

1 Title:

2 Social interactions within the family enhance the
3 capacity for evolutionary change

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33 Abstract:

34 Classical models of evolution seldom predict evolution in the wild. One explanation is
35 that the social environment has important, yet overlooked, effects on how traits
36 change in response to natural selection. We tested this idea with selection experiments
37 on burying beetles (*Nicrophorus vespilloides*), sub-social insects that exhibit
38 biparental care. Populations responded to selection for larger adults only when parents
39 cared for their offspring, and responded to selection for smaller adults only when we
40 prevented parents from providing care. Comparative analyses revealed a similar
41 pattern: evolutionary increases in species size within the genus *Nicrophorus* are
42 associated with the obligate provision of care. Synthesising our results with previous
43 studies, we suggest that cooperative social environments enhance the response to
44 selection whereas conflict can prevent further directional selection.

45

46 Main text:

47 Predicting the rate at which populations can evolve and adapt in a rapidly changing
48 world is a major challenge for evolutionary biology¹. A key problem is to explain how
49 rapidly traits change in response to selection. The breeder's equation summarizes
50 classical genetic models of evolution by suggesting that the magnitude of
51 evolutionary change in any given trait depends simply on the extent to which that trait
52 contributes to fitness (the strength of selection), and the degree to which it is
53 transmitted to the next generation by genetic variation (the trait's heritability)². Yet
54 these two parameters are seldom sufficient to predict how evolution will proceed in
55 the wild^{3,4}. One suggestion is that this is because the social environment has an
56 additional causal influence on the response to selection⁵⁻⁹. An individual's social
57 environment derives from its interactions with conspecifics. Variation in the social
58 environment can contribute to variation in an individual's phenotype, much as the
59 abiotic environment does^{10,11}. An important difference, though, is that there is genetic
60 variation in the social environment. This means that the social environment can be
61 inherited and can therefore change the response to selection of the traits that it
62 induces⁶⁻⁹.

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64 Specifically, mathematical analyses show that when there is a large and positive effect
65 of the social environment on trait expression, it increases a trait's response to

66 selection and accelerates evolutionary change. But if the effect of the social
67 environment is negative, it prevents any response in the trait to selection and impedes
68 evolutionary change^{6-9,12-16}. Previous experiments with domesticated species have
69 supported that latter prediction by showing that competitive interactions can prevent
70 selection for traits of greater economic value to farmers, such as increased body
71 size¹³⁻¹⁷. However, it is unclear whether the social environment can ever causally
72 accelerate trait evolution in animal populations. Nevertheless, theoretical work⁶⁻⁹ and
73 correlational analyses of the outcome of natural selection using large pedigreed
74 datasets collected from wild animals, both suggest it is likely¹⁸.

75

76 We tested whether the social environment within the family can promote the
77 evolution of burying beetle size (*Nicrophorus vespilloides*) using experiments on
78 wild-caught individuals. This species exhibits facultative biparental care, which
79 makes it ideal for experimental manipulations of the social environment (e.g. ref. 19).
80 Both parents work together to prepare the carrion nest by removing the fur or feathers
81 from the dead body, rolling the flesh into a ball and burying it underground. Larvae
82 hatch from eggs laid in the soil nearby and crawl to the carcass nest, where they take
83 up residence. There they feed on the flesh themselves, but are also tended by their
84 parents who guard them and transfer resources through regurgitation²⁰. However, if
85 parents are removed after nest preparation is complete, but before the larvae hatch,
86 then larvae can complete development without any post-hatching parental care at
87 all^{19,21}. After roughly five days, larvae disperse away from the carcass to pupate in the
88 soil.

89

90 We focused on the evolution of adult size for three reasons. First, size is strongly
91 associated with fitness in this species²⁰. Competition for the carrion breeding resource
92 can be intense, and larger beetles are more likely to win fights for ownership of
93 carcass (e.g. ref. 22). Second, adult size is known from previous work to vary with
94 aspects of the family social environment that larvae experience during development,
95 including social interactions with siblings²³ and parents²¹. Third, we found that the
96 heritability of adult size is very low. We used techniques from classical quantitative
97 genetics to estimate the heritability of adult size, in environments where parents
98 provided post-hatching care for offspring (hereafter Full Care), and in environments

99 where they provided no post-hatching care, because they were experimentally
100 removed (hereafter No Care). In both environments, the heritability of adult body size
101 did not differ from zero (estimate \pm s.e., Full Care: $h^2 = 0.08 \pm 0.12$; No Care: $h^2 =$
102 0.05 ± 0.30 , see Supplementary Materials). These estimates are similar to estimates
103 of the heritability of adult size in the congeneric *N. pustulatus*²⁴. The breeder's
104 equation² therefore predicts that body size should exhibit negligible change in
105 response to selection in the short term. This gave us the opportunity to separate the
106 effect of the social environment on the way in which body size responds to selection
107 from effects due to the heritability of body size alone (because the latter should be
108 virtually non-existent).

109
110 To test whether the social environment causally influences the response to selection,
111 we carried out an artificial selection experiment on eight laboratory populations (see
112 Methods). Importantly, we varied the social environment among the populations so
113 that we could analyse its causal influence on the response to selection: half the
114 populations experienced Full Care during development ($N = 4$ populations), the other
115 half had No Care ($N = 4$ populations). We then exposed half of the populations within
116 each Care environment to selection for increased adult body size (Large), while the
117 remaining populations experienced selection for decreased adult body size (Small, see
118 Methods). Thus we had four types of experimental populations, each replicated twice:
119 Full Care Large, Full Care Small, No Care Large, and No Care Small. We selected on
120 body size for seven generations, generating over 25,000 beetles.

121
122 For each experimental treatment, we measured the cumulative selection differential
123 and response to selection, and used these measures to estimate the realised heritability
124 of adult body size (see Methods). This gave us a measure of the extent to which body
125 size could be changed by artificial selection. The breeder's equation predicts that the
126 realised heritability of body size should not differ among the treatments. However, we
127 found instead that the realised heritability of adult body size varied among the four
128 types of experimental treatments (care \times selection \times cumulative selection differential:
129 $F_{3,44} = 6.87$, $P < 0.001$, Fig. 1). Furthermore, the realised heritability of body size was
130 relatively high, and significantly different from zero, for the Full Care Large
131 treatment (0.090 ± 0.021), where mean body size increased across the generations,

132 and for the No Care Small treatment (0.105 ± 0.033), where mean body size
133 correspondingly decreased. For these two treatments we therefore conclude that the
134 social environment during development enhanced the capacity for evolutionary
135 change in adult body size, and to a similar degree whether selection was for increased
136 or decreased body size.

137

138 By contrast, in the Full Care Small and the No Care Large treatments, the realised
139 heritability of adult body size was not significantly different from zero (Full Care
140 Small: -0.008 ± 0.023 ; No Care Large: 0.014 ± 0.033). Mean adult body size did not
141 change over the course of the selection experiment for individuals from either of these
142 treatments (Fig. 1).

143

144 The next step was to determine how the two contrasting social environments in our
145 selection experiment could influence evolutionary change in adult size. Previous work
146 has shown that the mass a larva attains by the time it disperses away from the carcass
147 strongly influences the size of the adult that then emerges²⁵. Furthermore, larval mass
148 at dispersal depends on the number of larvae competing during development for the
149 finite resources on a carcass²³. Building on these results, we identified three social
150 factors that influence larval mass at dispersal. The first is clutch size, because it
151 influences the number of larvae competing for carrion. However, it is not the sole
152 determinant of brood size on a carcass. Larger females lay a larger clutch²⁶ but have
153 fewer surviving larvae that disperse from the carcass (see Methods, Supplementary
154 Fig. 1), presumably due to a greater incidence of filial cannibalism²⁷. Brood size at
155 dispersal is therefore different from clutch size, and is the second factor influencing
156 larval mass at dispersal. The third factor is the presence or absence of parents after
157 hatching. This factor is important because it influences the relationship between brood
158 size and larval size at dispersal, especially for broods of 10 or fewer larvae. When
159 parents are present, and there are only a few larvae on the carcass, each consumes
160 more carrion and is larger at dispersal²³. However, when parents are absent, each larva
161 typically attains only a low mass by the time it disperses to pupate, because larvae
162 seemingly help each other to colonize and consume the carcass²³. Thus larvae in small
163 broods cannot attain a large mass at dispersal when parents are absent, but they can
164 when parents are present.

