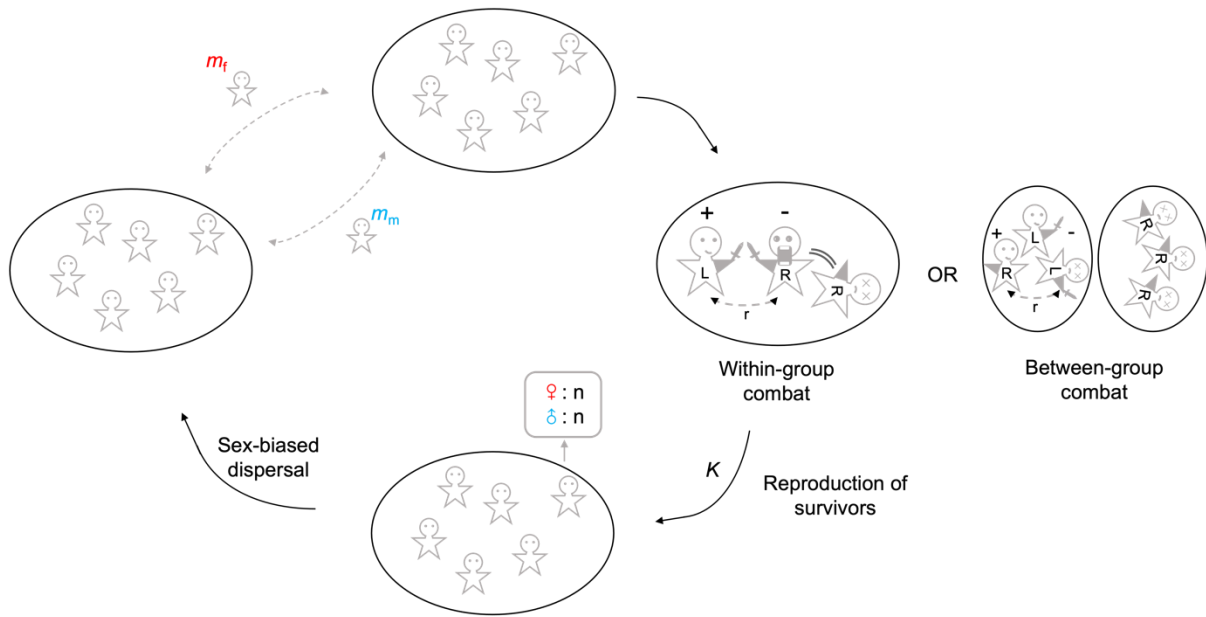


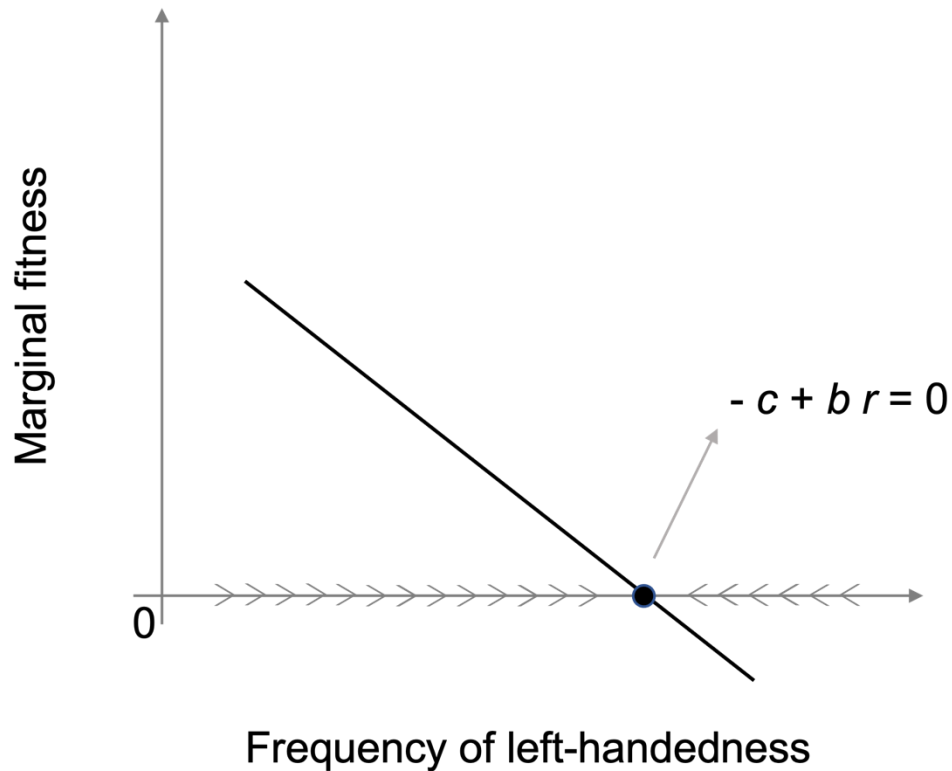
26	1.1 Population model
27	1.2 Fitness
28	1.3 Kin selection
29	1.4 Sex-biased dispersal
30	1.5 Parent-of-origin effects
31	1.6 Sex-specific effects
32	1.7 Parental genetic effects
33	2 Between-group Combat
34	2.1 Kin selection
35	2.2 Sex-biased dispersal
36	2.3 Parent-of-origin effects
37	2.4 Sex-specific effects
38	2.5 Parental genetic effects
39	
40	References



41

42 **Figure S1 | Model life cycle, details see §S1.1.**

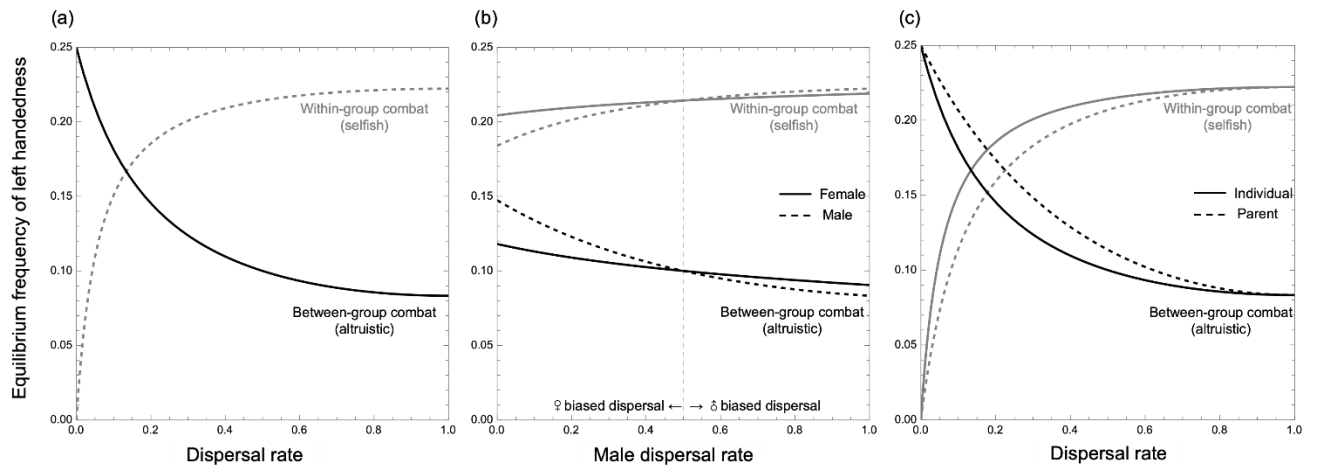
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44

45 **Figure S2 | Evolutionary equilibrium. The dark dot depicts the convergence stable value**
 46 **of the level of left-handedness, at which marginal fitness ($-c + br$, solid line) is zero. If**
 47 **the frequency of left-handedness increases above this equilibrium point (right side of**
 48 **the dot), marginal fitness becomes negative ($-c + br < 0$), such that selection acts to push**
 49 **it back towards the equilibrium. If the frequency of left-handedness decreases below the**
 50 **equilibrium point (left side of the dot), marginal fitness becomes positive ($-c + br > 0$),**
 51 **such that selection acts to push it back towards the equilibrium. (c denotes cost of left-**
 52 **handedness, b denotes benefit of left-handedness to social partners, and r denotes**
 53 **relatedness between social partners.)**

54



55

56 **Figure S3 | Incidence of left-handedness can be mediated by demographic features such**

57 **as dispersal, as higher dispersal reduces relatedness between social partners, and**

58 **relatedness modulates the convergence stable incidence of left-handedness. (a) Higher**

59 **dispersal is associated with lower relatedness and hence (i) higher incidence of left-**

60 **handedness in a within-group combat scenario in which left-handedness is marginally**

61 **selfish, and (ii) lower incidence of left-handedness in a between-group combat scenario**

62 **in which left-handedness is marginally altruistic. (b) Sex differences in left-handedness:**

63 **incidence of left-handedness can be mediated by sex and dispersal pattern (female/male**

64 **biased dispersal). (c) Parental genetic effects in left-handedness: incidence of left-**

65 **handedness can be mediated by dispersal, and further result in parent-offspring**

66 **disagreement on handedness. Here, we set female dispersal rate $m_f = 0.5$, the relative**

67 **importance of combat in relation to other types of competitions for females and males b_f**

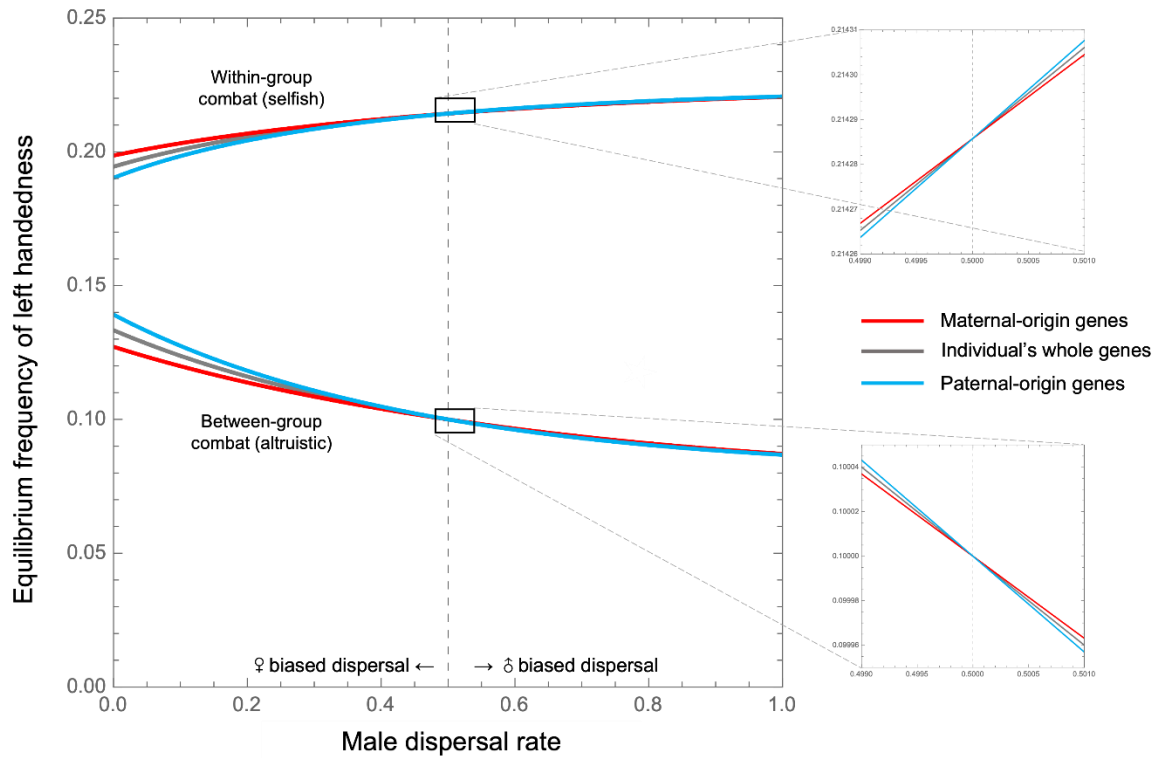
68 **$= b_m = 1$, the costs associated with left-handedness for females and males $c_f = c_m = 1$, and**

69 **the number of individuals each sex born in the same patch $n = 5$ (these parameter**

70 **values chosen are simply for illustration, details see §S1.3).**

71

72



73

74 **Figure S4 | Parent-of-origin effects in left-handedness: incidence of left-handedness can**

75 **be mediated by gene origin (maternal-origin versus paternal-origin) effects and**

76 **dispersal pattern (female/male biased dispersal) in the context of within-group combat**

77 **(left-handedness is selfish) versus between-group combat (left-handedness is altruistic).**

78 **Here, we set female dispersal rate $m_f = 0.5$, the relative importance of combat in relation**

79 **to other types of competitions for females and males $b_f = b_m = 1$, the costs associated**

80 **with left-handedness for females and males $c_f = c_m = 1$, and the number of individuals**

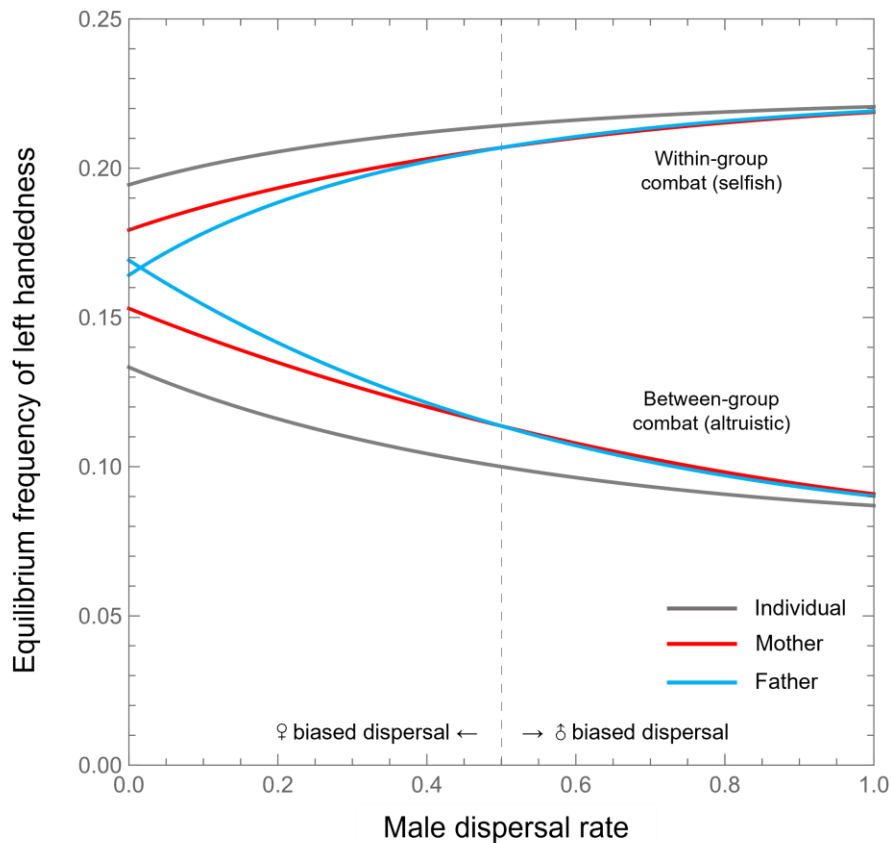
81 **each sex born in the same patch $n = 5$ (these parameter values chosen are simply for**

82 **illustration, details see §S1.3).**

83

84

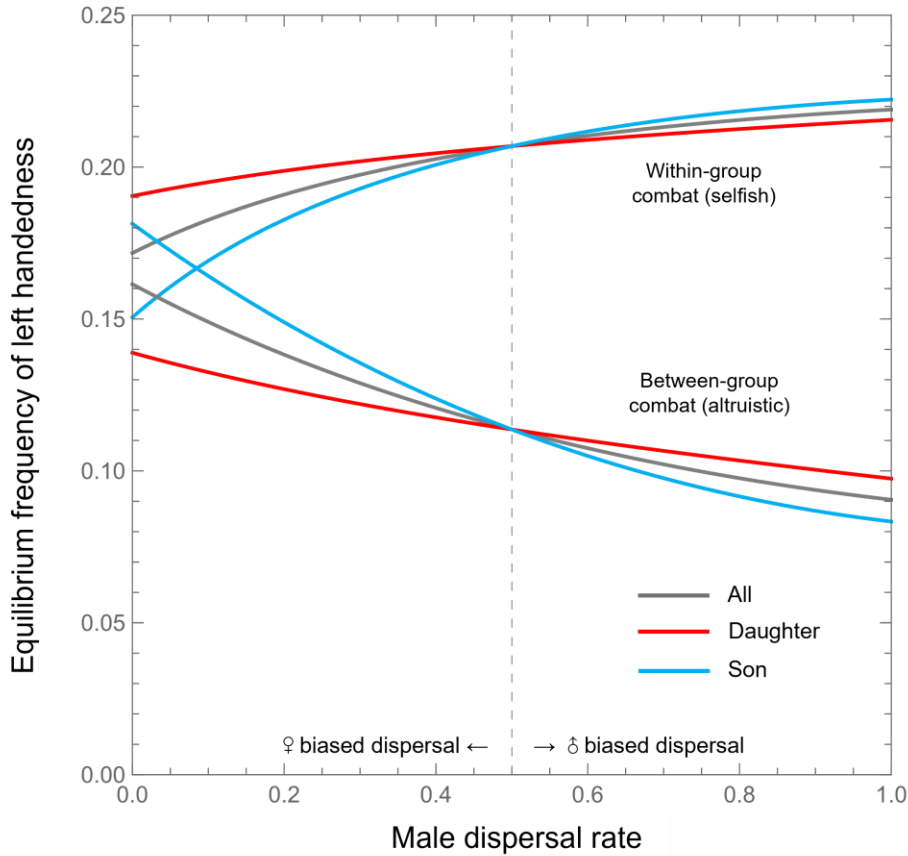
85



87

88 **Figure S5 | Maternal versus paternal genetic effects in left-handedness: incidence of left-**
 89 **handedness can be mediated by dispersal pattern (female/male biased), and further**
 90 **result in mother-father-offspring disagreement on handedness in the context of within-**
 91 **group combat (left-handedness is selfish) versus between-group combat (left-**
 92 **handedness is altruistic). Here, we set female dispersal rate $m_f = 0.5$, the relative**
 93 **importance of combat in relation to other types of competitions for females and males b_f**
 94 **$= b_m = 1$, the costs associated with left-handedness for females and males $c_f = c_m = 1$, and**
 95 **the number of individuals each sex born in the same patch $n = 5$ (these parameter**
 96 **values chosen are simply for illustration, details see §S1.3). Details see §§S1.7 and S2.5.**

97



98

99 **Figure S6 | Parental genetic effects on different offspring in left-handedness: incidence**

100 **of left-handedness can be mediated by dispersal pattern (female/male biased) in the**

101 **context of within-group combat (left-handedness is selfish) versus between-group**

102 **combat (left-handedness is altruistic). (Solid: all offspring, Dotted: daughters, Dashed:**

103 **sons.) Here, we set female dispersal rate $m_f = 0.5$, the relative importance of combat in**

104 **relation to other types of competitions for females and males $b_f = b_m = 1$, the costs**

105 **associated with left-handedness for females and males $c_f = c_m = 1$, and the number of**

106 **individuals each sex born in the same patch $n = 5$ (these parameter values chosen are**

107 **simply for illustration, details see §S1.3).**

108

109

		Female-biased dispersal		Male-biased dispersal	
		Left-handedness promoter	Left-handedness inhibitor	Left-handedness promoter	Left-handedness inhibitor
Prediction from kinship theory		M P Normal	M P Normal	M P Normal	M P Normal
Gene deletion	Maternal	M P Less left-handed	M P Normal	M P Normal	M P More left-handed
	Paternal	M P Normal	M P More left-handed	M P Less left-handed	M P Normal
Gene duplication	Maternal	M P More left-handed	M P Normal	M P Normal	M P Less left-handed
	Paternal	M P Normal	M P Less left-handed	M P More left-handed	M P Normal
Epimutation	Hypo-methylation	M P More left-handed	M P Less left-handed	M P More left-handed	M P Less left-handed
	Hyper-methylation	M P Less left-handed	M P More left-handed	M P Less left-handed	M P More left-handed
Uniparental disomy	Maternal	M P More left-handed	M P More left-handed	M P Less left-handed	M P Less left-handed
	Paternal	P M Less left-handed	P M Less left-handed	P M More left-handed	P M More left-handed
Crosses					

110

111 **Figure S7 | Phenotypic consequences on handedness of gene deletions, gene duplications, epimutations and uniparental disomies. (This expands upon**112 **Figure 3 of the main text.)**

113 **1 | Within-group combat**

114 **1.1 | Population model**

115 We develop a very simple population model purely for the purpose of illustration. We assume
116 a large population, separated into N patches (where N is large) each containing n women and
117 n men (where n may be small). Adults may engage in same-sex combat, and we model the
118 fitness consequences of this combat by modulating the survival of their offspring to
119 adulthood, which is mathematically equivalent to modulating the combatants' fecundity
120 (Taylor & Frank 1996). Specifically: we assign each female a large number K of offspring
121 fathered by each male in the patch, with an even sex ratio; all parents then die; and offspring
122 undergo random mortality, with each offspring's probability of survival depending on the
123 handedness of their parents and of their parents' social partners, reflecting their parents'
124 success in combat—including a surprise advantage to individuals with the rarer handedness
125 type—and also any intrinsic disadvantage of left-handers over right-handers (Figure S1).
126 Survivors then form subgroups of n woman and n men at random with their patch mates, and
127 N subgroups are chosen at random across the whole population with each being assigned a
128 patch in which to live, and all other subgroups perishing—i.e. a “tribe splitting” (Haldane
129 1932) or “group budding” (Gardner & West 2006) model of population structure. Finally,
130 with probability m_f for women and probability m_m for men, individuals may disperse away
131 from their assigned patch to take up a random spot in another patch vacated by another same-
132 sex disperser, such that these parameters modulate the relatedness structure of groups without
133 affecting fitness (Gardner & West 2006).

