5

6   Adjustment of sex allocation to co-foundress number and kinship under

7   local mate competition: an inclusive-fitness analysis

8

9   Andy Gardner[1] & Ian C.W. Hardy[2]*

10

11   [1] *School of Biology, University of St Andrews, Greenside Place, St Andrews, KY16 9TH, UK*

12   [2] *School of Biosciences, University of Nottingham, Sutton Bonington Campus,*

13   *Loughborough, LE12 5RD, UK*

14

15   **Corresponding author: Dr Ian C.W. Hardy, School of Biosciences, University of*

16   *Nottingham, Sutton Bonington Campus, Loughborough, LE12 5RD, UK*

17   *Tel: +44 (0) 115 9516177*

18   *Email: ian.hardy@nottingham.ac.uk.*

19   ORCID ID: 0000-0002-5846-3150

20

21   *A. Gardner: Email:* andy.gardner@st-andrews.ac.uk*, ORCID ID: 0000-0002-1304-3734*

22

33   **Abstract**

34   Hamilton's theory of local mate competition (LMC) describes how competition between male
35   relatives for mating opportunities favours a female-biased parental investment. LMC theory
36   has been extended in many ways to explore a range of genetic and life-history influences on
37   sex allocation strategies, including showing that increasing genetic homogeneity within mating
38   groups should favour greater female bias. However, there has been no quantitative theoretical
39   prediction as to how females should facultatively adjust their sex allocation in response to co-
40   foundress number and kinship. This shortfall has been highlighted recently by the finding that
41   sex ratios produced by sub-social parasitoid wasps in the family Bethylidae are affected by the
42   number of co-foundresses and by whether these are sisters or unrelated females. Here we close
43   this gap in LMC theory by taking an inclusive-fitness approach to derive explicit theoretical
44   predictions for this scenario. We find that, in line with the recent empirical results, females
45   should adopt a more female-biased sex allocation when their co-foundresses are less numerous
46   and are their sisters. Our model appears to predict somewhat more female bias than is observed
47   empirically; we discuss a number of possible model extensions that would improve realism
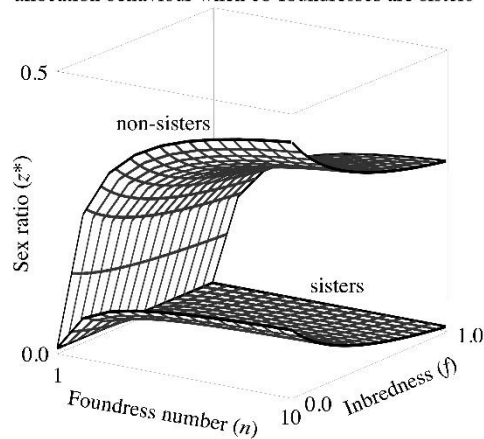48   and that would be expected to result in a closer quantitative fit with experimental data.
49
50
51   **Key words**: LMC, foundress kinship, sex ratio, parasitoid
52
53

Graphical Abstract

Sub-social parasitoids are predicted to adjust their sex allocation behaviour when co-foundresses are sisters

55

56   **Introduction**

57   The theory of sex allocation, which concerns the trade-off between female versus male
58   reproductive effort, has been described as the "jewel in the crown of evolutionary ecology"
59   (West & Herre 2002), and it provides among the best evidence of the precision of Darwinian
60   adaptation in the natural world (West 2009). Perhaps its most productive application has been
61   to scenarios in which mating groups comprise genetic relatives, such that wasteful competition
62   among males induces parents to decrease their investment into sons. Hamilton (1967) derived
63   an unbeatable sex allocation strategy for such "local mate competition" (LMC) under a diplo-
64   diploid mode of inheritance. This showed that a mother who is one of n unrelated females
65   contributing offspring to a mating group should make a proportional investment of $(n-1)/(2n)$
66   into sons, such that she should invest nearly all of her reproductive effort into daughters
67   (producing just enough sons to fertilize them) if she is the only mother present, and make a
68   nearly equal investment into daughters and sons if she is one of very many females contributing
69   offspring to the mating group, recovering Fisher's (1930) classic result for large, panmictic
70   populations.

71   Hamilton's (1967) analysis has subsequently been extended in a number of ways (reviewed
72   by West 2009), including to allow for a haplo-diploid mode of inheritance (Hamilton 1979)
73   and kinship among co-foundresses (Frank 1985, 1986a, 1986b, 1998, Bulmer 1986, Taylor
74   1988, Taylor & Crespi 1994, Courteau & Lessard 2000, Gardner et al. 2009, Rodrigues &
75   Gardner 2015). A very general result has been provided by Frank (1985, 1986a) who showed
76   that the unbeatable sex allocation under LMC is given by the product of three terms: ½,
77   reflecting the rarer-sex effect of Fisher (1930); R, capturing any asymmetry in the inclusive
78   fitness valuation of a son versus a daughter (such that $R < 1$ if daughters are valued more, $R >$
79   1 if sons are valued more, and $R = 1$ if both are valued equally); and $P_{d(a)t}$, representing Wright's

80 (1969) coefficient of panmixia, and hence the degree to which mating groups are genetically
81 heterogeneous. Frank (1985) has highlighted that the coefficient of panmixia may vary between
82 groups and hence that females might be favoured to adjust their sex allocation according to
83 their local assessment of both number and kinship of co-foundresses, though no explicit,
84 quantitative results have so far been derived for this particular scenario.

