

# 1 **The evolution of paternal care: a role for microbes?**

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9

## 10 **Abstract**

11 Paternal care is an evolutionary mystery. Despite extensive research, both theoretical and  
12 experimental, the reasons for its ubiquity remain unclear. Common explanations include kin  
13 selection, suggesting that the benefits to the offspring outweigh the costs to the father's future  
14 reproductive success, and limited accuracy in parentage assessment. However, these  
15 explanations do not cover the breadth of circumstances in which paternal care has been  
16 observed, particularly in conditions of uncertainty in paternity. Many recent studies presented  
17 associations between microbes and complex behavioural traits, including anxiety, depression,  
18 and autism spectrum disorders. Here we propose that microbes may play a key role in the  
19 evolution of paternal care. Using computational models, we demonstrate that microbes  
20 associated with increased paternal care could be favoured by natural selection. We find that  
21 microbe-induced paternal care could evolve under wider conditions than suggested by genetic  
22 models. Moreover, we show that microbe-induced paternal care is more likely to evolve  
23 when considering paternal care interactions that increase microbial transmission, such as  
24 feeding and grooming. Our results suggest that factors affecting the host microbiome, such as  
25 antibiotics or specific foods, could also affect paternal behaviour.

## 26 **Keywords**

27 Microbiome, paternal care, mathematical model, extra-pair mating, sexual conflict,  
28 nongenetic inheritance

29

## 30 **Introduction**

31 When should a father invest in caring for its offspring, rather than looking for additional  
32 mating opportunities? This question has been broadly addressed both theoretically and  
33 experimentally. Paternal care was frequently observed among avian species<sup>1</sup> (~85%), and  
34 was also found in mammalian species<sup>2</sup> (~5%), amphibians<sup>3</sup>, and many species of fish<sup>4</sup>. It is  
35 most commonly observed alongside maternal care, while exclusive paternal care is rare<sup>4,5</sup>. A  
36 father may demonstrate care for its offspring with several types of interactions<sup>4,5</sup>, such as  
37 feeding, grooming, or guarding against predators. It can also provide spousal care for the  
38 female while she cares for the young<sup>6,7</sup>. In many species there are synergistic effects<sup>8</sup>,  
39 significantly increasing offspring fitness when cared for by two parents and not  
40 singlehandedly by one.

41 A commonly proposed explanation for the prevalence of paternal care is kin selection<sup>9,10</sup>,  
42 suggesting that paternal care would be favoured whenever the paternal contribution to  
43 offspring fitness surmounts additional mating opportunities<sup>11,12</sup>, often limited by female  
44 availability and receptivity<sup>12</sup>. In some settings, such as caring for unrelated young, this  
45 explanation is insufficient, and alternative explanations are suggested<sup>13,14</sup>. Interestingly,  
46 studies relating paternal effort to certainty of paternity obtained mixed results<sup>15-21</sup>, and  
47 paternal care has been observed even in cases of very high probability of extra-pair paternity  
48 (e.g. in avian species<sup>22</sup> where extra-pair parenthood can range up to 95% in fairywrens<sup>23</sup>).

49 Here we consider the potential role of the microbes in host paternal care. The microbiome is a  
50 significant agent affecting host health and behaviour<sup>24-29</sup>. There are several proposed  
51 mechanisms for this phenomenon, broadly referenced as ‘gut-brain axis’<sup>29</sup>. Several studies  
52 have demonstrated a possible association between microbes and social behaviour<sup>30-35</sup>. Certain  
53 species of microbiome have been showed to alleviate symptoms of anxiety and depression<sup>33</sup>  
54 and improve social interactions<sup>36</sup>. Microbes are highly heritable, through  
55 gestation/incubation<sup>37,38</sup> or parental care<sup>39-41</sup>. Microbes can also be transmitted horizontally in  
56 a social setting<sup>42</sup>, through interactions<sup>41</sup> such as feeding, grooming and copulation. The effect  
57 of microbes on host behaviour has given rise to the idea that host manipulation by  
58 microorganisms may be driven by natural selection on the microbes<sup>29</sup>. Selection could drive  
59 such an effect when the induced behaviour increases microbial fitness, for example by  
60 increasing the rate of microbial transmission or proliferation<sup>29</sup>. Previous theoretical studies  
61 suggested that by encouraging host sociality<sup>43</sup> or altruism<sup>30</sup>, the microbes can help their own  
62 propagation.

63 We integrated the notion of microbe-associated behaviour into a mathematical model for the  
64 evolution of paternal care. A family is a unit with a high probability of microbial  
65 transmission<sup>44</sup>, since the members of the family partake in frequent and profound  
66 interactions. Caring for the young presents an excellent opportunity from microbial  
67 perspective, since providing care both increases odds of offspring survival<sup>11</sup> and establishes a  
68 higher transmission probability. Therefore, a microbial gene that is associated with host intra-  
69 family caring behaviour could be favoured by natural selection even when encouraging care  
70 towards genetically unrelated young individuals. The propagation of microbes carrying these  
71 genes may have driven the evolution of paternal care even in the absence of paternity.

## 72 Results

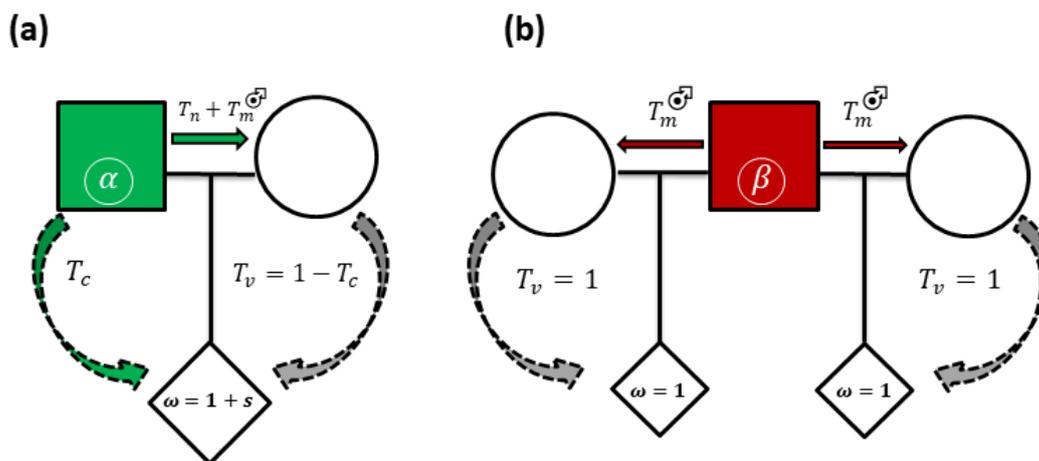
73 Let us first examine the case where males only adopt one of two pure strategies, either  
74 paternal care or lack thereof. Offspring fitness is increased by paternal care<sup>11</sup>, due to  
75 provision and protection from predation, by a factor of  $s > 0$ . There are, on average,  $n$   
76 available mating opportunities for a male who does not provide paternal care, and the  
77 expected level of paternity is assumed to be constant across them<sup>45</sup>. The male procures a  
78 higher benefit from providing paternal care than from not caring for the offspring when:

