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## Mothers front-load their investment to the egg stage when helped in a wild cooperative bird

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### **Data accessibility**

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The main datasets generated and analysed during the current study are available from the Dryad Digital Repository:

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<https://datadryad.org/stash/share/zpeQIUMYXxE04MamQW8orMkhFQyB0NPxuYYY6mLoFiE>

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33

34 **Abstract**

35 In many cooperative societies, including our own, helpers assist with the post-natal care of  
36 breeders' young, and may thereby benefit the *post-natal* development of offspring. Here we  
37 present evidence of a novel mechanism by which such post-natal helping could also have hitherto  
38 unexplored beneficial effects on *pre-natal* development: by lightening post-natal maternal  
39 workloads, helpers may allow mothers to increase their pre-natal investment per offspring. We  
40 present the findings of a decade-long study of cooperatively breeding white-browed sparrow  
41 weaver, *Plocepasser mahali*, societies. Within each social group, reproduction is monopolized by  
42 a dominant breeding pair, and non-breeding helpers assist with nestling feeding. Using a within-  
43 mother reaction norm approach to formally identify maternal plasticity, we demonstrate that when  
44 mothers have more female helpers they decrease their own *post-natal* investment per offspring  
45 (feed their nestlings at lower rates) but increase their *pre-natal* investment per offspring (lay larger  
46 eggs, which yield heavier hatchlings). That these plastic maternal responses are predicted by  
47 female helper number, and not male helper number, implicates the availability of post-natal  
48 helping *per se* as the likely driver (rather than correlated effects of group size), because female  
49 helpers feed nestlings at substantially higher rates than males. We term this novel maternal  
50 strategy "maternal front-loading" and hypothesize that the expected availability of *post-natal* help  
51 allows helped mothers to focus maternal investment on the *pre-natal* phase, to which helpers  
52 cannot contribute directly. Such cryptic maternally mediated helper effects on pre-natal  
53 development may markedly complicate attempts to identify and quantify the fitness consequences  
54 of helping.

## 55 Introduction

56 Maternal effects arising from variation in pre-natal maternal investment in the egg or fetus can  
57 have profound fitness consequences for mothers and offspring (Mousseau & Fox 1998; Krist  
58 2011; Pick *et al.* 2016). In social organisms, mothers are predicted to evolve investment strategies  
59 that maximize their fitness returns on investment according to their social environment (Hatchwell  
60 1999; Cunningham & Russell 2000; Russell *et al.* 2007; Bolund *et al.* 2009; Russell & Lummaa  
61 2009). Cooperatively breeding species are of particular interest in this regard, as helpers typically  
62 contribute to the post-natal feeding of the offspring of breeding females (hereafter ‘mothers’) and  
63 thus have the potential to impact the optimal level of maternal pre-natal investment per offspring  
64 (Russell *et al.* 2007; Russell & Lummaa 2009; Savage *et al.* 2015; Langmore *et al.* 2016). Where  
65 mothers are assisted by variable numbers of helpers throughout their lives, selection may be  
66 expected to favor plastic strategies in which mothers adjust their pre-natal investment per  
67 offspring according to the likely availability of help during the post-natal period (Russell & Lummaa  
68 2009).

69  
70 Different maternal strategies for adjusting pre-natal investment per offspring to the presence of  
71 helpers are hypothesized to evolve depending on how helpers impact the maternal payoff from  
72 pre-natal investment. Helpers have the potential to *decrease* the mother’s optimal level of pre-  
73 natal investment per offspring, leading to strategies in which mothers *reduce* pre-natal investment  
74 per offspring when assisted by more helpers (Russell *et al.* 2007; Russell & Lummaa 2009;  
75 Canestrari *et al.* 2011; Paquet *et al.* 2013). The ‘Load-Lightening Hypothesis’ (Hatchwell 1999;  
76 Russell *et al.* 2007) envisages that selection could favor such a maternal strategy if helpers (i)  
77 increase the overall provision of *post-natal* care to offspring (i.e., provide ‘additive post-natal care’;  
78 (Hatchwell 1999)) and thereby (ii) compensate, in part or whole, for any maternal reduction in *pre-*  
79 *natal* investment per offspring when helped (formally modelled as the ‘head start’ scenario in  
80 (Savage *et al.* 2015)). Notably, this hypothesis requires that helper-derived post-natal care can  
81 compensate for reductions in maternal pre-natal investment (i.e., that investment can be  
82 ‘substituted across stages’; (Savage *et al.* 2015)), which may not always be the case (Williams  
83 1994; Royle *et al.* 2005; Savage *et al.* 2015). Indeed, there is ample evidence that pre-natal  
84 conditions, and pre-natal maternal investment in particular, can have formative effects on

85 offspring phenotype and performance (Williams 1994; Henry & Uliaszek 1996; Hales & Barker  
86 2001; Royle *et al.* 2005; Krist 2011; Pick *et al.* 2016, 2019).

87

88 Helpers also have the potential to *increase* the mother's optimal level of pre-natal investment per  
89 offspring, leading to strategies in which mothers instead *increase* pre-natal investment per  
90 offspring when assisted by more helpers (Russell & Lummaa 2009; Savage *et al.* 2015; Langmore  
91 *et al.* 2016; Valencia *et al.* 2017). The 'Differential allocation hypothesis', for example, proposes  
92 that mothers should increase maternal investment under circumstances that increase their  
93 expected return on investment in their current breeding attempt, such as the presence of a high  
94 quality mate or more helpers (Burley 1986; Sheldon 2000; Valencia *et al.* 2006, 2017; Russell &  
95 Lummaa 2009; Horváthová *et al.* 2012; Langmore *et al.* 2016). This hypothesis was originally  
96 proposed in the context of non-cooperative species (Burley 1986; Sheldon 2000; Horváthová *et al.*  
97 *et al.* 2012), before being verbally extrapolated to cooperative breeders, with the suggestion that, as  
98 helpers commonly increase the reproductive value of offspring by providing additive post-natal  
99 care, mothers should increase investment per offspring when helped (Valencia *et al.* 2006, 2017;  
100 Carranza *et al.* 2008; Russell & Lummaa 2009; Langmore *et al.* 2016; Dixit *et al.* 2017). More  
101 specifically, the provision of additive *post-natal* care by helpers may increase the mother's return  
102 on *pre-natal* investment per offspring wherever pre- and post-natal investment have positive  
103 interactive effects on offspring fitness (such that *post-natal* helping increases the effect of  
104 maternal *pre-natal* investment on offspring fitness; (Savage *et al.* 2015)). Indeed, mathematical  
105 models incorporating such interactive effects of pre- and post-natal investment per offspring (the  
106 'silver spoon' scenario in (Savage *et al.* 2015)) predict that, where helpers contribute to post-natal  
107 care, mothers should *increase* both pre- and post-natal investment per offspring when helped.

