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## Maternity uncertainty in cobreeding beetles

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1 **Maternity uncertainty in cobreeding beetles: females lay**  
2 **more and larger eggs and provide less care**

3

4 **Running title:** Cobreeding females invest more in eggs but less in care

5

6 Jon Richardson\* & Per T. Smiseth

7 Institute of Evolutionary Biology, University of Edinburgh, Edinburgh, U.K.

8 \*Correspondence: J. Richardson, Institute of Evolutionary Biology, School of

9 Biological Sciences, University of Edinburgh, Charlotte Auerbach Road,

10 Edinburgh, EH9 3FL, U.K.

11 E-mail address: [jon.richardson@ed.ac.uk](mailto:jon.richardson@ed.ac.uk)

12 Telephone: +44 (0) 131 651 3631

13

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17

## 18 **Abstract**

19 Cobreeding, which occurs when multiple females breed together, is likely to be associated  
20 with uncertainty over maternity of offspring in a joint brood, preventing females from  
21 directing resources towards their own offspring. Cobreeding females may respond to such  
22 uncertainty by shifting their investment towards the stages of offspring development when  
23 they are certain of maternity and away from those stages where uncertainty is greater. Here  
24 we examined how uncertainty of maternity influences investment decisions of cobreeding  
25 females by comparing cobreeding females and females breeding alone in the burying  
26 beetle, *Nicrophorus vespilloides*. In this species, females sometimes breed together on a  
27 single carcass but females cannot recognise their own offspring. We found that cobreeding  
28 females shifted investment towards the egg stage of offspring development by laying more  
29 and larger eggs than females breeding alone. Furthermore, cobreeding females reduced  
30 their investment to post-hatching care of larvae by spending less time providing care than  
31 females breeding alone. We show that females respond to the presence of another female  
32 by shifting allocation towards egg laying and away from post-hatching care, thereby  
33 directing resources to their own offspring. Our results demonstrate that responses to  
34 parentage uncertainty are not restricted to males, but that, unlike males, females respond  
35 by shifting their investment to different components of reproduction within a single  
36 breeding attempt. Such flexibility may allow females to cope with maternity uncertainty as  
37 well as a variety of other social or physical challenges.

38

39 **Keywords:** cobreeding, maternity uncertainty, reproductive investment, egg size, parental  
40 care, burying beetle.

## 41 **Introduction**

42 Cobreeding occurs when multiple related or unrelated conspecific females breed together  
43 using a joint resource or breeding site (Emlen 1984; Brown 1987; Manning 1995 et al;  
44 Vehrencamp 1978; Hayes 2000; Vehrencamp 2000; Koenig & Dickinson 2004). In these  
45 cobreeding associations (also termed “communal breeding” or “joint nesting”), females rear  
46 a communal brood with each female contributing towards parental care (Emlen 1984;  
47 Brown 1987). Cobreeding occurs either because it provides adaptive benefits, such as  
48 reduced costs of nest building and parental care or improved nest defence, compared to  
49 breeding alone (e.g. Vehrencamp 1978; Scott 1994; Mappes et al. 1995; Riehl 2010a), or  
50 because the costs of evicting other females are too high (Komdeur et al. 2013). Regardless,  
51 cobreeding is likely to lead to significant conflict between females because offspring  
52 produced by different females will compete for limited resources (Koenig et al. 1995). Most  
53 prior work on cobreeding has focused on strategies used by females to increase their share  
54 of the group’s reproductive output by biasing or monopolising production of offspring  
55 and/or access to resources (i.e. reproductive skew). For example, in some species of birds,  
56 females selectively destroy eggs or kill offspring produced by other females (e.g. Elmen &  
57 Wrege 1986; Macedo & Bianchi 1997; Møller 1987; Mumme et al. 1983; Stouffer et al 1987;  
58 Vehrencamp 1977; Macedo & Melo 1999; Schmaltz et al. 2008). However, given that kin  
59 recognition is often absent or imperfect, cobreeding females are likely to face uncertainty  
60 over the maternity of offspring in the joint brood. In this case, they would have a limited  
61 ability to direct parental care towards their own offspring (Carrielo et al. 2004; Riehl 2010b).  
62 However, little is known about how uncertainty of maternity shapes the reproductive  
63 decisions of cobreeding females.

64           Here we suggest that cobreeding females may respond to maternity uncertainty by  
65 shifting their investment towards their own offspring rather than offspring that may have  
66 been produced by other females. Such behavioural responses to parentage uncertainty have  
67 been studied extensively in the context of sperm competition in species where males  
68 provide parental care (e.g. Westneat & Sherman 1993; Sheldon et al. 1997; Hunt & Simmons  
69 2002; Neff 2003; Suter et al. 2009; Alonzo & Klug 2012; Bose et al. 2016). Such studies show  
70 that males often facultatively reduce their contribution towards parental care in response to  
71 greater paternity uncertainty provided that males have access to cues about potential losses  
72 in paternity, and that they can expect higher paternity in future breeding attempts  
73 (Westneat & Sherman 1993; Wright 1998; Sheldon 2002; Alonzo 2010). Given that females  
74 often have certainty of maternity during egg laying or birth (except in species with  
75 intraspecific brood parasitism), there has been less interest in how females respond to  
76 maternity uncertainty. We consider the effect of maternity uncertainty on female  
77 reproductive decisions in communally breeding species where females do not recognise  
78 their own offspring. We suggest that cobreeding females should shift their investment  
79 towards those stages of offspring development when females have greater certainty of  
80 maternity. For example, when females have complete certainty of maternity for the eggs  
81 they lay, but there is maternity uncertainty of offspring after hatching, females should  
82 increase their investment in eggs and reduce their investment to parental care after  
83 hatching. Despite clear predictions, ours is the first study to examine whether cobreeding  
84 females respond to uncertainty of maternity by adjusting their investment to eggs and  
85 parental care.

