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1 **Biparental care is more than the sum of its parts:**
2 **experimental evidence for synergistic effects on offspring fitness**

3
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11

12 **Abstract**

13 Despite an extensive body of theoretical and empirical literature on biparental cooperation,
14 it is still unclear whether offspring fare equally, better, or worse when receiving care by two
15 parents versus a single parent. Some models predict that parents should withhold the
16 amount of care they provide due to sexual conflict, thereby shifting as much of the workload
17 as possible to their partner. This conflict should lead to offspring faring worse with two
18 parents. Yet, other models predict that when parents care for their offspring together, their
19 individual contributions can have synergistic (more than additive) effects on offspring
20 fitness. Under this scenario, biparental cooperation should lead to offspring faring better
21 with two parents. We address this fundamental question using a unique experimental design
22 where we compared offspring fitness when the two parents worked together (biparental
23 treatment) and when the two parents worked separately (uniparental treatment), while
24 keeping constant the amount of resources and number of offspring per parent across
25 treatments. This made it possible to directly compare the biparental treatment to the sum of
26 the male and female contributions in the uniparental treatment. Our main finding was that
27 offspring grew larger and were more likely to survive to adulthood when reared by both
28 parents than a single parent. This is the first empirical evidence for a synergistic effect of
29 biparental cooperation on offspring fitness and could provide novel insights into the
30 conditions favouring the evolution of biparental cooperation.

31

32 **Introduction**

33 Biparental care occurs when male and female parents cooperate to provide care for their
34 joint offspring. Although biparental care is relatively rare, it has evolved repeatedly in birds,
35 mammals, fishes, amphibians, and insects [1–3]. In general, biparental care is expected to
36 evolve when it increases offspring fitness to such an extent that it outweighs the fitness loss
37 to a caring parent in terms of lost breeding opportunities [4]. Nevertheless, when two
38 parents cooperate to rear their offspring, conflict inevitably arises over how much each
39 should contribute towards care [5–7]. This is because the benefit of care to each parent
40 depends on the combined effort of the two parents, whereas the cost depends on each
41 parent’s personal effort [6,8]. Thus, biparental care provides an excellent model system for
42 investigating the balance between cooperation and conflict between two unrelated
43 individuals [6,7].

44 Due to sexual conflict, each parent is under selection to reduce its personal cost by
45 shifting as much of the workload as possible over to its partner. Consequently, parents that
46 are working together are expected to withhold the amount of care they provide towards the
47 current brood, compared to when working alone [9]. This may result in offspring faring
48 worse when cared for by two parents than a single parent, as reported in a prior study on
49 zebra finches [10]. On the other hand, offspring may fare better with two parents if there are
50 synergistic (more than additive) effects of the individual contributions of the two parents on
51 offspring fitness [6,11,12]. This is referred to as complementarity and is predicted when
52 male and female parents specialise in different tasks during care [13]. Under this scenario,
53 the total beneficial effect of the combined effort of two parents on offspring performance
54 exceeds the sum of the beneficial effects of each individual parent when they provide care

55 separately. Since sexual conflict and complementarity are not mutually exclusive, it is likely
56 that there is a balance between cooperation and conflict in most systems [14]. Despite
57 extensive theoretical and empirical work on biparental care over the past few decades [e.g.,
58 13–17], it is still unclear whether this balance between cooperation and conflict leads to
59 offspring faring equally, better, or worse when receiving care by a single parent versus both
60 parents.

