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Maternal effects & inbreeding depression

Citation for published version:

Smiseth, P & Pilakouta, N 2016, 'Maternal effects alter the severity of inbreeding depression in the offspring: Maternal effects & inbreeding depression', *Proceedings of the Royal Society B-Biological Sciences*, vol. 283, no. 1838. <https://doi.org/10.1098/rspb.2016.1023>

Digital Object Identifier (DOI):

[10.1098/rspb.2016.1023](https://doi.org/10.1098/rspb.2016.1023)

Link:

[Link to publication record in Edinburgh Research Explorer](#)

Document Version:

Peer reviewed version

Published In:

Proceedings of the Royal Society B-Biological Sciences

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1 **Maternal effects alter the severity of inbreeding depression in the offspring**

2

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7

8 Running title: *Maternal effects & inbreeding depression*

9

10 **Abstract**

11 A maternal effect is a causal influence of the maternal phenotype on the offspring phenotype
12 over and above any direct effects of genes. There is abundant evidence that maternal effects can
13 have a major impact on offspring fitness. Yet, no previous study has investigated the potential
14 role of maternal effects in influencing the severity of inbreeding depression in the offspring.
15 Inbreeding depression is a reduction in the fitness of inbred offspring relative to outbred
16 offspring. Here, we tested whether maternal effects due to body size alter the magnitude of
17 inbreeding depression in the burying beetle *Nicrophorus vespilloides*. We found that inbreeding
18 depression in larval survival was more severe for offspring of large females than offspring of
19 small females. This might be due to differences in how small and large females invest in an
20 inbred brood because of their different prospects for future breeding opportunities. To our
21 knowledge, this is the first evidence for a causal effect of the maternal phenotype on the severity
22 of inbreeding depression in the offspring. In natural populations that are subject to inbreeding,
23 maternal effects may drive variation in inbreeding depression and therefore contribute to
24 variation in the strength and direction of selection for inbreeding avoidance.

25

26 **Keywords:** body size, burying beetle, inbreeding depression, maternal effects, *Nicrophorus*
27 *vespilloides*, offspring fitness, parental care

28 **Introduction**

29 Inbreeding results from matings between relatives and can lead to a general loss of
30 heterozygosity, which increases the likelihood that recessive, deleterious alleles are expressed
31 [1]. As a result, inbreeding is commonly associated with a reduction in the fitness of any
32 resulting offspring, known as inbreeding depression. Inbreeding depression is an important issue
33 in evolutionary biology and ecology because it can exert strong selection pressures on dispersal
34 strategies, mating systems, reproductive strategies, and social behaviors [2]. Furthermore,
35 inbreeding depression is a growing conservation concern, given that increasing rates of habitat
36 loss and habitat fragmentation can increase the likelihood of inbreeding [3,4], thereby
37 contributing to higher local extinction rates [5]. Even though there is abundant evidence for
38 inbreeding depression across a wide range of animal and plant taxa, the severity of inbreeding
39 depression can vary dramatically both among and within species [5,6]. Understanding the factors
40 that underlie this variation could have implications for the conservation of many endangered
41 populations, yet these dynamics are still not well understood. Earlier work has proposed that this
42 variation may be partly attributed to differences in the physical or social environment [7–9].
43 Environmental stresses, such as starvation and competition, tend to exacerbate inbreeding
44 depression [8,10], whereas benign conditions may moderate inbreeding depression [11,12].

45 We have recently shown that inbreeding depression is more severe in the absence of
46 maternal care, suggesting that the presence of the mother during offspring development can
47 buffer against inbreeding depression [12]. However, it is still unknown whether such a buffering
48 effect depends on the mother's phenotype. Maternal condition may affect the quantity or quality
49 of care provided to the offspring [13–17], so we might expect the severity of inbreeding
50 depression to be influenced by maternal traits such as body size, age, nutritional condition, and

51 health status. This type of a causal influence of the maternal phenotype on the offspring
52 phenotype would represent a maternal effect [18]. Even though the mechanisms and
53 consequences of maternal effects have been studied extensively [18,19], previous work has
54 overlooked the potential role of maternal effects in the context of inbreeding depression.