85   This gap in the theoretical development of LMC has recently been highlighted by an
86 empirical study of sex allocation in *Goniozus* wasps (Abdi et al. 2020); this found that
87 collective brood sex ratios are affected by both the number of foundresses and kinship among
88 co-foundresses. Briefly, *Goniozus* species are haplo-diploid parasitoids which have long been
89 known to exhibit female biased sex ratios and comply broadly with both the assumptions and
90 predictions of LMC theory (Hamilton 1967, 1979, Green et al. 1982, Hardy & Cook 1995,
91 Hardy et al. 1999, Khidr et al. 2013). Due to aggressive resource competition between females
92 and subsequent brood care (sub-social reproduction), the number of foundresses contributing
93 offspring to a mating group is thought to be typically just one. Yet adult females are able to
94 discriminate kinship and may tolerate each other's presence when relatedness is higher and
95 also when host resources are less limiting (Lizé et al. 2012; Abdi et al. 2020). When
96 experimentally induced to reproduce in multi-foundress groups, the sex ratios of broods
97 produced by sibling females were similar to sex ratios produced by single foundreses
98 (proportion of offspring that were male ≈ 0.10) while non-sibling foundresses produced sex
99 ratios were much higher (≈ 0.40; Abdi et al. 2020).

100   Here we close the theory gap by deriving explicit theoretical predictions for scenarios in
101 which a female may facultatively adjust her sex allocation according to the number of her co-
102 foundresses and whether they are her sisters or are unrelated females. We take an inclusive
103 fitness approach (Hamilton 1964), showing that the female's unbeatable sex ratio depends not
104 only on these two factors, but also on the average degree of inbredness across the whole
105 population. We provide solutions for both diplo-diploid and haplo-diploid modes of genetic
106 inheritance and find an improved fit between sex ratio predictions for haplo-diploidy and the
107 *Goniozus* sex ratios observed by Abdi et al. (2020). Despite this improvement, our model does
108 appear to predict somewhat more female bias than is observed empirically. Accordingly, we
109 discuss a number of possible model extensions – including partial male dispersal and local
110 resource competition – that would further improve realism and that would be expected to result
111 in a closer quantitative fit with the experimental data.

112
113 **Model and Results**

114 We consider a foundress group in which there are n females each making an equal contribution
115 of offspring to a mating group, with each female by default adopting a sex allocation strategy
116 z such that she contributes Nz sons and $N(1-z)$ daughters, where N is a large number. Their
117 offspring then mate at random amongst each other, with each female mating once and each
118 male potentially mating a large number of times. Following mating, the males die, and the
119 mated females disperse to form new foundress groups with other females drawn at random
120 from the entire population. We assume that these new foundress groups almost always
121 comprise unrelated females, but we do allow for a nonzero probability that co-foundresses are
122 sisters in order to investigate how females are favoured to behave in such circumstances.

123   To determine unbeatable sex allocation behaviour, we focus attention on one of the n
124 foundresses, and consider the inclusive-fitness consequences of her adopting an alternative sex
125 allocation strategy $z + \delta$, such that she instead contributes $N(z + \delta)$ sons and $N(1 - z - \delta)$
126 daughters to the mating group (full details are given in Box 1).

4

127   First, we consider a diplo-diploid (D) mode of inheritance. Here, we find that the unbeatable
128 sex allocation for a female whose group comprises herself and n-1 unrelated (U) other females
129 is given by

130

131 $$z_{D,U}^* = \frac{n-1}{2n} \tag{1}$$

132

133 which is exactly the result given by Hamilton (1967). This result is illustrated by the upper
134 surface in Figure 1a. Note that equation (1) holds irrespective of whether the number of
135 foundresses is constant or variable across groups and depends only on the number of
136 foundresses present in the female's own group (see Box 1 for details). In contrast, we find that
137 the unbeatable sex allocation for a female whose group comprises herself and n-1 of her sisters
138 (S) is given by

