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Selection on the joint actions of pairs leads to divergent adaptation

² and coadaptation of care-giving parents during pre-hatching care

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18 Abstract

The joint actions of animals in partnerships or social groups evolve under both natural selection, from 19 the wider environment, and social selection, imposed by other members of the pair or group. We used 20 experimental evolution to investigate how jointly expressed actions evolve upon exposure to a new 21 environmental challenge. Our work focused on the evolution of carrion nest preparation by pairs of 22 burying beetles *Nicrophorus vespilloides*, a joint activity undertaken by the pair but typically led by 23 the male. In previous work, we found that carrion nest preparation evolved to be faster in 24 experimental populations without post-hatching care (No Care lines) than with post-hatching care 25 (Full Care lines). Here we investigate how this joint activity evolved. After 15 generations of 26 experimental evolution, we created heterotypic pairs (No Care females with Full Care males, and No 27 Care males with Full Care females) and compared their carrion nest making with homotypic No Care 28 and Full Care pairs. We found that pairs with No Care males prepared the nest more rapidly than pairs 29 with Full Care males, regardless of the female's line of origin. This suggests that males led the way by 30 adapting their nest preparation behaviour to the No Care environment first, with females secondarily 31 co-adapting their behaviour to the male's behaviour by reducing their nest preparation behaviour. We 32 discuss how social coadaptations within pairs or groups could act as a post-mating barrier to gene 33 flow. 34

- 35
- 36 Keywords: nest-building | reproductive isolation | division of labour

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38 Introduction

When animals interact in partnerships, families or social groups, they are often in conflict, for 39 example, over mating (Chapman et al. 2003), parental care (Royle et al. 2012), or who gets to 40 reproduce (Emlen 1995). But, when the conflict is resolved or suppressed, their joint activities can 41 enhance the fitness of the whole collective. Joint actions commonly function to overcome ecological 42 adversity in the wider environment (e.g., Cornwallis et al. 2017), such as the threat of attack by 43 predators (e.g., Feeney et al. 2013), the potential theft of a key resource by rivals (e.g., Queller & 44 Strassman 1998) or the patchy availability of nutritional resources (e.g., Faulkes et al. 1997). It might 45 involve the joint construction of a nest or communal burrow (e.g., Hansell 2005), for example, or 46 collective defence against pathogens (e.g., Cremer 2019) or group care of dependent offspring (e.g., 47 Queller & Strassman 1998). Working together to achieve a common goal favours individuals whose 48 activities are well-coordinated with the actions of their partner, or other members of the family or 49 social collective, (e.g., Barta et al. 2014), perhaps through division of labour (e.g., Cooper & West 50 51 2018). It means that for each individual in the collective, there are two inter-related sources of selection on their behaviour: 1) natural selection from ecological challenges in the wider environment 52 that the team is working collectively to overcome and 2) social selection from the other members of 53 the pair or group to fine-tune individual contributions to the pair or group's collective activities 54 (Itzkowitz et al. 2001, Barta et al. 2014, Cooper & West 2018, McNamara et al. 1999). 55

56

Theory predicts that adapting to the heritable environments created by social partners can be more 57 rapid than adaptation to other environments. Selection imposed by the social environment changes the 58 genetic variation within the heritable environment and reinforcing selection in the subsequent 59 generations in a positive feedback loop (Moore, Brodie, and Wolf 1997, Agrawal, Brodie, and Wade 60 2001, Drown and Wade 2014). Furthermore, the social co-adaptation of the different group members 61 establishes favourable combinations of phenotypes within the family. These are known to exist within 62 animal families, for example (e.g., Zeh and Zeh 2000; Linksvayer, Fondrk, and Page Jr 2009; Hinde, 63 Johnstone, and Kilner 2010), particularly among provisioning adults who coordinate their activities 64 very precisely (e.g., Savage and Hinde 2019; Griffith 2019; Smiseth et al 2019). Favourable 65 phenotypic combinations potentially result from intergenomic epistasis in which the fitness of a social 66 trait depends on the genotype of the social partner (Wolf, Brodie, and Wade 2000; Wolf 2000). 67 68

