

1 **The constant philopater hypothesis: a new life history invariant for dispersal evolution**

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17 **Running title** – Dispersal and fecundity

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27 **Abstract** – Life history invariants play a pivotal role in the study of social adaptation: they
28 provide theoretical hypotheses that can be empirically tested, and benchmark frameworks
29 against which new theoretical developments can be understood. Here we derive a novel
30 invariant for dispersal evolution: the “constant philopater hypothesis” (CPH). Specifically, we
31 find that, irrespective of variation in maternal fecundity, all mothers are favoured to produce
32 exactly the same number of philopatric offspring, with high-fecundity mothers investing
33 proportionally more, and low-fecundity mothers investing proportionally less, into dispersing
34 offspring. This result holds for female and male dispersal, under haploid, diploid and
35 haplodiploid modes of inheritance, irrespective of the sex ratio, local resource availability,
36 and whether mother or offspring controls the latter’s dispersal propensity. We explore the
37 implications of this result for evolutionary conflicts of interest – and the exchange and
38 withholding of contextual information – both within and between families, and we show that
39 the CPH is the fundamental invariant that underpins and explains a wider family of invariance
40 relationships that emerge from the study of social evolution.

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42 **Keywords** – class structure, demography, heterogeneity, migration, parent-offspring conflict,
43 philopatry, reproductive value, seasonality, sex ratio, social evolution.

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53 **Introduction**

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55 A number of surprising invariance relationships have emerged from the study of social
56 evolution, whereby a cancelling-out of multiple partial effects of a genetic, ecological or
57 demographic parameter means that it has no net impact upon the evolution of a social
58 behaviour. For example, in the study of sex allocation under “local mate competition”
59 (Hamilton 1967), the number of sons produced by a mother is expected to be independent of
60 her fecundity, in what is known as the “constant male hypothesis” (CMH; Frank, 1985,
61 1987b; Yamaguchi, 1985). Specifically, the increased extent to which the sons of more-
62 fecund mothers engage in costly competition with male relatives for mating opportunities
63 means that a mother’s proportional investment into sons is expected to be inversely
64 proportional to her fecundity, such that her absolute investment into sons is invariant with
65 respect to her fecundity. Such invariance results provide an important stimulus for scientific
66 advancement. For example, the discovery of the CMH invariant spurred both empirical
67 testing and further development of theory in the field of sex allocation, which has continued
68 in a sustained way from the mid 1980s to the present day (Frank, 1985, 1987a,b,c; May &
69 Seger, 1985; Yamaguchi, 1985; Stubblefield & Seger, 1990; Foster & Benton, 1992;
70 Hasegawa & Yamaguchi, 1995; Petersen & Fischer, 1996; Flanagan et al., 1998; Wool &
71 Sulami, 2001; Ode & Rissing, 2002; Dagg & Vidal, 2004; Akimoto & Murakami, 2012;
72 Akimoto et al., 2012; Rodrigues & Gardner, 2015).

73 Such invariance results may cross over from their field of origin to illuminate other
74 topics, in which they give rise to new waves of theoretical and empirical research. For
75 example, a surprising discovery that sex ratios are unaffected by the rate of female dispersal –
76 owing to a cancellation of relatedness and kin-competition effects (Bulmer, 1986; Frank,
77 1986; Taylor, 1988a) – was subsequently shown to translate to the evolution of helping and
78 harming behaviours, stimulating a great deal of further theoretical and empirical study

79 (Taylor, 1992; Wilson et al., 1992; Taylor & Irwin, 2000; Irwin & Taylor, 2001; Perrin &
80 Lehmann, 2001; Gardner & West, 2006; Lehmann et al., 2006; Alizon & Taylor, 2008; El
81 Mouden & Gardner, 2008; Grafen & Archetti, 2008; Johnstone, 2008; Johnstone & Cant,
82 2008; Kümmerli et al., 2009; Gardner, 2010; Rodrigues & Gardner, 2012, 2013a, 2013b; Yeh
83 & Gardner, 2012). More generally, invariance with respect to transformation is the basis for
84 all analogy and the generalisation of all scientific knowledge to new domains.

85 Dispersal is a major life history trait and received a considerable amount of attention
86 from both theoreticians and empiricists and has been studied in relation to a variety of factors
87 such as kin competition (Hamilton & May, 1977; Léna et al., 1998; Ronce et al., 1998, 2000;
88 Leturque & Rousset, 2003; Kisdi, 2004; Innocent et al., 2010; Rodrigues & Johnstone, 2014),
89 spatial and/or temporal heterogeneity (Comins et al., 1980; Hastings, 1983; Holt, 1985;
90 Cohen & Levin, 1991; McPeck & Holt, 1992; Gandon & Michalakis, 1999; Leturque &
91 Rousset, 2002; Massol et al., 2010; Rodrigues & Johnstone, 2014), parent-offspring offspring
92 (Motro, 1983; Frank, 1986; Taylor, 1988b; Gandon, 1999; Starrfelt & Kokko, 2010),
93 intragenomic conflict (Farrell et al., 2015), budding dispersal (Gandon & Michalakis, 1999),
94 density-dependent dispersal (Crespi & Taylor, 1990; Travis et al., 1999; Poethke &
95 Hovestadt, 2002; De Meester & Bonte, 2010; Baguette et al., 2011) and other types of
96 condition-dependent dispersal (Ronce, 1998, 2000; Kisdi, 2004; Gyllenberg et al., 2011a,b).

97 One factor that is likely to have an important impact on the evolution of dispersal is
98 variation in fecundity among group members, i.e. reproductive skew (Vehrencamp, 1983;
99 Hager & Jones, 2009). The social evolutionary consequences of variation in fecundity has
100 received attention in relation to helping and harming behaviour (Frank, 1996; Johnstone,
101 2008; Bao & Wild, 2012; Rodrigues & Gardner, 2013a) and sex ratio (Yamaguchi, 1985;
102 Frank, 1985, 1987c; Stubblefield & Seger, 1990; Rodrigues & Gardner, 2015). However, the
103 implications for dispersal, and attendant conflicts of interest within and between families,
104 remain to be addressed.