139

140 $$z_{D,S}^* = \frac{(n-1)(1-f)}{4n(1+3f)} \tag{2}$$

141

142 where f describes the "inbredness" of females, i.e. the average consanguinity of their parents
143 (Frank 1985, 1986a, Bulmer 1994). This result is illustrated by the lower surface in Figure 1a.
144 The sex allocation predicted for sister groups (equation 2) is a constant fraction $(1-f)/(2(1+3f))$
145 of that predicted for non-sister groups (equation 1), independently of the number of co-
146 foundresses present, and this fraction decreases from ½ to 0 as the degree of inbredness
147 increases from 0 to 1, meaning that the proportional allocation to sons in sister groups is never
148 more than half of what it is in equal-sized non-sister groups. Note that a female's inbredness is
149 liable to depend on the sizes of groups encountered by her ancestors, such that (unlike for non-
150 sister diplo-diploid groups) it is likely that sex allocation behaviour predicted for sister groups
151 will depend not only on the local number of foundresses but also the on the distribution of
152 group sizes across the population. In the special case of all groups having the same size,
153 equation (2) reduces to $z_{D,S}^* = (n-1)^2/(4n^2)$ (see Box 1 for details).

154   Second, we consider a haplo-diploid (H) mode of inheritance. Here, we find that the
155 unbeatable sex allocation for a female whose group comprises herself and n-1 unrelated other
156 females is given by

157

158 $$z_{H,U}^* = \frac{(n-1)(1+f)}{2n(1+2f)}, \tag{3}$$

159

160 as is illustrated by the upper surface in Figure 1b. Note that, in contrast with the corresponding
161 result given for diplo-diploidy (equation 1), the sex allocation exhibited by non-sister groups
162 in haplo-diploid populations (equation 3) is dependent upon the degree of inbredness, and
163 hence is likely to depend on the distribution of group sizes across the population and not just
164 the size of the focal female's group. In the special case of all groups having the same size,
165 equation (3) reduces to $z_{H,U}^* = ((n-1)(2n-1))/(n(4n-1))$, as given by Hamilton (1979; see
166 Box 1 for details). More generally, the sex allocation predicted for haplo-diploid non-sister
167 groups (equation 3) is a constant fraction $(1+f)/(1+2f)$ of that predicted for diplo-diploid non-
168 sister groups (equation 1), independently of the number of co-foundresses present, and this
169 fraction decreases from 1 to 2/3 as the degree of inbredness increases from 0 to 1, meaning that
170 it is almost always lower than the corresponding result for diplo-diploid inheritance.

171   In contrast, we find that the unbeatable sex allocation for a female whose group comprises
172 herself and n-1 of her sisters is given by

5

173

174 $$z_{H,S}^* = \frac{(n-1)(1-f)}{8n(1+2f)},\tag{4}$$

175

176 as is illustrated by the lower surface in Figure 1b. This too is dependent upon the degree of
177 inbredness, and hence upon the distribution of group sizes across the whole population. In the
178 special case of all groups having the same size, equation (4) reduces to $z_{H,S}^* = (n-1)^2/(2n(4n$
179 $- 1))$. More generally, the sex allocation predicted for sister groups under haplo-diploidy
180 (equation 4) is a constant fraction $(1-f)/(4(1+f))$ of that predicted for non-sister groups under
181 haplo-diploidy (equation 3), and this fraction decreases from ¼ to 0 as the degree of inbredness
182 increases from 0 to 1, meaning that it is always lower than the corresponding result for non-
183 sister groups.

184
185
186
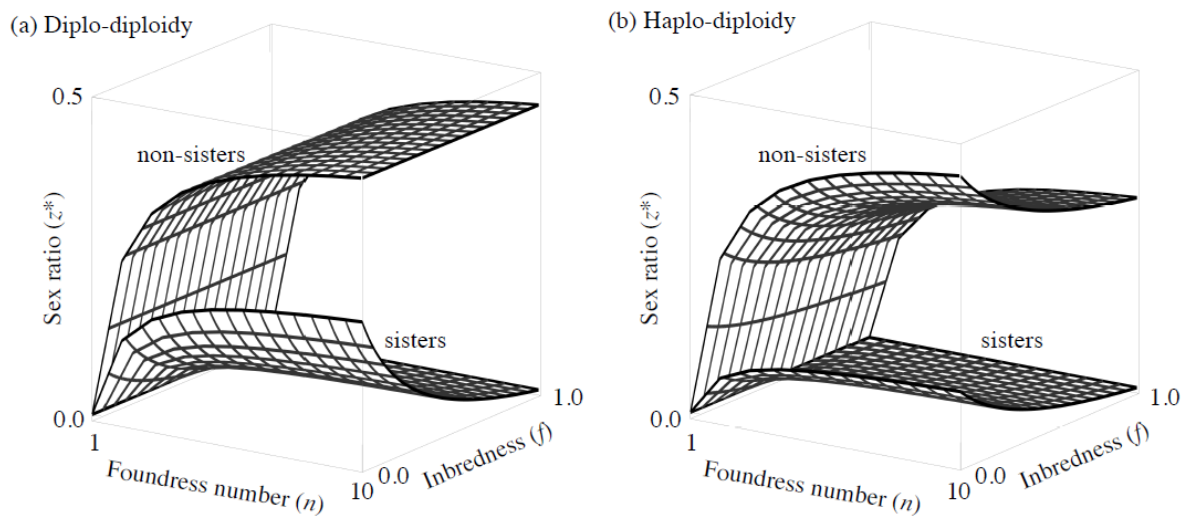
187
188
189 Figure 1: Predicted sex ratios in groups of sister or non-sister foundresses,
190 according to foundress number and inbredness. Panel (a) shows optima for diplo-
191 diploid inheritance and panel (b) shows optima for haplo-diploid inheritance.