61 Here, we address this fundamental gap in our understanding of biparental care, using
62 an experimental design where we compared parental behaviour and offspring performance
63 when the two parents worked together (biparental treatment) and when they worked
64 separately (uniparental treatment). The rationale for this design was that there was scope for
65 sexual conflict and synergy in the biparental treatment, whereas the potential for sexual
66 conflict and synergy was experimentally removed in the uniparental treatment. We first
67 measured parental behaviours to investigate (*i*) whether parents withhold care when
68 working together, as predicted due to sexual conflict, and (*ii*) whether the type of care
69 provided by male and female parents is more divergent when they work together than
70 separately, indicating task specialisation. We then measured offspring fitness-related traits to
71 determine whether (*i*) offspring perform equally well with two parents, as expected if the
72 beneficial effect of the parents' individual contributions is simply additive, (*ii*) offspring
73 perform better with two parents, as expected if biparental care has synergistic benefits, or
74 (*iii*) offspring perform worse with two parents, as expected if parents withhold care due to
75 sexual conflict. To allow a direct comparison between the biparental treatment and the sum
76 of the male and female contributions in the uniparental treatment, we kept constant the

77 amount of resources and the number of offspring (i.e., the potential workload) per parent
78 across treatments (Figure 1).

79 Our study species, *Nicrophorus vespilloides*, has a number of important attributes that
80 make it particularly well-suited for this experiment. Firstly, biparental care, female
81 uniparental care, and male uniparental care all occur in natural populations of this species,
82 with a relative frequency of 52%, 39%, and 3%, respectively [18,19]. Our biparental and
83 uniparental treatments therefore match conditions in the wild. Secondly, burying beetles
84 breed on carcasses of small vertebrates, which provide the sole source of food for the parents
85 and developing larvae. This made it possible to keep the amount of resources per parent and
86 offspring constant across treatments by providing the two parents in the biparental treatment
87 with two carcasses of a standardized size and each parent in the uniparental treatment with
88 one carcass (Figure 1). Thirdly, parents do not distinguish between their own larvae and
89 unrelated larvae [20]. This allowed us to standardize the number of offspring per parent by
90 providing parents with mixed-parentage broods of 30 larvae in the biparental treatment and
91 15 larvae in the uniparental treatment (Figure 1). Lastly, prior work in burying beetles has
92 found good evidence for sexual conflict over care, as well as task specialisation during care
93 [21–26]. Thus, the potential for both conflict and complementarity makes this species an
94 excellent study system for investigating whether offspring fare equally, better, or worse with
95 two parents working together or with a single parent working alone.

96

97 **Materials and Methods**

98 *Study species*

99 Biparental care in *N. vespilloides* is elaborate and complex. Once a carcass is found, parents
100 bury it into the soil, remove any fur or feathers, deposit antimicrobial secretions to its
101 surface, and lay eggs around it 24–48 hours after mating [27,28]. When the eggs hatch
102 approximately 60 hours later [29], the larvae crawl to the carcass and start feeding in a
103 crater created by the parents on the top of the carcass. The larvae can self-feed, but the
104 parents also provision larvae with predigested carrion [30]. There is some evidence for sex
105 differences in parental care with females spending more time provisioning food for the
106 larvae and staying on the carcass for longer than males [21–23,26]. Larvae disperse from the
107 carcass about five days after hatching, which corresponds to the end of the parental care
108 period. They pupate about 10–12 days after dispersal and eclose as adults about 10–12 days
109 after pupation.

110

111 *Animal husbandry*

112 We used virgin beetles from an outbred laboratory population maintained at the University
113 of Edinburgh. The beetles used in this study comprised of fifth- and sixth-generation beetles
114 from lines originally collected in Edinburgh, UK. They were housed individually in
115 transparent plastic containers (12 × 8 × 2 cm) filled with moist soil and kept at 22°C and a
116 16h:8h light cycle. All non-breeding adults were fed small pieces of raw organic beef twice a
117 week.

118

119 *Experimental design and procedures*

120 Our experimental design included a biparental treatment, where the two parents worked
121 together, and a uniparental treatment, where the two parents worked separately (Figure 1).

122 We kept constant the number of offspring (i.e., the potential workload) and the amount of
123 resources per parent across treatments (Figure 1) to allow a direct comparison of parental
124 effort and offspring performance between the biparental treatment and the sum of the
125 uniparental male and female contributions.