108

109 Cooperatively breeding birds provide a fruitful testing ground for these hypotheses, given the  
110 ability to estimate maternal pre-natal investment per offspring across different helping contexts  
111 by measuring egg traits. Several studies of cooperative birds have now reported that, after  
112 controlling for variation in clutch size, mothers with (more) helpers lay smaller eggs; the pattern  
113 predicted by the load-lightening hypothesis (e.g., *Malurus cyaneus* (Russell *et al.* 2007); *Corvus*  
114 *corone corone* (Canestrari *et al.* 2011); *Vanellus chilensis* (Santos & Macedo 2011); *Philetairus*  
115 *socius* (Paquet *et al.* 2013); see also Taborsky *et al.* (2007) for an experimental demonstration in

116 fish). Three studies of cooperative birds have reported no evident relationship between egg size  
117 and the availability of help (Koenig *et al.* 2009; Lejeune *et al.* 2016; Fortuna *et al.* 2021), and just  
118 one study has reported the reverse relationship. Iberian magpie (*Cyanopica cooki*) mothers with  
119 more helpers lay larger eggs *and* feed their nestlings at higher rates, consistent with the  
120 predictions of the differential allocation hypothesis (Valencia *et al.* 2006, 2017; Savage *et al.*  
121 2015). The situation may be more complex in some cases, however, as recent work suggests  
122 that the previously reported negative relationship between egg size and the availability of help in  
123 super fairy-wrens (Russell *et al.* 2007) becomes more positive under warmer conditions  
124 (Langmore *et al.* 2016). Given the overall weight of evidence for negative relationships across  
125 species, meta-analysis of these collated findings has led to the suggestion that helpers commonly  
126 *decrease* the mother's optimal level of pre-natal investment per offspring, and that the rationale  
127 of the load-lightening hypothesis may therefore commonly apply (Dixit *et al.* 2017).

128

129 Crucially though, it has yet to be demonstrated that any of these associations between helper  
130 number and egg size in cooperative birds arise specifically from maternal *plasticity* (i.e., *within-*  
131 *mother* variation in egg size; see (Taborsky *et al.* 2007)). They could arise instead from among-  
132 mother variation in egg size being correlated with among-mother variation in helper number (e.g.,  
133 mothers on higher quality territories might simply lay larger eggs and have more offspring that  
134 survive to become helpers). Indeed, a study that explicitly teased apart the effects of within- and  
135 among-mother variation in helper number found that the negative relationship initially detected  
136 between helper number and egg volume in red-winged fairy wrens (*Malurus elegans*) arose from  
137 among-mother variation in egg volume rather than maternal plasticity (within-mother variation),  
138 illustrating the importance of taking this approach (Lejeune *et al.* 2016). While this same approach  
139 has been used to identify plasticity in egg size according to abiotic conditions (e.g., temperature;  
140 (Langmore *et al.* 2016)), evidence of maternal plasticity in egg size according to the availability of  
141 help *per se* does not yet exist for cooperative birds. As such, it remains unclear whether avian  
142 mothers ever do adjust their pre-natal investment per offspring according to helper number, and  
143 whether any such maternal plasticity conforms to the predictions of the load-lightening or  
144 differential allocation hypotheses.

145

146 Here, we use a long-term field study of cooperatively breeding white-browed sparrow weavers,  
147 *Plocepasser mahali*, to test the key predictions of the load-lightening and differential allocation  
148 hypotheses for the evolution of maternal plasticity in pre-natal investment. We do so by testing  
149 for maternal plasticity in both pre-natal investment per offspring (egg volume) and post-natal  
150 investment per offspring (maternal nestling provisioning rate) according to the availability of help.  
151 We test for plasticity using a maternal reaction norm approach, in which we isolate the effects of  
152 *within*-mother variation in helper number on maternal investment (i.e., maternal plasticity) from  
153 potentially confounding effects of variation among mothers (van de Pol & Wright 2009; Lejeune  
154 *et al.* 2016). White-browed sparrow-weavers live in social groups of 2-12 birds, in which a single  
155 dominant female ('the mother') and male monopolize within-group reproduction and non-breeding  
156 subordinate 'helpers' of both sexes help to feed their nestlings (Lewis 1982; Harrison *et al.* 2013).  
157 Helpers are typically past offspring of the dominant breeding pair, and hence are usually helping  
158 to rear close kin (Harrison *et al.* 2013). Female helpers feed nestlings at approximately twice the  
159 rate of male helpers, and female helper number has a causal positive effect on the total rate at  
160 which broods are fed while male helper number does not (i.e., only female helpers provide  
161 demonstrably additive post-natal care; (Capilla-Lasheras *et al.* 2021)). That only female helpers  
162 provide additive post-natal care provides an unusual opportunity to distinguish the hypothesized  
163 pre-natal maternal responses to the availability of additive help (which should manifest in this  
164 species as maternal responses to the number of *female* helpers) from maternal responses to  
165 group size more generally (which could influence maternal investment through mechanisms other  
166 than helping; (Kokko *et al.* 2001; Kingma *et al.* 2014)).

167

168 Sparrow-weaver mothers lay small clutches of 1-3 eggs (modal clutch size = 2), and do not adjust  
169 their clutch size or the number of clutches laid per year according to helper numbers  
170 (Supplementary materials A). Indeed, given their small clutch size, subtle adjustments in pre-natal  
171 maternal investment may be more readily achieved through changes in investment per egg than  
172 through changes in clutch size. The focal hypotheses assume that laying mothers are able to  
173 predict the helper numbers that they will have during the post-natal rearing period, in order to  
174 adjust their own pre-natal investment per offspring accordingly. This should be straightforward in  
175 sparrow-weaver societies, as both male and female helper numbers at laying strongly predict  
176 male and female helper numbers respectively during the post-natal rearing period (Figure S1).

177 We assess pre-natal maternal investment per offspring by quantifying egg volume, which in this  
178 species is strongly correlated with egg mass at laying and strongly predicts nestling mass at  
179 hatching (see Results). Maternal variation in egg volume is therefore likely to have fitness  
180 implications for offspring (and their mothers), not least because nestling mass at hatching  
181 positively predicts nestling survival to fledging in this species (Capilla-Lasheras *et al.* 2021).

182

183 We test the following key predictions of the two focal hypotheses. The load-lightening hypothesis  
184 ('head start' scenario in (Savage *et al.* 2015)) predicts that sparrow-weaver mothers should  
185 decrease egg volume when assisted by more female, but not male, helpers. The differential  
186 allocation hypothesis ('silver spoon' scenario in (Savage *et al.* 2015)) predicts that sparrow-  
187 weaver mothers should increase both egg volume and their nestling provisioning rate when  
188 assisted by more female, but not male, helpers. To test these predictions, we first investigate  
189 whether within-mother variation in female and male helper numbers at laying predicts variation in  
190 egg volume (utilizing a large longitudinal data set; 271 clutches [490 eggs] laid by 62 mothers; 1-  
191 21 clutches [median 7] per mother). We then investigate whether within-mother variation in female  
192 and male helper numbers predicts variation in the mother's nestling feeding rate (again utilizing a  
193 large longitudinal data set; 108 broods being fed by 48 mothers; 1-10 broods [median 4] per  
194 mother). Our analyses control for the effects of variation in abiotic conditions (rainfall and  
195 temperature) as these could also influence mean levels of maternal investment (Bennion &  
196 Warren 1933; Blanckenhorn 2000) and/or any maternal response to the availability of help  
197 (Langmore *et al.* 2016).