105 Here we study the evolution of dispersal in groups where the fecundity of breeders
106 vary and report a new invariance result – the “constant philopater hypothesis” (CPH) – in the
107 context of dispersal evolution. We find that, irrespective of variation in maternal fecundity,
108 each mother is expected to make the same absolute investment into philopatric (i.e. non-
109 dispersing) offspring. This is because higher fecundity is associated with one’s offspring
110 facing more stringent kin competition for breeding opportunities when failing to disperse,
111 such that each mother’s proportional investment into philopatric offspring is expected to be
112 inversely proportional to her fecundity. We develop a mathematical kin-selection model to
113 show that the CPH holds for female and male dispersal, under haploid, diploid and
114 haplodiploid modes of inheritance, irrespective of the sex ratio, local resource availability,
115 and whether mother or offspring controls the latter’s dispersal propensity. We provide explicit
116 solutions for variation in resource availability within and between patches, considering both
117 spatial heterogeneity and also temporal heterogeneity for unpredictable and seasonal
118 environments, and we explore the implications of this result for evolutionary conflicts of
119 interest – and the exchange and withholding of contextual information – both within and
120 between families. Finally, we show that the CPH result is the fundamental invariant that
121 underpins and explains a family of other invariance results, including the previously described
122 “constant female hypothesis” (CFH; Frank, 1987c, 1998).

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Model and Results

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Model

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We assume an infinite island model (Wright, 1931; Hamilton & May, 1977;

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Rodrigues & Johnstone, 2014), with n mothers in every patch. There are different types of

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patches, i.e. type- t patches with $t \in T = \{1, 2, \dots, n_p\}$, and each type differing in its resource

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availability. Within each patch, each mother is randomly assigned a rank $i \in I = \{1, 2, \dots, n\}$,

131 and produces a large number of offspring in accordance with her rank, such that no two
132 mothers in the same patch share the same rank, and all mothers sharing the same rank and
133 patch type have the same fecundity. In the asexual version of the model we consider that all
134 offspring are daughters and clones of their mother, and in the sexual version of the model we
135 consider that a fraction σ_{it} of the offspring of a rank- i mother are sons and a fraction $1-\sigma_{it}$ are
136 daughters and that there is a haploid, diploid or haplodiploid mode of inheritance. After
137 reproduction, all mothers die, and the offspring of rank- i mothers either remain in their natal
138 patch with probability $1-z_{it}$ or else they disperse with probability z_{it} , with a fraction $1-c$ of
139 dispersers relocating to a new randomly-chosen patch and the remainder c perishing en route.
140 We assume that dispersal is controlled either by the offspring themselves or by their mother.
141 In the sexual version of the model, individuals mate at random within their patches following
142 dispersal, with each female mating once, after which all males die. Patches may maintain their
143 resource availability, and therefore remain of the same type, or change their resource
144 availability, and therefore change their type. Females then compete for breeding
145 opportunities, with n females being chosen at random within each patch to become the
146 mothers of the next generation, and all other females dying, which returns the population to
147 the beginning of the lifecycle.

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149 Evolution of dispersal

150 Applying kin-selection methodology (Hamilton, 1964; Taylor & Frank, 1996; Frank,
151 1997, 1998; Rousset, 2004; Taylor et al., 2007), we find that an increase in the probability of
152 dispersal of an offspring of a rank- i mother in a type- t patch is favoured when

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$$154 \quad -r_{it}\omega_t v_t + (1 - c)r_{it} \sum_{q \in T} p_q \omega_q v_q + \omega_t v_t h_t \sum_{j \in I} (U_{jt} \rho_{ijt}) > 0, \quad (1)$$

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156 where: ω_t is the probability that an individual wins a breeding site in a type- t patch; v_t is the
157 expected reproductive value of an individual in a type- t patch; p_m is the frequency of type- m
158 patches in the population; r_{it} is either the relatedness of a rank- i mother in a type- t patch to
159 one of her offspring (when dispersal is under maternal control), or else the relatedness of the
160 offspring to itself (when dispersal is under offspring control); h_t is the probability that a
161 random individual sampled after dispersal was born in the local patch (i.e. the probability of
162 philopatry); U_{jt} is the probability that this philopatric individual was produced by the rank- j
163 mother; and ρ_{ijt} is the relatedness of the rank- i mother (when dispersal is under maternal
164 control) or an offspring of the rank- i mother (when dispersal is under offspring control) to an
165 offspring of the rank- j mother in the same type- t patch (see Supporting Information for more
166 details).

167 If dispersal is under maternal control, then $r_{it} = \rho_{iit}$, as both of these quantities describe
168 the relatedness of the rank- i mother to her own offspring. However, if dispersal is under
169 offspring control, then r_i is the relatedness of the focal offspring to itself, whilst ρ_{iit} is its
170 relatedness to its siblings. Condition (1) holds for both the asexual and sexual models, and
171 also for haploid, diploid and haplodiploid modes of inheritance. Under the sexual
172 reproduction model, the quantities described in condition (1) are sex-specific: for instance, if
173 we are considering the dispersal of females, then U_{jt} is the probability that a random
174 philopatric female is a daughter of a rank- j mother in a type- t patch.

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176 The constant philopater hypothesis

177 Of key interest is the quantity $N_{it} = N_t U_{it}$, which describes the number of philopatric
178 offspring produced by a rank- i mother in a type- t patch, where N_t is the total number of
179 philopatric offspring in the focal patch. Note that: the relatedness of a mother to her offspring,
180 and the relatedness of the offspring to itself, are both independent of the mother's rank, so we
181 may write $r_{it} = r_t$ for all $i \in I$, and all $t \in T$; the relatedness of an offspring to its siblings is

182 independent of its mother's rank, so we may write $\rho_{iit} = \rho_t$ for all $i \in I$, and all $t \in T$; and the
 183 relatedness of a mother to another mother's offspring, and the relatedness of an offspring to
 184 another mother's offspring, is independent of the rank of either mother, so we may write
 185 $\rho_{ijt} = P_t$ for all $t \in T$, all $i \in I$, and all $j \in I, j \neq i$. Accordingly, $\sum_{j \in I} U_{jt} \rho_{ijt} = U_{it} \rho_t +$
 186 $P_t \sum_{j \in I, j \neq i} U_{jt} = U_{it} \rho_t + P_t(1 - U_{it})$, and condition (1) can be rewritten as

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$$188 \quad N_{it} > N_t \frac{1}{h_t \omega_t v_t} \frac{\omega_t v_t r_t - (1-c)r_t \sum_{m \in T} p_m \omega_m v_m - h_t \omega_t v_t P_t}{\rho_t - P_t} \quad (2)$$

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190 That is, the number of philopatric offspring produced by each rank- i mother in a type- t
 191 patch is favoured to converge upon the RHS of condition (2) and, because this quantity is
 192 independent of i , natural selection favours the number of philopatric offspring produced by
 193 each and every mother to converge upon the same number (i.e. $N_{it} = N_t^*$, and $U_{it} = U_t^*$),
 194 irrespective of the total number of offspring that she produces and her sex allocation. This
 195 result holds for both asexual and sexual reproduction under haploid, diploid, and haplodiploid
 196 inheritance, for female and/or male dispersal and for maternal or offspring control of
 197 dispersal. In analogy with the CMH, we term this invariant result the “constant philopater
 198 hypothesis” (CPH).