86           We address this gap using the burying beetle *Nicrophorus vespilloides*. Beetles in the  
87 genus *Nicrophorus* are excellent study systems for examining how females respond to

88 maternity uncertainty because they breed on carcasses of small vertebrates, either by  
89 cobreeding with other females or by breeding on their own (Eggert & Müller 1992; Scott  
90 1998). There is intense intraspecific competition over carcasses suitable for reproduction,  
91 with females attempting to monopolise access to the carcass (Bartlett & Ashworth 1988;  
92 Otronen 1988; Müller et al. 1990). Multiple females may breed communally on the same  
93 carcass when the carcass is relatively large, and females are matched for competitive ability  
94 (i.e. they are similar in size) (Eggert & Müller 1992; Trumbo 1992; Scott & Williams 1993;  
95 Trumbo & Wilson 1993; Eggert & Müller 2000; Komdeur et al. 2013). This is because it is  
96 harder for a single female to completely monopolise a larger carcass and because the costs  
97 of injury involved in attempting to evict competitors are likely to be higher when females  
98 are matched for size (Komdeur et al. 2013). Each cobreeding female lays eggs in the soil  
99 surrounding the carcass and provides elaborate post-hatching parental care to the joint  
100 brood, which includes direct provisioning of larvae with pre-digested carrion (Eggert et al.  
101 1998; Smiseth et al. 2005). Females use the timing of oviposition to selectively cull offspring  
102 produced by other females, thereby skewing reproduction to their own benefit (Eggert &  
103 Müller 2000). However, females cannot recognise their own offspring after hatching (Müller  
104 & Eggert 1990; Oldekop et al. 2007). Thus, cobreeding females are likely to face maternity  
105 uncertainty of hatched offspring in the communal brood. Furthermore, investment to egg  
106 laying and parental care are plastic traits as females flexibly adjust their reproductive  
107 behaviour in response to changes in their social or physical environment. For example,  
108 females lay larger eggs when breeding on larger carcasses (Richardson & Smiseth 2019) and  
109 increase their investment to parental care after experiencing competition (Pilakouta et al.  
110 2016). However, it is currently unclear whether female *N. vespilloides* adjust their

111 investment to eggs and/or parental care in response to uncertainty of maternity due to the  
112 presence of another female.

113         The aim of this study was to test if female burying beetles adjust their reproductive  
114 decisions when cobreeding with another female. We compared the number and size of eggs  
115 and the amount of post-hatching parental care by cobreeding females and females breeding  
116 alone. We generated cobreeding pairs by providing two size-matched females with a large  
117 mouse carcass. We compared cobreeding females with females breeding alone either on a  
118 similarly large carcass (i.e. the same total amount of resources as cobreeding pairs) or a  
119 carcass that was half the size given to cobreeding pairs (i.e. the same amount of resources  
120 per female in a cobreeding pair). We did this to separate the effects of cobreeding from  
121 potential effects due to resource availability. If females facultatively adjust their  
122 reproductive decisions in response to maternity uncertainty associated with cobreeding, we  
123 predicted that a cobreeding female would increase investment to her eggs by laying larger  
124 and/or more eggs but provide less post-hatching parental care than a female breeding  
125 alone. This is because a cobreeding female would have complete certainty of maternity for  
126 eggs that she lays, whilst there would be maternity uncertainty after hatching given that the  
127 brood would be comprised of a mixture of her own offspring and offspring produced by the  
128 other female.

129

## 130 **Methods**

131 Origin of study population and animal husbandry

132 We used virgin beetles from an outbred laboratory population maintained at the University  
133 of Edinburgh. The beetles used in our experiments were from the 5<sup>th</sup> and 6<sup>th</sup> generation of  
134 beetles descended from wild-caught beetles collected in Hermitage of Braid, Edinburgh, U.K.

135 We kept all beetles individually in transparent plastic containers (12 x 8 x 2 cm) filled with  
136 moist soil under a 16:8 light:dark cycle at 20°C and we fed them pieces of raw, organic beef  
137 twice a week.