The twin sources of selection on social traits, and the distinct patterns of inheritance and evolutionary dynamics of socially selected traits, make it difficult to predict how social traits might evolve upon exposure to a new ecological challenge in the wider environment. Would all individuals in the pair or group experience the same selection pressures in response to a new ecological challenge in the first instance, and only secondarily respond to selection induced by their behaviour to each other? Or

would selection act on a subset of the population who first adapt to ecological change, and their new
actions then provoke new social co-adaptations in other members of the pair or group? The latter
scenario seems more likely for social activities in which there are pre-existing leaders and followers
(e.g., Nagy et al. 2010), or where labour is already unevenly divided (e.g., Hager and Johnstone 2003;
Hinde, Johnstone, and Kilner 2010; Kölliker, Royle, and Smiseth 2012; Barta et al. 2014), though
whether this is indeed what happens has seldom been tested experimentally.

We investigated this problem by establishing lines of burying beetles Nicrophorus vespilloides and 81 allowing them to evolve in environments with a distinct ecological challenge that we imposed 82 experimentally. Burying beetles breed on the body of a small dead vertebrate (Scott 1998), commonly 83 in pairs but sometimes as lone adults or multi-adult groups (Müller et al. 2007). The parents jointly 84 convert the dead mouse or bird into a carrion nest by removing the fur or feathers, rolling it into a 85 ball, covering it in anti-microbial anal exudates, and burying it. Eggs are laid in the soil surrounding 86 the sunken carrion nest, and newly hatched larvae crawl to the nest where they aggregate. To help 87 their larvae take up residence on the carrion nest, and feed upon it, parents may make an incision in 88 the flesh prior to their arrival. The joint nest preparation activities of the parents are the focus of 89 interest here. Parents also guard and feed larvae after they hatch, though larvae can survive in the 90 laboratory with no post-hatching care at all (Eggert, Reinking, and Müller 1998). 91

92

In wild populations, pairs are under selection to prepare and bury the carrion nest as effectively and 93 efficiently as possible. Carrion nest preparation is key for concealing this vital resource from rivals 94 who might wish to use it for their own reproduction, including blowflies (Sun and Kilner 2020) and 95 other carrion-breeding insects, congenerics and conspecifics and microbes (Scott 1998). We imposed 96 selection on the pair's joint carrion preparation activities by removing parents 53h after pairing, just 97 before their offspring started to hatch (the 'No Care' lines). In two other experimentally evolving 98 lines, parents were allowed to stay with their larvae throughout their development and so were able to 99 provide both pre-hatching and post-hatching parental care (the 'Full Care' lines). 100

101

During the first twenty generations of experimental evolution, the No Care lines adapted rapidly to 102 our experimental intervention (Schrader, Jarrett, and Kilner 2015a; Schrader et al. 2017), and 103 exhibited divergent phenotypes in both larval (Jarrett et al. 2018a; Jarrett et al. 2018b; Rebar et al. 104 2020) and parental traits (Jarrett et al. 2018a; Duarte et al. 2021; Rebar et al. 2022). Of particular 105 relevance here, No Care parents evolved to frontload their parental care. They became more efficient 106 and more effective at converting carrion into a nest for their larvae, and in this way increased their 107 offspring's chance of surviving without post-hatching care (Duarte et al. 2021). In particular, No Care 108 parents were more likely to make an incision into the carcass prior to larval hatching. This incision is 109 noticeable upon inspecting the carcass and its presence prior to larval hatching strongly predicts brood 110

success when larvae are deprived of any post-hatching care (Duarte et al. 2021; Eggert, Reinking, and

Müller 1998; Jarrett et al. 2018a). Crucially, all the adaptations to a life without parental care that

occurred within fifteen generations of experimental evolution were consistent between replicate

populations, including the timing of making the feeding incision (Jarrett et al. 2018; Duarte et al.

115 2021).