199 The CPH emerges from a balance between the mortality risk of dispersing and the kin-
 200 competition consequences of philopatry. From condition (1) we see that: because both the
 201 relatedness of a mother to her own offspring and also the relatedness of an offspring to itself
 202 are independent of maternal rank, the impact of the mortality cost of dispersal is the same for
 203 all mothers within each patch ($-r_{it}v_t + (1-c)r_{it} \sum_{m \in T} p_m v_m = -r_{it}v_t + (1-c)r_{it} \sum_{m \in T} p_m v_m$ for all $i \in I$,
 204 and $t \in T$); because both the relatedness of a mother to another mother's offspring and also
 205 the relatedness of an offspring to another mother's offspring are independent of maternal rank
 206 ($\rho_{ijt} = P_t$ for all $t \in T$, all $i \in I$, and all $j \in I, j \neq i$), the offspring of all mothers experience the
 207 same strength of kin competition if all mothers produce the same number of philopatric

208 offspring ($h_t v_t U_t^* (r_t + (n-1)P_t)$ under maternal control, or $h_t v_t U_t^* (r_t + (n-1)\rho_t)$ under offspring
209 control); and, because any correlation that does arise between maternal rank and number of
210 philopatric offspring leads to stronger kin competition among the offspring of mothers who
211 produce more philopatric offspring, which favours such mothers to reduce their number of
212 philopatric offspring, any correlation between rank and number of philopatric offspring will
213 tend to disappear.

214 All mothers are favoured to produce the same number of philopatric offspring, but
215 various constraints may interfere with their ability to do so. One possible constraint is that
216 some low-ranking mothers are unable to produce the requisite number of philopatric offspring
217 even if none of their offspring disperse, on account of their low fecundity. In this case, the
218 CPH invariant breaks down, analogous to the breakdown of the CMH when some mothers are
219 of such low fecundity that they cannot produce the requisite number of sons even if all of
220 their offspring are male (Frank, 1985, 1987c).

221

222 Within-patch heterogeneity

223 Above we have shown that the CPH holds under a very general set of assumptions,
224 and we have expressed this result in terms of emergent quantities such as the relatedness and
225 the probability of philopatry. Here we express these emergent quantities as a function of the
226 underlying ecological and demographic parameters, which enables us to explicitly determine
227 the optimal dispersal behaviour of offspring in particular scenarios. Here we focus on a
228 particular case to illustrate how different model parameters mediate the optimal dispersal rates
229 of offspring. We then contrast the optimal dispersal behaviour of offspring under maternal
230 control with the optimal dispersal behaviour under offspring control to understand the role of
231 the CPH in mediating parent-offspring conflict over dispersal.

232 We focus on a particular case in which there are two asexually-reproducing mothers
233 per patch: a rank-1 mother with relatively-high fecundity (denoted by F_1), and a rank-2

234 mother with relatively-low fecundity (denoted by F_2). We denote the reproductive inequality
235 between females by s , where $s = 1 - (F_2/F_1)$. We find that the probability of dispersal of
236 offspring of high-fecundity mothers rises, whilst the probability of dispersal of offspring of
237 low-fecundity mothers falls, as the reproductive inequality between mothers rises (Fig. 1). On
238 the one hand, offspring of high-fecundity mothers and offspring of low-fecundity mothers
239 both suffer the same cost of dispersal (c), and the relatedness between a focal offspring and
240 herself is equal ($r_1 = r_2 = 1$), so the first term in inequality (1) is the same for both offspring
241 (i.e. $-c r_1 = -c r_2$). But, on the other hand, all else being equal, the number of philopatric
242 offspring of the high-fecundity mother is greater than that of the low-fecundity mother ($U_1 >$
243 U_2): accordingly, the expected relatedness between a focal offspring of the high-fecundity
244 mother and a random offspring in the patch is greater than the expected relatedness between a
245 focal offspring of the low-fecundity mother and a random offspring in the patch (i.e.
246 $h(U_1\rho_{11} + U_2\rho_{12}) > h(U_1\rho_{21} + U_2\rho_{22})$, where $\rho_{11} = \rho_{22} = 1$, and $\rho_{12} = \rho_{21} = \rho$). Therefore, the
247 selection pressure for dispersal of offspring of high-fecundity mothers is stronger than the
248 selection pressure for dispersal of offspring of low-fecundity mothers.

249 We also find that the mean probability of dispersal falls as the cost of dispersal rises
250 (Fig. 1). As the cost of dispersal rises, the first term in inequality (1) decreases and the second
251 term in inequality (1) increases. As the effect on the first term is stronger than the effect on
252 the second term, the overall effect of increasing the cost of dispersal is that dispersal becomes
253 less evolutionarily advantageous.

254 The number of philopatric offspring of the high-fecundity mother rises as the
255 reproductive inequality between the two mothers increases, and as the cost of dispersal
256 increases. So long as this number is not too high, low-fecundity mothers are able to match it
257 (i.e. $1 - z_1^* = (1-s)(1-z_2^*)$). However, if the number of philopatric offspring of high-fecundity
258 mothers is too high (due to high s and / or high c), then low-fecundity mothers cannot produce

259 the requisite number of philopatric offspring even if none of their offspring dispersal, and in
260 such scenarios the CPH breaks down (Fig. 1).