138 For our experiment, we selected sexually mature females (i.e. aged 10 days post-  
139 eclosion) from the stock population. Over a two-week period, we fed females small amounts  
140 of beef mince (approximately 0.3 g) containing one of two different fat-soluble dyes.  
141 Females were fed beef containing either Rhodamine B dye (Sigma-Aldrich, Dorset, U.K.) or  
142 Sudan Black dye (Fisher Scientific Ltd., Loughborough, U.K.) in a ratio of 0.4 g of dye per 20g  
143 of beef. These dyes are incorporated into the eggs during oviposition, and females produce  
144 pink and blue eggs, respectively (Scott 1997; Eggert & Müller 2000; Trumbo & Valletta 2007;  
145 Eggert et al. 2008), thereby allowing us to identify the eggs laid by an individual female. The  
146 dyes used have no effect on the timing of oviposition, female fecundity, hatching success, or  
147 larval survival and development (Scott 1997).

148

#### 149 Experimental procedures

150 After females had been fed on dyed beef for two weeks (i.e. when females were aged 24  
151 days post-eclosion), they were assigned to one of three treatments: the cobreeding  
152 treatment, in which a pair of females shared a single large mouse carcass (27–30 g), and the  
153 two controls treatments, in which a single female bred on her own either on a large carcass  
154 of the same size as that used by the cobreeding females (27–30 g) or on a small carcass that  
155 was half this size (12–15 g). We chose these carcass sizes because they are within the range  
156 used by this species (1–40 g) and because prior work shows that females breed communally  
157 on carcasses larger than 25 g (Eggert & Müller 1992; Komdeur et al. 2013). For the  
158 cobreeding treatment, we ensured that the two females had been fed different dyes so that



159 we could tell which female laid which eggs. In addition, we ensured that the two females  
160 were size-matched such that the maximum difference in pronotum width between them  
161 was <4% (mean  $\pm$  SE = 0.13%  $\pm$  0.010; range = 0 – 3.77%). There was no difference in body  
162 size between females assigned to the three treatments ( $F_{2,117} = 0.073$ ,  $p = 0.93$ ).

163         Once females had been assigned to a treatment, we mated each female with an  
164 unrelated, virgin male from the stock population. During mating, we placed each female in a  
165 transparent plastic container (11 x 11 x 3 cm) lined with moist soil together with her  
166 assigned mate for 24 hours. We did this to ensure that all females received sufficient sperm  
167 for fertilizing their eggs, allowing them to breed alone without male assistance when they  
168 were later provided with a carcass (Botteril-James et al. 2017). We excluded males from the  
169 experimental trials to remove any potential confounding effects that male presence may  
170 have on female behaviour or the dynamics between cobreeding females. After mating, we  
171 weighed each female so we could calculate her mass change during breeding (see below).

172         To initiate breeding, we transferred females to a larger transparent plastic container  
173 (28 x 16 x 10 cm) lined with 1 cm of moist soil and provided with a freshly thawed mouse  
174 carcass (Livefoods Direct Ltd., Sheffield, U.K.). For cobreeding pairs, we placed both females  
175 in the container at the same time, in opposite corners of the container and equidistant from  
176 the carcass. We individually identified each female in a cobreeding pair based on their  
177 colour, because the elytra of females that had been feeding on beef dyed with Rhodamine B  
178 had a distinct pink (rather than orange) colour. However, in order to ensure our  
179 identification was accurate, we also marked the two cobreeding females by providing them  
180 with either with one or two small spots of correction fluid on their elytra. This method of  
181 marking beetles is long-lasting, non-toxic and has no effect on their behaviour (Hagler &  
182 Jackson 2001; Richardson & Smiseth 2017). Nevertheless, we ensured that females assigned

183 to the control treatments were also marked in the same way as cobreeding females by  
184 randomly providing control females with either one or two small spots of correction fluid on  
185 their elytra.

186 We collected information on egg laying by placing each container on a flat-bed  
187 scanner (Canon CanoScan 9000F Mark II, Canon Inc., Tokyo, Japan) and scanning the bottom  
188 every hour until the completion of oviposition using VueScan professional edition software  
189 (Hamrick Software, Sunny Isles Beach, Florida, USA) (Ford & Smiseth 2016, Ford & Smiseth  
190 2017; Botterill-James et al. 2017; Ford et al. 2018). Eggs are visible at the bottom of the  
191 container and, because we used a thin layer of soil, the visible number of eggs is strongly  
192 correlated with the actual clutch size (Monteith et al. 2012). From each scanned image, we  
193 assigned pink eggs to females fed Rhodamine B dye, and blue eggs to females fed Sudan  
194 Black dye. We confirm that we were always able to assign eggs to each female. We also  
195 counted the number of new eggs laid each hour by each female, using this information to  
196 determine the start of egg laying (i.e., the time elapsed since the female was provided with  
197 a carcass until she laid the first egg), egg size (see below), hatching success (see below) and  
198 clutch size (i.e., the total number of eggs laid) for each female (Ford & Smiseth 2016). For  
199 each female, we measured the size of six randomly chosen eggs using ImageJ (Ambràmovic et  
200 al. 2004). For each egg, we measured its length and width in pixels three times. We then  
201 converted these measures to metric length (mm), and used the mean length and width to  
202 calculate a prolate spheroid volume for each egg ( $V$ ) as  $V = (1/6) \pi w^2 L$ , where  $w$  is width  
203 and  $L$  the length of the egg, respectively (Berrigan 1991). In addition, we checked scans  
204 after hatching to record the number of unhatched eggs. We estimated hatching success by  
205 subtracting the number of unhatched eggs from the clutch size to estimate the number of  
206 hatched eggs, and dividing the number of hatched eggs by clutch size.