134

135 **1.2 | Fitness**

136 We assume that an individual's payoff from combat is proportional to their competitive
137 ability relative to that of their same-sex social interactants. We assume that each individual's

138 competitive ability is proportional to the average disposition for the opposite handedness
139 within their social arena, such that the individual's competitive ability is greatest when their
140 own handedness is the opposite of all of their opponents—representing the surprise advantage
141 of the minority handedness type. For simplicity, we will often refer to handedness as if it
142 were a binary trait, so that an individual's disposition for left-handedness is the probability
143 that they will develop as left-handed, but more generally our analysis also applies to
144 scenarios in which individuals exhibit quantitative degrees of left- versus right-handedness.
145 That is: with probability x the focal individual is left-handed and has competitive ability $1-y$,
146 where y is the average disposition for left-handedness in the social arena; and with probability
147 $1-x$ the focal individual is right-handed and has competitive ability y . And the social arena is
148 made up of a proportion y of left-handed individuals with competitive ability $1-y$ and a
149 proportion $1-y$ of right-handed individuals with competitive ability y . Accordingly, the focal
150 individual's relative competitive ability is

$$x \frac{(1-y)}{y(1-y) + (1-y)y} + (1-x) \frac{y}{y(1-y) + (1-y)y} \quad (S1)$$

151 which simplifies to

$$\frac{x}{2y} + \frac{1-x}{2(1-y)} \quad (S2)$$

152 Hence, we may express the fitness of a focal juvenile by

$$w = \left(1 - b_f + b_f \left(\frac{x_{M_o}}{2y_{M_o}} + \frac{1-x_{M_o}}{2(1-y_{M_o})} \right) \right) (1 - c_f x_{M_o}) \left(1 - b_m \right. \\ \left. + b_m \left(\frac{x_{F_a}}{2y_{F_a}} + \frac{1-x_{F_a}}{2(1-y_{F_a})} \right) \right) (1 - c_m x_{F_a}) \quad (S3)$$

153 where x_{M_o} is the probability of the juvenile's mother developing as left-handed, x_{F_a} is the
154 probability of the juvenile's father developing as left-handed, y_{M_o} is the probability of a
155 random adult female from the juvenile's mother's group developing as left-handed, y_{F_a} is the
156 probability of a random adult male from the focal juvenile's father's group developing as left-

157 handed, b_f is the relative importance of combat compared with other types of competition for
 158 females, b_m is the relative importance of combat for males, c_f is the intrinsic cost of
 159 developing as left-handed for females and c_m is the intrinsic cost of developing as left-handed
 160 for males. Average fitness \bar{w} is found by substituting $x_{M0} = y_{M0} = z_f$, and $x_{Fa} = y_{Fa} = z_m$ in
 161 expression (S3) where z_f is the population average value of left-handedness for females, and
 162 z_m is the population average value of left-handedness for males. Accordingly, the relative
 163 fitness of the focal juvenile is given by $W = w/\bar{w}$ or

$$\begin{aligned}
 W = & \left(1 - b_f + b_f \left(\frac{x_{M0}}{2y_{M0}} + \frac{1 - x_{M0}}{2(1 - y_{M0})} \right) \right) \left(\frac{1 - c_f x_{M0}}{1 - c_f z_f} \right) \left(1 - b_m \right. \\
 & \left. + b_m \left(\frac{x_{Fa}}{2y_{Fa}} + \frac{1 - x_{Fa}}{2(1 - y_{Fa})} \right) \right) \left(\frac{1 - c_m x_{Fa}}{1 - c_m z_m} \right)
 \end{aligned}
 \tag{S4}$$

164

165 **1.3 | Kin selection**

166 *1.31 | Marginal fitness and evolutionary equilibrium*

167 We assume that genes at an autosomal locus G control their carrier's probability of
 168 developing as left-handed (see §S1.7 for the consequences of relaxing this assumption), that
 169 the two genes in this diploid locus have equal control over the individual's phenotype (see
 170 §S1.5 for the consequences of relaxing this assumption), and that genes are expressed in the
 171 same way by female and male carriers (see §S1.6 for the consequences of relaxing this
 172 assumption). We denote the genic value for left-handedness of a gene drawn from locus G
 173 from a focal juvenile by g . We further denote the additive genetic breeding value—i.e. the
 174 average of the corresponding genic values—for left-handedness of the focal juvenile's parent
 175 by \tilde{g} , the average breeding value of all the adults in the focal juvenile's parents' group by \tilde{g}' ,
 176 and the average breeding value of the population by \bar{g} . Employing Taylor-Frank kin-selection
 177 methodology (Taylor & Frank 1996), the condition for natural selection—the sum of direct

178 selection and indirect (i.e. kin) selection—to favour an increase in left-handedness is given by
 179 $dW/dg > 0$, where

$$\begin{aligned} \frac{dW}{dg} &= \frac{\partial W}{\partial x_{M_0}} \frac{dx_{M_0}}{d\tilde{g}} \frac{d\tilde{g}}{dg} + \frac{\partial W}{\partial y_{M_0}} \frac{dy_{M_0}}{d\tilde{g}'} \frac{d\tilde{g}'}{dg} + \frac{\partial W}{\partial x_{Fa}} \frac{dx_{Fa}}{d\tilde{g}} \frac{d\tilde{g}}{dg} + \frac{\partial W}{\partial y_{Fa}} \frac{dy_{Fa}}{d\tilde{g}'} \frac{d\tilde{g}'}{dg} \\ &= \left(\frac{\partial W}{\partial x_{M_0}} p_{OM} + \frac{\partial W}{\partial y_{M_0}} p_{JA} + \frac{\partial W}{\partial x_{Fa}} p_{OF} + \frac{\partial W}{\partial y_{Fa}} p_{JU} \right) \gamma \end{aligned} \quad (S5)$$

180 where p_{OM} is the consanguinity (i.e. probability of identity by descent; Bulmer 1994) between
 181 the focal juvenile and its mother, p_{JA} is the consanguinity between the focal juvenile and a
 182 random adult female in its parent group, p_{OF} is the consanguinity between the focal juvenile
 183 and its father, p_{JU} is the consanguinity between the focal juvenile and a random adult male in
 184 its parent group, $\gamma = dx_{M_0}/d\tilde{g} = dy_{M_0}/d\tilde{g}' = dx_{Fa}/d\tilde{g} = dy_{Fa}/d\tilde{g}'$ is the mapping
 185 between genotype and phenotype, and all the derivatives are evaluated at the population
 186 average $g = \bar{g}$. Accordingly, the condition for an increase in left-handedness to be favoured
 187 is:

$$\frac{\partial W}{\partial x_{M_0}} p_{OM} + \frac{\partial W}{\partial y_{M_0}} p_{JA} + \frac{\partial W}{\partial x_{Fa}} p_{OF} + \frac{\partial W}{\partial y_{Fa}} p_{JU} > 0 \quad (S6)$$

188 Here for the investigation on how kin selection mediates handedness generally, we assume
 189 there is no sex-biased dispersal ($m_f = m_m = m$), thus $p_O = p_{OM} = p_{OF}$, $p_J = p_{JA} = p_{JU}$, while this
 190 assumption will be relaxed in later sections (§S1.4 Sex-biased dispersal, §S1.5 Parent-of-
 191 origin effect, §S1.6 Sex-specific effects and §S1.7 Parental genetic effects). Using expression
 192 (S4) to calculate the corresponding partial derivatives, the condition for natural selection to
 193 favour an increase in left-handedness is

$$-\frac{(b_f + b_m)(1 - 2z)(r_J - r_O)}{2(1 - z)z} - \frac{c_f r_O}{1 - c_f z} - \frac{c_m r_O}{1 - c_m z} > 0 \quad (S7)$$

194 where $r_O = p_O/p_I$ is the relatedness between an individual and its offspring, $r_J = p_J/p_I$ is the
 195 relatedness of an individual to a random adult in its parent's group, $r_I = p_I/p_I$ is the relatedness
 196 of an individual to itself, and p_I is the consanguinity of a focal individual to itself. Letting

197 $f(z)$ be the LHS of expression (S7), then at evolutionary equilibrium (Figure S2) if there is
 198 an intermediate level of left-handedness z^* , this satisfies $f(z^*) = 0$. For example, setting $c_f =$
 199 $c_m = 1$, we have

$$z^* = \frac{1}{2} \frac{(b_f + b_m)(r_j - r_o)}{(b_f + b_m)r_j - (2 + b_f + b_m)r_o} \quad (\text{S8})$$

200

201 1.32 / Relatedness

202 The consanguinity between a juvenile and its parent p_o is given by

$$p_o = \frac{1}{2}p_I + \frac{1}{2}f \quad (\text{S9})$$

203 That is: with probability 1/2 the gene picked from the juvenile comes from that parent, in
 204 which case the consanguinity is that between the parent and itself, i.e. p_I ; and with probability
 205 1/2 the gene comes from the other parent, in which case the consanguinity is that of mating
 206 partners, f . The consanguinity between the focal juvenile and a random adult in its parents'
 207 social group p_J is:

$$p_J = \frac{1}{2} \left(\frac{1}{n}p_I + \frac{n-1}{n}(1-m)^2p_x \right) + \frac{1}{2}f \quad (\text{S10})$$

208 That is: with the probability 1/2 the juvenile's gene comes from the parent of the same sex as
 209 the adult, in which case with probability 1/n the adult is the parent and the consanguinity is
 210 p_I , and with probability $(n-1)/n$ the adult is not the parent then if neither of them disperses, i.e.
 211 $(1-m)^2$, their consanguinity would be that between two random juveniles born in the same
 212 patch, p_x , and with probability 1/2 the juvenile's gene comes from the parent of the opposite
 213 sex, in which case the consanguinity is that of mating partners, i.e. f . The consanguinity
 214 between an individual and itself, p_I , is given by

$$p_I = \frac{1}{2} + \frac{1}{2}f \quad (\text{S11})$$

215 That is: with probability $1/2$ we pick the individual's same gene twice, in which case the
 216 consanguinity is p_I , and with probability $1/2$ we pick one gene at the first time and pick the
 217 other at the second time, in which case the consanguinity is that of mating partners, i.e. f , and
 218 f is given by

$$f = (1 - m)^2 p_x \quad (\text{S12})$$

219 That is: with probability $(1 - m)^2$ neither mating partner disperses, in which case the
 220 consanguinity is that between two random juveniles born in the same patch p_x , and p_x is given
 221 by

$$p_x = \frac{1}{4} \left(\frac{1}{n} p_I + \frac{n-1}{n} (1 - m)^2 p_x \right) + \frac{1}{4} \left(\frac{1}{n} p_I + \frac{n-1}{n} (1 - m)^2 p_x \right) + \frac{1}{2} f \quad (\text{S13})$$

222 That is: with probability $1/4$ one juvenile's gene comes from her mother and the other
 223 juvenile's gene also comes from her mother, in which case the consanguinity is that between
 224 the two mothers, which is with probability $1/n$ the two individuals share one mother, and the
 225 consanguinity is that between the mother and herself, i.e. p_I , and with probability $(n - 1)/n$
 226 the two individuals do not share one mother, and if neither of the mothers disperses i.e.
 227 $(1 - m)^2$, and the consanguinity is that between two random juveniles born in the same
 228 patch, i.e. p_x , and with probability $1/4$ one juvenile's gene comes from her father and the
 229 other juvenile's gene also comes from her father, in which case the consanguinity is the same
 230 polynomials with the situation that the genes we pick both come from the juveniles' mothers,
 231 and with probability $1/2$ one juvenile's gene comes from her mother and the other juvenile's
 232 gene comes from her father, in which case the consanguinity is that of mating partners, i.e. f .
 233 Solving expressions (S9)-(S13) simultaneously, we obtain

$$f = \frac{(1 - m)^2}{1 + (1 - (1 - m)^2)(4n - 1)} \quad (\text{S14})$$

$$p_x = \frac{1}{1 + (1 - (1 - m)^2)(4n - 1)} \quad (\text{S15})$$

$$p_1 = \frac{1 + (1 - (1 - m)^2)(2n - 1)}{1 + (1 - (1 - m)^2)(4n - 1)} \quad (\text{S16})$$

$$p_j = \frac{1}{1 + (1 - (1 - m)^2)(4n - 1)} \quad (\text{S17})$$

$$p_0 = \frac{1 + (1 - (1 - m)^2)(n - 1)}{1 + (1 - (1 - m)^2)(4n - 1)} \quad (\text{S18})$$

234

235 *1.33 | Convergence stable strategy*

236 As $f'(z) < 0$ is true for all the values of z , the equilibrium value of left-handedness (Figure
 237 S2) is globally convergence stable (Christiansen 1991, Taylor 1996). We will use the term
 238 “optimum” or “optimal value” to be synonymous with this convergence stable strategy.

239 Substituting all the parameters of relatedness to expression (S8), we obtain the optimum of
 240 left-handedness z^* :

$$z^* = \frac{1}{2} \frac{(b_f + b_m)(1 - (1 - m)^2)(n - 1)}{(2 + b_f + b_m)(1 - (1 - m)^2)(n - 1) + 2} \quad (\text{S19})$$

241 We set the relative importance of combat relative to all types of competition for the female
 242 and male $b_f = b_m = 1$, and the number of individuals each sex born in the same patch $n = 5$ for
 243 Figure S3a.

244

245 **1.4 | Sex-biased dispersal**

246 *1.41 | Marginal fitness and evolutionary equilibrium*

247 Here we relax the assumption of no sex bias in dispersal i.e. $m_f \neq m_m$, hence $p_{JA} \neq p_{JU}$. In this
 248 section, the relative fitness function is the same as expression (S4), while the consanguinity
 249 and the conditions that favour the increase of left-handedness would change. Using
 250 expression (S4) to calculate the corresponding partial derivatives, we obtain the condition for
 251 an increase in left-handedness to be favoured when we consider within-group combat

$$-\frac{(b_f(r_{JA} - r_O) + b_m(r_{JU} - r_O))(1 - 2z)}{2(1 - z)z} - \frac{c_f r_O}{1 - c_f z} - \frac{c_m r_O}{1 - c_m z} > 0 \quad (S20)$$

252 where $r_{JA} = p_{JA}/p_I$ is the relatedness between a juvenile and a random adult female in its
 253 mother's social group, p_{JA} is the consanguinity between a juvenile and a random adult female
 254 in its mother's social group, $r_{JU} = p_{JU}/p_I$ is the relatedness between a juvenile and a random
 255 adult male in its father's social group, p_{JU} is the consanguinity between a juvenile and a
 256 random adult male in its father's social group. Letting $f(z)$ be the LHS of expression (S20),
 257 (S7), then at evolutionary equilibrium if there is an intermediate level of left-handedness z^* ,
 258 this satisfies $f(z^*) = 0$. For example, letting $c_f = c_m = 1$ i.e. no sex difference in the cost of
 259 developing as left-handed, we obtain

$$z^* = \frac{b_f r_{JA} + b_m r_{JU} - (b_f + b_m) r_O}{2(b_f r_{JA} + b_m r_{JU} - (2 + b_f + b_m) r_O)} \quad (S21)$$

260 This is the overall optima of left-handedness for all the loci involved, as $f'(z) < 0$ is true for
 261 all the values of z .

262

263 1.42 / Relatedness

264 Substituting the dispersal rate m in p_J (S10) with female dispersal rate m_f , we obtain the
 265 consanguinity between a juvenile and a random adult female in its mother's group p_{JA}

$$p_{JA} = \frac{1}{2} \left(\frac{1}{n} p_I' + \frac{n-1}{n} (1 - m_f)^2 p_x' \right) + \frac{1}{2} f' \quad (S22)$$

266 Substituting the dispersal rate m_f in p_{JA} (S22) with male dispersal rate m_m , we obtain the
 267 consanguinity between a juvenile and a random adult male in its father's group p_{JU}

$$p_{JU} = \frac{1}{2} \left(\frac{1}{n} p_I' + \frac{n-1}{n} (1 - m_m)^2 p_x' \right) + \frac{1}{2} f' \quad (S23)$$

268 Substituting the corresponding m with m_f and m_m in p_x (S13), we obtain the consanguinity
 269 between two random juveniles born in the same patch p_x'

$$p_x' = \frac{1}{4} \left(\frac{1}{n} p_I' + \frac{n-1}{n} (1 - m_f)^2 p_x' \right) + \frac{1}{4} \left(\frac{1}{n} p_I' + \frac{n-1}{n} (1 - m_m)^2 p_x' \right) + \frac{1}{2} f' \quad (S24)$$

270 Substituting the dispersal rate m in expression (S12) with m_f and m_m , we obtain the
 271 consanguinity between mating partners f'

$$f' = (1 - m_f)(1 - m_m)p_x' \quad (\text{S25})$$

272

273 1.43 | Convergence stable strategy

274 Substituting all the parameters of relatedness with expression (S22) in expression (S21), we
 275 obtain the optimal value of left-handedness z^* :

$$z^* = ((n - 1)(\Delta b \Delta m (\bar{m} - 1) + 4\bar{b}(\bar{m} - 2)\bar{m}n)) / (-8n + 2(n - 1)(\Delta b \Delta m (\bar{m} - 1) + 4(1 + \bar{b})(\bar{m} - 2)\bar{m}n)) \quad (\text{S26})$$

276 where $\Delta m = m_f - m_m$, $\bar{m} = (m_f + m_m)/2$, $\Delta b = b_f - b_m$, $\bar{b} = (b_f + b_m)/2$.

277

278 1.5 | Parent-of-origin effects

279 1.51 | Marginal fitness and evolutionary equilibrium

280 Here we consider how the origin of genes mediates the role of kin selection in the optimum
 281 of different set of genes under the circumstances of within-group combat. We now relax the
 282 assumption that the gene's influence on the phenotype is independent of its parent of origin,
 283 and we consider sex-specific dispersal as well ($m_f \neq m_m$). In this section, the relative fitness
 284 function is the same as expression (S4), while the conditions that favour the increase of left-
 285 handedness would change. If only the maternal-origin gene at locus G affects the individual's
 286 handedness phenotype, then:

$$\frac{dW}{dg} = \frac{\partial W}{\partial x_{M0}} \frac{dx_{M0}}{d\tilde{g}_M} \frac{d\tilde{g}_M}{dg} + \frac{\partial W}{\partial y_{M0}} \frac{dy_{M0}}{d\tilde{g}'_M} \frac{d\tilde{g}'_M}{dg} + \frac{\partial W}{\partial x_{Fa}} \frac{dx_{Fa}}{d\tilde{g}_M} \frac{d\tilde{g}_M}{dg} + \frac{\partial W}{\partial y_{Fa}} \frac{dy_{Fa}}{d\tilde{g}'_M} \frac{d\tilde{g}'_M}{dg} \quad (\text{S27})$$

287 where \tilde{g}_M is the genic value of an individual's maternal-origin genes at locus G, \tilde{g}'_M is the
 288 average genic value of the individual's female social partners' maternal-origin genes at locus

289 G, $\frac{dx_{M0}}{d\tilde{g}_M} = \frac{dy_{M0}}{d\tilde{g}'_M} = \frac{dx_{Fa}}{d\tilde{g}_M} = \frac{dy_{Fa}}{d\tilde{g}'_M} = \gamma_M$ describes the mapping between maternal-origin gene

290 and phenotype, $\frac{d\tilde{g}_M}{dg} = p_{OM|M}$ is the consanguinity between a juvenile and its mother
 291 conditional on picking the mother's maternal-origin genes, $\frac{d\tilde{g}_{M'}}{dg} = p_{JA|M}$ is the consanguinity
 292 between a juvenile and a random female adult in its parent group conditional on picking the
 293 adult female's maternal-origin genes, $\frac{d\tilde{g}_M}{dg} = p_{OF|M}$ is the consanguinity between a juvenile and
 294 its father conditional on picking the father's maternal-origin genes, $\frac{d\tilde{g}_{M'}}{dg} = p_{JU|M}$ is the
 295 consanguinity between a juvenile and a random male adult in its parent group conditional on
 296 picking the adult male's maternal-origin genes. We have $p_{O|M} = p_{OM|M} = p_{OF|M}$. Thus the
 297 condition that favours the increase of the probability of being left-handed from the
 298 perspective of maternal-origin genes is:

$$\frac{\partial W}{\partial x_{Mo}} r_{OM|M} + \frac{\partial W}{\partial y_{Mo}} r_{JA|M} + \frac{\partial W}{\partial x_{Fa}} r_{OF|M} + \frac{\partial W}{\partial y_{Fa}} r_{JU|M} > 0 \quad (S28)$$

299 where $r_{OM|M} = \frac{p_{OM|M}}{p_{I'}}$, $r_{JA|M} = \frac{p_{JA|M}}{p_{I'}}$, $r_{OF|M} = \frac{p_{OF|M}}{p_{I'}}$, $r_{JU|M} = \frac{p_{JU|M}}{p_{I'}}$. Similarly, if only the
 300 paternal-origin gene at locus G affects the individual's handedness phenotype, then the
 301 condition that favours the increase of the probability of being left-handed from the
 302 perspective of paternal-origin genes is:

$$\frac{\partial W}{\partial x_{Mo}} r_{OM|P} + \frac{\partial W}{\partial y_{Mo}} r_{JA|P} + \frac{\partial W}{\partial x_{Fa}} r_{OF|P} + \frac{\partial W}{\partial y_{Fa}} r_{JU|P} > 0 \quad (S29)$$

303 where $r_{OM|P} = \frac{p_{OM|P}}{p_{I'}}$, $r_{JA|P} = \frac{p_{JA|P}}{p_{I'}}$, $r_{OF|P} = \frac{p_{OF|P}}{p_{I'}}$, $r_{JU|P} = \frac{p_{JU|P}}{p_{I'}}$, and $p_{OM|P}$ is the
 304 consanguinity between a juvenile and its mother conditional on picking the mother's paternal-
 305 origin genes, $p_{JA|P}$ is the consanguinity between a juvenile and a random adult female in its
 306 parent group conditional on picking the adult female's paternal-origin genes, $p_{OF|P}$ is the
 307 consanguinity between a juvenile and its father conditional on picking the father's paternal-
 308 origin genes, $p_{JU|P}$ is the consanguinity between a juvenile and a random adult male in its
 309 parent group conditional on picking the adult male's paternal-origin genes. We have $p_{O|P} =$

310 $p_{OM|P} = p_{OF|P}$. Letting the LHS of the expression (S28) be $f(z_M)$ and that of condition (S29)
 311 be $f(z_P)$, then at evolutionary equilibrium if there is an intermediate level of left-handedness
 312 z_M^* and z_P^* , this satisfies $f(z_M) = 0$ and $f(z_P) = 0$ respectively, and we obtain

$$z_M^* = \frac{1}{2} \frac{b_f r_{JA|-M} + b_m r_{JU|-M} - (b_f + b_m) r_{O|-M}}{b_f r_{JA|-M} + b_m r_{JU|-M} - (2 + b_f + b_m) r_{O|-M}} \quad (S30)$$

$$z_P^* = \frac{1}{2} \frac{b_f r_{JA|-P} + b_m r_{JU|-P} - (b_f + b_m) r_{O|-P}}{b_f r_{JA|-P} + b_m r_{JU|-P} - (2 + b_f + b_m) r_{O|-P}} \quad (S31)$$

313 where $r_{O|-M} = \frac{p_{O|-M}}{p_{I'}}$, $r_{O|-P} = \frac{p_{O|-P}}{p_{I'}}$ and, z_M^* and z_P^* are the optima of left-handedness from the
 314 perspective of maternal- and paternal-origin genes, as $f'(z_M) < 0$ and $f'(z_P) < 0$ are true
 315 for all the values of z .