198

## 199 **Results**

### 200 **Maternal plasticity in pre-natal investment per offspring: individual mothers lay larger** 201 **eggs when they have more female helpers**

202 Sparrow-weavers show appreciable variation in egg volume both within and among mothers  
203 (Figure 1a). Egg volume appears to provide a valid proxy for pre-natal maternal investment per  
204 offspring, as higher volume eggs were heavier at laying (Figure 1b; LM:  $\beta_{\text{standardized}} \pm \text{Standard}$   
205  $\text{Error [S.E.]} = 0.946 \pm 0.016$ ;  $N = 390$  eggs with volume and laying mass data;  $\Delta\text{AIC} = 878.5$ ) and  
206 yielded heavier nestlings at hatching (Figure 1c; LM:  $\beta_{\text{standardized}} \pm \text{S.E.} = 0.468 \pm 0.048$ ;  $N = 342$

207 eggs with volume and hatchling mass data;  $\Delta\text{AIC} = 82.56$ ). These relationships also hold within  
208 mothers, illustrating that maternal *plasticity* in egg volume is also a key source of variation in egg  
209 mass at laying (LM:  $\beta_{\text{standardized}} \pm \text{S.E.}$  for the effect of *within*-mother variation in egg volume =  
210  $0.484 \pm 0.016$ ;  $N = 390$  eggs with volume and laying mass data from 63 mothers;  $\Delta\text{AIC} = 456.40$ )  
211 and nestling mass at hatching (LM:  $\beta_{\text{standardized}} \pm \text{S.E.}$  for the effect of *within*-mother variation in  
212 egg volume =  $0.282 \pm 0.048$ ;  $N = 342$  eggs with volume and hatchling mass data from 59 mothers;  
213  $\Delta\text{AIC} = 31.32$ ). Laying larger eggs may therefore have fitness consequences for mothers and the  
214 resulting offspring, as larger eggs yield heavier hatchlings (Figure 1c) and heavier hatchlings in  
215 this species are more likely to survive to fledging (Capilla-Lasheras *et al.* 2021).

216

217 Mothers that had more female helpers at laying laid larger eggs (Figure 2a; Table 1;  $\beta \pm \text{S.E.} =$   
218  $20.28 \pm 7.94$ ;  $\Delta\text{AIC} = 3.71$ ;  $N = 490$  eggs laid in 271 clutches by 62 mothers in 37 social groups  
219 [1-21 clutches [median = 7] measured per mother]). Partitioning the female helper number  
220 predictor within the best-supported model into its within- and among-mother components revealed  
221 evidence of maternal plasticity in egg volume (i.e., a maternal reaction norm to variation in female  
222 helper number): individual mothers laid larger eggs when they had more female helpers (Figure  
223 2b). Specifically, the effect size for within-mother variation in female helper number ( $\Delta$  female  
224 helper number;  $\beta \pm \text{S.E.} = 21.26 \pm 8.41$ ; Figure 2b) matched or exceeded that for among-mother  
225 variation in mean female helper number ( $\beta \pm \text{S.E.} = 12.51 \pm 23.57$ ). Accordingly, repeating model  
226 selection using the partitioned forms of both the female and male helper number predictors led to  
227 the retention of the  $\Delta$  female helper number term within the best-supported model (Table S2).  
228 The observed relationships between female helper number and egg volume cannot be readily  
229 attributed to correlated variation in abiotic environmental conditions affecting both variables as  
230 our models simultaneously allowed for effects of both rainfall and temperature on egg volume  
231 (see below and Supplementary materials B).

232

233 We found weaker evidence that male helper numbers predict variation in egg volume. When  
234 modelling the effects of population-level variation in female and male helper numbers, the best  
235 supported model containing a 'male helper number' effect was 1.40 AIC points below the top  
236 model (Table 1) and would be rejected under the nesting rule (see Table 1 legend). Accordingly,  
237 in the best-supported model that contained *both* the female helper number and male helper



238 number predictors, the effect size for female helper number ( $\beta \pm \text{S.E.} = 17.86 \pm 8.53$ ; Table 1)  
239 markedly exceeded that for male helper number ( $\beta \pm \text{S.E.} = 7.37 \pm 9.51$ ; Table 1). The same  
240 pattern was apparent when we repeated model selection using the partitioned forms of both the  
241 female and male helper number predictors: the effect size for within-mother variation in female  
242 helper number ( $\beta \pm \text{S.E.} = 18.88 \pm 8.99$ ) markedly exceeded that for within-mother variation in  
243 male helper number ( $\beta \pm \text{S.E.} = 7.51 \pm 10.12$ ) within the best-supported model that contained both  
244 terms (Table S2). Egg volume was also predicted by the position of the egg in the laying order  
245 (the first laid egg was consistently larger; Table 1) and by environmental temperature and rainfall  
246 (Table 1; the effects of these abiotic predictors are discussed in detail in Supplementary materials  
247 B). While our analyses allowed for an effect of clutch size on egg volume, no such association  
248 was detected (Table 1).

249

250 **Maternal plasticity in post-natal investment: individual mothers provision nestlings at**  
251 **lower rates when they have more female helpers**

252 Mothers that had more female helpers during the nestling period showed lower nestling  
253 provisioning rates (Figure 2c; Table 2;  $\beta \pm \text{S.E.} = -0.47 \pm 0.20$ ;  $\Delta\text{AIC} = 3.23$ ;  $N = 108$  broods being  
254 fed by 48 mothers in 34 social groups [1-5 broods [median = 2] per mother]). Partitioning the  
255 female helper number predictor within the best-supported model into its within- and among-  
256 mother components revealed evidence of maternal plasticity in nestling provisioning rate:  
257 individual mothers decreased their nestling provisioning rate when they had more female helpers.  
258 Specifically, the effect size for within-mother variation in female helper number ( $\Delta$  female helper  
259 number;  $\beta \pm \text{S.E.} = -0.47 \pm 0.29$ ; Figure 2d) matched that for among-mother variation in mean  
260 female helper number ( $\beta \pm \text{S.E.} = -0.46 \pm 0.30$ ). When the within- and among-mother effect sizes  
261 match in this way, the effect size for population-level variation in female helper number (i.e., prior  
262 to partitioning;  $\beta \pm \text{S.E.} = -0.47 \pm 0.20$ ) captures the within-mother effect (van de Pol & Wright  
263 2009). Accordingly, repeating model selection using the partitioned forms of both female and male

264 helper number led to the retention of  $\Delta$  female helper number within the best-supported model  
265 (Table S4).  
266  
267 Again, we found weaker evidence that male helper numbers predict variation in maternal nestling  
268 provisioning rate. When modelling the effects of population-level variation in female and male  
269 helper numbers, the best supported model containing a 'male helper number' effect was 0.93 AIC  
270 points below the top model (Table 2) and would be rejected under the nesting rule (see Table 2  
271 legend). Accordingly, in the best-supported model that contained both the female helper number  
272 and male helper number predictors, the effect size for female helper number ( $\beta \pm \text{S.E.} = -0.43 \pm$   
273  $0.20$ ; Table 2) was more strongly negative than that for male helper number ( $\beta \pm \text{S.E.} = -0.26 \pm$   
274  $0.23$ ; Table 2). The same pattern was apparent when we repeated model selection using the  
275 partitioned forms of both the female and male helper number predictors: the effect size for *within-*  
276 *mother* variation in female helper number ( $\beta \pm \text{S.E.} = -0.45 \pm 0.29$ ) was more strongly negative  
277 than that for *within-mother* variation in male helper number ( $\beta \pm \text{S.E.} = -0.16 \pm 0.34$ ) within the  
278 best-supported model that contained both terms (Table S4). Maternal nestling provisioning rates  
279 were also positively related to brood size (Table 2) and were predicted by environmental  
280 temperature and rainfall (Table 2; discussed in Supplementary materials B).