207 We collected information on female post-hatching parental care by conducting  
208 behavioural observations for each female. In this species, there is a peak in post-hatching  
209 parental care 24 h after hatching of the first larva in the brood (Smiseth et al. 2003). We  
210 therefore conducted behavioural observations for each female as close as possible to 24 h  
211 after her first eggs were expected to hatch (on average broods were observed  $30 \pm 0.33$  h  
212 after hatching of the first egg). For cobreeding females, we conducted observations based  
213 on the expected time of hatching for whichever female started laying first. We obtained  
214 information on expected time of hatching by adding 59 h, which is the time taken for eggs  
215 to hatch at 20°C (Smiseth et al. 2006), to the time at which a given female laid her first egg.  
216 Observations were conducted using instantaneous sampling every 1 min for 30 min  
217 following established protocols (Smiseth & Moore 2002; Smiseth et al. 2003; Smiseth et al.  
218 2005). For each female, we recorded parental behaviour as the number of sampling points  
219 out of 30 in which a female was providing (1) direct care, defined as when a female  
220 provisioned food to the brood by engaging in mouth-to-mouth contact with at least one  
221 larva, and (2) indirect care, defined as when a female was guarding the carcass by standing  
222 over the brood or maintaining the carcass by adding anal or oral secretions to the external  
223 surface, excavating the depression in the soil surrounding the carcass, or moving the carcass  
224 from below. We also recorded the number of sampling points that each female spent in  
225 close proximity to the brood, defined as when a female was within one pronotum width of  
226 the brood (approximately 5 mm). All other behaviours, such as self-grooming or being away  
227 from the carcass, were recorded as non-parental behaviours and not analysed further. After  
228 the observations, we left females to rear their broods until the larvae dispersed from the  
229 carcass 7 days later.

230           When all larvae had dispersed from the carcass, we recorded the number of  
231 dispersing larvae and the total brood mass. We calculated average larval mass at dispersal in  
232 each brood by dividing the total brood mass by the number of larvae in the brood. At the  
233 time of dispersal, we also weighed each female to measure her post-breeding mass. We  
234 then calculated mass change during breeding for each female by subtracting her pre-  
235 breeding mass from her post-breeding mass.

236

### 237 Statistical analyses

238 In total, we set up 141 broods ( $n = 41$  for cobreeding pairs,  $n = 49$  for females breeding  
239 alone on a large carcass and  $n = 50$  for females breeding alone on a small carcass). For our  
240 analyses of egg laying and parental behaviour, we excluded broods where females did not  
241 lay any eggs ( $n = 0$  for cobreeding pairs,  $n = 6$  for females breeding alone on a large carcass  
242 and  $n = 6$  for females breeding alone on a small carcass), where no eggs hatched ( $n = 8$  for  
243 cobreeding pairs,  $n = 13$  for females breeding alone on a large carcass and  $n = 13$  for females  
244 breeding alone on a small carcass), or where no larvae were alive at the time of the  
245 observation ( $n = 0$  for cobreeding pairs,  $n = 0$  for females breeding alone on a large carcass  
246 and  $n = 1$  for females breeding alone on a small carcass). We also excluded cobreeding pairs  
247 in which only one of the two female laid eggs ( $n = 2$ ) or one of the females died ( $n = 1$ ). This  
248 gave us a final sample size of  $n = 30$  for cobreeding pairs,  $n = 30$  for females breeding alone  
249 on a large carcass and  $n = 30$  for females breeding alone on a small carcass.

250           We analysed all data in R v. 3.6.0 (R Core Team, 2019). We used general linear mixed  
251 models with normally distributed error structures for the analysis of egg size, the time taken  
252 for females to lay their first egg and female mass change. For the analysis of number of  
253 eggs, we used a generalised linear mixed model with a Poisson error structure. We used a

254 generalised linear mixed model with a binomial error structure for the analysis of hatching  
255 success. Finally, we used generalised linear mixed models with binomial error structures for  
256 the analyses of parental care behaviour (i.e. time spent providing direct care, indirect care  
257 and in close proximity to the brood), because our count data was bounded at a maximum  
258 value of 30 (i.e. the total number of sampling points a female could be observed performing  
259 a particular behaviour) (Ratz & Smiseth 2018). We analysed egg-laying traits, parental care  
260 traits and female mass change at the level of the individual female and we accounted for  
261 the non-independence of observations of two females in our cobreeding treatment by  
262 including the identity of the pair as a random effect. We analysed number of dispersing  
263 larvae and average larval mass as brood level traits, using general linear models fitted with  
264 normally distributed error structures, because our experimental design did not allow us to  
265 distinguish the number or size of offspring produced by an individual female in a cobreeding  
266 pair. All models included treatment as a main effect (cobreeding, breeding alone on a large  
267 carcass, breeding alone on a small carcass). In addition, we included the number of eggs laid  
268 by an individual female as an additional covariate in the models for time until first egg and  
269 hatching success, whilst the number of larvae in the brood at the time of observation was  
270 included as an additional covariate in the models for parental care behaviour.