126 The parents used in this experiment were mated within two weeks after reaching
127 sexual maturity (i.e., 10–24 days after eclosion). We only mated unrelated males and
128 females that did not share any common ancestors for at least two generations. Just before
129 mating, we recorded the pre-breeding mass of each parent and measured their pronotum
130 width using digital calipers. Each experimental pair ($n = 130$) was then placed in a
131 transparent plastic container ($17 \times 12 \times 6$ cm) filled with 1 cm of moist soil and two freshly
132 thawed mouse carcasses of a standardized size (10–12 g). Half of these pairs were randomly
133 assigned to the uniparental treatment ($n = 65$) and the other half to the biparental treatment
134 ($n = 65$). There was no difference (two-sample t-test: $t_{129} = -0.07$, $P = 0.95$) between total
135 mass of the two carcasses assigned to the biparental treatment (mean \pm SD = 22.03 ± 0.97
136 g) and the uniparental treatment (22.05 ± 1.29 g). Immediately after egg laying, we
137 separated the parents from the eggs so that the larvae would hatch in isolation from the
138 parents. Parents in the biparental treatment were moved jointly, along with the two
139 carcasses, to a new container with moist soil. Parents in the uniparental treatment were
140 transferred to separate containers with moist soil, and each parent was provided with one of
141 the two carcasses given to them initially.

142 When the eggs started hatching, we used the newly hatched larvae to generate broods
143 of 15 or 30 larvae for the uniparental or biparental treatments, respectively (Figure 1). All
144 experimental broods included larvae of mixed parentage to eliminate any effects of parent-

145 offspring coadaptation [23,31,32]. In this species, parents do not distinguish between
146 unrelated foster broods and their own broods, as long as the larvae are at the same
147 developmental stage [20]. Since parents kill any larvae that arrive on the carcass before their
148 eggs are expected to hatch [33], we only provided parents with a brood once their own eggs
149 had hatched. We were not able to provide experimental broods to all parents, because we
150 were limited by the number of larvae that hatched at the same time. Thus, our final sample
151 sizes were $n = 40$ for the biparental treatment where both parents cared for a brood of 30
152 larvae and $n = 49$ for the uniparental treatment where the male and the female cared
153 separately for two broods of 15 larvae (Figure 1).

154 We conducted behavioural observations to compare the amount of care that male
155 and female parents provided to their offspring in the biparental versus the two uniparental
156 treatments. These observations were done 24 hours after parents were given a brood, as this
157 stage in larval development corresponds to a peak in post-hatching care in this species [30].
158 We used instantaneous sampling every 1 min for 30 min [21–24,34]. We recorded the
159 number of scans that a female spent providing (*i*) direct care, defined as provisioning food or
160 interacting with the larvae, and (*ii*) indirect care, defined as guarding or carcass maintenance
161 (i.e., deposition of secretions to the surface of the carcass or excavation of the crypt).

162 We checked the containers daily in the morning and in the afternoon to determine
163 whether the parents were present on the carcass or were away from the brood in the soil.
164 Parents that were away for more than two consecutive checks were deemed to have
165 abandoned the brood and were removed from the boxes to prevent infanticide. Based on the
166 last observation when the parent was present on the carcass, we were able to estimate the
167 duration of care by each parent. At the dispersal stage, we recorded the number of surviving

168 larvae and measured the total brood mass to calculate average larval mass in each brood.
169 After being weighed, all larvae from each brood were placed into large transparent
170 containers (17 × 12 × 6 cm) filled with moist soil. At eclosion, we recorded the number of
171 individuals that eclosed successfully. These data were used to calculate the survival rate for
172 each brood from the dispersal stage to the eclosion stage (“survival to adulthood”). We also
173 measured the parents' post-breeding mass at the dispersal stage. By subtracting each parent's
174 prebreeding mass from its postbreeding mass, we calculated its overall mass change over the
175 breeding attempt, which is a measure of somatic investment [34,35]. The parents were
176 transferred to individual containers (12 × 8 × 2 cm) filled with moist soil. They were
177 checked twice a week until death to determine their post-breeding lifespan, which served as
178 a proxy for residual reproductive value [35].

