

1           **Supplementary Material for Manuscript “*Kin selection as a modulator of human***  
2                           ***handedness: sex-specific, parental and parent-of-origin effects*”**

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10  
11   **A notebook file (.nb) that provides derivation of the equations and generates**  
12   **corresponding figures can be downloaded ([https://doi.org/10.17630/3fcf2892-b350-4e89-](https://doi.org/10.17630/3fcf2892-b350-4e89-a26f-6a51c921052a)**  
13   **[a26f-6a51c921052a](https://doi.org/10.17630/3fcf2892-b350-4e89-a26f-6a51c921052a)) and explored by using the freely available *Wolfram Player***  
14   **(download link: <https://www.wolfram.com/player/>).**

15  
16    This Supplementary Material includes:

17  
18    Figure S1

19    Figure S2

20    Figure S3

21    Figure S4

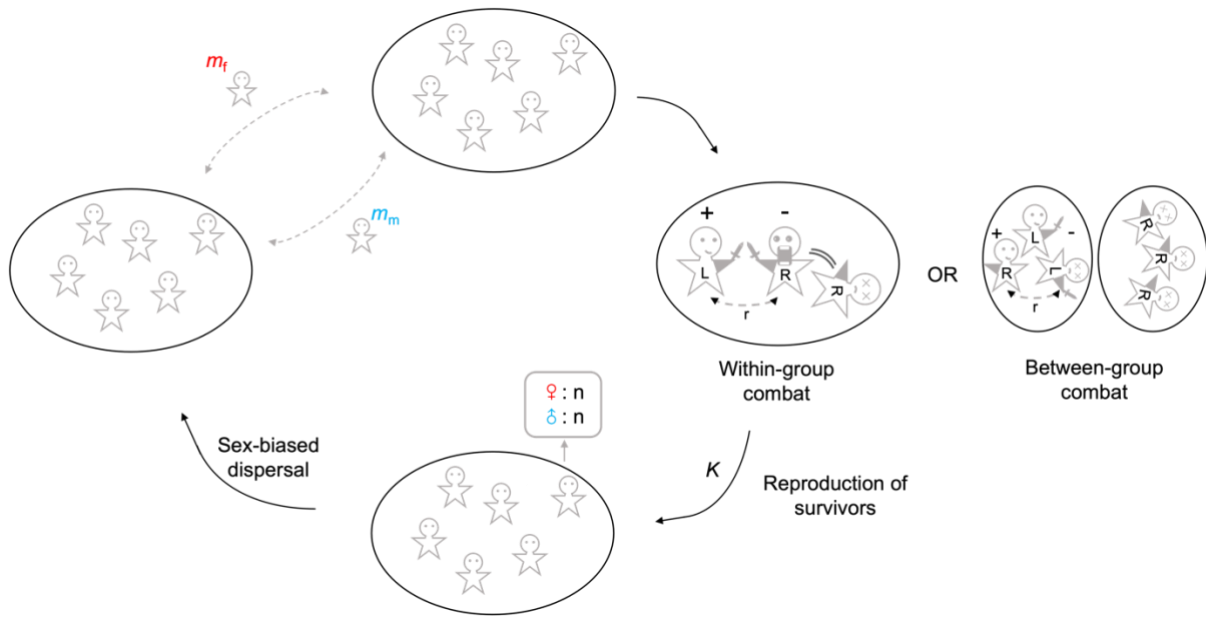
22    Figure S5

23    Figure S6

24    Figure S7

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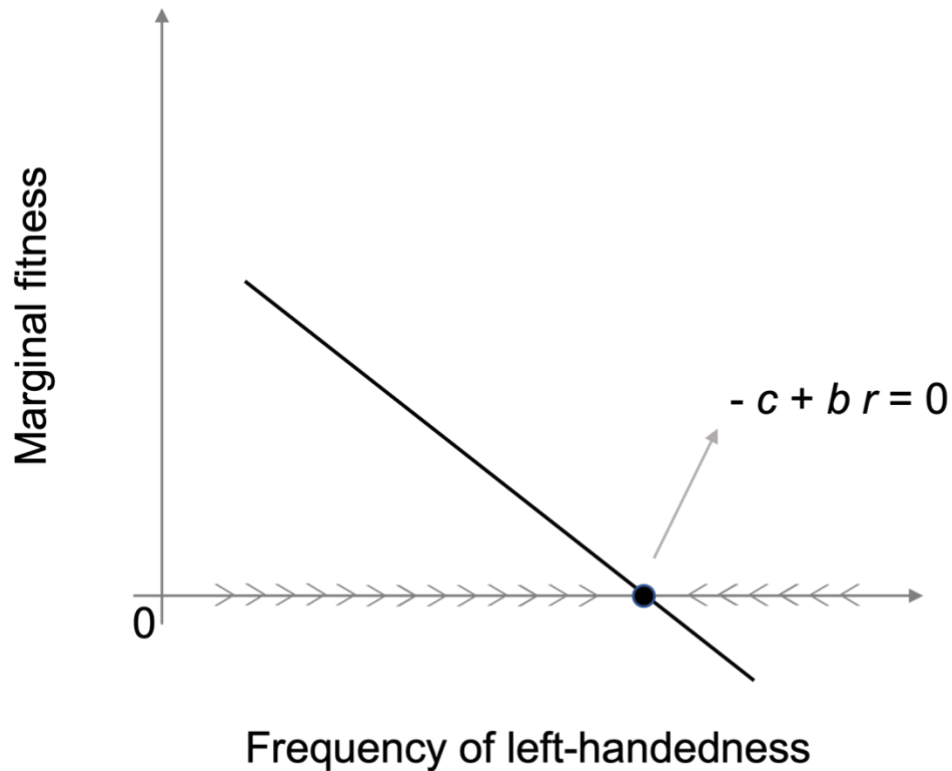
26	<b>1   Within-group Combat</b>
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38	2.4   Sex-specific effects
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41	<b>References</b>



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

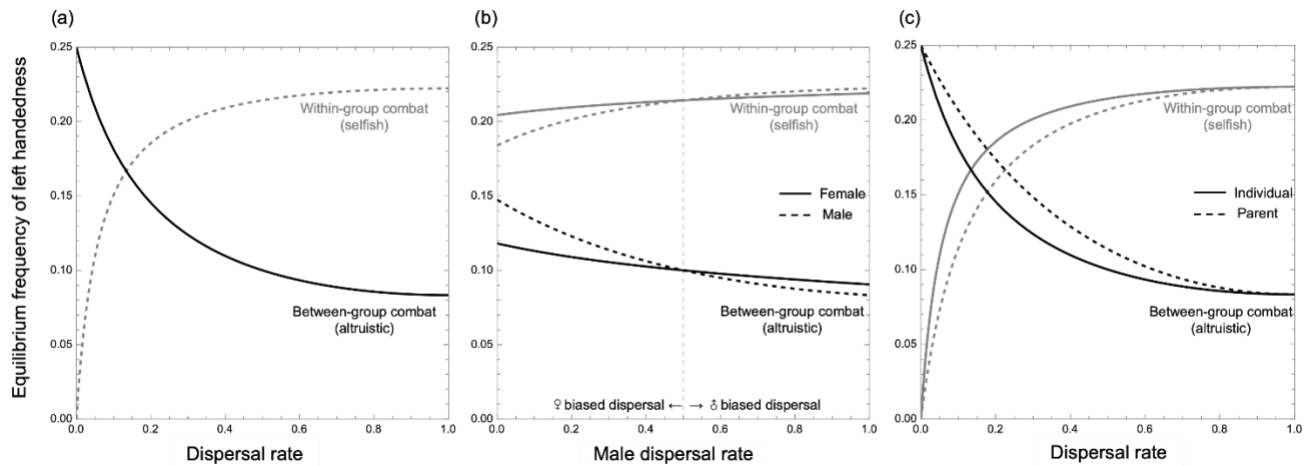
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46 **Figure S2 | Evolutionary equilibrium. The dark dot depicts the convergence stable value**  
 47 **of the level of left-handedness, at which marginal fitness ( $-c + br$ , solid line) is zero. If**  
 48 **the frequency of left-handedness increases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