55 Here, we use the burying beetle *Nicrophorus vespilloides* to examine whether maternal
56 body size, an important component of the maternal phenotype, affects the severity of inbreeding
57 depression in the offspring. Burying beetles are a highly suitable study system for addressing this
58 question. They have facultative biparental care, and male removal has no effect on offspring
59 fitness under laboratory conditions [20], allowing us to focus on maternal effects. Moreover, we
60 have previously shown that there is severe inbreeding depression in this species, with respect to
61 survival at the larval and pupal stages, as well as adult lifespan [12,21,22]. We have also shown
62 that inbreeding depression in the offspring is less severe when the mother is present than when
63 she is removed [12]. Given that small females provide less post-hatching care than large females
64 [16,17], we hypothesized that inbred offspring would suffer a greater reduction in fitness
65 (compared to outbred offspring) if they had a small mother than if they had a large mother. To
66 test this hypothesis, we used a 2×2 factorial design with the following treatment groups: (i) a
67 large female with outbred offspring, (ii) a small female with outbred offspring, (iii) a large
68 female with inbred offspring, and (iv) a small female with inbred offspring. Because inbreeding
69 depression affects traits across the entire life cycle in this species [12,21,22], we measured
70 several offspring fitness traits at different life stages: (i) hatching success, (ii) larval mass at
71 dispersal, (iii) survival rate from hatching to dispersal, (iv) survival rate from dispersal to
72 eclosion, and (v) lifespan after eclosion.

73

74 **Methods**

75 *Study species*

76 Burying beetles (*Nicrophorus vespilloides*) breed on carcasses of small vertebrates. Parents bury
77 the carcass and lay the eggs in the soil around it [23]. They prepare the carcass by removing any
78 fur or feathers and apply antimicrobial secretions to suppress bacterial and fungal growth [23–
79 25]. After hatching, larvae crawl to the carcass and start feeding in a crater created by the
80 parents. The larvae can self-feed, but parents also provision larvae with predigested carrion. In
81 addition, parents defend the brood from predators and conspecific competitors [26]. Although
82 both parents typically provide care, females stay on the carcass for longer and spend more time
83 provisioning food to the larvae [17,20,27–29]. The larvae disperse from the carcass about 5 days
84 after hatching, which corresponds to the end of the parental care period. They pupate about 10
85 days after dispersal and eclose as adults about 10 days after pupation.

86

87 *Beetle husbandry*

88 We used virgin beetles from an outbred laboratory population maintained at The University of
89 Edinburgh. The beetles used in this study comprised of second-generation beetles from lines
90 originally collected in Edinburgh, UK. They were housed individually in transparent plastic
91 containers (12 × 8 × 2 cm) filled with moist soil and kept at 20°C and constant light. All non-
92 breeding adults were fed small pieces of raw organic beef twice a week.

93

94 *Experimental design*

95 In the first part of our experiment, we generated small and large individuals. Because adult body
96 size is determined by larval mass at the dispersal stage [30,31], it is possible to generate

97 different-sized beetles by removing larvae from the carcass at different times after hatching
98 [16,17,32,33]. Thus, for each of 89 broods, we removed third-instar larvae weighing 100–150
99 mg and 200–250 mg to generate small and large adults, respectively. The main advantage of this
100 method was that it allowed us to generate small and large females that were full siblings. We
101 were thus able to remove any potential confounding genetic effects that might have arisen if we
102 had selected small and large individuals from our stock population. After each small or large
103 larva was removed from the carcass, it was placed in an individual container ($12 \times 8 \times 2$ cm)
104 filled with moist soil. At eclosion, we measured the pronotum width of all female beetles. As
105 intended, there was a substantial difference in the mean (\pm SD) pronotum width (mm) of females
106 from the two groups: 4.04 (\pm 0.24) for small females and 5.33 (\pm 0.24) for large females. There
107 was also no overlap in the range of pronotum widths for small (3.50–4.59 mm) and large females
108 (4.99–6.00 mm). Steiger [16] used similar size classes: 3.97 (\pm 0.21) for small females and 5.54
109 (\pm 0.23) for large females. These categories were based on the size range observed in both the
110 laboratory population and beetles collected in the field [16].

