 and maintenance, which allows for the preservation of the carcass for future offspring provisioning and
191 thus represents a type of parental care without direct interactions with offspring. We also recorded time
192 spent showing "no care", defined as when the parent was on the carcass but not engaged in direct or
193 indirect care, or the individual was off the carcass. Behaviors were recorded continuously as both a
194 duration and frequency (e.g., number of times an adult fed larvae). This gave each individual three
195 scores (direct care, indirect care, and no care) which together summed to 15 minutes.

196 We measured offspring traits related to fitness reared by males or females that had received full
197 or reduced care as larvae themselves. We did not manipulate the number of offspring but instead
198 allowed parents to cull the number without interference. Of the remaining 61 uniparental broods, we
199 measured the number of offspring reared, the mass of the offspring at dispersal, and the amount of time
200 larvae spent on the carcass from hatching to dispersal. Measurements of development times and larval
201 mass were the same as used in the experimental manipulation of the duration of parental care (see
202 previous section).

203

204 **STATISTICAL ANALYSES**

205

206 We performed all statistical analyses using JMP Pro (v. 16.0.0, http://jmp.com) and produced figures
207 in SigmaPlot (v. 14.5, http://www.sigmaplot.co.uk). Results are means ± SE unless otherwise noted.
208 Effects on continuous offspring traits were analyzed with nested ANOVA, with family nested within
209 treatment. We analyzed categorical data with Pearson's Chi-square goodness-of-fit test. We analyzed
210 parental care behaviors and continuous larval traits of grand offspring with two-way ANOVA or, a

211 GLM with a Poisson distribution for categorical data, with caretaker sex and parenting experienced as
212 factors.
213
214 *Results*
215
216 **EFFECT OF REDUCING PARENTAL CARE ON OFFSPRING DEVELOPMENT**
217
218 We set up 36 families, 18 in each treatment, of mixed-parentage broods with a single, unrelated female
219 caretaker in the full and reduced parental care treatments. Overall larval survival was high for both
220 treatments; from an initial 10 fostered larvae placed on carcass, 3-10 survived to dispersal from the
221 mouse with a mean 8.3 ± 0.4 surviving larvae for full care families and 8.7 ± 0.4 for reduced care ($F_{1,34}$
222 = 0.430, P = 0.516). Three (2%) larvae died after dispersal from the full care treatment, and three
223 (1.9%) died from the reduced care treatment. A further 14 (9.6%) died in the pupal stage in the full
224 care treatment, and 16 (10.4%) in the reduced care.
225 Larvae in the full care treatment developed faster on the carcass than larvae that received
226 reduced care (χ^2 = 18.86, P < 0.0001, N = 305). Larvae that received full care completed development
227 from hatch to dispersal in 7 - 8 days (mean = 7.4) and reduced care larvae dispersed in 8 - 9 days (mean
228 = 8.3 in reduced care families; **Fig. 1*A*)**. The largest effect of reduced care was on larval weight at
229 dispersal from the carcass (**Fig. 1*B***). There was statistically significant variation between care
230 treatments ($F_{1,269}$ = 433.253, P < 0.0001), as well as caretakers nested within treatments ($F_{34,269}$ =
231 10.155, P < 0.0001). Controlling for variation amongst families, larvae that received full care weighed
232 500.4 ± 4.4 mg, whilst larvae that received reduced care weighed 373.4 ± 4.2 mg. Larval weight at
233 dispersal was highly and positively correlated with adult size (r = 0.91, N = 248).