55



56

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

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

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

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

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

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

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

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

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

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

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

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

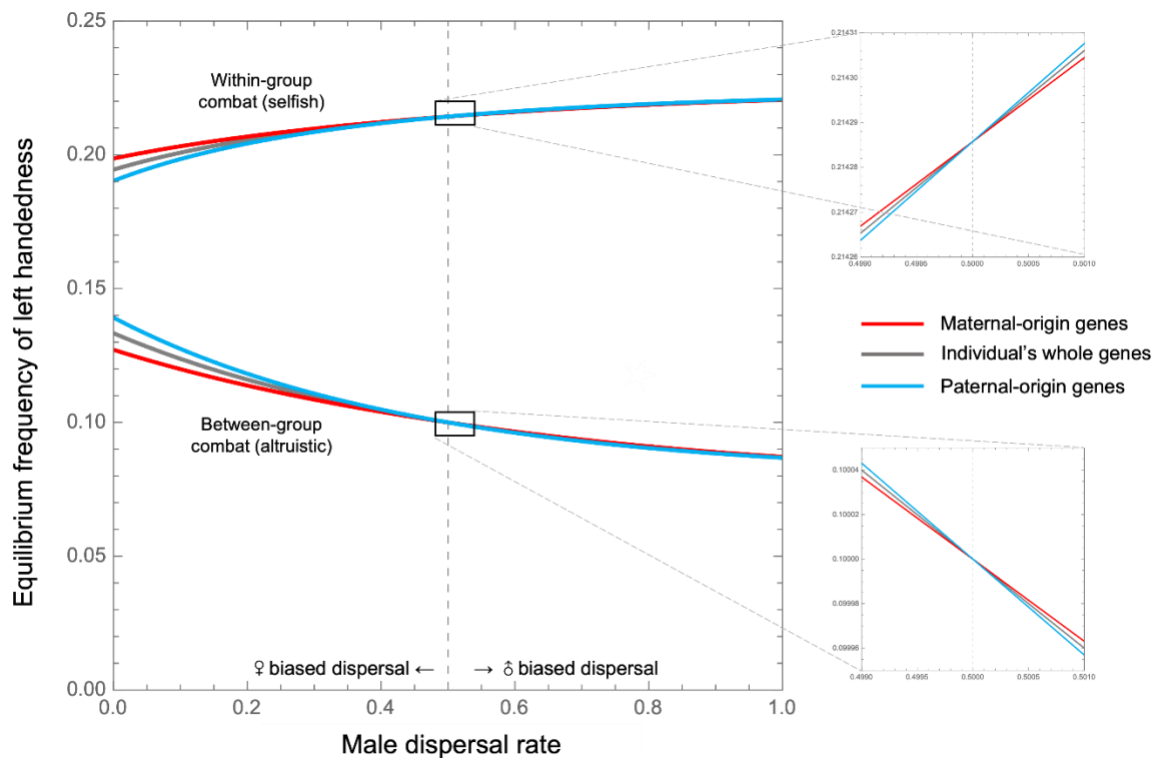
69  **$= b_m = 1$ , the costs associated with left-handedness for females and males  $c_f = c_m = 1$ , and**