## 281 Discussion

282 To test the predictions of the 'load-lightening' and 'differential allocation' hypotheses for the  
283 evolution of pre-natal investment strategies in cooperative breeders, we investigated the patterns  
284 of maternal plasticity in both pre- and post-natal investment per offspring in white-browed sparrow  
285 weaver societies. Using a within-mother reaction norm approach, our analyses revealed the first  
286 formal evidence of maternal plasticity in egg investment according to the availability of help in a  
287 cooperatively breeding bird (see Introduction and Taborsky *et al.* 2007). When sparrow-weaver  
288 mothers had more female helpers they laid larger eggs (and larger eggs yield heavier hatchlings,  
289 which are more likely to survive to fledging; (Capilla-Lasheras *et al.* 2021)). This maternal plastic  
290 response runs counter to the leading 'load-lightening hypothesis' (which predicts that helped  
291 mothers should lay smaller eggs; (Russell *et al.* 2007; Savage *et al.* 2015)) and counter to general  
292 expectation given empirical work to date (Dixit *et al.* 2017). The 'differential allocation hypothesis'  
293 does predict that helped mothers should lay larger eggs (as we observe), but is thought to predict  
294 that helped mothers should also feed their nestlings at higher rates (i.e., mothers should increase  
295 both pre- *and* post-natal investment per offspring when helped; see 'silver spoon' scenario in  
296 (Savage *et al.* 2015); the pattern observed at the population level in Iberian magpies (Valencia *et*  
297 *al.* 2006, 2017)). By contrast, our findings reveal a novel maternal strategy in which mothers with  
298 more (female) helpers appear to *increase* pre-natal investment per offspring (lay larger eggs) but  
299 *decrease* post-natal investment per offspring (feed their nestlings at lower rates). We term this  
300 strategy 'maternal front-loading', as mothers effectively front-load their investment to the pre-natal  
301 stage when helped. We consider adaptive explanations for this strategy below, along with its  
302 implications for identifying the benefits of helping in cooperative societies. Notably, maternal front-  
303 loading provides a mechanism by which *post-natal* helping could have beneficial effects on the  
304 *pre-natal* development of young.

305

306 While relationships between helper number and egg size have previously been reported in  
307 cooperatively breeding birds ((Dixit *et al.* 2017); and see Introduction), our findings are the first to  
308 demonstrate that such a pattern arises from within-mother plasticity. This is important, as recent  
309 work has highlighted that population-level relationships between helper number and egg size (i.e.,  
310 those reported to date: e.g., (Russell *et al.* 2007; Canestrari *et al.* 2011; Paquet *et al.* 2013;

311 Langmore *et al.* 2016; Valencia *et al.* 2017)), can arise from among-mother variation in egg size  
312 rather than within-mother plasticity (Lejeune *et al.* 2016). Furthermore, that sparrow-weaver  
313 mothers appear to adjust egg size according to female helper number and not male helper  
314 number implicates the availability of post-natal helping *per se* as the likely driver of this plastic  
315 maternal response, rather than correlated variation in group size (as female helpers feed nestlings  
316 at twice the rate of male helpers, and only female helper number has a causal positive effect on  
317 the overall rate of nestling provisioning; (Capilla-Lasheras *et al.* 2021)). Indeed, as female and  
318 male helper numbers at laying strongly predict helper numbers during the post-natal care period  
319 (Figure S1), sparrow-weaver mothers should have sufficient information at laying to adjust their  
320 egg volume to the future availability of post-natal help, were it adaptive to do so. Such a pattern  
321 of investment per egg could conceivably emerge as a by-product of a helper effect on the mother's  
322 optimal clutch size or number of clutches per year, with which egg volume could trade off (Lejeune  
323 *et al.* 2016). This mechanism cannot readily account for our findings, however, as sparrow-weaver  
324 mothers vary neither clutch size nor clutch number according to helper numbers (Supplementary  
325 materials A). Additional analyses also suggest that maternal plasticity in egg volume cannot be  
326 readily attributed to carry-over effects on maternal condition of helper actions in previous breeding  
327 attempts (see Supplementary materials C).

328

329 The 'differential allocation hypothesis' as applied to cooperative breeders does predict the pattern  
330 of egg investment observed here: mothers should lay larger eggs when helped (Russell &  
331 Lummaa 2009; Savage *et al.* 2015; Valencia *et al.* 2017). In general terms, the hypothesis  
332 proposes that mothers should increase maternal investment under circumstances that increase  
333 their return on investment in the current breeding attempt, such as having a more attractive mate  
334 or more helpers (Sheldon 2000; Russell & Lummaa 2009). Accordingly, theoretical models that  
335 apply the differential allocation rationale specifically to pre-natal investment in cooperative  
336 breeders (by having the mother's return on pre-natal investment per offspring increase when she  
337 has help with post-natal care; (Savage *et al.* 2015)), predict that mothers should increase both  
338 their pre- *and* post-natal investment per offspring when helped. These predictions are consistent  
339 with the patterns observed in the only other species to date in which mothers are thought to  
340 consistently lay larger eggs when they have more help: Iberian magpie mothers with helpers  
341 appear to lay larger eggs *and* provision their nestlings at higher rates than those without helpers

342 ((Valencia *et al.* 2006, 2017); but whether either reflects maternal plasticity is unknown). It is  
343 notable then that sparrow-weaver mothers instead increase pre-natal investment per offspring  
344 while *decreasing* post-natal investment per offspring when helped (i.e., engage in ‘maternal front-  
345 loading’); a pattern that is at odds with this set of predictions.

346

347 It is conceivable that the core rationale of the differential allocation hypothesis nevertheless can  
348 account for the pattern of egg investment observed here, as the biological processes and/or  
349 parameter space explored in the theoretical work to date (Savage *et al.* 2015) might not capture  
350 all relevant aspects of the biology at play. As per the differential allocation rationale, sparrow-  
351 weaver mothers could increase egg size with female helper number because the additive post-  
352 natal care that their female helpers will provide (Capilla-Lasheras *et al.* 2021) increases the  
353 mother’s expected return on investment per egg. For example, producing larger hatchlings may  
354 yield a greater payoff when those hatchlings stand to be fed at higher rates (Savage *et al.* 2015;  
355 Langmore *et al.* 2016). Our findings reveal that such additive post-natal care by helpers (Capilla-  
356 Lasheras *et al.* 2021) is accompanied here by mothers decreasing their own post-natal  
357 contributions when helped; a maternal strategy of post-natal ‘partial compensation’ commonly  
358 observed in cooperative breeders (Hatchwell 1999). As the evolution of such maternal post-natal  
359 partial compensation is generally attributed to post-natal care yielding diminishing returns  
360 (Hatchwell 1999; Heinsohn 2004), it would be valuable to now establish whether the integration  
361 of more strongly diminishing returns of post-natal care into existing models of the differential  
362 allocation hypothesis (Savage *et al.* 2015) would leave them predicting the maternal front-loading  
363 strategy observed here. The integration of stronger maternal trade-offs between pre- and post-  
364 natal investment and/or higher costs to mothers of post-natal investment might also resolve the  
365 apparent disparity.

