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1 **Maternal effects as a mechanism for manipulating male care and resolving**
2 **sexual conflict over care**

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12

13 **Abstract**

14 Understanding how sexual conflict influences male and female parental decisions is a long-
15 standing problem in behavioral ecology. Until now, most research on sexual conflict over
16 parental care has focused on behavioral mechanisms mediating the resolution of this conflict
17 through negotiation between parents. Here, we review evidence suggesting that maternal
18 effects that alter offspring phenotypes may provide females with a mechanism for
19 manipulating male care. We show that empirical studies on the role of maternal androgens in
20 birds with biparental care provide no support for female manipulation of male care. However,
21 we argue that it would be premature to conclude that maternal androgens play no role in
22 female manipulation of male care given methodological problems in previous work. We then
23 identify a number of additional mechanisms by which females may manipulate male care,
24 including egg components other than androgens, egg size and egg coloration. We show that
25 there is good evidence that egg coloration affects male care, suggesting that this mechanism
26 warrants further research. We also highlight that current evidence is derived from studies
27 using experimental design that target specific candidate mechanisms, such as maternal
28 androgens. Given the multitude of candidate mechanisms, we discuss an alternative approach
29 based on targeting ecologically relevant pre-natal conditions, such as food availability, and
30 monitoring subsequent effects on candidate mechanisms, offspring phenotypes, and male and
31 female care. Finally, we argue that it is timely to extend this work beyond birds with
32 biparental care to include other taxa and species with uniparental male care and cooperative
33 breeding.

34

35 *Key words:* begging, biparental care, egg coloration, egg size, female care, male care,
36 manipulation, maternal androgens, sexual conflict

37

38 **INTRODUCTION**

39 Understanding how sexual conflict shapes the evolution of male and female parental
40 strategies is a fundamental and long-standing problem in behavioral ecology (Clutton-Brock,
41 1991; Royle et al., 2012; Trivers, 1974). In the context of parental care, sexual conflict arises
42 because the benefits of care to the offspring are due to the combined effort of the two parents,
43 while the costs of care to each parent are due to its own personal effort. As a consequence of
44 this, each parent should be under selection to minimize its personal effort by shifting as much
45 as possible of the workload over to its partner (Houston et al., 2005). Thus, sexual conflict
46 poses an important theoretical problem because it undermines the evolutionary stability of
47 biparental care. Given this problem, most research into sexual conflict over parental care has
48 focused on identifying behavioral mechanisms that mediate the resolution of this conflict,
49 thereby allowing biparental care to remain evolutionarily stable (Harrison et al., 2009;
50 Houston et al., 2005; Lessells and McNamara, 2012).

51 Theoretical models have identified three behavioral mechanisms that may mediate the
52 resolution of sexual conflict over parental care (Lessells 2012; Lessells and McNamara,
53 2012): negotiation, matching and sealed-bid responses. Negotiation occurs when each parent
54 adjusts its level of care in direct response to its partner's contribution, such that the focal
55 parent partially compensates for a reduction in amount of care provided by its partner
56 (McNamara et al., 1999). Matching occurs when each parent adjusts its level of care to its
57 partner's contribution by matching any increase or reduction in its partner's contribution
58 (Johnstone and Hinde, 2006). Finally, sealed bids models assume that each parent makes an
59 initial fixed decision about how much care to provide that is independent of its partner's
60 decision (Houston and Davies, 1985). Although a meta-analysis of work on birds provides
61 overwhelming support for negotiation models (Harrison et al., 2009), there is empirical
62 support for all three models (e.g. Hinde, 2006; Schwagmeyer et al., 2002; Wright and Cuthill,

63 1989). In models of negotiation, matching or sealed-bid, the two parents use similar
64 behavioral strategies to influence the amount of care provided by their partner after the
65 hatching of their offspring, suggesting symmetry between male and female parents with
66 respect to how much influence they have on the resolution of sexual conflict. However, there
67 is mounting evidence that female birds can adjust the levels of hormones or other egg
68 components that influence offspring behavior or development in response to environmental
69 cues (Meylan et al., 2012; Saino et al., 2002; Von Engelhardt and Groothuis, 2011). Such
70 maternal effects may induce asymmetry between the sexes by providing females with a
71 mechanism for manipulating male contributions towards parental care by altering offspring
72 behavior or development (Moreno-Rueda, 2007; Müller et al., 2007). Maternal effects would
73 allow females to influence male care without the need to interact with the male partner while
74 he provides care, suggesting that maternal effects may be as relevant to species with
75 uniparental male care as to species with biparental care. Therefore, an important yet
76 unresolved issue in this field is whether females exercise greater control over the resolution of
77 sexual conflict via maternal effects (Moreno-Rueda, 2007; Müller et al., 2007).

78 The aim of this review is first to provide a brief overview over male involvement in
79 parental care and sexual conflict over the male's involvement in care, and then discuss
80 different maternal effects mechanisms by which females may influence male care. We
81 highlight that relatively few empirical studies have directly investigated female manipulation
82 in the context of sexual conflict. All of these studies were focused on testing the manipulating
83 androgens hypothesis (MAH) in birds with biparental care. The MAH focuses on the
84 mechanistic basis of female manipulation of male care in birds, and suggests that females
85 deposit androgens into the eggs in order to stimulate offspring begging, thereby elevating the
86 level of male care. We discuss potential methodological issues arising from previous
87 empirical tests of the MAH. We then identify a number of alternative mechanisms to

88 androgens, including other egg components, egg size and egg coloration, and suggest that the
89 results from studies on some of these mechanisms are consistent with female manipulation of
90 male care. Considering that females could use any one of these mechanisms to manipulate
91 male care, we propose another approach to test for female manipulation of male care that is
92 independent of the mechanistic basis of such manipulation. This approach would involve the
93 experimental manipulation of ecologically relevant pre-natal conditions (i.e., conditions that
94 are expected to trigger facultative changes in maternal effects), and the monitoring of
95 subsequent effects on candidate mechanisms, offspring phenotypes and male and female
96 parental effort. Finally, we argue that it is timely to expand work beyond the current focus on
97 birds with biparental care to include other animal taxa and species with uniparental male care
98 and cooperative breeding.