192
193
194

195 **Comparison of theory and observations**

196 Here we compare model predictions for the haplo-diploid mode of inheritance with sex ratios
197 observed in *Goniozus*. Abdi et al. (2020) provide data on the sexual composition of 123 broods
198 of offspring produced by *Goniozus nephantidis* (Muesebeck) females held in foundress groups
199 of size ranging from 1 to 8 and with multi-foundress groups consisting of sister females or non-
200 sister females. The results of null hypothesis significance testing using weighted logistic
201 analysis and the associated equations for the estimated minimal adequate models are presented
202 in Abdi et al. (2020), who also discussed the inclusion or exclusion of a large brood with an
203 outlying sex ratio which was especially influential due to the use of an intrinsically weighted
204 analysis. Here we include the outlier but use unweighted logistic analysis to de-emphasize the
205 influence of large broods. We obtain the following maximum likelihood estimates of the two
206 empirical relationships between sex ratio, z, and foundress number, n:

207 Regression for single foundresses and multiple non-sister foundresses:

208 $$z=1/(1+(1/(\exp(0.084n-1.132)))) \tag{5}$$

209

210 Regression for single foundresses and multiple sister foundresses:

211 $$z=1/(1+(1/(\exp(0.071n-2.072)))) \tag{6}$$

212

213   We explored likely values of f (the average inbredness of *G. nephantidis*) by calculating the
214 sums of squared differences between the observed sex ratio of each brood and the sex ratio
215 predicted by equations 3 and 4 for the given number of foundresses and foundress kinship,
216 across the range of candidate values of f (0 to 1): the best-fit value of f was zero. Using $f=0$, the
217 sex ratios predicted to be produced (equations 3 and 4) are plotted against n, along with the
218 estimated regressions (equations 5 and 6) and observed brood sex ratio data for *G. nephantidis*,
219 in Figure 2.

220

221
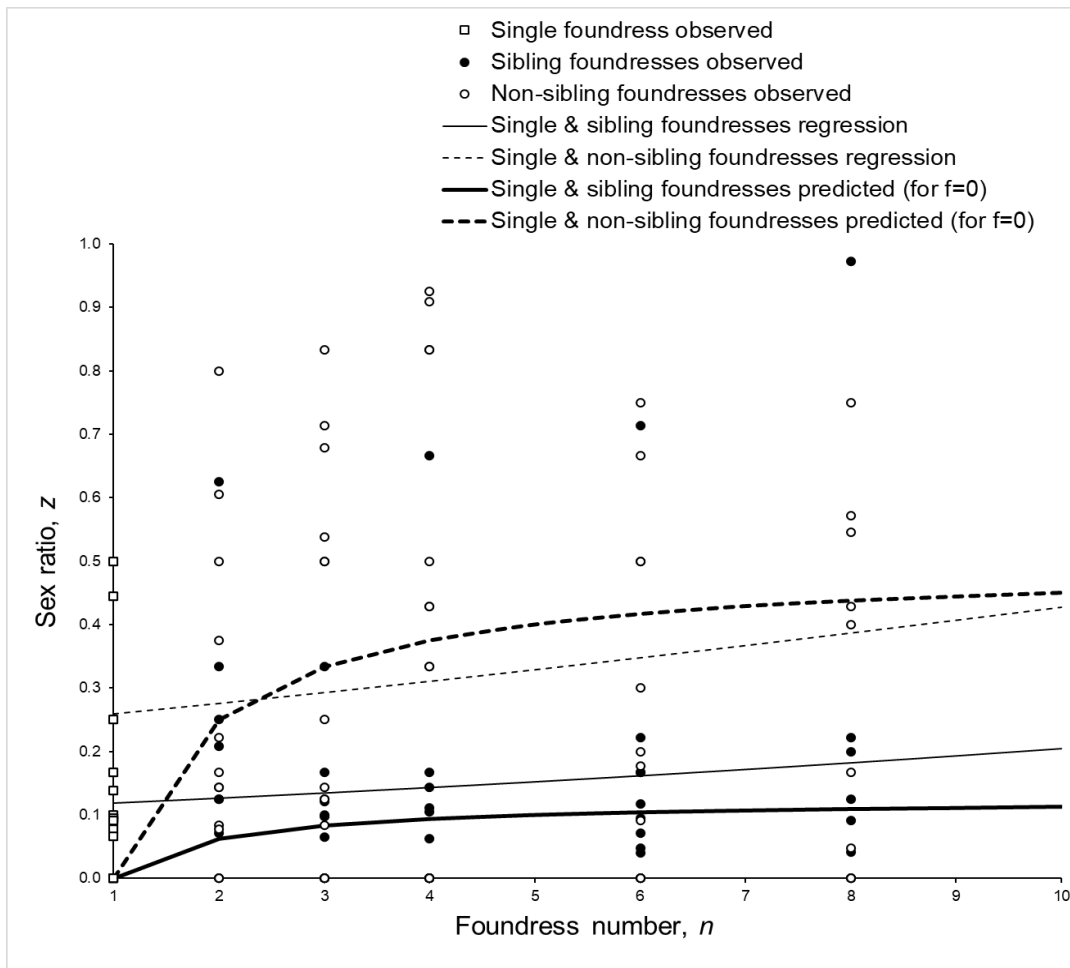
222
223
224   Figure 2: *Goniozus nephantidis* sex ratios: observed and predicted for the
225   haplo-diploid mode of inheritance. Note that, for the sake of illustration,
226   the prediction lines assume a degree of inbredness $f = 0$, as this is the best-
227   fitting value, but is likely unrealistic given the life-history of *G.*
228   *nephantidis* (see Discussion for more details).