165

166 We suggest that selection on these three elements of the social environment combined
167 to cause correlated change in body size in the Full Care Large lines and the No Care
168 Small lines (see Supplementary Materials). In the Full Care Large treatment (Fig. 2a),
169 we selected for larger adults. They produced larger clutches (Supplementary Fig. 2),
170 but produced fewer (Supplementary Fig. 3) and therefore larger dispersing larvae
171 (presumably due to greater levels of filial cannibalism). They matured into larger
172 adults themselves. Likewise, in the No Care Small treatment (Fig. 2b) we selected for
173 smaller adults and they laid a smaller clutch (Supplementary Fig. 2). Since these
174 broods developed without parents, the resulting smaller broods yielded smaller larvae
175 (Supplementary Fig. 3), which matured into smaller adults. In each treatment, we
176 effectively selected a social environment on the carcass that induced the production of
177 more individuals with either a larger (Full Care Large) or smaller (No Care Small)
178 body size. Furthermore, these selected individuals then produced a similar social
179 environment for their offspring. This explains why these lines responded to selection
180 on body size, despite the very low heritability of body size.

181

182 We observed very little change in body size in the other experimental populations (No
183 Care Large, Full Care Small). This was predicted by the classical estimates of
184 heritability, but it might also be attributed to effects of the social environment, which
185 could have cancelled out the effects of selection at each generation (see ref. 28). For
186 example, in the No Care Large treatment (Fig. 2c), selecting for larger adults yielded
187 smaller individuals in the next generation. The larger adults laid a larger clutch
188 (Supplementary Fig. 2), but with no parents present after hatching to cannibalize
189 offspring, these larger clutches yielded relatively large broods (Supplementary Fig. 3)
190 of smaller larvae, which matured into smaller adults. Similarly, in the Full Care Small
191 treatment (Fig. 2d) selection for smaller adults yielded larger adults in the following
192 generation. The smaller adults laid a smaller clutch (Supplementary Fig. 2), which in
193 turn yielded a smaller brood (Supplementary Fig. 3) of relatively large larvae that
194 matured into large adults.

195

196 We explicitly tested the conclusions set out in Fig. 2, by comparing the slope of the
197 regression between dam size and progeny size (see Supplementary Materials). Fig. 2a

198 and 2b predict that in the Full Care Large and No Care Small treatment, this
199 correlation should be positive, whereas Fig. 2c and Fig. 2d predict it should be
200 negative in the No Care Large and Full Care Small treatment. We found that the
201 slopes of these correlations differed significantly among treatments (care \times selection
202 \times dam pronotum: $\chi^2_1 = 4.13$, $P = 0.042$). The slopes were positive in the Full Care
203 Large (0.134 ± 0.090) and No Care Small treatments (0.094 ± 0.079). However,
204 although they were negative in the Full Care Small treatment (-0.059 ± 0.064), as we
205 predicted, they were positive in the No Care Large treatment (0.117 ± 0.098), which
206 we did not predict.

207
208 Our experiments thus find no clear evidence to support the suggestion that the social
209 environment within the family alone prevented evolutionary change in the Full Care
210 Small and No Care Large treatments. They do, however, show that social interactions
211 within the family enhanced the response to selection in the Full Care Large and No
212 Care Small treatment. More specifically, our experiments indicate that parental care is
213 essential to promote a rapid evolutionary increase in body size in *N. vespilloides*.

214
215 We tested the merits of this conclusion in a final comparative analysis across the
216 *Nicrophorus* genus, to link our experimental results back to the natural world (see
217 Methods). Different species of burying beetle are remarkably alike in their ecology
218 and appearance²⁹. They differ principally in their relative size and in the extent to
219 which parental care is essential for larval growth and survival³⁰. Observations of
220 natural burying beetle populations show that adult size is correlated with variation in
221 the size of carrion used by different species for reproduction²⁰. Variation in adult body
222 size is correlated with the partitioning of the carrion niche by sympatric species, and
223 enables larger species to favor larger carrion and smaller species to breed on smaller
224 carcasses²⁰. We mapped the changes in adult body size across the *Nicrophorus* genus
225 by measuring museum specimens of 49 of the 68 extant species²⁹ and placing them on
226 a recent molecular phylogeny of the genus (Fig. 3)³⁰. We found that there is
227 considerable variation in body size across the phylogeny, with multiple shifts to both
228 larger and smaller species relative to the ancestral phenotype (Fig. 3). Consistent with
229 our experimental results, we also found that the evolution of very large burying
230 beetles is associated with obligate provision of parental care (PGLS: estimate = $1.57 \pm$

231 0.66, $t_{12} = 2.40$, $P = 0.035$).

232

233 We conclude that the way in which the social environment influences a trait's
234 response to selection depends on whether it is associated with social interactions that
235 are cooperative or promote conflict (see ref. 10 for formal definitions of these terms).
236 Previous studies have shown that selection for increased size or productivity also
237 selects for increased aggression. Increased aggression reduces fitness so much that
238 any effects of selection on size cannot be transmitted to the next generation and this
239 prevents evolutionary change^{13,17}. This suggests that traits associated with social
240 environments that induce conflict have limited capacity for further directional
241 evolutionary change. Previous work has also demonstrated that, under these
242 conditions, the only way in which increased productivity or size can be artificially
243 selected is by imposing multilevel, group or kin selection^{12,13}. That is, a response to
244 selection can be restored only when an explicitly cooperative social environment is
245 artificially created at the same time³². Our experiment provides more direct evidence
246 that cooperative interactions enhance the response to selection, and can do so even
247 when selection acts on individuals. In the Full Care Large treatment, selection for
248 increased body size was possible because parents helped small broods of larvae to
249 attain a large size at dispersal. Likewise, in the No Care Small treatment (Fig. 2)
250 selection for decreased body size was possible because cooperative interactions
251 among larvae influence body size²³: in this case, selection for smaller individuals
252 decreased brood size and the fewer remaining larvae were increasingly unable to help
253 each other grow large. In short, cooperative interactions reinforced selection by
254 magnifying changes in body size across generations, so enhancing the capacity for
255 evolutionary change. Our general conclusion is that the response to selection is likely
256 to be reduced when trait expression is associated with conflict, but enhanced for traits
257 whose expression is associated with more cooperative social environments. Proper
258 characterization of the social environment in which traits are expressed is therefore
259 important not only for understanding a trait's current adaptive value¹⁰ but also for
260 predicting its future capacity to evolve and adapt.

