

Title: Constrained flexibility of parental cooperation limits evolutionary responses to harsh conditions

Running Title: Constrained plasticity of biparental care

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1 **Constrained flexibility of parental cooperation limits evolutionary responses to harsh**
2 **conditions**

3
4 **Abstract**

5 Parental care is predicted to evolve to mitigate harsh environments, thus adaptive
6 plasticity of care may be an important response to climate change. In biparental species, fitness
7 costs may be reduced with plasticity of behavior among partners. We investigated this prediction
8 with the burying beetle, *Nicrophorus orbicollis*, by exposing them to contrasting benign and
9 harsh thermal environments. We found strong fitness costs under the harsh environment, but
10 rather than select for more care, visualized selection was stabilizing. Examining different
11 components of care revealed positive directional selection gradients for direct care and strong
12 stabilizing selection gradients for indirect care, resulting in constrained evolutionary responses.
13 Further, because males and females did not coordinate their investments, the potential for
14 adaptive plasticity was not enhanced under biparental care. Females cared at capacity with or
15 without male partners, while males with partners reduced direct care but maintained indirect care
16 levels. Decision rules were not altered in different environments, suggesting no shift from sexual
17 conflict to cooperation. We suggest that the potential for parenting to ameliorate the effects of
18 our climate crisis may depend on the sex-specific evolutionary drivers of parental care, and that
19 this may be best reflected in components of care.

20
21 **Key words:** Biparental care, burying beetle, cooperation, environment, plasticity, temperature

22

23

24 **Introduction**

25 Parental care is expected to evolve to mitigate hostile and unpredictable environments
26 (Wilson 1975). However, the extent that ecological conditions further modify parenting once it
27 evolves may depend on plasticity of parental care in response to environmental stress; that is, the
28 phenotypic variation exposed to selection. One potential source of plasticity of care where such
29 variation might be exposed is biparental cooperation. Theoretically, the default of biparental
30 systems is sexual conflict over which parent cares (Lessells 2012), which can lead to overall care
31 deficits (McNamara et al. 2003, Lessells and McNamara 2012) and, ultimately, to one parent
32 being as effective or more effective at caring for offspring than two parents (Clutton-Brock 1991,
33 Smiseth et al. 2005, Trumbo 2006). However, the joint rearing of offspring may also allow
34 parents to breed under harsh conditions that would otherwise constrain single parent breeding
35 (Wilson 1975, Emlen 1982). This is because: 1) with more than one caregiver there is more
36 scope for increasing total care allocation (i.e., additive care; Ratnieks 1996, Clutton-Brock et al.
37 2001, Johnstone 2011, Savage et al. 2013), and 2) the efforts of a second parent may offset some
38 costs of care to the primary caregiver (i.e., load lightening; Crick 1992, Johnstone 2011). If true,
39 then transitions to stable biparental care and an increased capacity for cooperation should
40 coincide with expansion into increasingly harsh environments (Wesolowski 1994, 2004).

41 To date, tests of the ‘hostile environment’ hypothesis as it relates to cooperation over
42 offspring rearing have produced equivocal results (Wynne-Edwards and Timonin 2007,
43 AlRashidi et al. 2010, 2011, Öberg et al. 2015, Remeš et al. 2015, Wiley and Ridley 2016, Shen
44 et al. 2017, Vincze et al. 2017, Guindre-Parker and Rubenstein 2018, Lejeune et al. 2019, Lin et
45 al. 2019, Vági et al. 2020). However, the vast majority of insights derive from studies of birds –
46 a group for which biparental care is nearly ubiquitous and rarely decoupled from social

47 monogamy (Cockburn 2006). Hence, while reports of enhanced pair coordination under adverse
48 conditions (i.e., approaching egalitarian division of labor) accumulate from the bird literature
49 (AlRashidi et al. 2010, 2011, Vincze et al. 2017), the extent to which such causal links are
50 generalizable across taxa is unclear. Yet transitions to biparental care have occurred repeatedly
51 outside of the avian tree, including in diverse vertebrate (Reynolds et al. 2002) and invertebrate
52 lineages (Trumbo 2012, Suzuki 2013, Gilbert and Manica 2015). Such systems offer rich
53 opportunities to expand the taxonomic scope of investigations into the factors that shape
54 biparental care dynamics.

55 Burying beetles (Genus: *Nicrophorus*) provide an ideal complement to avian systems for
56 investigating the mechanisms of cooperation and conflict over offspring care (Smiseth 2019),
57 particularly in the context of environmental stress and plasticity. First, burying beetle parental
58 care reflects their ecology. The beetles breed on an ephemeral and widely desirable resource, a
59 dead vertebrate, resulting in both rapid development and parental care involving direct
60 provisioning of predigested food and defense of the developing young (Eggert and Müller 1997,
61 Scott 1998a). Burying beetles are also subsocial; they do not form social associations outside of
62 brief periods of parental care. Therefore, unlike most vertebrates, sources of variation in parental
63 investment can be readily dissociated from other pervasive aspects of social life. Second, we
64 know that there is capacity for plasticity of species that show biparental care because burying
65 beetle males do not work at their maximum. Indeed, parental care of burying beetles is sex-
66 biased, with females performing the majority of total caregiving duties (Eggert and Müller 1997,
67 Smiseth and Moore 2004, Benowitz and Moore 2016) while males provide less direct care in the
68 presence of a female partner (Parker et al. 2015, Pilakouta et al. 2018). The quantity or
69 composition of female behavior does not depend on the presence of a male. However, males of

70 this genus are also highly flexible and capable of adopting larger parental roles as needed to
71 compensate for compromised partner state (e.g., partner loss (Trumbo 1991, Smiseth et al. 2005,
72 Suzuki and Nagano 2009, Parker et al. 2015, Cunningham et al. 2019), handicapping (Creighton
73 et al. 2015), or inbreeding level (Mattey and Smiseth 2015). Finally, many burying beetles are
74 flexible in the social form of parenting they provide, with uniparental female care, uniparental
75 male care, and biparental care all expressed within natural populations (Trumbo 1991, Scott
76 1998a, Smiseth and Moore 2004, Suzuki and Nagano 2009, Benowitz et al. 2016). If it is true
77 that multiple parents provide more effective care to offspring in hostile conditions (i.e., through
78 additive and/or load-lightening effects), then members of the more flexible sex should also be
79 less inclined to withhold care in response to a generalized environmental stressor, which may
80 compromise the states of both parents.

81 Here, we use *Nicrophorus orbicollis* – a primarily biparental species and among the few
82 members of the temperate species complex to have successfully expanded into the warmer
83 climate of the US southeast (Trumbo 1990) – to examine the role that plasticity of parental
84 investment plays in mitigating harsh ambient conditions. High temperatures, as occur at low
85 latitudes, are generally implicated in more costly and less profitable reproduction in burying
86 beetles (Meierhofer et al. 1999, Müller et al. 2007, Steiger et al. 2007, Jacques et al. 2009,
87 Quinby 2016, Ong 2019, Feldman 2020). Individuals breeding under these conditions have been
88 found to suffer reduced lifespans and lower lifetime reproductive success (Laidlaw 2015). We
89 used a mixed factorial design with repeated measures to test whether beetles acclimated to high
90 temperature (i.e., harsh) breeding conditions respond by increasing parental investment. Further,
91 we quantified within-subject behavioral comparisons to examine the extent that sex-specific
92 plasticity and the capacity for biparental care drives responses to hostile environments. Contrary

93 to our prediction that plasticity of care will allow *N. orbicollis* to tolerate higher temperatures,
94 we find that there is stabilizing selection on total care with an optimum independent of the form
95 of care provided. This occurs because the components of care are under different forms of
96 selection, the components are not independent, and individual variation did not reflect a plastic
97 response to subtle variation in their partner's behavior.

98

99 **Methods**

100

101 *Study System*

102 *Nicrophorus orbicollis* is a large-bodied, ecological generalist that breeds on small (~20
103 g) to medium (~100 g) vertebrate carcasses in North American woodlands. The species has a
104 large latitudinal distribution (from southern Canada to northern Texas), with breeding seasons at
105 the southern margins characterized by higher temperatures (3–8°C on average) and a greater
106 frequency of reproductive failure (Trumbo 1990). As with most members of the genus, parental
107 care is elaborate and extends into the post-hatching stage (Eggert and Müller 1997, Scott 1998a).
108 During pre-hatching stages, parents work together to clean and prepare the carcass by removing
109 hair and applying anal secretions to prevent microbial growth. During the post-hatching stage,
110 parents continue to maintain the brood ball and also directly provision to begging young *via*
111 regurgitation. While larvae of most burying beetles can survive without parents (Schrader et al.
112 2015, Jarrett et al. 2018), *N. orbicollis* show obligate parental care, meaning that larvae depend
113 on direct provisioning for survival (Trumbo 1992, Capodeanu-Nägler et al. 2016, 2018). Parental
114 care is described as predominantly biparental on the basis that males and females typically
115 overlap with each other in the post-hatching stage (in 66% of cases; Benowitz and Moore 2016),

116 and both sexes perform the full repertoire of parenting behaviors (Scott and Traniello 1990,
117 Trumbo 1991, Scott 1998a). However, as is the case with any reproductive systems studied in
118 detail, individual investment is highly flexible and subject to environmental and social pressures
119 (Trumbo 1991, Scott 1998b, Creighton et al. 2015).

