

Can natural selection favour indiscriminate spite?

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1 Abstract

Spiteful behaviours occur when an actor harms its own fitness to inflict harm on the fitness of the recipient. Hamilton (1970) found that in order for spiteful genes to spread the spite had to be directed at individuals who were related to the actor with a negative relatedness. A number of papers have suggested scenarios where indiscriminate spite could be favoured, especially in small populations or small groups. However, it is not clear that a negative relatedness could arise without the harming behaviour being preferentially directed towards less related individuals (kin discrimination). We show that: (1) the evolution of spite requires kin discrimination; (2) previous models suggesting indiscriminate spite involve scenarios where the actor gains a direct, feedback benefit from harming others, and so the harming is selfish rather than spiteful; (3) selfish harming can be favoured most in small populations or groups because this is where the feedback benefit of harming is greatest.

keywords:

spite, inclusive fitness, cooperation, kin-selection, evolution, social evolution

22 **2 Introduction**

23 Spite is the hardest type of social trait to explain. Spiteful behaviour re-
24 duces the lifetime number of surviving offspring (fitness) of both the recipi-
25 ent and the performer (actor) of that behaviour (Hamilton, 1970) . In terms
26 of Hamilton's rule, $-C + RB > 0$, spite represents the case where there is a
27 fitness cost to the actor (positive C), and a fitness cost to the harmed recipi-
28 ent (negative B), which can only be favoured if the genetic relatedness term,
29 R , is negative (Hamilton, 1970). Understanding the meaning of negative
30 relatedness is therefore crucial for explaining how and why spite evolves.

31 It has been argued that the evolution of spite requires kin discrimina-
32 tion, allowing the actor to harm individuals in the social group with whom
33 they share relatively low genetic similarity (Foster et al., 2000, 2001; Gard-
34 ner and West, 2004b,a; Gardner et al., 2004; Lehmann et al., 2006; West
35 and Gardner, 2010). Specifically, spite can be favoured when harming less-
36 related individuals (primary recipients) reduces competition and therefore
37 benefits more-related individuals (secondary recipients). In this case, neg-
38 ative relatedness arises because the actor is less genetically similar to the
39 primary recipients than to the secondary recipients (Lehmann et al., 2006)
40 . In contrast, without kin discrimination, harming behaviours could not be
41 directed at individuals to whom the actor is negatively related, so indis-
42 criminate spite should be impossible.

43 Previous theoretical studies have suggested the possibility for indiscrimi-
44 nate spite. Indiscriminate meaning the trait does not affect other individ-
45 uals differentially based on their kinship. Hamilton (1970) found that non-
46 trivial negative relatedness will arise in any small population, and this led
47 to the prediction that indiscriminate spite could be favoured in sufficiently
48 small populations (Grafen, 1985; Vickery et al., 2003; Smead and Forber,
49 2012). Specifically, some authors have suggested that individuals could be
50 favoured to hold territories that are larger than needed for their own inter-

51 est (“super-territories”), in order to spitefully exclude others from resources
52 Knowlton and Parker (1979); Pleasants and Pleasants (1979); Parker and
53 Knowlton (1980).

54 Here, we resolve this disagreement over whether indiscriminate spite
55 can occur. Many harming traits will be costly to primary recipients ($B < 0$)
56 but provide a direct fitness benefit to the actor, because they reduce compe-
57 tition. Consequently, they are selfish ($-C > 0$) rather than spiteful ($-C < 0$)
58 (Hamilton, 1970; West and Gardner, 2010). We hypothesise that indiscrim-
59 inate harming traits like territory size have been misclassified as spiteful
60 when they are actually selfish. We aim to: (1) determine generally whether
61 indiscriminate harming evolves as a spiteful or a selfish trait; (2) examine
62 how different modelling approaches can change the meaning of negative re-
63 latedness and lead to misclassification of harming traits; (3) re-analyse the
64 Knowlton and Parker (1979) territory-size model to determine whether it
65 predicts spiteful behaviour.