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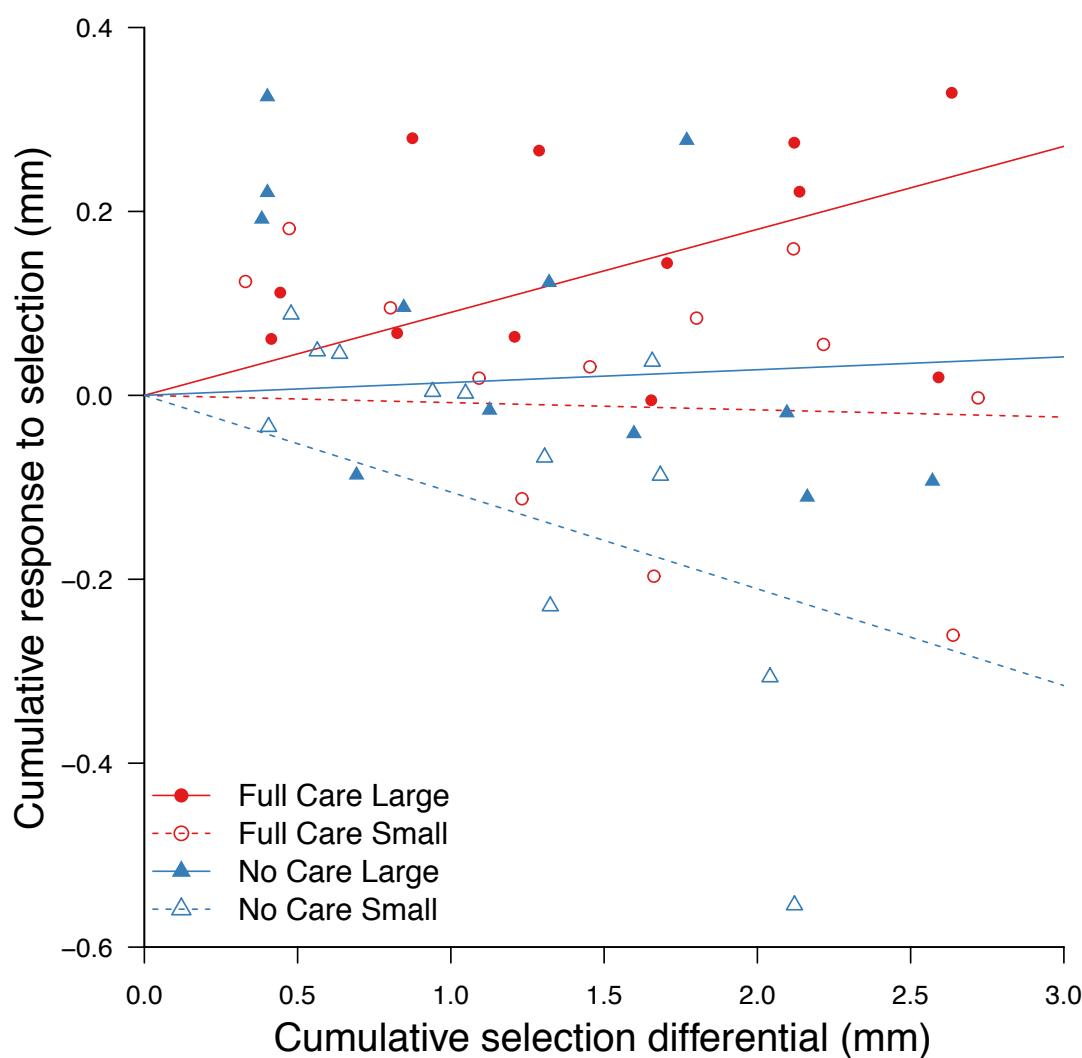
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405 Duarte and O. de Gasperin helped in the laboratory.

406

407 **Figures**

408 **Figure 1**

409 The realised heritability of body size, as a function of the different selection regimes
410 and social environments. The realised heritability is given by the regression slopes,
411 forced through the intercept. For each treatment the gradient of these regression lines
412 \pm S.E are: Full Care Large, 0.090 ± 0.021 ; Full Care Small, -0.008 ± 0.023 ; No Care
413 Large, 0.014 ± 0.033 ; No Care Small, -0.106 ± 0.033 . The cumulative selection
414 differential is the difference between the population mean and the mean of the
415 retained subset of the population. This is summed across the seven generations. The
416 cumulative response to selection is the difference between the mean of the population
417 and the mean of the population in the subsequent generation, and is also summed. The
418 two replicates for each treatment were pooled for the regression, as they did not differ
419 (see Supplementary Materials).