99

100 **MALE CARE AND SEXUAL CONFLICT**

101 Given that maternal effects can only influence the outcome of sexual conflict over parental
102 care if males contribute towards parental care, we start by providing a brief overview of the
103 taxonomic distribution and diversity of male involvement in parental care. Although male
104 parental care is relatively rare compared to female care, male care has evolved repeatedly
105 across a wide range of animal taxa, including birds, mammals, amphibians, fishes, arthropods
106 and annelids (Ridley, 1978; Royle et al., 2012). As hinted at earlier, male care occurs in two
107 distinct contexts: biparental care where the male cooperates with the female in providing care
108 for their joint offspring, and uniparental male care where the male is the sole care-giver.

109 Biparental care is common in birds (Cockburn, 2006), but it also occurs in a small number of
110 mammals, fishes, amphibians and arthropods (Balshine, 2012; Trumbo, 2012). Meanwhile,
111 uniparental male care is relatively common in fishes and amphibians (Balshine, 2012; Gross
112 and Sargent, 1985), and also occurs in some arthropods, such as sea spiders, assassin bugs and

113 giant waterbugs (Tallamy, 2001). Biparental care tends to involve elaborate forms of care,
114 such as progressive provisioning where parents repeatedly provide the offspring with food
115 after hatching and offspring often beg for food from the parents (Royle et al., 2012). In
116 contrast, uniparental male care tends to involve relatively simple forms of care, such as
117 guarding of eggs or juveniles. In species with uniparental male care and biparental care,
118 maternal effects provide one mechanism by which females could influence the resolution of
119 sexual conflict over parental care. Meanwhile, in species with biparental care, females could
120 influence male care via a combination of maternal effects prior to hatching or birth and
121 behavioral mechanisms such as negotiation and matching after hatching or birth. Thus, in
122 species with biparental care, the role of negotiation between the two parents after hatching
123 may depend on the extent to which male care is influenced by maternal effects on offspring
124 phenotypes.

125 In behavioral ecology, relatively simple cost-benefit analyses are used to derive the
126 optimal amount of male (and female) care (Fig. 1). The benefits of care are typically
127 measured in terms of enhanced offspring fitness (i.e. offspring survival and/or growth), and
128 the indirect benefits to the male parent can be calculated as the increase in offspring fitness
129 that is due to male care multiplied by the coefficient of relatedness between the male and the
130 offspring. Thus, one factor that may induce variation in the benefits of male care is losses in
131 paternity, which influences the coefficient of relatedness between the male and the offspring.
132 The costs of parental care, on the other hand, are measured in terms of reduced personal
133 fitness (i.e., current and future mating opportunities and/or future survival and reproductive
134 success). Loss of mating opportunities is an important cost of parental care to males in many
135 species given that parental care in general is a mutually exclusive activity with the pursuit of
136 additional mates (Alonzo, 2012; Houston and McNamara, 2002; Kokko and Jennions, 2008).

137 Models of parental care typically assume that the benefit function to the offspring
138 increases at a decelerating rate to reach an asymptote, while the cost function to the parent
139 increases either linearly or at an accelerating rate (Kilner and Hinde, 2012; Lessells and
140 McNamara, 2012). In either case, the optimal amount of male care is found by identifying the
141 level of care that maximizes the net balance between the indirect benefits and the direct costs
142 of care (Fig. 1). It is important to recognize that this level corresponds to the optimal amount
143 of male care from the male's own perspective. To find the optimal amount of male care from
144 the female's perspective, we need to recognize that the female gains the same indirect benefits
145 from male care as the male, but that she incurs no costs from the male's effort (unless she
146 pairs with the male for life). Thus, the optimum from the female's perspective is for the male
147 to provide the maximum amount of care (Fig. 1; Lessells and McNamara, 2012). In this
148 simple model, sexual conflict is represented as the divergence in the optimal amount of male
149 care between males and females. The actual amount of care that the male provides is
150 determined by the resolution of this conflict, which in turn depends on whether the female
151 somehow can influence the male's decision about how much care to provide. In the next
152 section, we will discuss how maternal effects might influence male care either by biasing the
153 amount of male care away from the male's optimum and towards her own optimum, or by
154 altering the benefit and/or cost functions of parental care to the male.