229
230   We evaluated how well the data fit the model predictions by calculating the sum of squared
231 departures from the observed mean sex ratio (SST) and the sums of squared departures (SSE)
232 from the model for haplo-diploids (equations 3 & 4), using data from all replicates, for a range
233 of values of f. For $f = 0$, the proportion of variation explained by the model ((SST-SSE)/SST)
234 was 0.0894. The model provided a better fit to the data than did the overall mean for $f \leq 0.35$
235 and for larger values it was worse. As LMC models give notoriously unrealistic predictions for
236 the single-foundress case (see below), we also calculated these values with single foundress
237 replicates excluded. The proportion of variation explained was 0.1167 and the model provided
238 a better fit than the mean sex ratio for $f \leq 0.5$.

239   Next we compared the variation explained by Hamilton's (1979) LMC model for haplo-
240 diploids ($z_{H,U}* = ((n - 1)(2n - 1))/(n(4n - 1))$) against the observed mean and found that this
241 model fits the data worse than does the overall mean sex ratio, whether or not single foundress
242 replicates are included. Finally, we calculated the proportion of variation explained by our
243 model for haplo-diploids (equations 3 & 4, $f = 0$, Fig. 2) compared to Hamilton's (1979) model
244 (shown plotted along with the same data in Fig. 10 of Abdi et al. 2020): across all replicates
245 23.2% of the variation was explained by including co-foundress and for multiple-foundress
246 replicates only this value was 24.44%. We conclude that the inclusion of facultative adjustment
247 according to whether co-foundresses are sisters or are unrelated females leads to a better match
248 between predicted and observed sex ratios.

249
250 **Discussion**
251
252 We have derived explicit theoretical predictions for sex allocation when females are able to
253 adjust their behaviour according to number and kinship of co-foundresses, for both diplo-
254 diploid and haplo-diploid modes of genetic inheritance. We have shown that females are
255 expected to decrease their allocation of reproductive resources to sons in the presence of both
256 fewer and more closely related co-foundresses, with the extent of sex ratio bias being
257 dependent upon female inbredness (and hence upon the distribution of group sizes across the
258 population) in all cases except for the classic diplo-diploid, non-sister-group scenario
259 considered by Hamilton (1967). These results are in agreement with the more general
260 qualitative predictions of LMC theory (Frank 1985) and are here rendered in explicit
261 quantitative form for the first time, enabling direct comparison with empirical data.

262   Our predictions are in line with the experimental data of Abdi et al. (2020) who varied
263 foundress number and relatedness in *Goniozus nephantidis*. Sex ratios of *G. nephantidis* appear
264 to be more affected by co-foundress relatedness than those of other studied insects and mites:
265 Shuker et al. (2004) report a meta-analysis across 7 studies, with all effect sizes, r, being <0.3
266 while, from logistic ANOVA statistics given in Abdi et al. (2020), for *G. nephantidis* $r = 0.438$.
267 This is most likely associated with the ability of adult *Goniozus* females to discriminate kinship
268 (Lizé et al. 2012; Abdi et al. 2020) which appears lacking in some studied parasitoids (Shuker
269 et al. 2004).

270   While the development of theory we present has been stimulated by the observed sex ratios
271 of *G. nephantidis* and its predictions match the fitted regressions quite closely, there are several
272 differences between the assumptions of the model and the life-history of *Goniozus* that can
273 affect sex ratio. First, the model assumes that local mating groups are sizable, with each
274 foundress contributing a large number, N, of offspring. *Goniozus* brood sizes more typically
275 take small integer values which constrains the values of possible brood sex ratios: for the single

276 foundress case the optimal sex ratio is $1/N$ if daughters are to be able to mate locally (Green et
277 al. 1982) and this especially likely accounts for disparities at $n=1$ in Figure 2.