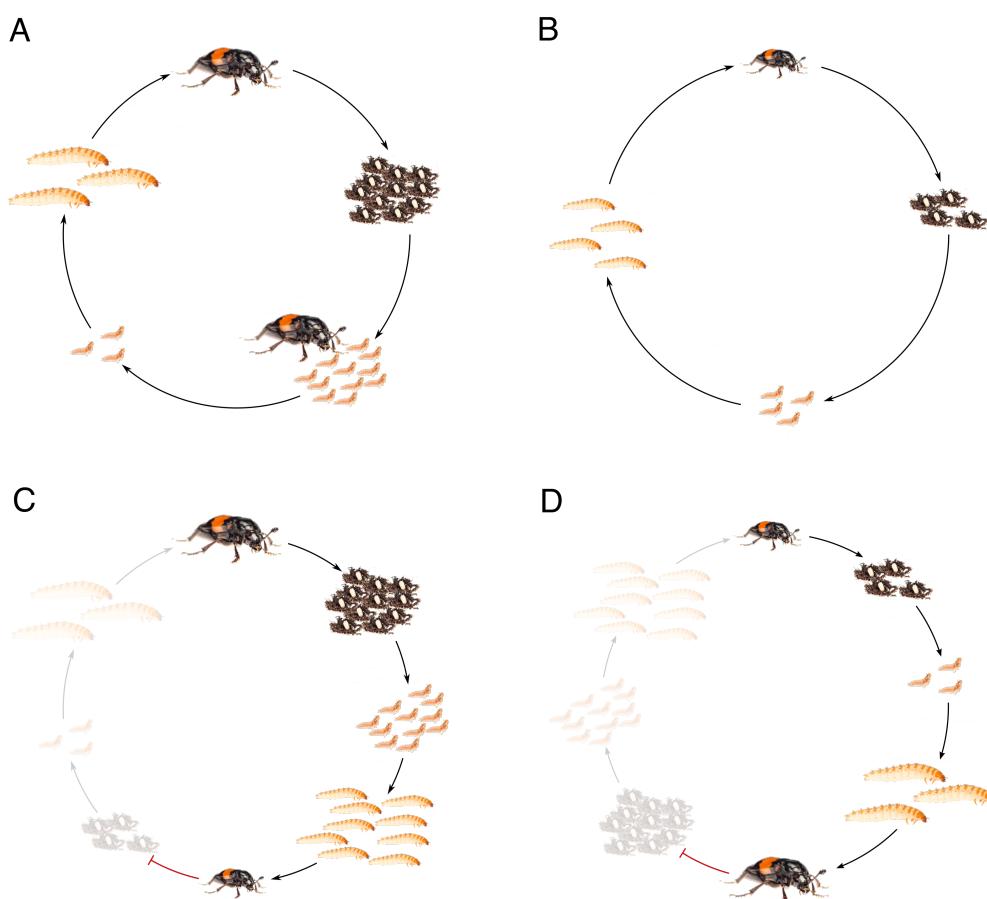


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421

422 Figure 2

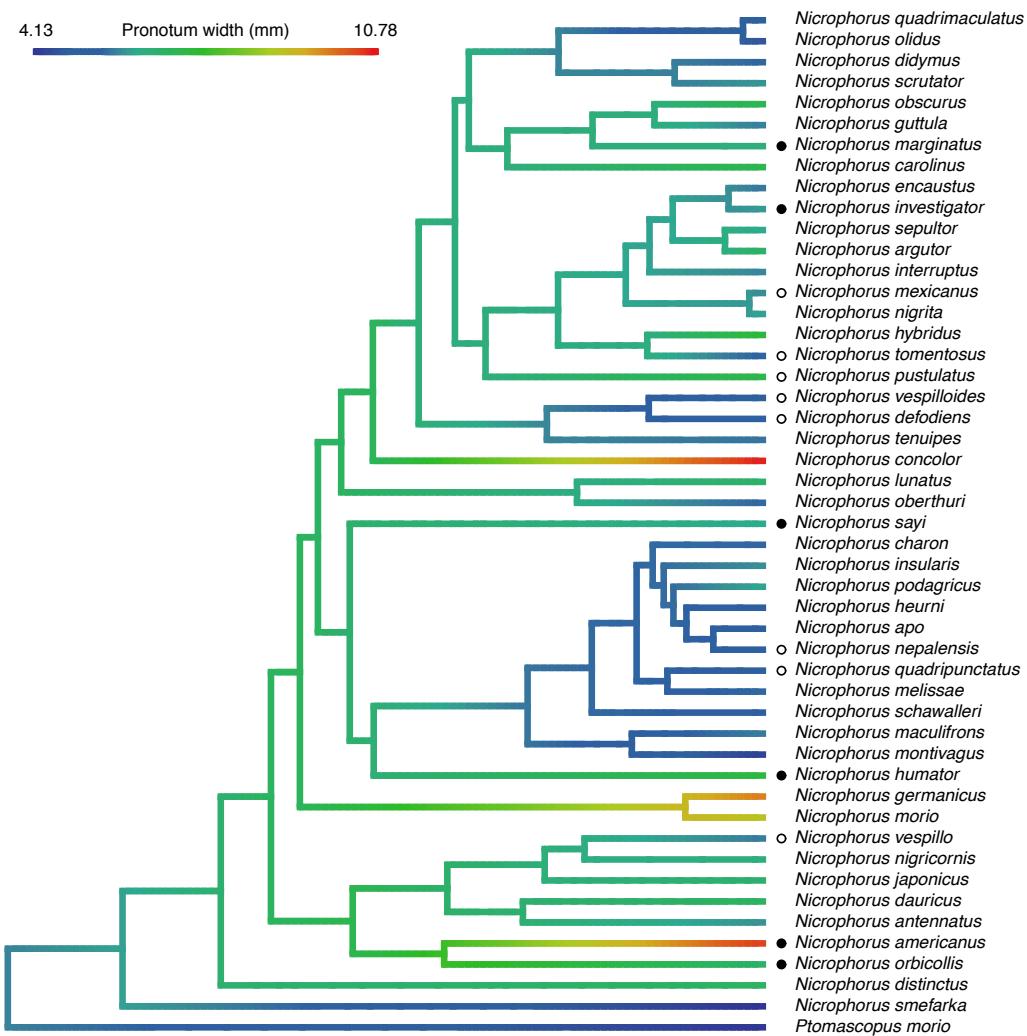
423 The effect of the social environment on the response to selection, in each of the
424 experimental treatments. (A) and (B) show how the social environment enhances the
425 capacity for evolutionary change; (C) and (D) show how the social environment could
426 prevent evolutionary change. (A) Full Care Large: large beetles lay many eggs, but
427 are more likely to cannibalize larvae and so have relatively small broods that yield
428 large larvae, which mature in large adults. (B) No Care Small: small beetles lay fewer
429 eggs, which yield a small brood of small larvae that mature into small adults. (C) No
430 Care Large: large beetles lay many eggs, which yield a larger brood of small larvae
431 that mature into small adults and are selected out of the experimental population; and
432 (D) Full Care Small: small beetles lay fewer eggs which yield a small brood of large
433 larvae that mature into small adults and are selected out of the experimental
434 population.



435
436
437

438 Figure 3

439 Adult pronotum width of burying beetle species mapped on an existing molecular
440 phylogeny³¹. Black circles indicate species with obligate post-hatching parental care;
441 open circles indicate facultative post-hatching parental care. Species with missing
442 data for parental care have no symbols. Body size data can be found in Supplementary
443 Table 2. Information regarding parental care can be found in Supplementary Table 3.



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451 **Materials and Methods**

452 The burying beetle genus *Nicrophorus* is distributed primarily throughout the
453 temperate regions of the Northern Hemisphere²⁹. So far as is known, the natural
454 history and reproductive biology of all *Nicrophorus* species are broadly similar^{20,29,31}
455 and centre on the use of small carrion as a breeding resource²⁰. Although the two other
456 extant genera in the Nicrophorinae also use carrion for reproduction, they lack the
457 elaborate parental care exhibited by *Nicrophorus* species and the associated social
458 interactions that it generates^{31,33}. These genera are also less speciose than
459 *Nicrophorus*: there are 68 known species in *Nicrophorus*, one in *Eonecrophorus* and
460 three in *Ptomascopus*²⁹. This suggests there is a correlation between the social
461 environment during development and the capacity for diversification in each of these
462 lineages.

463

464 **Estimating the heritability of body size in *N. vespilloides***

465 *Cultivating N. vespilloides in the lab*

466 All the individuals used in this experiment belonged to a captive colony (kept at a
467 constant temperature: 21°C, with a 16h:8h light:dark cycle) established at the
468 University of Cambridge in 2013 from wild-caught adults collected under licence
469 from local field sites at Byron's Pool and Wicken Fen in Cambridgeshire, U. K.
470 Adults were housed individually in plastic boxes (12 × 8 × 2cm) filled with moist soil
471 (Miracle Grow) and fed twice a week with ~0.3g of minced beef. For breeding, pairs
472 of unrelated individuals were placed into larger plastic boxes (17 × 12 × 6cm) half-
473 filled with moist soil, provided with a 8–13g freshly thawed mouse carcass and kept
474 in the dark to simulate natural underground conditions. The larvae disperse from the
475 carcass to pupate roughly eight days after pairing. Dispersing larvae were transferred
476 into population boxes (10 × 10 × 2cm), each subdivided into equal cells of 2 × 2 ×
477 2cm and filled with soil. Once pupation was complete (approximately 3 weeks after
478 dispersal), each sexually immature adult was moved to its own individual, uniquely
479 labeled box. Sexual maturity is reached approximately two weeks after eclosion, and
480 beetles were paired for reproduction at this time. No siblings or cousins were paired
481 for breeding.

482

483 *Methods*

484 We performed a full-sib/half-sib quantitative genetics experiment to estimate the
485 heritability of body size in *N. vespilloides*. We used two populations of beetles for this
486 experiment, both maintained under the same conditions as stock populations (Full
487 Care) for 11 generations without any selection for body size. Four females were
488 mated to a single male and then each female was given a recently defrosted mouse
489 (10–12g) to breed upon. Once the carcass had been prepared and all eggs laid,
490 approximately 53h after providing the mouse³⁴, the female and carcass were removed.
491 The female was placed in a new breeding box and provided with a fully prepared
492 carcass from a donor female. At that time we also prepared an equal number of
493 breeding boxes with just a donor-prepared carcass and no female. The breeding box
494 where the female laid her eggs was checked three times a day for larval hatching.
495 Once larvae started hatching, the larvae were transferred to either the carcass with
496 their mother (Full Care) or to the other carcass without an adult (No Care). Larvae
497 were added until a maximum of 12 larvae were present on each carcass, resulting in
498 mean (\pm s.e.) brood sizes of 7.85 ± 0.25 in the Full Care, and 8.21 ± 0.24 in the No
499 care environments.

500
501 We checked breeding boxes three times daily, and determined that the larvae were
502 ready to disperse when two or more larvae were seen crawling away from the remains
503 of the carcass²⁴. At this point the contents of the breeding box were removed and the
504 larvae were counted and weighed individually. The larvae were then placed into
505 individual cells within an eclosion box in the order in which they were weighed so we
506 could relate larval mass to adult size. After eclosion, we anaesthetized the adults with
507 CO₂. Once anaesthetized, each individual was placed flat under a Canon DSLR
508 camera and photographed. The camera was attached to a stand to ensue consistency in
509 the images obtained and connected to a computer for automatic image labeling. All
510 photographs contained a scale against which the pronotum width of each individual
511 was measured using a custom MatLab script. No statistical methods were used to
512 predetermine sample size.