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

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

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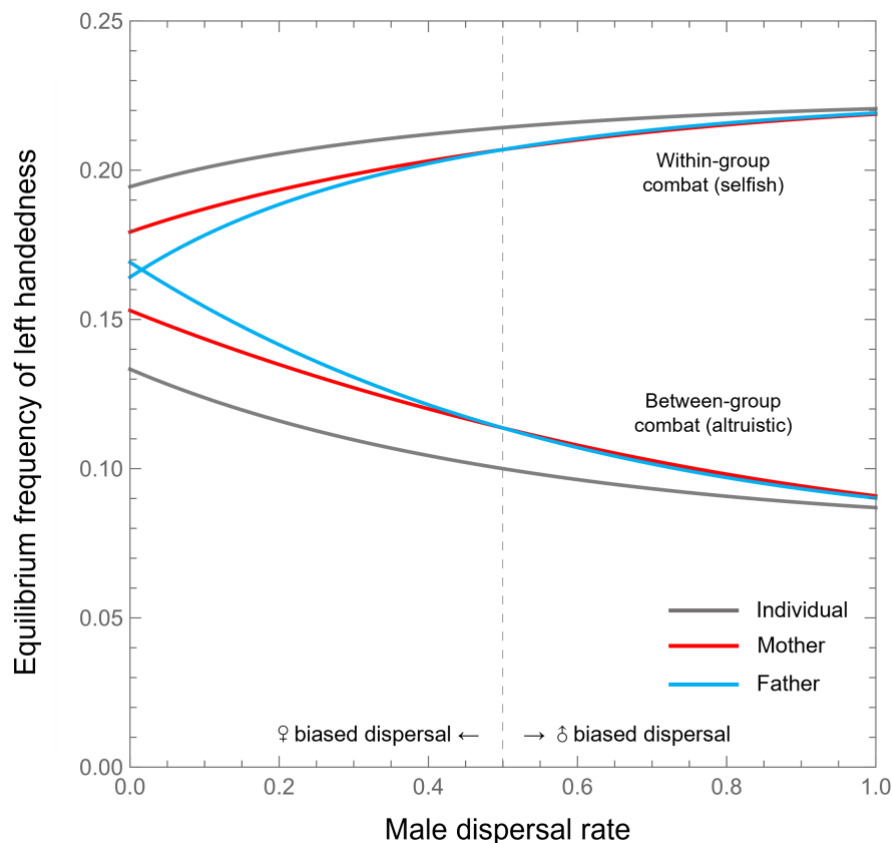
75 **Figure S4 | Parent-of-origin effects in left-handedness: incidence of left-handedness can**  
 76 **be mediated by gene origin (maternal-origin versus paternal-origin) effects and**  
 77 **dispersal pattern (female/male biased dispersal) in the context of within-group combat**  
 78 **(left-handedness is selfish) versus between-group combat (left-handedness is altruistic).**  
 79 **Here, we set female dispersal rate  $m_f = 0.5$ , the relative importance of combat in relation**  
 80 **to other types of competitions for females and males  $b_f = b_m = 1$ , the costs associated**  
 81 **with left-handedness for females and males  $c_f = c_m = 1$ , and the number of individuals**  
 82 **each sex born in the same patch  $n = 5$  (these parameter values chosen are simply for**  
 83 **illustration, details see §S1.3).**

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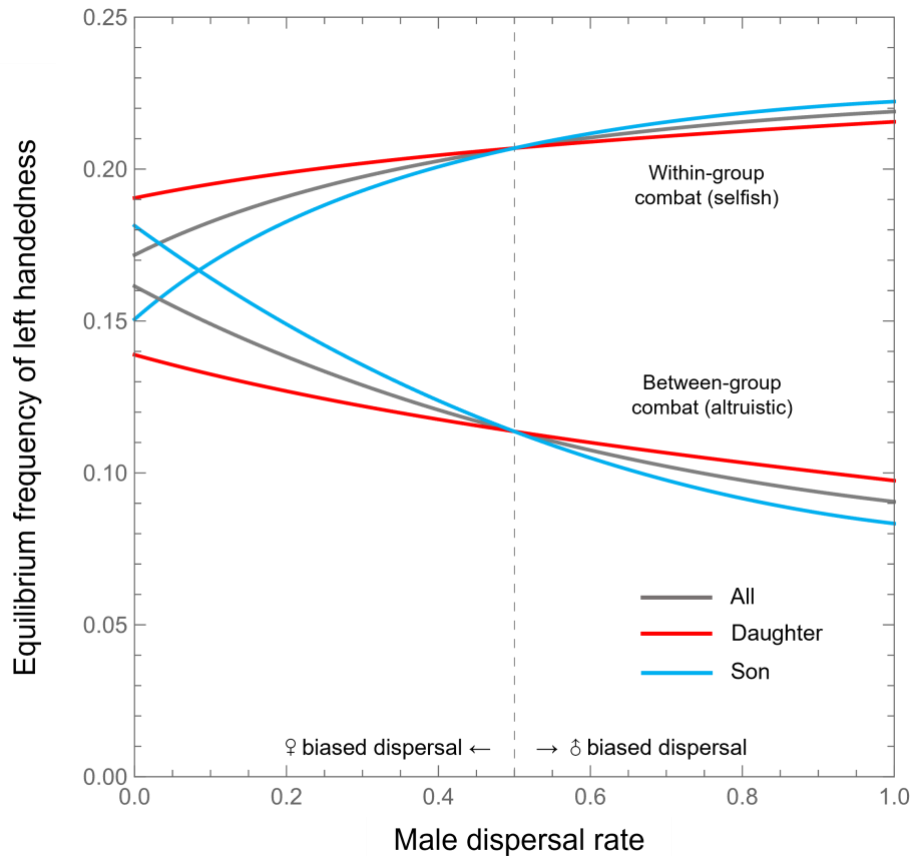
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89 **Figure S5 | Maternal versus paternal genetic effects in left-handedness: incidence of left-**  
90 **handedness can be mediated by dispersal pattern (female/male biased), and further**  
91 **result in mother-father-offspring disagreement on handedness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