179

180 *Data analysis*

181 We used linear models for continuous traits with normally distributed random errors
182 (average larval mass at dispersal, parent mass change, and parent post-breeding lifespan).
183 For discrete traits, we used generalized linear models fitted with a negative binomial error
184 distribution (brood size at dispersal) or a quasipoisson error distribution (amount of direct
185 care, amount of indirect care, duration of care). For proportion data (probability of brood
186 abandonment, offspring survival to adulthood), we used generalized linear models fitted
187 with a binomial and quasibinomial distribution, respectively. Quasipoisson and
188 quasibinomial distributions were used to account for overdispersion by including a
189 dispersion parameter that describes additional variance in the data.

190 We first compared parental behaviour and offspring performance between the
191 biparental treatment and the uniparental treatment. To this end, we calculated the sum of
192 the male and female contributions for the following variables: amount of direct and indirect
193 care, duration of care, mass change of each parent, brood size at dispersal, and number of
194 offspring surviving to adulthood. For average larval mass, we calculated total brood mass by
195 adding up the brood mass across the two uniparental treatments and divided that by the
196 total number of larvae across the two broods. Each of these variables was then used as a
197 response variable with treatment (uniparental or biparental) as a factor.

198 Carcass size was added as a covariate to the models for average larval mass and
199 brood size at dispersal, because the amount of resources available may influence offspring
200 growth and survival, respectively. Based on prior evidence that the parents' body size can
201 influence offspring fitness in this species [36,37], we also added male and female pronotum
202 width as covariates to the models for average larval mass, brood size at dispersal, and
203 survival to adulthood.

204 We next compared the behaviours of male and female parents across treatments. The
205 response variables were amount of direct and indirect care, duration of care, parental mass
206 change over the breeding attempt, and parent post-breeding lifespan. The explanatory
207 variables were parent sex (male or female), treatment (uniparental or biparental), and the
208 interaction between the two. Decisions about which variables to include in the final models
209 were based on AIC values following criteria from Burnham and Anderson [38]. All analyses
210 were performed using R version 3.4.2 [39]. The ggplot2 package was used for generating
211 figures [40].

212

213 **Results**

214 *Parental behaviour*

215 Broods received a similar total amount of care (direct care: $t_{86} = 0.83$, $P = 0.50$; indirect care:
216 $t_{86} = -1.55$, $P = 0.13$; duration of care: $t_{86} = 0.13$, $P = 0.89$) regardless of whether the two
217 parents worked together (i.e., biparental treatment) or separately (i.e., uniparental
218 treatment). Nevertheless, examining each sex separately revealed that males provided less
219 care and females provided more care when working with a partner than when working
220 alone (Figures 2a, 2b, and 2c). This pattern was true for amount of direct care (treatment \times
221 parent sex: LR $\chi^2_{1,173} = 39.83$, $P < 0.0001$), amount of indirect care (treatment \times parent sex:
222 LR $\chi^2_{1,173} = 11.29$, $P < 0.001$), as well as duration of care (treatment \times parent sex: LR $\chi^2_{1,173} =$
223 8.36 , $P = 0.004$). Similarly, females were less likely to abandon the brood in the biparental
224 (5%) than the uniparental treatment (18%), whereas males were more likely to abandon the
225 brood in the biparental (35%) than the uniparental treatment (30%) (treatment \times parent sex:
226 LR $\chi^2_{1,173} = 4.29$, $P = 0.038$). The average probability of abandonment was the same across
227 treatments (LR $\chi^2_{1,173} = 0.50$, $P = 0.48$).