66 **3 Harming traits**

67 We first modelled natural selection acting on a harming trait, following the
68 approach of Lehmann et al. (2006). The trait has a fitness effect on a focal ac-
69 tor ($-C$) and on two categories of recipients: the harmed primary recipients
70 and the unharmed secondary recipients who benefit from reduced compe-
71 tition (fitness effects B_1 and B_2 , respectively). We assume that fitness effects
72 on the actor, primary recipients, and secondary recipients must sum to zero
73 because of competition for finite resources (Rousset and Billiard, 2000):

$$-C + B_1 + B_2 = 0, \quad (1)$$

74 implying that any decrease in fitness for one category necessarily means
75 an increase in fitness for another. This model could apply to any finite

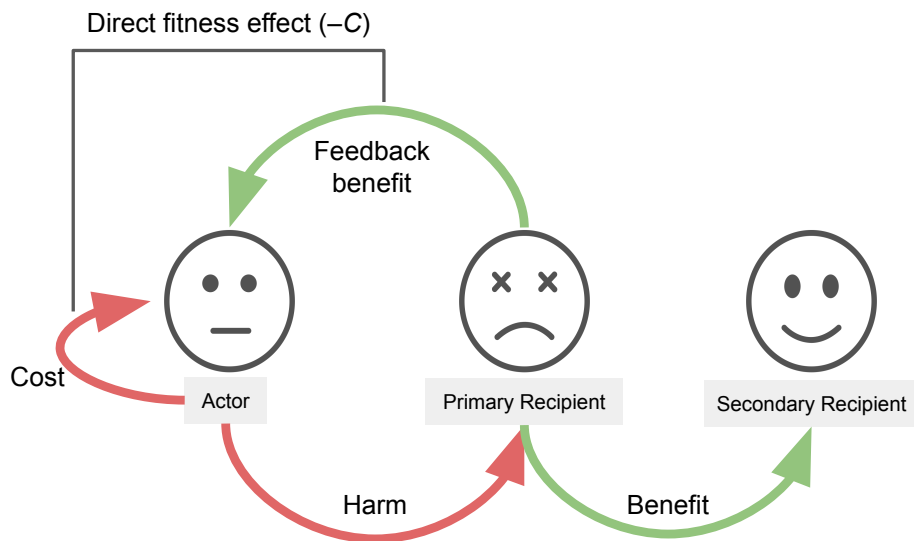


Figure 1: Partitioning the fitness effects of a harming trait. When a focal actor harms a primary recipient, this reduces competition and therefore benefits the unharmed secondary recipients and the actor itself (feedback benefit). Some modelling approaches include the actor in the set of secondary recipients. However, the total direct fitness effect ($-C$ in Hamilton's rule) includes the fecundity cost of expressing the harming trait plus the feedback benefit.

76 population of constant size or to a local economic neighbourhood in which
 77 there is a zero-sum competition for access to the next generation (Queller,
 78 1994). Key examples of such local competition include poly-embryonic
 79 wasps competing for resources inside a host (Gardner and West, 2004b;
 80 Gardner et al., 2007) or male fig wasps competing for females inside a fig
 81 (West and Gardner, 2010).

82 To predict the direction of natural selection acting on the harming trait,
 83 we considered the fate of a mutant harming allele in a population of indi-
 84 viduals with a fixed, resident genotype. The success of the mutant allele
 85 depends on its inclusive fitness effect (Hamilton, 1964): the sum of effects
 86 from a focal actor's mutant trait on its own fitness and on the total fitness of

87 each recipient category, weighted by their genetic similarity with the actor.
88 Under the usual assumptions of weak selection and additive gene action,
89 the inclusive fitness effect for our model is:

$$\Delta W_{IF} = -C + B_1 Q_1 + B_2 Q_2, \quad (2)$$

90 where, Q_1 and Q_2 are probabilities of sharing identical genes between the
91 focal actor and a random individual from the primary and secondary re-
92 cipients, respectively. We note that the fitness effects in eq. (2) could alter-
93 natively be weighted by relatedness coefficients, where genetic similarity is
94 measures with respect to a reference population (e.g., $R_i = (Q_i - \bar{Q})/(1 - \bar{Q})$,
95 where \bar{Q} is the average genetic similarity to the whole population, including
96 the actor; Hamilton 1970)

97 In the following sections, we examine two different ways of defining the
98 category of secondary recipients and therefore partitioning the fitness ef-
99 fects of harming. Both methods correctly predict the direction of selection
100 (they give the same sum as in eq. (2)). The first partitioning also maintains
101 complete separation of direct and indirect (kin-selected) fitness effects ($-C$
102 and RB , respectively), making it appropriate for classifying harming traits
103 as selfish ($-C > 0$) or spiteful ($-C < 0$). In contrast, the second partition-
104 ing obscures the separation of direct and indirect fitness effects, making it
105 inappropriate for classifying traits in this way.