116

In common with many other species (Henshaw et al. 2019), burying beetles divide the duties of 117 parental care between the sexes. Males carry out more of the pre-hatching duties of care and take the 118 lead in preparing the carrion nest (Walling et al. 2008; De Gasperin et al. 2016), while females are 119 more involved with post-hatching care (Walling et al. 2008). Previous work on burying beetles 120 suggests that task specialisation causes the sexes to be dependent upon each other, in the sense that 121 they each perform more effectively when paired (Pilakouta et al. 2018). After fifteen generations of 122 experimental evolution, we conducted crosses between the experimental lines to investigate whether 123 No Care males alone had unilaterally adapted their carrion preparation in the No Care lines, or 124 125 whether this was true of both sexes. We generated homotypic pairings (No Care adults paired with each other, and Full Care adults paired with each other) and heterotypic pairings (No Care adults 126 paired with Full Care adults). With this experimental design, we were able to test the extent to which 127 each sex had co-adapted its nest preparation behaviour to that of its partner. We also used these data 128 to investigate whether the presence of a feeding incision predicted the survival of the brood when 129 parents were present or absent after hatching. 130

131

We predicted that if the males alone unilaterally adapted in the No Care lines, then carried prepared 132 by No Care males should consistently bear a feeding incision with a higher probability than carrion 133 prepared by Full Care males-regardless of the female's line of origin. If the No Care females had co-134 adapted to the No Care males, then carrion prepared by homotypic No Care pairs should be more 135 likely to carry an incision than carrion prepared by No Care females paired with Full Care males. By 136 contrast, if the sexes had each unilaterally evolved changes in their nest preparation behaviour in the 137 No Care lines, then the Full Care homotypic pairings should be least likely to bear a feeding incision 138 53h after pairing, while the No Care homotypic pairings should be most likely to have an incision at 139 this point and both heterotypic pairings should lie somewhere between the two. 140

141

142 Methods

143 Experimental evolution

144 The experimentally evolving lines used in this work have been described in detail elsewhere

145 (Schrader et al. 2017). In brief, we established a large founding population of 671 N. vespilloides

individuals by interbreeding wild-caught individuals from four different woodlands in 32 pairs. Only

one pair of the 32 comprised individuals from the same woodland population. Offspring from each of

the 32 pairs were represented in each of the four replicate experimental lines. In two lines, larvae

- experienced Full Care (FC) in each generation, with both parents allowed to stay in the breeding box
- to feed and interact with their offspring. In the remaining No Care (NC) lines, both parents were
- removed from the breeding box at each generation, 53 h after they were paired, once carcass
- preparation was complete but before any larvae had hatched (see Schrader et al. 2017 for more details
- on the experimental set up). Pairs only bred once and only had one partner. FC lines had 30 pairs
- breeding per generation, and NC lines had 45 pairs to account for failures. Siblings and cousins were
- prevented from breeding. The lines were organised into two blocks, separated by a week, to ease the
- 156 workload (hence NC1, FC1 in Block 1 and NC2, FC2 in Block 2). The experimental work reported
- ¹⁵⁷ here used lines that had been exposed to 15 generations of experimental evolution.
- 158

159 Experimental design

The design of the experiment is shown in Figure 1. Prior to testing, the four lines went through a 160 common garden environment of Full Care (where all parents were allowed to interact with their larvae 161 162 throughout development). The aim was to standardise parental effects across all four treatments so that any residual variation could be attributed to evolutionary change. To set up the common garden 163 generation, the FC1 and NC1 parents were bred three weeks after eclosing as adults, and the FC2 and 164 NC2 parents were bred at two weeks after eclosing as adults. This synchronised breeding of 165 individuals from the two blocks ensured that the adults generated for the focal experiment were 166 matched in age at first breeding across treatments. The lines were then crossed: homotypic pairs 167 involved crossing the two replicate lines that had experienced the same parental manipulation (i.e., 168 $FC1 \times FC2$ and $NC1 \times NC2$, Fig 1a, b), while heterotypic pairs involved crossing populations that 169 had experienced different parental manipulations (i.e., FC1 × NC1 and FC2 × NC2, Fig 1a, b). It was 170 not feasible logistically to perform every possible cross between every replicate line (Fig 1a). With 171 the experimental design we used, we can isolate the evolutionary effects of parental care treatment 172 (NC v FC) on males and females (Fig 1a), but we cannot partition effects of replicate line (1 v 2) from 173 parental care treatment (NC v FC). Note that when we carried out this experiment, we had detected no 174 evidence of divergence between replicate lines with parental care treatments. 175