234 Even though larvae in the full care treatment developed faster on the carcass, duration of total
235 post-embryonic development (hatch to eclosion) was influenced primarily by larval mass at dispersal
236 ($F_{1,232}$ = 77.283, P < 0.0001) and not on care treatment ($F_{1,232}$ = 1.311, P = 0.2535; **Fig. 1*C***). There was
237 statistically significant variation attributable to caretaker ($F_{34,261}$ = 9.301, P < 0.0001), larval weight
238 ($F_{1,261}$ = 34.501, P < 0.0001) and duration of parental care received ($F_{1,261}$ = 13.47, P = 0.0003) on time
239 spent after dispersal to pupation. The same factors influenced duration of pupal development (pupae
240 to adult eclosion) with statistically significant variation arising from larval weight ($F_{1,231}$ = 55.586, P
241 < 0.0001), caretaker ($F_{34,231}$ = 3.173, P < 0.0001), but not duration of parental care received ($F_{1,231}$ =
242 0.883, P = 0.348). Thus, the duration of care received influenced the speed with which the larvae
243 developed on the carcass, but this only shifted development time.
244
245 **EFFECT OF VARIATION IN PARENTAL CARE ENVIRONMENT ON SUBSEQUENT GENERATIONS**
246
247 We next established 89 uniparental broods using the resulting offspring from the reduced and full care
248 treatments (26 full care males, 20 full care females, 24 reduced care males, and 17 reduced care
249 females). There is no evidence that the type of parenting received influenced whether parents
250 abandoned prior to showing parental care to larvae. Focal male caretakers were more likely to abandon
251 before eggs hatched (reduced care males: 11/24 breeding attempts; full care males: 11/26 breeding
252 attempts) than female caretakers (reduced care females: 2/17 breeding attempts; full care females 2/20
253 breeding attempts). Once larvae hatched, most focal parents stayed for the entire larval development
254 on the carcass. When caretakers did abandon larvae, it was almost exclusively males (10/29 males,
255 1/33 females; χ^2 = 11.640, df = 1, P = 0.0012). The one female that abandoned early had received full
256 care; for males, four had received full care and six received reduced care.
257 Parental care behavior of both males and females was affected by the length of care they
258 received as larvae. There are strong differences between uniparental females and males in this species

259 (**Fig. 2**). Females spent more time on the carcass during the observation period than did males ($F_{1,55}$ =
260 17.610, P < 0.001; **Fig. 2*A***) regardless of the duration of parental care they received ($F_{1,55}$ = 1.878, P
261 = 0.176) and there was not a statistically significant interaction between the duration of care received
262 and sex of the caregiver on amount of time spent on the carcass ($F_{1,55}$ = 1.332, P = 0.253). Direct care,
263 or the time parents spent regurgitating to their larvae, was strongly influenced by the duration of
264 parental care received ($F_{1,55}$ = 6.761, P = 0.012); individuals that received reduced care provided more
265 direct care themselves and this pattern was consistent for both males and females (**Fig. 2*B***); there was
266 no interaction between the sex of the caregiver and the effect of parenting received ($F_{1,55}$ = 0.111, P =
267 0.741). Females provided more direct care than males under both treatments ($F_{1,55}$ = 12.699, P =
268 0.0008). In contrast, indirect care, or time spent maintaining the carcass, was not affected by the
269 duration of parental care received ($F_{1,55}$ = 1.181, P = 0.282; **Fig. 2*C***) or sex of the caregiver ($F_{1,55}$ =
270 3.072, P = 0.085), and there was no interaction between these treatments ($F_{1,55}$ = 0.705, P = 0.405).
271 Overall, the care a parent received as a larva did not result in negative effects on grandoffspring.
272 Using GLM with Poisson distribution, there was no statistically significant effect of caregiver sex (χ^2
273 = 0.269, df = 1, P = 0.604), care received by the parent (χ^2 = 0.007, P = 0.932) or their interaction (χ^2
274 = 0.439, P = 0.508). Carcass mass did not have a statistically significant influence (χ^2 = 0.118, P =
275 0.731). There was no effect of caregiver sex on average larval mass ($F_{1,56}$ = 1.855, P = 0.179), care
276 received by parent ($F_{1,56}$ = 1.340, P = 0.252) or their interaction ($F_{1,56}$ = 0.477, P = 0.493), controlling
277 for carcass mass as a covariate ($F_{1,56}$ = 0.047, P = 0.829; **Fig. 3*A***). Females reared more offspring than
278 did males in general ($F_{1,56}$ = 15.521, P = 0.0002), but there was no effect of parental treatment on the
279 number of offspring reared ($F_{1,56}$ = 0.095, P = 0.759; **Fig. 3*B***) and no interaction between caregiver
280 sex and the duration of parental care received ($F_{1,56}$ = 0.429, P = 0.515). Carcass mass as a covariate
281 was also not statistically significant ($F_{1,56}$ = 1.562, P = 0.217).
282