106 **3.1 Is indiscriminate harming spiteful, or selfish?**

107 We determined the conditions for a harming trait to be classified as spite-
108 ful or selfish. For this purpose, we assume that the focal actor, primary
109 recipients, and secondary recipients are mutually exclusive categories. This
110 ensures that the actor is not a recipient of its own behaviour, and so the $-C$
111 term in the inclusive fitness effect (eq. (2)) captures all effects of the actor's

112 harming behaviour on its own fitness. From eq. (2), we derived the typical
113 two-party version of Hamilton's rule by eliminating the fitness effect on sec-
114 ondary recipients, using $B_2 = C - B_1$ (from eq. (1)). After rearrangement, the
115 inclusive fitness effect is positive, and the harming trait is favoured, when:

$$-C + \frac{Q_1 - Q_2}{1 - Q_2} B_1 > 0, \quad (3)$$

116 which is Hamilton's rule with the relatedness between actor and primary
117 recipients given by $(Q_1 - Q_2)/(1 - Q_2) \equiv R_1$. This is the genetic similarity
118 between the actor and an individual from the potential primary recipients,
119 measured relative to an individual from the potential secondary recipients.

120 Equation (3) implies that indiscriminate spite cannot evolve. This is be-
121 cause negative relatedness (and hence an indirect fitness benefit of harming)
122 will arise only if harm can be directed at primary recipients who are less
123 similar to the actor than secondary recipients are ($Q_1 < Q_2$). Negative relat-
124 edness requires discrimination. However, if the actor were indiscriminate
125 — harming a random subset of a population or local economic neighbour-
126 hood — then its expected similarity to these primary recipients would be
127 the same as to the set of potential secondary recipients ($Q_1 = Q_2$), and relat-
128 edness would be zero ($R = 0$). This implies that indiscriminate harming will
129 be favoured when it is a selfish trait with a positive direct fitness benefit
130 ($-C > 0$).

131 3.2 Why does misclassification occur?

132 Misclassification of harming traits can occur because the fitness effects of
133 social traits can be partitioned in different ways (Frank, 1998). An alterna-
134 tive way of partitioning the effects of harming is to include the actor in the
135 set of secondary recipients who may benefit from reduced competition. In
136 fact, it is often implicitly assumed that the set of potential secondary recip-

137 ients is the entire population (or economic neighbourhood), including the
 138 focal actor (Hamilton, 1970, 1971; Grafen, 1985; Vickery et al., 2003; Smead
 139 and Forber, 2012). To make this explicit, we re-write the inclusive fitness
 140 effect as

$$\Delta W_{IF} = -c + b_1 Q_1 + b_2 \bar{Q}. \quad (4)$$

141 We use lower-case letters to indicate that the fitness effects no longer match
 142 those from eq. (2). Hence, b_2 is now the benefit of reduced competition that
 143 may be experienced by all individuals in population (including the actor),
 144 and \bar{Q} is the probability of genetic identity between the focal actor and a
 145 random individual the entire population (including itself). It follows that
 146 $-c$ is not a total direct fitness effect because it excludes the secondary benefit
 147 of harming that feeds back to the focal actor (reduced competition;).

148 We used eq. (4) to derive an analogue of Hamilton's rule, which reveals
 149 a different version of negative relatedness. For example, in a population
 150 (or economic neighbourhood) of N individuals, an actor could indiscriminately
 151 harm a random subset of individuals with genetic similarity Q_1 to
 152 the actor. If the entire population is in the set of secondary recipients, then
 153 the expected genetic similarity between the actor and these recipients is
 154 $Q_2^p = \frac{1}{N}1 + \frac{N-1}{N}Q_1$ (where the first term accounts for the actor's similar-
 155 ity to itself). Eliminating the fitness effect on secondary recipients (using
 156 $b_2 = c - b_1$, shows that indiscriminate harming is favoured when:

$$-c + \frac{-1}{N-1}b_1 > 0. \quad (5)$$

157 Where $-1/(N-1)$ is the relatedness between actor and primary recipients,
 158 measured with respect to the entire population, $(Q_1 - \bar{Q})(1 - \bar{Q}) \equiv R_{1,p}$. This
 159 is the version of negative relatedness that has led to predictions of indis-
 160 criminate spite in small populations (Hamilton, 1970; Grafen, 1985).