155

156 **MATERNAL EFFECTS AND RESOLUTION OF SEXUAL CONFLICT**

157 Maternal effects have received growing attention as important mechanisms that can promote
158 adaptation in complex and changing environments (Groothuis et al., 2005; Meylan et al.,
159 2012; Mousseau and Fox, 1998). Maternal effects can broadly be described as the causal
160 effect of the female's phenotype on the phenotype of the developing offspring over and above
161 the direct effects of genes that the offspring inherit from their mother (Mousseau and Fox,

162 1998). When adaptive, maternal effects are expected to influence the offspring's phenotype in
163 a way that maximize either the offspring's fitness (i.e. anticipatory maternal effects; Marshall
164 and Uller, 2007) or the mother's own fitness (i.e. selfish maternal effects; Marshall and Uller,
165 2007). Such adaptive maternal effects can be mediated through a wide range of epigenetic
166 mechanisms. For example in oviparous species, females might adjust the offspring's
167 phenotype through a variety of egg components, such as nutrients (e.g. proteins, lipids and
168 carotenoids), or hormones (e.g. androgens and corticosterone) (Badyaev, 2008; Von
169 Engelhardt and Groothuis, 2011). If the environmental conditions prior to breeding predict the
170 conditions that the offspring are likely to encounter after hatching, the mother could adjust the
171 offspring's development based on cues from the pre-natal environment to match the
172 offspring's phenotype to the post-hatching conditions before the offspring have developed
173 their own ability to do so (Burgess and Marshall, 2014). As predicted, several studies have
174 demonstrated adjustments in maternal effects to various pre-natal environmental conditions,
175 such as food availability or mate quality (Benton et al., 2005; Sheldon, 2000). For example, in
176 barn swallows (*Hirundo rustica*) and zebra finches (*Taeniopygia guttata*), females deposit
177 more androgens in eggs when they are mated with attractive males (Gil et al., 1999; Gil et al.,
178 2006).

179 Maternal effects may play a role in the resolution of sexual conflict over parental care
180 by providing females with a potential mechanism for influencing male care through
181 adjustments of the offspring's phenotype. Maternal effects may influence the male's decision
182 on how much care to provide by changing the offspring's phenotype, thereby altering the
183 benefits and/or costs of parental care. For example, males often adjust the amount of care they
184 provide in response to the offspring's phenotype, such as the offspring's size (Smiseth et al.,
185 1998) and/or begging behavior (MacGregor and Cockburn, 2002; Müller et al., 2007; Smiseth
186 and Moore, 2004), presumably because these cues provide males with information on the

187 benefits of continued parental care. In this context, females would be under selection to adjust
188 the offspring's phenotype such that it extracts as much care as possible from the male, thereby
189 shifting more of the costs of care towards the male. Whether such maternal effects should
190 increase offspring fitness (anticipatory maternal effects) and/or female fitness (selfish
191 maternal effects) depends on whether the increase in male care is offset by a corresponding
192 decrease in female care, and the extent to which any decrease in female care increases the
193 female's future reproductive potential (Marshall and Uller, 2007). For example, if females are
194 under selection to invest in current reproduction, females might maintain their level of care in
195 response to an increase in male care. In this situation, we would expect maternal effects to
196 improve offspring rather than female fitness. On the other hand, if females are under selection
197 to favor investment in future reproduction, females might respond to an increase in male care
198 by reducing their level of care. Thus, in this situation, we would expect maternal effects to
199 improve female rather than offspring fitness. In light of this argument, we suggest that the
200 extent to which maternal effects should increase offspring and/or female fitness may depend
201 on the life history of the species (Marshall and Uller, 2007; Stearns, 1992).

202 So far, we have discussed female manipulation of male care without defining what we
203 mean by the term 'manipulation'. We define female manipulation as the outcome of any
204 mechanism used by the female to influence the amount of care provided by her male partner
205 in a way that increases the female's and/or offspring's fitness at the expense of the male's
206 fitness. We assign fitness following Smiseth et al. (2012) such that offspring survival from
207 egg formation is assigned as part of the offspring's direct fitness. Although there are other
208 definitions of manipulation, the definition provided above is consistent with previous
209 definitions as one individual altering the behaviour of another against the best interests of the
210 latter (eg. Dawkins, 1999). Based on the cost-benefit analysis introduced earlier, it is possible
211 to distinguish between two forms of female manipulation: (1) deception, which occurs when

212 maternal effects somehow bias the amount of care provided by the male away from the male's
213 optimum and towards the female's own optimum (Fig. 2a), and (2) incentivization, which
214 occurs when maternal effects somehow modify the benefit and/or cost functions of care such
215 that it increases the male's optimal amount of care (Fig. 2b-c). The distinction between these
216 two forms of manipulation is significant because they are likely to differ with respect to their
217 evolutionary stability. Deception is likely to be evolutionarily unstable because the male
218 should be under selection to evolve counter-strategies that help re-store his optimum. For
219 example, if females deposit compounds into the eggs that stimulate begging offspring to
220 exaggerate their true needs, males could simply respond over evolutionary time by becoming
221 progressively less responsive to offspring begging. Theoretical considerations suggest that,
222 although deceptive manipulation may be evolutionary unstable, it might nevertheless drive
223 subsequent evolutionary changes in parental care. As shown in a recent theoretical study, if
224 there is a slight difference in the costs and/or benefits of care to males and females, the sex
225 with the lower costs or higher benefits of care will evolve to become both more able to
226 provide care and to provide much higher levels of care than the other sex (McNamara and
227 Wolf, 2015). Thus, deception might drive the evolution of stable sex differences in parental
228 care strategies by inducing slight initial differences in the costs and/or benefits of care
229 between male and female parents.

230 Incentivization, on the other hand, is likely to be evolutionarily stable because, with
231 this form of manipulation, maternal effects induces changes in benefit and/or cost functions of
232 parental care, thereby altering the amount of care that is optimal from the male's perspective.
233 For example, if females reduce their initial investment in eggs such that the offspring require
234 an increase in the amount of post-hatching parental care, males should respond by increasing
235 their contribution towards parental care due to the corresponding shift in the benefit function
236 of care. The difference between deception and incentivization is that the male provides more

237 care than is optimal to the male in the former case while the male provides the optimal
238 amount of given the current circumstances determined by maternal effects in the latter care.
239 Below, we provide an overview of possible mechanisms by which females might manipulate
240 male care.