$$79 \quad \frac{1+s}{n} > 1 \quad (1)$$

80 Where  $n$  = available mating opportunities,  $s$  = increase in offspring fitness due to paternal  
81 care.

82 Now, we extend the model to include microbes as a reproductive unit that can affect paternal  
83 care behaviour. For simplicity, we neglect the effect of host genetic background in the  
84 microbe model and assume that host paternal behaviour is determined by its microbes. Let us  
85 consider microbes of type  $\alpha$ , which are associated with paternal care behaviour, and microbes  
86 of type  $\beta$ , which have no effect on paternal care behaviour. Microbes can be transmitted to  
87 the offspring either from the mother, with probability  $T_v$ , or from the father, with  
88 probability  $T_c$  when the father cares for the offspring. Microbes can also be transmitted from  
89 the father to the mother during mating with probability  $T_m^{\ominus}$ , and possibly through nurture of  
90 the mother, with probability  $T_n$ . In many species, mate nurturing behaviour is more common  
91 from father to mother than vice versa<sup>6,7</sup>. For simplicity, we assume that each host is inhabited  
92 by a single type of microbe at a given time. A transmission probability thus includes the  
93 probabilities that a microbe transmits to a new individual, establishes, and replaces the  
94 resident microbe, encompassing the competition dynamics between different microbial

95 strains. The transmission pathways and transmission probabilities of the two microbes are  
 96 illustrated in Fig. 1. We consider a model where the mother cares for the offspring<sup>46,47</sup>, and  
 97 additionally can transmit microbes during gestation<sup>38</sup> and natively<sup>37</sup>, so overall maternal  
 98 transmission is higher than paternal transmission ( $T_v > T_c$ ). We also assume that paternal  
 99 care involves more interaction – and potential for microbe transmission – than a singular  
 100 mating encounter ( $T_c > T_m^{\text{♂}}$ ). Since the probability of transmitting microbes during mating<sup>48</sup>  
 101 is asymmetric between the sexes, with a higher probability for male-to-female transmission,  
 102 we neglect the probability of female-to-male transmission. We initially assume that males  
 103 have full paternity in their brood and relax that assumption later (see Fig. 3).



**Figure 1. Illustration of microbe transmission pathways within the family.** (a) where the father carries microbes of type  $\alpha$ , inducing paternal care. (b) where the father carries microbes of type  $\beta$ , that have no effect on behaviour. Males carrying  $\beta$  do not care for the offspring and can be involved in  $n$  additional matings (illustrated is the case  $n = 1$ ).  $T_v$  – vertical transmission probability through maternal influence (prenatal and postnatal).  $T_c$  – probability of transmission through paternal care.  $T_m^{\text{♂}}$  – probability of male-to-female microbe transmission during mating.  $T_n$  – probability of transmission through male-to-female nurture.

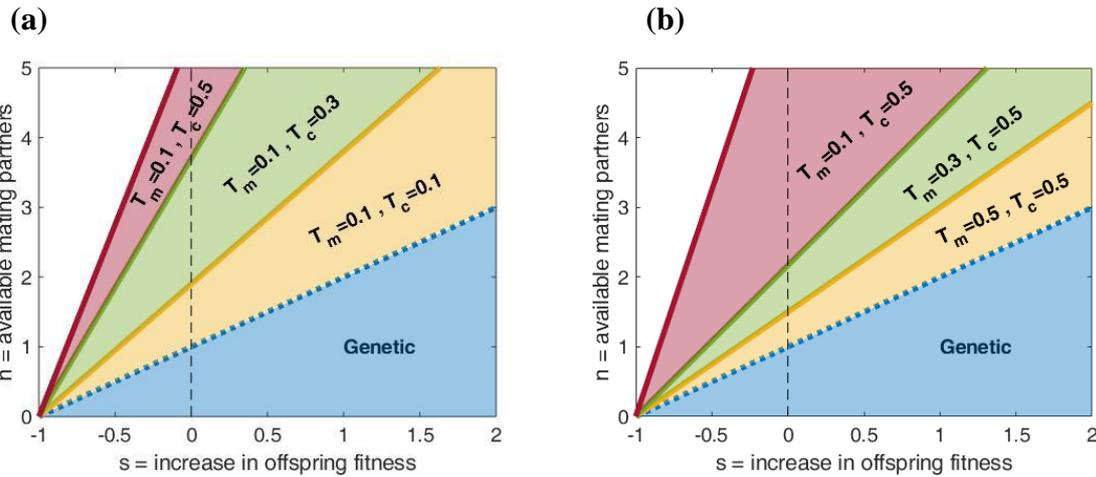
104 Reproduction is divided into two stages. First is mating, where males and females randomly  
 105 pair and mate. During this phase, microbes can be exchanged between the participating  
 106 individuals. We assume a delay in the effect of the microbes on behaviour and neglect the

107 possibility of a male altering its paternal behaviour due to contracting different microbes at  
108 the mating stage. The second phase is the transmission of microbes to the offspring. We  
109 assume  $T_c + T_v = 1$ , meaning that all the microbes of the offspring are obtained from its  
110 parents. In the case of lack of paternal care  $T_v = 1$ , meaning the offspring will receive its  
111 mother's microbes. We assume that during infancy, the offspring are interacting almost  
112 exclusively with individuals within the familial unit<sup>49-52</sup>. Consequently, we neglect the  
113 probability of contagion by the general population. The non-caring male paternal care has  
114  $n > 1$  mating opportunities but contributes no microbes to the offspring through care ( $T_c =$   
115  $0$ ). The fitness of an offspring whose father does not provide paternal care is  $\omega_\beta = 1$ , while  
116 an offspring that receives paternal care has increased fitness  $\omega_\alpha = 1 + s$ .