161 However, although the term $\frac{-1}{N-1}b_1$ resembles an indirect fitness benefit
162 ($RB > 0$), it actually accounts for the secondary benefit of harming that feeds
163 back to the focal actor. Another way of seeing this is to derive an analogue of
164 Hamilton's rule from eq. (4), this time eliminating the fitness effect on pri-
165 mary recipients (using $b_1 = c - b_2$). For example, in a well-mixed population
166 of N individuals, indiscriminate harming is favoured when:

$$-c + \frac{1}{N}b_2 > 0, \quad (6)$$

167 where, $1/N$ is the relatedness between actor and the entire population (in-
168 cluding itself), measured with respect to primary recipients ($(\bar{Q} - Q_1)(1 -$
169 $Q_1) \equiv R_{2,p}$). The term $(1/N)b_2$ accounts for the fraction of the secondary
170 benefit (reduced competition) that feeds back to the focal actor, which gets
171 larger as the actor makes up a larger fraction of the population.

172 Our key distinction here is that harming behaviours can be either benefi-
173 cial or costly to the actor ($-C > 0$ or $-C < 0$), whereas spiteful behaviours are
174 strictly costly to the actor ($-C < 0$). We showed that indiscriminate harming,
175 when it is favoured, is favoured because it is directly beneficial to the actor
176 ($-C > 0$). Moreover, indiscriminate harming will be most favoured in small
177 populations (or small economic neighbourhoods) because this is where the
178 focal actor can benefit most from reducing competition.

179 **3.3 Re-visiting super-territories**

180 We next re-examined the territory size model from Knowlton and Parker
181 (1979); Parker and Knowlton (1980). We first analysed the model to fully
182 separate direct and indirect fitness effects (applying eq. (2)), asking whether
183 the model predicts selfish behaviour, as expected. We then used the alter-
184 native approach (applying eq. (4)) to illustrate why previous studies have
185 interpreted territory size as a spiteful trait.

186 We considered a finite, deme-structured population with $d \in \mathbb{Z}^+$ demes
187 and $n \in \mathbb{Z}^+$ individuals competing for territory in each deme; total pop-
188 ulation size is $N = dn$ (Wright, 1943). Individuals that secure a territory
189 have offspring and then die, afterwards a fraction, m , of their offspring dis-
190 perse randomly throughout the entire population. All individuals have a
191 genetically-determined strategy for the size of territory that they try to ob-
192 tain (a continuous trait). Taking over a larger territory has three key effects:
193 (1) it incurs a fecundity cost for the actor (we assume a linear cost with in-
194 creasing trait size, with slope $a \in [0, 1]$); (2) it harms the actor's deme mates
195 by taking resources away and reducing their fecundity; (3) it reduces the
196 competition faced by all remaining offspring in the population to secure a
197 territory in the next generation.

198 We first assumed that the actor, primary recipients, and secondary recip-
199 ients are mutually exclusive categories (eq. (2)). In Appendix A, we derive
200 an expression for the fitness, W , of a focal actor as a function of its own
201 territory-size strategy, x ; the average strategy of its deme mates (primary
202 recipients), y ; and the average strategy of individuals in other demes (sec-
203 ondary recipients), z . We used this neighbour-modulated fitness function to
204 derive the inclusive fitness effect, by taking partial derivatives with respect
205 to the strategies of the different categories of individuals (Taylor and Frank,
206 1996; Rousset and Billiard, 2000):

$$\Delta W_{IF} = \frac{\partial W}{\partial x} + \frac{\partial W}{\partial y} Q_1 + \frac{\partial W}{\partial z} Q_2 \quad (7)$$

$$= -C + B_1 Q_1 + B_2 Q_2 \quad (8)$$

207 where, all partial derivatives are evaluated in a monomorphic population
208 ($x = y = z$) with respect to a dummy variable g . In Appendix B, we derive
209 expressions for Q_1 and Q_2 , and with these we determined the equilibrium
210 of the model (\hat{z} , where directional selection stops) by solving $\Delta W_{IF} = 0$. We

211 also checked that the equilibrium is a convergence-stable strategy, denoted
212 z^* , meaning that if the population is perturbed from the equilibrium then
213 natural selection will push it back $\left(\frac{d\Delta W_{IF}}{dz}\Big|_{z=z^*}\right)$.