241

242 **HOW CAN FEMALES MANIPULATE MALE CARE?**

243 As stated earlier, maternal effects might provide females with a means for manipulating male
244 care through a number of different mechanisms, such as hormones (e.g. androgens and
245 corticosteroids), or nutrients (e.g. proteins, lipids, carotenoids Badyaev, 2008). Until now, the
246 study of female manipulation of male care has been intimately linked to the mechanistic basis
247 of such manipulation. The reason for this is that the original hypothesis, known as the
248 manipulating androgens hypothesis (MAH), focused on androgens as the specific mechanism
249 by which female birds may manipulate male care. In this section, we will start by discussing
250 the logic of the MAH before reviewing empirical evidence for potential effects of maternal
251 androgens on male care. Given that the general logic of the MAH applies to any mechanism
252 females potentially could use to manipulate male, we then review evidence suggesting that
253 these mechanisms could allow females to manipulate male care.

254

255 **Manipulating androgens**

256 The manipulating androgens hypothesis (MAH) is a verbal hypothesis proposing that female
257 birds can manipulate male care by depositing androgens such as testosterone in the eggs,
258 thereby stimulating offspring begging and ultimately increasing the male's contribution
259 towards food provisioning (Moreno-Rueda, 2007; Müller et al., 2007). The MAH was
260 proposed against a background of growing evidence that female birds deposit androgens into
261 their eggs (Gil et al., 2007; Schwabl, 1996), and that females can adjust how much androgens

262 they deposit into their eggs in response to pre-natal cues that predict the environmental
263 conditions the offspring would experience after hatching (Mazuc et al., 2003; Sandell et al.,
264 2007; Von Engelhardt and Groothuis, 2011). Furthermore, there was also growing evidence
265 that maternal androgens stimulate offspring begging (Schwabl, 1996; Smiseth et al., 2011;
266 Von Engelhardt and Groothuis, 2011). Thus, the MAH suggests that females deposit
267 androgens in the eggs as a mechanism for manipulating male care, given that their effects on
268 offspring begging could be used to extract more care from the male. However, for this to be
269 possible, it is essential for female manipulation of offspring begging to have a differential
270 impact on the costs of care for males and females. For this to be the case, males must be more
271 responsive to an increase in offspring begging than females (Moreno-Rueda, 2007). There is
272 some evidence that this requirement is met, as studies on some birds and insects show that
273 males respond more strongly to an increase in nestling begging (MacGregor and Cockburn,
274 2002; Müller et al., 2007; Smiseth and Moore, 2004).

275 Currently, six experimental studies have tested the MAH, all of which have been
276 conducted on birds with biparental care (Table 1). Four studies tested the MAH by
277 experimentally elevating levels of yolk androgen, one injected flutamide (an androgen
278 blocking agent) in the eggs, and one measured testosterone levels of the fourth egg and cross-
279 fostered the remaining clutch (Table 1). All studies monitored subsequent effects of these
280 experimental treatments on offspring begging and/or male food provisioning (Table 1). None
281 of these studies found any evidence for a causal effect of yolk androgen levels on male
282 parental effort. In fact, one study found evidence that contradicts the MAH, as only female
283 great tits (*Parus major*) reduced their food provisioning towards enlarged broods when an
284 androgen-blocking agent was injected to the eggs (Tschirren and Richner, 2008). The only
285 study to report some evidence in support of the MAH found that injection of testosterone into
286 the eggs of yellow-legged gulls (*Larus michahellis*) increased a component of nestling

287 begging (i.e., chatter calls) that was more strongly correlated with male provisioning rates
288 than with female ones (Noguera et al., 2013). However, given that this study did not directly
289 test for a causal effect of the manipulation of testosterone on the provisioning of the two
290 parents, this evidence should be interpreted with care.

291 As outlined above, there is no clear-cut evidence in support of the MAH, suggesting
292 that we perhaps should reject the hypothesis. However, such a conclusion would be premature
293 given that the lack of evidence in support of the MAH could be due to methodological
294 shortcomings with the previous experiments. For example, previous studies of the MAH
295 recorded the effects of elevated levels of maternal testosterone on parental provisioning rates
296 after the stage in the nestling's development when maternal testosterone has its strongest
297 effect on nestling begging. Previous work suggests that maternal effects on nestling begging
298 may be more pronounced during the first few days after hatching (Schwabl, 1996). However,
299 all studies that investigated the effect of testosterone on male parental effort recorded effects
300 on male provisioning rates 5–10 days after hatching (Table 1). For example, in the study on
301 house wrens (*Troglodytes aedon*), maternal testosterone was found to affect nestling begging
302 on days 4–5 after hatching but not on days 9–10 after hatching (Barnett et al., 2011).
303 Nevertheless, this study tested for effects of maternal testosterone on male provisioning rates
304 on days 9–10 after hatching (Barnett et al., 2011), when the potential effects of maternal
305 testosterone on begging no longer appear. Thus, further work on birds is needed to test the
306 MAH, and such work should now ensure that any effects on male care are measured during
307 the first few days after hatching.

308 A second potential methodological issue is that these studies focused on one specific
309 mechanism: the effect of maternal androgens on offspring begging. The historical emphasis
310 on maternal androgens as the focal mechanism by which females can manipulate male care is
311 understandable in light of the early discovery that female birds deposit testosterone into eggs.

312 However, the basic logic of the MAH applies to any maternal effect that females can adjust in
313 response to pre-natal cues predicting the environmental conditions the offspring are likely to
314 experience, and that might influence male care through its effect on the offspring's phenotype.
315 Thus, in the following parts of this section, we discuss evidence suggesting that other such
316 maternal effects might provide females with a means for manipulating male care.