117 The condition for fixation of microbe type  $\alpha$  (see Methods for full derivation) is given by:

$$118 \quad \frac{1+s}{n} > \frac{T_m}{T_c*(1-T_m)+T_m+T_n*(1-T_c)} \quad (2)$$

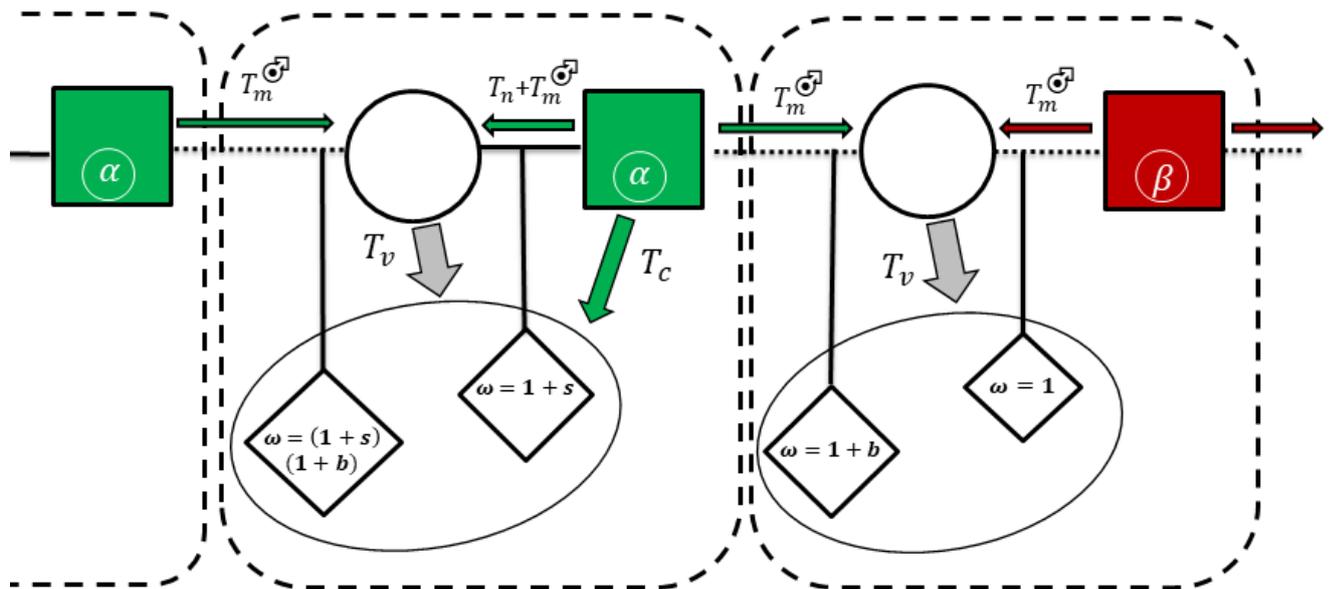
119 Fig. 2 presents the parameter range that allows for the evolution of paternal care in the model.  
120 In the genetic case, the cost-benefit isocline is given by  $\frac{1+s}{n} > 1$  (Eq. 1). The range of  
121 conditions where a gene for paternal care evolves is shown by the blue area (Fig. 2). The  
122 conditions where a microbe inducing paternal care evolves can be much wider, shown by the  
123 areas below the yellow, green and red lines. The range widens with  $T_c$ , the probability of  
124 microbe transmission through paternal care (Fig. 2a) and narrows with  $T_m$ , the transmission  
125 probability during mating (Fig. 2b). These results demonstrate that paternal care can evolve  
126 even in the paradoxical case where paternal "care" decreases offspring fitness, if the overall  
127 probability of transmission through mating is sufficiently low in comparison with the  
128 probability of transmission through paternal care.



129

**Figure 2. Microbes can expand the conditions for the evolution of paternal care.**  $T_c$  – probability of microbe transmission from father to offspring through paternal care.  $T_m$  – probability of transmission from male to female during mating. The area below each graph represents the conditions allowing paternal care to evolve in the population. A microbe associated with paternal care behaviour can widen the range of conditions where paternal care prevails, and the effect increases with the transmission probability of the paternal microbes to the offspring during care. Microbe-induced paternal care can even evolve in some paradoxical cases where paternal “care” decreases offspring fitness. Other parameters:  $T_n = 0$ .

130 Now, let us consider a different social structure, where both males and females can engage in  
 131 extra-pair mating, but offspring are brought up by social pairs<sup>22,53–55</sup>. The offspring of extra-  
 132 pair mating are raised along with the rest of the mother’s brood in the nest. We assume that a  
 133 male has limited resources, which it distributes among its efforts to pursue additional mating  
 134 opportunities and its paternal duties<sup>12</sup>. The more the father invests in its offspring, the fitter  
 135 they will be, but the father will have fewer extra-pair progeny. The fitness of an offspring  
 136 cared for by its social father is increased by a factor of  $1 + s$ . For each offspring in a social  
 137 brood, there is a probability,  $P_C$ , that this offspring is not biologically sired by its social  
 138 father. This corresponds to the availability of females interested in extra-pair matings<sup>16</sup>,  
 139 taking into account due to mate guarding, sperm competition, and cryptic female  
 140 choice<sup>56</sup>. The fitness of such an extra-pair offspring is increased by a factor of  $1 + b$ , due to  
 141 direct or indirect benefits gained from extra-pair mating<sup>22,57</sup>.



142

**Figure 3. Illustration of microbe transmission pathways within families with extra-pair mating.** Males carrying microbes of type  $\beta$  do not care for the offspring, while males carrying microbes of type  $\alpha$  care for the offspring in their social nest. All males and females engage in extra-pair mating.  $T_v$  – vertical transmission probability through maternal influence (prenatal and postnatal).  $T_c$  – probability of transmission through paternal care.  $T_m$  – probability of male-to-female transmission during mating.  $T_n$  – probability of transmission through male-to-female nurture. Offspring sired by an extra-pair mate are  $1 + b$  times more fit than offspring sired by the social mate. Offspring that receive paternal care are  $1 + s$  times more fit than offspring that do not receive it.

143

144 Let  $\omega_{xyz}$  be the fitness of an offspring with a social father of type  $x$ , a mother of type  $y$  and a

145 biological father of type  $z$  (denoted by  $\omega_{xy}$  if the social father  $x$  is also the biological father).

146 From our assumptions  $\omega_{\alpha\beta\alpha} = \omega_{\alpha\beta\beta} = \omega_{\alpha\alpha\alpha} = \omega_{\alpha\alpha\beta} = (1 + b) * (1 + s)$ ,  $\omega_{\beta\alpha\alpha} = \omega_{\beta\alpha\beta} =$

147  $\omega_{\beta\beta\alpha} = \omega_{\beta\beta\beta} = (1 + b)$ , while  $\omega_{\alpha\alpha} = \omega_{\alpha\beta} = (1 + s)$ , and  $\omega_{\beta\alpha} = \omega_{\beta\beta} = 1$ .