278   Second, the model implicitly assumes that the sexual composition of offspring groups is the
279 same at the time of sex allocation and the time at offspring mating. *Goniozus* broods normally
280 experience some developmental mortality that can alter the sexual composition of broods: this
281 can both select for less biased primary sex ratios than would be predicted in the absence of
282 mortality and also can obscure patterns of sex allocation (Green et al. 1982; Khidr et al. 2013).
283 In the experiment reported by Abdi et al. (2020) offspring mortality was unusually high due to
284 the sustained confinement of multiple-foundresses and it remains possible that the brood sex
285 ratios observed do not accurately reflect sex allocation decisions made by foundresses.

286   Third, the model assumes strictly local mating with males dying and only mated females
287 dispersing. In *Goniozus* males are winged and are observed, in laboratory trials, to disperse
288 from natal broods (Hardy et al. 1999); if non-local mating occurs in nature this would select
289 for less female biased sex ratios than are predicted by models assuming strict LMC (Nunney
290 & Luck 1988, West 2009). This effect is likely masked in Figure 2 on account of the degree of
291 inbredness (f) being treated as a free parameter whose value may be adjusted to improve the
292 goodness of fit, with the best fit obtained when females are considered to be completely outbred
293 ($f = 0$). The life-history of *Goniozus* suggests that some degree of inbredness ($f > 0$) is expected,
294 which would select for a more female biased sex ratio, and therefore compensate for the
295 discrepancy between prediction and observation in the opposite direction arising as a
296 consequence of partial LMC. A more direct estimate of inbredness using molecular markers
297 would be a useful goal for future investigation of the *Goniozus* mating system. Relatedly, the
298 model assumes almost complete dispersal of females following mating, and hence negligible
299 competition among related females for reproductive resources. Incorporating limited dispersal
300 of females would be expected to reduce the extent of female bias in sex allocation for both
301 sister and non-sister groups (*cf.* Bulmer 1986, Frank 1986b, Taylor 1988).

302   A further assumption of the present theoretical model is that females are able to recognise
303 each other as sisters versus non-sisters *per se*, although the model is agnostic as to whether this
304 involves environmental or genetic kin recognition (Grafen 1990). A possibility is that females
305 are able to recognise co-foundresses who eclosed from the same host, without being able to
306 discriminate between those that are actually sisters versus non-sisters (including both more
307 distantly-related kin and non-kin co-foundresses), or that both types of recognition may be used
308 (Lizé et al., 2012, have shown that kin discrimination in one species of *Goniozus* utilizes
309 genetically-based and familiarity-based mechanisms). Discrimination based only on familiarity
310 was considered by Taylor and Crespi (1994) in an analysis of how females are expected to
311 adjust their sex allocation in response to their own dispersal status and that of their co-
312 foundresses; this instantiated Frank's (1985) qualitative prediction that closer kinship should
313 result in a more female-biased sex ratio, though without allowing for the possibility of
314 foundress number variation within populations. On account of familiar females being, on
315 average, less related than confirmed sisters, we would expect adjustment of sex ratios in
316 response to familiarity *per se* to lead to less female bias than is predicted by the present model.

317   Finally, a limitation of the present analysis is that it has, following the experimental design
318 of Abdi et al. (2020), focused on the comparison between sister versus non-sister foundress
319 groups and has not explored sex allocation behaviour within groups containing mixtures of
320 sisters and non-sisters (possible for $n>2$). Mixed groups present a particular mathematical
321 challenge in that they allow for (though do not in all cases necessitate) individuals within a
322 group finding themselves in different circumstances and hence being favoured to exhibit
323 different sex allocation behaviours. When each female's strategy is conditional upon not only

324
325
326
327
328
329
330

her own circumstances but also the circumstances of her co-foundresses, strategies are required to be solved simultaneously rather than individually. A similar complexity would arise in the presence of partial LMC, whereby the mating success of eclosing males depends upon sex allocation strategies employed globally as well as locally. Such scenarios provide an interesting avenue for future theoretical attention.