214 We found that the equilibrium of our model, $z^* = 1/(aN)$, is identical
215 to that originally predicted by (Parker and Knowlton, 1980); however, our
216 analysis shows that the optimal territory size strategy is selfish rather than
217 spiteful. Territory size cannot be spiteful in this model because the actor's
218 genetic similarity to individuals in other demes is always equal to or less
219 than the similarity to deme mates ($Q_1 \geq Q_2$). Accordingly, the relatedness
220 to primary recipients (measured relative to secondary recipients) is never
221 negative ($R_1 \geq 0$), and so there is no indirect benefit of larger territory size.
222 Moreover, when offspring dispersal is limited ($m < 1$) and deme mates are
223 positively related ($R_1 > 0$), there is no indirect benefit of smaller territory
224 size (as a form of helping). This is because limited dispersal increases com-
225 petition among offspring within the deme, which promotes harming and
226 exactly cancels the effect of positive relatedness (Taylor, 1992). Territory
227 size therefore evolves for its direct benefit only, with larger territories pro-
228 moted by a smaller fecundity cost to the actor (smaller a) and smaller pop-
229 ulation size (smaller N). Specifically, the direct fitness effect at equilibrium
230 ($z = z^*$) is

$$-C = \frac{aN(d-1)(1-m)^2}{N-1}, \quad (9)$$

231 which is either positive (when $m < 1$) or zero (when $m = 1$). In the case of full
232 offspring dispersal ($m = 1$), the equilibrium is the point where the fecundity
233 cost to the actor is exactly balanced by the feedback benefit experienced by
234 its offspring (reduced competition for space in the next generation). As the
235 population approaches this equilibrium, however, direct fitness is always
236 positive ($-C > 0$), confirming that territory size evolves as a selfish trait
237 (fig. 2).