271

## 272 **Results**

### 273 **Egg laying**

274 Cobreeding females laid eggs that were, on average, 8.87% and 8.85% larger than females  
275 breeding alone on large or small carcasses, respectively (Table 1; Figure 1A). However, there  
276 was no difference in the size of eggs laid by females breeding alone regardless of carcass  
277 size (Table 1; Figure 1A). Furthermore, cobreeding females laid clutches that were, on

278 average, 24.7% and 46.4% larger than females breeding alone on large or small carcasses,  
279 respectively (Table 1; Figure 1B), whilst there was no difference in the number of eggs laid  
280 by females breeding alone on either size of carcass (Table 1; Figure 1B).

281 After controlling for clutch size, there was no difference in the number of hatched  
282 eggs between cobreeding females and females breeding alone on large or small carcasses  
283 (Table 1). However, females breeding alone on small carcasses had, on average, 6.3% more  
284 hatched eggs than females breeding alone on large carcasses (Table 1). Furthermore,  
285 cobreeding females took, on average, 31.7% and 55.2% longer to lay their first egg  
286 compared to females breeding alone on large and small carcasses, respectively (Table 1;  
287 Figure 2). There was no difference between females breeding alone on either size of carcass  
288 in the amount of time until the first egg was laid (Table 1; Figure 2).

289

290 Post-hatching parental care

291 Cobreeding females spent, on average, 59.5% and 66.3% fewer sampling points providing  
292 direct care than females breeding alone on large or small carcasses, respectively (Table 1;  
293 Figure 3A). However, there was no difference in the amount of care provided by females  
294 breeding alone regardless of carcass size (Table 1; Figure 3A). Furthermore, the summed  
295 amount of direct care provided by the two females in a cobreeding pair was less than that  
296 provided by females breeding alone on either large or small carcasses (Tukey HSD;  
297 cobreeding pair vs female breeding alone on large carcasses: estimate  $\pm$  SE =  $-0.54 \pm 0.19$ ;  $z$   
298 =  $-2.81$ ,  $p = 0.010$ , mean difference = 19.8% fewer sampling points; cobreeding pair vs  
299 female breeding alone on small carcass: estimate  $\pm$  SE =  $-0.66 \pm 0.18$ ;  $z = -3.49$ ,  $p = 0.0014$ ,  
300 mean difference = 33.3% fewer sampling points).

301           There was no difference in the amount of indirect care provided by cobreeding  
302 females and females breeding alone on smaller carcasses (Table 1; Figure 3B). However,  
303 females breeding alone on large carcasses spent, on average, 54.3% and 41.1% more  
304 sampling points engaging in indirect care than cobreeding females and females breeding  
305 alone on small carcasses (Table 1; Figure 3B). In addition, there was no difference between  
306 cobreeding females and females breeding alone on large or small carcasses with respect to  
307 the amount of time spent in proximity to the brood (Table 1). The number of offspring in the  
308 brood at the time of the observation had no effect on the amount of direct or indirect care  
309 provided by females, or the amount of time females spent in proximity to the brood (Table  
310 1).

311

#### 312 Female mass change

313 Females breeding alone on large carcasses gained, on average, 78.9% more weight during  
314 breeding than cobreeding females (Table 1; Figure 4). However, there was no difference in  
315 mass change between cobreeding females and females breeding alone on small carcasses or  
316 between females breeding alone regardless of carcass size (Table 1; Figure 4).

317

#### 318 Number and size of offspring at dispersal

319 There was no difference in the total number of offspring in the brood between cobreeding  
320 pairs and females breeding alone on large or small carcasses (Table 2). Similarly, there was  
321 no difference in the number of offspring between females breeding alone on either large or  
322 small carcasses (Table 2). Furthermore, there was no difference in the average mass of  
323 larvae in broods reared by cobreeding pairs and broods reared by females alone on either

324 large or small carcasses (Table 2). Finally, there was no difference in the average mass of  
325 larvae in broods reared by females breeding alone on large or small carcasses (Table 2).

326

## 327 **Discussion**

328 Here we show that female burying beetles respond facultatively to maternity uncertainty  
329 associated with cobreeding by shifting their investment towards those stages of the  
330 offspring's development when they have complete certainty of maternity (i.e., egg laying),  
331 and away from those stages when there is maternity uncertainty (i.e., after hatching). As  
332 predicted, cobreeding females laid more and larger eggs than females breeding alone on  
333 either large or small carcasses. Furthermore, cobreeding females spent less time providing  
334 direct care to the brood than females breeding alone on either large or small carcasses.  
335 Thus, cobreeding females responded to maternity uncertainty by shifting their reproductive  
336 investment towards egg laying at the expense of post-hatching parental care. Below we  
337 provide a more detailed discussion of the wider implications of our results for our  
338 understanding of cobreeding and female responses to maternity uncertainty.