316

317 1.52 / Relatedness

318 The consanguinity between mother and offspring from the perspective of the mother's own
 319 maternal-origin genes is

$$p_{OM|-M} = \frac{1}{2} \left(\frac{1}{2} + \frac{1}{2} f' \right) + \frac{1}{2} (1 - m_f)(1 - m_m) \left(\frac{1}{2} \left(\frac{1}{n} p_{I'} + \frac{n-1}{n} (1 - m_f)^2 p_{x'} \right) + \frac{1}{2} f' \right) \quad (S32)$$

320 That is: with probability 1/2 of picking the juvenile's gene that is inherited from the mother,
 321 in which case the consanguinity is, with probability 1/2 this gene is the mother's maternal-
 322 origin genes, and the consanguinity is that between the mother's maternal gene to itself which
 323 is 1, and with probability 1/2 the juvenile's gene picked is not the mother's maternal-origin
 324 genes, and the consanguinity if that between mating partners i.e. f' , and with probability 1/2
 325 of picking the individual's gene that is inherited from the father, in which case the
 326 consanguinity is that between the father and the mother's maternal-origin genes, which is the
 327 probability that neither the mother nor the father disperses $(1 - m_f)(1 - m_m)$, and then with
 328 probability 1/2 of picking the father's gene that comes from his mother, and with probability

329 $1/n$ the father and the mother share the same mother, and the consanguinity is that of the
 330 mother to herself i.e. p_I' , and with the probability $(n-1)/n$ the father and the mother do not
 331 share mother, with probability that neither of the two mothers disperse $(1 - m_f)^2$, and the
 332 consanguinity is that between two random juveniles born in the same patch i.e. p_x' , plus the
 333 probability $1/2$ of picking the father's genes that come from his father, times the
 334 consanguinity between mating partners f' . The consanguinity between a juvenile and its
 335 father's maternal-origin genes $p_{OF|M}$ is

$$\begin{aligned}
 p_{OF|M} = & \frac{1}{2}(1 - m_f)(1 - m_m) \left(\frac{1}{2} \left(\frac{1}{n} p_I' + \frac{n-1}{n} (1 - m_f)^2 p_x' \right) + \frac{1}{2} f' \right) \\
 & + \frac{1}{2} \left(\frac{1}{2} + \frac{1}{2} f' \right)
 \end{aligned} \tag{S33}$$

336 That is: with probability $1/2$ of picking the juvenile's gene that comes from its mother, in
 337 which case the consanguinity is that between the mother and the father's maternal-origin
 338 genes, which is with probability $(1 - m_f)(1 - m_m)$ that neither the mother nor the father
 339 disperses, and with probability $1/2$ of picking the mother's maternal-origin genes, with
 340 probability $1/n$ that the mother and father share the same mother, and the consanguinity is
 341 that of the mother to herself i.e. p_I' , and with probability $(n-1)/n$ the mother and father do not
 342 share mother, with probability $(1 - m_f)^2$ neither of the two mothers disperses, and the
 343 consanguinity is that between two random juveniles born in the same patch i.e. p_x' , with
 344 probability $1/2$ of picking the mother's paternal-origin genes, and the consanguinity is that
 345 between mating partners i.e. f' , and with probability $1/2$ of picking the juvenile's gene that
 346 comes from the father, in which case the consanguinity is, with probability $1/2$ this gene is
 347 the father's maternal-origin genes, then and the consanguinity is that of the father's maternal-
 348 origin gene to itself which is 1, and with probability $1/2$ the juvenile's gene is not the father's
 349 maternal-origin gene, then the consanguinity is that between mating partners f' . Hence we

350 have $p_{O|M} = p_{OM|M} = p_{OF|M}$. The consanguinity between a juvenile and the maternal-
 351 origin genes of a random female in its mother's social group $p_{JA|M}$ is

$$\begin{aligned}
 p_{JA|M} = & \frac{1}{2} \left(\frac{1}{n} p_I' + \frac{n-1}{n} (1 - m_f)^2 \left(\frac{1}{2} \left(\frac{1}{n} p_I' + \frac{n-1}{n} (1 - m_f)^2 p_x' \right) + \frac{1}{2} f' \right) \right) \\
 & + \frac{1}{2} (1 - m_f)(1 - m_m) \left(\frac{1}{2} \left(\frac{1}{n} p_I' + \frac{n-1}{n} (1 - m_f)^2 p_x' \right) + \frac{1}{2} f' \right)
 \end{aligned}
 \tag{S34}$$

352 That is: with probability 1/2 of picking the juvenile's maternal-origin gene, in which case the
 353 consanguinity is that between the juvenile's mother and the maternal-origin genes of a
 354 random adult female in the mother's social group (including the mother), which is with
 355 probability 1/n that the adult female is the juvenile's mother, then the consanguinity is that of
 356 an individual to itself i.e. p_I' , plus the probability $(n-1)/n$ that the adult female is not the
 357 juvenile's mother, then the consanguinity is with probability $(1 - m_f)^2$ that neither of these
 358 two females disperses, and with probability 1/2 of picking the maternal-origin gene of the
 359 juvenile's mother, then with probability 1/n that the two females share one mother, and the
 360 consanguinity is that of the mother to herself i.e. p_I , and with probability $(n-1)/n$ that the two
 361 females do not share one mother, with probability $(1 - m_f)^2$ that neither of the mothers of
 362 these two females disperses, and the consanguinity is that between two random juveniles born
 363 in the same patch i.e. p_x' , and with probability 1/2 of picking the gene of the paternal-origin
 364 genes of the juvenile's mother, times the consanguinity of mating partners i.e. f' , and with
 365 probability 1/2 of picking the juvenile's paternal-origin gene, in which case the consanguinity
 366 is that between the juvenile's father and the maternal-origin gene of a random adult female in
 367 the mother's social group, which is the probability $(1 - m_f)(1 - m_m)$ that neither of the
 368 adult female nor the juvenile's father disperses, and with probability 1/2 of picking the
 369 maternal-origin gene of the father, with probability 1/n that the juvenile's father and the adult
 370 female share one mother, and the consanguinity is that of the mother to herself i.e. p_I' , and
 371 with probability $(n-1)/n$ that the juvenile's father and the female do not share one mother,

372 with probability $(1 - m_f)^2$ that neither of the mothers of these two individuals disperses, and
 373 the consanguinity is that between two random juveniles born in the same patch i.e. p_x' , with
 374 probability 1/2 of picking the paternal-origin gene of the father, then the consanguinity is that
 375 between mating partners i.e. f' . The consanguinity between the focal juvenile and the
 376 maternal-origin gene of a random male in its father's social group p_{JU-M} is

$$\begin{aligned}
 p_{JU-M} = & \frac{1}{2}(1 - m_f)(1 - m_m) \left(\frac{1}{2} \left(\frac{1}{n} p_I' + \frac{n-1}{n} (1 - m_f)^2 p_x' \right) + \frac{1}{2} f' \right) \\
 & + \frac{1}{2} \left(\frac{1}{n} p_I' \right. \\
 & \left. + \frac{n-1}{n} (1 - m_m)^2 \left(\frac{1}{2} \left(\frac{1}{n} p_I' + \frac{n-1}{n} (1 - m_f)^2 p_x' \right) + \frac{1}{2} f' \right) \right)
 \end{aligned} \tag{S35}$$

377 That is: with probability 1/2 of picking the juvenile's gene that comes from the mother, in
 378 which case the consanguinity is that between the juvenile's mother and the maternal-origin
 379 genes of a random adult male in the father's social group, which is with probability $(1 -$
 380 $m_f)(1 - m_m)$ that neither the mother nor the adult male disperses, with probability 1/2 of
 381 picking the mother's maternal-origin genes, with probability 1/n these two genes come from
 382 the same mother and the consanguinity is that of the mother to herself i.e. p_I' , and with
 383 probability $(n-1)/n$ these two genes come from different mothers, with probability $(1 - m_f)^2$
 384 that neither of the two mothers disperses, and the consanguinity is that between two random
 385 juveniles born in the same patch i.e. p_x' , and with probability 1/2 of picking the mother's
 386 paternal-origin gene, and the consanguinity is that of mating partners i.e. f' , and with
 387 probability 1/2 of picking the juvenile's gene that comes from the father, in which case the
 388 consanguinity is that between the juvenile's father and the maternal-origin genes of a random
 389 adult male in the father's social group (including this father), which is with probability 1/n
 390 these two genes come from the same mother, and the consanguinity is that of the mother to
 391 herself i.e. p_I' , with probability $(n-1)/n$ these two genes comes from different mothers, with
 392 probability $(1 - m_m)^2$ neither of the two males disperses, and with probability 1/2 of picking

393 the father's maternal-origin gene, with probability $1/n$ the juvenile's father and the random
394 male in the father's group share one mother, and the consanguinity is that between the mother
395 and herself i.e. p_I' , with probability $(n-1)/n$ the two males do not share one mother, with
396 probability $(1 - m_f)^2$ that neither of the two mothers of the two males disperses, and the
397 consanguinity is that between two random juveniles born in the same patch p_x' , with
398 probability $1/2$ of picking the juvenile's father's paternal-origin gene, and the consanguinity is
399 that between mating partners i.e. f' . The consanguinity between a juvenile and its mother
400 from the perspective of the mother's paternal-origin gene $p_{OM|P}$ is

$$p_{OM|P} = \frac{1}{2} \left(\frac{1}{2} f' + \frac{1}{2} \right) + \frac{1}{2} (1 - m_f)(1 - m_m) \left(\frac{1}{2} f' + \frac{1}{2} \left(\frac{1}{n} p_I' + \frac{n-1}{n} (1 - m_m)^2 p_x' \right) \right) \quad (S36)$$

401 That is: with probability $1/2$ of picking the juvenile's gene that comes from the mother, in
402 which case the consanguinity is that between the mother and the mother's paternal-origin
403 gene, which is with probability $1/2$ the gene is the mother's maternal-origin genes, and the
404 consanguinity is that between the mother's maternal-origin genes and its paternal-origin genes
405 i.e. f' , and with probability $1/2$ the juvenile's gene picked is the mother's paternal-origin
406 genes, then the consanguinity is 1, and with probability $1/2$ of picking the juvenile's gene that
407 comes from its father, in which case the consanguinity is that between the mother's maternal-
408 origin genes and the father, which is with probability $(1 - m_f)(1 - m_m)$ neither of the
409 mother and father disperses, and with probability $1/2$ of picking the father's maternal-origin
410 gene, and the consanguinity is that between mating partners i.e. f' , and with probability $1/2$ of
411 picking the father's paternal-origin gene, and with probability $1/n$ the mother and father share
412 the same father, and the consanguinity is that of the mother to herself i.e. p_I' , and with
413 probability $(n-1)/n$ the mother and father do not share father, with probability $(1 - m_m)^2$
414 neither of the two fathers disperses, and the consanguinity is that between two random

415 juveniles born in the same patch i.e. p_x' . From expression (S32) and (S33), according to the
 416 same rule we can get $p_{O|P} = p_{OM|P} = p_{OF|P}$. The consanguinity between a juvenile and a
 417 random adult female in its mother's social group (including the mother) from the perspective
 418 of the adult female's paternal-origin genes $p_{JA|P}$ is

$$p_{JA|P} = \frac{1}{2} \left(\frac{1}{n} p_I' + \frac{n-1}{n} (1 - m_f)^2 \left(\frac{1}{2} f' + \frac{1}{2} \left(\frac{1}{n} p_I' + \frac{n-1}{n} (1 - m_m)^2 p_x' \right) \right) \right) \quad (S37)$$

$$+ \frac{1}{2} (1 - m_f)(1 - m_m) \left(\frac{1}{2} f' + \frac{1}{2} \left(\frac{1}{n} p_I' + \frac{n-1}{n} (1 - m_m)^2 p_x' \right) \right)$$

419 That is: with probability 1/2 of picking the juvenile's gene that come from the mother, in
 420 which case the consanguinity is that between the juvenile's mother and the paternal-origin
 421 genes of a random adult female in the mother's social group, which is with probability 1/n the
 422 adult female is the juvenile's mother, times the consanguinity of the mother to herself p_I , and
 423 with probability $(n-1)/n$ that the adult female is not the juvenile's mother, and with
 424 probability $(1 - m_f)^2$ that neither of the two females disperses, with probability 1/2 of picking
 425 the juvenile's mother's maternal-origin gene, and the consanguinity is that between the
 426 mother's maternal-origin genes and paternal-origin genes i.e. f' , and with probability 1/2 of
 427 picking the mother's paternal-origin genes, with probability 1/n the juvenile's mother and the
 428 random female in the mother's group share one father, and the consanguinity is that between
 429 the father and himself i.e. p_I , and with probability $(n-1)/n$ the two females do not share one
 430 father, with probability $(1 - m_m)^2$ neither of the two fathers of the two females disperses, and
 431 the consanguinity is that between two random juveniles born in the same patch i.e. p_x' , and
 432 with probability 1/2 of picking the juvenile's gene that comes from the father, in which case
 433 the consanguinity is that between the juvenile's father and the paternal-origin genes of a
 434 random adult female in the mother's group, which is with probability $(1 - m_f)(1 - m_m)$ that
 435 neither the adult female nor the father disperses, and with probability 1/2 of picking the
 436 father's maternal-origin gene, and the consanguinity is that between mating partners i.e. f' ,

437 with probability $1/2$ of picking the father's paternal-origin gene, and with probability $1/n$ that
438 the adult female and the father share one father, and the consanguinity is that of the father to
439 himself i.e. p_I' , and with probability $(n-1)/n$ the adult female and the father do not share one
440 father, and with probability $(1 - m_m)^2$ neither of the two fathers disperses, and the
441 consanguinity is that between two random juveniles born in the same patch i.e. p_x' . The
442 consanguinity between a juvenile and the paternal-origin gene of a random adult male in its
443 father's social group (including the father) $p_{JU|P}$ is:

$$\begin{aligned}
p_{JU|P} = & \frac{1}{2}(1 - m_f)(1 - m_m) \left(\frac{1}{2}f' + \frac{1}{2} \left(\frac{1}{n}p_I' + \frac{n-1}{n}(1 - m_m)^2p_x' \right) \right) & (S38) \\
& + \frac{1}{2} \left(\frac{1}{n}p_I' \right. \\
& \left. + \frac{n-1}{n}(1 - m_m)^2 \left(\frac{1}{2}f' + \frac{1}{2} \left(\frac{1}{n}p_I' + \frac{n-1}{n}(1 - m_m)^2p_x' \right) \right) \right)
\end{aligned}$$

444 That is: with probability $1/2$ of picking the juvenile's maternal-origin gene, in which case the
445 consanguinity is that between the juvenile's mother and the paternal-origin genes of a random
446 adult male in the father's social group, which is the probability $(1 - m_f)(1 - m_m)$ that
447 neither of the juvenile's mother nor the adult male disperses, and with probability $1/2$ of
448 picking the maternal-origin gene of the mother, and the consanguinity is that between mating
449 partners i.e. f' , and with probability $1/2$ of picking the paternal-origin gene of the mother,
450 with probability $1/n$ the juvenile's mother and the adult male share one father, and the
451 consanguinity is that of the father to himself i.e. p_I' , and with probability $(n-1)/n$ the
452 juvenile's mother and the adult male do not share one father, with probability $(1 - m_m)^2$
453 neither of the fathers disperses, and the consanguinity is that between two random juveniles
454 born in the same patch i.e. p_x' , and with probability $1/2$ of picking the juvenile's paternal-
455 origin gene, in which case the consanguinity is that between the juvenile's father and the
456 paternal-origin gene of a random adult male in the father's social group, which is with

457 probability $1/n$ the adult male is the juvenile's father, and the consanguinity is that of the
458 father to himself i.e. p_I' , and with probability $(n-1)/n$ the adult male is not the juvenile's
459 father, with probability $(1 - m_m)^2$ that neither of the fathers disperses, and with probability
460 $1/2$ that picking the maternal-origin gene of the juvenile's father, and the consanguinity is
461 that between mating partners i.e. f' , and with probability $1/2$ of picking the paternal-origin
462 gene of the juvenile's father, with probability $1/n$ the two males share one father, and the
463 consanguinity of the father to himself i.e. p_I' , and with probability $(n-1)/n$ the two males do
464 not share one father, with probability $(1 - m_m)^2$ that neither of the fathers disperses, and the
465 consanguinity is that between two random juveniles born in the same patch i.e. p_x' . Solving
466 expressions (S32)-(S38) with the solutions of p_I' , p_x' and f' from previous section
467 simultaneously, we obtain

$$p_{O|M} = ((-2\Delta m(M - 2\bar{m} + 1)(1 - \bar{m}) + 2(1 - \bar{m})(M\Delta m - 2\Delta m\bar{m} + 2m_f + 2\bar{m} - 4)n - 8(2 - \bar{m})\bar{m}n^2)) / ((8n(2\bar{m} - 1 - 4\bar{m}^2 + 3M - 4(2 - \bar{m})\bar{m}n))) \quad (S39)$$

$$p_{JA|M} = -((-2\Delta m(1 - m_f)^2(1 - \bar{m}) + 2\Delta m(1 - \bar{m})(5 - m_m + m_f(2m_f - 5 + m_m))n + (8 + m_f^4 - m_f^3(5 - m_m) - (4 - m_m)H_m - m_f(8 + (4 - m_m)(1 - m_m)m_m) - m_f^2(m_m - 10 + m_m^2))n^2)) / ((8n^2(2\bar{m} - 1 - 4\bar{m}^2 + 3M - 4(2 - \bar{m})\bar{m}n))) \quad (S40)$$

$$p_{JU|M} = (2\Delta m(1 - m_m)^2(1 - \bar{m}) - 2\Delta m(1 - \bar{m})(1 + M - 2\bar{m} + 2H_m)n + (2\Delta m(1 - \bar{m})(M - 2\bar{m} + H_m) - 8)n^2) / ((8n^2(2\bar{m} - 1 - 4\bar{m}^2 + 3M - 4(2 - \bar{m})\bar{m}n))) \quad (S41)$$

$$p_{O|P} = (((M - 2\bar{m} + 1) + 2\Delta m(1 - \bar{m}) + 2(1 - \bar{m})(2\Delta m\bar{m} - M\Delta m + 2m_m + 2\bar{m} - 4)n - 8(2 - \bar{m})\bar{m}n^2)) / ((8n(2\bar{m} - 1 - 4\bar{m}^2 + 3M - 4(2 - \bar{m})\bar{m}n))) \quad (S42)$$

$$\begin{aligned}
p_{J|A|-P} = & (-2\Delta m(1 - m_f)^2(1 - \bar{m}) + 2\Delta m(1 - \bar{m})(1 - 2\bar{m} + M + 2H_f)n \\
& + (-8 - 4\Delta m(1 - \bar{m})(M - \bar{m} + H_f - m_f)n^2)) / ((8n^2(2\bar{m} - 1 \\
& - 4\bar{m}^2 + 3M - 4(2 - \bar{m})\bar{m}n))
\end{aligned} \tag{S43}$$

$$\begin{aligned}
p_{J|U|-P} = & (-2\Delta m(1 - m_m)^2(1 - \bar{m}) + 2\Delta m(1 - \bar{m})(5 + M - 2\bar{m} + 2H_m)n \\
& + (-8 + m_f^2(H_m - 3m_m + 6) - m_f^3(1 - m_m) \\
& - H_m(4 + H_m - m_m) + m_f(H_m - 8 + 6m_m - m_m^3))n^2) \\
& / (8n^2(2\bar{m} - 1 - 4\bar{m}^2 + 3M - 4(2 - \bar{m})\bar{m}n))
\end{aligned} \tag{S44}$$

468 where $\Delta m = m_f - m_m$, $\bar{m} = (m_f + m_m)/2$, $M = m_f m_m$, $\Delta b = b_f - b_m$, $\bar{b} = (b_f + b_m)/2$,

469 $H_f = (m_f - 2)m_f$, $H_m = (m_m - 2)m_m$.