283 *Discussion*

284

285 Adaptive parental effects are expected to evolve to help offspring overcome challenging environments
286 through modification of offspring phenotypes or buffering (Wilson 1975; Mousseau and Fox 1998;
287 West-Eberhard 2003; Badyaev and Uller 2009), yet parents can have negative impacts on offspring
288 (Rauter and Moore 2002; Royle et al. 2012) especially if parental and offspring environments do not
289 match (Marshall and Uller 2007; Sheriff and Love 2013; Bateson et al. 2014). We tested the hypothesis
290 that parental care can act as a buffer because it allows parents to compensate for their own poor
291 developmental environment when they become parents themselves. Experimentally reducing parental
292 care greatly influenced offspring traits that are aligned with fitness, including duration of the vulnerable
293 stage on the carcass (**Fig. 1*A***; Robertson 1993; Eggert & Müller 1997) and body size (**Fig. 1*B***; Otronen
294 1988). However, there was no difference in the size or number of offspring when those same offspring
295 themselves were parents. This consistency of offspring outcomes was enabled by a shift in the
296 expression of the components of parental care behavior. Parents that received reduced parental care
297 themselves spent more time directly transferring nutrients to offspring, as opposed to parents that
298 received full care, who invested more in indirect mechanisms to enable nutrient acquisition of larvae
299 (i.e., maintenance of a food resource). As a result, parents that received reduced parental care
300 constrained the negative effects of their own poor developmental environment to a single generation.
301 Together, these data suggest that parents behaviorally compensate for their own poor rearing
302 environment, showing experience-dependent parental care and an adaptive parental effect ensuring that
303 poor developmental environments do not persist.

304 Beetles that received full parental care were larger and developed faster on the carcass, although
305 larger beetles overall took longer to develop into adult beetles. Why might development on the carcass
306 be different relative to other developmental periods? On a local level, developmental rate can be

307 directly influenced by variation in parental care. Parents regurgitate to larvae, and direct provisioning
308 has been shown to increase offspring size or growth rate across taxa (Naef-Daenzer and Keller 1999;
309 Lock et al. 2004; Lock 2012). The carcass is the only source of nutrition for both larvae and parents
310 during early larval development (Keppner et al. 2023). In other *Nicrophorus* species, multiple parental
311 behaviors increase larval growth and survival, such as reducing exploitation competition by removing
312 bacteria (Cotter and Kilner 2010; Arce et al. 2012), selective culling of the brood (Bartlett 1987;
313 Bartlett and Ashworth 1988), and maintenance of a larval cavity in the carcass (Capodeanu-Nägler et
314 al. 2018; Duarte et al. 2021). An ultimate explanation for rapid development on the carcass may be that
315 there is selection arising from competition or predation for offspring to leave the carcass quickly.
316 Studies in the wild find that *N. orbicollis* nests are frequently discovered by scavengers or taken over
317 by conspecifics, which generally eat larvae and eggs during successful takeovers (Robertson 1993).
318 High predation risk has been associated with more rapid development rates in the nest across bird
319 species (Martin et al. 2011). Thus, we suggest that local provisioning rates serve to enhance offspring
320 growth rates while on the carcass, reducing the risk at this vulnerable stage, while still allowing larvae
321 to attain large adult size.

322 Parental effects range from short-term effects that dissipate when offspring pass a certain
323 developmental stage (Gluckman et al. 2005), to effects that persist for multiple generations, even for
324 the same traits (e.g., stress reactivity; Meaney 2001; Mustoe et al. 2014; Sheriff et al. 2017). Previous
325 work in other *Nicrophorus* species and other taxa have documented such transgenerational effects of
326 poor parental care environments (e.g., Meaney 2001; Champagne 2008; Lock 2012; Kilner et al. 2015).
327 An unanswered question is why the effects of poor developmental environment are propagated across
328 generations under some circumstances but not in others. The persistence of parental effects likely
329 depends both abiotic and biotic factors, such as the durability of physiological mechanisms that
330 transmit them (Weaver et al. 2004; Horsthemke 2018) and concordance between the parent and
331 offspring environments (Gluckman et al. 2005; Marshall and Uller 2007; Bateson et al. 2014).