317

318 **Other egg components**

319 There is mounting evidence that females deposit a wide range of compounds into their eggs,
320 some of which are known to influence nestling begging. For example, female birds deposit
321 several non-androgen hormones, including corticosteroids, into their eggs (Smiseth et al.,
322 2011; Von Engelhardt and Groothuis, 2011). There is evidence that females adjust the
323 deposition of corticosteroids in response to pre-natal environmental variations (Meylan et al.,
324 2012). For example, studies on tree-spined sticklebacks (*Gasterosteus aculeatus*) (Giesing et
325 al., 2011), Japanese quails (*Coturnix japonica*) (Hayward et al., 2005) and barn swallows
326 (Saino et al., 2005) show that females deposit more corticosteroids in their eggs when they are
327 exposed to more stressful pre-natal conditions. However, existing evidence suggests that
328 elevated levels of maternal corticosteroids have a detrimental effect on the offspring (Von
329 Engelhardt and Groothuis, 2011). For example, a study on the tropical damselfish
330 *Pomacentrus amboinensis* show that maternal cortisol reduces the body size of fry at hatching
331 (McCormick, 1998). Furthermore, in yellow-legged gulls elevated maternal corticosterone
332 suppresses nestling begging and growth (Rubolini et al., 2005). Thus, given that
333 corticosteroids seem to suppress offspring growth and development, it seems unlikely that
334 females could manipulate male care by elevating the levels of these hormones.

335 Insects have a hormone system that is quite different from that of vertebrates (Nijhout,
336 1998). Nevertheless, there is evidence suggesting that female insects also deposit hormones in

337 their eggs (De Loof et al., 2013). For example, many insects, including the silkmoth *Bombyx*
338 *mori*, produce eggs that are rich in ecdysteroids and juvenile hormones (Gharib and de Reggi,
339 1983). Ecdysteroids and juvenile hormones are involved in the regulation of numerous aspects
340 of insect development, physiology, and behavior (Nijhout, 1998). It is currently unknown
341 whether female insects adjust the deposition of ecdysteroids or juvenile hormones based on
342 pre-natal environmental cues. Nevertheless, there is some evidence that elevated juvenile
343 hormone levels can stimulate larval begging in the burying beetle *Nicrophorus vespilloides*
344 (Crook et al., 2008). In this and other species of the genus *Nicrophorus*, males often assist the
345 female during breeding by providing care for the developing larvae, suggesting that females
346 potentially could deposit juvenile hormones into the eggs as a mechanism for manipulating
347 male involvement in care. Thus, further work is now needed to examine the role of juvenile
348 hormones and ecdysteroids as mechanisms for manipulating male care in these beetles and
349 other insects with biparental care or uniparental male care.

350 Females also deposit various non-hormonal compounds into their eggs, including
351 carotenoids. Carotenoids are fat-soluble pigments (von Schantz et al., 1999) that are
352 exclusively obtained from the diet, and the amount of carotenoids in the diet may therefore
353 reliably reflect food availability prior to breeding (Blount et al., 2000). There is evidence from
354 studies on birds that maternal deposition of carotenoids varies with pre-natal conditions as
355 females of several species increase their deposition of carotenoids in egg yolk when
356 supplemented with a carotenoid-rich diet (Berthouly et al., 2007; Ewen et al., 2008; McGraw
357 et al., 2005). Such an increase in yolk carotenoids often result in higher phenotypic quality of
358 the offspring (Berthouly et al., 2007; Biard et al., 2005; Marri and Richner, 2014).
359 Furthermore, carotenoids are known to stimulate begging intensity in great tits (Helfenstein et
360 al., 2008) and affect the nestling's mouth coloration in hihis (*Notiomystis cincta*) (Thorogood
361 et al., 2008). Thus, given that carotenoids stimulate offspring growth and begging, it is

362 possible that females could deposit carotenoids into their eggs to manipulate male care. Thus,
363 there is now a need for further work to examine whether maternal carotenoids might influence
364 the amount of care provided by the male (Dugas, 2015).

365

366 **Egg size**

367 Egg size is often used as a proxy for the amount of energy and nutrients that female parents
368 invest into each egg (Bernardo, 1996; Christians, 2002). There is evidence that females adjust
369 egg size depending on the environmental conditions, as experimental studies on insects,
370 amphibians or fishes have found that females increase egg size under more stressful
371 environmental conditions (Fox et al., 1997; Kaplan, 1992; Taborsky, 2006; Vijendravarma et
372 al., 2010). For example, in cooperative breeding species, there is evidence that females lay
373 smaller eggs as the number of helpers increases, as has been reported for several bird species
374 (Canestrari et al., 2011; Paquet et al., 2013; Russell et al., 2007; Santos and Macedo, 2011)
375 and as well for one fish species (Taborsky et al., 2007). This adjustment in egg size suggests
376 that the females reduce their investment in eggs in response to predictable cues about the
377 number of helpers that would provide care for the offspring. As predicted by a recent game-
378 theoretical model, females might reduce egg size if an increase in post-hatching care by the
379 parents and their helpers can compensate for the effects of the reduction in egg size (Savage et
380 al., 2015). Although this model applies to cooperatively breeding species, its logic may apply
381 to species with biparental care or uniparental male care by substituting the number of helpers
382 with the male's ability to provide post-hatching care. Thus, there is now a need for studies
383 investigating whether females may adjust egg size in response to cues about the male's ability
384 to provide care in species with biparental care or uniparental male care.