366

367 While it may ultimately prove possible to reconcile the differential allocation hypothesis with the  
368 maternal investment strategy observed here (see above), our findings do highlight a simpler  
369 explanation for sparrow-weaver mothers laying larger eggs when helped. The differential  
370 allocation hypothesis envisages that helpers increase the maternal *benefit* of pre-natal investment  
371 per offspring (e.g., via the provision of additive post-natal care; (Savage *et al.* 2015)). However,  
372 helpers may instead reduce the maternal *cost* of pre-natal investment per offspring by reducing

373 maternal post-natal workloads. Maternal front-loading may therefore reflect an anticipatory  
374 strategy in which the expected lightening of maternal *post-natal* workloads allows helped mothers  
375 to focus their investment on the *pre-natal* phase, to which helpers cannot contribute directly. Such  
376 a maternal strategy may therefore be of particular benefit when pre-natal investment has  
377 differentially large effects on offspring fitness. Under this scenario, the maternal increase in egg  
378 investment when helped is a consequence of the helper effect on the mother's post-natal  
379 workload, whereas under the differential allocation hypothesis the increase is typically considered  
380 a product of the additive effect of helpers on the overall provision of post-natal care (Russell &  
381 Lummaa 2009; Langmore *et al.* 2016; Dixit *et al.* 2017; Valencia *et al.* 2017). Species in which  
382 helpers lighten maternal post-natal workloads but do *not* have additive effects on post-natal care  
383 (because the maternal reduction in post-natal work rate completely compensates for helper  
384 contributions; (Hatchwell 1999)) would therefore provide a fruitful testing ground for testing these  
385 alternative, though not mutually exclusive, hypotheses. As maternal post-natal load-lightening is  
386 often reported in cooperative breeders (Hatchwell 1999; Heinsohn 2004; Russell *et al.* 2007;  
387 Kingma *et al.* 2010), the maternal front-loading strategy observed here could ultimately prove  
388 more commonplace once more studies formally characterize maternal plasticity in egg investment  
389 (Lejeune *et al.* 2016). Indeed, recent evidence suggesting that superb fairy-wren mothers with  
390 helpers lay larger eggs than those without when conditions are warm (Langmore *et al.* 2016)  
391 could reflect maternal front-loading in warm conditions, if the reported population-level  
392 relationship between egg size and the availability of help arose via maternal plasticity, and if post-  
393 natal load-lightening also occurred under such warm conditions (which it could well do; (Russell  
394 *et al.* 2008)).

395

396 Where mothers do front-load their investment to the pre-natal stage when helped (as observed  
397 here), post-natal helping may have hitherto unexplored beneficial effects on the pre-natal  
398 development of offspring. The potential for such cryptic 'pre-natal helper effects' has important  
399 implications for attempts to identify and quantify the benefits of helping in cooperative societies.  
400 First, while it has been suggested that studies of helper effects on offspring should control for  
401 variation in egg size in order to ensure that maternal *reductions* in egg size by helped mothers do  
402 not 'conceal' helper effects on offspring (Russell *et al.* 2007), our findings highlight a danger of  
403 this approach. If, as here, plastic mothers lay *larger* eggs when helped, controlling for variation in

404 egg size could lead to the *underestimation* of helper effects on offspring, by factoring out helper  
405 effects that arise indirectly via maternal investment in the egg. Second, while helper-induced  
406 reductions in maternal post-natal workloads are typically thought to benefit mothers (e.g., by  
407 improving maternal survival; (Hatchwell 1999; Russell *et al.* 2007)), our findings highlight that  
408 anticipatory changes in egg investment may actually pass these benefits, in part or whole, to the  
409 offspring being reared. Indeed, as helpers commonly lighten maternal post-natal workloads  
410 (Hatchwell 1999; Heinsohn 2004; Russell *et al.* 2008; Kingma *et al.* 2010), it is conceivable that  
411 a maternal front-loading response of the type observed here has actually contributed to the  
412 positive relationships already described in numerous species between helper numbers and  
413 offspring survival or performance.

414

## 415 **Conclusion**

416 Our findings provide the first formal evidence of maternal plasticity in pre-natal investment per  
417 offspring according to the availability of help in a natural population (Taborsky *et al.* 2007). They  
418 reveal a plastic maternal pre-natal response that runs directly counter to the predictions of the  
419 leading load-lightening hypothesis and to general expectation given the limited empirical work to  
420 date (Dixit *et al.* 2017). The patterns of maternal plasticity in *post-natal* investment that we also  
421 document suggest that the overall maternal strategy does not match the existing predictions of  
422 the differential allocation hypothesis either (Savage *et al.* 2015), and instead highlight an  
423 alternative explanation for mothers increasing their egg size when helped: by lightening maternal  
424 post-natal workloads, helpers may allow mothers to focus their investment on the pre-natal stage,  
425 to which helpers cannot contribute directly. The novel ‘maternal front-loading’ strategy that  
426 sparrow-weaver mothers appear to employ has important implications for attempts to both identify  
427 and quantify the benefits of helping; the best-studied form of animal cooperation.

## 428 **Materials and Methods**

### 429 **General Field Methods**

430 White-browed sparrow-weavers live in semi-arid regions of East and Southern Africa. Our study  
431 population is located in Tswalu Kalahari Reserve in the Northern Cape Province of South Africa  
432 (27°16'S, 22°25' E). Fieldwork was carried out from September to April between 2007 and 2016  
433 inclusive. Approximately 40 social groups were monitored, each defending a small exclusive  
434 territory within an overall study site of approximately 1.5 km<sup>2</sup>. Sparrow-weaver groups were easily  
435 monitored and distinguished in the field as all group members foraged together, engaged in  
436 communal weaving and territory defense, and roosted within in a single tree or cluster of trees  
437 close to the center of their territory. All birds in the study population were fitted with a single metal  
438 ring and three color rings for identification from the time they were first detected in the population  
439 (under SAFRING license 1444). The sex of each bird could be determined after six months of age  
440 using the sex difference in bill color (Leitner *et al.* 2009).

441

442 Each social group contains a single behaviourally dominant female. The dominant female is easily  
443 identified in the field because she displays a distinct set of behaviours: being behaviourally  
444 dominant to other females, being the only female observed to incubate the eggs or enter the nest  
445 during the incubation phase, and closely associating with and frequently duetting with the  
446 dominant male (Walker *et al.* 2016). Genetic analyses have confirmed that the dominant female  
447 is always the mother of any eggs or chicks produced on their group's territory; subordinate  
448 females never breed (Harrison *et al.* 2013). For brevity, we therefore refer throughout the paper  
449 to the dominant female as the 'mother'.

450

451 Each group's territory was regularly monitored (every one or two days while nests were present)  
452 to detect new clutches. Once a new clutch was found, egg length and maximum width were  
453 measured with a plastic calliper to the nearest 0.1 mm. Nests were then checked daily until the  
454 clutch had been completed. Clutches were then checked 8 days after the first egg was laid (to  
455 confirm the progression of incubation), before daily checks were resumed 15 days after the first  
456 egg was laid, until the fate of every egg had been determined (hatch or failure). Hatchlings were  
457 weighed on their first day of life using a portable scale to the nearest 0.01 g.