120

121 *Field collection and husbandry*

122 *Nicrophorus orbicollis* were captured from Whitehall Forest, Athens GA, in the summer
123 of 2020. Beetles were baited into hanging traps with salmon and collected twice weekly to breed
124 an outbred laboratory colony. Simultaneously, ThermoChron® iButton temperature loggers
125 (©Maxim Integrated Products, Inc., San Jose, CA, U.S.A) were deployed ~10–12 cm
126 underground at trap locations throughout our collection site to estimate the range of temperatures
127 beetles likely experience in their subterranean brood chambers. *Nicrophorus orbicollis* begin
128 emerging from hibernation in early spring and reach peak densities around midsummer (between
129 late June and early August; Ulyshen and Hanula 2004). In 2020, mean daily temperatures during
130 these two potential breeding windows – late spring/early summer (31 May–03 July) and mid/late
131 summer (15 July–22 August) – ranged between $21.71 \pm 1.38^\circ\text{C}$ and $23.82 \pm 0.77^\circ\text{C}$, respectively
132 (Fig S1). Diurnal temperature fluctuations were between 0.75°C and 7.71°C . To capture this
133 variation in the laboratory, we programmed two incubators to ramp between set points of diurnal
134 temperatures over the course of 10:14 hour reverse light: dark cycles, simulating early and late
135 summer breeding conditions, respectively. The first treatment, hereafter the ‘benign’ thermal
136 environment, was set to ramp between 19°C (night) and 20°C (day), while the second, hereafter
137 the ‘harsh’ thermal environment, was set to ramp between 23°C (night) and 24°C (day). Focal
138 individuals for the experiment were selected from F01 and F02 colony lines, which were bred on

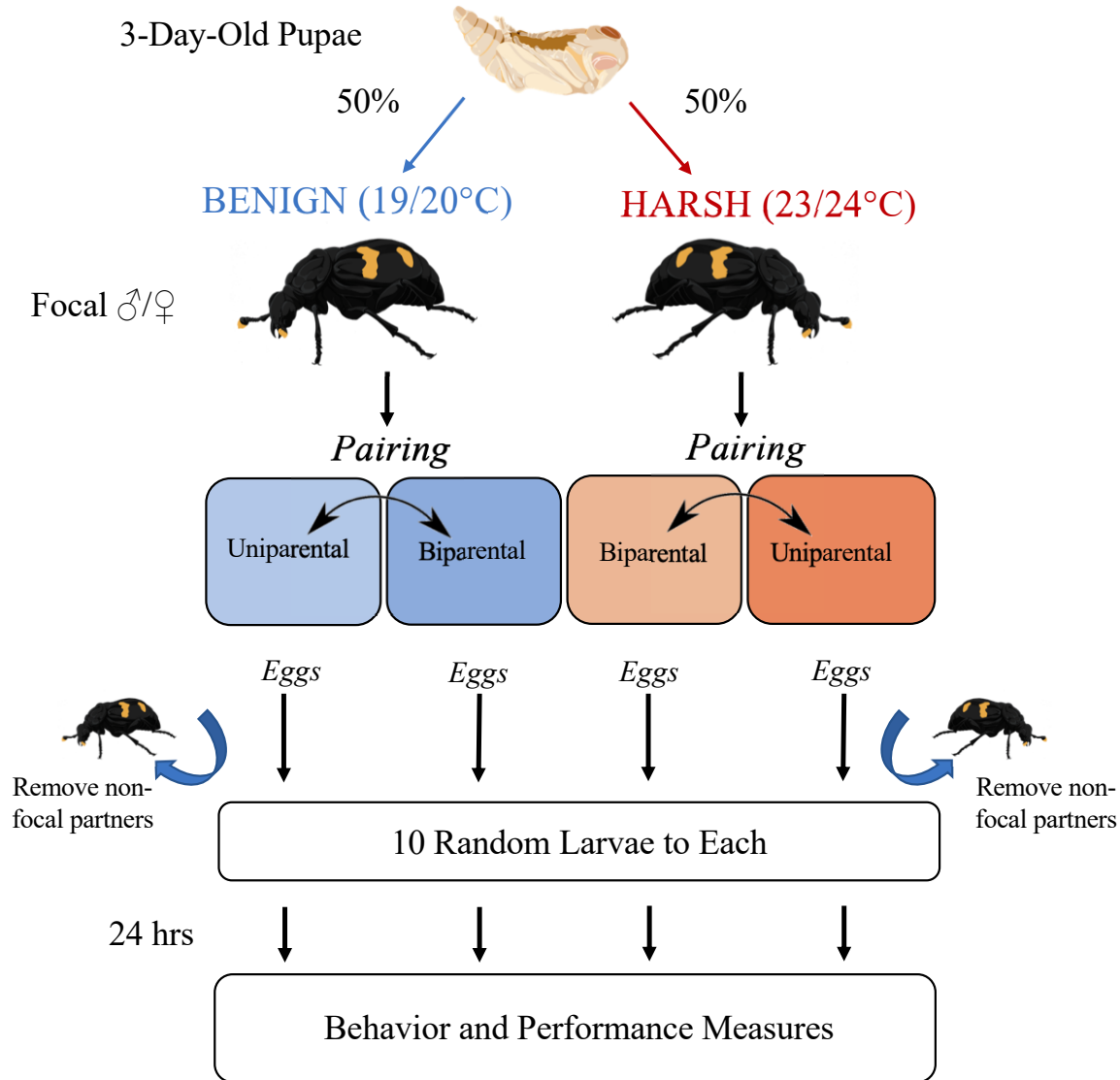
139 countertops at room temperature ($20\pm 0.5^{\circ}\text{C}$). Larvae were divided evenly between the treatment
140 incubators on the third day of pupal development to facilitate acclimation (adults eclosed into the
141 environment in which they would ultimately breed) while controlling for possible early
142 developmental effects of temperature. All virgins selected for the experiment were at least 14
143 days of age.

144

145 *Breeding trials*

146 Breeding trials were carried out between October 2020 and January 2021. We used a
147 mixed factorial design as outlined in Figure 1, in which social condition (uniparental or
148 biparental) was measured as a within-subject factor and thermal environment (Benign or Harsh)
149 was measured as a between-subject factor. The goal was to achieve a balanced experimental
150 design with respect to the number of individuals undergoing repeated trials ($N = 20$ males and
151 females per thermal environment), which would allow us to explicitly quantify differences in
152 individual plasticity between the two thermal environments. To facilitate this, we randomized the
153 order in which focal individuals were exposed to either social condition. To create the biparental
154 condition, individuals were paired to a focal individual of the opposite sex within the same
155 thermal environment. To create the uniparental condition, individuals were paired to a random
156 unrelated beetle of the opposite sex (also within the same thermal environment) who would be
157 removed between egg laying and hatching. Individuals who successfully completed their first
158 trial would continue on to a second trial in the opposite social condition, while individuals that
159 failed their first trial within seven days of pairing were restarted. Beetles were allowed one
160 failure on their first attempt.

161



162
163 **Figure 1:** Schematic of mixed factorial experimental design. Focal individuals of each sex were
164 divided evenly between the treatment incubators on the third day of pupal development to
165 facilitate thermal acclimation (thermal environment = between-subject factor). At pairing,
166 individuals were assigned randomly to a starting social condition (uniparental or biparental) and
167 restarted in the opposite social condition upon successful completion of a first trial (social
168 condition = within-subject factor). In uniparental trials, non-focal parents were removed after egg
169 laying. All eggs were collected prior to hatching and each widowed parent or biparental pair was
170 allocated a standardized number of larvae (N=10) of random genetic origin. Behavioral and
171 performance measures were collected starting 24 hours into care.
172

173 At the start of each trial pairs were placed in a plastic box (17.2 x 12.7 x 6.4 cm; Pioneer
174 Plastics, Dixon, KY, USA) filled with approximately two cm of moistened potting soil and

175 containing a freshly thawed mouse carcass between 40 and 45 g (RodentPro, Evansville, IN,
176 USA). Boxes were returned to the incubator where they were kept on a darkened shelf beneath
177 blackout curtains to simulate an underground breeding environment. From pairing, breeding
178 boxes were checked twice daily for eggs. Pairs with no eggs after seven days were restarted on a
179 new mouse. Two days after eggs were first recorded, the brood ball and focal beetle(s) were
180 transferred to a new breeding box (non-focal parents were removed) such that eggs could be
181 collected and counted. This step was performed to facilitate brood standardization, which
182 ensured that comparisons of performance would be attributed to parental care rather than
183 differences in fertility or genetic quality. Eggs were placed in petri dishes with damp filter paper
184 and monitored every 8 hours until larvae appeared. At this stage, synchronously hatching broods
185 were randomly mixed, and each pair of fertile parents was given exactly 10 larvae. Broods that
186 failed to hatch within five days of laying were recorded as unfertilized, and the pair was
187 restarted.