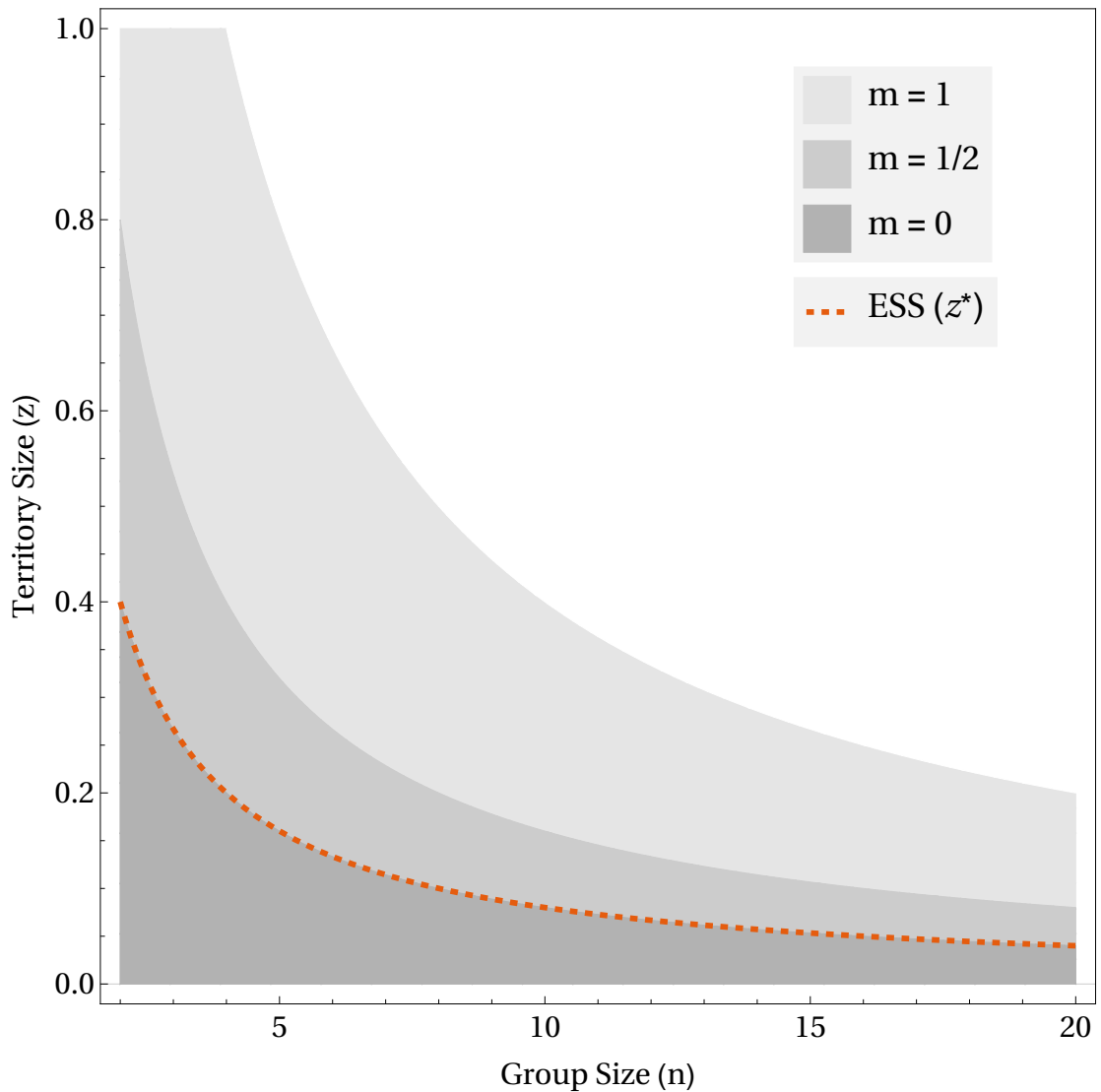


Figure 2: Territory size and direct fitness, the shaded regions indicate where direct fitness is greater than zero for a given migration rate (m). Larger territory size is promoted by smaller population size (smaller dn) and reduced offspring migration from the deme (smaller m), both of which increase the direct benefit to an actor for harming its deme mates. However, reduced migration also increases the relatedness among deme mates, which inhibits larger territory size. Ultimately, the optimal territory size strategy (z^* , dashed line) is independent of migration rate and evolves as if the population were fully mixed ($m = 1$). Other parameters used: $d = 2$, $c = 0.25$.

238 We next assumed that the set of secondary recipients is the entire pop-
 239 ulation, including the focal actor (as in eq. (4)). In this case, the inclusive
 240 fitness effect is

$$\begin{aligned}\Delta W_{IF} &= \frac{\partial W}{\partial x} + \frac{\partial W}{\partial y} Q_1 + \frac{\partial W}{\partial z} \bar{Q} \\ &= -c + b_1 Q_1 + b_2 \bar{Q}.\end{aligned}\tag{10}$$

241 Where z_p is the average territory size strategy in the entire population (in-
 242 cluding the focal actor), and all partial derivatives are evaluated at $x = y =$
 243 z_p . As expected, solving for the equilibrium of eq. (10) gives the same an-
 244 swer as before, $z^* = 1/aN$.

245 However, we can now see why territory size could be misclassified as
 246 spiteful. For example, in a fully mixing population at the equilibrium ($m =$
 247 1 ; $z_p = z^*$), the first term in eq. (10) is:

$$-c = -\frac{aN}{N-1},\tag{11}$$

248 which is always negative. This term reflects the fecundity cost of the focal
 249 actor's territory size strategy, however, it is not the total direct fitness effect
 250 because it excludes the feedback benefit experienced by the actor's offspring
 251 (reduced competition). As noted above, when $m = 1$ this feedback benefit
 252 should exactly balance the fecundity cost at equilibrium. Following eq. (5)
 253 or eq. (6), we can calculate the feedback benefit as $(-1/(N-1))b_1$ or $(1/N)b_2$
 254 (both evaluated at $z_p = z^*$), which gives the expected result, $aN/(N-1)$. The
 255 partitioning in eq. (10) therefore splits the total direct fitness effect of terri-
 256 tory size into two separate terms, $-c + (-1/(N-1))b_1$ or $-c + (1/N)b_2$, which
 257 could be misinterpreted as a direct fitness cost ($-C < 0$) and an indirect
 258 fitness benefit ($RB > 0$).

259 4 Discussion

260 We examined a general model of harming traits and a specific model where
261 larger territory size is an indiscriminate harming trait. In both models we
262 found that: (1) the evolution of spite requires kin discrimination; (2) with-
263 out kin discrimination, harming can be favoured but only when there is a
264 sufficient direct, feedback benefit to the actor (reduced competition); (3) in-
265 discriminate harming can be favoured most in small populations (or small
266 economic neighbourhoods), where the feedback benefit to the actor is great-
267 est; (4) previous studies have misclassified indiscriminate harming as spite,
268 partly because they misinterpret the feedback benefit as an indirect (kin-
269 selected) benefit ($RB > 0$). Overall, our results support the hypothesis that
270 indiscriminate harming traits are selfish rather than spiteful.