111 In the second part of our experiment, we used a 2×2 factorial design with the following
112 treatment groups: (i) a large female with outbred offspring, (ii) a small female with outbred
113 offspring, (iii) a large female with inbred offspring, and (iv) a small female with inbred offspring.
114 To produce outbred offspring for treatments (i) and (ii), we paired outbred virgin beetles that had
115 no common ancestors for at least two generations. To produce inbred offspring for treatments
116 (iii) and (iv), we paired outbred virgin beetles that were full siblings. All male and female parents
117 were mated within 15 days after reaching sexual maturity (i.e., 10–25 days after eclosion). On the
118 day of mating, we measured each female's prebreeding mass, which was later used to estimate
119 the female's mass change over the breeding attempt (see below). Each experimental pair ($n=276$)

120 was placed in a transparent plastic container ($17 \times 12 \times 6$ cm) filled with 1 cm of moist soil and a
121 freshly thawed mouse carcass (Livefoods Direct Ltd, Sheffield, UK) of a standardized size (24–
122 26 g). After mating, we checked the containers twice a day for the presence of eggs. As soon as
123 the first eggs were laid, we removed the male from the container. In this species, the amount of
124 care provided by the male is highly variable and male removal has no effect on offspring fitness
125 under laboratory conditions [20]. Right before larvae started hatching, we recorded the number
126 of eggs laid (clutch size) by counting the number of eggs visible at the bottom of the transparent
127 breeding box [33,34]. Because each box contained a very thin layer of soil, the number of eggs at
128 the bottom of the box was very close to the actual clutch size [34].

129 When all larvae had dispersed from the carcass, we weighed the female again. By
130 subtracting each female's prebreeding mass from her postbreeding mass, we calculated her mass
131 change over the breeding attempt, as a measure of somatic investment and thus allocation to
132 future reproduction [32,35]. Females were then transferred to individual containers ($12 \times 8 \times 2$
133 cm) filled with moist soil. They were checked twice a week until death to measure their post-
134 breeding lifespan, as a measure of their residual reproductive value [33].

135 At the dispersal stage, we also recorded the number of unhatched eggs visible at the
136 bottom of the box, the number of surviving larvae, and the total mass of the brood. By
137 subtracting the number of unhatched eggs from the clutch size recorded earlier, we estimated the
138 number of eggs that hatched. We then divided the number of eggs that hatched successfully by
139 clutch size to calculate hatching success. We also calculated the average larval mass in each
140 brood by dividing total brood mass by the number of larvae. We placed all larvae from each
141 brood into large transparent containers ($17 \times 12 \times 6$ cm) filled with moist soil. Approximately 20
142 days later, we recorded the number of individuals that eclosed successfully from each brood to

143 calculate the survival rate from dispersal to eclosion. At this stage, up to six beetles from each
144 brood were placed into individual containers ($12 \times 8 \times 2$ cm). We tracked the adult lifespan of
145 these offspring ($n = 872$) by checking them twice a week until death. The sample sizes for
146 matings with at least one offspring surviving until eclosion were as follows: $n = 46$ for large
147 females with outbred broods, $n = 54$ for small females with outbred broods, $n = 40$ for large
148 females with inbred broods, and $n = 43$ for small females with inbred broods.

149

150 *Data analysis*

151 All analyses were done using R version 3.2.3. We used linear models for continuous traits with
152 normally distributed random errors (average larval mass, adult offspring lifespan, female mass
153 change, and female post-breeding lifespan). For discrete traits, we used generalized linear
154 models fitted with a Poisson error distribution (clutch size). For proportion data, we used
155 generalized linear models fitted with a binomial distribution (survival to dispersal and survival to
156 eclosion) or a binomial distribution corrected for overdispersion (hatching success). Proportion
157 data were entered into the models using the ‘cbind’ function. In all of these models, we analysed
158 absolute differences rather than log-transformed measures [36], as relative measures of
159 inbreeding depression are potentially biased [37].