98



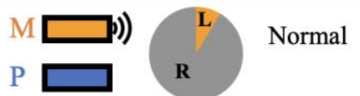







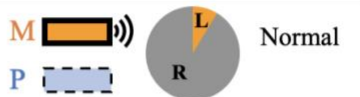



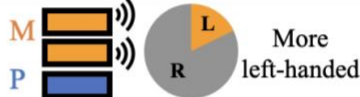


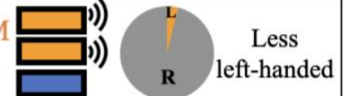
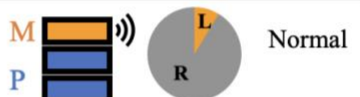









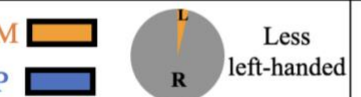




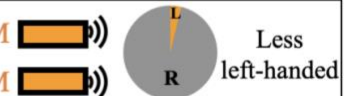





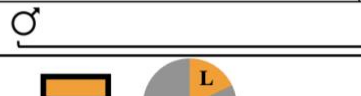
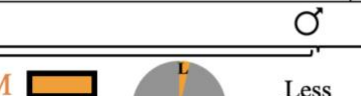
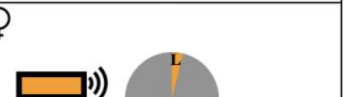
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100 **Figure S6 | Parental genetic effects on different offspring in left-handedness: incidence**  
 101 **of left-handedness can be mediated by dispersal pattern (female/male biased) in the**  
 102 **context of within-group combat (left-handedness is selfish) versus between-group**  
 103 **combat (left-handedness is altruistic). (Solid: all offspring, Dotted: daughters, Dashed:**  
 104 **sons.) Here, we set female dispersal rate  $m_f = 0.5$ , the relative importance of combat in**  
 105 **relation to other types of competitions for females and males  $b_f = b_m = 1$ , the costs**  
 106 **associated with left-handedness for females and males  $c_f = c_m = 1$ , and the number of**  
 107 **individuals each sex born in the same patch  $n = 5$  (these parameter values chosen are**  
 108 **simply for illustration, details see §S1.3).**

109

110



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

111

112 **Figure S7 | Phenotypic consequences on handedness of gene deletions, gene duplications, epimutations and uniparental disomies. (This expands upon**113 **Figure 3 of the main text.)**

## 114 **1 | Within-group combat**

### 115 **1.1 | Population model**

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

135

### 136 **1.2 | Fitness**

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

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

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

152 which simplifies to

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

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

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

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

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

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

165

### 166 **1.3 | Kin selection**

#### 167 *1.31 | Marginal fitness and evolutionary equilibrium*

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

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

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

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

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

189 Here for the investigation on how kin selection mediates handedness generally, we assume  
 190 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  
 191 assumption will be relaxed in later sections (§S1.4 Sex-biased dispersal, §S1.5 Parent-of-  
 192 origin effect, §S1.6 Sex-specific effects and §S1.7 Parental genetic effects). Using expression  
 193 (S4) to calculate the corresponding partial derivatives, the condition for natural selection to  
 194 favour an increase in left-handedness is

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

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

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

$$z^* = \frac{1}{2} \frac{(b_f + b_m)(r_j - r_0)}{(b_f + b_m)r_j - (2 + b_f + b_m)r_0} \quad (\text{S8})$$