228 Females gained more mass and males gained less mass when the two parents worked
229 together compared to when they worked separately (treatment \times parent sex: $F_{1,143} = 8.59$, P
230 $= 0.004$; Figure 2d). However, total mass change did not differ between the uniparental and
231 biparental treatments ($t_{86} = 1.33$, $P = 0.19$). Post-breeding lifespan did not depend on sex
232 ($F_{1,170} = 1.56$, $P = 0.21$), treatment ($F_{1,170} = 0.15$, $P = 0.70$), or the interaction between sex and
233 treatment ($F_{1,170} = 0.46$, $P = 0.50$).

234

235 *Offspring performance*

236 Larvae reared by parents who worked together were larger at the end of the parental care
237 period than larvae reared by parents who worked separately (LR $\chi^2_{1,86} = 11.18$, $P < 0.001$;
238 Figure 3a). This difference in average larval mass was not associated with a trade-off
239 between offspring size and number, since there was no evidence for a difference in brood
240 size at the dispersal stage between the biparental and uniparental treatments (LR $\chi^2_{1,86} =$
241 0.01 , $P = 0.92$). In addition to having a higher larval mass, offspring reared by both parents
242 had a higher survival rate to adulthood than offspring reared by a single parent (LR $\chi^2_{1,86} =$
243 4.83 , $P = 0.03$; Figure 3b).

244 In terms of the covariates included in the above models, average larval mass was
245 higher on larger carcasses (LR $\chi^2_{1,86} = 4.86$, $P = 0.028$) and when the female was larger (LR
246 $\chi^2_{1,86} = 4.12$, $P = 0.042$) but not when the male was larger (LR $\chi^2_{1,86} = 0.20$, $P = 0.65$). Brood
247 size at dispersal was not influenced by the male's body size (LR $\chi^2_{1,86} = 0.08$, $P = 0.78$), the
248 female's body size (LR $\chi^2_{1,86} = 0.09$, $P = 0.76$), or the size of the carcass (LR $\chi^2_{1,86} = 1.16$, $P =$
249 0.28). Lastly, offspring of larger males (LR $\chi^2_{1,86} = 4.03$, $P = 0.04$) and larger females (LR
250 $\chi^2_{1,86} = 5.40$, $P = 0.02$) were more likely to survive to adulthood.

251

252 **Discussion**

253 In this study, we first tested (*i*) whether parents withhold care when working together, as
254 predicted due to sexual conflict, and (*ii*) whether the type of care provided by male and
255 female parents is more divergent when they work together than separately, indicating task
256 specialisation. We found that males, but not females, provided less care when working with
257 a partner, and there was no evidence for task specialisation. We then tested whether (*i*)
258 offspring perform equally well with two parents, as expected if the beneficial effect of the

259 parents' individual contributions is simply additive, (*ii*) offspring perform better with two
260 parents, as expected if biparental care has synergistic benefits, or (*iii*) offspring perform
261 worse with two parents, as expected if parents withhold care due to sexual conflict. In
262 accordance with the second scenario, we found that larvae reared by both parents were
263 larger at the end of the parental care period and more likely to survive to adulthood than
264 offspring reared by a single parent. To our knowledge, this is the first empirical evidence for
265 a synergistic effect of biparental care on offspring fitness. Below, we offer potential
266 explanations for our results and discuss their implications for our understanding of
267 biparental care.

268 Our first main finding was that parents adjusted their effort depending on whether
269 they were caring alone or together. Males provided less care, whereas females provided
270 more care, when working with a partner. This pattern may be a consequence of sexual
271 conflict over care where males, but not females, withheld the amount of care they provided
272 to shift some of the workload over to their partner. This would suggest that females were
273 exploited by males, because they were forced to increase their effort to compensate for their
274 partner's reduced effort. However, an alternative explanation is that females had the upper
275 hand in sexual conflict over carcass consumption. Previous work on this species suggests
276 that sexual conflict over carcass consumption is closely linked to sexual conflict over
277 parental care and may be equally important [24,25]. In our study, females consumed more
278 of the carcass and gained more mass in the biparental than in the uniparental treatment,
279 whereas the opposite was true for males. Mouse carcasses are a highly nutritional resource
280 for parents who feed on the carcass before and during a breeding attempt to replenish their
281 energy reserves. Thus, if females controlled access to the carcass in the biparental treatment,

282 the lower level of care by males might reflect that males were prevented from feeding on the
283 carcass and were thus unable or unwilling to provide an equal amount of care [24,25].