148 We denote the total resources available to a male by  $E$ . These resources are allocated between

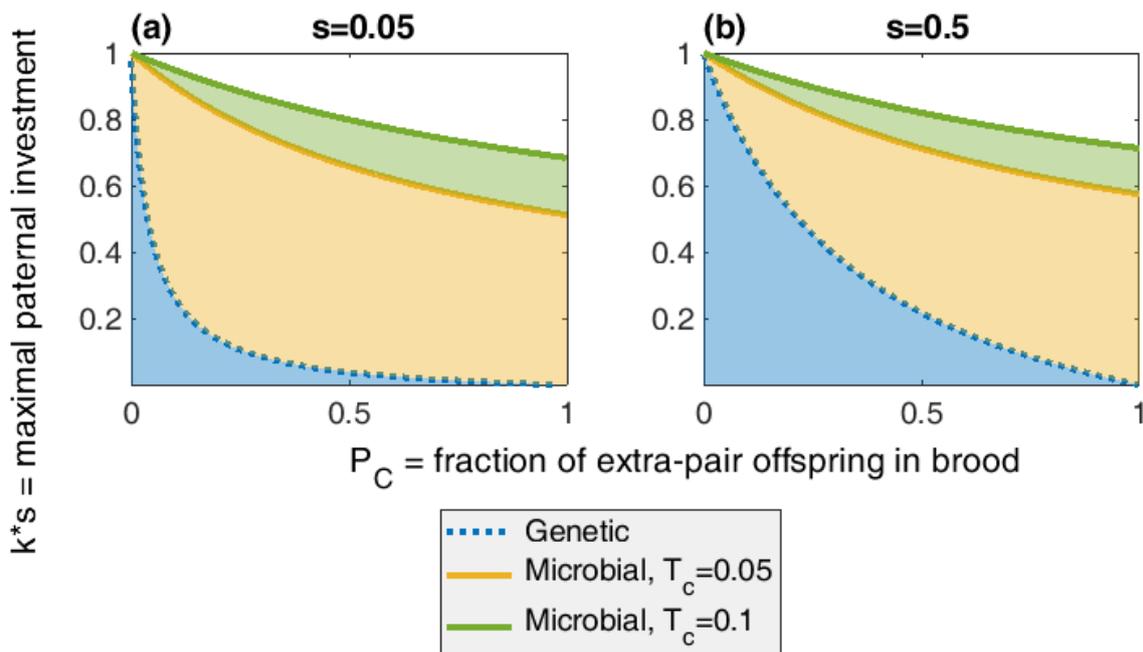
149 its paternal care and its efforts of seeking extra-pair mates<sup>12,58</sup>. The amount of paternal care is

150 given by  $s$ , the increase in offspring fitness. As paternal care increases, the caring father

151 would be less successful in siring extra-pair offspring<sup>53,54</sup>. The success of a caring father in

152 seeking additional mates is given by  $n_\alpha = n * (1 - k \frac{s}{E})$ , where  $0 \leq ks \leq E$ . The factor  $k$

153 represents the cost/benefit ratio between two effects of paternal care: the increase in offspring  
 154 fitness and the decrease in paternal mating opportunities.  
 155 We find the conditions for fixation of an  $\alpha$  gene, coding for paternal care, and similarly for  
 156 the fixation of microbes of type  $\alpha$ , inducing host paternal care (see Methods for mathematical  
 157 derivations).



158

**Figure 4. The evolution of paternal care in face of extra-pair offspring in brood.** The figure represents the maximal paternal investment,  $ks$ , that allows for the evolution of paternal care induced by either genes or microbes. The solid lines represent the microbial case and the dotted line represents the genetic case. Generally, in the microbial case, paternal care evolves under wider conditions. The range narrows with an increase in extra-pair paternity in both the genetic and microbial cases. However, the effect is reduced when the transmission probability through paternal care ( $T_c$ ) is high. The different plots (a),(b) represent different values of  $s$ , increase in offspring fitness due to paternal care. In both the microbial and the genetic cases, the range of paternal investment that allows for evolution of paternal care increases with  $s$ . In the microbial case, this effect is weaker when the ratio of transmission through caring and mating is high ( $T_c/T_m$ ). Other parameters:  $b = 0.2, T_n = 0.05, T_n = 0$ .

159 Fig. 4 shows the maximal paternal investment that still allows for a gene or a microbe of type  
 160  $\alpha$  (paternal care) to spread to fixation. A high degree of extra-pair paternity in the population

161 has a dual effect in the same direction. First, it allows for more opportunities to breed as an  
162 extra-pair sire. Secondly, it reduces the genetic relatedness of the social father to the offspring  
163 in its nest, and thus the fitness benefits it receives from paternal care. This effect is stronger  
164 in the genetic case, since from microbial perspective, paternal care for a genetically unrelated  
165 young individual contributes the same fitness benefits as for a genetically related one.

166 The dynamics between the two microbe types ( $\alpha$  and  $\beta$ ) are strongly affected by the ratio  
167 between transmission probability through paternal care ( $T_c$ ) and transmission probability  
168 through mating ( $T_m$ ). A higher  $T_c$  allows for a wider range of conditions in which microbe-  
169 induced paternal care can evolve. An increase in offspring fitness due to paternal care ( $s$ ) also  
170 widens the range of conditions where paternal care can evolve, but this effect is minor when  
171 microbial transmission through paternal care is significantly higher than transmission through  
172 mating ( $T_c \gg T_m$ ).

## 173 Discussion

174 In this work, we present an alternative explanation to a long-standing evolutionary  
175 conundrum: the ubiquity of paternal care. We show that when considering paternal care to be  
176 induced by microbes rather than by the father's genes, the range of conditions in which  
177 paternal care could evolve widens. We expect that microbe-induced paternal care could play  
178 a more significant role in circumstances where genetic relatedness falls short of explaining  
179 the observed degree of paternal investment, such as adoption<sup>59</sup>, species where extra-pair  
180 paternity is common<sup>22</sup> and the well-known behaviour of cooperative breeding and  
181 eusociality<sup>60,61</sup>. Our model predicts that microbe-induced paternal care would more easily  
182 evolve when parent-offspring interactions are of high transmission ability<sup>50,51,62-64</sup> (high  $T_c$ ,  
183 resulting from interactions corresponding to feeding, grooming).