271 4.1 Classifying harming traits

272 For the purposes of classifying harming traits, we found that it is easiest
273 to treat the actor, primary recipients, and secondary recipients as separate
274 categories. This makes it straightforward to separate the total direct and
275 indirect fitness effects of harming ($-C$ and RB , respectively) and ensures
276 that non-zero relatedness will always be associated with an indirect fitness
277 effect. For example, spiteful harming ($-C < 0$, $B < 0$) requires that harm is
278 directed at primary recipients to whom the actor is negatively related (with
279 respect to secondary recipients; $Q_1 < Q_2$ and $R_1 < 0$), resulting in a positive
280 indirect fitness effect ($R_1B > 0$) (Lehmann et al., 2006). In contrast, when
281 harming is indiscriminate, the actor has zero relatedness to primary recip-
282 ients (with respect to secondary recipients; $Q_1 = Q_2$ and $R_1 = 0$), meaning
283 that harming can be favoured as a selfish trait only ($-C > 0$, $B < 0$).

284 We showed that misclassification of indiscriminate harming is due to
285 an implicit assumption that the focal actor is a secondary recipient of its
286 own behaviour (Hamilton, 1970; Grafen, 1985; Vickery et al., 2003; Smead

287 and Forber, 2012). This means that some of the actor's direct benefit of
288 harming has been accounted for by a fraction of the fitness effects on recip-
289 ients, giving the appearance of an indirect benefit ($RB > 0$). For example,
290 in a well-mixed population where all individuals (including the actor) are
291 considered secondary recipients, a fraction of the fitness effect on primary
292 recipients ($-1/(N - 1)B_1$) actually contributes to the direct benefit of indis-
293 criminate harming.

294 Others have suggested that harming traits should be classified based
295 on their primary effects only, rather than their total fitness effects (Krupp,
296 2013). This means that indiscriminate harming traits like larger territory
297 size, which may be associated with a survival or fecundity cost ($-c < 0$ in
298 the terms of our model), would be classified as spiteful, despite the feedback
299 benefit to the focal actor. We argue, however, that a classification based on
300 total fitness effects ($-C$ and RB) is more useful (Hamilton, 1964; West et al.,
301 2007). This is because it emphasises the fundamental distinction between
302 spiteful harming, which is favoured by indirect fitness benefits and requires
303 kin discrimination, versus selfish harming, which is favoured by direct fit-
304 ness benefits and does not require kin discrimination (West and Gardner,
305 2010). Similar arguments have been made for maintaining the distinction
306 between altruistic helping ($-C < 0, B > 0$) and mutually-beneficial helping
307 ($-C > 0, B > 0$) (West et al., 2007).

308 **4.2 Indiscriminate harming in nature**

309 We found that selfish indiscriminate harming can be favoured most in small
310 populations or small economic neighbourhoods (e.g., small groups with rel-
311 atively local competition). This is because harming primary recipients leads
312 to reduced competition for all individuals in the population or group, and a
313 focal actor receives a larger fraction of this secondary benefit when it makes
314 up a larger fraction of the population or group. Indiscriminate harming can

315 therefore be thought of as producing a type of public good for secondary
316 recipients (Tullock, 1979), analogous to indiscriminate helping, which is of-
317 ten thought of as a public good for primary recipients. A key difference is
318 that indiscriminate helping is inhibited by local competition (Taylor, 1992;
319 Griffin et al., 2004); in contrast, indiscriminate harming requires local com-
320 petition so that the focal actor can actually benefit the reduced competition
321 that results from its harming (Gardner et al., 2004).

322 So where can we expect to find indiscriminate harming in nature? As
323 recognised by Hamilton (1970), very small populations will tend to extinc-
324 tion, so harming traits in these populations are unlikely to be observed. An
325 alternative may be small groups with relatively local competition, such that
326 harming an individual reduces competition for local resources. One poten-
327 tial example is in fig wasps, where males fight for access to females, and
328 the intensity of fighting increases sharply as the number of males in the fig
329 declines (Reinhold, 2003; West et al., 2001). Further potential examples in-
330 clude competition among female honey bees for a colony and other cases
331 where males engage in local competition for mates (e.g., *Melittobia* para-
332 sitoids; West (2002)).

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423 **A Territory Size model**

424 Here, we derive an expression for the fitness of a focal actor with a mutant
425 territory size strategy, based on the models of Knowlton and Parker (1979);
426 Parker and Knowlton (1980). We consider a population that is structured
427 into d demes of n individuals competing for territories, where each deme
428 has A units of available territory. The focal actor’s strategy, x , represents a
429 continuous number of territory units that it attempts to gain ($x > 0$). The
430 average strategy of the actor’s deme mates is y , and the average strategy in
431 all other demes is z .