188

189 *Behavior and performance measures*

190 Behavioral observations were carried out 24 hours after introducing larvae, as previous
191 work indicates that offspring provisioning peaks around this time (Smiseth et al. 2003). Breeding
192 boxes were placed in a dark, temperature-controlled observation room (20°C) and allowed to
193 acclimate for 30 minutes, ensuring that observed differences in parenting could not be attributed
194 solely to temperature-dependent activity. Observations took place under red light over a 30-
195 minute period. Behaviors were recorded every minute *via* instantaneous scan sampling. These
196 included any instances of direct provisioning (i.e., mouth-to-mouth contact suggesting
197 regurgitation of food to larvae), oral pre-treatment of feeding substrates (i.e., opening up the

198 cavity or self-feeding to facilitate subsequent regurgitations), offspring association (i.e., in
199 physical contact with larvae but not provisioning), carrion maintenance (i.e., positioned under
200 brood ball or walking over brood ball exuding antimicrobial secretions), self-grooming, and off
201 brood ball. Individual behaviors were then grouped into two broad categories – direct care (direct
202 provisioning, oral pre-treatment of feeding substrates, and offspring association) and indirect
203 care (carrion maintenance) – to arrive at 2x budget scores (ranging between 0 and 30) for each
204 parent in each trial. “Self-grooming” and “off brood ball” were regarded as non-caring behaviors
205 and were interpreted only in the inverse. For biparental pairs, total direct and indirect care were
206 calculated by summing the time budget scores of the two parents.

207 After completing observations, brood boxes were returned to incubators and subsequently
208 checked three times per day for parental desertion. Desertion was inferred when beetles were
209 observed buried in the dirt away from the brood ball for three consecutive observations
210 (Hopwood et al. 2015, Parker et al. 2015, Benowitz and Moore 2016). At this point, beetles were
211 removed, and we recorded the duration of care (in days). Final weights were taken for each
212 beetle at the end of a breeding trial, and those due for a second trial were fed and returned to the
213 incubator for 1–2 days prior to restarting. To calculate and compare performance across trials,
214 we measured two traits implicated in parental performance: total number of offspring surviving
215 to the end of a breeding trial and mean larval mass (Parker et al. 2015). These measures were
216 taken only after larvae dispersed naturally from the brood ball, to ensure maximal feeding time.

217

218 *Statistical analyses*

219 All statistical analyses were conducted in R v. 4.0.3 (R Core Development Team 2019)
220 using the package lme4 (Bates et al. 2015). We first examined evidence for fitness costs

221 associated with the high temperature environment. Because a large number of deaths were
222 recorded over the course of our experiment, our first analysis was of parental longevity. We used
223 a Cox proportional hazard regression model implemented in the R package ‘survival’ (Therneau
224 and Lumley 2015) to test the association between thermal environment and mortality, adjusting
225 for sex. Our second analysis was of reproductive parameters. We used two-tailed *t*-tests to
226 contrast the means of fecundity, fertility, and development time across all trials. To compare
227 realized performance (number and mean mass of dispersing larvae), we used simple linear
228 regression with thermal environment as a main effect and breeding history (binary specifying at
229 least one previous breeding success between parents) as a covariate, to account for variation in
230 parental experience within our study design.

231 After identifying costs associated with thermal stress, we split the dataset by thermal
232 environment and examined evidence for variation in behaviors under selection. We explored
233 how care influenced fitness through environment-specific performance gradients. We first
234 plotted the relationship between standardized offspring mass and care allocation by social
235 condition. Overall selection was visualized using total care (sum of all direct and indirect care).
236 We next calculated standardized selection gradients (Lande and Arnold 1983, Brodie et al. 1995)
237 for different components of care using number of larvae and mean larval mass to estimate
238 fitness. We examined both linear and non-linear selection on components of parenting
239 (maximum number of days parents attended, cumulative direct care, and cumulative indirect
240 care). We then examined intra-environmental variation in parenting as a function of social
241 condition by performing a mixed model analysis of variance (ANOVA) for each metric followed
242 by specified *a priori* pairwise contrasts, comparing uniparental and biparental care behavior
243 within a sex, implemented using the lsmeans package (Lenth 2016). To control for repeated

244 measures of focal parents, we included male and female IDs as random block effects in the
245 model design.

246 Our final analysis examined variation among individuals. We asked whether variation of
247 parenting behavior reflected individual plasticity by examining patterns of individual behavior
248 across the two thermal acclimation environments. To achieve this, we split the dataset by sex,
249 retaining only individuals with repeated measures of behavior, and quantified how much
250 behavioral variation *within* environments could be attributed to social plasticity. We first
251 performed separate repeated-measures ANOVAs for each sex and thermal environment, using
252 social condition as the within-subject factor and individual ID nested within trial number as the
253 error term. To understand how individual male and female behaviors varied *between*
254 environments, we carried out repeated-measures multivariate ANOVAs (RM MANOVA) using
255 the R package, MANOVA.RM (Friedrich et al. 2019). The three behavioral metrics were
256 specified as response variables and thermal environment was specified as a between-subject
257 factor. To facilitate comparisons of duration of care given temperature-dependent larval
258 development rates, attendance times were divided by the mean development times within each
259 thermal environment. Wald-type statistics (WTS) and resampling *P*-values are reported for
260 within- and between-subject factors and their interaction.

261

262 **Results**

263 Over the course of this experiment, we initiated 358 breeding trials spread over two thermal
264 environments and three social conditions. Only 165 trials resulted in larvae that survived through
265 the 24-hr behavioral observation period. These included 32 biparental pairs, 29 uniparental
266 males, and 30 uniparental females in the harsh environment, and 26 biparental pairs, 23

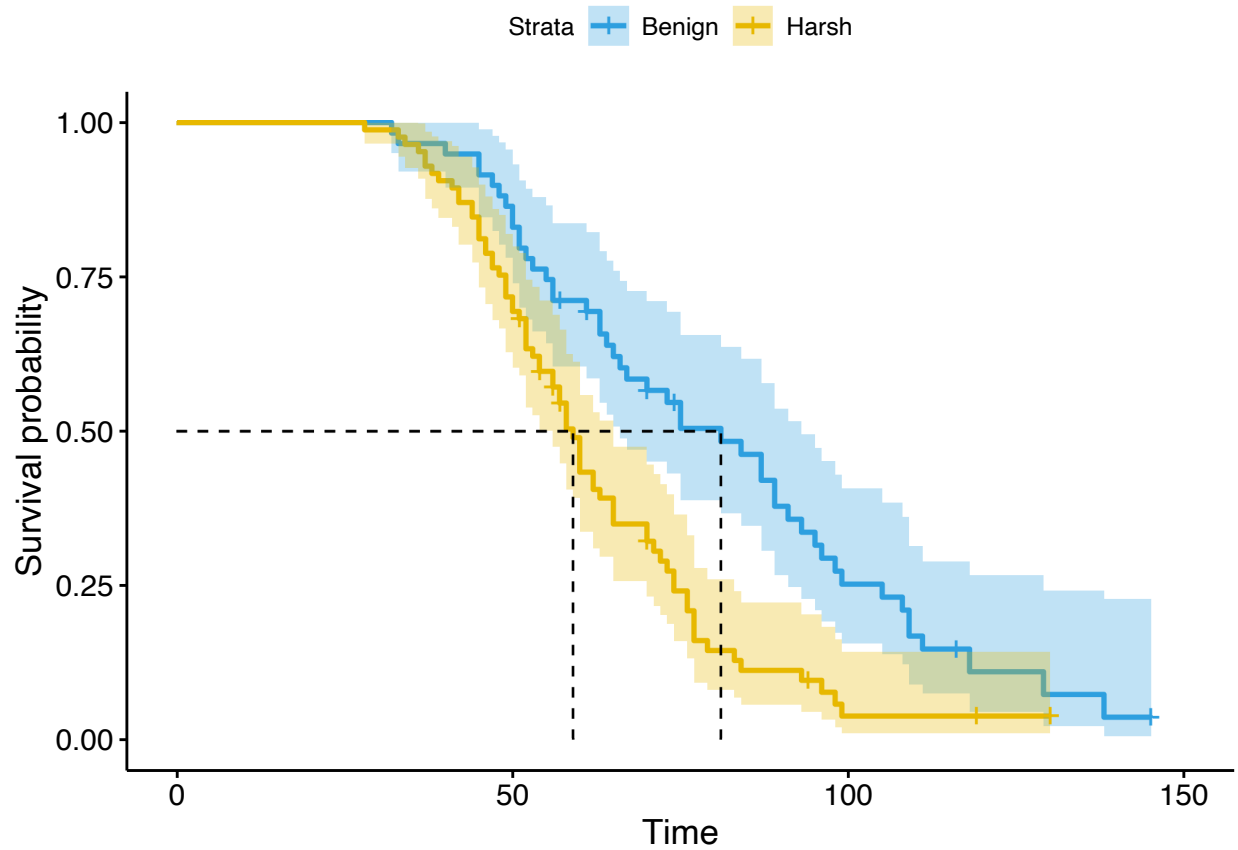
267 uniparental males, and 25 uniparental females in the benign environment. The final number of
268 focal individuals with repeated measures amounted to 18 males and 20 females in the harsh
269 environment and 20 males and 20 females in the benign environment.