339 Our main finding was that cobreeding females laid more and larger eggs and spent  
340 less time providing direct care for larvae than females breeding alone. This effect was not  
341 due to differences in the amount of resources available during breeding, as cobreeding  
342 females laid more and larger eggs and provided less care after hatching than females  
343 breeding alone regardless of whether the latter bred on large or small carcasses. Instead,  
344 females responded to the presence of another female by shifting resource allocation  
345 towards eggs at the expense of care towards the larvae. Females have complete certainty of  
346 maternity of any eggs that they lay, whilst there is maternity uncertainty after hatching  
347 given that females caring for a joint brood cannot recognise their own larvae from those of



348 the other female (Müller & Eggert 1990; Eggert & Müller 1992; Eggert & Müller 2000;  
349 Oldekop et al. 2007; Komdeur et al. 2013). Our results add to our understanding of  
350 cobreeding by showing that cobreeding females facultatively adjust their investment  
351 between different stages of offspring development in response to changes in certainty of  
352 maternity. The ability of females to respond to cues about maternity uncertainty may allow  
353 them to minimise some of the costs of cobreeding by directing more resources towards  
354 their own offspring, thereby reducing the risk that resources are allocated to unrelated  
355 offspring.

356         We found that cobreeding females gained less mass during reproduction than  
357 females breeding alone on a large carcass, while there was no difference in mass gain  
358 between cobreeding females and females breeding alone on a small carcass or between  
359 females breeding alone on large or small carcasses. In this species, parents gain mass during  
360 breeding because they feed from the carcass. Previous work suggests that mass gain during  
361 breeding serves as a proxy for investment to future reproduction (Creighton et al. 2009;  
362 Billman et al. 2014). In this species, parents adjust their investment to future reproduction  
363 by gaining more mass during breeding when exposed to nutritional stress (Gray et al. 2018;  
364 Richardson et al. 2019) or when breeding on poorer quality carcasses (Billman et al. 2014).  
365 However, our results indicate that females do not respond to maternity uncertainty by  
366 consuming more carrion, suggesting cobreeding is not associated with a shift towards  
367 greater investment to future reproduction.

368         Our results highlight that there is contrast between how females respond to  
369 maternity uncertainty in the context of cobreeding and how males respond to paternity  
370 uncertainty in the context of sperm competition. There is good evidence that males  
371 facultatively respond to paternity uncertainty by reducing their investment to the current

372 breeding attempt, thereby leaving more resources to invest in future reproductive attempts  
373 (e.g. Neff & Gross 2001; Neff 2003). In contrast, our results suggest that cobreeding females  
374 respond to maternity uncertainty by shifting their investment between different stages of  
375 offspring development within a single reproductive episode. This difference may reflect that  
376 males do not contribute resources to the zygote, and that males therefore cannot respond  
377 to paternity uncertainty by shifting their investment towards the pre-hatching stage of  
378 offspring development. Thus, males may only be able to respond to paternity uncertainty by  
379 reducing their investment in the current breeding attempt and saving resources for future  
380 reproductive opportunities. In contrast, females invest considerable resources into eggs,  
381 allowing them to facultatively shift their investment towards the egg stage of offspring  
382 development when there is maternity uncertainty after hatching. Alternatively, cobreeding  
383 females may not shift their allocation towards future reproduction if it is unlikely that the  
384 probability of breeding alone is greater in the future (Westneat & Sherman 1993). Indeed,  
385 cobreeding with another female may indicate that competition for carcasses is high and that  
386 future breeding opportunities are likely to be limited. Thus, females may respond to cues  
387 gained from the presence of a cobreeding females by directing their investment away from  
388 future breeding attempts, as suggested by previous work showing that females increase  
389 their investment to reproduction when there is competition for breeding resources  
390 (Pilakouta et al. 2016). Nevertheless, our results indicate that males and females show  
391 different responses to uncertainty of parentage, which may have consequences for how  
392 each sex responds to reproductive competition.

393         Finally, we found that cobreeding females took longer to begin egg laying than  
394 females breeding alone. This finding is surprising given that initiating egg laying earlier  
395 would allow a given female to produce larvae that reached the carcass and began feeding

396 sooner, thereby gaining a competitive advantage over the offspring of the other female  
397 (Smiseth et al. 2007). There are a number of potential explanations for why cobreeding  
398 females took longer to begin egg laying. Firstly, cobreeding females may delay egg laying in  
399 order to selectively kill the larvae produced by the other female. Previous work in this  
400 species shows that females use the timing of oviposition to shift between infanticidal culling  
401 and parental care (Eggert & Müller 1990; Eggert & Müller 2000). Thus, cobreeding females  
402 may delay egg laying to increase the chances that they can accurately direct infanticidal  
403 behaviour towards the larvae of the other female. Alternatively, cobreeding females may  
404 delay egg laying because they spend time fighting for control of the carcass with the other  
405 female, as is the case when multiple females arrive on a carcass in this species (Bartlett &  
406 Ashworth 1988; Safryn & Scott 2000). Finally, cobreeding females may delay the start of egg  
407 laying in order to feed more from the carcass prior to oviposition. In this species, females  
408 feed from the carcass in order to acquire the resources necessary for egg production  
409 (Wilson & Knollenberg 1984). Given that cobreeding females laid more and larger eggs, they  
410 may need to consume resources for longer in preparation for the production of eggs (Gray  
411 et al. 2018; Richardson et al. 2019). These explanations are not mutually exclusive and  
412 decisions about the timing of oviposition could be maintained by a combination of adaptive  
413 benefits and physiological and social constraints in the context of cobreeding.