470

471 *1.53 / Convergence stable strategy*

472 By solving the expression $dW/dg = 0$, we could get the optimal value of left-handedness from

473 the perspective of maternal-origin genes z_M^* :

$$\begin{aligned}
z_M^* = & ((2\bar{b}(n - 1)(-H_f(2 + H_f) + H_m(2 + H_m) - 2\Delta m(1 - \bar{m})(2 + H_f + H_m)n \\
& - 16(2 - \bar{m})\bar{m}n^2))) / ((-8\bar{b}\Delta m(1 - \bar{m})(2 + H_f + H_m) + 16\Delta m(1 \\
& - \bar{m})(\bar{b}(2 + H_f + H_m) - 1 + 2\bar{m} - M)n + 2(2\bar{b}m_f^4 - 32 \\
& - 4m_f^3(2\bar{b} - 1 + m_m) + 4m_f^2(\bar{b} - 5 + 3m_m) + 4m_f(10 + 6\bar{b} \\
& - 4(\bar{b} + 1)m_m - 3m_m^2 + m_m^3) + 2m_m(10b_f - 10\bar{b}m_m + 2(2\bar{b} \\
& - 1)m_m^2 - \bar{b}m_m^3 + 2(6 + 5b_m + m_m)))n^2 - 64(\bar{b} + 1)(2 \\
& - \bar{m})\bar{m}n^3))
\end{aligned} \tag{S45}$$

474 where $\Delta m = m_f - m_m$, $\bar{m} = (m_f + m_m)/2$, $M = m_f m_m$, $\Delta b = b_f - b_m$, $\bar{b} = (b_f + b_m)/2$,

475 $H_f = (m_f - 2)m_f$, $H_m = (m_m - 2)m_m$. Solving the expression $dW/dg = 0$, we obtain the

476 optimal value of left-handedness from the perspective of paternal-origin genes z_P^* :

$$\begin{aligned}
z_P^* = & ((2\bar{b}(n-1)(-(H_f(2+H_f)) + H_m(2+H_m) - 2\Delta m(1-\bar{m})(2+H_f+H_m)n \\
& + 16(2-\bar{m})\bar{m}n^2))) / ((-8\Delta m\bar{b}(1-\bar{m})(2+H_f+H_m) \\
& + 8\Delta m(1-\bar{m})(b_m H_f - 2(b_m + m_f)m_m + b_m m_m^2 \\
& + 2(b_m - 1 + 2\bar{m}) + b_f(2+H_f+H_m))n \\
& + 4(16 + \bar{b}m_f^4 - 4(5+3\bar{b})m_m - 2(\bar{b}-5)m_m^2 + 2(2\bar{b}-1)m_m^3 \\
& - \bar{b}m_m^4 - 2m_f^3(2\bar{b}-1+m_m) + 2m_f^2(5\bar{b}-1+3m_m) \\
& + 2m_f(4(\bar{b}+1)m_m - 6 - 10\bar{b} - 3m_m^2 + m_m^3))n^2 + 64(\bar{b} \\
& + 1)(2-\bar{m})\bar{m}n^3)) \tag{S46}
\end{aligned}$$

477 The optimal value of left-handedness for the perspective of the whole genes of the individual

478 z^* is:

$$z^* = \frac{(n-1)(\Delta b \Delta m(1-\bar{m}) + 4\bar{b}(2-\bar{m})\bar{m})}{2(n-1)(\Delta b \Delta m(1-\bar{m}) + 8n + 4(\bar{b}+1)(2-\bar{m})\bar{m})} \tag{S47}$$

479 We set the female dispersal rate $m_f = 0.5$, the relative importance of combat relative to all
480 types of competition for the female and male $b_f = b_m = 1$, and the number of individuals each
481 sex born in the same patch $n = 5$ for Figure S4. For the two zoomed-in parts, the range of
482 male dispersal rate m_m is from 0.499 to 0.501, the range for the equilibrium frequency of left-
483 handedness is from 0.21426 to 0.21431.

484

485 **1.6 | Sex-specific effects**

486 *1.61 | Marginal fitness and evolutionary equilibrium*

487 Here we consider how sex effects add to the mediation of kin selection on handedness. In this
488 section, the fitness functions of the focal juvenile are the same as previous sections. We use
489 g_1 to denote the genic value for the locus G1, which affects handedness only when it is
490 carried by a female. We use g_2 and to denote the genic value for the locus G2 which affects
491 handedness only when it is carried by a male. The relative fitness functions are the same as

492 expression (S4). Then we explore the optimal value of the level of left-handedness for locus
 493 G_1 which only controls the handedness trait of females. For juveniles, the relationship
 494 between the phenotype and genotype is:

$$\begin{aligned} \frac{dW}{dg_1} &= \frac{\partial W}{\partial x_{M_0}} \frac{dx_{M_0}}{d\tilde{g}_{1f}} \frac{d\tilde{g}_{1f}}{dg_1} + \frac{\partial W}{\partial y_{M_0}} \frac{dy_{M_0}}{d\tilde{g}_{1f}'} \frac{d\tilde{g}_{1f}'}{dg_1} + \frac{\partial W}{\partial x_{Fa}} \frac{dx_{Fa}}{d\tilde{g}_{1m}} \frac{d\tilde{g}_{1m}}{dg_1} + \frac{\partial W}{\partial y_{Fa}} \frac{dy_{Fa}}{d\tilde{g}_{1m}'} \frac{d\tilde{g}_{1m}'}{dg_1} \\ &= \left(\frac{\partial W}{\partial x_{M_0}} p_{OM} + \frac{\partial W}{\partial y_{M_0}} p_{JA} \right) \gamma_{1f} + \left(\frac{\partial W}{\partial x_{Fa}} p_{OF} + \frac{\partial W}{\partial y_{Fa}} p_{JU} \right) \gamma_{1m} \end{aligned} \quad (S48)$$

495 where \tilde{g}_{1f} is the additive breeding value of a juvenile for its mother's genes in locus G_1 , \tilde{g}_{1f}'
 496 is the breeding value of the juvenile for a random adult female's genes in locus G_1 , \tilde{g}_{1m} is the
 497 breeding value of the juvenile for its father's genes in locus G_1 , \tilde{g}_{1m}' is the breeding value of
 498 the juvenile for a random adult male's genes in locus G_1 , and γ_{1f} and γ_{1m} is the mapping
 499 between genotype and phenotype for the focal females and males respectively. According to
 500 our assumption that locus G_1 would only take an effect if its carrier is a female, we have $\gamma_{1f} =$
 501 1, $\gamma_{1m} = 0$. Then expression (S48) can be simplified to

$$\frac{dW}{dg_1} = \frac{\partial W}{\partial x_{M_0}} p_{OM} + \frac{\partial W}{\partial y_{M_0}} p_{JA} \quad (S49)$$

502 Then the condition that favours the increase of left-handedness is

$$\frac{\partial W}{\partial x_{M_0}} r_{OM} + \frac{\partial W}{\partial y_{M_0}} r_{JA} > 0 \quad (S50)$$

503 Letting the LHS of expression (S50) be $f(z)$, as $f'(z) < 0$ is true for all the values of z ,
 504 hence at evolutionary equilibrium if there is an intermediate level of left-handedness z_f^* , this
 505 satisfies $f(z^*) = 0$, we obtain the optimum of left-handedness for all the loci that only
 506 control the handedness when they are carried by females

$$z_f^* = \frac{1}{2} \frac{b_f(r_{OM} - r_{JA})}{(1 + b_f)r_{OM} - b_f r_{JA}} \quad (S51)$$

507 Now we explore the optimum value of the probability of developing as left-handedness for
 508 locus G_2 which only controls the handedness trait of males. For a juvenile, the relationship
 509 between the phenotype and genotype is

$$\begin{aligned}
\frac{dW}{dg_2} &= \frac{\partial W}{\partial x_{M0}} \frac{dx_{M0}}{d\tilde{g}_{2f}} \frac{d\tilde{g}_{2f}}{dg_2} + \frac{\partial W}{\partial y_{M0}} \frac{dy_{M0}}{d\tilde{g}_{2f}'} \frac{d\tilde{g}_{2f}'}{dg_2} + \frac{\partial W}{\partial x_{Fa}} \frac{dx_{Fa}}{d\tilde{g}_{2m}} \frac{d\tilde{g}_{2m}}{dg_2} \\
&\quad + \frac{\partial W}{\partial y_{Fa}} \frac{dy_{Fa}}{d\tilde{g}_{2m}'} \frac{d\tilde{g}_{2m}'}{dg_2} \tag{S52} \\
&= \left(\frac{\partial W}{\partial x_{M0}} p_{OM} + \frac{\partial W}{\partial y_{M0}} p_{JA} \right) \gamma_{2f} + \left(\frac{\partial W}{\partial x_{Fa}} p_{OF} + \frac{\partial W}{\partial y_{Fa}} p_{JU} \right) \gamma_{2m}
\end{aligned}$$

510 where \tilde{g}_{2f} is the additive breeding value of a juvenile for its mother's genes in locus G_2 , \tilde{g}_{2f}'
511 is the breeding value of the juvenile for a random adult female's genes in locus G_2 , \tilde{g}_{2m} is the
512 breeding value of the juvenile for its father's genes in locus G_2 , \tilde{g}_{2m}' is the breeding value of
513 the juvenile for a random adult male's genes in locus G_2 , γ_{2f} and γ_{2m} is the mapping between
514 genotype and phenotype for an adult female or male respectively. According to our
515 assumption that locus G_2 would only take an effect if its carrier is a male, thus $\gamma_{2f} = 0$, $\gamma_{2m} = 1$.
516 Then dW_f/dg_{2f} can be simplified to

$$\frac{dW}{dg_2} = \frac{\partial W}{\partial x_{Fa}} p_{OF} + \frac{\partial W}{\partial y_{Fa}} p_{JU} \tag{S53}$$

517 Using the same way as deriving the optimal value of locus G_1 , z_{f}^* , we could obtain the
518 optimal value of left-handedness z_m^* for all the loci that only control handedness when they
519 are carried by males:

$$z_m^* = \frac{1}{2} \frac{b_m(r_{OF} - r_{JU})}{(1 + b_m)r_{OF} - b_m r_{JU}} \tag{S54}$$

520 1.62 / Convergence stable strategy

521 Combining with parent-of-origin effects, we can write the optimal value of left-handedness
522 for all the loci that control female's handedness from the perspective of maternal-origin
523 genes, z_{fM}^* , and that from the perspective of paternal-origin genes, z_{fP}^* , as well as the optimal
524 value of left-handedness for all the loci that control male's handedness from the perspective
525 of maternal-origin genes and paternal-origin genes respectively: z_{mM}^* and z_{mP}^* :

$$z_{fM}^* = \frac{1}{2} \frac{b_f(r_{OM|M} - r_{JA|M})}{(1 + b_f)r_{OM|M} - b_f r_{JA|M}} \quad (S55)$$

$$z_{fP}^* = \frac{b_f(r_{OM|P} - r_{JA|P})}{(1 + b_f)r_{OM|P} - b_f r_{JA|P}} \quad (S56)$$

$$z_{mM}^* = \frac{1}{2} \frac{b_m(r_{OF|M} - r_{JU|M})}{(1 + b_m)r_{OF|M} - b_m r_{JU|M}} \quad (S57)$$

$$z_{mP}^* = \frac{1}{2} \frac{b_m(r_{OF|P} - r_{JU|P})}{(1 + b_m)r_{OF|P} - b_m r_{JU|P}} \quad (S58)$$

526 where $r_{OM|P} = p_{OM|P}/p_I$, $r_{OF|P} = p_{OF|P}/p_I$, $r_{JA|P} = p_{JA|P}/p_I$, $r_{JU|P} = p_{JU|P}/p_I$. Substituting all
 527 the relatedness in expressions (S51), (S54) and (S55)-(S58), we obtain the optimal values of
 528 left-handedness when it is involved in within-group combat:

$$z_f^* = ((b_f(n-1)(H_f - H_m - 4(2 - \bar{m})\bar{m}n)) / ((-8n + 2(n - 1)(-2b_f\Delta m(1 - \bar{m}) - 4(1 + b_f)(2 - \bar{m})\bar{m}n))) \quad (S59)$$

$$\begin{aligned} z_{fM}^* = & ((b_f(-2\Delta m(1 - m_f)^2(1 - \bar{m}) + 4\Delta m(2 + H_f)(1 - \bar{m})n \\ & + (m_f(2 + m_f(5 + H_f - 2m_f)) + 2(7 + H_f - 2m_f)m_m \\ & - (5 + m_f)m_m^2)n^2 - 8(2 - \bar{m})\bar{m}n^3)) \\ & / ((-4b_f\Delta m(1 - m_f)^2(1 - \bar{m}) + 4\Delta m(1 - \bar{m})(m_f - 1 + 2b_f(2 \\ & + H_f) + m_m - M)n + 2(-8 + m_f(10 + H_f - 3m_f + b_f(2 + m_f(5 \\ & + H_f - 2m_f))) + 6m_m + (2b_f(7 + H_f - 2m_f) - m_f(4 + H_f - m_f))m_m \\ & - (3m_f - 1 + b_f(5 + H_f))m_m^2 - (1 - m_f)m_m^3)n^2 - 16(1 + b_f)(2 \\ & - \bar{m})\bar{m}n^3)) \end{aligned} \quad (S60)$$

$$\begin{aligned} z_{fP}^* = & ((b_f(-2\Delta m(H_f + 1)(1 - \bar{m}) + 4H_f\Delta m(1 - \bar{m})n + ((H_f - m_f)(2 + H_f + m_f) \\ & + 2(m_f^2 - 5)m_m - (H_f - 3)m_m^2)n^2 - 8(\bar{m} - 2)\bar{m}n^3)) \\ & / ((-4b_f\Delta m(1 - m_f)^2(1 - \bar{m}) + 4\Delta m(1 - \bar{m})(2\bar{m} - 1 + 2b_fH_f \\ & - M)n + 2(8 + (H_f - m_f)(2 + m_f + b_f(2 + H_f + m_f)) - 10m_m \\ & + (-(H_f - 2m_f)(1 + m_f) + 2b_f(m_f^2 - 5))m_m + (5 - 3m_f - b_f(H_f \\ & - 3))m_m^2 - (1 - m_f)m_m^3)n^2 + 16(1 + b_f)(2 - \bar{m})\bar{m}n^3)) \end{aligned} \quad (S61)$$

$$z_m^* = ((b_m(n-1)(H_m - H_f - 4(2 - \bar{m})\bar{m}n)) / ((-8n + 2(n - 1)(2b_m\Delta m(1 - \bar{m}) - 4(1 + b_m)(2 - \bar{m})\bar{m}n))) \quad (S62)$$

$$z_{mM}^* = ((2b_m(-\Delta m(1 - m_m)^2(1 - \bar{m}) + 4H_m\Delta m(1 - \bar{m})n + (m_f^2(H_m - 3) - (H_m - m_m)(2 + H_m + m_m) - 2m_f(m_m^2 - 5))n^2 - 8(2 - \bar{m})\bar{m}n^3)) / ((-4b_m\Delta m(1 - m_m)^2(1 - \bar{m}) + 4\Delta m(1 - \bar{m})(2\bar{m} - 1 - M + 2b_mH_m)n + 2(-8 - m_f^3(m_m - 1) + m_f^2(-5 + 3m_m + b_m(H_m - 3)) - (H_m - m_m)(2 + m_m + b_m(2 + H_m + m_m)) + m_f(10 + m_m(H_m - m_m - 4) - 2b_m(-5 + m_m^2)))n^2 - 16(1 + b_m)(2 - \bar{m})\bar{m}n^3)) \quad (S63)$$

$$z_{mP}^* = ((-2b_m\Delta m(n-1)(-(1 - m_m)^2(1 - \bar{m}) - 2\Delta m(1 - \bar{m})(3 + H_m)n + 8(2 - \bar{m})\bar{m}n^2)) / ((-4b_m\Delta m(n-1)(-(H_m + 1)(1 - \bar{m}) - 2\Delta m(1 - \bar{m})(3 + H_m)n + 8(2 - \bar{m})\bar{m}n^2) + 2n(-2\Delta m(M - 2\bar{m} + 1)(1 - \bar{m}) - 2(1 - \bar{m})(2\bar{m} - 4 + 2m_m + 2\Delta m\bar{m} - M\Delta m)n + 8(2 - \bar{m})\bar{m}n^2))) \quad (S64)$$

529 where $\Delta m = m_f - m_m$, $\bar{m} = (m_f + m_m)/2$, $M = m_fm_m$, $\Delta b = b_f - b_m$, $\bar{b} = (b_f + b_m)/2$,
530 $H_f = (m_f - 2)m_f$, $H_m = (m_m - 2)m_m$. To plot z_f^* and z_m^* (Figure S3b) we set the female
531 dispersal rate $m_f = 0.5$, the relative importance of combat relative to all types of competition
532 for the female and male $b_f = b_m = 1$, and number of the number of individuals each sex born
533 in the same patch $n = 5$.

534

535 **1.7 | Parental genetic effects**

536 *1.71 | Marginal fitness and evolutionary equilibrium*

537 Now we consider the parental effects, i.e. the effect on the phenotype of the parents of the
538 focal juvenile is caused by the genes carried by the grandparents of the focal juvenile,
539 regardless of the parents' genotype. In this section, the fitness function and relatedness

540 remain the same as previous ones, while the conditions that favours the increase of left-
541 handedness change according to specific situations. Depending on whether there is difference
542 between maternal and paternal effects, and/or between the parental effects on daughters
543 versus those on sons, there can be nine situations: 1) When both parents control the parental
544 effect and all offspring experience the parental effect in their handedness (we denote the
545 optima for left-handedness as z_{PO}^*). 2) When both parents control the parental effect and only
546 daughters experience the parental effect in their handedness (z_{PD}^*). 3) When both parents
547 control the parental effect and only sons experience the parental effect in their handedness
548 (z_{PS}^*). 4) When only mother controls the parental effect and all offspring experience the
549 parental effect in their handedness (z_{MO}^*). 5) When only mother controls the parental effect
550 and only daughters experience the parental effect in their handedness (z_{MD}^*). 6) When only
551 mother controls the parental effect and only sons experience the parental effect in their
552 handedness (z_{MS}^*). 7) When only father controls the parental effect and all offspring
553 experience the parental effect in their handedness (z_{FO}^*). 8) When only father controls the
554 parental effect and only daughters experience the parental effect in their handedness (z_{FD}^*). 9)
555 When only father controls the parental effect and only sons experience the parental effect in
556 their handedness (z_{FS}^*).