513
514 We analyzed data for each care regime separately, using the package ASreml-R 3.0³⁵
515 in R version 3.3.0³⁶. Models included a fixed effect of the number of larvae surviving
516 per brood (mean-centered), a random effect of brood ID to estimate variance due to

517 permanent environmental (including maternal) effects, and a random effect of the
518 pedigree term to estimate the additive genetic variance. (We were unable to partition
519 variance due to maternal effects from that of the permanent environment because no
520 females had multiple broods within a single environment). We then tested the
521 significance of the additive genetic variance in adult size by comparing models with
522 and without the pedigree term using a likelihood ratio test. We estimated χ^2_{nDF} as
523 twice the difference in model log likelihoods; given that we were testing the effect of
524 a single variance component ($nDF = 1$), we assumed that the test statistic was
525 asymptotically distributed as an equal mix of χ^2_0 and χ^2_1 (ref. 37). The heritability of
526 adult size was calculated as V_A / V_p where V_p is the sum of the variance components
527 (additive genetic, permanent environment, and residual) from the model, having
528 conditioned on the fixed effects. We used Wald F -tests to estimate the significance of
529 fixed effects.

530

531 *Results*

532 The experiment yielded 186 maternal full-sib families and 56 paternal half-sib
533 families in the Full Care environment, and 84 maternal full-sib families and 22
534 paternal half-sib families in the No Care environment. Mean (\pm s.e.) brood size in the
535 Full Care was 7.69 ± 0.24 and 5.31 ± 0.30 in the No Care.

536

537 We found no evidence for significant additive genetic variance in adult size in either
538 the Full Care ($V_A = 0.013 \pm 0.021$, $\chi^2_{0,1} = 0.46$, $P = 0.25$) or No Care ($V_A = 0.008 \pm$
539 0.045 , $\chi^2_{0,1} = 0.03$, $P = 0.43$, Supplementary Table 1) environments. The heritability
540 estimates of adult size were correspondingly close to zero, with large standard errors
541 ($h^2_{Full} = 0.08 \pm 0.12$; $h^2_{No} = 0.05 \pm 0.30$). Permanent environment effects (ie effects of
542 the Care treatment and brood size) explained a significant amount of the total
543 phenotypic variation in adult size (conditional on fixed effects) in both Full Care (V_{PE}
544 $= 0.046 \pm 0.012$, $\chi^2_{0,1} = 16.22$, $P < 0.001$; proportion of total phenotypic variance
545 conditional on fixed effects $= 0.263 \pm 0.065$) and No Care ($V_{PE} = 0.054 \pm 0.025$, $\chi^2_{0,1}$
546 $= 6.05$, $P = 0.007$; proportion $= 0.361 \pm 0.157$) environments. For completeness, we
547 ran the same models without any fixed effects (see ref. 38), but this had no
548 meaningful effect on our results.

549

550 **Selection experiment**

551 One way to analyse the effect of the social environment on the response to selection is
552 to use cross-fostering to partition out sources of variance in body size to direct, sib-
553 social, or maternal effects³⁹⁻⁴¹ and thereby deduce the underlying genetic architecture.
554 However, the downside of this approach is that it requires detailed knowledge of
555 precisely how the social environment influences trait expression: if one key element is
556 overlooked then the analyses are too incomplete to be able to predict the response to
557 selection with any accuracy. For this reason, we chose instead to use an artificial
558 selection experiment. We manipulated the social environment, imposed selection and
559 measured the response. In this way we could confidently attribute any change in the
560 response to selection to our manipulations of the social environment, without making
561 any *a priori* assumptions about which particular aspects of the social environment
562 were important in influencing trait expression.

563

564 All the individuals used in the selection experiment belonged to a captive colony
565 established at Cambridge University in 2013 from wild caught adults collected under
566 licence from local field sites at Byron's Pool and Wicken Fen in Cambridgeshire,
567 U.K. Full details of the protocols used are given in (ref. 19).

568

569 *Methods*

570 From the genetically diverse founding population, we started eight populations
571 consisting of four treatments with two replicates per treatment, randomly allocating
572 individuals to treatments. We had two treatments, Provision of Care and Selection for
573 Size, resulting in a 2×2 factorial experiment. Provision of Care was manipulated by
574 either leaving or removing both parents 53 hours after pairing, after carcass
575 preparation and egg laying were complete³⁴, resulting in a Full Care treatment, and a
576 No Care treatment, respectively. We then imposed two selection regimes on the Full
577 Care and No Care populations: Large and Small. We selected the largest third of the
578 population with the Large regime, and the smallest third of the population under the
579 Small regime. Selection was imposed at the population level and not at the family
580 level. Once the population had been selected, individuals were paired haphazardly,
581 although we ensured cousins and siblings did not breed. All beetles were maintained
582 under the conditions described above. Each population was maintained with at least

583 25 families per generation, by breeding 40 pairs of beetles for the Full Care
584 populations and 60 pairs for the No Care populations. When it became impossible to
585 sustain populations of this size, the experiment ceased. (We bred extra pairs in the No
586 Care population to ensure there were enough successful families: failure rates are high
587 when initially removing parental care).

588

589 At eclosion members of the same sex from each family were temporarily housed in a
590 box together and anaesthetised with CO₂. Once anaesthetized, each individual was
591 photographed and the body size measured in the same method as described above.
592 Each individual was given a unique ID that we used to identify individuals that were
593 retained to breed in the next generation.

594

595 To estimate the potential for evolutionary change in body size in each population, we
596 calculated the realised heritability of body size, as the slope of the regression of the
597 cumulative response to selection against the cumulative strength of selection⁴². Post-
598 hoc pairwise comparisons were adjusted for multiple testing⁴³. No statistical methods
599 were used to predetermine sample size.

600

601 *Results*

602 The realised heritability did not differ significantly between replicate populations for
603 each treatment ($F_{40} = 2.08$, $P = 0.10$). Replicates were therefore pooled for all
604 subsequent analyses. After running the global model, we used pairwise comparisons
605 to compare measures of realised heritability across the different treatments. The Full
606 Care Large and Full Care Small treatments significantly differed from one another in
607 realised heritability ($F_{22} = 9.90$, $P_{adj} = 0.015$), as did the Full Care Large and No Care
608 Small ($F_{22} = 26.44$, $P_{adj} = 0.006$). There was marginal support for a difference in
609 realised heritability between Full Care Large and No Care Large ($F_{22} = 3.95$, $P_{adj} =$
610 0.072). Realised heritability in the No Care Small treatment differed significantly
611 from that in the Full Care Small ($F_{22} = 5.92$, $P_{adj} = 0.03$) and the No Care Large
612 populations ($F_{22} = 6.36$, $P_{adj} = 0.03$). The Full Care Small and No Care Large did not
613 differ from one another in their realised heritability ($F_{22} = 0.30$, $P_{adj} = 0.59$). Realised
614 heritability estimates for each population are in Supplementary Table 2.

615

616 **The effects of the social environment on adult size**

617 The social environment that larvae experience during development influences the size
618 the larvae attain by the time they disperse from the carcass and this, in turn, is
619 strongly correlated with adult size²⁵. Three factors contribute to this social
620 environment (see main text): clutch size, brood size at dispersal and the presence (or
621 absence) of parents during larval development²³. To understand how these different
622 elements of the social environment might have caused the outcome of the selection
623 experiment, we began by investigating how clutch size and brood size are related to
624 adult size.

625

626 *a) Relationship between female size and clutch size, or brood size at dispersal*

627 To assess the effect of female size on clutch size we analysed data from²⁶ where we
628 manipulated female size experimentally and destructively counted the total clutch size
629 for a breeding attempt after 53 hours when egg laying has ceased³⁴. Brood size data
630 were taken from a stock population maintained in the laboratory under the same
631 conditions as the Full Care populations, and assayed when the selected populations
632 were in generation five. Brood size was measured at the point of larval dispersal away
633 from the carcass. Both clutch size and brood size were analysed with a Poisson
634 distribution and a log link function with female size and carcass mass fitted as
635 covariates.