176

177 Burying beetle husbandry

- Adult beetles were kept individually in boxes measuring $12 \times 8 \times 2$ cm filled with compost for two
- weeks after eclosion until they were sexually mature. Individuals were fed ~ 0.3 g of minced beef
- 180 twice a week. Once individuals were sexually mature, they were paired for breeding. The pair of
- beetles was added to a larger box measuring $17 \times 12 \times 6$ cm half filled with fresh compost. A mouse
- carcass, sourced from Live Foods Direct Ltd, was weighed and recorded (mean \pm sd = 11.60 \pm 0.87g;
- range = 10.00-13.18g) and placed into the box, after which the pair of beetles was added. The pair of
- beetles prepared the mouse carcass for the first two days, whilst the female laid eggs in the soil

surrounding the carcass. At \sim 53 h, when carcass preparation and egg laying had been completed, we removed the parents in the No Care treatment. For the Full Care treatment, the parents were left in the box until the larvae dispersed, typically eight days after pairing.

188

189 Eight days after pairing, the larvae had completely eaten the carcass and were ready to complete

development. We removed the larvae, counted them, and weighed the whole brood to the nearest

191 0.0001g. After they had been weighed, the larvae were placed into an eclosion box, measuring $10 \times$

 10×2 cm, with 25 individual cells, each $2 \times 2 \times 2$ cm. An individual larva was placed in each cell

and covered with peat that was sifted to remove large chunks of soil. Each box held one brood. Water

194 was sprayed over the top to prevent desiccation during subsequent development, which typically

195 lasted 18–21 days.

196

197 Statistical analysis

All analyses were performed in R (version 3.5.1) (R Development Core Team 2018) using Bayesian

models in Stan (Stan Development Team 2021) implemented in *brms* (Bürkner 2017; 2018).

200 Additional packages used for the analysis and plotting of data in this paper include: *tidyverse*

201 (Wickham 2017), ggplot2 (Wickham 2009), tidybayes (Kay 2019), and modelr (Wickham 2018).

Bayesian models run through *brms* provide an estimate of the slope (β) with 95% credible intervals

(CI), which gives an indication as to the effect of the variable in question. If the 95% CIs for the β

estimate did not overlap with 0, we assessed the model's predictive ability by comparing the model

205 containing the variable of interest with a simpler model that did not contain the variable (or

²⁰⁶ interaction of variables) of interest. We compared these models using leave-one-out (loo) cross-

validation and calculated the relative weight of each model to evaluate which model had the highest

likelihood of predicting future data (Vehtari et al. 2017). Models fit in this manner move away from

the dichotomy of deciding whether a variable is significant or non-significant and assess both the

strength of a variable's effect, and the predictive ability of the model. Post-hoc contrasts between

different pairs were performed using the "hypothesis" function in *brms*.

212

We tested our predictions by focusing on the presence of a feeding incision on the prepared carrion nest at 53h after pairing, using data from both the No Care and Full Care post-hatching environments (see Fig. 1) since parents in both treatments had experienced the same opportunity to create a feeding

incision by this point. (Note, that when we refer to the 'No Care environment' and the 'Full Care

environment', we mean the within-generation treatment at the end of the experiment (shown in Fig.

1). We refer to the evolving lines as either the 'Full Care lines' or the 'No Care lines'). We treated the

219 presence or absence of a feeding incision on the carcass as a dummy variable with a Bernoulli

distribution where 0 = no feeding incision and 1 = feeding incision present.

222 The adaptive value of the feeding incision

We also investigated the fitness consequences of the feeding incision by asking how its presence or 223 absence influenced the likelihood that a brood would succeed (i.e., that the brood would have at least 224 one surviving larva at dispersal). We anticipated the relationship between the feeding incision and 225 brood success would be dependent on the care environment, and so split the No Care and Full Care 226 environment data and analysed each separately. For this analysis, we analysed brood success (success 227 vs fail) assuming a Bernoulli distribution. The model included male line of origin (i.e., descended 228 from a No Care or Full Care line) and female line of origin (i.e., descended from a No Care or Full 229 Care line) and their interaction, along with the presence or absence of a feeding incision as a two-level 230 factor. 231

232

233 Adaptation and co-adaptation

We tested whether the lines of origin of both males and females each independently predicted the 234 presence of a feeding incision on a carcass. We coded males and females from the Full Care lines as 1 235 and individuals from the No Care lines as 0. The model included both the female and male lines of 236 origin and their interaction. Simpler models were then considered by first removing the interaction 237 between female and male lines of origin, then secondly removing each line of origin in turn, and 238 finally considering a model without either line of origin. For all analyses, the standardised (mean = 0, 239 sd = 1) mass of the carcass, and the standardised size of the male and the female were included as 240 covariates. Other covariates included in specific models are outlined below. 241