557

558 *1) Parental control of offspring phenotype (z_{PO}^*)*

559 We consider there is only locus G controlling the phenotype of handedness, and there is no
560 difference in who carries the genes influence the phenotype of offspring, and it affects the
561 handedness phenotype of daughters and sons in the same way. We denote the genic value as
562 g_f and g_m for the juvenile females and males, G_f and G_m for the breeding value for the
563 maternal grandparent and paternal grandparent of the focal juvenile respectively, G'_f for the
564 breeding value of the parent of a random adult in the focal juvenile's mother's group, G'_m for

565 the breeding value of the parent of a random adult in the focal juvenile's father's group. The
 566 relationship between the phenotype and genotype can be described as:

$$\begin{aligned} \frac{dW}{dg} &= \frac{\partial W}{\partial x_{M_o}} \frac{dx_{M_o}}{dG_f} \frac{dG_f}{dg} + \frac{\partial W}{\partial y_{M_o}} \frac{dy_{M_o}}{dG_f'} \frac{dG_f'}{dg} + \frac{\partial W}{\partial x_{Fa}} \frac{dx_{Fa}}{dG_m} \frac{dG_m}{dg} + \frac{\partial W}{\partial y_{Fa}} \frac{dy_{Fa}}{dG_m'} \frac{dG_m'}{dg} \\ &= \left(\frac{\partial W}{\partial x_{M_o}} p_{JMGP} + \frac{\partial W}{\partial y_{M_o}} p_{JMAP} \right) \gamma_{Pf} \\ &\quad + \left(\frac{\partial W}{\partial x_{Fa}} r_{JPGP} + \frac{\partial W}{\partial y_{Fa}} r_{JPUP} \right) \gamma_{Pm} \end{aligned} \quad (S65)$$

567 where p_{JMGP} is the consanguinity between the focal juvenile female and its maternal
 568 grandparent (here we treat the maternal grandparent as a "tetraploidy"), p_{JMAP} is the
 569 coefficient of the consanguinity between the focal juvenile female and the parent of a random
 570 adult female (here "A" denotes "Aunt") in the focal juvenile's mother's group, p_{JPGP} is the
 571 coefficient of the consanguinity between the focal juvenile female and its paternal
 572 grandparent, p_{JPUP} is the coefficient of the consanguinity between the focal juvenile female
 573 and the parent of a random adult male (here "U" denotes "Uncle") in the focal juvenile's
 574 father's group, $\gamma_{Pf} = \frac{dx_{M_o}}{dG_f} = \frac{dy_{M_o}}{dG_f'}$ is the mapping between the gene of parents and its
 575 expressed phenotype in a female offspring, $\gamma_{Pm} = \frac{dx_{Fa}}{dG_m} = \frac{dy_{Fa}}{dG_m'}$ is the mapping between the
 576 gene of parents and its expressed phenotype in a male offspring, and under our assumption γ_{Pf}
 577 $= \gamma_{Pm} = 1$. The condition that favours the increase of left-handedness is:

$$\frac{\partial W_f}{\partial x_{M_o}} r_{JMGP} + \frac{\partial W_f}{\partial y_{M_o}} r_{JMAP} + \frac{\partial W_f}{\partial x_{Fa}} r_{JPGP} + \frac{\partial W_f}{\partial y_{Fa}} r_{JPUP} > 0 \quad (S66)$$

578 where $r_{JMGP} = p_{JMGP}/p_I$, $r_{JMAP} = p_{JMAP}/p_I$, $r_{JPGP} = p_{JPGP}/p_I$, $r_{JPUP} = p_{JPUP}/p_I$. Letting the LHS of
 579 expression (S66) be $f(z)$, $f'(z) < 0$ is true for all the values of z , hence at evolutionary
 580 equilibrium if there is intermediate level of left-handedness z_{PO}^* that satisfies $f(z_{PO}^*) = 0$,
 581 we obtain the optimum of left-handedness from the perspective of parent's genes:

$$z_{PO}^* = \frac{1}{2} \left(1 - \frac{r_{JMGP} + r_{JPGP}}{r_{JMGP} + b_f(-r_{JMAP} + r_{JMGP}) + r_{JPGP} + b_m r_{JPGP} - b_m r_{JPUP}} \right) \quad (S67)$$

582 if we set $b_f = b_m = 1$, expression (S67) can be re-written as: $\frac{1}{2} + \frac{1}{2} \frac{1}{\frac{p_{JAveAUP}}{p_{JAveGP}} - 2}$, where p_{AveAUP} is
583 the consanguinity between an individual and the parent of the individual's parent's social
584 partner, and $p_{AveAUP} = 1/2 (p_{JMAP} + p_{JPUP})$, p_{AveGP} is the consanguinity between an individual
585 and its grandparent, and $p_{AveGP} = 1/2 (p_{JMGP} + p_{JPGP})$. If we set $b_f = b_m = 1$, expression (S8) can
586 be re-written as: $\frac{1}{2} + \frac{1}{2} \frac{1}{\frac{p_J}{p_J} - 2}$. We use ratio $r_1 = p_{AveAUP}/p_{AveGP}$ for considering the optima from
587 the perspective of parents, and $r_2 = p_J/p_O$ for considering the optimum from the perspective of
588 the offspring. As r_1 is always greater than r_2 , parents always favour a lower value of left-
589 handedness in their offspring than the offspring would, in the context of within-group
590 combat.

591

592 2) Parental control of daughter's phenotype (z_{PD}^*)

593 Under our assumption that only daughters experience parental effect, $\gamma_{Pf} = 1$, $\gamma_{Pm} = 0$. The
594 condition that favours the increase of left-handedness is

$$\frac{\partial W}{\partial x_{Mo}} r_{JMGP} + \frac{\partial W}{\partial y_{Mo}} r_{JMAP} > 0 \quad (S68)$$

595 with similar process of obtaining z_{PO}^* we obtain the optimal value of left-handedness from
596 the perspective of parent's genes to its daughter

$$z_{PD}^* = \frac{1}{2} \frac{b_f(r_{JMAP} - r_{JMGP})}{b_f r_{JMAP} - (1 + b_f) r_{JMGP}} \quad (S69)$$

597

598 3) Parental control of son's phenotype (z_{PS}^*)

599 Under our assumption that only sons experience parental effect, $\gamma_{Pf} = 0$, $\gamma_{Pm} = 1$. The
600 condition that favours the increase of left-handedness is:

$$\frac{\partial W}{\partial x_{Fa}} r_{JPGP} + \frac{\partial W}{\partial y_{Fa}} r_{JPUP} > 0 \quad (S70)$$

601 with similar process, we obtain the optimal value of left-handedness from the perspective of
 602 parent's genes to its son:

$$z_{PS}^* = \frac{1}{2} \frac{b_m(r_{JPGP} - r_{JPUP})}{r_{JPGP} + b_m r_{JPGP} - b_m r_{JPUP}} \quad (S71)$$

603

604 *4) Maternal control of offspring phenotype (z_{MO}^*)*

605 In this case, the relationship between phenotype and genotype is

$$\frac{dW}{dg} = \left(\frac{\partial W}{\partial x_{Mo}} p_{JMGM} + \frac{\partial W}{\partial y_{Mo}} p_{JMAM} \right) \gamma_{Ff} + \left(\frac{\partial W}{\partial x_{Fa}} p_{JPGM} + \frac{\partial W}{\partial y_{Fa}} p_{JPUM} \right) \gamma_{Fm} \quad (S72)$$

606 where p_{JMGM} is the consanguinity between the focal juvenile female and its maternal
 607 grandmother, p_{JMAM} is the consanguinity between the focal juvenile female and the mother of
 608 a random adult female in the focal juvenile's mother's group, p_{JPGM} is the consanguinity
 609 between the focal juvenile female and its paternal grandmother, p_{JPUM} is the consanguinity
 610 between the focal juvenile female and the mother of a random adult male in the focal
 611 juvenile's father's group. γ_{Ff} is the mapping between the gene of mother and its expressed
 612 phenotype in a female offspring, γ_{Fm} is the mapping between the gene of mother and its
 613 expressed phenotype in a male offspring. Under our assumption that all offspring experience
 614 maternal effect, $\gamma_{Ff} = \gamma_{Fm} = \gamma$. The condition that favours the increase of left-handedness is

$$\frac{\partial W}{\partial x_{Mo}} r_{JMGM} + \frac{\partial W}{\partial y_{Mo}} r_{JMAM} + \frac{\partial W}{\partial x_{Fa}} p_{JPGM} + \frac{\partial W}{\partial y_{Fa}} p_{JPUM} > 0 \quad (S73)$$

615 where $r_{JMGM} = p_{JMGM}/p_I$, $r_{JMAM} = p_{JMAM}/p_I$, $r_{JPGM} = p_{JPGM}/p_I$, $r_{JPUM} = p_{JPUM}/p_I$. With similar
 616 process as previous situations, we obtain the optimal value of left-handedness from the
 617 perspective of mother's genes to her offspring

$$z_{MO}^* = \frac{1}{2} \left(1 - \frac{r_{JMGM} + r_{JPGM}}{r_{JMGM} + b_f(r_{JMGM} - r_{JMAM}) + r_{JPGM} + b_m r_{JPGM} - b_m r_{JPUM}} \right) \quad (S74)$$

618

619 *5) Maternal control of daughter's phenotype (z_{MD}^*)*

620 Changing γ_{Ff} to 1, γ_{Fm} to 0 obtains the condition for an increase in left-handedness to be
 621 favoured

$$\frac{\partial W}{\partial x_{M0}} r_{JMGM} + \frac{\partial W}{\partial y_{M0}} r_{JMAM} > 0 \quad (S75)$$

622 With similar process, we obtain the optimal value of left-handedness from the perspective of
 623 mother's genes to her daughters

$$z_{MD}^* = \frac{1}{2} \frac{b_f(r_{JMAM} - r_{JMGM})}{b_f r_{JMAM} - (1 + b_f)r_{JMGM}} \quad (S76)$$

624

625 *6) Maternal control of son's phenotype (z_{MS}^*)*

626 Changing γ_{Ff} to 0, γ_{Fm} to 1 obtains the condition for an increase in left-handedness to be
 627 favoured

$$\frac{\partial W}{\partial x_{Fa}} r_{JPGM} + \frac{\partial W}{\partial y_{Fa}} r_{JPUM} > 0 \quad (S77)$$

628 With similar process, we obtain the optimal value of left-handedness from the perspective of
 629 mother's genes to her sons

$$z_{MS}^* = \frac{1}{2} \frac{b_m(r_{JPGM} - r_{JPUM})}{r_{JPGM} + b_m r_{JPGM} - b_m r_{JPUM}} \quad (S78)$$

630

631 *7) Paternal control of offspring phenotype (z_{FO}^*)*

632 In this case, the relationship between phenotype and genotype is

$$\frac{dW}{dg} = \left(\frac{\partial W}{\partial x_{M0}} p_{JMGF} + \frac{\partial W}{\partial y_{M0}} p_{JMAF} \right) \gamma_{Mf} + \left(\frac{\partial W}{\partial x_{Fa}} p_{JPGF} + \frac{\partial W}{\partial y_{Fa}} p_{JPUF} \right) \gamma_{Mm} \quad (S79)$$

633 where p_{JMGF} is the consanguinity between the focal juvenile female and its maternal
 634 grandfather, p_{JMAF} is the consanguinity between the focal juvenile female and the father of a
 635 random adult female in its mother's group, p_{JPGF} is the consanguinity between the focal
 636 juvenile female and its paternal grandfather, p_{JPUF} is the consanguinity between the focal
 637 juvenile female and the father of a random adult male in its father's group, γ_{Mf} is the mapping

638 between the gene of father and its expressed phenotype in a female offspring, γ_{Mm} is the
 639 mapping between the gene of parents and its expressed phenotype in a male offspring. Under
 640 our assumption that all offspring experience paternal effect, $\gamma_{Mf} = \gamma_{Mm} = \gamma$. The condition that
 641 favours the increase of left-handedness is

$$\frac{\partial W}{\partial x_{Mo}} r_{JMGF} + \frac{\partial W}{\partial y_{Mo}} r_{JMAF} + \frac{\partial W}{\partial x_{Fa}} r_{JPGF} + \frac{\partial W}{\partial y_{Fa}} r_{JPUF} > 0 \quad (S80)$$

642 where $r_{JMGF} = p_{JMGF}/p_I$, $r_{JPGF} = p_{JPGF}/p_I$, $r_{JMAF} = p_{JMAF}/p_I$, $r_{JPUF} = p_{JPUF}/p_I$. With similar
 643 process as previous situations, we obtain the optimal value of left-handedness from the
 644 perspective of father's genes to his offspring

$$z_{FO}^* = \frac{1}{2} \left(1 - \frac{r_{JMGF} + r_{JPGF}}{r_{JMGF} + b_f(r_{JMGF} - r_{JMAF}) + r_{JPGF} + b_m r_{JPGF} - b_m r_{JPUF}} \right) \quad (S81)$$

645

646 8) *Paternal control of daughter's phenotype* (z_{FD}^*)

647 Changing γ_{Mf} to 1, γ_{Mm} to 0 obtains the condition for an increase in left-handedness to be
 648 favoured

$$\frac{\partial W}{\partial x_{Mo}} r_{JMGF} + \frac{\partial W}{\partial y_{Mo}} r_{JMAF} > 0 \quad (S82)$$

649 With similar process, we obtain the optimal value of left-handedness from the perspective of
 650 father's genes to his daughters

$$z_{FD}^* = \frac{1}{2} \frac{b_f(r_{JMAF} - r_{JMGF})}{b_f r_{JMAF} - (1 + b_f) r_{JMGF}} \quad (S83)$$

651

652 9) *Paternal control of son's phenotype* (z_{FS}^*)

653 Changing γ_{Mf} to 0, γ_{Mm} to 1 obtains the condition for an increase in left-handedness to be
 654 favoured

$$\frac{\partial W}{\partial x_{Fa}} r_{JPGF} + \frac{\partial W}{\partial y_{Fa}} r_{JPUF} > 0 \quad (S84)$$

655 With similar process, we obtain the optimal value of left-handedness from the perspective of
 656 father's genes to his sons

$$z_{FS}^* = \frac{1}{2} \frac{b_m(r_{JPGF} - r_{JPUF})}{r_{JPGF} + b_m r_{JPGF} - b_m r_{JPUF}} \quad (S85)$$

657

658 1.72 / Relatedness

659 The consanguinity between the focal juvenile and its maternal grandmother p_{JMGM} is

$$\begin{aligned} p_{JMGM} = & \frac{1}{2} \left(\frac{1}{2} p_I' + \frac{1}{2} f' \right) \\ & + \frac{1}{2} (1 - m_f)(1 - m_m) \left(\frac{1}{n} \left(\frac{1}{2} p_I' + \frac{1}{2} f' \right) \right) \\ & + \frac{n-1}{n} \left(\frac{1}{2} (1 - m_f)^2 p_x' + \frac{1}{2} f' \right) \end{aligned} \quad (S86)$$

660 That is: with probability 1/2 the gene we pick comes from the juvenile's mother, in which
 661 case the consanguinity is that between the mother and the maternal grandmother, which is
 662 with probability 1/2 the gene comes from the maternal grandmother, and the consanguinity is
 663 that between the maternal grandmother and herself i.e. p_I' , and with probability 1/2 the gene
 664 comes from the maternal grandfather, and the consanguinity is that between mating partners
 665 i.e. f' , and with probability 1/2 that the gene we pick comes from the juvenile's father, in
 666 which case the consanguinity is that between the juvenile's father and the maternal
 667 grandmother, which is with probability $(1 - m_f)(1 - m_m)$ neither the mother nor the father
 668 disperses from their natal patch, and with probability 1/n the mother and the father share one
 669 mother, and with probability 1/2 the gene comes from their mother, and the consanguinity is
 670 p_I' , and with probability 1/2 the gene comes from their father, and the consanguinity is that
 671 between two random mating partner i.e. f' , and with probability $(n-1)/n$ the mother and the
 672 father do not share one mother, and with probability 1/2 the gene comes from the paternal
 673 grandmother, with probability $(1 - m_f)^2$ neither of the two females disperses, and the

674 consanguinity is that between two random juveniles born in the same patch i.e. p_x' , and with
 675 probability $1/2$ the gene comes from the paternal grandfather, and the consanguinity is f' . The
 676 consanguinity between the focal juvenile and its maternal grandfather p_{JMGF} is

$$\begin{aligned}
 p_{JMGF} = & \frac{1}{2} \left(\frac{1}{2} f' + \frac{1}{2} p_I' \right) \\
 & + \frac{1}{2} (1 - m_f)(1 - m_m) \left(\frac{1}{n} \left(\frac{1}{2} f' + \frac{1}{2} p_I' \right) \right. \\
 & \left. + \frac{n-1}{n} \left(\frac{1}{2} f' + \frac{1}{2} (1 - m_m)^2 p_x' \right) \right) \quad (S87)
 \end{aligned}$$

677 That is: with probability $1/2$ the gene we pick comes from the juvenile's mother, in which
 678 case the consanguinity is that between the mother and her father, which is with probability
 679 $1/2$ the gene we pick comes from the maternal grandmother, and the consanguinity is that
 680 between mating partners i.e. f' , and with probability $1/2$ the gene we pick comes from the
 681 maternal grandfather, and the consanguinity is that between the grandfather and himself p_I' ,
 682 and with probability $1/2$ the gene we pick comes from the juvenile's father, in which case the
 683 consanguinity is that between the juvenile's father and maternal grandfather, which is with
 684 probability $(1 - m_f)(1 - m_m)$ neither the mother nor the father disperses, and with
 685 probability $1/n$ the mother and the father share one father, with probability $1/2$ the gene we
 686 pick comes from their mother, and the consanguinity is that between two random mating
 687 partner i.e. f' , and with probability $1/2$ the gene we pick comes from their father, and the
 688 consanguinity is p_I' , and with probability $(n-1)/n$ the mother and the father do not share one
 689 father, with probability $1/2$ the gene we pick comes from the paternal mother, and the
 690 consanguinity is that between two random mating partners f' , and with probability $1/2$ that
 691 the genes we pick come from the paternal father, with probability $(1 - m_m)^2$ neither of the
 692 two males disperses, and the consanguinity is that between two random juveniles born in the
 693 same patch i.e. p_x' . The consanguinity between the focal juvenile and the mother of a random
 694 adult female in its mother's social group p_{JMAM} is

$$\begin{aligned}
p_{\text{JMAM}} = & \frac{1}{2} \left(\frac{1}{n} \left(\frac{1}{2} p_1' + \frac{1}{2} f' \right) \right. \\
& + \frac{n-1}{n} (1 - m_f)^2 \left(\frac{1}{n} \left(\frac{1}{2} p_1' + \frac{1}{2} f' \right) \right. \\
& \left. \left. + \frac{n-1}{n} \left(\frac{1}{2} (1 - m_f)^2 p_x' + \frac{1}{2} f' \right) \right) \right) \quad (\text{S88}) \\
& + \frac{1}{2} (1 - m_f)(1 - m_m) \left(\frac{1}{n} \left(\frac{1}{2} p_1' + \frac{1}{2} f' \right) \right. \\
& \left. + \frac{n-1}{n} \left(\frac{1}{2} (1 - m_f)^2 p_x' + \frac{1}{2} f' \right) \right)
\end{aligned}$$

695 That is: with probability 1/2 the gene we pick comes from the juvenile's mother, in which
696 case the consanguinity is that between the juvenile's mother and the mother of a random
697 adult female in the juvenile's mother's social group, which is, with probability 1/n the
698 random adult female ("aunt" hereafter) is the juvenile's mother, and the consanguinity is that
699 between the juvenile's mother and maternal grandmother which is $\frac{1}{2} p_1' + \frac{1}{2} f'$, and with
700 probability $(n-1)/n$ the aunt is not the juvenile's mother, with the probability $(1 - m_f)^2$
701 neither of the two females disperses, and with probability 1/n the aunt and the juvenile's
702 mother share one mother, with probability $(n-1)/n$ the aunt and the juvenile's mother do not
703 share one mother, with probability 1/2 that the mother's gene comes from her mother, with
704 probability $(1 - m_f)^2$ neither the grandmother nor the mother of the aunt disperses, and the
705 consanguinity is that between two random juvenile born in the same patch i.e. p_x' , and with
706 probability 1/2 that the mother's gene came from her father, in which case the consanguinity
707 is that between two random mating partners f' , with probability 1/2 the gene we pick comes
708 from the juvenile's father, and with probability $(1 - m_f)(1 - m_m)$ neither the aunt nor the
709 father disperses, with probability 1/n the aunt and the father share one mother, with
710 probability 1/2 the gene comes from their mother, and the consanguinity is that between the
711 grandmother and herself i.e. p_1' , and with probability 1/2 the gene comes from the juvenile's

712 paternal grandfather, and the consanguinity is f' , and with probability $(n-1)/n$ the aunt and the
713 father do not share one mother, with probability $1/2$ the gene comes from the juvenile's
714 paternal grandmother, with probability $(1 - m_f)^2$ neither the mother of the juvenile's aunt
715 nor the paternal grandmother disperses, and the consanguinity is that between two random
716 juveniles born in the same patch p_x' , and with probability $1/2$ the gene comes from the
717 juvenile's paternal grandfather, and the consanguinity is f' . The consanguinity between the
718 focal juvenile and the father of a random adult female in its mother's group p_{JMAF} is

$$\begin{aligned}
p_{JMAF} = & \frac{1}{2} \left(\frac{1}{n} \left(\frac{1}{2} f' + \frac{1}{2} p_I' \right) \right. \\
& + \frac{n-1}{n} (1 - m_f)^2 \left(\frac{1}{n} \left(\frac{1}{2} f' + \frac{1}{2} p_I' \right) \right. \\
& \left. \left. + \frac{n-1}{n} \left(\frac{1}{2} f' + \frac{1}{2} (1 - m_m)^2 p_x' \right) \right) \right) \quad (S89) \\
& + \frac{1}{2} (1 - m_f)(1 - m_m) \left(\frac{1}{n} \left(\frac{1}{2} f' + \frac{1}{2} p_I' \right) \right. \\
& \left. + \frac{n-1}{n} \left(\frac{1}{2} f' + \frac{1}{2} (1 - m_m)^2 p_x' \right) \right)
\end{aligned}$$

719 That is: with probability $1/2$ the gene we pick comes from the juvenile's mother, in which
720 case the consanguinity is that between the mother and the father of the aunt, which is, with
721 probability $1/n$ the aunt is the juvenile's mother, and with probability $1/2$ the gene comes
722 from the juvenile's maternal grandmother, and the consanguinity is f' , with probability $1/2$
723 the gene comes from the juvenile's maternal grandfather, and the consanguinity is that of the
724 maternal grandfather to himself p_I' , and with probability $(n-1)/n$ the aunt is not the juvenile's
725 mother, with probability $(1 - m_f)^2$ neither of the two females disperses, with probability $1/n$
726 the aunt and the mother have a same father, with probability $1/2$ the gene comes from the
727 mother's mother, and the consanguinity is f' , and with probability $1/2$ the gene comes from
728 the mother's father, and the consanguinity is p_I' , and with probability $(n-1)/n$ the aunt and the