284 Our second main finding was that offspring fared better when receiving care by both
285 parents than a single parent. These synergistic fitness benefits of care were evident before
286 offspring independence (i.e., larval mass) and persisted after independence (i.e., survival to
287 adulthood). The mass of a larva at the dispersal stage is a crucially important fitness
288 component in this species. Because larvae do not feed after dispersal and before eclosion,
289 larval mass determines adult size [41]. In turn, adult size influences lifespan, fecundity, and
290 the likelihood of acquiring a carcass for breeding [35,36,42,43]. Thus, the higher larval mass
291 of offspring reared by two parents may have downstream fitness benefits with respect to the
292 offspring's reproductive success as adults. Interestingly, the only other study to directly test
293 how offspring fare with one versus two parents found the opposite pattern. Using zebra
294 finches, Royle et al. [10] compared a biparental treatment to a female uniparental treatment
295 (but not a male uniparental treatment) and showed that nestlings reared by a single female
296 received more care per offspring than those reared by both parents. This difference in
297 parental investment had consequences for offspring fitness later in life, with male offspring
298 from uniparental broods being more sexually attractive than male offspring from biparental
299 broods [10].

300 Synergistic effects are predicted when there is task specialisation between male and
301 female parents [13]. In burying beetles, parents provide care by provisioning food to the
302 larvae, grooming larvae, maintaining the carcass, and guarding the carcass from predators
303 and competitors. Under task specialisation, we would expect a greater divergence in
304 parental care behaviours when parents work together than when they work separately, but

305 this was not the case here. We found that female parents provided more direct care (food
306 provisioning) and more indirect care (carcass maintenance) in the biparental treatment than
307 the uniparental treatment, whereas male parents provided less direct care and less indirect
308 care in the biparental than the uniparental treatment. Thus, even though there were sex
309 differences in care (with females providing more care than males), there was no evidence for
310 task specialisation.

311 Our study provides no evidence for the mechanistic basis of the synergistic effects we
312 observed, but one possibility is that they were driven by differences in carrion consumption
313 between treatments. Given that carrion consumption by the parents can negatively affect
314 offspring fitness in this species [44], the lower offspring performance in the uniparental
315 treatment could be due to higher carcass consumption by the parents. However, this
316 explanation is not supported by our results, since there was no difference in the parents'
317 total mass change between treatments.

318 A more likely explanation is that these synergistic effects are related to a component
319 of parental care that we did not measure directly. For example, *N. vespilloides* parents deposit
320 oral and anal fluids onto the carcass during larval development. These secretions contain a
321 wide range of compounds, which have been shown to increase larval survival by facilitating
322 the vertical transmission of symbiotic microbiota [45] and by preventing bacterial and fungal
323 growth on the decomposing carcass [27]. In the absence of these secretions, microbes can
324 compromise larval health and degrade the quality of the carcass as a food resource to the
325 offspring [27]. The lysozymes in these secretions can vary between individuals [46], so
326 secretions from two parents are likely to be more diverse than secretions from a single

327 parent. We encourage future research to investigate the mechanistic basis of the synergistic
328 effects of biparental cooperation.

329 Overall, this work shows that offspring fare better in broods with two parents despite
330 one of the parents providing less care (in this case, the male). These findings contradict the
331 assumption that sexual conflict between parents reduces offspring fitness by causing parents
332 to withhold parental investment [10,47]. We suggest that synergistic effects may be more
333 common than currently appreciated and that the lack of empirical evidence for
334 complementarity may be due to the lack of studies explicitly testing for it. It is important to
335 note that it is not possible to detect synergistic effects by only studying parents who are
336 providing care together (as is typically done in most studies of biparental care). Instead, it is
337 essential to use an experimental design where some parents are allowed to work together
338 and some work separately, while the number of offspring per parent is kept constant.