414           Here we focused on how maternity uncertainty as a consequence of cobreeding  
415 leads to facultative adjustment of investment to different stages of offspring development.  
416 In contrast, prior work on cobreeding has focused on the strategies used to increase the  
417 proportion of a female's own offspring in the joint brood (i.e. reproductive skew). These  
418 approaches will overlap as responses to changes in maternity uncertainty can be interpreted  
419 as strategies to achieve reproductive skew and *vice versa*. For instance, in the context of our

420 study, laying more and larger eggs may represent a strategy by cobreeding females to  
421 achieve reproductive skew. This is because laying more eggs would allow cobreeding  
422 females to increase the proportion of their own offspring in the subsequent brood. This is  
423 the case in the smooth-billed ani (*Crotophaga ani*), where females lay more eggs when  
424 breeding in larger groups (Schmaltz et al. 2008). Furthermore, laying larger eggs may lead to  
425 reproductive skew if it allows cobreeding females to produce more competitive offspring. In  
426 *N. vespilloides* offspring hatching from larger eggs are larger at dispersal in the absence of  
427 parental care (Monteith et al. 2012) and early-hatched larvae outcompete their siblings for  
428 access to carrion (Smiseth et al. 2007). Thus, examining our results in the context of  
429 reproductive skew might lead to the interpretation that cobreeding females increase their  
430 investment to egg laying in order to achieve reproductive skew and as a direct result have  
431 fewer resources to invest in parental care. However, this explanation is unsatisfactory as  
432 there is no evidence that increased investment to egg laying comes at the cost of reduced  
433 parental care in this species (Andrews et al. 2016). In fact, there is a positive correlation  
434 between clutch size and time spent providing indirect care (Andrews et al. 2016). Thus, our  
435 results are better explained by a response to maternity uncertainty rather than a strategy to  
436 achieve reproductive skew. This being the case, we propose that the strategies used to  
437 achieve reproductive skew seen in other cobreeding species could also be interpreted in the  
438 context of responses to maternity uncertainty. As described above, the logic of this  
439 argument is that directing resources towards eggs in response to maternity uncertainty may  
440 indirectly achieve reproductive skew because laying more and/or larger eggs means a  
441 female contributes a larger number of more competitive offspring than other females. To  
442 distinguish between these approaches we encourage more work on reproductive decisions  
443 in cobreeding species, as well as in species with intraspecific brood parasitism (Yom-Tov

444 1980; Yom-Tov 2001), to further investigate how and when parents shift their investment  
445 decisions in response to uncertainty of maternity and whether such responses have evolved  
446 to help achieve reproductive skew and/or allow females to better cope with maternity  
447 uncertainty.

448         In conclusion, our results advance our understanding of cobreeding by  
449 demonstrating that females respond to maternity uncertainty by facultatively adjusting  
450 their investment between different stages of offspring development. Female responses  
451 differ from those previously reported in males, as females adjust their investment within,  
452 rather than between, breeding attempts. Such plasticity in investment between different  
453 stages of offspring development may generalise to other contexts by allowing individuals to  
454 cope with a variety of social and environmental challenges. For example, flexible investment  
455 to eggs and/or offspring within a single breeding attempt may allow individuals to better  
456 cope with competition for resources (Kawecki 1995), intraspecific brood parasitism or  
457 stochastic environments where the risk of offspring mortality fluctuates during  
458 development due to changes in temperature, resource availability or the risk of predation or  
459 infection.

460

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470

#### 471 **Data accessibility**

472 Analyses reported in this article can be reproduced using the data provided by Richardson &  
 473 Smiseth 2020.

474

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476 **Figure legends**

477 **Figure 1** – Effect of cobreeding on (A) the average size of eggs (mm<sup>3</sup>) and (B) the number of  
478 eggs laid. Data was analysed at the level of the individual female. White boxes represent  
479 females breeding alone on a large carcass, grey bars represent females breeding alone on a  
480 small carcass and black boxes represent females cobreeding alongside another female on a  
481 large carcass. Centre lines show the medians; box limits indicate the 25th and 75th  
482 percentiles; whiskers extend 1.5 times the interquartile range from the 25th and 75th  
483 percentiles. N = 30 for all treatments.

484

485 **Figure 2** – Effect of cobreeding on the amount of time elapsed (hours) from being provided  
486 with a mouse carcass until the first egg was laid. Data was analysed at the level of the  
487 individual female. White boxes represent females breeding alone on a large carcass, grey  
488 bars represent females breeding alone on a small carcass and black boxes represent females  
489 cobreeding alongside another female on a large carcass. Centre lines show the medians; box  
490 limits indicate the 25th and 75th percentiles; whiskers extend 1.5 times the interquartile  
491 range from the 25th and 75th percentiles. N = 30 for all treatments.