Box 1 | Inclusive fitness derivation

General

The focal female produces $N_d = N(1 - z - \delta)$ daughters and $N_s = N(z + \delta)$ sons, and the $n - 1$ other females in her foundress group collectively produce $N_f = (n\text{-}1)N(1 - z)$ daughters and $N_m = (n\text{-}1)Nz$ sons. Accordingly, the total inclusive-fitness (Hamilton 1964) value the focal female places upon the mating group is

$$H = N_d p_d v_f + N_f p_f v_f + (N_d + N_f) \frac{N_s}{N_s + N_m} p_s v_m + (N_d + N_f) \frac{N_m}{N_s + N_m} p_m v_m \qquad \text{(B1.1)}$$

where p_d is her consanguinity (i.e. probability of identity by descent; Bulmer 1994) to her daughters, p_s is her consanguinity to her sons, p_f is her consanguinity to the daughters of her co-foundresses, p_m is her consanguinity to the sons of her co-foundresses, v_f is the reproductive value (Fisher 1930, Hamilton 1972, Bulmer 1994) of a mated female's eggs and v_m is the reproductive value of the sperm that fertilise a mated female's eggs. The inclusive-fitness effect of a small deviation δ in the focal female's sex allocation strategy is $\Delta H = (\partial H / \partial \delta |_{\delta=0}) \delta$ and, accordingly, the unbeatable sex allocation strategy (Hamilton 1967) satisfies $\Delta H |_{z=z^*} = 0$, which yields

$$z^* = \frac{(n-1)(p_s - p_m)v_m}{n(p_d v_f + p_s v_m)} . \qquad \text{(B1.2)}$$

The right hand side of equation (B1.2) is equivalent to the expression $\frac{1}{2} R P_{d(a)t}$ derived by Frank (1985; see also Hamilton 1979, Frank 1986a), using a different, lengthier and less-accessible approach, where the ½ term captures the rarer-sex effect, the $R = (2 p_s v_m)/(p_d v_f + p_s v_m)$ term is a coefficient of inheritance asymmetry between the sexes and the $P_{d(a)t} = ((n\text{-}1)/n)(p_s - p_m)/p_s$ term is an index of panmixia as assessed by the focal female conditional upon the information she has available to her – potentially including number and relatedness of co-foundresses. Note that, as p_m is the only determinant of z^* that is affected if a female conditions her sex allocation upon whether her co-foundresses are or are not her sisters, and since z^* is linear in p_m, it is evident that kin discrimination is not expected to affect the overall sex ratio of the population compared with a scenario in which females cannot discriminate kin (*cf.* Faria & Gardner 2020). Nor would any ability to detect variation in genetic relatedness among sisters affect the average sex allocation employed in response to sister co-foundresses (*cf.* Faria & Gardner 2020). Moreover, as n is the only determinant of z^* that is affected if a female conditions her sex allocation upon the number of her co-foundresses, and since z^* is a concave function of n, it is evident that kin discrimination is expected to reduce the overall sex ratio of the population compared with a scenario in which females cannot adjust their sex allocation in response to co-foundress number (*cf.* Faria & Gardner 2020).

Diplo-diploidy

Under diplo-diploidy, $p_d = p_s = (1 + 3f)/4$, where f is the consanguinity of the focal female's parents and hence describes her "inbredness" (Frank 1985, 1986a), and $v_f = v_m$ (Fisher 1930, Bulmer 1994). Accordingly, if the focal female is unrelated to her co-foundresses, such that $p_m = 0$, then her unbeatable sex allocation strategy is given by equation (1) of the main text.

If instead the focal female's co-foundresses are her sisters, then $p_m = (1+7f)/8$ and her unbeatable sex allocation strategy is given by equation (2) of the main text. Note that this equation depends on the focal female's inbredness, which depends on the frequency of sib-matings (and hence the size of foundress groups) among her ancestors. If the number of foundresses is n in all foundress groups, not just in the focal female's foundress group, then inbredness may be expressed as $f = 1/(4n-3)$, such that the unbeatable sex allocation strategy is $z_{D,S}{}^* = (n-1)^2/(4n^2)$. If the number of foundresses is variable, then $f = 1/(4v-3)$ and $z_{D,S}{}^* = ((n-1)(v-1))/(4nv)$, where v is the harmonic mean foundress number (specifically, taken across all females, it is the harmonic mean of the number of foundresses in their mothers' foundress groups; *cf.* Frank 1985).

Haplo-diploidy

Under haplo-diploidy, $p_d = (1 + 3f)/4$, $p_s = (1 + f)/2$ and $v_f = 2v_m$ (Hamilton 1972, Bulmer 1994). Accordingly, if the focal female is unrelated to her co-foundresses, such that $p_m = 0$, then her unbeatable sex allocation strategy is given by equation (3) of the main text. If the number of foundresses contributing to different mating groups is constant, then $f = 1/(4n-3)$ and $z_{H,U}{}^* = ((n-1)(2n-1))/(n(4n-1))$. If the number of foundresses is variable, then $f = 1/(4v-3)$ and $z_{H,U}{}^* = ((n-1)(2v-1))/(n(4v-1))$.

Finally, if the focal female's co-foundresses are her sisters, then $p_m = (3+5f)/8$ and her unbeatable sex allocation strategy is given by equation (4) of the main text. If the number of foundresses contributing to different mating groups is constant, then $f = 1/(4n-3)$ and $z_{H,S}{}^* = (n-1)^2/(2n(4n-1))$, and if the number of foundresses is variable, then $f = 1/(4v-3)$ and $z_{H,U}{}^* = ((n-1)(v-1))/(2n(4v-1))$.