201

### 202 1.32 / Relatedness

203 The consanguinity between a juvenile and its parent  $p_0$  is given by

$$p_0 = \frac{1}{2}p_1 + \frac{1}{2}f \quad (\text{S9})$$

204 That is: with probability 1/2 the gene picked from the juvenile comes from that parent, in  
 205 which case the consanguinity is that between the parent and itself, i.e.  $p_1$ ; and with probability  
 206 1/2 the gene comes from the other parent, in which case the consanguinity is that of mating  
 207 partners,  $f$ . The consanguinity between the focal juvenile and a random adult in its parents'  
 208 social group  $p_J$  is:

$$p_J = \frac{1}{2} \left( \frac{1}{n}p_1 + \frac{n-1}{n}(1-m)^2p_x \right) + \frac{1}{2}f \quad (\text{S10})$$

209 That is: with the probability 1/2 the juvenile's gene comes from the parent of the same sex as  
 210 the adult, in which case with probability 1/n the adult is the parent and the consanguinity is  
 211  $p_1$ , and with probability  $(n-1)/n$  the adult is not the parent then if neither of them disperses, i.e.  
 212  $(1-m)^2$ , their consanguinity would be that between two random juveniles born in the same  
 213 patch,  $p_x$ , and with probability 1/2 the juvenile's gene comes from the parent of the opposite  
 214 sex, in which case the consanguinity is that of mating partners, i.e.  $f$ . The consanguinity  
 215 between an individual and itself,  $p_I$ , is given by

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

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

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

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

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

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

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

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

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

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

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

235

236 *1.33 | Convergence stable strategy*

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

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

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

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

245

## 246 **1.4 | Sex-biased dispersal**

247 *1.41 | Marginal fitness and evolutionary equilibrium*

248 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  
 249 section, the relative fitness function is the same as expression (S4), while the consanguinity  
 250 and the conditions that favour the increase of left-handedness would change. Using  
 251 expression (S4) to calculate the corresponding partial derivatives, we obtain the condition for  
 252 an increase in left-handedness to be favoured when we consider within-group combat



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

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

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

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

263

#### 264 1.42 / Relatedness

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

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

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

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

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

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

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

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

273

#### 274 1.43 | Convergence stable strategy

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

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

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

278

### 279 1.5 | Parent-of-origin effects

#### 280 1.51 | Marginal fitness and evolutionary equilibrium

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

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

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

290 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

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

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

300 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  
301 paternal-origin gene at locus G affects the individual's handedness phenotype, then the  
302 condition that favours the increase of the probability of being left-handed from the  
303 perspective of paternal-origin genes is:

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

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

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

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

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

314 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  
 315 perspective of maternal- and paternal-origin genes, as  $f'(z_M) < 0$  and  $f'(z_P) < 0$  are true  
 316 for all the values of  $z$ .

317

### 318 1.52 / Relatedness

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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



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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

471

472 *1.53 / Convergence stable strategy*

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

474 the perspective of maternal-origin genes  $z_M^*$ :

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

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

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

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

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

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

479  $z^*$  is:

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

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

485

## 486 **1.6 | Sex-specific effects**

### 487 *1.61 | Marginal fitness and evolutionary equilibrium*

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

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

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

496 where  $\tilde{g}_{1f}$  is the additive breeding value of a juvenile for its mother's genes in locus  $G_1$ ,  $\tilde{g}'_{1f}$   
 497 is the breeding value of the juvenile for a random adult female's genes in locus  $G_1$ ,  $\tilde{g}_{1m}$  is the  
 498 breeding value of the juvenile for its father's genes in locus  $G_1$ ,  $\tilde{g}'_{1m'}$  is the breeding value of  
 499 the juvenile for a random adult male's genes in locus  $G_1$ , and  $\gamma_{1f}$  and  $\gamma_{1m}$  is the mapping  
 500 between genotype and phenotype for the focal females and males respectively. According to  
 501 our assumption that locus  $G_1$  would only take an effect if its carrier is a female, we have  $\gamma_{1f} =$   
 502 1,  $\gamma_{1m} = 0$ . Then expression (S48) can be simplified to