160 All models included the following factors: offspring inbreeding status (outbred or
161 inbred), maternal body size (large or small), and the interaction between the two. A statistically
162 significant interaction would suggest that maternal body size affects the severity of inbreeding
163 depression in the offspring (i.e., the extent to which inbred offspring perform less well compared
164 to outbred offspring). Carcass size was added as a covariate in all models, because the amount of
165 resources available may influence female reproductive decisions and offspring performance.

166 Indeed, we found that females laid more eggs on larger carcasses (LR $\chi_1^2=8.87$, $P<0.01$), and
167 larvae had a higher survival rate on larger carcasses (LR $\chi_1^2=6.47$, $P=0.01$). There was also a
168 nonsignificant trend for females to gain more mass on larger carcasses ($F=3.20$, $P=0.08$). In
169 addition, we added maternal age as a covariate in all models, because it can influence female
170 reproductive decisions and offspring performance. Accordingly, we found that younger females
171 laid fewer eggs (LR $\chi_1^2=8.56$, $P<0.01$) and their offspring had a higher survival rate from
172 hatching to dispersal (LR $\chi_1^2=28.8$, $P<0.0001$). Lastly, we added sex as a covariate in the model
173 for adult lifespan of the offspring and found that male offspring had a shorter lifespan after
174 eclosion than female offspring ($F=9.16$, $P<0.001$). Decisions on which covariates to include in
175 the final models were based on AIC scores.

176

177 **Results**

178 *Effects of inbreeding*

179 There was no difference in clutch size, mass change, or post-breeding lifespan between females
180 that were mated to their brothers and females that were mated to unrelated males (Tables 1 and
181 S1). However, inbreeding had significant effects on the offspring's fitness (Tables 2 and S1).

182 Inbred larvae suffered substantial inbreeding depression in three of the five traits we measured:

183 survival from hatching to dispersal, survival from dispersal to eclosion, and adult lifespan

184 (Figure 1). There was no evidence for inbreeding depression in hatching success or larval mass at

185 the dispersal stage (Tables 2 and S1).

186

187 *Effects of female body size*

188 Small females laid fewer eggs, gained relatively less mass over the breeding attempt, and had a
189 shorter post-breeding lifespan than large females (Tables 1 and S1). Small females also produced
190 larvae that had a lower mass at the dispersal stage than larvae of large females (Tables 2 and S1).
191 However, female body size had no effect on hatching success, survival to dispersal, survival to
192 eclosion, or adult lifespan of the offspring (Tables 2 and S1).

193

194 *Interaction between inbreeding and female size*

195 There was a significant interaction between offspring inbreeding status and female size on
196 survival to dispersal (Table 2). This interaction reflected that offspring of large females suffered
197 a greater reduction in fitness due to inbreeding than offspring of small females (Figure 2). In
198 other words, inbreeding depression in survival to dispersal was more severe for offspring of large
199 mothers than those of small mothers (Figure 1). There was no interaction on hatching success,
200 larval mass, survival to eclosion, or offspring lifespan after eclosion (Table 2). Similarly, there
201 was interaction on female reproductive decisions or residual reproductive value (Table 1).

202

203 **Discussion**

204 In this study, we tested whether the mother's phenotype can influence the severity of inbreeding
205 depression in her offspring. We found evidence for inbreeding depression in three of the five
206 traits we measured: survival from hatching to dispersal, survival from dispersal to eclosion, and
207 post-eclosion lifespan (Table 1). In addition, we found a significant interaction between
208 inbreeding and maternal body size on survival to dispersal. This interaction reflected that
209 inbreeding depression in this trait was more severe for offspring of large females than offspring
210 of small females (Figure 2). There was no such interaction on survival to eclosion or post-

211 eclosion lifespan. Although we found an interaction in only one of these fitness traits, we note
212 that this trait was also the one with the highest level of inbreeding depression (Figure 1). In
213 summary, our key finding is that offspring of large females suffered a lower survival rate from
214 hatching to dispersal if they were inbred than if they were outbred, whereas inbred and outbred
215 offspring of small females had a similar survival rate (Figure 2). To our knowledge, this is the
216 first evidence for a causal effect of the maternal phenotype on the severity of inbreeding
217 depression in the offspring.