184 Previous work has discussed possible explanations for the broad existence of paternal care.  
185 Suggested explanations<sup>60</sup> include gaining practice in caring for young, resulting in higher  
186 chances for successful parenthood in the following year<sup>14</sup>; increasing indirect fitness<sup>65,66</sup>; and  
187 increasing chances of mating or territory acquisition<sup>67,68</sup>. In addition, mating may not be  
188 random with regard to the paternal trait. Since female choice is a key factor in determining  
189 male reproductive success, sexual selection may act directly on the paternal trait<sup>10,66,69</sup>.  
190 Another suggested explanation is inaccurate perceived paternity<sup>70,71</sup>, or the limited accuracy  
191 of assessing offspring paternity by phenotypic signals. Lower accuracy helps preserve a  
192 stable level of paternal care<sup>15,18,72</sup>. However, when the cost of caring is high, and the expected  
193 level of paternity is low, selection is expected to favour more suspicious males that reduce  
194 their paternal investment with increased risk of extra-pair mating<sup>9,18,72-75</sup>. Nevertheless,  
195 paternal care has been demonstrated to prevail even in these cases in natural systems<sup>22,23,54,76</sup>.  
196 We demonstrate that the microbial perspective can explain stable levels of paternal care even  
197 under high levels of extra-pair mating, and when paternal investment is high.  
198 Increased extra-pair mating may impose both costs and benefits on the female. In our model,  
199 the sum of costs and benefits is represented by the parameter  $b > 0$ , assuming that the  
200 benefits exceed the costs. The benefits of extra-pair mating for females<sup>55,77-79</sup> may be  
201 obtaining a higher quality or more compatible sire<sup>78</sup> and bet-hedging by increasing the  
202 genetic diversity of offspring<sup>80</sup>. The possible costs include loss of care by social mate<sup>81</sup>, male  
203 sexual aggression<sup>82</sup>, increased sibling competition<sup>83,84</sup>, and the risk of contracting sexually  
204 transmitted pathogens<sup>85</sup>. Microbes may mediate some of these costs. As demonstrated by our  
205 results, care by the social mate prevails under wider conditions when induced by the  
206 microbes. Within-brood aggression between half-siblings<sup>83</sup> could also be mitigated by  
207 microbes, since relatedness among the microbes of the sibling is not expected to be  
208 significantly affected by the genetic relatedness among them.

209 Our model can be extended in several ways. We examined two extremes, paternal care  
210 governed exclusively by host genes or exclusively by microbial genes. However, evolution of  
211 paternal care is likely driven by a selection on reproductive units in both levels, possibly  
212 leading to intermediate results. Additionally, it is possible to consider that when host genes  
213 and microbial genes experience conflicting selective pressures, selection on the host would  
214 drive the evolution of resistance genes to the microbial influence. In this case, we expect the  
215 host-microbe coevolution to generate oscillatory rock-paper-scissors evolutionary dynamics,  
216 that can allow the long-term maintenance of paternal care. Similar dynamics have been found  
217 by some of us with respect to microbe-induced cooperation and host resistance<sup>86</sup>.

218 We may consider uneven potential reproductive opportunities among males. According to  
219 empirical studies<sup>57,87–89</sup>, extra-pair mating success varies and has some correlation with male  
220 quality. This would have consequences on paternal strategy, where males who expect meagre  
221 success as philanderers may benefit more from increasing paternal investment. The  
222 availability of reproductive opportunities can also be restricted by the abundance of males  
223 pursuing extra-pair mating. Another extension would be allowing more female strategies. We  
224 assumed a constant level of maternal care. Yet, studies show females may reduce their care if  
225 the male provides sufficiently intensive care or increase their care to compensate for lack of  
226 male care<sup>16,90,91</sup>. Females may also vary the level of care offered to an offspring with the  
227 quality of its father, a strategy known as “differential allocation”<sup>92,93</sup>. Both these behaviours  
228 could reduce the benefits of paternal behaviour in favour of siring extra-pair offspring. In  
229 addition, we may consider maternal investment to be governed by microbial genes as well.

230 Microbial influence over female reproductive behaviour could increase the frequency of  
231 extra-pair offspring within a brood to the extent that still allows for paternal care by the social  
232 mate.

233 Our model joins the rank of previous models concerning the role of different nongenetic  
 234 elements in the evolution of social traits<sup>30,94–96</sup>. Recent evidence suggests that microbes hold a  
 235 significant role in shaping host evolution<sup>25,30,97,98</sup>. However, it is worth noting that the  
 236 assumptions presented here are not limited to the microbiome and apply to any class of  
 237 nongenetic elements that are capable of both vertical and horizontal/oblique<sup>99,100</sup> transfer and  
 238 of influencing complex behavioural phenotypes. Examples of such elements may include  
 239 epigenetic states<sup>101,102</sup> and culture<sup>94,103–106</sup>.

240 Our theoretical results demonstrate a possible explanation to a widely studied and unresolved  
 241 question in evolutionary biology – why males care for the offspring. Previous studies  
 242 demonstrated hormonal regulation of paternal care<sup>107–110</sup>, yet the mechanism by which  
 243 microbes may regulate paternal behaviour is still to be experimentally validated.

244 Nevertheless, our results suggest that factors affecting the host microbiome (for example  
 245 antibiotics<sup>111,112</sup>, probiotics<sup>113,114</sup>, specific foods<sup>115,116</sup>) may also modify paternal behaviour.

## 246 **Methods**

### 247 **Model Parameters**

	<b>Meaning</b>	<b>Range</b>
<b><math>p_\alpha, p_\beta</math></b>	frequency of individuals carrying gene/microbe of type $\alpha$ or $\beta$ , respectively	$p_\alpha + p_\beta = 1$
<b><math>n</math></b>	number of mating opportunities for a male that does not provide paternal care	$n > 1$
<b><math>E</math></b>	total male resources allocated between its parental care and efforts of seeking extra-pair mates	$E = 1$
<b><math>s</math></b>	increase in offspring fitness due to paternal care	$0 \leq k * s \leq 1$
<b><math>b</math></b>	increase in offspring fitness due to benefits gained from extra-pair mating	$0 \leq b \leq 1$
<b><math>T_m</math></b>	probability of male-to-female microbe	$0 \leq T_m \leq 1$

	transmission during mating	
$T_c$	probability of microbe transmission through paternal care	$0 \leq T_c \leq 1$
$T_n$	probability of transmission through male-to-female nurture	$0 \leq T_n \leq 1$
$k$	cost/benefit ratio between two effects of paternal care: the increase in offspring fitness and the decrease in paternal mating opportunities	$0 \leq k * s \leq 1$
$P_c$	fraction of extra-pair offspring in brood (population mean)	$0 \leq P_c \leq 1$

248

### 249 Family structure I: full-sibs in brood, microbial case

250 We assume that the male who does not provide paternal care has  $n$  mating opportunities,  
 251 where  $n > 1$ . Under random mating, the effective probabilities of the males in mating  
 252 encounters are given by the following expressions:

$$253 \quad \widetilde{p}_\beta = \frac{n * p_\beta}{n * p_\beta + p_\alpha}$$

$$254 \quad \widetilde{p}_\alpha = 1 - \widetilde{p}_\beta$$

255 The frequency of microbe  $\alpha$  in the offspring generation is given by:

$$256 \quad p'_\alpha = \widetilde{p}_\alpha p_\alpha \cdot \frac{\omega_{\alpha\alpha}}{\bar{\omega}} + \widetilde{p}_\alpha p_\beta (T_c + T_n (T_n + T_m)) \frac{\omega_{\alpha\beta}}{\bar{\omega}} + \widetilde{p}_\beta p_\alpha (1 - T_m) \frac{\omega_{\beta\alpha}}{\bar{\omega}}$$