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

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

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

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

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

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

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

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

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

518 Using the same way as deriving the optimal value of locus  $G_{1,zf^*}$ , we could obtain the  
519 optimal value of left-handedness  $z_m^*$  for all the loci that only control handedness when they  
520 are carried by males:

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

### 521 1.62 / Convergence stable strategy

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

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

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

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

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

527 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  
528 the relatedness in expressions (S51), (S54) and (S55)-(S58), we obtain the optimal values of  
529 left-handedness when it is involved in within-group combat:

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

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

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



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

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

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

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

535

## 536 1.7 | Parental genetic effects

### 537 1.71 | Marginal fitness and evolutionary equilibrium

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

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

558

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

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

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

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

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

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

579 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  
 580 expression (S66) be  $f(z)$ ,  $f'(z) < 0$  is true for all the values of  $z$ , hence at evolutionary  
 581 equilibrium if there is intermediate level of left-handedness  $z_{PO}^*$  that satisfies  $f(z_{PO}^*) = 0$ ,  
 582 we obtain the optimum of left-handedness from the perspective of parent's genes:

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

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

592

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

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

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

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

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

598

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

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

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

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

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

604

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

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

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

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

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

616 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  
 617 process as previous situations, we obtain the optimal value of left-handedness from the  
 618 perspective of mother's genes to her offspring

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

619

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

621 Changing  $\gamma_{Ff}$  to 1,  $\gamma_{Fm}$  to 0 obtains the condition for an increase in left-handedness to be  
 622 favoured

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

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

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

625

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

627 Changing  $\gamma_{Ff}$  to 0,  $\gamma_{Fm}$  to 1 obtains the condition for an increase in left-handedness to be  
 628 favoured

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

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

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

631

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

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

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

634 where  $p_{JMGM}$  is the consanguinity between the focal juvenile female and its maternal  
 635 grandfather,  $p_{JMAM}$  is the consanguinity between the focal juvenile female and the father of a  
 636 random adult female in its mother's group,  $p_{JPGF}$  is the consanguinity between the focal  
 637 juvenile female and its paternal grandfather,  $p_{JPUF}$  is the consanguinity between the focal  
 638 juvenile female and the father of a random adult male in its father's group,  $\gamma_{Mf}$  is the mapping

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

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

643 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  
 644 process as previous situations, we obtain the optimal value of left-handedness from the  
 645 perspective of father's genes to his offspring

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

646

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

648 Changing  $\gamma_{Mf}$  to 1,  $\gamma_{Mm}$  to 0 obtains the condition for an increase in left-handedness to be  
 649 favoured

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

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

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

652

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

654 Changing  $\gamma_{Mf}$  to 0,  $\gamma_{Mm}$  to 1 obtains the condition for an increase in left-handedness to be  
 655 favoured

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

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

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

658

### 659 1.72 / Relatedness

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

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

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



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

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

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

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

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

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

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

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

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

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

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

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

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

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

749 That is: with probability 1/2 the gene we pick comes from the juvenile's mother, in which  
750 case the consanguinity is with probability  $(1 - m_f)(1 - m_m)$  neither the mother nor the  
751 father disperses, with probability 1/n the mother and the father share one mother, with  
752 probability 1/2 the gene comes from the maternal grandmother, and the consanguinity is  $p_1$ ,  
753 with probability 1/2 the gene comes from the maternal grandfather, and the consanguinity is  
754  $f'$ , and with probability  $(n-1)/n$  the mother and the father do not share one mother, with  
755 probability 1/2 the gene comes from the maternal grandmother, with probability  $(1 - m_f)^2$   
756 neither of the two females disperses, and the consanguinity is  $p_x'$ , with probability 1/2 the  
757 gene comes from the maternal grandfather, and the consanguinity is  $f'$ , with probability 1/2  
758 the gene we pick comes from the juvenile's father, in which case the consanguinity is, with  
759 probability 1/2 the gene comes from the paternal grandmother, and the consanguinity is  $p_1'$ ,  
760 with probability 1/2 the gene comes from the paternal grandfather, and the consanguinity is  
761  $f'$ . The consanguinity between the focal juvenile and its paternal grandfather  $p_{JPGF}$  is

$$p_{JPGF} = \frac{1}{2}(1 - m_f)(1 - m_m) \left( \frac{1}{n} \left( \frac{1}{2}f' + \frac{1}{2}p_1' \right) + \frac{n-1}{n} \left( \frac{1}{2}f' + \frac{1}{2}(1 - m_m)^2 p_x' \right) \right) + \frac{1}{2} \left( \frac{1}{2}f' + \frac{1}{2}p_1' \right) \quad (S93)$$