636

637 We found that clutch size increased with female size even when accounting for
638 carcass mass ($t = 3.63$, $P = 0.001$), whereas brood size at dispersal decreased with
639 female size ($t = -2.06$, $P = 0.04$, Supplementary Fig. 1).

640

641 The next step was to relate these effects of the social environment to the results of our
642 selection experiment. If the outcome of the selection experiment is attributable to
643 different elements of the social environment, then we predict we should see
644 divergence in clutch size, and brood size at dispersal among the different
645 experimental treatments.

646

647 *b) Measurement of clutch size in the experimentally selected populations*

648 Based on the results in Supplementary Fig. 1, we predict that clutch size should be

649 greater in populations where adults are selected to be larger (i.e. Full Care Large and
650 No Care Large) than in populations where adults are selected to be smaller (i.e. Full
651 Care Small and No Care Small). To test this prediction, we estimated clutch size in all
652 eight populations at generation five by counting the number of eggs visible on the
653 bottom of the breeding box. We know from previous work that this measure is
654 strongly correlated with total clutch size²⁶. We analysed estimated clutch size using a
655 generalised linear model with a Poisson error structure, and log link function. We
656 included carcass size as a covariate.

657

658 As predicted, we found that clutch size in generation five of the selection experiment
659 was greater in the Large selected lines than in the Small selected lines ($z = -7.53$, $P <$
660 0.001), independent of the parental care treatment ($z = 1.32$, $P = 0.19$, Supplementary
661 Fig. 2). There was no interaction between selection regime and parental care on clutch
662 size ($z = -0.38$, $P = 0.70$).

663

664 *c) Measurement of brood size in the experimentally selected populations*

665 We predicted that brood size at larval dispersal should also differ among the
666 experimental populations. Specifically, based on the results in Supplementary Fig. 1,
667 we predicted that members of the Full Care Large populations should have a smaller
668 brood size than members of the Full Care Small populations. In addition, since there
669 is no possibility of filial cannibalism in the No Care populations, we predicted that in
670 these populations brood size should vary in the same way as clutch size, and therefore
671 should be greater in the No Care Large populations than in the No Care Small
672 populations. We measured brood size at larval dispersal in Generation 7 of the
673 selection experiment and pooled both replicates. We analysed estimated brood size
674 using a generalised linear model with a Poisson error structure, and log link function,
675 and tested our prediction by searching for a significant interaction between parental
676 care (Full Care, No Care) and selection regime (Large, Small) on brood size at
677 dispersal. We included carcass size as a covariate.

678

679 As predicted, we found a significant interaction between parental care and selection
680 regime on brood size at larval dispersal in generation seven ($z = -4.89$, $P < 0.001$).
681 Full Care Large populations had fewer offspring at dispersal than the Full Care Small

682 populations, whereas No Care Large populations had more offspring at dispersal than
683 No Care Small populations (Supplementary Fig. 3).

684

685 *d) Testing predictions from Figure 3*

686 From Fig. 3, we predicted that the slopes of offspring size regressed against dam size
687 would differ among the experimental treatments. Specifically, we predicted that the
688 slope would be positive for the Full Care Large and No Care Small lines, because
689 these were the lines in which we observed phenotypic change. And we predicted that
690 the slope would be negative in the No Care Large and Full Care Small lines. We took
691 all the data from all the lines and combined both replicates per treatment for the seven
692 generations of the experiment.

693

694 We used R³⁶ and the package lme4⁴⁴ to run a linear mixed model, where we ran a
695 model coding the three-way interaction of Care treatment (Full Care or No Care),
696 selection regime (Large or Small) and dam pronotum width. Also included in the
697 model was carcass size and generation. Dam ID was fit as a random term.

698 Significance was determined by removing the three-way interaction from the model
699 and comparing the output with the full model. The slopes for each experimental
700 treatment were obtained in the same way, but with the appropriate subset of the data
701 for each experimental treatment.

702

703 **Phylogenetic analysis of body size**

704 We collected data on *Nicrophorus* body size using the beetle collections at the Natural
705 History Museum in London. We took standardized photographs of representatives
706 from all the *Nicrophorus* species included in a recently published molecular
707 phylogeny³¹, with a constant distance between subject and camera, and including a
708 scale-bar in each picture. There was no sexual size dimorphism in our dataset ($t = -$
709 1.453, $P = 0.15$). Therefore body size data from both sexes were pooled for each
710 species. We used the standard practice of quantifying body size by measuring
711 pronotum width, and used a MatLab script to calibrate photographic measurements of
712 pronotum width with the scale bar in each image, using the same method for both
713 experiments detailed above. The full datasets can be found in Supplementary Table 3.
714 Post-hatching parental care was classified as ‘facultative’ or ‘obligate’ using data

715 from the published literature and from personal communication with other burying
716 beetle researchers ($N = 14$ species, Supplementary Table 4). ‘Obligate’ parental care
717 was defined as the failure of larvae to survive to the third instar when parents were
718 removed.

719

720 We used a phylogenetic generalised least squares regression (PGLS) to analyse the
721 relationship between body size and parental care using R version 3.3.0³⁶ with
722 packages ape⁴⁵, picante⁴⁶ and caper⁴⁷. Care was coded with a dummy variable that was
723 treated as a factor in (1 = obligate post-hatching parental care, 0 = facultative post-
724 hatching parental care). Species without a parental care classification were coded NA.

725

726 We removed data obtained through personal communication systematically and
727 repeated the analysis to check whether these data affected our conclusions. They did
728 not. We removed *N. americanus* (est = 0.88 ± 0.35 , $t_{11} = 2.54$, $P = 0.028$), *N.*
729 *marginatus* (est = 1.72 ± 0.72 , $t_{11} = 2.40$, $P = 0.035$), and *N. nepalensis* (est = $1.52 \pm$
730 0.71 , $t_{11} = 2.13$, $P = 0.056$) from our analysis separately, and without all three species
731 (est = 0.85 ± 0.42 , $t_9 = 2.05$, $P = 0.07$). The results without *N. nepalensis*, and without
732 all three species, were still marginally significant. More importantly, a large effect
733 size in the same direction was retained: that is, larger species have obligate care (see
734 Main Text).