257 Offspring fitness increases with paternal care. An offspring that receives paternal care has a  
 258 fitness of  $\omega_\alpha = 1 + s$ , while an offspring whose father does not provide paternal care has a  
 259 fitness of  $\omega_\beta = 1$ . The mean offspring population fitness is given by:

$$260 \quad \bar{\omega} = \widetilde{p}_\alpha p_\alpha \omega_\alpha + \widetilde{p}_\alpha p_\beta \omega_\alpha + \widetilde{p}_\beta p_\alpha \omega_\beta + \widetilde{p}_\beta p_\beta \omega_\beta$$

261 The change in the frequency of microbe  $\alpha$  in the next generation is given by

$$262 \quad \Delta p = p'_\alpha - p = \frac{p * (1 + s) * [(1 - p) * (T_c + T_n - T_c * T_m - T_c * T_n) + T_m]}{p * (1 + s) + n * (1 - p)} - T_m * p$$

263 To find the equilibrium ( $p^*$ ), we find  $p$  for which  $\Delta p = 0$ . The possible equilibria are  $p^* =$   
 264 0 and  $p^* = 1$ , meaning the microbe of type  $\alpha$  inducing paternal care either goes extinct or  
 265 reaches fixation.

266 Stability analysis:

$$267 \quad \frac{\partial \Delta p}{\partial p} \Big|_{p^*=0} = \frac{(s + 1) * (T_c + T_m + T_n - T_c * T_m - T_c * T_n)}{n} - T_m$$

$$268 \quad \frac{\partial \Delta p}{\partial p} \Big|_{p^*=1} = T_c * T_m - T_n - T_c + T_c * T_n - \frac{T_m * (s - n + 1)}{s + 1}$$

269 The value of the derivative  $\frac{\partial \Delta p}{\partial p} \Big|_{p^*=0}$  and  $\frac{\partial \Delta p}{\partial p} \Big|_{p^*=1}$  can be either positive or negative,  
 270 depending on the values of  $T_c, T_m, T_n, n, s$ . Hence, the equilibria may be stable, oscillatory or  
 271 unstable. The condition for stable fixation of microbe  $\alpha$  is  $\frac{\partial \Delta p}{\partial p} \Big|_{p^*=1} < 0$ , which is given by  
 272 the following inequality:

$$273 \quad s > \left( \frac{T_m}{T_c * (1 - T_m) + T_m + T_n * (1 - T_c)} \right) * n - 1$$

## 274 Family structure II: extra-pair mating, genetic case

275

### 276 Mating opportunities

277  $p$  – the proportion of hosts carrying microbes of type  $\alpha$  before the mating season.

278 The success of a caring father in extra-pair matings is reduced proportionally to his paternal  
 279 care ( $s$ ). The parental investment is represented by  $ks$ , where  $k$  is the cost/benefit ratio  
 280 between two effects of paternal care: the increase in offspring fitness and the decrease in  
 281 paternal mating opportunities.

282 The representation of the different male types in additional mating encounters is given by the  
 283 following expressions:

$$284 \quad \alpha \text{ males: } \frac{p \cdot (1 - ks)}{p(1 - ks) + 1 - p} \qquad \beta \text{ males: } \frac{1 - p}{p(1 - ks) + 1 - p}$$

285 Offspring types:

286  $p_{xy}$  – proportion of offspring where the father is  $x$  and the mother is  $y$

287  $p_{xyz}$  – proportion of offspring where the social mate is  $x$ , the mother is  $y$ , and the extra-pair

288 mate (genetic father of offspring) is  $z$

289 The proportion of each offspring type is determined by the fraction of each type of parent

290 ( $\alpha/\beta$  female,  $\alpha/\beta$  male) and the proportion of extra-pair offspring within a brood ( $P_c$ ).

Proportion of offspring types	Probability of $\alpha/\beta$ offspring	Offspring fitness
$p_{\alpha\alpha} = p \cdot p \cdot (1 - P_c)$	$p_o(\alpha) = 1$	$\omega = 1 + s$
$p_{\alpha\alpha\alpha} = p \cdot p \cdot P_c \cdot \frac{p \cdot (1 - k \cdot s)}{p(1 - k \cdot s) + 1 - p}$	$p_o(\alpha) = 1$	$\omega = (1 + s) \cdot (1 + b)$
$p_{\alpha\alpha\beta} = p \cdot p \cdot P_c \cdot \frac{p \cdot (1 - k \cdot s)}{p(1 - k \cdot s) + 1 - p}$	$p_o(\alpha) = T_c + (1 - T_m)(1 - T_c)$	$\omega = (1 + s) \cdot (1 + b)$
	$p_o(\beta) = T_m \cdot (1 - T_c)$	
$p_{\alpha\beta} = p \cdot (1 - p) \cdot (1 - P_c)$	$p_o(\alpha) = T_n(1 - T_c) + T_c$	$\omega = 1 + s$
	$p_o(\beta) = (1 - T_n)(1 - T_c)$	
$p_{\alpha\beta\alpha} = p \cdot (1 - p) \cdot (1 - P_c) \cdot \frac{p \cdot (1 - k \cdot s)}{p(1 - k \cdot s) + 1 - p}$	$p_o(\alpha) = (T_n + T_m)(1 - T_c) + T_c$	$\omega = (1 + s) \cdot (1 + b)$
	$p_o(\beta) = (1 - T_n - T_m)(1 - T_c)$	
$p_{\alpha\beta\beta} = p \cdot (1 - p) \cdot (1 - P_c) \cdot \frac{p \cdot (1 - k \cdot s)}{p(1 - k \cdot s) + 1 - p}$	$p_o(\alpha) = T_c + T_n(1 - T_c)$	$\omega = (1 + s) \cdot (1 + b)$
	$p_o(\beta) = (1 - T_n)(1 - T_c)$	
$p_{\beta\alpha} = (1 - p) \cdot p \cdot (1 - P_c)$	$p_o(\alpha) = (1 - T_m)$	$\omega = 1$
	$p_o(\beta) = T_m$	
$p_{\beta\alpha\alpha} = (1 - p) \cdot p \cdot P_c \cdot \frac{p \cdot (1 - k \cdot s)}{p(1 - k \cdot s) + 1 - p}$	$p_o(\alpha) = 1 - T_m$	$\omega = 1 + b$
	$p_o(\beta) = T_m$	