385 A reduction in egg size by females may influence the amount of male care indirectly
386 by stimulating the offspring's begging behavior, as described above for the MAH. For

387 example, given smaller eggs may hatch offspring with lower energy reserves (Christians,
388 2002; Krist 2011), offspring hatching from smaller eggs may beg at higher levels because
389 they have higher hunger levels. We are unaware of any previous work investigating effects of
390 egg size on offspring begging. Thus, further work is needed to test for effects of egg size on
391 offspring begging. Potentially males may visually assess egg size during the egg stage, in
392 which case males may adjust the amount of care they provide in direct response to egg size
393 rather than its potential effects on offspring begging. Males may be expected to adjust the
394 amount of care they provide in response to egg size given that egg size is strongly correlated
395 with offspring condition early after hatching (Christians, 2002). Smaller eggs often hatch into
396 offspring with lower energy reserves and lower survival prospects, especially under adverse
397 environmental conditions (Benton and Grant, 1999; Fox et al., 1997). Thus, a reduction in egg
398 size might alter the benefit function of male care given that parental care is thought to have
399 evolved to enhance offspring fitness by buffering adverse environmental conditions (Royle et
400 al., 2012). If so, a reduction in egg size might be expected to alter the benefit function of care,
401 thereby creating an incentive for males to increase their contribution towards care.

402 Currently, little is known about the causal effect of egg size on the amount of care
403 provided by males. For example, if the negative effects of a reduction in egg size can be
404 compensated by post-natal parental care (i.e. “head start” hypothesis sensu Savage et al.,
405 2015), we would expect a negative correlation between eggs size and the amount of male
406 care. There is no evidence that this is the case from the few studies that directly investigated
407 the relationship between egg size and parental care in birds with biparental care (Krist, 2009;
408 Quillfeldt and Peter, 2000). However, it is important to note that these studies did not test for
409 sex-specific effects of egg size on parental care, and that it is therefore possible that egg size
410 is negatively correlated with male care but positively correlated with female care. Thus, there
411 is now need for experimental studies specifically designed to test for effects of egg size on

412 male and female care. It may appear challenging to disentangle between adjustments in egg
413 size as a female strategy specifically used to manipulate male care and adjustments in egg size
414 as a general female life history strategy that is independent of male manipulation. However,
415 evidence that adjustments of egg size are associated with a decrease in male fitness and an
416 increase in female and/or offspring fitness would support the hypothesis that females adjust
417 egg size to manipulate male care. Additionally, in species where egg size *per se* influences
418 male care, it would be possible to experimentally test whether egg size provides females with
419 a means to manipulate male care by providing parents with different-sized dummy eggs and
420 monitor subsequent effects on male contributions towards care.

421

422 **Egg coloration**

423 Egg coloration may not seem an obvious mechanism for female manipulation of male care.
424 However, there is growing evidence that variation in egg coloration affects male care in some
425 birds with biparental care (Moreno et al., 2006b; Sanz and García-Navas, 2009; Soler et al.,
426 2005), suggesting that egg coloration may provide females with a mechanism for
427 manipulating male care. The evolution of egg coloration in birds has received considerable
428 attention given its diversity both between and within species (Kilner, 2006; Underwood and
429 Sealy, 2002). The sexually selected egg color hypothesis (SSEC) suggests that the blue-green
430 pigmentation of avian eggs, which is caused by the antioxidant biliverdin, may act as a post-
431 mating sexual signal that communicates the female's condition or genetic quality to the male
432 (Moreno and Osorno, 2003). Studies on pied flycatchers (*Ficedula hypoleuca*) and spotless
433 starlings (*Sturnus unicolor*) show that experimental manipulation of the female's condition
434 influences the blue-green coloration of the eggs (Moreno et al., 2006a; Soler et al., 2008). The
435 SSEC suggests that males gain a fitness benefit by adjusting their investment in response to
436 variation in egg coloration, because egg coloration reflects female's genetic quality and/or

437 condition. If so, males may increase the amount of care they provide when females lay eggs
438 that are more pigmented because the offspring of better mates would merit more parental
439 effort according to the differential allocation hypothesis (Moreno and Osorno, 2003).

440 In support of the SSEC, several studies have found evidence for a positive effect of
441 egg coloration on male care (Moreno et al., 2006b; Sanz and García-Navas, 2009; Soler et al.,
442 2005 but see Krist and Grim, 2007; Stoddard et al., 2012). It is noteworthy that experimental
443 manipulation of egg coloration had a significant positive effect on male but not female
444 provisioning rates in spotless starlings (Soler et al., 2008), American robins (*Turdus*
445 *migratorius*) (English and Montgomerie, 2011) and house wrens (Walters et al., 2014). Given
446 that egg coloration seems to influence male care only, females could use this mechanism as a
447 means for manipulating male care. Although these results on the effects of egg coloration on
448 male have not traditionally been interpreted as evidence for female manipulation of care,
449 current evidence suggest that egg coloration is the most promising mechanism by which
450 females might manipulate male care. To confirm that egg coloration provides a mechanism
451 for female manipulation of male care, we need further studies that investigate the fitness
452 consequences of egg coloration for males and females. If egg coloration is used as a
453 mechanism for female manipulation of male care, we would expect egg coloration to enhance
454 the female's current or future reproductive potential at the expense of the male's future
455 reproductive potential.