492

493 **Figure 3** – Effect of cobreeding on the number of scans (out of 30) in which females  
494 provided (A) direct care and (B) indirect care. Data was analysed at the level of the  
495 individual female. Behaviour was recorded using instantaneous sampling every 1 min for 30  
496 min. White boxes represent females breeding alone on a large carcass, grey bars represent  
497 females breeding alone on a small carcass and black boxes represent females cobreeding  
498 alongside another female on a large carcass. Centre lines show the medians; box limits

499 indicate the 25th and 75th percentiles; whiskers extend 1.5 times the interquartile range  
500 from the 25th and 75th percentiles. N = 30 for all treatments.

501

502 **Figure 4** – Effect of cobreeding on mass change (g) over the breeding attempt. Data was  
503 analysed at the level of the individual female. White boxes represent females breeding  
504 alone on a large carcass, grey bars represent females breeding alone on a small carcass and  
505 black boxes represent females cobreeding alongside another female on a large carcass.  
506 Centre lines show the medians; box limits indicate the 25th and 75th percentiles; whiskers  
507 extend 1.5 times the interquartile range from the 25th and 75th percentiles. N = 30 for all  
508 treatments.

509

Table 1 – Effects of breeding treatment (cobreeding female, female breeding alone on large carcass or female breeding alone on small carcass) on egg laying traits, post-hatching parental care traits and female mass change. We provide likelihood ratio  $\chi^2$  (LR  $\chi^2$ ) and p-values for effects from linear mixed models and generalized linear mixed models analysed at the level of individual female. We also provide parameter estimates (Est), standard errors (SE), test statistics (z) and p-values from Tukey HSD post-hoc contrasts. Significant p-values are indicated in bold type.

Trait		LR $\chi^2$	p	Cobreeding female vs female breeding alone on large carcass			Cobreeding female vs female breeding alone on small carcass			Female breeding on small carcass vs female breeding on large carcass		
				Est ( $\pm$ SE)	z	p	Est ( $\pm$ SE)	z	p	Est ( $\pm$ SE)	z	p
Average egg size (mm <sup>3</sup> )	Treatment	9.87	<b>0.007</b>	0.15 (0.060)	2.57	<b>0.031</b>	0.15 (0.059)	2.56	<b>0.031</b>	0.00036 (0.069)	0.005	0.99
Number of eggs	Treatment	20.17	<b>&lt;0.001</b>	0.23 (0.091)	2.54	<b>0.022</b>	0.41 (0.092)	4.44	<b>&lt;0.001</b>	-0.18 (0.097)	-1.86	0.063
Time to first egg (h)	Treatment	15.09	<b>&lt;0.001</b>	5.68 (2.31)	2.46	<b>0.027</b>	8.48 (2.31)	3.68	<b>&lt;0.001</b>	-2.80 (2.63)	-1.07	0.28
Hatching success (%)	Treatment	16.24	<b>0.002</b>	0.51 (0.32)	1.59	0.11	-0.81 (0.37)	-2.16	0.062	1.32 (0.37)	3.58	<b>0.0011</b>
	Clutch size	15.48	<b>&lt;0.001</b>	-	-	-	-	-	-	-	-	-
Time spent providing direct care (sampling points)	Treatment	53.40	<b>&lt;0.001</b>	-1.26 (0.24)	-5.14	<b>&lt;0.001</b>	-1.71 (0.24)	-7.05	<b>&lt;0.001</b>	0.45 (0.24)	1.87	0.065
	Brood size	1.09	0.29	-	-	-	-	-	-	-	-	-
Time spent providing indirect care (sampling points)	Treatment	18.63	<b>&lt;0.001</b>	-0.93 (0.22)	-4.14	<b>&lt;0.001</b>	-0.21 (0.23)	-0.88	0.377	-0.72 (0.23)	-3.08	<b>0.0042</b>
	Brood size	0.0013	0.97	-	-	-	-	-	-	-	-	-
Time spent close to the brood (sampling points)	Treatment	5.78	0.055	-0.21 (0.37)	-0.56	0.57	-0.86 (0.37)	-2.32	0.062	0.64 (0.38)	1.71	0.17
	Brood size	0.040	0.84	-	-	-	-	-	-	-	-	-
Female mass change (g)	Treatment	8.51	<b>0.014</b>	-0.022 (0.0059)	-3.68	<b>&lt;0.001</b>	-0.008 (0.0058)	-1.34	0.17	-0.014 (0.0068)	-2.04	0.082

Table 2 – Effects of breeding treatment (cobreeding pair, female alone on large carcass or female alone on small carcass) on offspring performance. We provide test statistics (F) and p-values from linear models analysed at the level of the brood. We also provide parameter estimates (Est), standard errors (SE), test statistics (t) and p-values from Tukey HSD post-hoc contrasts.

Trait				Cobreeding pair vs female alone on large carcass			Cobreeding pair vs female alone on small carcass			Female alone on small carcass vs female alone on large carcass		
		F <sub>2,87</sub>	p	Est (±SE)	t	p	Est (±SE)	t	p	Est (±SE)	T	p
Number of offspring	Treatment	1.00	0.37	4.07 (2.88)	1.41	0.34	1.70 (2.88)	0.59	0.82	2.37 (2.88)	0.82	0.69
Average larval mass (g)	Treatment	0.98	0.38	0.012 (0.0088)	1.32	0.57	0.0022 (0.0088)	0.27	0.81	0.010 (0.0088)	1.08	0.57