332 Moreover, the persistence of parental effects likely depends on whether they arise from an evolved
333 interaction between parents and offspring development, or are merely a disruption of normal
334 development (Gluckman et al. 2005). Adaptive parental effects are predicted to induce variation in
335 offspring traits that are functionally related to the environment that triggered them (e.g., Tollrian 1995;
336 Duckworth et al. 2015; Sheriff et al. 2017; Sharda et al. 2021). In our study, *N. orbicollis* that received
337 poor parenting changed their own parental care behavior to reduce the influence of a poor
338 developmental environment, which also requires that offspring are receptive to changes in parental
339 care behavior (Smiseth et al. 2003). Together, these data imply that parental care acts a developmental
340 buffer across generations and may indicate evolution for this purpose in *N. orbicollis,* particularly given
341 how important body size is for competitive interactions in this species (Robertson 1993; Creighton
342 2005; Schrempf et al. 2021). While there are many processes that may alter the persistence of parental
343 effects, the results of this study suggest that changes in parental care enables the reversal of poor
344 developmental environments.

345 Parental care, and behavior more broadly, is often hypothesized to act as a buffer on both
346 ecological and evolutionary timescales (Huey et al. 2003; Duckworth 2009; Muñoz and Losos 2018).
347 Parental care strategies show tremendous variation across taxa (Brockmann 1997; Scott 1998a; Mank
348 et al. 2005; Cockburn 2006; Benowitz et al. 2016; Potticary and Duckworth 2021) and have arisen
349 across a wide diversity of ecological conditions (Wilson 1975; Jetz and Rubenstein 2011). Our results
350 may provide one explanation for why there can be so much variation in parental care (e.g., Meierhofer
351 et al. 1999) given its importance to offspring development (Royle et al. 2016). It has been broadly
352 suggested that variable environments are expected to produce systems that have greater flexibility, in
353 order to maintain consistent function across changing environments (Kitano 2004; Kashtan and Alon
354 2005; Kashtan et al. 2007; Chenard and Duckworth 2021). That is, environments that are challenging
355 in many ways may require flexible parental care to maintain consistent function, such as large offspring
356 body size, across environments. *N. orbicollis* live in highly heterogenous and variable environments

357 (Collard et al. 2021; Wettlaufer et al. 2023; Potticary et al. in press), larger beetles win access to
358 carcasses (Robertson 1993; Creighton 2005; Schrempf et al. 2021), and larger *Nicrophorus* species are
359 more likely to show obligate care (Jarrett et al. 2017). Together, this may indicate that the great
360 variation observed both in how individual burying beetles show care (Scott 1998b; Meierhofer et al.
361 1999) and who shows care (e.g., uniparental to biparental to communal; Trumbo 1992; Scott 1998a;
362 Benowitz et al. 2016) may emerge from selection for consistency of offspring phenotypes relative to
363 the prevailing environmental context (Creighton 2005).

364 Organisms are not passive recipients of the environment, but rather influence their environment
365 in the short term and evolve in response to social and ecological conditions in the long term (Lewontin
366 1983). We found that removing parental care induced strong changes in traits associated with fitness.
367 Offspring that received poor parenting responded by increasing uniparental care when they became
368 parents and shifting the type of nutrient-transfer behavior they showed, resulting in the amelioration of
369 poor developmental environments experienced by parents. Parenting may be an effective evolutionary
370 mechanism for buffering poor past and present environments, including those imposed during the
371 parents' development. This buffering may be enabled by dynamic changes in the units of parental care
372 – the component behaviors themselves.

373

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375

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380

Author Contributions

ALP and AJM conceived of study and developed methods. ALP, AJM, and CBC collected life history data. ALP conducted behavioural observations. AJM performed statistical analyses. ALP and AJM created figures. ALP, AJM, and CBC all contributed to writing and editing the manuscript. ALP was funded by a USDA cooperative agreement to AJM.

Data Accessibility

The data underlying this article are available in the Dryad Digital Repository (doi: pending).