270

271 *Fitness Costs of Thermal Stress*

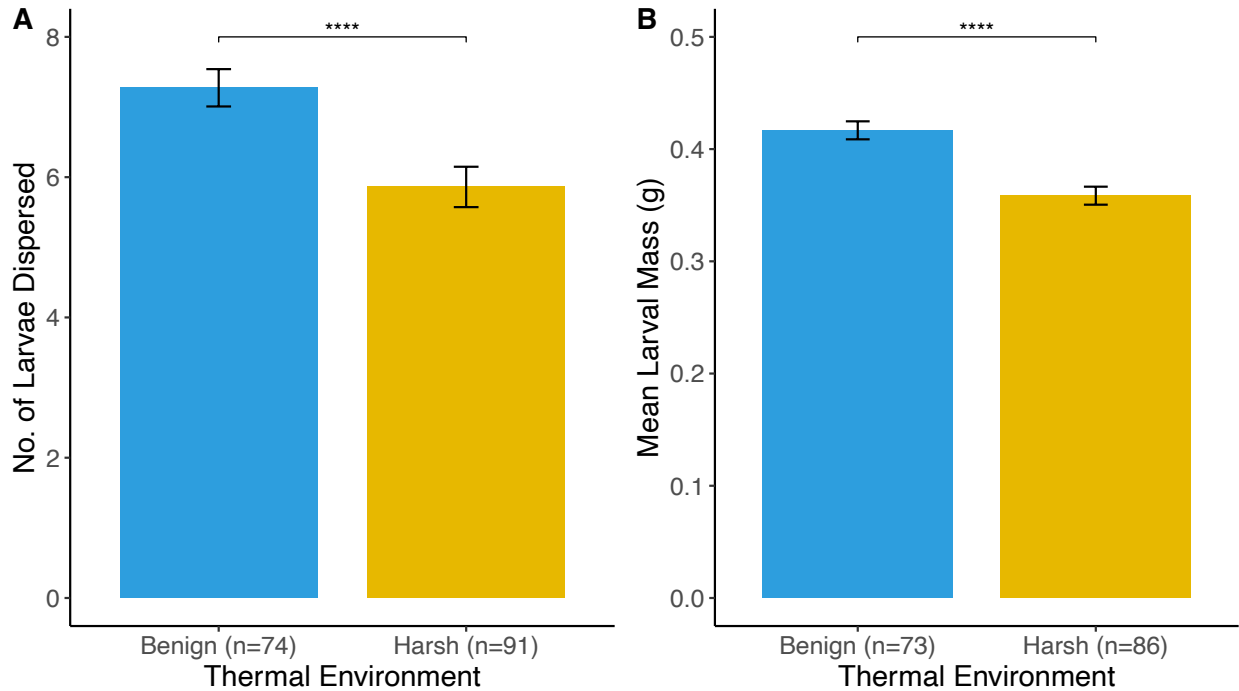
272 We observed strong adverse effects on fitness associated with thermal stress. Focal
273 beetles in the harsh environment suffered a 47.6% higher mortality risk compared to counterparts
274 in the benign environment (95% CI (1.43, 3.09), $P < 0.001$; Fig 2), with males outliving females
275 (HR = 0.62, 95% CI (0.43, 0.90), $P = 0.013$). Within breeding trials, mortality accounted for
276 21.7% of failures among inexperienced breeders, and 31.6% among experienced breeders
277 (compared to 12.9% and 10.2% in the benign environment, respectively). Reduced fecundity and
278 infertility were other sources of breeding failure, with beetles laying fewer ($t_{207.59} = -2.68$, $P =$
279 0.008) and less fertile ($t_{211.25} = -2.13$, $P = 0.034$) eggs under thermal stress. In trials that
280 progressed through the dispersal stage, larvae developed significantly faster in the harsh
281 environment (6.04 ± 1.47 days) compared to the benign (7.23 ± 1.38 ; $t_{155.41} = -5.24$, $P < 0.001$) and
282 were reduced for both number ($F = 16.769$, $df = 1, 162$, $P < 0.001$) and mass ($F = 22.346$, $df = 1,$
283 156 , $P < 0.001$; Fig 3). Parental breeding history had no effect on either larval number ($F = 4.458$,
284 $df = 1, 162$, $P = 0.409$) or larval mass ($F = 0.019$, $df = 1, 156$, $P = 0.891$).

285



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Figure 2: Survival curves calibrated from the mortality times of 144 beetles (25 censored) assigned to the benign (blue line; N = 59) and harsh (orange line; N = 85) thermal environments. Dotted lines indicate median lifespans for each environment, in days.

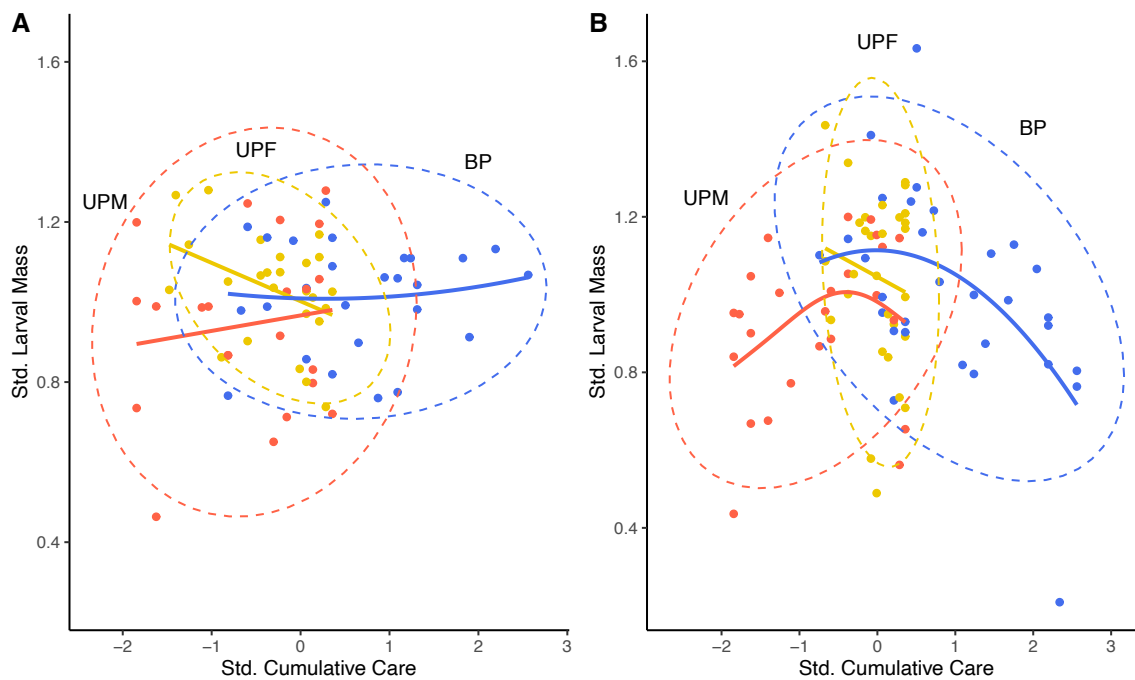


291
292 **Figure 3:** Comparisons of average breeding performance across all social conditions between the
293 benign and harsh thermal environment. Performance is compared based on (A) number of larvae
294 dispersed, and (B) mean larval mass (in g). Asterisks indicate significant differences at
295 $\alpha=0.0001$.
296

297 *Selection on Care*

298 Visualizing selection, we found that care provided negligible fitness benefits under
299 benign conditions (Fig 4A) and became harmful under stressful conditions (Fig 4B). Duration of
300 parental attendance had significant linear effects on the number of offspring reared to dispersal in
301 both environments (Table 1a, b). However, selection acting on distinct components of care
302 differed between the two thermal environments. While there was no statistically significant
303 selection acting on direct or indirect care in the benign environment, we found significant
304 directional and stabilizing selection for different care components specific to the harsh
305 environment. Total provisioning effort showed a positive linear relationship with brood size,
306 whereas significant nonlinear effects on both larval size and number were detected in association
307 with extreme values of indirect care. Thus, the harsh environment selected for increased time in

308 direct provisioning and intermediate time in carcass maintenance. Variation was largely
309 attributed to the number and sex of parents, as all behaviors varied significantly with social
310 condition under both environmental conditions (Table 2a,b) and pairwise comparisons identified
311 only indirect care as being significantly increased for biparental pairs relative to uniparental
312 females (Table 3).
313



314
315 **Figure 4:** Relationship between standardized total parental time allocation to care (direct +
316 indirect) and standardized mean larval mass in the (A) benign environment, and (B) harsh
317 environment. Data points belonging to each of three social conditions (uniparental male (UPM),
318 uniparental female (UPF), and biparental (BP)) are differentiated by color (red = UPM, yellow =
319 UPF, blue = BP). Labeled ellipses illustrate 95% confidence intervals, and approximate splines
320 illustrate overall trends in the data.