218 Until now, very few studies have considered maternal effects in the context of inbreeding
219 depression, and all of these were conducted on plants [38–41]. Moreover, none of these studies
220 established a causal link between maternal effects and the magnitude of inbreeding depression.
221 For example, Wolfe [38] found that maternal effects influenced early-life fitness traits in
222 *Hydrophyllum appendiculatum*, while inbreeding depression affected late-life fitness traits. He
223 proposed two plausible explanations for this pattern: (i) maternal effects substantially reduce the
224 severity of inbreeding depression in early-life fitness traits, so no inbreeding depression is
225 detected during this life stage, or (ii) inbreeding depression is more severe in later life stages
226 because of the cumulative effect of smaller fitness reductions in earlier life stages [38]. Since it
227 was not possible to distinguish between these two explanations, it was unclear whether there was
228 an effect of the maternal phenotype on the severity of inbreeding depression in this species.

229 Here, we demonstrate that maternal body size can alter the severity of inbreeding
230 depression in larval survival in the burying beetle *N. vespilloides*. Inbred offspring of large
231 females suffered lower survival from hatching to dispersal than outbred ones, whereas offspring
232 of small females had the same survival rate regardless of their inbreeding status. The fact that
233 there was no detectable inbreeding depression in this trait for offspring of small females suggests

234 that maternal effects completely masked the deleterious effects of inbreeding on early-life
235 offspring performance. In a population where the majority of females are small, such a masking
236 effect could effectively hide the inbred genotype from natural selection, with potential
237 consequences for the level of genetic load in the population [38].

238 We expected that inbreeding depression would be less severe for offspring of large
239 females than those of small females, because females that are in better condition might have the
240 capacity to provide more care. Yet, we found evidence for the opposite pattern. One plausible
241 explanation is that large females have larger clutches (Table 1), resulting in more intense sibling
242 competition, which might in turn exacerbate the severity of inbreeding depression. We think this
243 is unlikely given our earlier work showing that sibling competition does not exacerbate
244 inbreeding depression in this species [22]. Additionally, our mean brood size was relatively
245 small (potentially due to seasonal variation in reproductive success [42]), suggesting a low level
246 of sibling competition in our study. An alternative explanation is that small and large females
247 differ in how they invest in an inbred brood because of their prospects for future breeding
248 opportunities. Large females have a longer lifespan (J Moorad, unpublished data) and are more
249 successful at acquiring and defending a carcass against conspecific competitors [30]. Thus, large
250 females have a higher residual reproductive value than small females, who may only breed once
251 due to their shorter lifespan and lower competitive ability. If this is the case, a small female
252 might maximize her reproductive effort during a breeding attempt regardless of her offspring's
253 inbreeding status. On the other hand, when a large female mates with a relative and produces a
254 brood of inbred, low-quality offspring, she might reduce her investment in current reproduction
255 in order to take advantage of additional breeding opportunities in the future. Such adjustments in
256 maternal investment could be mediated through changes in prehatching effort (e.g., egg size,

257 nutrients deposited into the eggs) and/or posthatching effort (e.g., provisioning rate), leading to a
258 reduction in the survival of inbred offspring reared by large mothers. Nevertheless, this
259 interpretation assumes that *N. vespilloides* females have the ability to recognise their relatives
260 and/or the inbreeding status or overall quality of their offspring. Further work is needed to
261 determine whether females behave differently towards inbred and outbred offspring.

262 We expect inbreeding to be relatively rare in *N. vespilloides*, which makes this species a
263 good model for understanding how the fitness costs of inbreeding are influenced by maternal
264 effects in species that do not regularly inbreed. There are two important reasons it is useful to
265 focus on species where inbreeding is relatively rare: (i) inbreeding depression is a greater
266 concern for species with no prior history of inbreeding because deleterious, recessive alleles have
267 not yet been purged from the population, and (ii) once a species has a significant history of
268 inbreeding, parental behaviours and other family interactions might be modified by selection due
269 to inbreeding. Thus, species with a history of inbreeding might not be appropriate as models for
270 endangered species that have only recently become subject to inbreeding. In principle, all
271 populations are potentially at risk of inbreeding in the future, given increasing habitat loss and
272 other human-induced disturbances that increase the chances of inbreeding [3]. It is therefore
273 important to improve our understanding of how populations that become subject to inbreeding
274 may cope with inbreeding depression.