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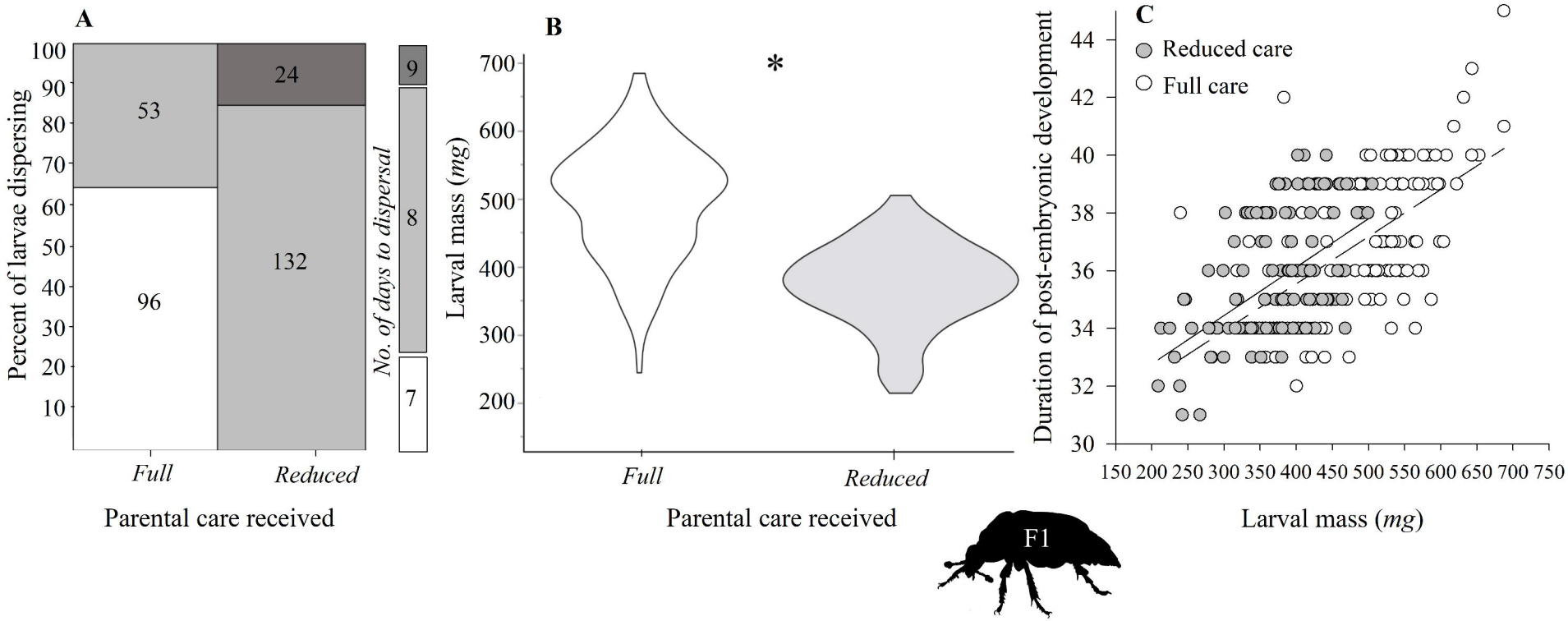
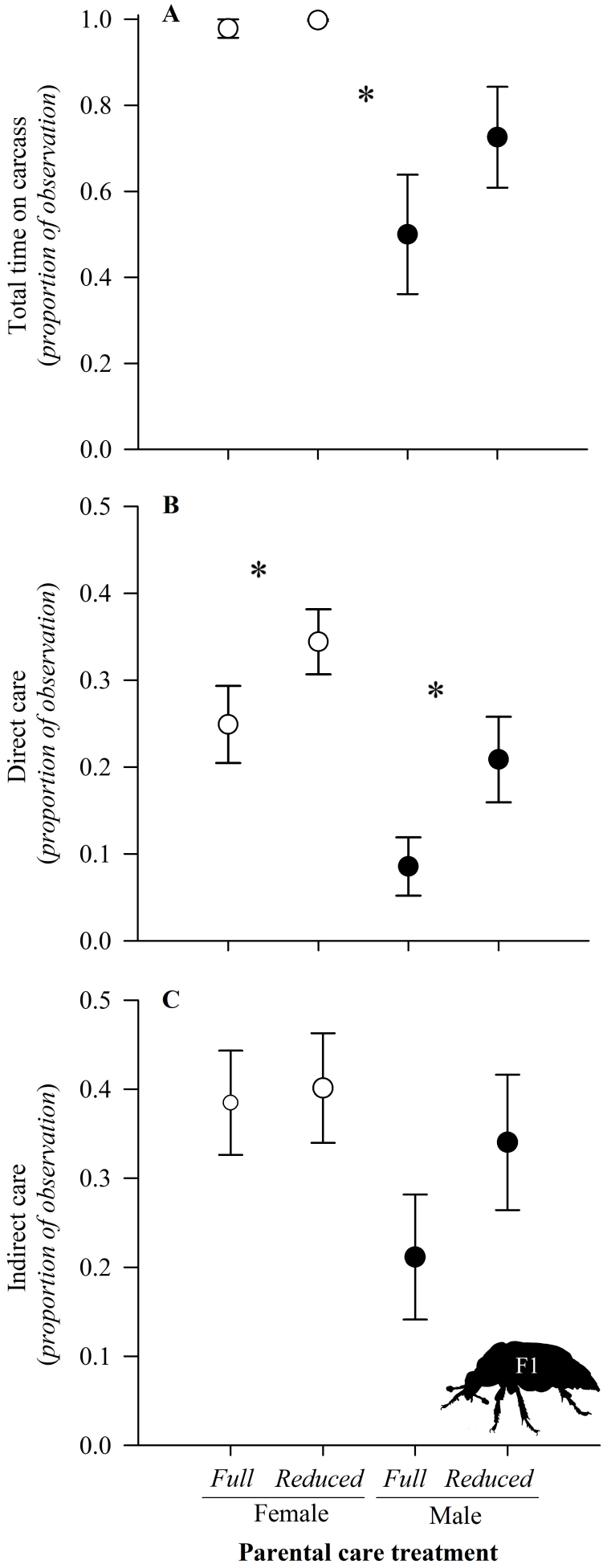
Figure legends