735

736 **Supplementary Figures and Figure Captions**

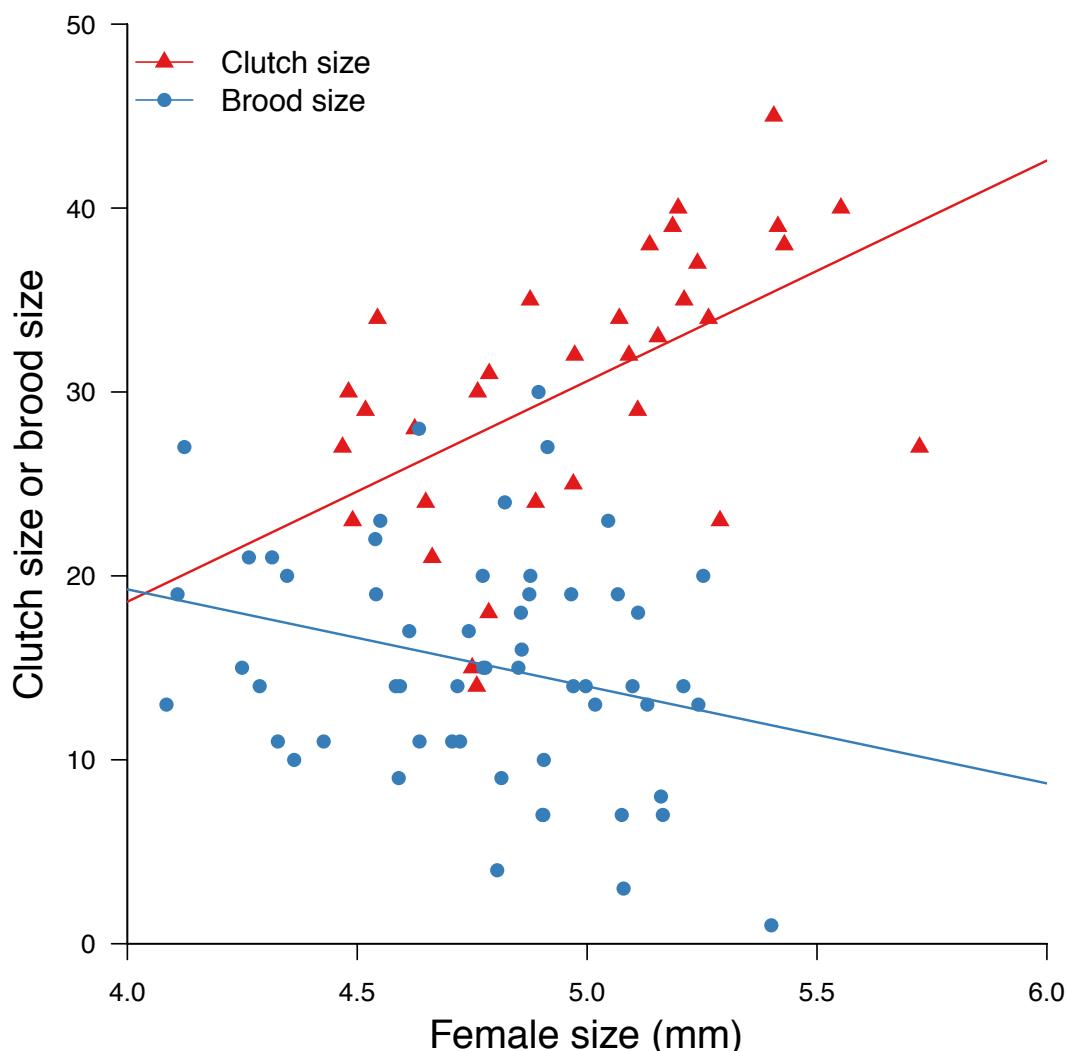
737 Supplementary Fig. 1

738 The relationship between female size and a) clutch size (in red triangles); and b)
739 brood size (in blue circles). Clutch size (red line, N = 33) increases with female size.

740 Data were taken from²⁶. Brood size (blue line, N = 55), decreases with female size.

741 Female size refers to pronotum width. Each datapoint corresponds to a different

742 female.



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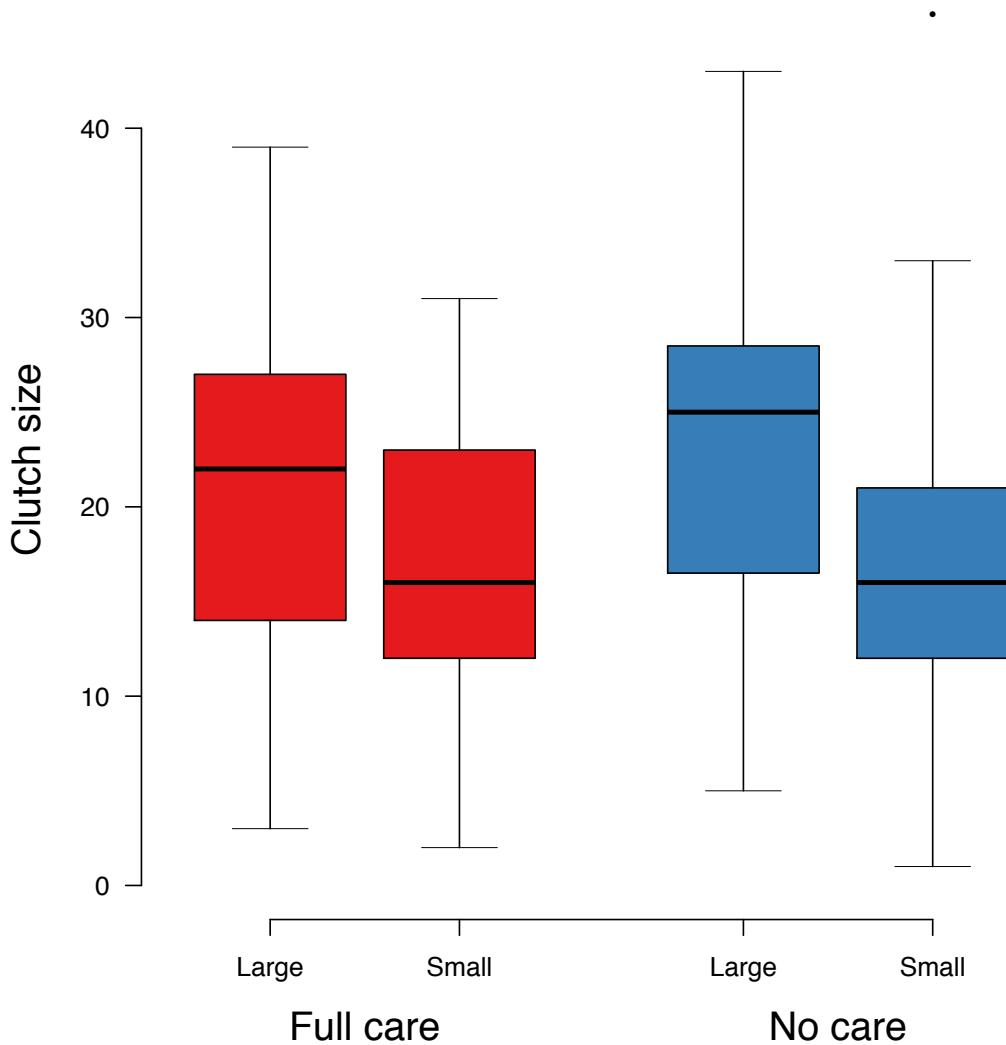
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748

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750 Supplementary Fig. 2

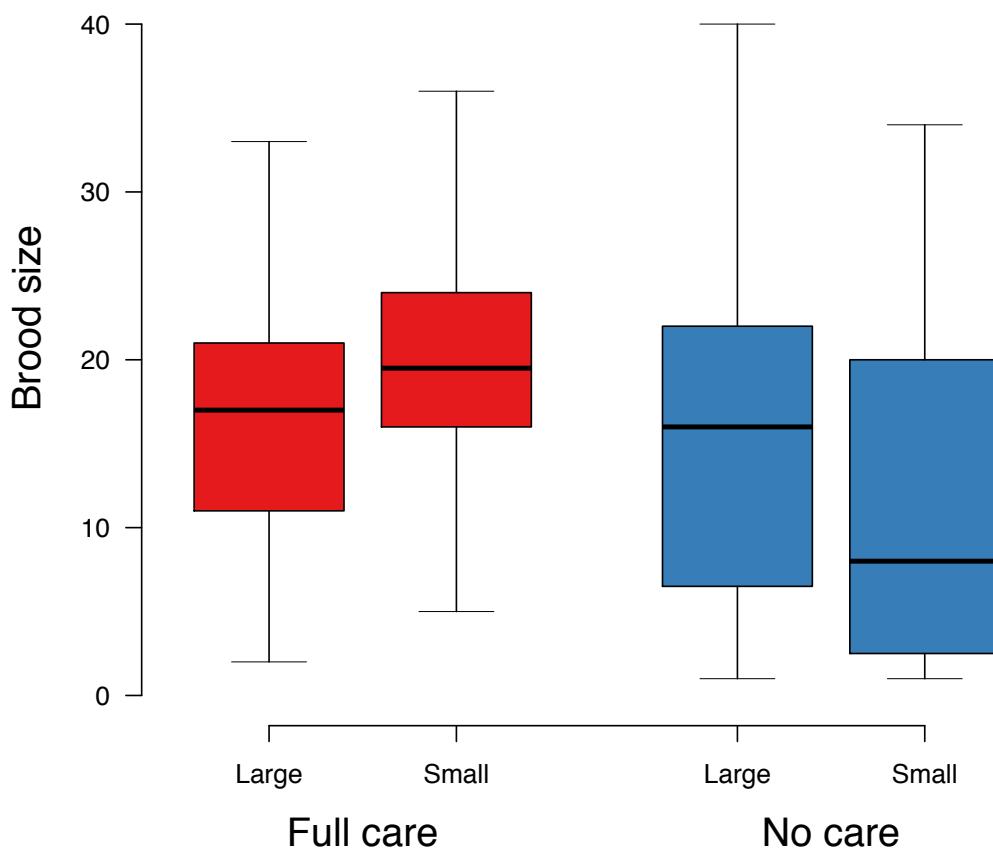
751 Clutch size at generation five in the four different experimental treatments in the
752 selection experiment: Full Care Large (N=38) and Full Care Small (N=39) (in red);
753 No Care Large (N=51) and No Care Small (N=44) (in blue). Both replicates per
754 treatment are combined. Box plots show median and interquartile ranges.