762 That is: with probability 1/2 the gene we pick comes from the juvenile's mother, in which  
763 case the consanguinity is, with probability  $(1 - m_f)(1 - m_m)$  neither the mother nor the  
764 father disperses, and with probability 1/n the mother and the father share one mother, with  
765 probability 1/2 the gene comes from the maternal grandmother, and the consanguinity is  $f'$ ,  
766 with probability 1/2 the gene comes from the maternal grandfather, and the consanguinity is  
767  $p_1'$ , and with probability  $(n-1)/n$  the mother and the father do not share one mother, with  
768 probability 1/2 the gene comes from the maternal grandmother, and the consanguinity is  $f'$ ,  
769 with probability 1/2 the gene comes from the maternal grandfather, with probability  
770  $(1 - m_m)^2$  neither of the two males disperses, and the consanguinity is  $p_x'$ , with probability

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

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

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

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

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

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

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

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

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

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

822

823 *1.73 / Convergence stable strategy*

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

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



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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

828 considering within-group combat

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

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

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

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

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

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

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

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

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

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

834

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

843

## 844 **2 | Between-group combat**

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

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

853

## 854 **2.1 | Kin selection**

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

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

865 which simplifies to

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

866 Accordingly, the fitness of a juvenile  $w'$  is

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

867 Similarly, the average fitness of a random juvenile  $\bar{w}'$  can be described by evaluating  
 868 expression (S121) at  $x_{M0} = y_{M0} = z_f$ ,  $x_{Fa} = y_{Fa} = z_m$ , and the relative fitness of the focal  
 869 juvenile  $W'$  is  $w'/\bar{w}'$

$$W' = \left(1 - b_f + b_f \left(\frac{y_{M0}}{2z} + \frac{1 - y_{M0}}{2(1 - z)}\right)\right) \left(\frac{1 - c_f x_{M0}}{1 - c_f z_f}\right) \left(1 - b_m\right) \\ + b_m \left(\frac{y_{Fa}}{2z} + \frac{1 - y_{Fa}}{2(1 - z)}\right) \left(\frac{1 - c_m x_{Fa}}{1 - c_m z_m}\right) \quad (\text{S122})$$

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

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

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

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

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

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

878

## 879 **2.2 | Sex-biased dispersal**

880 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  
 881 section, the relative fitness function is the same as expression (S122). Using expressions  
 882 (S122) to calculate the corresponding partial derivatives, we obtain the condition for an  
 883 increase in left-handedness to be favoured when we consider between-group combat

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

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

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

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

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

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

895

### 896 **2.3 | Parent-of-origin effects**

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



903 intermediate level of left-handedness  $z_M^{**}$  and  $z_P^{**}$ , which satisfies  $f(z_M^{**}) = 0$  and

904  $f(z_P^{**}) = 0$ , respectively, we obtain the optima

$$z_M^{**} = \frac{1}{2} \frac{b_f r_{jA|M} + b_m r_{jU|M}}{2r_{O|M} + b_f r_{jA|M} + b_m r_{jU|M}} \quad (S129)$$

$$z_P^{**} = \frac{1}{2} \frac{b_f r_{jA|P} + b_m r_{jU|P}}{2r_{O|P} + b_f r_{jA|P} + b_m r_{jU|P}} \quad (S130)$$

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

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

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

908 genes,  $z_M^{**}$

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

909 With similar process, we obtain the optimal value left-handedness  $z_P^{**}$ :

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

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

911  $z'^*$  is

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

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

918

## 919 2.4 | Sex-specific effects

920 Here we consider how sex effects add to the mediation of kin selection on handedness under

921 the circumstances of between-group combat. In this section, the conditions that favour the

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

942

## 943 2.5 | Parental genetic effects

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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



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

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

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

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

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

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

966

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

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

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

973

974

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