456

457 **Other mechanisms**

458 Above, we have reviewed some of the most likely mechanisms females could use to
459 manipulate male care based on information in the published literature. However, it is possible
460 that females could use a variety of other egg characteristics providing (1) that females can
461 adjust this characteristic in response to pre-natal conditions, (2) that it affects an aspect of the

462 offspring's phenotype that the male can access, and (3) that the male adjust his level of care in
463 response to this trait. For example, in many fishes with male care, males often cannibalize
464 some of the eggs to lower their energetic costs of care (Klug and Bonsall, 2007; Manica,
465 2002). If so, females could potentially modify some eggs properties that increase the cost of
466 cannibalism to the males, thereby increasing the offspring's fitness at the expense of the
467 male's own fitness. In support of this suggestion, the evolution of care in harvestmen seem to
468 coincide with mucus or attachment of debris on the surface of the eggs, possibly representing
469 an adaptation whereby females can reduce male cannibalism (Requena et al., 2009).
470 Furthermore, in an assassin bug species with male care, the eggs are darker compared with an
471 ecologically similar species with female care, which may reflect that the former have a thicker
472 egg wall to increase the costs of male egg cannibalism (Gilbert et al., 2010).

473

474 **FUTURE RESEARCH DIRECTIONS**

475 **Mechanisms versus maternal effects?**

476 As discussed above, previous experimental work on female manipulation of male care have
477 focused on the MAH, and have tested this hypothesis by manipulating the level of androgen
478 in the eggs and monitoring subsequent effects on offspring begging and/or male care (Table
479 1). The advantage of this experimental approach is that it is explicit about the specific
480 mechanism by which females might manipulate male care. However, an obvious disadvantage
481 of this experimental approach is that females might manipulate male care through a different
482 mechanism than the one that was targeted in the experimental manipulation, including other
483 compounds deposited into eggs, egg size and egg coloration. One potential solution to this
484 problem is to repeat the experiment such that it targets every possible mechanism that could
485 be used by females. However, this strategy is likely to be labor-intensive and may remain

486 inconclusive as females might manipulate male care through a mechanism that is yet to be
487 discovered.

488 An alternative approach to the one used hitherto is to consider the ecological context
489 of the maternal effects that females are expected to use as a means to manipulate male care.
490 Thus, rather than targeting a specific candidate mechanism, experiments could target some
491 aspect of the pre-natal environmental conditions and then monitor subsequent effects on male
492 and female parental care and male, female and offspring fitness (Fig. 3). For example, if
493 females and/or offspring benefit from higher levels of male care when food availability is low,
494 we might expect females to adjust some unknown maternal effect in response to food
495 availability, with subsequent effects on the offspring's phenotype (e.g., offspring begging)
496 and the amount of male care. The strength of this approach is that it is independent of the
497 specific mechanism by which females manipulate male parental care. Thus, this approach
498 reduces the risk of incorrectly rejecting female manipulation due to not targeting the correct
499 mechanism and would even work in systems where there is no prior information on potential
500 candidate mechanisms.

501 A potential weakness of this approach is that, in order to demonstrate effects on male
502 and female parental care due to the pre-natal environmental conditions, it is important to
503 exclude potential effects due the post-natal environmental conditions. Separating these effects
504 is essential because the pre-natal conditions might correlate with the post-natal conditions,
505 and the effects of the pre-natal conditions mediated through maternal effects on the eggs are
506 likely to be weaker than the effects of the post-natal conditions on the level of parental care
507 after hatching (Krist, 2011). In order to overcome this problem, it is therefore essential to
508 implement cross-fostering experiments within this approach. Such cross-fostering
509 experiments would allow us to disentangle the effects of the pre-natal environmental
510 conditions on male and female parental care from those of the post-natal environmental

511 conditions (see for example Hinde et al., 2009; Paquet et al., 2015). Another disadvantage of
512 this approach is that it provides no information on the mechanism by which females
513 manipulate male care. This problem could be addressed by testing between possible candidate
514 mechanisms once maternal manipulation of male care has been documented. This could be
515 done based on the same experimental design as described above, but by monitoring
516 subsequent effects on a wide range of possible candidate mechanisms. Once candidate
517 mechanisms have been identified, experiments should be conducted that specifically target
518 each candidate mechanism.

519

520 **Beyond biparental care**

521 Until now, female manipulation of male care has only been considered for birds with
522 biparental care. However, given that maternal effects are mediated through the offspring's
523 phenotype, they provide females with a mechanism for manipulating male care even if
524 females do not interact with the male while he provides care. Thus, maternal effects may be as
525 important in species with uniparental male care as in species with biparental care. Indeed,
526 species with uniparental male care might be better suited as models for studying female
527 manipulation of male care because its role in the resolution of sexual conflict is not
528 confounded by effects due to other mechanisms of conflict resolution, such as negotiation or
529 matching. For example, many fishes might be very well suited as study systems to test for
530 female manipulation of male care in species with uniparental male care (Gross and Sargent,
531 1985).

532 Finally, we note that female manipulation also might occur in cooperatively breeding
533 species, where females gain help to raise their offspring from both their male partner and a
534 variable number of helpers. Helpers are non-breeding individuals that assist the breeders by
535 providing care to their offspring, for example by provisioning additional food to the nest

536 (Brown, 1987; Emlen, 1991). Thus, the presence of helpers represents a predictable
537 improvement in the rearing conditions that females can assess prior to breeding (Fig. 3).
538 There is some evidence that females use the number of helpers as a cue to strategically adjust
539 the size of the eggs that they lay (Russell et al., 2007; Taborsky et al., 2007), or the amount of
540 nutrients (Russell et al., 2007) and hormones (Paquet et al., 2013) deposited into the eggs. In
541 these species, females may manipulate the amount of care provided by both the male and the
542 helpers. Thus, as more than one individual could be manipulated by the breeding females,
543 there is no need for a sex-specific effect on parental effort as any decrease in female care
544 could be overcompensated by an increase in the amount of care provided by the male and the
545 helpers.