261

262 Between-patch heterogeneity

263 *Temporally-stable environments* – We now consider a heterogeneous population in which
264 there are type-1 patches with high resource-availability and type-2 patches with low resource-
265 availability. We define the reproductive inequality between patches as $s_b = 1 - (F_{12}/F_{11})$, and
266 the reproductive inequality within patches as $s_1 = 1 - (F_{21}/F_{11}) = s_2 = 1 - (F_{22}/F_{12}) = s$. We first
267 consider a spatially-heterogeneous environment in which patches retain their type over
268 generations. We find that the average probability of dispersal is higher from low-quality type-
269 2 patches than from high-quality type-1 patches (Fig. 2, panel (c)). As a result, high-quality
270 patches have more non-dispersing offspring than low-quality patches. However, in both types
271 of patches, higher-ranking mothers disperse more offspring than lower-ranking mothers, and,
272 as long as inequality within patches is sufficiently small, both high- and low-rank mothers
273 produce exactly the same number of philopatric offspring irrespective of the quality of their
274 patch (Fig. 2, panel (f)).

275

276 *Temporally-unpredictable environments* – We next consider unpredictable environments in
277 which a patch's type in the next generation is independent of its type in the current
278 generation. Under such circumstances, the expected reproductive value is identical across
279 patches. Thus, $v_t = v$, for all $t \in T$. Moreover, the relatedness coefficients are also identical
280 across patches. Thus, $r = r_t$, $\rho_t = \rho$, and $P_t = P$. Therefore, inequality (2) becomes

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$$282 \quad 1 > n \frac{1}{h_t \omega_t} \frac{\omega_t r - (1-c)r \sum_{m \in T} p_m \omega_m - h_t \omega_t P}{\rho - P}. \quad (3)$$

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284 This means that, at equilibrium, $h_t^* = h^*$ and $\omega_t^* = \omega^*$, and therefore natural selection favours
285 the number of philopatric offspring produced by each and every mother to converge upon the
286 same number (i.e. $N_{it} = N_t^* = N^*$, and $U_{it} = U_t^* = U^*$). Thus, in unpredictable environments, the
287 CPH holds not only within each patch, but also between patches (Fig. 2, panel (e)).

288

289 *Seasonal environments* – Finally, we consider seasonal environments in which a patch always
290 changes its type from one generation to the next. We find that the average probability of
291 dispersal is higher from high-quality type-1 patches than from low-quality type-2 patches
292 (Fig. 2, panel (a)). As a result, low-quality patches have more philopatric offspring than high-
293 quality patches. However, in both types of patches, higher rank mothers disperse more
294 offspring than lower rank mothers, and, as long as inequality within patches is sufficiently
295 small, both high- and low-rank mothers produce exactly the same number of philopatric
296 offspring irrespective of the quality of their patch (see Fig. 2, panel (d)).

297

298 Parent-offspring conflict

299 Although the CPH result obtains irrespective of whether dispersal is controlled by the
300 offspring themselves or by their mother, we find that the level of dispersal that is favoured
301 does depend upon whose control it is under. This recovers Motro's (1983) result that an
302 evolutionary conflict of interest often exists between mother and offspring with regards to
303 dispersal, with mothers generally preferring that their offspring disperse at a rate that is higher
304 than the rate at which the offspring would prefer to disperse themselves. This is on account of
305 the mother being equally related to those offspring that disperse and their siblings that benefit
306 from the resulting relaxation of kin competition, and her offspring being more related to
307 themselves than they are to each other (see also Frank, 1986; Taylor, 1988b; Gandon, 1999;
308 Starrfelt & Kokko, 2010).

309 Our model has crucially incorporated heterogeneity in maternal condition, and this
310 allows us to investigate how such heterogeneity mediates the parent-offspring conflict of
311 interests with respect to dispersal. Here, we determine whether the potential for conflict is
312 greater in families with more resources (i.e. families with high-fecundity rank-1 mothers) or
313 fewer resources (i.e. families with low-fecundity rank-2 mothers). We consider two scenarios:
314 one in which offspring have complete information about their mothers' rank (i.e. conditional
315 dispersal); and one in which offspring have no information about their mothers' rank (i.e.
316 unconditional dispersal). We first focus on cases in which offspring have complete
317 information about their mothers' rank. Here, we find that mothers always prefer greater
318 dispersal rates of offspring than the offspring, irrespective of the resources available for each
319 family (Fig. 3). However, the difference between the optimal behaviour from the mother's
320 perspective and the optimal behaviour from the offspring's perspective is not the same for the
321 different types of families. In particular, we find that for lower inequality, conflict is more
322 pronounced within resource-poor families than within resource-rich families (Fig. 3). As
323 inequality between families rises the optimal dispersal rate of offspring in resource-rich
324 families rises, whereas the optimal dispersal rate of offspring in resource-poor families falls,
325 irrespective of who controls the dispersal rate of offspring. When the inequality between
326 families is sufficiently large, resource-poor families hit a threshold beyond which all their
327 offspring are philopatric, independently of who controls the dispersal rate of offspring. At this
328 point the conflict within resource-poor families ceases, whilst it still exists within resource-
329 rich families (Fig. 3). In summary, when inequality is low, resource-poor mothers suffer more
330 parent-offspring conflict over offspring dispersal than resource-rich families, but they still
331 produce a fair amount offspring. When inequality is high, there is less conflict within
332 resource-poor families, but their fecundity is very low.

333 We next contrast cases in which offspring have complete information about their
334 mothers' rank with cases in which offspring have no information about their mothers' rank.

335 This allows us to investigate the circumstances under which mothers are selectively favoured
336 to inform their offspring as to their rank versus withholding this contextual information. We
337 find that when offspring know that they have rank-1 mothers, parent-offspring conflict is less
338 strong than when offspring do not know the rank of their mothers (Fig. 3, panel (a)). This
339 suggests that rank-1 mothers should disclose full information about their status to their
340 offspring in order to minimise parent-offspring conflict. In contrast, we find that when
341 offspring know that they have rank-2 mothers, parent-offspring conflict is stronger than when
342 offspring do not know the rank of their mothers, as long as inequality is sufficiently small
343 (Fig. 3, panel (b)). This suggests that rank-2 mothers should withhold information about their
344 status from their offspring in order to minimise parent-offspring conflict. These conflicting
345 selective forces generate an informational battleground between rank-1 and rank-2 mothers, in
346 which rank-1 mothers are favoured to disclose maternity information to offspring in the group
347 whilst rank-2 mothers are favoured to withhold it.