242

243 **Results**

244 The adaptive value of the feeding incision

In the No Care environment, the presence of a feeding incision before larval hatching increased the 245 success of the brood ($\beta = 1.02$, [0.28, 1.91], Fig. 2). Brood success could not be further explained by 246 any other divergence between the populations of origin, as the null model without female or male 247 background had the lowest loo values and half the model weight (Table 1). However, in the Full Care 248 environment, the presence of a feeding incision did not influence the success of the brood ($\beta = 0.21$, [-249 1.53, 2.27], Fig. 2). Brood success was partly explained by the female's line of origin, but this model 250 had no more explanatory power than the null model as shown by the small Δloo and almost equal loo 251 weight (Table 1). 252

253

254 Adaptation and co-adaptation

Replicating our previous finding (Jarrett et al. 2018a, Duarte et al. 2021), we found that homotypic No

²⁵⁶ Care pairs were more likely to insert a feeding incision by 53h after pairing than homotypic Full Care

- pairs (Fig. 3, NN versus FF *post-hoc* comparison in Table 2).
- 258

Focusing first on males, we found that a feeding incision was more likely to be made if the male was

- drawn from a No Care population than a Full Care population (Fig. 3, Table 3). This was true
- regardless of the female's line of origin. The No Care homotypic pair and the heterotypic pair of a No
- ²⁶² Care male and a Full Care female (Fig. 2, Table 3) did not differ in their likelihood of creating a
- ²⁶³ feeding incision (Fig. 3; NN versus FN *post-hoc* comparison in Table 2). Therefore, we conclude that
- No Care males have unilaterally adapted their carcass preparation behaviour in response to the No
- 265 Care treatment.
- 266
- ²⁶⁷ Turning to females, we found evidence that the presence of a feeding incision depended on the
- female's line of origin matching the male's line of origin (Fig. 3; interaction between sex and line of
- origin: $\beta = 1.06$, [-0.02, 2.15]). We accounted for the strong effect of a No Care male's presence by
- focusing on comparisons with pairs involving Full Care males. Here, we found that a feeding incision
- was more likely to be made when a No Care female was paired with a No Care male, than with a Full
- 272 Care male (NN vs NF comparison in Table 2). It was also more likely when a Full Care male was
- paired with a Full Care female rather than a No Care female (FF vs NF comparison in Table 2).
- Therefore, we conclude that females have co-adapted their carrion preparation behaviour to match the male's behaviour.
- 276

277 Discussion

We have previously shown that pairs of burying beetles evolved to prepare their carrion nest more 278 rapidly when they were persistently prevented from interacting with their larvae after hatching 279 (Duarte et al. 2021). Specifically, pairs evolved to hasten their insertion of a feeding incision in the 280 carrion so that it was more likely to be present before their larvae hatched in the No Care lines than in 281 the Full Care lines. The presence of a feeding incision contributes significantly to brood fitness when 282 broods are deprived of any post-hatching care, because there is a greater chance that at least one larva 283 survives until dispersal (Fig. 3; Duarte et al. 2021; Eggert, Reinking, and Müller 1998; Jarrett et al. 284 2018a). 285

286

We used this instance of experimental evolution to investigate a general problem. How do the joint 287 actions of a pair (or group) evolve in response to change in the wider environment – in this case the 288 enforced removal of parents prior to larval hatching? By setting up crosses within and between our 289 experimental No Care and Full Care lines, we dissected the evolution of carrion preparation behaviour 290 to determine how individual changes in males and females contributed to the accelerated expression 291 of this pair-level trait in the No Care lines. We found that No Care males had unilaterally evolved to 292 ensure the feeding incision was inserted sooner in the absence of post-hatching care. Nests prepared 293 by No Care males were more likely to bear a feeding incision, regardless of the female's line of 294 origin. The likelihood that a feeding incision would be made prior to larval hatching was secondarily 295

influenced by females, and the extent to which females were co-adapted to the behaviour of the male.
Although both sexes contribute to carrion preparation, males take the lead in carrying out this duty of
care. This might explain why evolutionary change in this pair-level trait was driven by the males in
our experiments, with secondary co-adaptation by females, rather than *vice versa*.