755

756 Supplementary Fig. 3

757 Brood size at larval dispersal in the four different experimental treatments in the
758 selection experiment: Full Care Large (N=54) and Full Care Small (N=52) (in red);
759 No Care Large (N=47) and No Care Small (N=15) (in blue). Both replicates per
760 treatment were combined. Box plots show the median and interquartile ranges of the
761 data.



762

763

764 **Tables**

765 Supplementary Table 1

766 The variance components for pronotum width in the Full Care and No Care

767 environments.

	$h^2 \pm se$	$V_A \pm se$	$V_{PE} \pm se$	$V_R \pm se$
Full Care	0.08 ± 0.12	0.01 ± 0.02	0.04 ± 0.01	0.12 ± 0.01
No Care	0.05 ± 0.30	0.01 ± 0.04	0.05 ± 0.02	0.09 ± 0.02

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795 Supplementary Table 2

796 The realised heritabilities, and the associated standard errors, of adult body size for
797 each of the eight experimental populations (i.e. the four experimental treatments, each
798 replicated twice). For each population, the slope of the regression of cumulative
799 response to selection against cumulative selection differential of each population was
800 tested against zero. The t-values and P-values give the results of these tests.

801

Population	Realised heritability	Standard error	t value	P value
Full Care Large 1	0.048	0.025	1.929	0.112
Full Care Large 2	0.130	0.024	5.401	0.003
Full Care Small 1	-0.042	0.041	-1.030	0.350
Full Care Small 2	0.022	0.019	1.140	0.306
No Care Large 1	0.067	0.064	1.047	0.343
No Care Large 2	-0.023	0.024	-0.917	0.401
No Care Small 1	-0.134	0.051	-2.617	0.047
No Care Small 2	-0.076	0.043	-1.771	0.137

802

803

804 Supplementary Table 3

805 The *Nicrophorus* species which were measured for size. The sample size (N) is the
806 number of individuals photographed and measured from collections held in the
807 Natural History Museum, London.

808

Species	Number of photographs (N)	Mean pronotum width (mm)	Standard deviation
<i>Nicrophorus americanus</i>	27	10.56	1.04
<i>Nicrophorus antennatus</i>	8	5.92	0.76
<i>Nicrophorus apo</i>	2	5.20	0.55
<i>Nicrophorus argutor</i>	5	6.67	0.42
<i>Nicrophorus carolinus</i>	40	6.99	0.93
<i>Nicrophorus charon</i>	9	5.52	0.65
<i>Nicrophorus concolor</i>	37	10.78	0.99
<i>Nicrophorus dauricus</i>	6	6.77	0.52
<i>Nicrophorus defodiens</i>	60	5.43	0.59
<i>Nicrophorus didymus</i>	28	5.51	0.60
<i>Nicrophorus distinctus</i>	14	6.73	0.46
<i>Nicrophorus encaustus</i>	5	5.67	0.50
<i>Nicrophorus germanicus</i>	24	9.92	1.38
<i>Nicrophorus guttula</i>	50	5.72	0.73
<i>Nicrophorus heurni</i>	12	5.35	0.55
<i>Nicrophorus humator</i>	33	7.16	0.85
<i>Nicrophorus hybridus</i>	8	7.26	0.89
<i>Nicrophorus insularis</i>	8	5.87	0.48
<i>Nicrophorus interruptus</i>	35	5.81	0.60
<i>Nicrophorus investigator</i>	105	5.99	0.77
<i>Nicrophorus japonicus</i>	16	6.58	0.98
<i>Nicrophorus kieticus</i>	29	4.34	0.53
<i>Nicrophorus lunatus</i>	5	6.65	1.10
<i>Nicrophorus maculifrons</i>	12	5.72	0.91
<i>Nicrophorus marginatus</i>	69	6.38	0.96
<i>Nicrophorus mexicanus</i>	20	5.84	0.76
<i>Nicrophorus montivagus</i>	18	4.32	0.53
<i>Nicrophorus morio</i>	7	9.00	0.88
<i>Nicrophorus nepalensis</i>	90	5.22	0.58
<i>Nicrophorus nigricornis</i>	4	6.34	1.00
<i>Nicrophorus nigrita</i>	15	6.07	0.99
<i>Nicrophorus oberthuri</i>	9	5.51	0.60
<i>Nicrophorus obscurus</i>	36	6.97	0.99
<i>Nicrophorus olidus</i>	20	4.66	0.62
<i>Nicrophorus orbicollis</i>	39	6.65	0.82
<i>Nicrophorus podagricus</i>	80	6.10	0.62
<i>Nicrophorus przewalskii</i>	4	6.59	0.20
<i>Nicrophorus pustulatus</i>	18	7.05	0.93
<i>Nicrophorus quadrimaculatus</i>	4	4.92	0.76
<i>Nicrophorus quadripunctatus</i>	56	5.05	0.67
<i>Nicrophorus sayi</i>	40	6.12	0.65
<i>Nicrophorus scrutator</i>	7	5.94	1.50
<i>Nicrophorus semenowi</i>	3	5.18	0.90
<i>Nicrophorus sepultor</i>	12	6.12	0.54

<i>Nicrophorus smefarka</i>	4	4.13	0.42
<i>Nicrophorus tenuipes</i>	20	5.63	0.39
<i>Nicrophorus tomentosus</i>	50	5.46	0.59
<i>Nicrophorus vespillo</i>	50	5.72	0.77
<i>Nicrophorus vespilloides</i>	70	4.83	0.59
<i>Ptomascopus morio</i>	23	4.16	0.56

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811 Supplementary Table 4

812 Variation in the provision of parental care across burying beetle species. ‘Obligate’
813 care means that larvae cannot survive to their third instar unless they are cared for by
814 their parents; ‘facultative’ care means larvae can survive without their parents.

Species	Parental care	Source of information
<i>Nicrophorus americanus</i>	Obligate	D. Howard pers. comm.
<i>Nicrophorus defodiens</i>	Facultative	(30)
<i>Nicrophorus humator</i>	Obligate	BP Springett cited in (30)
<i>Nicrophorus investigator</i>	Obligate	BP Springett cited in (30)
<i>Nicrophorus marginatus</i>	Obligate	D. Howard pers. comm.
<i>Nicrophorus mexicanus</i>	Facultative	(48)
<i>Nicrophorus nepalensis</i>	Facultative	S.-J. Sun pers. Comm.
<i>Nicrophorus orbicollis</i>	Obligate	(30,49)
<i>Nicrophorus pustulatus</i>	Facultative	(30,49)
<i>Nicrophorus quadripunctatus</i>	Facultative	(50)
<i>Nicrophorus sayi</i>	Obligate	(30)
<i>Nicrophorus tomentosus</i>	Facultative	(30)
<i>Nicrophorus vespillo</i>	Facultative	(51), B.J.M. Jarrett, unpub data
<i>Nicrophorus vespilloides</i>	Facultative	(19,21,49)

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