348

349 Allomaternal control of dispersal

350 Above, we have considered that control of offspring dispersal occurs either by the
351 offspring themselves or by their mothers. Whilst this may often be the case, in other situations
352 mothers may control the dispersal traits of offspring other than their own. This may be
353 particularly important when differences in fecundity between mothers are also extended to
354 other behavioural traits such as dominance over other group members. First we consider a
355 case in which the high-fecundity breeder has full control over the dispersal of her own
356 offspring, but varies in the degree of control, denoted by α , over the offspring of the low-
357 fecundity mother, with $0 \leq \alpha \leq 1$. We find that the CPH holds as long as the high-fecundity
358 mother does not exert any control over the dispersal of the low-fecundity mother's offspring
359 (i.e. when $\alpha = 0$; Fig. 4). However, when the degree of control by the high-fecundity mother
360 increases, the dispersal probability of their own offspring decreases, whilst the dispersal

361 probability of the low-fecundity mother's offspring increases (Fig. 4, panel(a)). Indeed, when
362 the high-fecundity mother reaches a certain degree of control, all of the low-fecundity
363 mother's offspring are forced to disperse (i.e. $z_2 = 1$). We obtain similar results when we
364 allow the low-fecundity mother control the dispersal of the high-fecundity mother's offspring,
365 where we denote the degree of control of the low-fecundity mother by β . When the degree of
366 control by the low-fecundity mother increases, the dispersal probability of their own offspring
367 decreases, whilst the dispersal probability of the low-fecundity mother's offspring increases
368 (Fig. 4, panel(b)). If the degree of control is sufficiently high, all offspring of high-fecundity
369 rank-1 mothers are forced to disperse, whilst all offspring of low-fecundity rank-2 mothers
370 remain in the local patch. When the low-fecundity mother has no control over the high-
371 fecundity mother's offspring (i.e. when $\beta = 0$), the CPH holds, but not otherwise (i.e. when β
372 > 0 ; Fig. 4).

373

374 The CPH underpins a family of invariance results

375 To the extent that any trait may be coincident with an individual's dispersal status, the
376 CPH underpins a whole family of invariance results. For example, if dispersing individuals
377 engage in aggressive behaviour whilst non-dispersing individuals are more docile (e.g. El
378 Mouden & Gardner, 2008), then the present CPH result could be reframed as a "constant non-
379 aggressor hypothesis". The important caveat here is that such derivative invariants are only
380 expected to hold insofar as the focal trait is tightly coupled to dispersal status, and the fact
381 that incomplete coupling leads to a failure of these invariants whilst the CPH continues to
382 hold confirms that the CPH is the more fundamental invariant.

383 One such derivative invariant that has been previously described is the "constant
384 female hypothesis" (CFH; Frank, 1987c, 1998). This is concerned with "local resource
385 competition" (Clark, 1978) scenarios in which females are philopatric and males are the
386 dispersing sex, and the CFH predicts that more fecund mothers will invest relatively less into

387 daughters than will less fecund mothers, such that all mothers will produce the same number
388 of daughters, irrespective of their fecundity. This is because the selection gradient acting on
389 the sex allocation strategy shows properties that are identical to those of the selection gradient
390 acting on dispersal. Namely, if we assume that the sex-ratio of a mother (i.e. σ_{it}) is now an
391 evolving trait, rather than a parameter, the selection gradient acting on the sex allocation
392 strategy of a mother is given by

393

$$394 \quad -\omega_f r_{if} + \omega_m r_{im} + \omega_f \sum_{j \in I} (U_j \rho_{ij}) > 0. \quad (4)$$

395

396 As in the CPH, the relatedness coefficients are independent of the mother's rank. Thus, $r_i = r$
397 and $\rho_{ii} = \rho$ for all $i \in I$; $\rho_{ij} = P$ for all $i \in I$, and all $j \in I$, $j \neq i$. Thus, mothers adjust their sex
398 ratio such that each and every mother converge upon the same number of daughters (i.e. $N_i =$
399 N^* , and $U_i = U^*$).

400 However, this invariant result only holds when all daughters are philopatric. If females
401 exhibit at least some propensity to disperse, then the selection gradient acting on the sex ratio
402 is given by

403

$$404 \quad -(\omega_f(1 - z_i) + \omega_f z_i(1 - c))r_f + \omega_m r_{im} + \omega_f(1 - z_i)h \sum_{j \in I} (U_j \rho_{ij}) > 0. \quad (5)$$

405

406 This means that the first term of the selection gradient now depends on the fecundity of the
407 focal mother, and therefore the CFH no longer holds. The CPH, by contrast, does hold,
408 irrespective of the sex ratio produced by each mother. That is, it is the CPH that underpins the
409 CFH, and not the reverse.

410

411

412

Discussion

413

414

415 We have described a new life-history invariant result for dispersal evolution.
416 Specifically, we have found that natural selection favours all mothers to produce the same
417 number of philopatric offspring, irrespective of variation between mothers in the total number
418 of offspring that they produce. This is because kin competition, arising from a failure to
419 disperse, is related to the number, rather than the proportion, of a mother's philopatric
420 offspring. In analogy with the similar "constant male hypothesis" (CMH) of the sex allocation
421 literature (Frank, 1987c, 1998), we term this result the "constant philopater hypothesis"
422 (CPH).

423 Such invariance results provide testable predictions in their own right, and also
424 promote the interplay of theory and empirical testing by reducing the extent to which
425 extraneous genetic, ecological and demographic parameters are confounding in comparative
426 analyses (e.g. West et al., 2001; Rodrigues & Gardner, 2015). Moreover, they also facilitate
427 the development and conceptualisation of theory. For example, the invariant relationship
428 between helping and harming, on the one hand, and degree of population viscosity, on the
429 other hand (Taylor, 1992; El Mouden & Gardner, 2008), has been used to demonstrate that
430 heterogeneity in resource availability per se – and not any conflating effect of viscosity itself
431 – modulates the evolution of helping and harming in viscous populations (Rodrigues &
432 Gardner, 2012, 2013a). The CPH invariance prediction is readily amenable to empirical
433 testing, as it is robust to variation in difficult-to-measure quantities such as the mortality risk
434 associated with dispersal. Social groups in different species often comprise multiple breeders
435 that vary in their fecundity (reproductive skew), and in some cases there is variation in the
436 proportion / number of dispersers produced by each breeder (e.g. Crespi & Taylor 1990;
437 Innocent et al., 2010). Our theory predicts that dispersal rates (or the fraction of dispersal

438 morphs) should be higher for more productive breeders, and that at the same time the number
439 of philopatric offspring should be equal for each breeder.