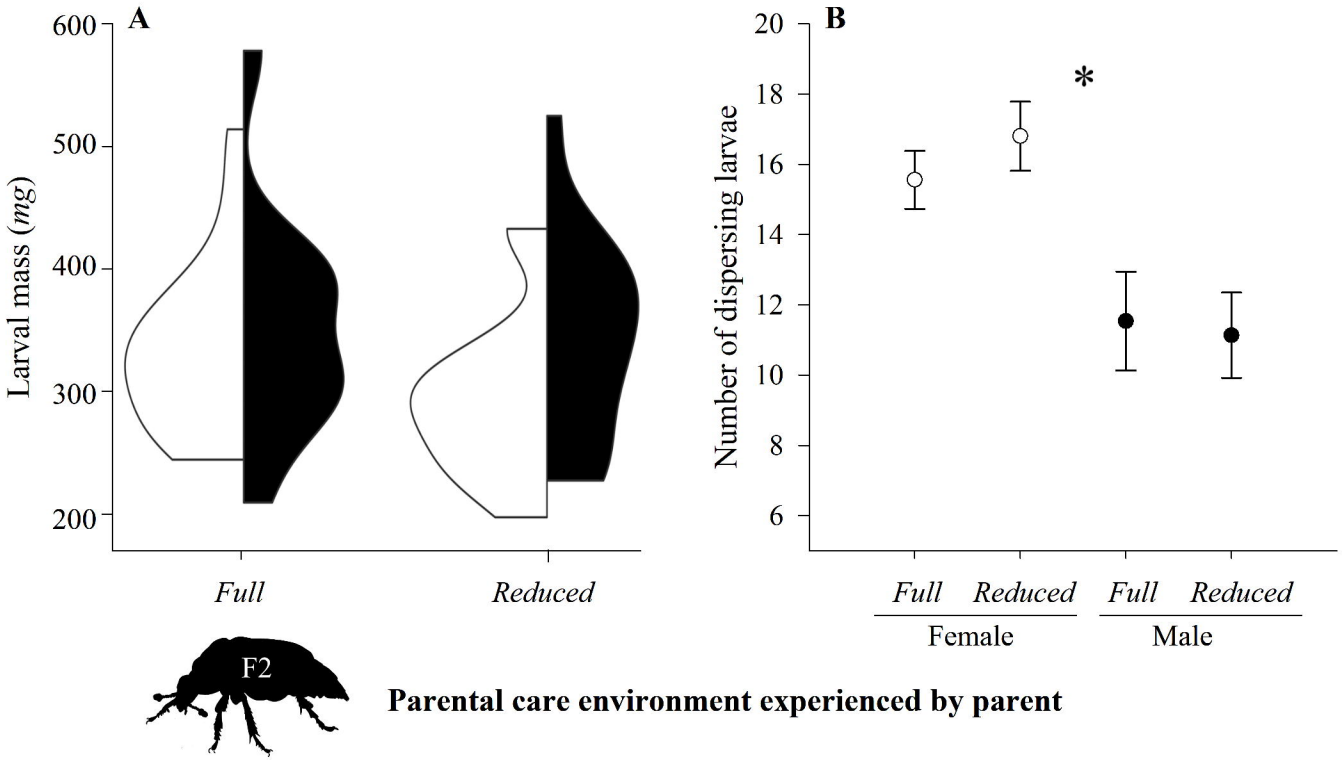
Figure 1. Care influences larval developmental time and size. ***(A)*** Mosaic plot indicating the percent of larvae dispersing from the carcass after 7, 8, or 9 days (white, light grey, or dark grey, respectively). Larvae that received full care developed faster on the carcass than larvae receiving reduced care. Sample sizes noted within mosaic plot. ***(B)*** Violin plot of distribution of final larval weight between individuals that received the full or reduced care treatment (Full care: N = 149, Reduced care: N = 156). Asterisks indicate statistically significant contrasts ($P < 0.05$). ***(C)*** Duration of larval period (in days) from larval hatch until ecolsion, or emergence of adult beetles, was statistically dependent on larval weight at dispersal and not on care treatment (N = 233). Grey circles and solid line refer to larvae that received reduced care, while open circles and the dashed line refer to individuals that received full care.