458

459 The composition of each social group was assessed every week throughout each field season,  
460 with birds being identified on the basis of their color-ring combination. Birds were also routinely  
461 caught while roosting within their group's territory at night, and this information also contributed  
462 to group composition assessments. Group compositions were typically very stable over time, with  
463 group members residing within the same social group for many months to many years at a time  
464 (i.e., group composition not being affected by short-term fluctuations in environmental conditions).  
465 For every breeding attempt in our analyses, we used these group compositions to calculate the  
466 number of male and female helpers that the dominant female (mother) had on the day of laying  
467 (for the egg volume analyses) and on the days that provisioning behaviour was recorded (for the  
468 maternal provisioning rate analyses). All subordinate group members over the age of 6 months  
469 were considered helpers, as analyses of helper contributions suggest that subordinates < 6  
470 months old contribute little to nestling provisioning (Lewis 1982; Capilla-Lasheras 2020).

471

#### 472 **Nestling provisioning behaviour**

473 Nestling provisioning behaviour was recorded for 174 breeding attempts between September  
474 2007 and April 2016. We collected provisioning data using video recordings of the birds visiting  
475 the nest (viewed from below the nest) between the 10<sup>th</sup> and 12<sup>th</sup> day inclusive after the first egg  
476 of a given clutch had hatched (this is the period of highest nestling post-natal demand; the nestling  
477 period lasts approximately 20-25 days). At least five days before video recording started, we (i)  
478 caught and marked the vent of each group member other than the dominant female using hair  
479 dye (Capilla-Lasheras *et al.* 2021) to aid their identification on the video and (ii) deployed a tripod  
480 on the ground beneath the nest to acclimatize the birds to its presence prior to recording. On  
481 recording days, the video camera was set up and recording started soon after sunrise, at standard  
482 times relative to sunrise in order to track seasonal changes in sunrise timings. Provisioning  
483 behaviour was recorded for approximately three hours per day per brood. Video recordings were  
484 then watched using VLC media player to determine the rate at which each group member visited  
485 the nest (here after their 'provisioning rate'), identifying each visitor via their sex (based on bill  
486 coloration (Leitner *et al.* 2009)), unique vent pattern and color-ring combination. Prior analyses  
487 using within-nest cameras have confirmed that during this peak provisioning period all nest visits  
488 by all group members entail the delivery of a single food item by the visitor that is then eaten by

489 the chicks (the only exception being nest-maintenance visits that were easily excluded from the  
490 data set on the basis of the visitor conspicuously carrying grass (Walker 2015)).

491

492 We then calculated the provisioning rate of mothers (feeds / hour). In some cases, we were unable  
493 to reliably identify every visiting bird within the provisioning video, yielding some uncertainty in  
494 our estimate of maternal provisioning rate. We therefore only carried forward maternal  
495 provisioning rate estimates to our statistical analyses where the maximum possible maternal  
496 provisioning rate (i.e., if one considered the mother the feeder in *all* cases of uncertain feeder  
497 identity) did not exceed the observed maternal provisioning rate (calculated solely on the basis of  
498 the mother's identified visits) by more than 33% or 3 feeds / hour. Applying this filtering criteria,  
499 there was less than 10% uncertainty for more than 90% of maternal provisioning rate estimations.  
500 Where estimates of maternal provisioning rate were available for multiple mornings for a given  
501 breeding attempt, the measures were averaged to yield a single mean maternal provisioning rate  
502 for each breeding attempt for analysis (as maternal provisioning rate estimates for a given  
503 breeding attempt were highly correlated over successive mornings of video recording). This  
504 yielded a data set for analysis of mean maternal provisioning rate for 48 different dominant  
505 females (mothers) feeding 108 broods in 34 social groups.

506

#### 507 **Environmental data**

508 Daily rainfall data were collected from two rainfall gauges located to the west (27° 16' 58.9" S,  
509 22° 23' 02.1" E) and east (27° 17' 42.1" S, 22° 27' 34.9" E) of the study site, 7.60 km apart from  
510 each other. These two rainfall measurements were highly correlated during the study period  
511 (Pearson's product-moment correlation:  $r = 0.875$ , 95% CI = 0.867 – 0.882,  $df = 3,347$ ). We  
512 therefore calculated average daily values across both gauges and used this as a proxy for rainfall  
513 conditions at the study site.

514

515 Temperature data for a 0.25 degree latitude x 0.25 degree longitude area that encompassed the  
516 study site was extracted from the GLDAS-2.1 Noah 0.25 degree 3-hourly data set (Rodell *et al.*  
517 2016), accessed via the NASA's Goddard Earth Sciences Data and Information Services Center  
518 online data system (Giovanni; <http://disc.sci.gsfc.nasa.gov/giovanni>). From this, we calculated the  
519 daily maximum temperature and daily mean temperature (i.e., the average of all eight measures

520 available per 24 hour period) for all days of our study. The daily mean temperatures from this data  
521 set were highly correlated with those obtained directly within our study site using a 2700  
522 Watchdog weather station (Spectrum Technologies Inc) deployed for part of the study period  
523 (partial coverage of 2010-2015; Pearson's product-moment correlation:  $r = 0.973$ , 95%CI = 0.970  
524 – 0.975,  $df = 1,771$ ).

525

## 526 **Statistical analysis**

### 527 *Modelling maternal pre-natal investment per offspring: egg volume.*

528 Linear mixed models with Gaussian error structure were used to investigate the predictors of egg  
529 volume (calculated based on length and maximum breadth following the formula given in  
530 (Narushin 2005)). Four terms were included as random intercepts: breeding season (referring to  
531 each of the nine different September-April breeding seasons studied), social group ID, clutch ID  
532 and maternal ID. The following were included as fixed effect predictors: egg position within the  
533 clutch, clutch size, number of female helpers, number of male helpers and the interaction between  
534 helper number (both females and males) and (i) egg position, and (ii) clutch size. To control for  
535 the potential effects of temperature and rainfall on egg volume, we also fitted the following two  
536 indices as fixed effect predictors: a 'heat waves' index (the number of days in which the maximum  
537 daily temperature exceeded 35°C within a time window spanning the 13 days prior to egg laying)  
538 and a rainfall index (the total rainfall that fell within a time window spanning 44-49 days prior to  
539 egg laying). The specific time windows used for the calculation of these indices were determined  
540 objectively by the application of a sliding window approach prior to this modelling step (see  
541 Supplementary materials B). The 'heat waves' index as defined here (i.e., number of days above  
542 35°C) has been shown to appropriately capture hot-weather events in the Kalahari and it impacts  
543 the reproductive biology of several Kalahari bird species (Cunningham *et al.* 2013b, a). Between  
544 2007 and 2016 inclusive, we collected egg length and width information (and therefore volume)  
545 from 906 eggs that were detected in the field with less than four days of uncertainty around their  
546 laying date. We focused our analysis on the 490 of these for which we also knew laying order  
547 (allowing determination of the 'egg position within the clutch' variable): 490 eggs from 271  
548 clutches laid by 62 dominant females (mothers) across 37 social groups (mean = 7.90 eggs per  
549 mothers; range 1 – 21 eggs per mother).