$p_{\beta\alpha\beta} = (1-p) \cdot p \cdot P_c$ $\cdot \frac{p \cdot (1-k \cdot s)}{p(1-k \cdot s) + 1-p}$	$p_o(\alpha) = 1 - 2T_m$	$\omega = 1 + b$
	$p_o(\beta) = 2T_m$	
$p_{\beta\beta} = (1-p) \cdot (1-p) \cdot (1-P_c)$	$p_o(\beta) = 1$	$\omega = 1$
$p_{\beta\beta\alpha} = (1-p) \cdot (1-p) \cdot (1-P_c)$ $\cdot \frac{p \cdot (1-k \cdot s)}{p(1-k \cdot s) + 1-p}$	$p_o(\alpha) = T_m$	$\omega = 1 + b$
	$p_o(\beta) = 1 - T_m$	
$p_{\beta\beta\beta} = (1-p) \cdot (1-p) \cdot (1-P_c)$ $\cdot \frac{p \cdot (1-k \cdot s)}{p(1-k \cdot s) + 1-p}$	$p_o(\beta) = 1$	$\omega = 1 + b$

292

291 The mean offspring fitness is given by:

$$\begin{aligned}
 293 \quad \bar{\omega} = P_c * (p_{\alpha\beta\alpha} * \omega_{\alpha\beta\alpha} + p_{\alpha\beta\beta} * \omega_{\alpha\beta\beta} + p_{\alpha\alpha\alpha} * \omega_{\alpha\alpha\alpha} + p_{\alpha\alpha\beta} * \omega_{\alpha\alpha\beta} + p_{\beta\beta\alpha} * \omega_{\beta\beta\alpha} \\
 294 \quad + p_{\beta\beta\beta} * \omega_{\beta\beta\beta} + p_{\beta\alpha\alpha} * \omega_{\beta\alpha\alpha} + p_{\beta\alpha\beta} * \omega_{\beta\alpha\beta}) + (1 - P_c) \\
 295 \quad * (p_{\alpha\alpha} * \omega_{\alpha\alpha} + p_{\alpha\beta} * \omega_{\alpha\beta} + p_{\beta\beta} * \omega_{\beta\beta} + p_{\beta\alpha} * \omega_{\beta\alpha})
 \end{aligned}$$

296 The frequency of the  $\alpha$  gene in the next generation would be:

$$\begin{aligned}
 297 \quad p'_\alpha = \frac{1}{\bar{\omega}} * P_c * \left( \frac{1}{2} * p_{\alpha\beta\alpha} * \omega_{\alpha\beta\alpha} + 0 * p_{\alpha\beta\beta} * \omega_{\alpha\beta\beta} + p_{\alpha\alpha\alpha} * \omega_{\alpha\alpha\alpha} + \frac{1}{2} * p_{\alpha\alpha\beta} * \omega_{\alpha\alpha\beta} + \frac{1}{2} \right. \\
 298 \quad \left. * p_{\beta\beta\alpha} * \omega_{\beta\beta\alpha} + 0 * p_{\beta\beta\beta} * \omega_{\beta\beta\beta} + p_{\beta\alpha\alpha} * \omega_{\beta\alpha\alpha} + \frac{1}{2} * p_{\beta\alpha\beta} * \omega_{\beta\alpha\beta} \right) + \frac{1}{\bar{\omega}} \\
 299 \quad * (1 - P_c) * \left( p_{\alpha\alpha} * \omega_{\alpha\alpha} + \frac{1}{2} * p_{\alpha\beta} * \omega_{\alpha\beta} + 0 * p_{\beta\beta} * \omega_{\beta\beta} + \frac{1}{2} * p_{\beta\alpha} * \omega_{\beta\alpha} \right)
 \end{aligned}$$

300 We calculate the equilibria as before,  $\Delta p = p'_\alpha - p = 0$ . Three equilibria points exist:  $p^* =$

301  $0$ ,  $p^* = 1$ , and a polymorphic solution that under some conditions occurs within the range

302  $0 < p < 1$ .

303 We examine the derivative of  $\Delta p$  at  $p^* = 1$  and  $p^* = 0$ . When  $\left. \frac{\partial \Delta p}{\partial p} \right|_{p^*=1} < 0$  it means there

304 exists some critical  $p^*$  (either  $p^* = 0$  or the polymorphic solution  $p^* > 0$ ) from which the  $\alpha$

305 gene will spread in the population to fixation,  $p = 1$ . When  $\frac{\partial \Delta p}{\partial p} \Big|_{p^*=0} > 0$  and  $\frac{\partial \Delta p}{\partial p} \Big|_{p^*=1} < 0$

306 it means that  $\alpha$  gene will spread to fixation from  $p = 0$ .

$$307 \quad \frac{\partial \Delta p}{\partial p} \Big|_{p^*=1} = \frac{k * s}{2 * (1 - k * s)} - \frac{s * (1 - P_c) * (k + 1)}{2 * (P_c * b + 1) * (1 - k * s) * (s + 1)}$$

308 Differentiating the above expression with respect to  $k$ , we get:

$$309 \quad \frac{\partial \left( \frac{\partial \Delta p}{\partial p} \Big|_{p^*=1} \right)}{\partial k} = \frac{P_c * s * (b + 1)}{2 * (P_c * b + 1) * (k * s - 1)^2}$$

310 The above expression is positive for all  $0 < s, P_c, b, k$ . Thus, the function  $\frac{\partial \Delta p}{\partial p} \Big|_{p^*=1}$  is

311 increasing with  $k$ . We want to find the range of  $k$  for which  $\frac{\partial \Delta p}{\partial p} \Big|_{p^*=1} < 0$ . Thus, solving

312  $\frac{\partial \Delta p}{\partial p} \Big|_{p^*=1} = 0$  for  $k$  will give the maximal  $k$  for which this holds.

$$313 \quad k^1 = \frac{1 - P_c}{P_c + s + P_c * b + P_c * b * s}$$

314 Now we will do the same for  $\frac{\partial \Delta p}{\partial p} \Big|_{p^*=0}$ ,

$$315 \quad \frac{\partial \Delta p}{\partial p} \Big|_{p^*=0} = -\frac{k * s}{2} + \frac{s * (1 - P_c) * (k + 1)}{2 * (P_c * b + 1)}$$

316 Differentiating the above expression in relation to  $k$ , we get:

$$317 \quad \frac{\partial k \left( \frac{\partial \Delta p}{\partial p} \Big|_{p^*=0} \right)}{\partial k} = -\frac{P_c * s * (b + 1)}{2 * (P_c * b + 1)}$$

318 The above expression is negative for all  $0 < s, P_c, b$ . Thus, the function  $\frac{\partial \Delta p}{\partial p} \Big|_{p^*=0}$  is

319 decreasing when  $k$  is increasing. We want to find the range of  $k$  for which  $\frac{\partial \Delta p}{\partial p} \Big|_{p^*=0} > 0$ .