321
322

323 **Table 1:** Linear (β) and nonlinear (γ) standardized selection gradients (Lande and Arnold 1983,
 324 Brodie et al. 1995) relating brood performance (measured as number of larvae dispersed and
 325 mean larval mass (in g)) to behavioral measures of parenting effort. Selection gradients are
 326 presented separately for the (a) benign, and (b) harsh environment. Statistically significant
 327 gradients (at $\alpha=0.05$) are highlighted in bold.
 328

Behavioral Measure	N	Larval Number				Mean Larval Mass				
		β	<i>P</i>	γ	<i>P</i>	N	β	<i>P</i>	γ	<i>P</i>
(a) Benign Environment										
Days Attended	74	0.124 (± 0.034)	<0.001	-0.259 (± 0.078)	0.078	73	0.028 (± 0.021)	0.179	-0.006 (± 0.050)	0.907
Total Indirect Care	74	0.058 (± 0.035)	0.097	-0.025 (± 0.052)	0.632	73	-0.004 (± 0.020)	0.832	-0.005 (± 0.032)	0.867
Total Direct Care	74	0.042 (± 0.034)	0.228	0.008 (± 0.050)	0.868	73	0.028 (± 0.019)	0.164	-0.021 (± 0.031)	0.513
(b) Harsh Environment										
Days Attended	91	0.161 (± 0.052)	0.002	-0.089 (± 0.131)	0.497	86	0.039 (± 0.027)	0.167	0.035 (± 0.068)	0.610
Total Indirect Care	90	-0.001 (± 0.052)	0.992	-0.165 (± 0.069)	0.020	85	-0.037 (± 0.027)	0.179	-0.100 (± 0.035)	0.006
Total Direct Care	90	0.102 (± 0.051)	0.049	0.008 (± 0.060)	0.896	85	0.021 (± 0.026)	0.416	-0.053 (± 0.029)	0.069

329

330 **Table 2:** Mixed model ANOVAs testing the effects of social condition (uniparental male,
 331 uniparental female, and biparental) on parental effort (the total time allocated to indirect or direct
 332 care during a 30-minute observation) for three forms of care. Results are reported separately for
 333 the benign and harsh environment, with male and female IDs treated as random factors.
 334

Model	MS	Num <i>df</i>	Den <i>df</i>	<i>F</i>	<i>P</i>
(a) Benign Environment					
Days Attended	20.06	2	71.00	8.60	< 0.001
Total Indirect Care	5.00	2	37.75	12.34	< 0.001
Total Direct Care	96.68	2	40.05	6.22	0.004
(b) Harsh Environment					
Days Attended	14.37	2	57.81	15.65	< 0.001
Total Indirect Care	18.05	2	61.10	27.36	< 0.001
Total Direct Care	124.98	2	63.29	3.20	0.047

335

336

337 **Table 3:** *a priori* determined pairwise comparisons of parental effort among pairs within the
 338 same acclimation environment, benign or harsh. For each dataset, biparental (BP) is the reference
 339 group against which uniparental female (UPF) and uniparental male (UPM) observations are
 340 contrasted. Effects with statistically significant *P*-values (at $\alpha=0.05$) are shown in bold.
 341

<i>Contrast</i>		<i>t</i>	<i>P</i>
<i>Days Attended:</i>			
Benign Environment	BP – UPF	-0.836	0.684
	BP – UPM	3.080	0.010
Harsh Environment	BP – UPF	0.069	0.997
	BP – UPM	4.967	< 0.001
<i>Total Indirect Care:</i>			
Benign Environment	BP – UPF	3.885	0.001
	BP – UPM	4.119	< 0.001
Harsh Environment	BP – UPF	3.952	0.006
	BP – UPM	7.127	< 0.001
<i>Total Direct Care:</i>			
Benign Environment	BP – UPF	1.250	0.430
	BP – UPM	3.408	0.005
Harsh Environment	BP – UPF	0.391	0.919
	BP – UPM	2.328	0.064

342

343 *Plasticity of Biparental Care*

344 For plasticity of biparental care to help mitigate increased environmental costs of parenting,
 345 males and females should adjust investment strategies to complement, rather than overlap, with
 346 care components of their partner. We found sex-specific tradeoffs in parenting behaviors,
 347 consistent with covariance underpinning potential responses. Repeated measures ANOVA tests
 348 identified social condition as an important factor explaining within-subject variation of parenting
 349 behavior, but these effects were sex-specific (Table 3). Females were not plastic and appeared to
 350 care at capacity regardless of thermal environment or social condition. Conversely, male
 351 parenting effort varied significantly between social conditions, most dramatically in terms of
 352 duration of care (Table 4). Further, males in the harsh environment significantly reduced their
 353 provisioning effort when paired with a female but maintained the same levels of indirect care
 354 (Table 4). Between-treatment comparisons largely recapitulated these sex-specific patterns:
 355 social condition emerged as a significant predictor of overall within-subject behavioral variation

356 in males (WTS = 15.691, $P < 0.001$) but not in females (WTS = 4.816, $P = 0.185$). Neither males
 357 nor females showed significant differences in parenting behavior between thermal environments
 358 (Males: WTS = 0.399, $P = 0.945$; Females: WTS = 3.752, $P = 0.295$). Moreover, adaptive
 359 plasticity of biparental care did not mitigate effects of environmental stress because the
 360 interaction of within-treatment (social condition) and between-treatment (thermal environment)
 361 effects was not significant.

362

363 **Table 4:** Repeated-measures ANOVAs quantifying behavioral plasticity of individual female
 364 and male parenting behaviors (days in attendance and time allocation to indirect and direct care
 365 during a 30-minute observation). Test statistics are reported separately for each sex and thermal
 366 environment (benign and harsh), where social condition (uniparental or biparental) is the within-
 367 subject factor and individual ID nested within trial number is the error term. Effects with
 368 statistically significant P -values (at $\alpha=0.05$) are shown in bold.

369

Behavior	Test statistic	<i>Benign</i>		<i>Harsh</i>	
		Female	Male	Female	Male
Days Attending	<i>F</i> (df)	0.730 (1,19)	18.4 (1,19)	3.307 (1,19)	4.994 (1,17)
	<i>P</i>	0.403	< 0.001	0.085	0.039
Indirect Care	<i>F</i> (df)	0.231 (1,19)	0.699 (1,19)	0.632 (1,19)	0.252 (1,17)
	<i>P</i>	0.637	0.413	0.436	0.622
Direct Care	<i>F</i> (df)	0.101 (1,19)	3.165 (1,19)	0.012 (1,19)	4.754 (1,17)
	<i>P</i>	0.755	0.091	0.912	0.044

370

371

372 Discussion

373 In this study, we investigated the potential of plasticity of biparental care to ameliorate a
 374 harsh environment in a burying beetle, *Nicrophorus orbicollis*. Our prediction was that offspring
 375 receiving more care through additive or load lightening benefits of multiple caregivers would
 376 fare better under harsh environmental conditions. We tested this by exposing families with
 377 different parental compositions to thermal stress and identifying behavioral correlates of
 378 performance using standardized selection gradients. The patterns that emerged were opposite to
 379 expectations: the harsh environment favored intermediate, not high overall parental investment,

380 but the type of care was important, and components were not independent of each other.
381 Plasticity of biparental care did not help overcome constraints because decision rules for
382 investment were sex-specific and were unaltered by generalized stress on the family. The
383 consequence was that in biparental pairs under environmental stress, females overinvested, and
384 males contributed only to care types that caused a decrease in fitness in excess. These results
385 challenge our understanding of the adaptive role of biparental care in hostile environments.