339 In conclusion, our study provides evidence for a synergistic effect of biparental care
340 on offspring fitness by showing that offspring grow better and are more likely to survive to
341 adulthood when reared by two parents working together than by a single parent working
342 alone. Evolutionary theory has long considered the role of synergistic effects [11,13,17], but
343 until now, we have lacked empirical support for their existence. Our results can therefore
344 provide valuable insights into the conditions that might favour the evolution of biparental
345 care.

346

347 **Authors' contributions**

348 N.P. and P.T.S. conceived and designed the experiment. N.P and E.J.H.H performed the
349 experiment. N.P. performed the data analysis and wrote the first draft of the manuscript.
350 P.T.S. edited the manuscript. All authors read and approved the final manuscript.

351

352 **Competing interests**

353 We declare that we have no competing interests.

354

355 **Data accessibility**

356 Data have been deposited on the Dryad Digital Repository:

357 <http://datadryad.org/review?doi=doi:10.5061/dryad.s7n04j8>.

358

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366

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474 **Figure 1.** Experimental design illustration (not drawn to scale). Males (blue) and females
475 (orange) in the uniparental treatment were separated after egg laying and were each
476 provided with one mouse of a standardized size and a mixed-parentage brood of 15 larvae.
477 Parents in the biparental treatment were allowed to stay together and were provided with
478 two mice of a standardized size and a mixed-parentage brood of 30 larvae.