440 In terms of reaction-norms, the CPH means that mothers with fecundity below a
441 certain threshold should produce no dispersing offspring, while mothers with fecundity above
442 that threshold should exhibit a positive correlation between their fecundity and the dispersal
443 rate of their offspring. Such reaction norms with a critical threshold have also been observed
444 in the context of the evolution of dispersal conditional on the overall number of individuals in
445 a patch (Crespi & Taylor, 1990; Ezoe & Iwasa, 1997; Kisdi, 2004; Rodrigues & Johnstone,
446 2014). Under certain conditions, this means that differences in density between patches before
447 dispersal are eroded after dispersal. Specifically, we have shown that the CPH holds both
448 within and between patches when the environment is temporally unpredictable but not for
449 other types of temporal variation. This implies that there are two forces mediating the
450 evolution of dispersal: one acting between patches that tends to equalise or enhance
451 differences in density between them; and one acting within patches that tends to equalise
452 differences in number of philopatric offspring among group members. These two forces may
453 be operating simultaneously in natural population, and future empirical studies should take
454 both into consideration.

455 We have shown that the adaptive adjustment of offspring dispersal conditional on
456 maternal fecundity may have a dramatic impact on the amount of kin competition that each
457 offspring experiences. More specifically, this means that variation in fecundity among
458 breeders is not translated into an equivalent variation in kin competition among offspring.
459 Indeed, owing to the CPH, the amount of kin competition may be precisely the same,
460 irrespective of a mother's fecundity. This has wide-reaching implications for the evolution of
461 social behaviour within groups. We have shown how the CPH underlies the "constant female
462 hypothesis", an invariant result that has been previously described in the sex allocation
463 literature (Frank, 1987c, 1998). Another topic for which the CPH may have important

464 implications is reproductive skew, which has been shown to promote the evolution of
465 harming by high-fecundity mothers and helping by low-fecundity mothers (Johnstone, 2008).
466 Crucially, that result has been derived under the assumption that, while helping and harming
467 are conditional on a mother's fecundity, dispersal of offspring is not. An immediate
468 consequence of the CPH is that, if offspring disperse conditionally, according to maternal
469 fecundity, the asymmetry in the level of kin competition between high- and low-fecundity
470 mothers vanishes, such that helping and harming are no longer favoured. This suggests a
471 promising avenue for future theoretical and empirical study.

472 We have also shown that there will typically be a conflict of interests between parent
473 and offspring with respect to the latter's probability of dispersing, and that the intensity of
474 such conflict is modulated by heterogeneity in parental condition, and hence is liable to vary
475 between families. We find that if inequality in fecundity is sufficiently low, the intensity of
476 parent-offspring conflict is greater in resource-poor families but, by contrast, if the inequality
477 is sufficiently high, the conflict within resource-poor families may vanish, with parents and
478 offspring agreed that there should be no dispersal. To the extent that within-family conflict
479 has a negative impact on a mother's fecundity, this result suggests that parent-offspring
480 conflict may either reinforce inequality between families (when inequality is relatively low)
481 or may attenuate inequality between families (when inequality is relatively high).

482 On account of our finding that parent and offspring dispersal optima depend upon the
483 degree of heterogeneity in fecundity across families, we have uncovered a new informational
484 battleground over dispersal, with high-fecundity mothers being favoured to disclose full
485 information about their status to all the offspring in the group, and low-fecundity mothers
486 being favoured to withhold this information. The resolution of this informational conflict will
487 depend upon the specific biology of particular species (for reviews see Godfray, 1995; Kilner
488 & Hinde, 2008). There are many examples of mothers disclosing contextual information to
489 their offspring: in daphnia, for instance, mothers provide accurate information about the

490 presence of predators in the local environment, and offspring respond to this information by
491 developing a protective helmet (Tollrian & Dodson, 1999). Conversely, there are examples of
492 mothers withholding information or actively deceiving their offspring with regards to the
493 circumstances in which they find themselves: in black-headed gulls, *Larus ridibundus*, for
494 instance, mothers appear to adjust yolk androgen concentration in eggs in order to manipulate
495 the offspring's perception of their birth order in the brood (Eising et al., 2001).

496 More generally, we suggest that the resolution of this informational conflict will
497 depend on whether mothers are: (i) constrained to either honestly communicate their rank to
498 their offspring or else withhold this information; or (ii) able to honestly communicate,
499 withhold the information or deceive their offspring with regards to their rank. If deception is
500 not an option, then in this simple binary scenario an offspring will always be able to correctly
501 determine her mother's rank, either because her mother honestly communicates the fact that
502 she is of rank-1 or else because her mother communicates no information, which enables the
503 offspring to infer that she is of rank-2, and this system of signalling will be stably maintained
504 by the coincidence of interests of the rank-1 mother and her offspring. However, if
505 unconstrained deception is an option, then all mothers are expected to communicate that they
506 are of rank-1, which provides no useful information to their offspring, and hence this system
507 of communication is expected to collapse. The resolution of this conflict represents a further
508 avenue for future research.

509 Our model provides an explanation for different patterns of dispersal within social
510 groups depending on the degree of control by each group member, which can change the sign
511 of rank-dependent dispersal. If each mother controls the dispersal of their own offspring or if
512 offspring control their own dispersal, then we should expect a positive correlation between
513 mother's fecundity and offspring propensity to disperse – i.e. positive rank-dependent
514 dispersal. Under allomaternal control of offspring dispersal the mother with a higher degree
515 of control is expected to force offspring of other mothers to disperse and therefore their own

516 offspring are less likely to disperse. If, for instance, the dominant mother controls the
517 dispersal of offspring in the social group, then we should expected negative rank-dependent
518 dispersal. For example, in meerkats the dominant is more likely to force distantly related
519 offspring to disperse than their close relatives, and therefore offspring of lower rank mothers
520 are more likely to disperse than offspring of higher rank mothers (i.e. negative rank-
521 dependent dispersal rates; Clutton-Brock et al., 2010). By contrast, in the red-fronted lemurs,
522 there is no correlation between dispersal and kinship, and therefore we should not expect
523 negative rank-dependent dispersal rates (Kappeler & Fichtel, 2012, reviewed in Clutton-
524 Brock, 2013). More generally, while in our model we have considered a simple control
525 parameter, more species-specific resolution models can be adopted (e.g. Godfray, 1995;
526 Kilner & Hinde, 2008). These possibilities also represent avenues for future theoretical and
527 empirical exploration.