729 mother do not have a same father, with probability $1/2$ the gene comes from the juvenile's
730 maternal grandmother, and the consanguinity is f' , and with probability $1/2$ the gene comes
731 from the juvenile's grandfather, with probability $(1 - m_m)^2$ neither of the maternal
732 grandfather nor the aunt's father disperses, and the consanguinity is p_x' ; and with probability
733 $1/2$ that the gene we pick come from the juvenile's father, in which case the consanguinity is
734 that between the father and the father of the aunt, which is, with probability $(1 - m_f)(1 -$
735 $m_m)$ neither the aunt nor the father disperses, and with probability $1/n$ the aunt and the father
736 share one father, with probability $1/2$ the gene comes from the paternal grandmother, and the
737 consanguinity is f' , with probability $1/2$ the gene comes from the paternal grandfather, and
738 the consanguinity is p_1' , and with probability $(n-1)/n$ the aunt and the father do not share one
739 father, with probability $1/2$ the gene comes from the paternal grandmother, and the
740 consanguinity is f' , with probability $1/2$ the gene comes from the paternal grandfather, with
741 probability $(1 - m_m)^2$ neither of the maternal grandfather nor the aunt's father disperses, and
742 the consanguinity is p_x' . Hence the consanguinity between the focal juvenile and the parent of
743 the aunt p_{JMAP} can be given as

$$p_{JMAP} = \frac{1}{2}p_{JMAM} + \frac{1}{2}p_{JMAF} \quad (S90)$$

744 Similarly, p_{JMGP} which is the consanguinity between the focal juvenile and its maternal
745 grandparents, can be given as

$$p_{JMGP} = \frac{1}{2}p_{JMGM} + \frac{1}{2}p_{JMGF} \quad (S91)$$

746 Now we consider the consanguinity through paternal grandparents. The consanguinity
747 between the focal juvenile and its paternal grandmother p_{JPGM} is

$$p_{JPGM} = \frac{1}{2}(1 - m_f)(1 - m_m) \left(\frac{1}{n} \left(\frac{1}{2}p_1' + \frac{1}{2}f' \right) + \frac{n-1}{n} \left(\frac{1}{2}(1 - m_f)^2 p_x' + \frac{1}{2}f' \right) \right) + \frac{1}{2} \left(\frac{1}{2}p_1' + \frac{1}{2}f' \right) \quad (S92)$$

748 That is: with probability 1/2 the gene we pick comes from the juvenile's mother, in which
749 case the consanguinity is with probability $(1 - m_f)(1 - m_m)$ neither the mother nor the
750 father disperses, with probability 1/n the mother and the father share one mother, with
751 probability 1/2 the gene comes from the maternal grandmother, and the consanguinity is p_I ,
752 with probability 1/2 the gene comes from the maternal grandfather, and the consanguinity is
753 f' , and with probability $(n-1)/n$ the mother and the father do not share one mother, with
754 probability 1/2 the gene comes from the maternal grandmother, with probability $(1 - m_f)^2$
755 neither of the two females disperses, and the consanguinity is p_x' , with probability 1/2 the
756 gene comes from the maternal grandfather, and the consanguinity is f' , with probability 1/2
757 the gene we pick comes from the juvenile's father, in which case the consanguinity is, with
758 probability 1/2 the gene comes from the paternal grandmother, and the consanguinity is p_I' ,
759 with probability 1/2 the gene comes from the paternal grandfather, and the consanguinity is
760 f' . The consanguinity between the focal juvenile and its paternal grandfather p_{JPGF} is

$$p_{JPGF} = \frac{1}{2}(1 - m_f)(1 - m_m) \left(\frac{1}{n} \left(\frac{1}{2}f' + \frac{1}{2}p_I' \right) + \frac{n-1}{n} \left(\frac{1}{2}f' + \frac{1}{2}(1 - m_m)^2 p_x' \right) \right) + \frac{1}{2} \left(\frac{1}{2}f' + \frac{1}{2}p_I' \right) \quad (S93)$$

761 That is: with probability 1/2 the gene we pick comes from the juvenile's mother, in which
762 case the consanguinity is, with probability $(1 - m_f)(1 - m_m)$ neither the mother nor the
763 father disperses, and with probability 1/n the mother and the father share one mother, with
764 probability 1/2 the gene comes from the maternal grandmother, and the consanguinity is f' ,
765 with probability 1/2 the gene comes from the maternal grandfather, and the consanguinity is
766 p_I' , and with probability $(n-1)/n$ the mother and the father do not share one mother, with
767 probability 1/2 the gene comes from the maternal grandmother, and the consanguinity is f' ,
768 with probability 1/2 the gene comes from the maternal grandfather, with probability
769 $(1 - m_m)^2$ neither of the two males disperses, and the consanguinity is p_x' , with probability

770 1/2 the gene we pick comes from the juvenile's father, in which case the consanguinity is,
 771 with probability 1/2 the gene comes from the paternal grandmother, and the consanguinity is
 772 f' , and with probability 1/2 the gene comes from the paternal grandfather, and the
 773 consanguinity is p_I' . The consanguinity between the focal juvenile and the mother of a
 774 random adult male in its father's social group p_{JPUM} is

$$\begin{aligned}
 p_{JPUM} = & \frac{1}{2}(1 - m_f)(1 - m_m) \left(\frac{1}{n} \left(\frac{1}{2} p_I' + \frac{1}{2} f' \right) + \frac{n-1}{n} \left(\frac{1}{2} (1 - m_f)^2 p_x' + \frac{1}{2} f' \right) \right) \\
 & + \frac{1}{2} \left(\frac{1}{n} \left(\frac{1}{2} p_I' + \frac{1}{2} f' \right) \right. \\
 & + \frac{n-1}{n} (1 - m_m)^2 \left(\frac{1}{n} \left(\frac{1}{2} p_I' + \frac{1}{2} f' \right) \right. \\
 & \left. \left. + \frac{n-1}{n} \left(\frac{1}{2} (1 - m_f)^2 p_x' + \frac{1}{2} f' \right) \right) \right)
 \end{aligned}
 \tag{S94}$$

775 That is: with probability 1/2 the gene we pick comes from the juvenile's mother, in which
 776 case the consanguinity is, with probability $(1 - m_f)(1 - m_m)$ neither the mother nor the
 777 father's social partner ("uncle" hereafter) disperses, with probability $1/n$ the mother and the
 778 uncle share one mother, with probability 1/2 the gene comes from the maternal grandmother,
 779 and the consanguinity is p_I' , with probability 1/2 the gene comes from the maternal
 780 grandfather, and the consanguinity is f' , with probability $(n-1)/n$ the mother and the uncle do
 781 not share one mother, with probability 1/2 the gene comes from the maternal grandmother,
 782 with probability $(1 - m_f)^2$ neither of the maternal grandmother nor the uncle's mother
 783 disperses, and the consanguinity is p_x' , with probability 1/2 the gene comes from the maternal
 784 grandfather, and the consanguinity is f' , and with probability 1/2 the gene we pick comes
 785 from the juvenile's father, in which case the consanguinity is, with probability $1/n$ the uncle
 786 is the juvenile's father, and with probability 1/2 the gene comes from the paternal
 787 grandmother, and the consanguinity is p_I' , with probability 1/2 the gene comes from the
 788 paternal grandfather, and the consanguinity is f' , with probability $(n-1)/n$ the uncle is not the

789 juvenile's father, with probability $(1 - m_m)^2$ neither of the two males disperses, with
790 probability $1/n$ the uncle and the father have a same mother, with probability $1/2$ the gene
791 comes from the paternal grandmother, and the consanguinity is p_I' , with probability $1/2$ the
792 gene comes from the paternal grandfather, and the consanguinity is f' , with probability $(n-$
793 $1)/n$ the uncle and the father do not have a same mother, with probability $1/2$ the gene comes
794 from the paternal grandmother, with probability $(1 - m_f)^2$ neither of the paternal
795 grandmother nor the uncle's mother disperses, and the consanguinity is p_x' , with probability
796 $1/2$ the gene comes from the paternal grandfather, and the consanguinity is f' . The
797 consanguinity between the focal juvenile and the father of an uncle p_{JPUF} is

$$\begin{aligned}
p_{JPUF} = & \frac{1}{2}(1 - m_f)(1 - m_m) \left(\frac{1}{n} \left(\frac{1}{2}f' + \frac{1}{2}p_I' \right) + \frac{n-1}{n} \left(\frac{1}{2}f' + \frac{1}{2}(1 - m_m)^2 p_x' \right) \right) \\
& + \frac{1}{2} \left(\frac{1}{n} \left(\frac{1}{2}f' + \frac{1}{2}p_I' \right) \right. \\
& + \frac{n-1}{n} (1 - m_m)^2 \left(\frac{1}{n} \left(\frac{1}{2}f' + \frac{1}{2}p_I' \right) \right. \\
& \left. \left. \left. + \frac{n-1}{n} \left(\frac{1}{2}f' + \frac{1}{2}(1 - m_m)^2 p_x' \right) \right) \right) \right)
\end{aligned} \tag{S95}$$

798 That is: with probability $1/2$ the gene we pick comes from the juvenile's mother, in which
799 case the consanguinity is, with probability $(1 - m_f)(1 - m_m)$ neither the mother nor the
800 uncle disperses, and with probability $1/n$ the mother and the uncle share one father, and with
801 probability $1/2$ the gene comes from the maternal grandmother, and the consanguinity is f' ,
802 and with probability $1/2$ the gene comes from the maternal grandfather, and the consanguinity
803 is p_I' , and with probability $(n-1)/n$ the mother and the uncle do not share one father, with
804 probability $1/2$ the gene comes from the maternal grandmother, and the consanguinity is f' ,
805 with probability $1/2$ the gene comes from the maternal grandfather, with probability
806 $(1 - m_m)^2$ neither the uncle's father of nor the paternal grandfather disperses, and the
807 consanguinity is p_x' , with probability $1/2$ the gene we pick comes from the juvenile's father,

808 in which case the consanguinity is, with probability $1/n$ the uncle is the juvenile's father, and
809 the consanguinity is that between the juvenile's father and its paternal grandfather which is
810 $\frac{1}{2}f' + \frac{1}{2}p_1'$, and with probability $(n-1)/n$ the uncle is not the juvenile's father, with probability
811 $(1 - m_m)^2$ neither of the two males disperses, and with probability $1/n$ the uncle and the
812 father have a same father, with probability $1/2$ the gene comes from the paternal
813 grandmother, and the consanguinity is f' , with probability $1/2$ the gene comes from the
814 paternal grandfather, and the consanguinity is p_1 , and with probability $(n-1)/n$ the uncle and
815 the father do not have a same father, with probability $1/2$ the gene comes from the paternal
816 grandmother, and the consanguinity is f' , with probability $1/2$ the gene comes from the
817 paternal grandfather, with probability $(1 - m_m)^2$ neither the grandfather nor the uncle's
818 father disperses, and the consanguinity is p_x' . Hence the consanguinity between the focal
819 juvenile and its paternal grandparents p_{JPGP} is

$$p_{JPGP} = \frac{1}{2}p_{JPGM} + \frac{1}{2}p_{JPGF} \quad (S96)$$

820 Similarly, the consanguinity between the focal juvenile and the parent of an uncle p_{JPUP} is

$$p_{JPUP} = \frac{1}{2}p_{JPUM} + \frac{1}{2}p_{JPUF} \quad (S97)$$

821

822 *1.73 / Convergence stable strategy*

823 Solving expression (S86), we can get all the consanguinities:

$$\begin{aligned} p_{JMGM} = & (-2\Delta m(M - 2\bar{m} + 1)(1 - \bar{m}) \\ & + (m_f(10 + H_f - 2m_f) - 8 + 6m_m - m_f(6 + H_f - m_f)m_m \\ & + (2 - 3m_f)m_m^2 - (1 - m_f)m_m^3)n - 4\bar{m}(2 - \bar{m})n^2)/(8n(2\bar{m} - 1 \\ & - 4\bar{m}^2 + 3M - 4\bar{m}(2 - \bar{m})n)) \end{aligned} \quad (S98)$$

$$p_{\text{JMGF}} = (2\Delta m(M - 2\bar{m} + 1)(1 - \bar{m})) \quad (\text{S99})$$

$$\begin{aligned} &+ (m_f^2(2 - 3m_m) - 8 - m_f^3(1 - m_m) + m_m(10 + H_m - 2m_m) \\ &- m_f(m_m(6 + H_m - m_m) - 6))n - 4\bar{m}(2 - \bar{m})n^2 / (8n(2\bar{m} - 1 \\ &- 4\bar{m}^2 + 3M - 4\bar{m}(2 - \bar{m})n)) \end{aligned}$$

$$p_{\text{JMGP}} = 1/8 - (7(M - 2\bar{m} + 1)) / (8(2\bar{m} - 1 - 4\bar{m}^2 + 3M - 4\bar{m}(2 - \bar{m})n)) \quad (\text{S100})$$

$$p_{\text{JMAM}} = -(((-2\Delta m(H_f + 1)(1 - \bar{m}) - \Delta m(-10 + 2m_f^3 + m_f(H_m - 6m_m + 16)) \quad (\text{S101})$$

$$\begin{aligned} &- 3m_f^2(3 - m_m) - H_m + 4m_m)n + (8 + m_f^4 - m_f^3(5 - m_m) \\ &+ (H_m - 3m_m + 4)m_m + m_f(3 - m_m)(H_m - 4) - m_f^2(m_m - 11 \\ &+ m_m^2))n^2) / ((8n^2(2\bar{m} - 1 - 4\bar{m}^2 + 3M - 4\bar{m}(2 - \bar{m})n)) \end{aligned}$$

$$p_{\text{JMAF}} = ((-2\Delta m(H_f + 1)(1 - \bar{m}) - \Delta m(H_f(2m_f - 5) - 2 + 4m_m) \quad (\text{S102})$$

$$\begin{aligned} &+ m_f(3m_f - 8)m_m - (1 - m_f)m_m^2)n + (m_f^4 - 8 - m_f^3(5 - m_m) \\ &+ m_m(4 + H_m - m_m) - m_f((H_m - 3m_m + 6)m_m - 4) - m_f^2(m_m \\ &- 5 + m_m^2))n^2) / ((8n^2(2\bar{m} - 1 - 4\bar{m}^2 + 3M - 4\bar{m}(2 - \bar{m})n)) \end{aligned}$$

$$p_{\text{JMAP}} = \frac{m_m(4 + m_m(n - 1)) - 3m_f^2(n - 1) - 8n - 2m_f(2 + m_m - (4 - m_m)n)}{8n(2\bar{m} - 1 - 4\bar{m}^2 + 3M - 4\bar{m}(2 - \bar{m})n)} \quad (\text{S103})$$

$$p_{\text{JPGM}} = (-2\Delta m(M - 2\bar{m} + 1)(1 - \bar{m})) \quad (\text{S104})$$

$$\begin{aligned} &+ (-8 + m_f(10 + H_f - 2m_f) + 6m_m - M(6 + H_f - m_f) \\ &+ (2 - 3m_f)m_m^2 - (1 - m_f)m_m^3)n - 4\bar{m}(2 - \bar{m})n^2 / (8n(2\bar{m} - 1 \\ &- 4\bar{m}^2 + 3M - 4\bar{m}(2 - \bar{m})n)) \end{aligned}$$

$$p_{\text{JPGF}} = (2\Delta m(M - 2\bar{m} + 1)(1 - \bar{m}) + (-8 + m_f^2(2 - 3m_m) - m_f^3(1 - m_m)) \quad (\text{S105})$$

$$\begin{aligned} &+ m_m(10 + H_m - 2m_m) - m_f(-6 + m_m(6 + H_m - m_m)))n \\ &- 4\bar{m}(2 - \bar{m})n^2 / (8n(2\bar{m} - 1 - 4\bar{m}^2 + 3M - 4\bar{m}(2 - \bar{m})n)) \end{aligned}$$

$$p_{\text{JPGP}} = 1/8 - (7(M - 2\bar{m} + 1)) / (8(2\bar{m} - 1 - 4\bar{m}^2 + 3M - 4\bar{m}(2 - \bar{m})n)) \quad (\text{S106})$$

$$p_{\text{JPUM}} = ((2\Delta m(H_m + 1)(1 - \bar{m}) + \Delta m(-2 - m_f^2(1 - m_m) + H_m(2m_m - 5) \quad (\text{S107})$$

$$+ m_f(3H_m - 2m_m + 4))n + (-8 + m_f^3(1 - m_m) - m_f^2(3 + H_m - 3m_m) + m_f(4 + (H_m - m_m)(2 + m_m)) + m_m(4 + m_m(5 + H_m - 3m_m)))n^2) / ((8n^2(2\bar{m} - 1 - 4\bar{m}^2 + 3M - 4\bar{m}(2 - \bar{m})n)))$$

$$p_{\text{JPUP}} = ((-2\Delta m(H_m + 1)(1 - \bar{m}) - \Delta m(-10 + 6m_f - m_f^2) \quad (\text{S108})$$

$$+ (H_m - 6m_m + 16)m_m - 3(3 - m_f)m_m^2 + 2m_m^3)n + (-8 - m_f^3(1 - m_m) + m_f^2(5 + H_m - 3m_m) - m_m(-12 + m_m(11 + H_m - 3m_m)) + m_f(-4 + m_m(2 + m_m - m_m^2)))n^2) / ((8n^2(2\bar{m} - 1 - 4\bar{m}^2 + 3M - 4\bar{m}(2 - \bar{m})n)))$$

$$p_{\text{JPUP}} = \frac{m_f^2(n - 1) - 8n + m_m(-4 - 3m_m(n - 1) + 8n) - 2m_f(m_m - 2 + m_m n)}{8n(2\bar{m} - 1 - 4\bar{m}^2 + 3M - 4\bar{m}(2 - \bar{m})n)} \quad (\text{S109})$$

824 where $\Delta m = m_f - m_m$, $\bar{m} = (m_f + m_m)/2$, $M = m_f m_m$, $\Delta b = b_f - b_m$, $\bar{b} = (b_f + b_m)/2$,

825 $H_f = (m_f - 2)m_f$, $H_m = (m_m - 2)m_m$, and by substituting these values, we obtain z_{PO}^* ,

826 z_{PD}^* , z_{PS}^* , z_{MO}^* , z_{MD}^* , z_{MS}^* , z_{FO}^* , z_{FD}^* and z_{FS}^* for the optimal values of left-handedness when

827 considering within-group combat

$$z_{\text{PO}}^* = (((n - 1)(\Delta m(b_f(-4 + 3m_f + m_m) - b_m(m_f - 4 + 3m_m)) - 8\bar{b}\bar{m}(2 - \bar{m})n))) / ((-2\Delta m(b_f(3m_f - 4 + m_m) - b_m(m_f - 4 + 3m_m)) - 4(8 - 4(2 + b_m)m_f + (1 - \Delta b)m_f^2 + 2M(3 + 2\bar{b}) + m_m(-8 - b_f(4 - m_m) + m_m - b_m m_m))n - 16\bar{m}(\bar{b} + 1)(2 - \bar{m})n^2)) \quad (\text{S110})$$

$$z_{\text{PD}}^* = ((b_f(n - 1)(-2m_f(2 + m_m) + (H_m - 2m_m)(n - 1) - 2m_f(2 - m_m)n + m_f^2(3 + n))) / ((-2(8 + H_f - 6m_f - 8m_m + 6m_f m_m + m_m^2)n - 8\bar{m}(2 - \bar{m})n^2 + 2b_f(n - 1)(-2m_f(2 + m_m) + (H_m - 2m_m)(n - 1) - 2m_f(2 - m_m)n + m_f^2(3 + n)))) \quad (\text{S111})$$

$$\begin{aligned}
z_{\text{PS}}^* = & ((b_m(n-1)(m_f^2(n-1) - 2m_f(2-m_m)(n-1) + m_m(-4(1+n) + m_m(3 \\
& + n)))) / ((2b_m\Delta m(m_f - 4 + 3m_m) \\
& - 2(8 + (1 + 2b_m)m_f^2 + m_f(-8 - 4b_m(2 - m_m) + 6m_m) \\
& + m_m(m_m - 8 - 2b_m m_m))n - 8\bar{m}(1 + b_m)(2 - \bar{m})n^2))
\end{aligned} \tag{S112}$$

$$\begin{aligned}
z_{\text{MO}}^* = & (((n-1)(2\Delta m(b_f(H_f + 1) + b_m(H_m + 1))(1 - \bar{m}) + \Delta m(2b_m - 2b_f(3 \\
& - m_m) + b_m m_m(2 - m_f(2 - m_m) + H_m - 2m_m) + b_f m_f(8 - 2m_m \\
& - 2m_f(2 - \bar{m})))n - 8\bar{b}\bar{m}(2 - \bar{m})n^2))) \\
& / ((2(2n(-2\Delta m(1 - 2\bar{m} + M)(1 - \bar{m}) \\
& + (-8 + m_f(10 + H_f - 2m_f) + 6m_m - m_f(6 + H_f - m_f)m_m \\
& + (2 - 3m_f)m_m^2 - (1 - m_f)m_m^3)n - 4\bar{m}(2 - \bar{m})n^2) + b_m(n \\
& - 1)(2\Delta m(H_m + 1)(1 - \bar{m}) + \Delta m(2 + m_m(2 - m_f(2 - m_m) + H_m \\
& - 2m_m))n - 4\bar{m}(2 - \bar{m})n^2) + b_f(n-1)(2\Delta m(H_f + 1)(1 - \bar{m}) \\
& + \Delta m(-2(3 - m_m) + m_f(8 - 2m_m - 2m_f(2 - \bar{m})))n \\
& - 4\bar{m}(2 - \bar{m})n^2)))
\end{aligned} \tag{S113}$$