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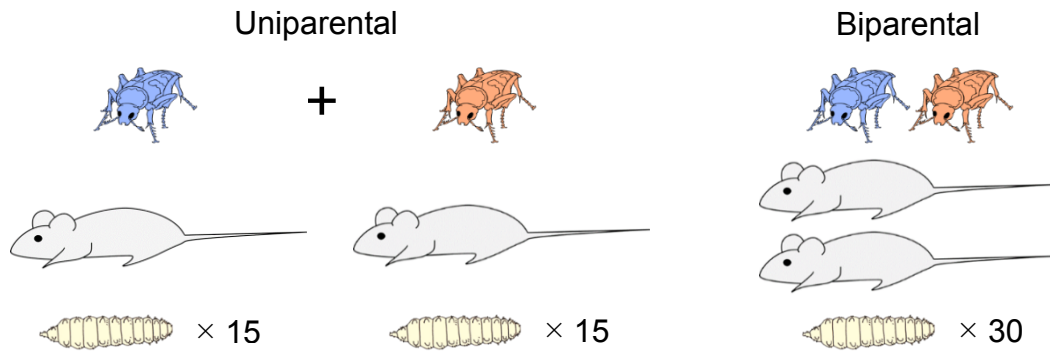
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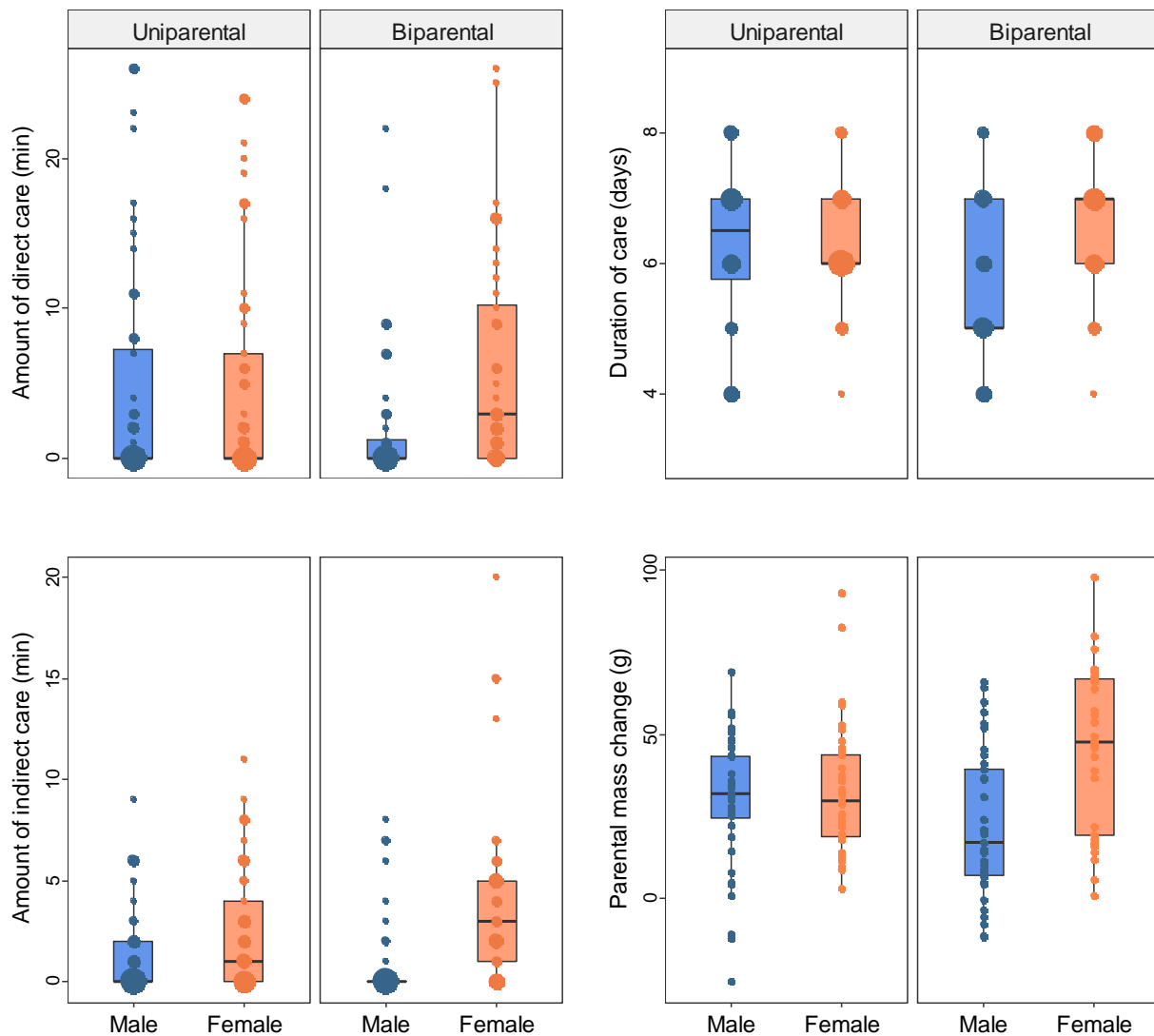
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489 **Figure 2.** Boxplots showing the amount of direct care (a), amount of indirect care (b),
 490 duration of care (c), and mass change (d) by males (blue) and females (orange) in the
 491 uniparental ($n = 49$) and biparental ($n = 40$) treatments. Direct care refers to food
 492 provisioning and interactions with larvae (e.g., grooming). Indirect care refers to carcass
 493 maintenance and guarding. The amount of direct and indirect care provided by parents was
 494 measured using scan sampling during 30-min behavioural observations. Duration of care
 495 refers to the number of days each parent was present on the carcass before abandoning the
 496 brood. Filled circles indicate individual data points with the size of the circle representing
 497 the frequency of observations.



506 **Figure 3.** Boxplots showing average offspring mass (a) and number of surviving offspring
507 (b) at the dispersal stage in the uniparental (green) and biparental (purple) treatments ($n = 49$
508 and $n = 40$, respectively). Filled circles indicate individual data points with the size of the
509 circle representing the frequency of observations.
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