275 Our study shows that maternal effects have the potential to influence the magnitude of
276 inbreeding depression in the offspring. We encourage future research to investigate this
277 previously unexplored issue in other taxa, since this pattern may be widespread in natural
278 populations that suffer from inbreeding depression. If that is the case, it could have important
279 implications for conservation efforts. Maternal effects are inextricably linked to maternal

280 condition, which may vary over time within a population due to seasonal changes in weather and
281 food availability [43–45]. Maternal effects may therefore contribute to temporal variation in
282 inbreeding depression in natural populations that are subject to environmental variability. In
283 species where estimates of inbreeding depression (δ) are sensitive to maternal condition, a better
284 understanding of the role of maternal effects may be important for the conservation and
285 management of endangered populations. The presence of maternal effects might cause
286 researchers to overestimate or underestimate inbreeding depression as a threat to population
287 viability depending on the state of females at the time of data collection and on the particular
288 subsample of females used in the study.

289 Our findings also have general implications for evolutionary biology, because if maternal
290 condition influences inbreeding depression in the offspring, we might expect selection for
291 inbreeding avoidance to depend on the average maternal condition in the population. Depending
292 on the parents' capacity to moderate the deleterious effects of inbreeding in the offspring, there
293 might be selection for inbreeding avoidance, tolerance, or even preference. Existing theory [46–
294 48] has overlooked the possibility that maternal effects might influence animal inbreeding
295 strategies. Until now, theoretical models have focused on how the costs of dispersal, mating
296 system, mate encounter rate, and kin recognition might shape the balance between inbreeding
297 tolerance and avoidance [46–48]. We propose that incorporating maternal effects into such
298 models may help us better understand and predict when animals should avoid, tolerate, or prefer
299 inbreeding, which has so far been challenging [2].

300 In summary, our study provides novel insights into the role of maternal effects in altering
301 the expression of inbreeding depression. We show that inbreeding depression in larval survival
302 was less severe for offspring of small females than for offspring of large females. This pattern

303 might be driven by differences in how small and large females invest in an inbred (low-quality)
304 brood because of their different prospects for future reproduction. We recommend that future
305 research investigates how other maternal traits, such as age, nutritional condition, and health
306 status, might affect the severity of inbreeding depression within or among populations. In natural
307 populations that are subject to inbreeding, maternal effects may contribute to both variation in
308 the magnitude of inbreeding depression and variation in the strength and direction of selection
309 for inbreeding avoidance.

310

311 **Data accessibility**

312 The raw data are available on the Dryad Digital Repository (doi:10.5061/dryad.r754h).

313

314 **Authors' contributions**

315 NP conceived of the study, designed the study, collected data, carried out the statistical analyses,
316 and wrote the manuscript. PTS helped design the study and provided feedback on the
317 manuscript.

318

319 **Competing interests**

320 We have no competing interests.

321

322 **Funding**

323 NP and PTS were funded by the Institute of Evolutionary Biology and the School of Biological
324 Sciences at University of Edinburgh. NP was also supported by a Student Research Award from
325 the American Society of Naturalists.

326

327 **Acknowledgments**

328 We thank the Edinburgh Countryside Rangers for permission to collect beetles at Corstorphine
329 Hill. We are also grateful to Deborah Charlesworth, Emma Cunningham, Lucy Ford, Jacob
330 Moorad, Matthieu Paquet, and Craig Walling for helpful discussions on the experimental design
331 and data analysis. Lastly, we thank Hope Klug, Sandra Steiger, and one anonymous reviewer for
332 helpful comments on the manuscript.

333

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- 438

439 **Figure Captions**

440

441 **Figure 1** Inbreeding depression (δ) in offspring with large mothers (grey bars) or small mothers
442 (white bars). Inbreeding depression was calculated as a proportional change in mean fitness of
443 outbred (w_o) and inbred (w_i) offspring, using the equation $\delta = (w_o - w_i)/w_o$. Survival to dispersal
444 is the offspring survival rate from hatching to dispersal, which corresponds to the end of the
445 parental care period. Survival to eclosion is the offspring survival rate from dispersal to eclosion.
446 Adult lifespan refers to the number of days an individual was alive after eclosion.