550

551 *Modelling maternal post-natal investment: maternal nestling provisioning rate*

552 Linear mixed models with Gaussian error structure were used to investigate the predictors of  
553 maternal provisioning rate (calculated as a single mean value for each breeding attempt; see  
554 above). Three terms were included as random intercepts: breeding season (see above), social  
555 group ID, and maternal ID. The following were included as fixed effect predictors: brood size,  
556 number of female helpers, number of male helpers and the interactions between helper number  
557 (both females and males) and brood size. To control for the potential effects of temperature and  
558 rainfall on maternal provisioning rate, we also fitted the following two indices as fixed effect  
559 predictors: 'heat waves' index (the total number of days within a time window spanning 51-58  
560 days prior to egg laying in which the maximum daily temperature exceeded 35°C) and a rainfall  
561 index (the total amount of rainfall that fell within a time window spanning 61-78 days prior to egg  
562 laying). The specific time windows used for the calculation of these indices were determined by  
563 the application of a sliding window approach prior to this modelling step (see Supplementary  
564 materials B for methods and interpretation). The final data set contained 108 measures of mean  
565 maternal provisioning rate for 108 broods born to 48 dominant females (mothers) across 34 social  
566 groups.

567

568 *General statistical procedures*

569 To identify the predictors of the focal response term in our mixed effects models we used an  
570 information-theoretic (IT) approach. Starting from a global model that contained the fixed effect  
571 variables and interactions predicted to have an effect on the focal response term (see above for  
572 details), we fitted all possible models containing simpler combinations of these fixed effect  
573 predictors and ranked them for model fit based on Akaike's Information Criterion (AIC, (Burnham  
574 & Anderson 2002)). With this approach, the best-supported model is the one with the lowest AIC  
575 value.  $\Delta$ AIC values were then calculated for every model, as the difference between the AIC of  
576 the focal model and that of the best-supported model (thus, the  $\Delta$ AIC for the best-supported model  
577 is zero, and models with progressively weaker fits have progressively larger positive  $\Delta$ AIC  
578 values). We gave consideration to models with  $\Delta$ AIC values  $< 6$  (Richards 2008; Richards *et al.*  
579 2011) and subsequently reduced this  $\Delta 6$  top model set by applying the 'nesting rule' described in  
580 (Richards 2008). Simulations have shown that the addition of uninformative variables to a top  
581 model can weaken AIC support by less than six points, leading to the retention within the  $\Delta 6$  top

582 model set of more complex versions of better supported models, which contain such  
583 uninformative variables (Richards 2008; Arnold 2010). The nesting rule aims to avoid this scenario  
584 by discarding models that are more complex versions of better-supported simpler (nested) models  
585 (Richards 2008; Arnold 2010). The subset of models retained after applying the nesting rule are  
586 flagged in the right-hand column in all model output tables. When quadratic terms were included  
587 in a given model, linear coefficients were always present. Intercept-only models were always  
588 considered. For AIC comparisons, models were fitted using maximum likelihood. All predictors  
589 were standardized prior to analysis by mean centering and dividing by one standard deviation,  
590 with the exception of those relating to helper numbers (to facilitate comparisons of the effect size  
591 estimates for male and female helper numbers by keeping them on the same scale; using  
592 standardized helper number predictors instead yielded identical conclusions). Statistical analyses  
593 were performed in R version 3.6.1. (R Core Team 2019), and statistical models were fitted using  
594 the R package 'lme4' (Bates *et al.* 2015).

595

596 A common concern in studies of the effects of helper numbers on fitness-related traits in  
597 cooperative species, is that positive correlations between the two could arise not from a causal  
598 effect of helpers on the focal trait but instead from both helper numbers and the focal trait being  
599 positively impacted by territory (and/or maternal) quality (Cockburn 1998; Cockburn *et al.* 2008).  
600 We addressed this concern in two different ways. First, we excluded young individuals (< 6 six  
601 months old) from our calculations of the number of male and female helpers (see above; as they  
602 contribute little to helping), given that transient resource peaks could leave recent and current  
603 productivity positively correlated, potentially yielding a spurious correlation between helper  
604 number and current productivity if recently fledged young were considered helpers. Second, we  
605 first carried out our analyses using the number of (male and female) helpers as the focal predictor,  
606 and then partitioned this variable into its within- and among-mother components:  $\Delta$  (male or  
607 female) helper number and  $\mu$  (male or female) helper number respectively (van de Pol & Wright  
608 2009). ' $\mu$  helper number' is the mean helper number that a mother had across all of her breeding  
609 attempts in the relevant data set, whereas ' $\Delta$  helper number' is the difference between her helper  
610 number in the focal clutch or brood and ' $\mu$  helper number'. This approach allows us to statistically  
611 isolate the effects of within-mother ( $\Delta$ ) variation in helper number (which is both within-mother

612 and within-territory, as each mother in our analyses only ever held one territory), which are  
613 indicative of maternal *plasticity*, in the knowledge that its effects cannot be attributed to variation  
614 in quality *among* mothers or their territories. A recent study has shown that partitioning within-  
615 and among-individual effects following this approach provides a robust estimation of the within-  
616 individual effect size, the parameter of interest in this study (Westneat *et al.* 2020).

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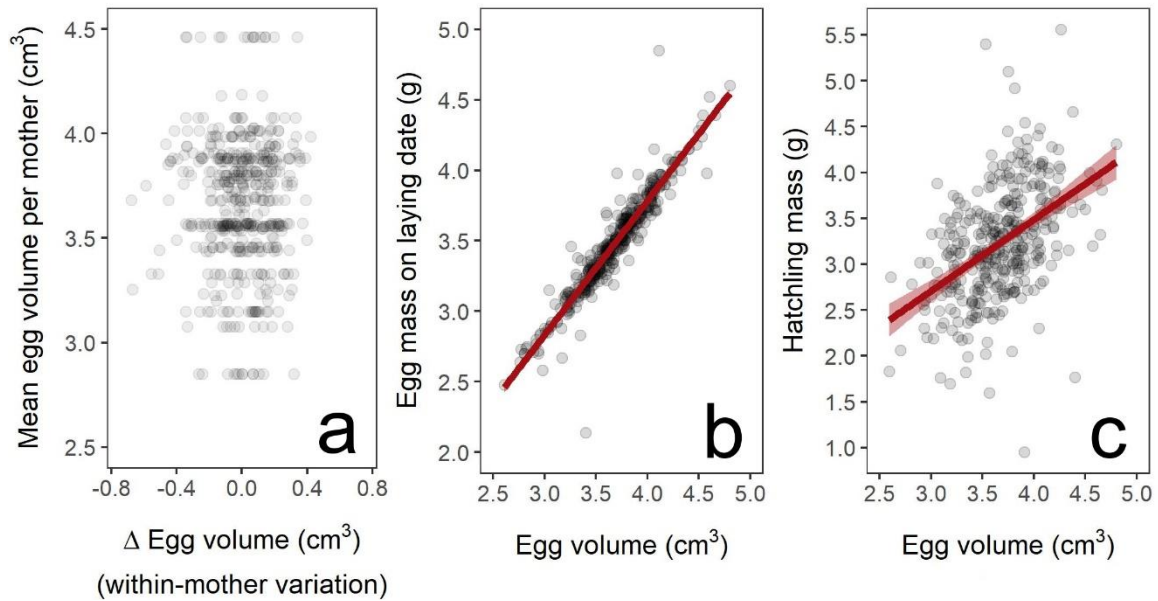
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777 **Figures and Tables**