386 The thermal stress we imposed had strong deleterious fitness effects compared to a more
387 benign temperature. Not only did adults acclimated to the warmer environment suffer reduced
388 lifespans and lower reproductive potential per bout, but offspring were also less likely to survive
389 to dispersal and attained lower body mass than counterparts in the benign environment. Our
390 results are consistent with both field and laboratory studies of the genus noting significant
391 performance declines along gradients of temperatures (Meierhofer et al. 1999, Müller et al. 2007,
392 Steiger et al. 2007, Jacques et al. 2009, Quinby 2016, Ong 2019, Feldman 2020). Given these
393 severe fitness costs, we expected there would be selection pressure to cope with extreme
394 temperatures.

395 Because environmental hostility exacerbates offspring vulnerabilities, systems with
396 dependent young should benefit from the capacity to increase parental investment when
397 confronted with more extreme environments (Wilson 1975, Wesolowski 1994, 2004). Burying
398 beetles are known for the level of plasticity they show in parental care, especially in response to
399 social condition, with uniparental female, uniparental male, and biparental care possible for
400 many species including *N. orbicollis* (Trumbo 1991, Scott 1998a, Smiseth and Moore 2004,
401 Suzuki and Nagano 2009, Benowitz et al. 2016). We predicted that given this extant plasticity,
402 care by two parents would have greater capacity to respond to increased offspring need. Contrary

403 to this expectation, our high-stress environment did not induce strong and consistent directional
404 selection relative to the benign environment. Instead, overall care was associated with significant
405 nonlinear effects – an indication of strong stabilizing selection (Schluter 1988). This translated to
406 fewer and smaller offspring among caregivers with both the lowest and the highest cumulative
407 behavioral investments (Fig 4B). We detected no improvements in performance among families
408 with two caregivers as opposed to one (Fig 4B). In fact, because two caregivers are effectively
409 capable of twice the sum total effort, biparental pairs accounted for much of the performance
410 reduction in the upper tails of the care distribution. These results are consistent with independent
411 investigations carried out in Oregon (Feldman 2020) and Canada (Ong 2019), which report
412 significantly reduced performance and limited compensation among biparental pairs exposed to
413 experimental warming treatments. Our study provides a mechanism for these effects: reduced
414 offspring performance at higher temperatures does not result from biparental care *per se*, but
415 from temperature-dependent thresholds in optimal care allocation, which are most likely to be
416 exceeded when two parents are active at the nest.

417 Our original prediction – that parents should compensate for environmental stress by
418 increasing the amount of time they spend caring – was based on an assumption of unconstrained
419 potential to evolve more care to offspring. Clearly parents should have the ability to re-allocate
420 time from non-caring to caring behaviors, as males can shift to care from no-care when females
421 are not present. However, care in burying beetles comes in different forms, and our analysis
422 suggests that there is conflicting selection resulting in a constraint on changes in care
423 composition. In the harsh environment, increased direct care was under directional selection,
424 with more care associated with greater offspring number and mass. In contrast, indirect care was
425 under stabilizing selection for both offspring number and mass (Table 1). It is possible that

426 negative genetic correlations between indirect care and direct care, as described in quantitative
427 genetic work in the related *N. vespilloides* (Walling et al. 2008), limit independent responses of
428 care components under conflicting selection regimes. However, such tradeoffs would not explain
429 the lack of adaptive plasticity seen in biparental pairs.

430 Our expectation was that because burying beetles show flexibility in parenting in
431 response to social parameters (Trumbo 1991, Smiseth et al. 2005, Suzuki and Nagano 2009,
432 Creighton et al. 2015, Matthey and Smiseth 2015, Parker et al. 2015), and males caring with
433 females have spare capacity, the application of a generalized stressor should promote shifts from
434 conflict to cooperation. Instead, we found that both males and females adhered to predicted sex-
435 specific rules for parental investment – males were plastic and females were not, as seen in the
436 related *N. vespilloides* (Smiseth et al. 2005, Royle et al. 2014) – irrespective of the selective
437 environment. Specifically, females cared at capacity even when exposed to heat stress and
438 provided with male helpers, allowing us to reject any ‘load lightening’ benefits of two caregivers
439 (Crick 1992, Johnstone 2011). Males in the presence of females withheld direct care and deserted
440 broods earlier, consistent with sexual conflict. The main difference between biparental pairs and
441 uniparental females across environments was an increase in indirect care, underpinned by the
442 fact that neither males nor females showed plasticity of this behavior. Reductions in offspring
443 fitness with additive care were most likely due to tradeoffs with direct care at the individual
444 level. Hence, when ambient conditions turn unfavorable, two parents are not more efficient at
445 caring for offspring than one.

446 Given the predominance of biparental care in *N. orbicollis*, why have mechanisms for
447 enhancing coordination not evolved? In systems where brood care responsibilities are shared by
448 more than one individual, social factors are expected to have an outsized influence on investment

449 decisions, and the ability to mount coordinated responses may help buffer environmental
450 variation (Heinsohn 2004, Ridley and Raihani 2008).-Models of biparental care such as partial
451 compensation (Houston and Davies 1985), negotiation (McNamara et al. 1999), and turn-taking
452 (Johnstone et al. 2014) assume that male and female strategies are optimized to resolve conflict
453 over offspring care. However, if biparental care of burying beetles did not evolve to mitigate
454 offspring need, then the dynamics predicted under these models may not hold true. As in the
455 related *N. vespilloides*, sexual conflict may continue to structure interactions between the sexes
456 (Boncoraglio and Kilner 2012, Parker et al. 2015), at least in terms of a lack of a response by
457 males to offspring need. In burying beetles, the prevailing theory for why males of some species
458 join females is that mating opportunities are limited elsewhere and pairs fare better than single
459 parents in defense of the valuable but temporally and spatially unpredictable resources (Scott
460 1990, 1994, 1998a, Trumbo 1991). If true, then the impetus for the evolution of care may be
461 different for males and females. While females should focus efforts on meeting the needs of
462 offspring, males should remain impervious to offspring needs except in the extreme case that the
463 female dies or abandons the nest. Thus, males adopt an ‘insurance policy’ strategy for
464 participation of care (Parker et al. 2015). This is supported by evidence in a variety of burying
465 beetle species for compensatory responses to partner removal (Smiseth et al. 2005, Suzuki and
466 Nagano 2009, Royle et al. 2014) and no compensation for subtler perturbations in the family
467 environment, such as reduced partner provisioning, (Suzuki and Nagano 2009, Suzuki 2020),
468 increased offspring begging (Suzuki 2020) or, as we show here, the application of a generalized
469 stressor. Overall, research on burying beetles suggest that there can be sex-specific evolutionary
470 pathways for biparental care consistent with sexual conflict as one of the drivers of the evolution
471 of care in this genus (Boncoraglio and Kilner 2012, Parker et al. 2015).

472 The prediction that cooperative parental strategies enhance resilience in harsh or hostile
473 environments is not novel (Wilson 1975, Emlen 1982), but climate change has afforded new
474 urgency to understanding its practical significance (Lucey et al. 2015, Manfredini et al. 2019,
475 Henriques and Osmond 2020). Our study has shown that burying beetles at southern range
476 margins will face steep reproductive challenges associated with rising temperatures alone, and
477 that these will not be alleviated through biparental cooperation. Despite the predominance of
478 biparental social structures in this species strategies for coordinated care are unrefined. The
479 implication of our work is that the potential for parenting to ameliorate the effects of climate
480 change is likely to depend on the evolutionary drivers of parental care, which may be sex
481 specific and be best reflected in components of care.

482

483 **References:**

- 484 AlRashidi, M., A. Kosztolányi, C. Küpper, I. C. Cuthill, S. Javed, and T. Székely. 2010. The
485 influence of a hot environment on parental cooperation of a ground-nesting shorebird, the
486 Kentish plover *Charadrius alexandrinus*. *Frontiers in Zoology* 7:1.
- 487 AlRashidi, M., A. Kosztolányi, M. Shobrak, C. Küpper, and T. Székely. 2011. Parental
488 cooperation in an extreme hot environment: Natural behaviour and experimental evidence.
489 *Animal Behaviour* 82:235–243.
- 490 Bates, D. M., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models
491 using lme4. *Journal of statistical software* 67:1–48.
- 492 Benowitz, K. M., E. C. McKinney, and A. J. Moore. 2016. Difference in parenting in two species
493 of burying beetle, *Nicrophorus orbicollis* and *Nicrophorus vespilloides*. *Journal of Ethology*
494 34:3.