546 In cooperatively breeding species, female manipulation of the amount of care provided
547 by the other group members may also vary with the relatedness between the female and the
548 helpers given that it would be more advantageous for females to manipulate unrelated helpers
549 from an inclusive fitness perspective (Savage et al., 2013). This idea is supported by evidence
550 from previous work on sociable weavers (*Philetairus socius*) showing that offspring beg less
551 when expecting to be fed by more helpers (Paquet et al., 2015). Thus, in this species, the
552 number of helpers in the group co-varies with pre-natal maternal effects on offspring begging.
553 Currently, there are few studies on how parents and helpers respond to changes in offspring
554 begging levels in cooperatively breeding species, but the results obtained so far are consistent
555 with female manipulation of the male and the helpers. For example, in Arabian babblers
556 (*Turdoides squamiceps*), where there is high relatedness within breeding groups, the two
557 parents and the helpers respond in the same way to experimentally manipulated begging
558 (Wright, 1998). On the other hand, in superb fairy-wrens (*Malurus cyaneus*), where the
559 breeding male and the helpers often are unrelated to the brood, the breeding female does not
560 respond to increased begging while the male and the helpers respond by increasing their

561 feeding rates (MacGregor and Cockburn, 2002). Finally, in sociable weavers adult helpers
562 feed at a higher rate when less related to the breeding female, but not with that of the breeding
563 male (Doutrelant et al., 2011), suggesting that female manipulation is directed towards
564 primarily unrelated helpers. Studying the maternal effect of helpers' number and relatedness
565 to the mother on individual provisioning behavior is thus a promising research avenue to
566 investigate female manipulation in cooperative breeders.

567

568 **CONCLUSION**

569 Female manipulation of male care has often been assumed to be a rare phenomenon, and its
570 existence has been largely overlooked in the study of sexual conflict over parental care
571 (Lessells and McNamara, 2012). Here, we show that females might use various maternal
572 effects mechanisms for manipulating male care, including androgens deposited into eggs,
573 other egg components, egg size and egg coloration. Given the number of potential
574 mechanisms, we suggest that future work on female manipulation of male care use
575 experimental designs that are independent of the specific underlying mechanism and that they
576 instead focus on the pre-natal conditions that are expected to influence maternal effects, such
577 as food availability.

578

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585

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855 **Figure legends**

856

857 **Figure 1**

858 A simple cost-benefit analysis for the optimal amount of male care. rB represents the benefit
859 function of male care, defined as the effect of specific amount of male care on the offspring's
860 fitness multiplied by the relatedness coefficient between the offspring and the male. C
861 represents the cost function of male care, defined as the effect of specific amounts of male
862 care on the male's ability to invest in other offspring. The optimal amount of male care to the
863 male is the amount of care that provides the largest possible net benefit given rB and C , and is
864 represented by M^* and the vertical solid line. The optimal amount of male care to the female
865 is represented by F^* and the vertical dashed line. The conflict battleground is the difference in
866 the optimal amount of male care between the two sexes and is represented by the horizontal
867 double line.

868

869 **Figure 2**

870 Graphical representation of the two different forms of maternal manipulation: deception (a)
871 and incentivization (b–c). Deception occurs when females bias the actual amount of care the
872 male provides (M_a) away from the male's optimum (M^*) and towards the female's own
873 optimum (F^*). Incentivization occurs when female increase male care by altering the shape of
874 either the benefit function (b) or the cost function (c) of male care. Thus, with incentivization,
875 the male still provides the optimal amount of care to the male, but this optimum has changed
876 as a consequence of maternal effects on the benefits or the costs of care.

877

878

879 **Figure 3**

880 Illustration of potential causal pathways by which females may manipulate male parental
881 effort via maternal effects that influence offspring traits. Pre-natal conditions, such as food
882 availability and male parental quality, influence some maternal effects mechanism, such as
883 deposition of androgens into the eggs. These maternal effects alter the offspring's phenotype
884 by for example stimulating offspring begging, which in turn lead to an increase in male
885 parental care. Ultimately, this increase in male parental care should enhance the fitness of the
886 female and/or the offspring at the expense of the fitness of the male.

Table 1: Summary of the experiments and main results from the 6 previous studies that investigated the MAH.

Species	Treatment	Effect on begging	Effect on male provisioning	Time begging measured	Time provisioning measured	Reference
House wren <i>Troglodytes aedon</i>	T injected in eggs	+ ^a	no	day 4-5 and 9-10	day 9-10	(Barnett et al., 2011)
Pied flycatcher <i>Ficedula hypoleuca</i>	cross fostering and 4 th egg measured for T	NM	no	NM	day 5	(Laaksonen et al., 2011)
Collared Flycatcher <i>Ficedula albicollis</i>	T+A4 injected in eggs	NM	no	NM	day 9	(Ruuskanen et al., 2009)
Great tit <i>Parus major</i>	antiandrogen injection	NM	no ^b	NM	day 10	(Tschirren and Richner, 2008)
Canary <i>serinus canaria</i>	T injected in eggs	No	no	1 hour then daily for 10 days	day8-10	(Müller et al., 2010)
Yellow-legged Gull <i>Larus michaellis</i>	T injected in 3rd eggs	+	Yes? ^c	2 days	2 days	(Noguera et al., 2013)

NM: Not measured

^a: Effect on begging at day 4-5 but not 9-10

^b: In enlarged broods females feed more unmanipulated chicks

^c: Positive relation between begging and male provisioning