References

Abdi, M. K., Lupi, D. & Hardy, I. C. W. 2020. Co-foundress confinement elicits kinship effects in a naturally sub-social parasitoid. Journal of Evolutionary Biology, 33: 1068-1085.

Bulmer, M. G. 1986. Sex ratio theory in geographically structured populations. Heredity, 56: 69–73.

Bulmer, M. G. 1994. Theoretical evolutionary ecology. Sinauer Associates, Sunderland, MA.

Courteau, J. & Lessard, S. 2000. Optimal sex ratios in structured populations. Journal of Theoretical Biology, 207: 159-175.

Faria, G. S. & Gardner, A. 2020. Does kin discrimination promote cooperation? Biology Letters, 16: 20190742.

Fisher, R.A. 1930. The genetical theory of natural selection. Clarendon Press, Oxford.

344 Frank, S. A. 1985. Hierarchical selection theory and sex ratios. II. On applying the theory, and a test
345   with fig wasps. Evolution 39: 949-964.

346 Frank, S. A. 1986a. Hierarchical selection theory and sex ratios. I. General solutions for structured
347   populations. Theoretical Population Biology 29: 312-342.

348 Frank, S. A. 1986b. The genetic value of sons and daughters. Heredity 56: 351-354.

349 Frank, S. A. 1998. Foundations of social evolution. Princeton University Press, Princeton.

350 Gardner, A., Arce, A. & Alpedrinha, J. 2009. Budding dispersal and the sex ratio. Journal of
351   Evolutionary Biology 22: 1036-1045.

352 Grafen, A. 1990. Do animals really recognize kin? Animal Behaviour 39: 42-54.

353 Green, R. F., Gordh, G., Hawkins, B. A. 1982. Precise sex ratios in highly inbred parasitic wasps. The
354   American Naturalist 120: 653–665.

355 Hamilton, W. D. 1964. The genetical evolution of social behaviour I & II. Journal of Theoretical
356   Biology 7:1–52.

357 Hamilton, W. D. 1967. Extraordinary sex ratios. Science 156: 477-488.

358 Hamilton, W. D. 1972. Altruism and related phenomena, mainly in social insects. Annual Review of
359   Ecology, Evolution, and Systematics 3: 193–232.

360 Hamilton, W. D. 1979. Wingless and fighting males in fig wasps and other insects. In: Sexual selection
361   and reproductive competition in insects (Blum, M. S. & Blum, N.A. (eds.). pp. 167–220. Academic
362   Press, London.

363 Hardy, I. C. W. & Cook, J. M. 1995. Brood sex-ratio variance, developmental mortality and virginity
364   in a gregarious parasitoid wasp. Oecologia 103: 162-169.

365 Hardy, I. C. W., Pedersen, J. B., Sejr, M. K. & Linderoth, U. H. 1999. Local mating, dispersal and sex
366   ratio in a gregarious parasitoid wasp. Ethology 105: 57-72.

367 Khidr, S. K., Mayes, S. & Hardy, I. C. W. 2013. Primary and secondary sex ratios in a gregarious
368   parasitoid with local mate competition. Behavioral Ecology 24: 435-443.

369 Lizé, A., Khidr, S. K. & Hardy, I. C. W. 2012. Two components of kin recognition influence parasitoid
370   aggression in resource competition. Animal Behaviour 83: 793-799.

371 Nunney, L. & Luck, R. F. 1988. Factors influencing the optimal sex ratio in structured populations.
372   Theoretical Population Biology 33: 1-30.

373 Rodrigues, A. M. M. & Gardner, A. 2015. Simultaneous failure of two sex-allocation invariants:
374   implications for sex-ratio variation within and between populations. Proceedings of the Royal
375   Society of London Series B — Biological Sciences 282: 20150570.

376 Shuker, D. M., Reece, S. E., Taylor, J. A. L. & West, S. A. 2004. Wasp sex ratios when females on a
377   patch are related. Animal Behaviour 68: 331-336.

378 Taylor, P. D. & Crespi, B. J. 1994. Evolutionarily stable strategy sex ratios when correlates of
379   relatedness can be assessed. The American Naturalist 143: 297-316.

380 Taylor, P.D. 1988. Inclusive fitness models with two sexes. Theoretical Population Biology 34: 145-
381   168.

382 West, S. A. & Herre, E. A. 2002. Using sex ratios: why bother? In: Sex ratios: concepts and research
383   methods, (Hardy, I. C. W., ed.). pp. 399-413. Cambridge University Press, Cambridge, UK.

384 West, S. A. 2009. Sex allocation. Princeton University Press, Princeton.

385 Wright, S. 1969. Evolution and the genetics of populations, Vol. 2, University of Chicago Press,
386   Chicago, IL.