$$\begin{aligned}
z_{\text{MD}}^* = & ((b_f(n-1)(2\Delta m(H_f + 1)(1 - \bar{m}) + \Delta m(-2(3 - m_m) + m_f(8 - 2m_m \\
& - 2m_f(2 - \bar{m})))n - 4\bar{m}(2 - \bar{m})n^2))) \\
& / ((2(n(-2\Delta m(1 - 2\bar{m} + M)(1 - \bar{m}) \\
& + (-8 + m_f(10 + H_f - 2m_f) + 6m_m - m_f(6 + H_f - m_f)m_m \\
& + (2 - 3m_f)m_m^2 - (1 - m_f)m_m^3)n - 4\bar{m}(2 - \bar{m})n^2) + b_f(n \\
& - 1)(2\Delta m(H_f + 1)(1 - \bar{m}) + \Delta m(-2(3 - m_m) + m_f(8 - 2m_m \\
& - 2m_f(2 - \bar{m})))n - 4\bar{m}(2 - \bar{m})n^2)))
\end{aligned} \tag{S114}$$

$$\begin{aligned}
z_{\text{MS}}^* = & ((b_m(n-1)(2\Delta m(H_m+1)(1-\bar{m}) + \Delta m(2+m_m(2-m_f(2-m_m)+H_m \\
& - 2m_m))n - 4\bar{m}(2-\bar{m})n^2))) / ((2n(-2\Delta m(1-2\bar{m}+M)(1-\bar{m}) \\
& + (-8+m_f(10+H_f-2m_f) + 6m_m - m_f(6+H_f-m_f)m_m \\
& + (2-3m_f)m_m^2 - (1-m_f)m_m^3)n - 4\bar{m}(2-\bar{m})n^2) + 2b_m(n \\
& - 1)(2\Delta m(H_m+1)(1-\bar{m}) + \Delta m(2+m_m(2-m_f(2-m_m)+H_m \\
& - 2m_m))n - 4\bar{m}(2-\bar{m})n^2)))
\end{aligned} \tag{S115}$$

$$\begin{aligned}
z_{\text{FO}}^* = & -(((n-1)(-2\Delta m(b_f(H_f+1) + b_m(H_m+1))(1-\bar{m}) - \Delta m(b_m(-6 \\
& + m_m(8+H_m-2m_m) + m_f(2+H_m)) + b_f(2+m_f(2-2m_m \\
& - 2m_f(2-\bar{m}))))n - 8\bar{b}\bar{m}(2-\bar{m})n^2))) \\
& / ((4n(-2\Delta m(1-2\bar{m}+M)(1-\bar{m}) \\
& + (8+m_f(H_f-6) - 10m_m + m_f(6-H_f+m_f)m_m \\
& + (4-3m_f)m_m^2 - (1-m_f)m_m^3)n + 4\bar{m}(2-\bar{m})n^2) - 2b_m(n \\
& - 1)(-2\Delta m(H_m+1)(1-\bar{m}) - \Delta m(-6+m_m(8+H_m-2m_m) \\
& + m_f(2+H_m))n - 4\bar{m}(2-\bar{m})n^2) - 2b_f(n-1)(-2\Delta m(H_f+1)(1 \\
& - \bar{m}) - \Delta m(2+m_f(2-2m_m-2m_f(2-\bar{m})))n \\
& - 4\bar{m}(2-\bar{m})n^2)))
\end{aligned} \tag{S116}$$

$$\begin{aligned}
z_{\text{FD}}^* = & ((b_f(n-1)(2\Delta m(H_f+1)(1-\bar{m}) + \Delta m(2+m_f(2-2m_m \\
& - 2m_f(2-\bar{m})))n + 4\bar{m}(2-\bar{m})n^2))) \\
& / ((2n(-2\Delta m(1-2\bar{m}+M)(1-\bar{m}) \\
& + (8+m_f(H_f-6) - 10m_m + m_f(6-H_f+m_f)m_m \\
& + (4-3m_f)m_m^2 - (1-m_f)m_m^3)n + 4\bar{m}(2-\bar{m})n^2) \\
& + 2b_f(n-1)(2\Delta m(H_f+1)(1-\bar{m}) - \Delta m(2+m_f(2-2m_m \\
& - 2m_f(2-\bar{m})))n - 4\bar{m}(2-\bar{m})n^2)))
\end{aligned} \tag{S117}$$

$$\begin{aligned}
z_{FS}^* = & -(((b_m(n-1)(-m_f^2(H_m+1) - n)(n-1) + 2m_f(n-1)(H_m+1) - (2 \\
& - m_m)n) + m_m((2 - m_m)(H_m+1) + (-6 + m_m(8 + H_m \\
& - 2m_m))n - (4 - m_m)n^2)))) / ((2n(-2\Delta m(1 - \bar{m}) + M)(1 - \bar{m}) \\
& + (8 + m_f(-6 + H_f) - 10m_m + m_f(6 - H_f + m_f)m_m \tag{S118} \\
& + (4 - 3m_f)m_m^2 - (1 - m_f)m_m^3)n + 4\bar{m}(2 - \bar{m})n^2) - 2b_m(n \\
& - 1)(-2\Delta m(H_m+1)(1 - \bar{m}) - \Delta m(-6 + m_m(8 + H_m - 2m_m) \\
& + m_f(2 + H_m))n - 4\bar{m}(2 - \bar{m})n^2)))
\end{aligned}$$

828 where $\Delta m = m_f - m_m$, $\bar{m} = (m_f + m_m)/2$, $M = m_f m_m$, $\Delta b = b_f - b_m$, $\bar{b} = (b_f + b_m)/2$,
829 $H_f = (m_f - 2)m_f$, $H_m = (m_m - 2)m_m$. We set the female dispersal rate $m_f = 0.5$, the
830 relative importance of combat relative to all types of competition for the female and male $b_f =$
831 $b_m = 1$, and number of the number of individuals each sex born in the same patch $n = 5$ for
832 Figure S3c, S5 and S6.

833

834 Here we show what if there are differences between the parental genetic effects on daughters
835 and those on sons in the context of within-group combats, hence left-handedness is
836 marginally selfish. Under female-biased dispersal, the relatedness between the parent and the
837 social partner through daughters' side would be lower than that through sons' side, hence
838 genes carried by parents would favour a higher level of left-handedness for daughters than for
839 sons; while under male-biased dispersal, the relatedness between social partners through
840 daughters' side would be higher than that through sons' side, genes carried by parent would
841 favour a lower expression level of left-handedness for daughters than for sons (Figure S6).

842

843 **2 | Between-group combat**

844 Here we make an illustration of the scenario where left-handedness is marginally altruistic,
845 when between-group combat is the most frequent form of combat, as left-handed individuals
846 are more likely to win the fights for their group, and this incurs a cost to themselves. The

847 models here are based on the same life cycle, but with different fitness function. We
848 investigate with the same process as that in “Within-group combat”, starting from “Kin
849 selection”, through “Sex-biased dispersal”, “Parent-of-origin effect”, “Sex-specific effects” to
850 “Parental genetic effects”. All the consanguinities are the same as those in the context of
851 “Within-group combat”.

852

853 **2.1 | Kin selection**

854 We assume that an individual's payoff from between-group combat is proportional to the ratio
855 of the competitive ability of the local group and the average competitive ability in the whole
856 population. We assume that each group's competitive ability is proportional to the average
857 disposition to the opposite handedness within their social arena. That is, with proportion y the
858 members of the focal group are left-handed and have competitive ability $1-z$, where z is the
859 average proportion of left-handers in the whole population. And with proportion $1-y$ the
860 members of the focal group are right handed and have competitive ability z . And the average
861 competitive ability in the whole population is made up of the proportion z of left-handed
862 individuals in an average group with competitive ability $1-z$ and the proportion $1-z$ of right-
863 handed individuals in an average group with competitive ability z , which gives

$$y \frac{(1-z)}{z(1-z) + (1-z)z} + (1-y) \frac{z}{z(1-z) + (1-z)z} \quad (\text{S119})$$

864 which simplifies to

$$\frac{y}{2z} + \frac{1-y}{2(1-z)} \quad (\text{S120})$$

865 Accordingly, the fitness of a juvenile w' is

$$w' = \left(1 - b_f + b_f \left(\frac{y_{Mo}}{2z} + \frac{1-y_{Mo}}{2(1-z)} \right) \right) (1 - c_f x_{Mo}) \left(1 - b_m \right. \\ \left. + b_m \left(\frac{y_{Fa}}{2z} + \frac{1-y_{Fa}}{2(1-z)} \right) \right) (1 - c_m x_{Fa}) \quad (\text{S121})$$

866 Similarly, the average fitness of a random juvenile \bar{w}' can be described by evaluating
 867 expression (S121) at $x_{Mo} = y_{Mo} = z_f$, $x_{Fa} = y_{Fa} = z_m$, and the relative fitness of the focal
 868 juvenile W' is w'/\bar{w}'

$$W' = \left(1 - b_f + b_f \left(\frac{y_{Mo}}{2z} + \frac{1 - y_{Mo}}{2(1 - z)}\right)\right) \left(\frac{1 - c_f x_{Mo}}{1 - c_f z_f}\right) (1 - b_m) \quad (S122)$$

$$+ b_m \left(\frac{y_{Fa}}{2z} + \frac{1 - y_{Fa}}{2(1 - z)}\right) \left(\frac{1 - c_m x_{Fa}}{1 - c_m z_m}\right)$$

869 Similarly using expression (S122), we obtain the condition for an increase in left-handedness
 870 to be favoured when we consider between-group combat

$$\frac{(b_f + b_m)(1 - 2z)r_j}{2(1 - z)z} - \frac{c_f r_o}{1 - c_f z} - \frac{c_m r_o}{1 - c_m z} > 0 \quad (S123)$$

871 Letting the LHS of expression (S7) be $f(z)$, then at evolutionary equilibrium, if there is an
 872 intermediate level of left-handedness z'^* , this satisfies $f(z'^*) = 0$, we get the optimal value
 873 of developing as left-handed for a random individual when we consider between-group
 874 combat

$$z'^* = \frac{1}{2} \frac{(b_f + b_m)r_j}{r_j(b_f + b_m) \mp 2r_o} \quad (S124)$$

875 Substituting all the parameters of relatedness to expression (S124), we can get the optimal
 876 value of left-handedness for the genes at locus G when left-handedness is altruistic, z'^*

$$z'^* = \frac{1}{2} \frac{b_f + b_m}{2 + b_f + b_m + 2(1 - (1 - m)^2)(n - 1)} \quad (S125)$$

877

878 2.2 | Sex-biased dispersal

879 Here we relax the assumption of no sex bias in dispersal i.e. $m_f \neq m_m$, hence $p_{JA} \neq p_{JU}$. In this
 880 section, the relative fitness function is the same as expression (S122). Using expressions
 881 (S122) to calculate the corresponding partial derivatives, we obtain the condition for an
 882 increase in left-handedness to be favoured when we consider between-group combat

$$-\frac{(b_f r_{JA} + b_m r_{JU})(1-2z)}{2(1-z)z} - \frac{c_f r_O}{1-c_f z} - \frac{c_m r_O}{1-c_m z} > 0 \quad (S126)$$

883 Letting $f(z)$ be the LHS of expression (S126), than at evolutionary equilibrium, if there is an
 884 intermediate level of left-handedness, this satisfies $f(z'^*) = 0$, we obtain the optimum of
 885 left-handedness in the context of between-group combat. For example, letting $c_f = c_m = 1$, i.e.
 886 there is no sex difference in the cost of developing as left-handed, we have

$$z'^* = \frac{1}{2} \frac{b_f r_{JA} + b_m r_{JU}}{b_f r_{JA} + b_m r_{JU} + 2r_O} \quad (S127)$$

887 This is the convergence stable strategy, i.e. the overall optima level of left-handedness for all
 888 the loci involved, as $f'(z) < 0$ is true for all the values of z . Here all the consanguinity are
 889 the same as the previous section under the situation of “within-group combat”, substituting all
 890 the parameters of relatedness to expression (S21), we obtain the optimal value of left-
 891 handedness z'^*

$$z'^* = (2\Delta b \Delta m (1 - \bar{m}) + b_f (4 + H_f - H_m) n + b_m (4 - H_f + H_m) n) / (4\Delta b \Delta m (1 - \bar{m}) + 2(8(1 - \bar{m})^2 + b_f (4 + H_f - H_m + b_m (4 - H_f + H_m)) n + 16(2 - \bar{m}) \bar{m} n^2)) \quad (S128)$$

892 where $\Delta m = m_f - m_m$, $\bar{m} = (m_f + m_m)/2$, $\Delta b = b_f - b_m$, $\bar{b} = (b_f + b_m)/2$, $H_f = (m_f -$
 893 $2)m_f$, $H_m = (m_m - 2)m_m$.

894

895 **2.3 | Parent-of-origin effects**

896 Here we consider how the origin of genes mediates the role of kin selection in the optima of
 897 different set of genes, under the circumstances of between-group combat. In this section the
 898 conditions that favour the increase of left-handedness in the population and the relatedness
 899 are the same as previous section “§S1.5 Parental-of-origin effects” when considering within-
 900 group combat, while the relative fitness function change to expression (S122). Letting the
 901 LHS of the expression (S28) be $f(z)$, then at evolutionary equilibrium, if there is an

902 intermediate level of left-handedness $z_M'^*$ and $z_M''^*$, which satisfies $f(z_M'^*) = 0$ and

903 $f(z_P'^*) = 0$, respectively, we obtain the optima

$$z_M'^* = \frac{1}{2} \frac{b_f r_{JA|-M} + b_m r_{JU|-M}}{2r_{O|-M} + b_f r_{JA|-M} + b_m r_{JU|-M}} \quad (S129)$$

$$z_P'^* = \frac{1}{2} \frac{b_f r_{JA|-P} + b_m r_{JU|-P}}{2r_{O|-P} + b_f r_{JA|-P} + b_m r_{JU|-P}} \quad (S130)$$

904 $f'(z) < 0$ is true for all the values of z , thus $z_M'^*$ and $z_P'^*$ are the optimal values of left-

905 handedness from the perspective of maternal- and paternal-origin genes, respectively.

906 Substituting all the parameters of relatedness, we obtain optimal value of maternal-origin

907 genes, $z_M'^*$

$$\begin{aligned} z_M'^* = & ((b_m(-2\Delta m(H_m + 1)(1 - \bar{m}) + 2\Delta m(1 - \bar{m})(1 - M - 2\bar{m} + 2H_m)n \\ & + (8 - 2\Delta m(1 - \bar{m})(M - 2\bar{m} + H_m))n^2) + b_f(H_f \\ & + 1)(-2\Delta m(1 - \bar{m}) + 2\Delta m(1 - \bar{m})(5 - 2\bar{m} + 2H_f + M)n \\ & + (8 + m_f^4 - m_f^3(5 - m_m) - (4 - m_m)H_m - m_f(8 + (H_m \\ & - 3m_m + 4)m_m) - m_f^2(-10 + 3m_m + H_m))n^2))) \\ & / ((2(-2b_m\Delta m(H_m + 1)(1 - \bar{m}) - 2\Delta m(1 - \bar{m})(b_m + 2(M \\ & - 2\bar{m} + 1) + b_m(M - m_f) + b_m(2H_m - m_m))n + (b_m(8 \\ & - 2\Delta m(1 - \bar{m})(M - 2\bar{m} + H_m)) - 4(1 - \bar{m})(-4 - m_f^2(1 \\ & - m_m) + m_m + m_m^2 - m_f(m_m^2 - 3)))n^2 + 16(2 - \bar{m})\bar{m}n^3 \\ & + b_f(-2\Delta m(H_f + 1)(1 - \bar{m}) + 2\Delta m(1 - \bar{m})(5 - 2\bar{m} + 2H_f \\ & + M)n + (8 + m_f^4 - m_f^3(5 - m_m) - (4 - m_m)H_m - m_f(8 \\ & + (H_m - 3m_m + 4)m_m) - m_f^2(-10 + H_m + 3m_m))n^2))) \end{aligned} \quad (S131)$$

908 With similar process, we obtain the optimal value left-handedness $z_P'^*$:

$$\begin{aligned}
z_P'^* = & ((-2b_m\Delta m(1 - \bar{m})(H_m + 1) + 2b_m\Delta m(1 - \bar{m})(5 + M - 2\bar{m} \\
& + 2H_m)n - 8b_f n^2 + b_m(-8 + (4 - m_f)H_f - H_m(4 + H_m \\
& - m_m) + M(4 + 2\bar{m}\Delta m + M - 4m_f - \Delta m))n^2 - 2b_f\Delta m(1 \\
& - \bar{m})(H_f + 1 + (2\bar{m} - 1 - 2H_f - M)n + ((2\bar{m} - 3)m_f \\
& - m_m)n^2))) / ((2(-2b_m\Delta m(1 - \bar{m})(H_m + 1) + 2\Delta m(1 \\
& - \bar{m})(2(M - 2\bar{m} + 1) + b_m(5 + M - 2\bar{m} + 2H_m))n \\
& + (b_m(-8 + (4 - m_f)H_f - H_m(4 + H_m - m_m) + M(4 \\
& + 2\bar{m}\Delta m + M - 4m_f - \Delta m)) - 4(1 - \bar{m})(4 - m_f^2(1 - m_m) \\
& + H_m - m_m - m_f(1 + m_m^2)))n^2 - 16(2 - \bar{m})\bar{m}n^3 \\
& + b_f(-8n^2 - 2\Delta m(1 - \bar{m})(H_f + 1 + (2\bar{m} - 1 - 2H_f - M)n \\
& + ((2\bar{m} - 3)m_f - m_m)n^2))))))
\end{aligned} \tag{S132}$$

909 The optimal value of left-handedness for the perspective of the whole genes of the individual

910 z'^* is

$$\begin{aligned}
z'^* = & (2\Delta b\Delta m(1 - \bar{m}) + (b_f(4 + H_f - H_m) + b_m(4 - H_f \\
& + H_m))n) / (4\Delta b\Delta m(1 - \bar{m}) - 2(b_m(H_f - H_m - 4) - 8 \\
& - b_f(4 + H_f - H_m) - 8\bar{m}(2 - \bar{m})(n - 1))n)
\end{aligned} \tag{S133}$$

911 where $\Delta m = m_f - m_m$, $\bar{m} = (m_f + m_m)/2$, $\Delta b = b_f - b_m$, $\bar{b} = (b_f + b_m)/2$, $H_f = (m_f -$
912 $2)m_f$, $H_m = (m_m - 2)m_m$. We set the female dispersal rate $m_f = 0.5$, the relative importance
913 of combat relative to all types of competition for the female and male $b_f = b_m = 1$, and the
914 number of individuals each sex born in the same patch $n = 5$ for Figure S4. For the zoomed-in
915 parts, the range of male dispersal rate m_m is from 0.499 to 0.501, the range of the equilibrium
916 frequency of left-handedness is from 0.09995 to 0.10005.