300

The strength of our conclusions is tempered by the fact that our experimental design lacked any 301 control pairings within replicate lines. (We had to sacrifice this treatment due to logistical 302 constraints). Nevertheless, from other data we have collected from these populations, we have no 303 reason to suppose that the replicate lines, within either the No Care or Full Care treatments, had 304 diverged by this stage of experimental evolution (Schrader, Jarrett, and Kilner 2015a; Schrader et al. 305 2017; Jarrett et al. 2018a; Jarrett et al. 2018b; Rebar et al. 2020; Duarte et al. 2021). If our conclusions 306 are broadly correct, then our expectation is that the evolution of other group or pair-level traits in 307 response to environmental change should be initiated unilaterally by the individual that takes that lead 308 in shaping these collective actions, and that this in turn will provoke swift social co-adaptation by 309 other members of the pair or group. 310

311

The coadaptation of male and female traits is likely to have favoured a distinct combination of

socially interacting genes in the two sexes (*cf* Linksvayer, Fondrk, and Page Jr 2009). For this reason,

previous theoretical analyses have suggested that socially coadapted traits within the family that are

divergent between populations could function as a post-mating mechanism for reproductive

isolation—because they cause hybrids to perform less well (e.g., Zeh and Zeh 2000; Gavrilets 2000;

Martin & Hosken 2003; Brandvain & Haig 2005). Evidence from burying beetles is consistent with

this view. *Nicrophorus vespilloides* has recently been split into two species, with *N. hebes* now

recognised as a distinct bog-breeding specialist that lives mostly in Canada (Sikes et al. 2016).

320 Speciation is sufficiently recent that *N. hebes* can still hybridise with Alaskan populations of *N*.

vespilloides to produce viable offspring. Nevertheless, hybrids perform less well, partly because

322 hybrid larvae are less viable (at least in a No Care post-hatching environment). Experimental work

indicates that hybrid pairings produce fewer eggs and have lighter broods than pure-bred populations

324 (Sikes et al. 2016). The reduced performance of hybrids could also be due to coadaptation between

325 care-giving adults, although this possibility remains to be tested explicitly.

326

327 Social coadaptations contribute to post-mating reproductive isolation in other species (e.g., Zeh and

Zeh 2000; Gavrilets 2000; Martin & Hosken 2003; Brandvain & Haig 2005). The key barrier is the

high level of coordination between interacting individuals. This is true whether coordination results

from cooperation or conflict. It is seen in viviparous species, for example, through the highly specific

331 structures that have evolved to coordinate the supply of resources from mother to offspring in

viviparous fish (Schrader & Travis 2008; Furness et al. 2019) and placental mammals (Roy 2022).

- We have shown here that the highly coordinated activities jointly undertaken by male and female
- burying beetles in converting carrion into an edible nest can also become coadapted and cause
- heterotypic pairings to perform less well. In future work, it would be interesting to test whether the
- coadaptations involved in other types of coordinated cooperative social activities, such as the
- 337 construction of nests or burrows, collective immunity, or the joint defence of a key resource, could
- also potentially function as a post-mating barrier to gene flow between populations.
- 339

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- 348

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479 Figures

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Figure 1 | (A) Experimental design, showing all possible crosses between lines, including all replicate 483 lines within parental care treatments. Green boxes indicate the crosses that were made, red boxes 484 indicate the crosses that were not made. FC = Full Care, NC = No Care; numbers refer to replicate 485 lines. (B) The experimental design in detail. Four lines were generated from a source population that 486 formed two replicate Full Care (in red) and two replicate No Care (in blue) lines. The Full Cares lines 487 evolved in a Full Care environment (red solid lines) and the No Care lines evolved in a No Care 488 environment (blue dashed lines) for 15 generations (see Schrader et al. 2017 for more information 489 about the experimental set up). After 15 generations of breeding in these contrasting environments, 490 individuals from each population were passed through a common garden regime, in which all broods 491