- 495 Benowitz, K. M., and A. J. Moore. 2016. Biparental care is predominant and beneficial to
496 parents in the burying beetle *Nicrophorus orbicollis* (Coleoptera: Silphidae). *Biological*
497 *Journal of the Linnean Society* 119:1082–1088.
- 498 Boncoraglio, G., and R. M. Kilner. 2012. Female burying beetles benefit from male desertion:
499 Sexual conflict and counter-adaptation over parental investment. *PLoS ONE* 7:e31713.
- 500 Brodie, E. D., A. J. Moore, and F. J. Janzen. 1995. Visualizing and quantifying natural selection.
501 *Trends in Ecology & Evolution* 10:313–318.
- 502 Capodeanu-Nägler, A., E. M. Keppner, H. Vogel, M. Ayasse, A. K. Eggert, S. K. Sakaluk, and
503 S. Steiger. 2016. From facultative to obligatory parental care: Interspecific variation in
504 offspring dependency on post-hatching care in burying beetles. *Scientific Reports* 6:29323.
- 505 Capodeanu-Nägler, A., M. A. Prang, S. T. Trumbo, H. Vogel, A. K. Eggert, S. K. Sakaluk, and
506 S. Steiger. 2018. Offspring dependence on parental care and the role of parental transfer of
507 oral fluids in burying beetles. *Frontiers in Zoology* 15:33.
- 508 Clutton-Brock, T. H. 1991. *The Evolution of Parental Care*. Princeton University Press,
509 Princeton, New Jersey, U.S.A.
- 510 Clutton-Brock, T. H., A. F. Russell, L. L. Sharpe, P. N. M. Brotherton, G. M. McIlrath, S. White,
511 and E. Z. Cameron. 2001. Effects of helpers on juvenile development and survival in
512 meerkats. *Science* 293:2446–2449.
- 513 Cockburn, A. 2006. Prevalence of different modes of parental care in birds. *Proceedings of the*
514 *Royal Society B: Biological Sciences* 273:1375–1383.
- 515 Creighton, C. J., A. N. Smith, A. Komendat, and M. C. Belk. 2015. Dynamics of biparental care
516 in a burying beetle: Experimental handicapping results in partner compensation. *Behavioral*
517 *Ecology and Sociobiology* 69:265–271.

- 518 Crick, H. Q. P. 1992. Load-lightening in cooperatively breeding birds and the cost of
519 reproduction. *Ibis* 134:56–61.
- 520 Cunningham, C. B., L. Ji, E. C. McKinney, K. M. Benowitz, R. J. Schmitz, and A. J. Moore.
521 2019. Changes of gene expression but not cytosine methylation are associated with male
522 parental care reflecting behavioural state, social context and individual flexibility. *Journal*
523 *of Experimental Biology* 222:1–9.
- 524 Eggert, A.-K., and J. K. Müller. 1997. Biparental care and social evolution in burying beetles:
525 lessons from the larder. Pages 216–236 *in* J. Choe and B. Crespi, editors. *The Evolution of*
526 *Social Behavior in Insects and Arachnids*. Cambridge University Press, Cambridge,
527 Massachusetts, USA.
- 528 Emlen, S. T. 1982. The evolution of helping. 1. An ecological constraints model. *American*
529 *Naturalist* 119:29–29.
- 530 Feldman, N. S. 2020. Does environmental variability explain male parental care in a burying
531 beetle? Purdue University, Hammond, IN, U.S.A.
- 532 Friedrich, S., F. Konietschke, and M. Pauly. 2019. Resampling-based analysis of multivariate
533 data and repeated measures designs with the R package MANOVA. RM. R Package version
534 3.4.0.
- 535 Gilbert, J. D. J., and A. Manica. 2015. The evolution of parental care in insects: A test of current
536 hypotheses. *Evolution* 69:1255–1270.
- 537 Guindre-Parker, S., and D. R. Rubenstein. 2018. Multiple benefits of alloparental care in a
538 fluctuating environment. *Royal Society Open Science* 5:172406.
- 539 Heinsohn, R. G. 2004. Parental care, load-lightening, and costs. Pages 67–80 *in* W. D. Koenig
540 and J. L. Dickenson, editors. *Ecology and Evolution of Cooperative Breeding in Birds*.

- 541 Cambridge University Press, Cambridge, U.K.
- 542 Henriques, G. J. B., and M. M. Osmond. 2020. Cooperation can promote rescue or lead to
543 evolutionary suicide during environmental change. *Evolution* 74:1255–1273.
- 544 Hopwood, P. E., A. J. Moore, T. Tregenza, and N. J. Royle. 2015. Male burying beetles extend,
545 not reduce, parental care duration when reproductive competition is high. *Journal of*
546 *Evolutionary Biology* 28:1394–1402.
- 547 Houston, A. I., and N. B. Davies. 1985. The evolution of cooperation and life history in the
548 dunnock *Prunella modularis*. Pages 471–487 in R. M. Sibley and R. H. Smith, editors.
549 *Behavioral Ecology*. Blackwell Scientific, Oxford, U.K.
- 550 Jacques, B. J., S. Akahane, M. Abe, W. Middleton, W. W. Hoback, and J. J. Shaffer. 2009.
551 Temperature and food availability differentially affect the production of antimicrobial
552 compounds in oral secretions produced by two species of burying beetle. *Journal of*
553 *Chemical Ecology* 35:871–877.
- 554 Jarrett, B. J. M., E. Evans, H. B. Haynes, M. R. Leaf, D. Rebar, A. Duarte, M. Schrader, and R.
555 M. Kilner. 2018. A sustained change in the supply of parental care causes adaptive
556 evolution of offspring morphology. *Nature Communications* 9:3987.
- 557 Johnstone, R. A. 2011. Load lightening and negotiation over offspring care in cooperative
558 breeders. *Behavioral Ecology* 22:436–444.
- 559 Johnstone, R. A., A. Manica, A. L. Fayet, M. C. Stoddard, M. A. Rodriguez-Gironés, and C. A.
560 Hinde. 2014. Reciprocity and conditional cooperation between great tit parents. *Behavioral*
561 *Ecology* 25:216–222.
- 562 Laidlaw, C. T. 2015. Latitudinal variation in lifetime survival and reproduction in a burying
563 beetle. Brigham Young University.

- 564 Lande, R., and S. J. Arnold. 1983. The measurement of selection on correlated characters.
565 Evolution 37:1210–1226.
- 566 Lejeune, L., J. L. Savage, A. C. Bründl, A. Thiney, A. F. Russell, and A. S. Chaine. 2019.
567 Environmental effects on parental care visitation patterns in blue tits *Cyanistes caeruleus*.
568 Frontiers in Ecology and Evolution 7:356.
- 569 Lenth, R. V. 2016. Least-squares means: The R package lsmeans. Journal of Statistical Software
570 69:1–33.
- 571 Lessells, C. M. 2012. Sexual Conflict. Pages 150–170 in N. J. Royle and P. T. Smiseth, editors.
572 The Evolution of Parental Care. Oxford University Press, Oxford, UK.
- 573 Lessells, C. M., and J. M. McNamara. 2012. Sexual conflict over parental investment in repeated
574 bouts: Negotiation reduces overall care. Proceedings of the Royal Society B: Biological
575 Sciences 279:1506–1514.
- 576 Lin, Y. H., S. F. Chan, D. R. Rubenstein, M. Liu, and S. F. Shen. 2019. Resolving the paradox of
577 environmental quality and sociality: The ecological causes and consequences of cooperative
578 breeding in two lineages of birds. American Naturalist 194:207–216.
- 579 Lucey, N. M., C. Lombardi, L. Demarchi, A. Schulze, M. C. Gambi, and P. Calosi. 2015. To
580 brood or not to brood: Are marine invertebrates that protect their offspring more resilient to
581 ocean acidification? Scientific Reports 5:12009.
- 582 Manfredini, F., M. Arbetman, and A. L. Toth. 2019. A potential role for phenotypic plasticity in
583 invasions and declines of social insects. Frontiers in Ecology and Evolution 7:375.
- 584 Matthey, S. N., and P. T. Smiseth. 2015. Complex effects of inbreeding on biparental cooperation.
585 American Naturalist 185:1–12.
- 586 McNamara, J. M., C. E. Gasson, and A. I. Houston. 1999. Incorporating rules for responding into

- 587 evolutionary games. *Nature* 401:368–371.
- 588 McNamara, J. M., A. I. Houston, Z. Barta, and J. L. Osorno. 2003. Should young ever be better
589 off with one parent than with two? *Behavioral Ecology* 14:301–310.
- 590 Meierhofer, I., H. H. Schwarz, and J. K. Müller. 1999. Seasonal variation in parental care,
591 offspring development, and reproductive success in the burying beetle, *Nicrophorus*
592 *vespillo*. *Ecological Entomology* 24:73–79.
- 593 Müller, J. K., V. Braunisch, W. Hwang, and A. K. Eggert. 2007. Alternative tactics and
594 individual reproductive success in natural associations of the burying beetle, *Nicrophorus*
595 *vespilloides*. *Behavioral Ecology* 18:196–203.
- 596 Öberg, M., D. Arlt, T. Pärt, A. T. Laugen, S. Eggers, and M. Low. 2015. Rainfall during parental
597 care reduces reproductive and survival components of fitness in a passerine bird. *Ecology*
598 *and Evolution* 5:345–356.
- 599 Ong, J. Y. 2019. Coping with thermal challenges: Reaction norms of life history traits in a
600 burying beetle with biparental care. Queen’s University, Kingston, Ontario.
- 601 Parker, D. J., C. B. Cunningham, C. A. Walling, C. E. Stamper, M. L. Head, E. M. Roy-Zokan,
602 E. C. McKinney, M. G. Ritchie, and A. J. Moore. 2015. Transcriptomes of parents identify
603 parenting strategies and sexual conflict in a subsocial beetle. *Nature Communications*
604 6:8449.
- 605 Pilakouta, N., E. J. H. Hanlon, and P. T. Smiseth. 2018. Biparental care is more than the sum of
606 its parts: Experimental evidence for synergistic effects on offspring fitness. *Proceedings of*
607 *the Royal Society B: Biological Sciences* 285:20180875.
- 608 Quinby, B. M. 2016. Latitudinal variation in life history strategies in the burying beetle,
609 *Nicrophorus orbicollis*. Purdue University, Hammond, Indiana.