447

448 **Figure 2** Mean (\pm SE) survival rate from hatching to dispersal for outbred (grey) or inbred
449 (white) offspring of small or large females. Inbred offspring of large females suffered lower
450 survival from hatching to dispersal than outbred ones, whereas offspring of small females had
451 the same survival rate regardless of their inbreeding status.

452

453 **Table 1.** Effects of inbreeding (outbred or inbred offspring), maternal body size (large or small female),
 454 and their interaction on female reproductive decisions (clutch size and mass change) and residual
 455 reproductive value (postbreeding lifespan).

	Offspring inbreeding status		Female size		Interaction	
	<i>F</i> / <i>LR</i> χ_1^2	<i>P</i>	<i>F</i> / <i>LR</i> χ_1^2	<i>P</i>	<i>F</i> / <i>LR</i> χ_1^2	<i>P</i>
Clutch size	1.90	0.17	263	<0.0001	0.03	0.86
Female mass change (%)	0.11	0.74	11.1	<0.01	0.20	0.65
Female postbreeding lifespan (days)	0.09	0.77	9.7	<0.01	2.21	0.14

456 We provide information on the test statistic (*F* or *LR* χ_1^2 for linear models or generalized linear models,
 457 respectively) and *P*-value for each variable. Statistically significant *P*-values are indicated in bold.

458

459

460 **Table 2.** Effects of inbreeding (outbred or inbred offspring), maternal body size (large or small
 461 female), and their interaction on offspring fitness traits.

	Offspring inbreeding status		Female size		Interaction	
	<i>F</i> / <i>LR</i> χ_1^2	<i>P</i>	<i>F</i> / <i>LR</i> χ_1^2	<i>P</i>	<i>F</i> / <i>LR</i> χ_1^2	<i>P</i>
Hatching success (%)	1.83	0.18	1.09	0.30	3.01	0.08
Average larval mass (mg)	0.11	0.74	30.3	<0.001	1.05	0.31
Survival to dispersal (%)	17.8	<0.0001	0.05	0.82	9.49	<0.01
Survival to eclosion (%)	21.5	<0.0001	2.24	0.13	1.01	0.32
Offspring adult lifespan (days)	24.9	<0.001	1.40	0.24	0.32	0.57

462 Survival to dispersal refers to the offspring survival rate from hatching to dispersal, and survival to
 463 eclosion refers to the offspring survival rate from dispersal to eclosion. We provide information on the
 464 test statistic (*F* or *LR* χ_1^2 for linear models or generalized linear models, respectively) and *P*-value for
 465 each variable. Statistically significant *P*-values are indicated in bold.

466

467 **Table S1.** Means (\pm SE) for all response variables.

	Large female		Small female	
	Outbred offspring	Inbred offspring	Outbred offspring	Inbred offspring
Clutch size	18.4 \pm 1.2	19.6 \pm 1.3	10.0 \pm 0.8	10.7 \pm 1.1
Hatching success (%)	93.2 \pm 2.0	90.9 \pm 1.5	87.5 \pm 2.2	86.7 \pm 3.4
Average larval mass (mg)	216 \pm 4	212 \pm 4	188 \pm 5	194 \pm 4
Survival to dispersal (%)	53.2 \pm 4.5	39.3 \pm 4.5	43.4 \pm 4.0	47.0 \pm 4.8
Survival to eclosion (%)	95.3 \pm 1.5	89.6 \pm 3.0	92.9 \pm 2.1	87.5 \pm 2.9
Female mass change (%)	12.2 \pm 1.5	13 \pm 2.1	7.5 \pm 1.5	5.9 \pm 1.8
Maternal post-breeding lifespan (days)	45.7 \pm 1.6	47.8 \pm 1.7	42.9 \pm 1.1	43.2 \pm 1.4
Offspring lifespan (days)	43.4 \pm 0.6	40.7 \pm 0.7	43.0 \pm 0.6	39.5 \pm 0.7