320 Thus, solving  $\frac{\partial \Delta p}{\partial p} \Big|_{p^*=0} = 0$  for  $k$  will give the maximal  $k$  for which this holds.

321 
$$k^0 = \frac{1 - Pc}{Pc + Pc * b}$$

322 Now, the range of  $k$  that allows for the evolution of the  $\alpha$  gene to fixation is  $0 < k <$   
323  $\min(k^0, k^1)$ .

324 Let us examine the expression,

325 
$$\delta k = k^1 - k^0 = (Pc - 1) * \left[ \frac{1}{Pc * (1 + b)} - \frac{1}{Pc * (1 + b) + s * (1 + Pc)} \right]$$

326 The part in round brackets is negative, and the part in square brackets is positive. Thus, the  
327 entire expression is always negative, meaning  $0 < k^1 < k^0$ .

328 Overall,

329 
$$\text{Maximal } k(Pc, b, s) = k^0$$

### 330 **Family structure II: extra-pair mating, microbial case**

331 Next, we introduce the microbial influence over the paternal behaviour. We define  $T_{sm}$  as the  
332 transmission probability of a microbe from a father providing paternal care to an offspring in  
333 its brood, and  $T_{ep}$  as the transmission probability of a microbe from an extra-pair mate to the  
334 offspring in the female's brood.

335 
$$T_{sm} = T_c + (T_n + T_m) * (1 - T_c)$$

336 
$$T_{ep} = T_m * (1 - T_c)$$

337 In this case, the frequency of the microbe  $\alpha$  in the next generation is given by:

$$\begin{aligned}
 338 \quad p'_\alpha &= \frac{1}{\bar{\omega}} * P_C * ((T_{sm} + T_{ep}) * p_{\alpha\beta\alpha} * \omega_{\alpha\beta\alpha} + T_{sm} * p_{\alpha\beta\beta} * \omega_{\alpha\beta\beta} + p_{\alpha\alpha\alpha} * \omega_{\alpha\alpha\alpha} \\
 339 \quad &+ (1 - T_{ep}) * p_{\alpha\alpha\beta} * \omega_{\alpha\alpha\beta} + T_m * p_{\beta\beta\alpha} * \omega_{\beta\beta\alpha} + 0 * p_{\beta\beta\beta} * \omega_{\beta\beta\beta} \\
 340 \quad &+ (1 - T_m) * p_{\beta\alpha\alpha} * \omega_{\beta\alpha\alpha} + (1 - 2 * T_m) * p_{\beta\alpha\beta} * \omega_{\beta\alpha\beta}) + \frac{1}{\bar{\omega}} * (1 - P_C) \\
 341 \quad &* (p_{\alpha\alpha} * \omega_{\alpha\alpha} + T_{sm} * p_{\alpha\beta} * \omega_{\alpha\beta} + 0 * p_{\beta\beta} * \omega_{\beta\beta} + (1 - T_m) * p_{\beta\alpha} * \omega_{\beta\alpha})
 \end{aligned}$$

342 We calculate the equilibria as for the genetic case,  $\Delta p = p'_\alpha - p = 0$ . Three equilibria exist:

343  $p^* = 0, p^* = 1$ , and a polymorphic solution that under some conditions exists within the

344 range  $0 < p < 1$ .

345 For the microbial case, differentiating  $\frac{\partial \Delta p}{\partial p} |_{p^*=1}$  with respect to  $k$ , we get:

$$346 \quad \frac{\partial \left( \frac{\partial \Delta p}{\partial p} |_{p^*=1} \right)}{\partial k} = \frac{P_C * T_m * s * (1 - T_c) * (b + 1)}{(P_C * b + 1) * (k * s - 1)^2}$$

347 The expression above is positive for  $0 < T_m, s, P_C, b, k, T_c < 1$ . This means that  $\frac{\partial \Delta p}{\partial p} |_{p^*=1}$

348 increases with  $k$ . We want to find the range in which  $\frac{\partial \Delta p}{\partial p} |_{p^*=1} < 0$ .

349 solving  $\frac{\partial \Delta p}{\partial p} |_{p^*=1} = 0$  for  $k$  will give the maximal  $k$  for which this holds.

350  $k^1$

$$351 \quad = \frac{T_m * s * (1 + P_C * b) + (1 + s) * (1 + P_C * b) * (T_c * (1 - T_m) + T_n * (1 - T_c))}{T_m * s^2 * (1 + P_C * b) + s * (1 + s) * (1 + P_C * b) * (T_c * (1 - T_m) + T_n * (1 - T_c)) + s * (1 + s) * P_C * T_m * (1 - T_c) * (1 + b)}$$

352 Similarly, differentiating  $\frac{\partial \Delta p}{\partial p} |_{p^*=0}$  with respect to  $k$ , we get:

$$353 \quad \frac{\partial \left( \frac{\partial \Delta p}{\partial p} |_{p^*=0} \right)}{\partial k} = - \frac{P_C * T_m * s * (b + 1)}{P_C * b + 1}$$

354 The above expression is negative for all  $0 < b, T_c, T_n, s < 1$ . Thus, the function  $\frac{\partial \Delta p}{\partial p} |_{p^*=0}$  is

355 decreasing when  $k$  is increasing. We want to find the range of  $k$  for which  $\frac{\partial \Delta p}{\partial p} |_{p^*=0} > 0$ .

356 Thus, solving  $\frac{\partial \Delta p}{\partial p} |_{p^*=0} = 0$  for  $k$  will give the maximal  $k$  for which this holds.

357 
$$k^0 = \frac{(P_c * b + 1) * (s + 1) * (T_c + T_n - T_c * T_n)}{P_c * T_m * s * (b + 1)} - \frac{(P_c * b + 1) * (T_c - s + T_c * s)}{P_c * s * (b + 1)}$$

358 Now, the range of  $k$  that allows for the evolution of the  $\alpha$  microbe to fixation is  $0 < k <$

359  $\min(k^0, k^1)$ .

360 In this case  $\delta k$  can be either positive or negative, depending on the parameter values, hence

361 the minimum needs to be calculated dynamically.

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## **Author Contributions**

Y.G. and L.H. designed the study and formulated the model. Y.G. and O.L.-E. derived the analytical equations and implemented the code. Y.G. and L.H. analysed the results and wrote the manuscript.

## **Competing interests**

The authors declare no competing interests.