528 The CPH result emerges from key symmetries in relatedness, for instance the
529 independence of the relatedness between two mothers breeding in the same patch with respect
530 to their rank and hence their share of the group's total fecundity. This situation obtains in the
531 present model owing to our assumption that rank is not inherited. However, more generally,
532 rank may be heritable, to some extent, such that high-ranking females tend to be the daughters
533 of highly-fecund mothers, in which case they may be more likely to breed alongside sisters
534 than are females of lower rank, which could lead to a positive correlation between rank /
535 fecundity and relatedness to group mates. Alternatively, whilst we have considered the cost of
536 dispersal to be paid in terms of mortality, dispersal may also incur fecundity costs, which
537 again could lead to a positive correlation between fecundity and relatedness, owing to low-
538 fecundity dispersers being unrelated to their group mates.

539 Finally, although our results hold under a wide range of model assumptions, we have
540 not studied the effects of many other potentially-relevant factors. It is likely that, in some of
541 these cases, our model will fail to conform to empirical data. However, by highlighting those

542 scenarios in which our model's key assumptions are not met, our result may be used to
543 illuminate otherwise obscured biological details, concerning a species' ecology, demography,
544 phenotypic plasticity or cognition. In this respect, the model also establishes a baseline
545 scenario, which may help to understand and interpret new empirical data and future
546 mathematical results.

547

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549

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822

Figure legends

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825 **Figure 1. Convergence stable dispersal rates in heterogeneous groups.** The CS dispersal
826 strategies of offspring of high-fecundity rank-1 breeders (z_1^* , solid lines) and of offspring of
827 low-fecundity rank-2 breeders (z_2^* , dashed lines) as a function of the reproductive inequality
828 (s) for varying cost of dispersal (c). The dispersal rate of offspring of high-fecundity breeders
829 is greater than that of offspring of low-fecundity breeders (i.e. $z_1^* > z_2^*$). All breeders produce
830 the same number of offspring that remain in the natal patch as long as low-fecundity mothers
831 give birth to a sufficiently high number of offspring.

832

833 **Figure 2. Convergence stable dispersal rates in heterogeneous populations.** The CS
834 dispersal strategies of offspring of high-fecundity rank-1 breeders (z_{1X}^* , solid lines) and of
835 offspring of low-fecundity rank-2 breeders (z_{2X}^* , dashed lines) in high resource-availability
836 rank-1 patches (z_{X1}^*) and in low resource-availability rank-2 patches (z_{X2}^*) as a function of
837 the reproductive inequality (s) for temporally stable, unpredictable, and seasonal
838 environments. (a,d) In temporally seasonal environments average dispersal is higher from
839 rank-1 patches, and the CPH holds as long as inequality is sufficiently small. (b,e). In
840 temporally unpredictable environments average dispersal is higher from rank-1 patches, and
841 the CPH holds both within and between patches as long as inequality is sufficiently small.
842 (c,f) In temporally stable environments average dispersal is higher from rank-2 patches, and
843 the CPH holds as long as inequality is sufficiently small. Parameter values: $c = 0.50$, $p = 0.50$.

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845 **Figure 3. Parent-offspring conflict.** The CS dispersal strategies of mothers (solid lines) and
846 of daughters under complete maternity information (offspring_C, dotted lines) and under no
847 maternity information (offspring_U, dashed lines) for (a) rank-1 resource-rich families, and (b)
848 rank-2 resource-poor families. Under lower reproductive inequality, parent-offspring conflict

849 is more intense for low-fecundity families. For resource-rich families, parent-offspring
850 conflict is more intense under no-maternity information irrespective of the inequality between
851 families. For resource-poor families, parent-offspring conflict is less intense under no-
852 maternity information to the left of the vertical dashed line. The number of philopatric
853 offspring is in arbitrary units. Parameter values: $c = 0.25$.

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855 **Figure 4. Allomaternal control of dispersal.** The CS dispersal strategies of offspring and the
856 number of philopatric offspring as a function of rank-1 high-fecundity and rank-2 low-
857 fecundity mothers degree of control. When mothers control the dispersal of their own
858 offspring (i.e. $\alpha = 0$, and $\beta = 0$) the CPH holds. (a,c) When high-fecundity mothers increase
859 their control over the dispersal of low-fecundity mothers' offspring, the dispersal of low-
860 fecundity mothers' offspring rises whilst the dispersal of their own offspring falls. (b,d) When
861 low-fecundity mothers increase their control over the dispersal of high-fecundity mothers'
862 offspring, the dispersal of high-fecundity mothers' offspring rises whilst the dispersal of their
863 own offspring falls. (c,d) The CPH breaks down when mothers do not control the dispersal of
864 their own offspring or when offspring do not control their own dispersal. The number of
865 philopatric offspring is in arbitrary units. Parameter values: $c = 0.25$, $s = 0.5$.

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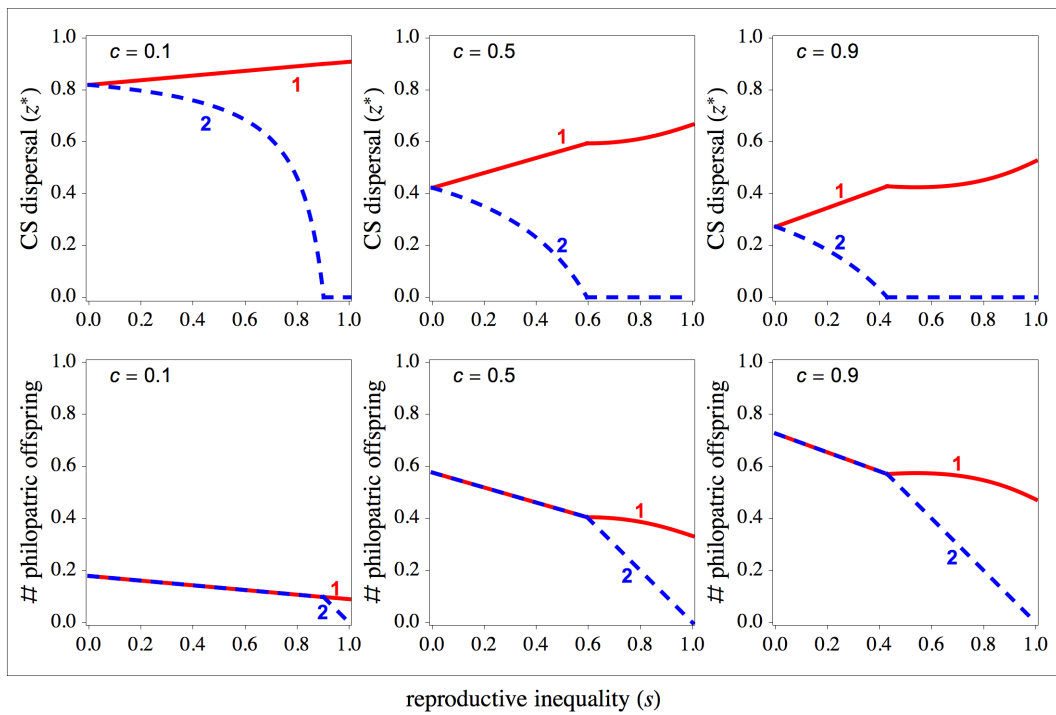