- 610 R Core Development Team. 2019. R: A language and environment for statistical computing.
- 611 Ratnieks, F. L. W. 1996. Evolution of unstable and stable biparental care. *Behavioral Ecology*
- 612 7:490–493.
- 613 Remeš, V., R. P. Freckleton, J. Tökölyi, A. Liker, and T. Székely. 2015. The evolution of
- 614 parental cooperation in birds. *Proceedings of the National Academy of Sciences of the*
- 615 *United States of America* 12:13603–13608.
- 616 Reynolds, J. D., N. B. Goodwin, and R. P. Freckleton. 2002. Evolutionary transitions in parental
- 617 care and live bearing in vertebrates. *Philosophical Transactions of the Royal Society B:*
- 618 *Biological Sciences* 357:269–281.
- 619 Ridley, A. R., and N. J. Raihani. 2008. Task partitioning increases reproductive output in a
- 620 cooperative bird. *Behavioral Ecology* 19:1136–1142.
- 621 Royle, N. J., A. F. Russell, and A. J. Wilson. 2014. The evolution of flexible parenting.
- 622 Savage, J. L., A. F. Russell, and R. A. Johnstone. 2013. Maternal costs in offspring production
- 623 affect investment rules in joint rearing. *Behavioral Ecology* 24:750–758.
- 624 Schluter, D. 1988. Estimating the form of natural selection on a quantitative trait. *Evolution*
- 625 42:849–861.
- 626 Schrader, M., B. J. M. Jarrett, and R. M. Kilner. 2015. Using experimental evolution to study
- 627 adaptations for life within the family. *American Naturalist* 185:610–619.
- 628 Scott, M. P. 1990. Brood guarding and the evolution of male parental care in burying beetles.
- 629 *Behavioral Ecology and Sociobiology* 26:31–39.
- 630 Scott, M. P. 1994. The benefit of paternal assistance in intra- and interspecific competition for
- 631 the burying beetle, *Nicrophorus defodiens*. *Ethology Ecology and Evolution* 6:537–543.
- 632 Scott, M. P. 1998a. The ecology and behavior of burying beetles. *Annual Review of Entomology*

- 633 43:595–618.
- 634 Scott, M. P. 1998b. Facultative adjustment of the duration of parental care by burying beetles.
635 *Journal of Insect Behavior* 11:597–603.
- 636 Scott, M. P., and J. F. A. Traniello. 1990. Behavioural and ecological correlates of male and
637 female parental care and reproductive success in burying beetles (*Nicrophorus spp.*).
638 *Animal Behaviour* 39:274–283.
- 639 Shen, S. F., S. T. Emlen, W. D. Koenig, and D. R. Rubenstein. 2017. The ecology of cooperative
640 breeding behaviour. *Ecology Letters* 20:708–720.
- 641 Smiseth, P. T. 2019. Coordination, cooperation, and conflict between caring parents in burying
642 beetles. *Frontiers in Ecology and Evolution* 7:1–5.
- 643 Smiseth, P. T., C. T. Darwell, and A. J. Moore. 2003. Partial begging: An empirical model for
644 the early evolution of offspring signalling. *Proceedings of the Royal Society B: Biological
645 Sciences* 270:1773–1777.
- 646 Smiseth, P. T., C. Dawson, E. Varley, and A. J. Moore. 2005. How do caring parents respond to
647 mate loss? Differential response by males and females. *Animal Behaviour* 69:551–559.
- 648 Smiseth, P. T., and A. J. Moore. 2004. Behavioral dynamics between caring males and females
649 in a beetle with facultative biparental care. *Behavioral Ecology* 15:621–628.
- 650 Steiger, S., K. Richter, J. K. Müller, and A. K. Eggert. 2007. Maternal nutritional condition and
651 genetic differentiation affect brood size and offspring body size in *Nicrophorus*. *Zoology*
652 110:360–368.
- 653 Suzuki, S. 2013. Biparental care in insects: Paternal care, life history, and the function of the
654 nest. *Journal of Insect Science* 13:131.
- 655 Suzuki, S. 2020. Biparental negotiation or larval begging? Determinant of male provisioning in a

- 656 burying beetle (*Nicrophorus quadripunctatus*). Behaviour 157:719–729.
- 657 Suzuki, S., and M. Nagano. 2009. To compensate or not? Caring parents respond differentially to
658 mate removal and mate handicapping in the burying beetle, *Nicrophorus quadripunctatus*.
659 Ethology 115:1–6.
- 660 Therneau, T. M., and T. Lumley. 2015. Package ‘survival.’ R package version 3.2.7.
- 661 Trumbo, S. T. 1990. Reproductive Success, Phenology and Biogeography of Burying Beetles
662 (Silphidae, Nicrophorus). American Midland Naturalist 124:1–11.
- 663 Trumbo, S. T. 1991. Reproductive benefits and the duration of paternal care in a biparental
664 burying beetle, *Nicrophorus orbicollis*. Behaviour 117:82–105.
- 665 Trumbo, S. T. 1992. Monogamy to communal breeding: exploitation of a broad resource base by
666 burying beetles *Nicrophorus*. Ecological Entomology 17:289–298.
- 667 Trumbo, S. T. 2006. Infanticide, sexual selection and task specialization in a biparental burying
668 beetle. Animal Behaviour 75:1159–1167.
- 669 Trumbo, S. T. 2012. Patterns of parental care in invertebrates. Pages 81–100 in M. K. Nick J.
670 Royle, Per T. Smiseth, editor. The Evolution of Parental Care. Oxford University Press,
671 Oxford, U.K.
- 672 Ulyshen, M. D., and J. L. Hanula. 2004. Diversity and seasonal activity of carrion beetles
673 (Coleoptera: Silphidae) in northeastern Georgia. Journal of Entomological Science 39:460–
674 463.
- 675 Vági, B., Z. Végvári, A. Liker, R. P. Freckleton, and T. Székely. 2020. Climate and mating
676 systems as drivers of global diversity of parental care in frogs. Global Ecology and
677 Biogeography 29:1373–1386.
- 678 Vincze, O., A. Kosztolányi, Z. Barta, C. Küpper, M. Alrashidi, J. A. Amat, A. Argüelles Ticó, F.

679 Burns, J. Cavitt, W. C. Conway, M. Cruz-López, A. E. Desucre-Medrano, N. dos Remedios,
680 J. Figuerola, D. Galindo-Espinosa, G. E. García-Peña, S. Gómez Del Angel, C. Gratto-
681 Trevor, P. Jönsson, P. Lloyd, T. Montalvo, J. E. Parra, R. Pruner, P. Que, Y. Liu, S. T.
682 Saalfeld, R. Schulz, L. Serra, J. J. H. St Clair, L. E. Stenzel, M. A. Weston, M. Yasué, S.
683 Zefania, and T. Székely. 2017. Parental cooperation in a changing climate: fluctuating
684 environments predict shifts in care division. *Global Ecology and Biogeography* 26:347–358.

685 Walling, C. A., C. E. Stamper, P. T. Smiseth, and A. J. Moore. 2008. The quantitative genetics of
686 sex differences in parenting. *Proceedings of the National Academy of Sciences of the*
687 *United States of America* 105:18430–18435.

688 Wesolowski, T. 1994. On the origin of parental care and the early evolution of male and female
689 parental roles in birds. *American Naturalist* 143:39–58.

690 Wesolowski, T. 2004. The origin of parental care in birds: A reassessment. *Behavioral Ecology*
691 15:530–523.

692 Wiley, E. M., and A. R. Ridley. 2016. The effects of temperature on offspring provisioning in a
693 cooperative breeder. *Animal Behaviour* 117:187–195.

694 Wilson, E. O. 1975. *Sociobiology: The New Synthesis*. Belknap, Cambridge, U.K.

695 Wynne-Edwards, K. E., and M. E. Timonin. 2007. Paternal care in rodents: Weakening support
696 for hormonal regulation of the transition to behavioral fatherhood in rodent animal models
697 of biparental care. *Hormones and Behavior* 52:114–121.

698