- received Full Care to minimise variation between lines due to parental effects. The populations were
- then crossed. The two control groups involved crossing the populations that had evolved under the
- same social environment during development: Full Care pairs (left red solid box) were formed by
- ⁴⁹⁵ males and females from FC1 and FC2; and No Care pairs (right blue dashed box) were formed by
- ⁴⁹⁶ males and females from NC1 and NC2. The two experimental groups (middle red dashed boxes)
- 497 involved crossing populations that have evolved under different social environments during
- development. We only crossed one Full Care line with its No Care replicate (FC1 with NC1, and FC2
- with NC2) for both sets of crosses. The offspring from each pair were then randomly allocated one of
 the social environments (Full Care or No Care) as a treatment during larval development.
- 501 502



Figure 2 | The proportion of successful broods when the feeding incision in the carcass was either
 present or absent prior to larval hatching, in a No Care and Full Care post-hatching environment.
 Predicted values (and 95% credible intervals) are shown derived from the model with carcass mass
 and female and male standardised size as other covariates.

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Figure 3 | The proportion (and 95% credible intervals that describe the posterior distribution of the estimate) of prepared carrion nests found with an incision hole at 53 h after pairing, in relation to both the male and female's line of origin. Predicted means are shown and are derived from the model containing the lines of origin of the male and the female and their interaction, as well as all other

522 covariates.

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524 Tables

529

Table 1 | Summary of the model comparisons for brood success in No Care and Full Care environments, and, in the case of the No Care environment, whether the inclusion of the feeding incision as an explanatory variable alters which model best explains the data. A Δ loo of 0 indicates it has the lowest looic value, with the difference and standard errors of the difference listed for each

model. The looic weight is also listed for each model and sums to 1 for each set of models.

Mo	odel	Brood success		Brood success		Brood success	
		No Care with incision		No Care without incision		Full Care	
		Δloo	loo	Δloo	loo	Δloo	loo
			weight		weight		weight
Fen	nale	4.67 ± 2.77	0.05	2.21 ± 3.01	0.05	1.72 ± 1.79	0.14
×N	/lale						
Fen	nale	4.21 ± 1.28	0.06	3.54 ± 1.13	0.08	2.67 ± 1.85	0.09
+ N	/lale						
Fen	nale	1.67 ± 1.25	0.21	1.89 ± 0.96	0.19	0	0.33
Ma	le	2.07 ± 0.37	0.18	1.85 ± 0.86	0.19	1.45 ± 4.50	0.16
Nul	11	0	0.50	0	0.49	0.24 ± 3.68	0.29

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Table 2 | Post-hoc contrasts between all four combinations of female and male line of origin on the 542 predicted probability of the presence of a feeding incision. The difference between the posterior 543 distributions of the two pairs we are contrasting is shown, summarised by the mean and 90% CIs of 544 the resulting distribution. Treatments are listed with female first and male second (for example, FN is 545 a Full Care female paired with a No Care male). All comparisons are one-tailed save the FN vs NF 546 comparison. We predicted that the NN would have greatest probability of making an incision and FF 547 having the lowest probability, and so comparisons with these treatments were one-tailed accordingly. 548 We had no *a priori* expectation for FN vs NF, which is why it is a two-tailed comparison. Credible 549 intervals are 90% CIs except for the two-tailed test of FN vs NF which have 95% CIs. The final 550 column identifies which of the two pairs in the contrast is most likely to make the incision, when the 551 modulus of the contrast is greater than 0. 552

Contrast	Estimate	Credible	Pair more likely
		intervals	to make incision
FF vs NN	-0.95	[-1.53, -0.36]	NN
FF vs NF	0.74	[0.05, 1.44]	FF
FF vs FN	-0.62	[-1.18, -0.05]	FN
NN vs NF	-1.69	[-2.38, -1.03]	NN
NN vs FN	-0.33	[-0.86, 0.22]	neither
FN vs NF	-2.02	[-3.21, -0.73]	FN

Table 3 | Summary of the model comparisons the presence of the feeding incision. A Δloo of 0

indicates it has the lowest looic value, with the difference and standard errors of the difference listed

⁵⁵⁶ for each model. The looic weight is also listed for each model and sums to 1 for each set of models.

557	Model	reeding note	
		Δloo	loo
558			weight
559	Female	0.11 ± 4.21	0.41
560	× Male		
561	Female	1.84 ± 0.80	0.17
562	+ Male		
563	Female	17.71 ± 8.65	0.00
564	Male	0	0.42
565			
566	Null	15.56 ± 8.46	0.00