Figure 2. Parental behavior of females and males affected by the care they received as larvae. ***(A)*** Females spent more time on the carcass during the observation period than did males regardless of how much care they received. In addition, ***(B)*** both females and males that experienced reduced care increased the amount of direct care given to their offspring but ***(C)*** not indirect care. Error bars are

589 mean ± SEM. N = 15 observations for all treatments except Full care males, where N = 14 observations.
590 Asterisks indicate statistically significant contrasts ($P < 0.05$).
591
592 **Figure 3. Sex of parent influences offspring outcomes but not the parental developmental**
593 **environment.** ***(A)*** Violin plot of average larval mass for female (open violin) or male parents (closed
594 violin) that received full or reduced care. There was no statistically significant effect of caregiver sex,
595 the care they received as a larva, or their interaction, on larval mass. (***B)*** Females reared more offspring
596 than did males, but there was no effect of parental treatment on the number of offspring reared. Namely,
597 the care a parent received as a larva did not result in negative effects on grandoffspring. Full care males:
598 N = 13 breeding attempts, full care females: N = 18, and N = 15 for both reduced care males and
599 females. Female data are indicated with open circles, while male data are closed circles. Error bars are
600 ± SEM. Asterisks indicate statistically significant contrasts ($P < 0.05$).
601


A
Percent of larvae dispersing
100
90
80
70
60
50
40
30
20
10
53
24
96
132
9
8
7
No. of days to dispersal
Full
Reduced
Parental care received
B
Larval mass (mg)
700
600
500
400
300
200
*
Full
Reduced
Parental care received
C
Reduced care
Full care
Duration of post-embryonic development
44
42
40
38
36
34
32
30
150 200 250 300 350 400 450 500 550 600 650 700 750
Larval mass (mg)
F1


A
Total time on carcass
(proportion of observation)
1.0
0.8
0.6
0.4
0.2
0.0
*
B
Direct care
(proportion of observation)
0.5
0.4
0.3
0.2
0.1
0.0
*
*
C
Indirect care
(proportion of observation)
0.5
0.4
0.3
0.2
0.1
0.0
F1
Full
Reduced
Full
Reduced
Female
Male
Parental care treatment


A
600
500
400
300
200
Larval mass (mg)
Full
Reduced
B
20
18
16
14
12
10
8
6
Number of dispersing larvae
*
Full
Reduced
Full
Reduced
Female
Male
F2
Parental care environment experienced by parent