917

918 2.4 | Sex-specific effects

919 Here we consider how sex effects add to the mediation of kin selection on handedness under
920 the circumstances of between-group combat. In this section, the conditions that favour the

921 increase of left-handedness, the relatedness are the same as the previous section “§S1.6 Sex-
 922 specific effects” when considering within-group combat, while the relative fitness function
 923 changes to expression (S122). For locus G_1 which only controls the handedness trait of
 924 females, using similar methods as previous sections, letting the LHS of expression (S50) be
 925 $f(z)$, $f'(z) < 0$ is true for all the values of z and all of the four coefficients of relatedness
 926 above, at evolutionary equilibrium, if there is an intermediate level of left-handedness $z_f'^*$,
 927 this satisfies $f(z_f'^*) = 0$, we obtain the optimal value of left-handedness $z_f'^*$ for all the loci
 928 that control handedness only when they are carried by females

$$z_f'^* = \frac{1}{2} \frac{b_f r_{JA}}{r_{OM} + b_f r_{JA}} \quad (S134)$$

929 Similarly, we obtain the optimal value of locus G_2 when left-handedness is altruistic, $z_m'^*$

$$z_m'^* = \frac{1}{2} \frac{b_m r_{JU}}{r_{OF} + b_m r_{JU}} \quad (S135)$$

930 Similarly, we can obtain the optimal value for the locus G_1 from the perspective of maternal-
 931 origin genes, $z_{fM}'^*$, and that from the perspective of paternal-origin genes, $z_{fP}'^*$, and the
 932 optimal value for the locus G_2 from the perspective of maternal-origin genes and paternal-
 933 origin genes respectively: $z_{mM}'^*$ and $z_{mP}'^*$

$$z_{fM}'^* = \frac{1}{2} \frac{b_f r_{JA|M}}{r_{OM|M} + b_f r_{JA|M}} \quad (S136)$$

$$z_{fP}'^* = \frac{1}{2} \frac{b_f r_{JA|P}}{r_{OM|P} + b_f r_{JA|P}} \quad (S137)$$

$$z_{mM}'^* = \frac{1}{2} \frac{b_m r_{JU|M}}{r_{OF|M} + b_m r_{JU|M}} \quad (S138)$$

$$z_{mP}'^* = \frac{1}{2} \frac{b_m r_{JU|P}}{r_{OF|P} + b_m r_{JU|P}} \quad (S139)$$

934 Substituting all the relatedness in expressions (S134)-(S139) we obtain the optimal values of
 935 left-handedness when considering between-group combat:

$$z_f^{f*} = \frac{b_f(H_m - H_f + 2(2 - \Delta m(1 - \bar{m}))n)}{8n + 8\bar{m}(2 - \bar{m})(n - 1)n + 2b_f(H_m - H_f + 2(2 - \Delta m(1 - \bar{m}))n)} \quad (\text{S140})$$

$$\begin{aligned} z_{fM}^{f*} = & ((b_f((8 + H_f(4 + H_f - m_f) - H_m(4 - m_m)) \\ & + M(H_f - H_m + 2\bar{m} + 2m_m - M))n^2 - 2\Delta m(1 - \bar{m})(H_f + 1 \\ & + (2\bar{m} - 5 - 2H_f - M)n))) / ((2(2\Delta m(1 - \bar{m})(M - 2\bar{m} + 1)n \\ & + b_f(8 + H_f(4 + H_f - m_f) - H_m(4 - m_m) + M(H_f - H_m + 2\bar{m} \\ & + 2m_m - 4 - M))n^2 + 2n^2(-(1 - \bar{m})(-4 + M\Delta m - 2\bar{m}\Delta m + 2\bar{m} \\ & + 2m_f) + 4(2 - \bar{m})\bar{m}n) - 2b_f\Delta m(1 - \bar{m})(H_f + 1 + (2\bar{m} - 5 - 2H_f \\ & - M)n))) \end{aligned} \quad (\text{S141})$$

$$\begin{aligned} z_{fP}^{f*} = & -(((b_f(-8n^2 - 2\Delta m(1 - \bar{m})(H_f + 1 + (2\bar{m} - 1 - 2H_f - M)n + ((2\bar{m} \\ & - 3)m_f - m_m)n^2)))) / ((2(2\Delta m(1 - \bar{m})(M - 2\bar{m} + 1)(1 - m_m)n \\ & + 8b_f n^2 - 2(1 - \bar{m})(2\bar{m} + 2m_m - 4 + 2\bar{m}\Delta m - M\Delta m)n^2 \\ & + 8(2 - \bar{m})\bar{m}n^3 + 2b_f\Delta m(1 - \bar{m})(H_f + 1 + (2\bar{m} - 1 - 2H_f - M)n \\ & + ((2\bar{m} - 3)m_f - m_m)n^2)))) \end{aligned} \quad (\text{S142})$$

$$z_m^{f*} = \frac{b_m(H_f - H_m + 2(2 + \Delta m - \Delta m\bar{m})n)}{8n + 8\bar{m}(2 - \bar{m})(n - 1)n + 2b_m(H_f - H_m + 2(2 + \Delta m - \Delta m\bar{m})n)} \quad (\text{S143})$$

$$\begin{aligned} z_{mM}^{f*} = & ((-b_m(-2(1 - \bar{m})(H_m + 1)\Delta m - 2\Delta m(1 - \bar{m})(1 + M - 2\bar{m} + 2H_m)n \\ & + (-8 + 2\Delta m(1 - \bar{m})(M - 2\bar{m} + H_m))n^2))) \\ & / ((2(n(-2\Delta m(1 - \bar{m})(M - 2\bar{m} + 1) \\ & + 2(1 - \bar{m})(M\Delta m - 4 - 2\bar{m}\Delta m + 2\bar{m} + 2m_f)n - 8(2 - \bar{m})\bar{m}n^2) \\ & + b_m(2(1 - \bar{m})(H_m + 1)\Delta m - 2\Delta m(1 - \bar{m})(1 + M - 2\bar{m} + 2H_m)n \\ & + (-8 + 2\Delta m(1 - \bar{m})(M - 2\bar{m} + H_m))n^2)))) \end{aligned} \quad (\text{S144})$$

$$\begin{aligned}
z_{mP}{}^{*} = & -(((b_m \Delta m (-2(1 - \bar{m})(H_m + 1) + 2\Delta m(1 - \bar{m})(5 + M - 2\bar{m} + 2H_m)n \\
& + (-8 + (4 - m_f)H_f - H_m(4 + H_m - m_m) + M(4 + 2\bar{m}\Delta m + M \\
& - 4m_f - \Delta m)n^2))) / ((2(n(-2\Delta m(1 - \bar{m})(M - 2\bar{m} + 1) \\
& - 2(1 - \bar{m})(2\bar{m} - 4 + 2\bar{m}\Delta m + 2m_m - M\Delta m)n + 8(2 - \bar{m})\bar{m}n^2) \\
& + b_m(2(1 - \bar{m})(H_m + 1)\Delta m - 2\Delta m(1 - \bar{m})(5 + M - 2\bar{m} + 2H_m)n \\
& + (8 - H_f(4 - m_f) + m_m(-8 - (H_f - 3m_f + 4)m_f + 10m_m - M \\
& - M\Delta m - 5m_m^2 + m_m^3))n^2))))))
\end{aligned} \tag{S145}$$

936 where $\Delta m = m_f - m_m$, $\bar{m} = (m_f + m_m)/2$, $M = m_f m_m$, $\Delta b = b_f - b_m$, $\bar{b} = (b_f + b_m)/2$,
937 $H_f = (m_f - 2)m_f$, $H_m = (m_m - 2)m_m$. We set the female dispersal rate $m_f = 0.5$, the
938 relative importance of combat relative to all types of competition for the female and male $b_f =$
939 $b_m = 1$, and number of the number of individuals each sex born in the same patch $n = 5$ for
940 Figure S3b.

941

942 2.5 | Parental genetic effects

943 Here we consider how parental effects mediate handedness considering handedness under the
944 circumstances of between-group combat. In this section the coefficients of relatedness and all
945 the nine situations are the same as previous section “§S1.7 Parental genetic effects” when
946 considering within-group combat, but the relative fitness function changes to expression
947 (S122). Using similar methods as previous sections, letting the LHS of expression (S66) be
948 $f(z)$, $f'(z) < 0$ is true for all the values of z and all of the four relatedness, then at
949 evolutionary equilibrium, if there is an intermediate level of left-handedness $z_{PO}{}^{*}$, this
950 satisfies $f(z_{PO}{}^{*}) = 0$, we obtain the optimum of left-handedness from the perspective of
951 parent’s genes

$$z_{PO}{}^{*} = \frac{1}{2} \frac{b_f r_{JMAP} + b_m r_{JPUP}}{b_f r_{JMAP} + r_{JMGP} + r_{JPGP} + b_m r_{JPUP}} \tag{S146}$$

952 Similarly, we can obtain the optimal value of left-handedness from the perspective of parent's
 953 genes to its daughter

$$z_{PD}'^* = \frac{1}{2} \frac{b_f r_{JMAP}}{b_f r_{JMAP} + r_{JMGP}} \quad (S147)$$

954 the optimal value of left-handedness from the perspective of parent's genes to its son

$$z_{PS}'^* = \frac{1}{2} \frac{b_m r_{JPUP}}{r_{JPGP} + b_m r_{JPUP}} \quad (S148)$$

955 the optimal value of left-handedness from the perspective of mother's genes to her offspring

$$z_{MO}'^* = \frac{1}{2} \frac{b_f r_{JMAM} + b_m r_{JPUM}}{b_f r_{JMAM} + r_{JMGM} + r_{JPGM} + b_m r_{JPUM}} \quad (S149)$$

956 the optimal value of left-handedness from the perspective of mother's genes to her daughters

$$z_{MD}'^* = \frac{1}{2} \frac{b_f r_{JMAM}}{b_f r_{JMAM} + r_{JMGM}} \quad (S150)$$

957 the optimal value of left-handedness from the perspective of mother's genes to her sons

$$z_{MS}'^* = \frac{1}{2} \frac{b_m r_{JPUM}}{r_{JPGM} + b_m r_{JPUM}} \quad (S151)$$

958 the optimal value of left-handedness from the perspective of father's genes to his offspring

$$z_{FO}'^* = \frac{1}{2} \frac{b_f r_{JMAF} + b_m r_{JPUF}}{b_f r_{JMAF} + r_{JMGF} + r_{JPGF} + b_m r_{JPUF}} \quad (S152)$$

959 the optimal value of left-handedness from the perspective of father's genes to his daughters

$$z_{FD}'^* = \frac{1}{2} \frac{b_f r_{JMAF}}{b_f r_{JMAF} + r_{JMGF}} \quad (S153)$$

960 and the optimal value of left-handedness from the perspective of father's genes to his sons

$$z_{FS}'^* = \frac{1}{2} \frac{b_m r_{JPUF}}{r_{JPGF} + b_m r_{JPUF}} \quad (S154)$$

961 Substituting all of the relatedness, we obtain the optimal values of left-handedness when
 962 considering between-group combat

$$\begin{aligned}
z_{\text{PO}}'^* = & ((-(2\Delta m(-2\Delta b + b_f m_f - b_m m_m + \bar{m}\Delta b)) + (2b_f(4 + \bar{m}\Delta m + H_f + M \\
& - 2m_f) + 2b_m(4 - 4m_m - \bar{m}(m_f - 3m_m)))n)) / ((-2\Delta m(b_f(-4 \\
& + 3m_f + m_m) - b_m(-4 + m_f + 3m_m)) + 2(2b_f(4 + \bar{m}\Delta m + H_f \\
& + M - 2m_f) + 2(8 + H_f - 12\bar{m} + 6M + H_m) + b_m(8 - 8m_m \\
& - 2\bar{m}(m_f - 3m_m)))n + 16\bar{m}(2 - \bar{m})n^2))
\end{aligned} \tag{S155}$$

$$\begin{aligned}
z_{\text{PD}}'^* = & ((b_f(3m_f^2(n - 1) + 8n + 2m_f(2 + m_m + (m_m - 4)n) + m_m(-4 + m_m \\
& - m_m n)))) / ((8n(2 - 4\bar{m} + \bar{m}^2 + M + \bar{m}(2 - \bar{m})n) + 2b_f(3m_f^2(n \\
& - 1) + 8n + 2m_f(2 + m_m + (m_m - 4)n) + m_m(m_m - 4 \\
& - m_m n))))
\end{aligned} \tag{S156}$$

$$\begin{aligned}
z_{\text{PS}}'^* = & (b_m(m_f^2(n - 1) - 8n + m_m(-4 - 3m_m(n - 1) + 8n) - 2M + 4m_f \\
& - 2Mn)) / ((-2b_m\Delta m(-4 + m_f + 3m_m) \\
& + 2(16\bar{m} - 8 - 4\bar{m}^2 - 8b_m + 8b_m m_m + b_m m_f - 6b_m m_m \bar{m} \\
& + 4M)n - 8\bar{m}(2 - \bar{m})n^2))
\end{aligned} \tag{S157}$$

$$\begin{aligned}
z_{\text{MO}}'^* = & ((-2\Delta m(b_f(H_f + 1) + b_m(H_m + 1))(1 - \bar{m}) - \Delta m(b_f(-10 + 2m_f^3 \\
& + m_f(H_m - 6m_m + 16) - 3m_f^2(3 - m_m) - H_m + 4m_m) + b_m(-2 \\
& - m_f^2(1 - m_m) + H_m(-5 + 2m_m) + m_f(3H_m - 2m_m + 4)))n \\
& + (b_f(8 + m_f^4 + m_f^3(m_m - 5) + (H_m - 3m_m + 4)m_m - m_f(m_m \\
& - 3)(-4 + H_m) - m_f^2(-11 + m_m + m_m^2)) + b_m(8 + m_f^3(m_m \\
& - 1) + m_f^2(3 + H_m - 3m_m) - m_m(4 + m_m(5 + H_m - 3m_m)) \\
& + m_f(-4 + m_m(6 + m_m - m_m^2))))n^2)) / ((-4\Delta m(b_f(H_f + 1) \\
& + b_m(H_m + 1))(1 - \bar{m}) - 2\Delta m(-4(M - 2\bar{m} + 1)(1 - \bar{m}) \\
& + b_f(-10 + 2m_f^3 + m_f(H_m - 6m_m + 16) + 3m_f^2(m_m - 3) - H_m \\
& + 4m_m) + b_m(-2 - m_f^2(1 - m_m) + H_m(-5 + 2m_m) + m_f(3H_m \\
& - 2m_m + 4)))n + 2(b_f(8 + m_f^4 + m_f^3(m_m - 5) + (H_m - 3m_m \\
& + 4)m_m - m_f(m_m - 3)(-4 + H_m) - m_f^2(-11 + m_m + m_m^2)) \\
& + 2(8 + m_f^2(4 - 3m_m) - m_f^3(1 - m_m) + m_m(-6 + H_m) - m_f(10 \\
& + m_m(-6 + H_m - m_m))) + b_m(8 - m_f^3(1 - m_m) + m_f^2(3 + H_m \\
& - 3m_m) - m_m(4 + m_m(5 + H_m - 3m_m)) + m_f(-4 + m_m(6 + m_m \\
& - m_m^2))))n^2 + 16\bar{m}(2 - \bar{m})n^3))
\end{aligned} \tag{S158}$$

$$\begin{aligned}
z_{\text{MD}}'^* = & ((b_f(-2\Delta m(H_f + 1)(1 - \bar{m}) - \Delta m(-10 + 2m_f^3 + m_f(H_m - 6m_m + 16) \\
& - 3m_f^2(3 - m_m) - H_m + 4m_m)n + (8 + m_f^4 + m_f^3(m_m - 5) \\
& + (H_m - 3m_m + 4)m_m + m_f(3 - m_m)(-4 + H_m) - m_f^2(m_m - 11 \\
& + m_m^2))n^2))) / ((-4b_f\Delta m(H_f + 1)(1 - \bar{m}) - 2\Delta m(-2(M - 2\bar{m} \\
& + 1)(1 - \bar{m}) + b_f(-10 + 2m_f^3 + m_f(H_m - 6m_m + 16) + 3m_f^2(m_m \\
& - 3) - H_m + 4m_m))n + 2(8 + m_f^2(4 - 3m_m) - m_f^3(1 - m_m) \\
& + m_m(-6 + H_m) - m_f(10 + m_m(-6 + H_m - m_m))) + b_f(8 + m_f^4 \\
& + m_f^3(m_m - 5) + (H_m - 3m_m + 4)m_m - (M - 3m_f)(-4 + H_m) \\
& - m_f^2(-11 + m_m + m_m^2)))n^2 + 8\bar{m}(2 - \bar{m})n^3))
\end{aligned} \tag{S159}$$

$$\begin{aligned}
z_{\text{MS}}'^* = & ((b_m(2\Delta m(H_m + 1)(1 - \bar{m}) - \Delta m(-2 - m_f^2(1 - m_m) + H_m(2m_m - 5) \\
& + m_f(3H_m - 2m_m + 4))n + (8 + m_f^3(m_m - 1) + m_f^2(3 + H_m \\
& - 3m_m) - m_m(4 + m_m(5 + H_m - 3m_m)) + m_f(-4 + m_m(6 + m_m \\
& - m_m^2)))n^2)) / ((-4b_m\Delta m(H_m + 1)(1 - \bar{m}) - 4\Delta m(-(M - 2\bar{m} \\
& + 1)(1 - \bar{m}) + b_m(-2 - m_f^2(1 - m_m) + H_m(-5 + 2m_m) + m_f(H_m \\
& - 6m_m + 4)))n + 2(8 + m_f^2(4 - 3m_m) - m_f^3(1 - m_m) + m_m(-6 \\
& + H_m) - m_f(10 + m_m(-6 + H_m - m_m)) + b_m(8 - m_f^3(1 - m_m) \\
& + m_f^2(3 + H_m - 3m_m) - m_m(4 + m_m(5 + H_m - 3m_m)) + m_f(-4 \\
& + m_m(6 + m_m - m_m^2)))n^2 + 8\bar{m}(2 - \bar{m})n^3)) \quad (\text{S160})
\end{aligned}$$

$$\begin{aligned}
z_{\text{FO}}'^* = & ((-2\Delta m(b_f(H_f + 1) + b_m(H_m + 1))(1 - \bar{m}) - \Delta m(b_f(-2 + H_f(-5 + 2m_f) \\
& + 4m_m + m_f(3m_f - 8)m_m - (1 - m_f)m_m^2) + b_m(-10 + 6m_f \\
& - m_f^2(H_f - 6m_f + 16)m_m + 3(m_f - 3)m_m^2 + 2m_m^3))n + (b_f(-8 \\
& + m_f^4 + m_f^3(m_m - 5) + m_m(4 + H_m - m_m) - m_f(-4 + (m_m \\
& - 3)H_m) - m_f^2(m_m - 5 + m_m^2)) + b_m(-8 - m_f^3(1 - m_m) \\
& + m_f^2(5 + H_m - 3m_m) - m_m(-12 + m_m(11 + H_m - 3m_m)) \\
& + m_f(-4 + m_m(2 + m_m - m_m^2)))n^2)) / ((-4\Delta m(b_f(H_f + 1) \\
& + b_m(H_m + 1))(1 - \bar{m}) - 2\Delta m(-4(M - 2\bar{m} + 1)(1 - \bar{m}) + b_f(-2 \\
& + H_f(2m_f - 5) + 4m_m + M(3m_f - 8) - (1 - m_f)m_m^2) + b_m(-10 \\
& + 6m_f - m_f^2(H_f - 6m_f + 16)m_m + 3(m_f - 3)m_m^2 + 2m_m^3))n \\
& + 2(-16 - 16\Delta b + 12m_f + 4b_fm_f - 4b_mm_f + 4m_f^2 + 5b_fm_f^2 \\
& + 5b_mm_f^2 - 2m_f^3 - 5b_fm_f^3 - b_mm_f^3 + b_fm_f^4 + (4(5 + b_f + 3b_m) \\
& + 2(-6 - 2b_f - \Delta b)m_f - (6 + 2\bar{b} + 4b_m)m_f^2 + (2 + b_f \\
& + b_m)m_f^3)m_m + (-8 + 6m_f - b_f(3 + H_f - 3m_f) + b_m(-11 + m_f \\
& + m_f^2))m_m^2 + (2 + 2\bar{b} + 4b_m - 2(1 + \bar{b})m_fm_m^3 - b_mm_m^4)n^2 \\
& - 16\bar{m}(2 - \bar{m})n^3)) \quad (\text{S161})
\end{aligned}$$

$$\begin{aligned}
z_{FD}'^* = & ((-2b_f\Delta m(H_f + 1)(1 - \bar{m}) - \Delta m(-2 + H_f(2m_f - 5) + 4m_m \\
& + m_f(3m_f - 8)m_m - (1 - m_f)m_m^2)n + (-8 + m_f^4 + m_f^3(m_m \\
& - 5) + m_m(4 + H_m - m_m) - m_f(-4 - H_m(3 - m_m)) - m_f^2(m_m \\
& - 5 + m_m^2))n^2))) / ((2(-2b_f\Delta m(H_f + 1)(1 - \bar{m}) - \Delta m(-2(M \\
& - 2\bar{m} + 1)(1 - \bar{m}) + b_f(-2 + H_f(2m_f - 5) + 4m_m \\
& + m_f(3m_f - 8)m_m - (1 - m_f)m_m^2))n + (-8 + m_f^2(2 - 3m_m) \\
& - m_f^3(1 - m_m) + m_m(10 + H_m - 2m_m) - m_f(-6 + m_m(6 + H_m \\
& - m_m)) + b_f(-8 + m_f^4 + m_f^3(m_m - 5) + m_m(4 + H_m - m_m) \\
& - m_f(-4 - H_m(3 - m_m)) - m_f^2(m_m - 5 + m_m^2)))n^2 \\
& - 4\bar{m}(2 - \bar{m})n^3)))
\end{aligned} \tag{S162}$$

$$\begin{aligned}
z_{FS}'^* = & ((b_m(-2\Delta m(H_m + 1)(1 - \bar{m}) - \Delta m(-10 + 4m_f - H_f + m_m(H_f - 6m_f \\
& + 16) + 3(-3 + m_f)m_m^2 + 2m_m^3)n + (-8 - m_f^3(1 - m_m) \\
& + m_f^2(5 + H_m - 3m_m) - m_m(-12 + m_m(11 + H_m - 3m_m)) \\
& + m_f(-4 + m_m(2 + m_m - m_m^2)))n^2))) \\
& / ((2(-2b_m\Delta m(H_m + 1)(1 - \bar{m}) - \Delta m(-2(M - 2\bar{m} + 1)(1 - \bar{m}) \\
& + b_m(-10 + 4m_f - H_f + m_m(H_f - 6m_f + 16) + 3(-3 + m_f)m_m^2 \\
& + 2m_m^3))n + (-8 + m_f^2(2 - 3m_m) - m_f^3(1 - m_m) + m_m(10 \\
& + H_m - 2m_m) - m_f(-6 + m_m(6 + H_m - m_m)) + b_m(-8 - m_f^3(1 \\
& - m_m) + m_f^2(5 + H_m - 3m_m) - m_m(-12 + m_m(11 + H_m \\
& - 3m_m)) + m_f(-4 + m_m(2 + m_m - m_m^2)))n^2 \\
& - 4\bar{m}(2 - \bar{m})n^3)))
\end{aligned} \tag{S163}$$

963 where $\Delta m = m_f - m_m$, $\bar{m} = (m_f + m_m)/2$, $M = m_fm_m$, $\Delta b = b_f - b_m$, $\bar{b} = (b_f + b_m)/2$,

964 $H_f = (m_f - 2)m_f$, $H_m = (m_m - 2)m_m$.

965

966 Here we show what if there are differences between the parental genetic effects on daughters

967 and those on sons in the context of between-group combats, hence left-handedness is

968 marginally altruistic. Under female-biased dispersal, genes carried by parents would favour a
969 lower level of left-handedness for daughters than for sons; while under male-biased dispersal,
970 genes carried by parent would favour a higher level of left-handedness for daughters than for
971 sons (Figure S6).

972

973

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