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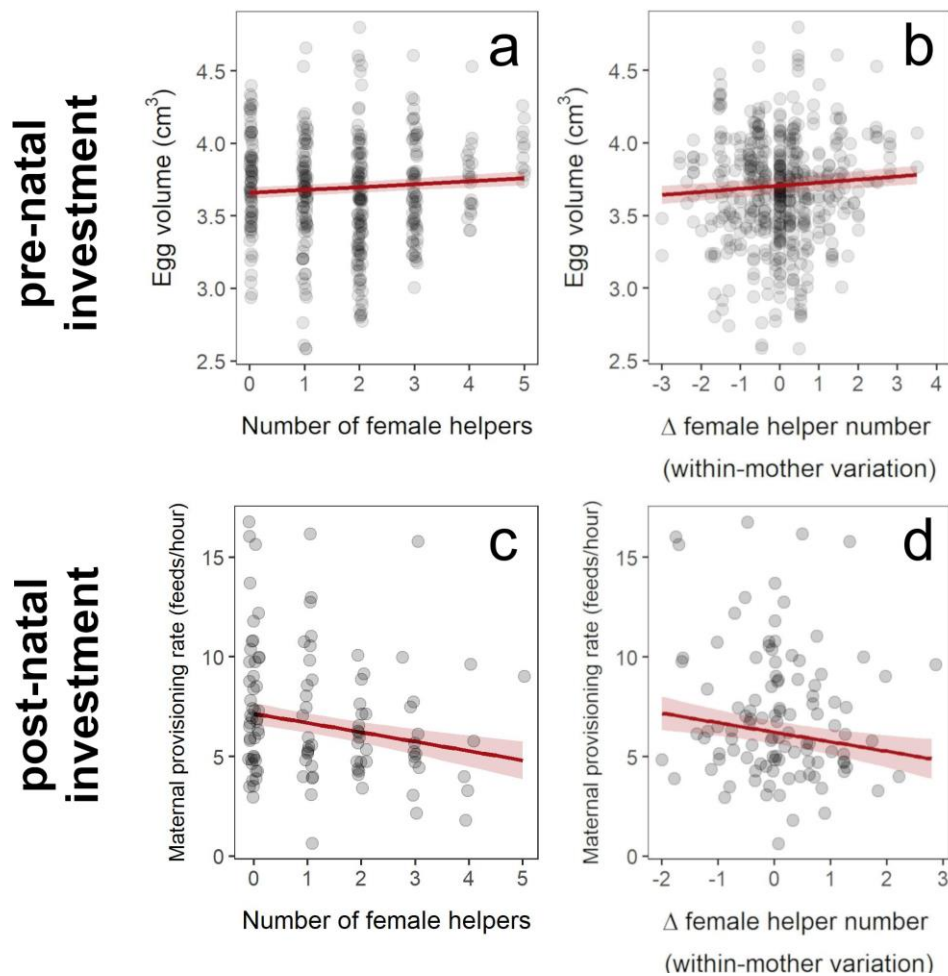
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**Figure 1. Patterns and implications of maternal variation in egg volume.** (a) Egg volume showed high variation both within (x-axis) and among mothers (y-axis).  $\Delta$  egg volume represents the difference in egg volume between the focal egg and that mother's own mean egg volume (i.e., within-mother variation; hence the negative and positive values). (b) Variation in egg volume positively predicted egg mass (g) on the day of laying and (c) nestling mass (g) on the day of hatching. Mean model predictions  $\pm$  standard error (SE) are plotted in red.



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789 **Figure 2. Maternal plasticity in pre-natal (egg volume) and post-natal (nestling provisioning**  
790 **rate) investment according to female helper numbers. (a)** Female helper number positively  
791 predicts egg volume at the population level (Table 1; prior to partitioning variation in helper  
792 number). **(b)** Within-mother variation in female helper number (' $\Delta$  female helper number') also  
793 positively predicts egg volume, providing evidence of maternal plasticity (see results & Table S2).  
794 **(c)** Female helper number negatively predicts maternal nestling provisioning rate at the population  
795 level (Table 2). **(d)** Within-mother variation in female helper number (' $\Delta$  female helper number')  
796 also negatively predicts maternal nestling provisioning rate, providing evidence of maternal  
797 plasticity (see results & Table S4). Grey dots illustrate raw data points and red lines present model  
798 predictions ( $\pm$  SE).

799 **Table 1.** The top-performing models (i.e., those within  $\Delta AIC < 2$  of the top model) explaining  
 800 variation in egg volume. Only the top model would be retained under the nesting rule ('Retained'  
 801 (Richards 2008); see methods). The longer list of models within  $\Delta AIC < 6$  of the top model is  
 802 presented as Table S1. The first model not containing number of female helpers as a predictor  
 803 scored a  $\Delta AIC$  value of 3.71 (see Table S1). Model coefficients (effect sizes) are shown along  
 804 with number of model parameters ('k'), AIC, and  $\Delta AIC$ . Other tested predictors not shown in this  
 805 table (as they were not present in the models within this set) were as follows: clutch size, clutch  
 806 size x female helper number, egg position x female helper number and egg position x male helper  
 807 number.

Intercept	Number female helpers	Number male helpers	Rainfall <sup>1</sup>	Rainfall <sup>2</sup>	Egg position	Heat waves	Clutch size x Number male helpers	k	AIC	$\Delta AIC$	Retained
3638.00	20.28		-553.60	-859.80	-43.20	-41.71		11	6671.1	0.00	✓
3631.00	17.86	7.37	-545.70	-855.40	-42.96	-42.46		12	6672.5	1.40	
3638.00	20.51		-555.30	-865.60	-47.81	-41.56	3.77	12	6672.7	1.59	

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810 **Table 2.** The top-performing models (i.e., those within  $\Delta AIC < 2$  of the top model) explaining  
 811 variation in maternal provisioning rate. Only the top model would be retained under the nesting  
 812 rule ('Retained' (Richards 2008) ; see methods). The longer list of models within  $\Delta AIC < 6$  of the  
 813 top model is presented as Table S3. The first model not containing number of female helpers as  
 814 a predictor scored a  $\Delta AIC$  value of 3.23 (see Table S3). Model coefficients (effect sizes) are  
 815 shown along with number of model parameters ('k'), AIC, and  $\Delta AIC$ .

Intercept	Number female helpers	Number male helpers	Brood size	Rainfall <sup>1</sup>	Rainfall <sup>2</sup>	Heat waves	Number female helpers X Brood size	Number male helpers X Brood size	k	AIC	$\Delta AIC$	Retained
7.63	-0.47		1.51	4.98	7.18	0.69			10	526.3	0.00	✓
7.85	-0.43	-0.26	1.92	4.86	7.34	0.62		-0.34	12	527.2	0.93	
7.88	-0.45	-0.21	1.49	4.76	7.15	0.64			11	527.5	1.18	
7.63	-0.46		1.48	5.07	7.15	0.69	0.04		11	528.3	1.97	

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