Figure 1

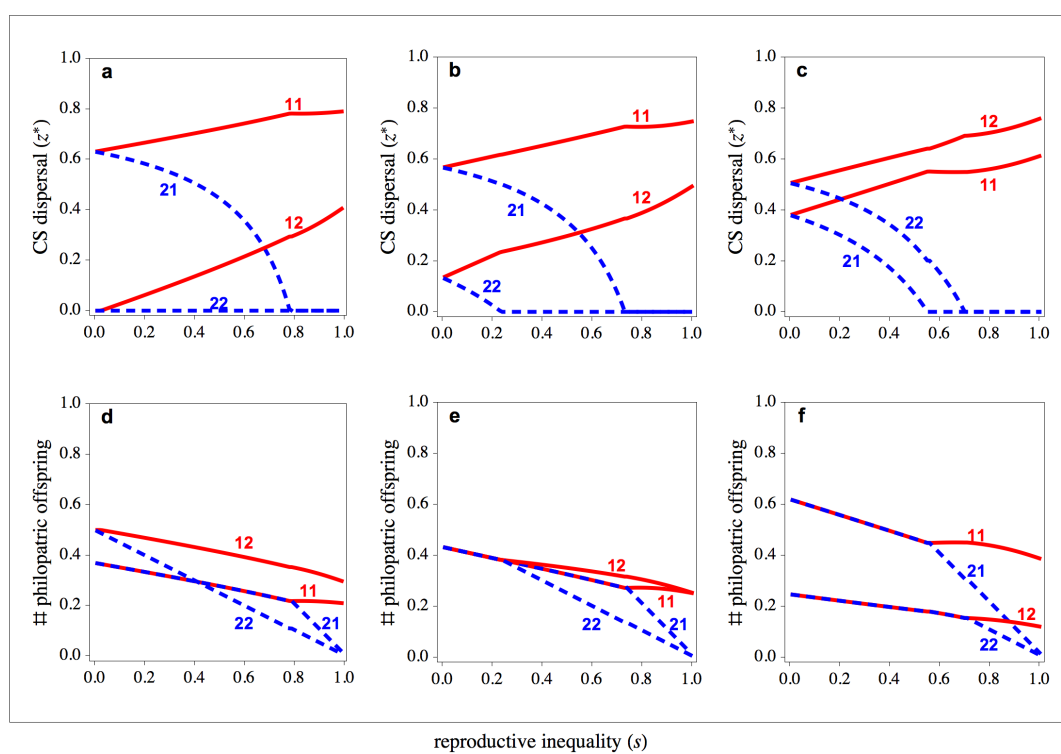


Figure 2

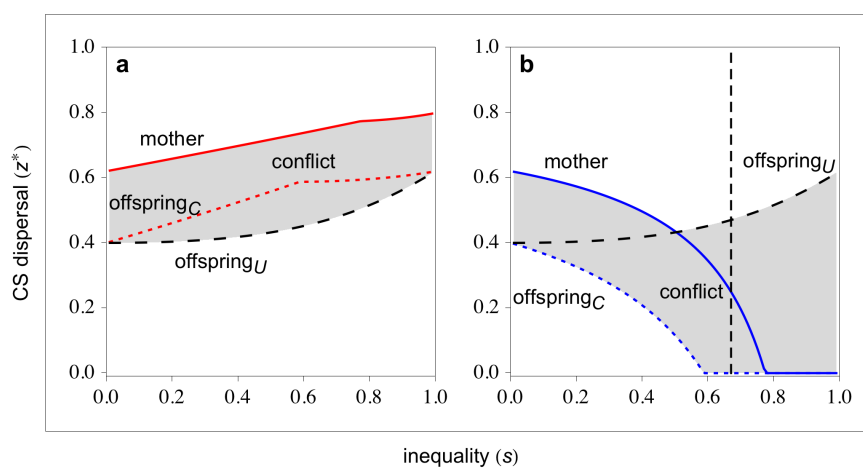


Figure 3

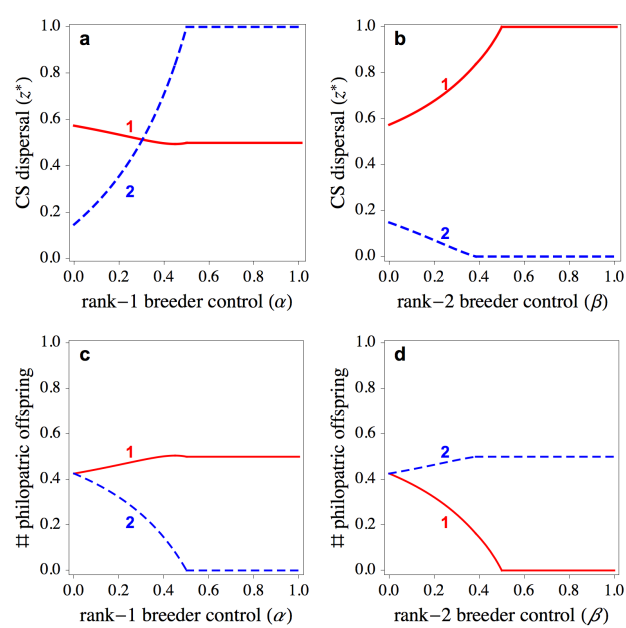


Figure 4