432 We first calculate the expected offspring production (expected fecundity,
433 F) for the focal actor, an individual in the actor’s deme, and an individual
434 in another deme. These expected values depend on: (1) the probability
435 of an individual acquiring a territory (assuming that available spaces are
436 acquired completely randomly); (2) the cost associated with the individual’s
437 strategy (assuming fecundity declines linearly with increasing territory size
438 strategy; $f(x) = 1 - ax$, where $0 < a < 1$). For the focal actor, there are A/y
439 spaces available in the deme, and we use the simplifying assumption that
440 a mutant individual has priority to claim the territory units denoted by its
441 strategy (Knowlton and Parker, 1979). Therefore, the focal actor has a $1/n$
442 probability of acquiring a territory, and its expected fecundity is:

$$F_x = \frac{A}{y} \frac{1}{n} f(x). \quad (\text{A.1})$$

443 The space available for others in the patch depends on whether or not the
 444 focal actor claims a territory. The actor gains access to the patch with prob-
 445 ability A/ny , and in this case $(A-x)/y$ spaces remain; otherwise, A/y spaces
 446 are available. The expected fecundity for one of the $n-1$ deme mates of the
 447 focal actor is therefore:

$$F_y = \left(\frac{A}{ny} \frac{A-x}{y} f(y) + \left(1 - \frac{A}{ny} \right) \frac{A}{y} f(y) \right) (n-1)^{-1}. \quad (\text{A.2})$$

448 Finally, for an individual in another deme in the population, there are A/z
 449 spaces available, and so the expected fecundity for one of these individuals
 450 is:

$$F_z = \frac{A}{z} \frac{1}{n} f(z), \quad (\text{A.3})$$

451 We next calculate the focal actor's fitness, $W(x, y, z)$, which is the num-
 452 ber of its offspring that survive to compete for a territory in the next gen-
 453 eration. This can be partitioned into two terms, the first term accounting
 454 for offspring that compete on the focal actor's natal deme (those that did
 455 not disperse, with probability $1-m$, and those that dispersed but landed on
 456 the natal deme, with probability m/d) and the second term accounting for
 457 offspring that disperse with probability m to compete in the $d-1$ non-natal
 458 demes:

$$\omega = \frac{\left(1 - m + \frac{m}{d} \right) F_x n}{(1-m)F_x + (n-1)(1-m)F_y + \frac{1}{d}(mF_x + (n-1)mF_y) + \frac{d-1}{d}nmF_z} + \frac{\frac{d-1}{d}nmF_x}{(1-m)nF_z + \frac{1}{d}(mF_x + (n-1)mF_y) + \frac{d-1}{d}nmF_z}. \quad (\text{A.4})$$

459 where, the denominator of the first and second terms account for, respec-
 460 tively, all offspring competing in the focal actor's natal deme and all off-
 461 spring competing in any other deme in the population. Equation (A.4) is
 462 the fitness function used to calculate the inclusive fitness effect in eq. (8) of

463 the main text. To express the focal individual's fitness in terms of x , y , and
 464 z_p (the average territory size strategy in the entire population, including the
 465 focal individual), we substituted $(x + (n-1)y - dnz_p)/(n - nd)$ for z in eq. (A.4).
 466 This gives the fitness function used to calculate the inclusive fitness effect
 467 in eq. (9) of the main text.

468 **B Deriving probabilities of genetic identity**

469 Here, we derive probabilities of genetic identity by descent in a finite deme-
 470 structured population, following the approach of (Taylor et al., 2000). In
 471 particular, we needed the probability of identity between the focal actor
 472 and a randomly selected deme mate (Q_1), between the actor and a randomly
 473 selected individual in another deme (Q_2), and between the actor and a ran-
 474 domly selected individual in the entire population (including itself, Q_2^p),
 475 defined as:

$$Q_2^p = \frac{1}{d} \left(\frac{1}{n} + \frac{(n-1)}{n} Q_1 \right) + \frac{d-1}{d} Q_2. \quad (\text{B.1})$$

476 This is distinct from equation A.1 in Taylor et al. (2000) in that we separate
 477 out the individual from the group using the term $\frac{1}{n} + \frac{(n-1)}{n} Q_1$ which in Taylor
 478 et al. (2000) would be just Q_1 . The above yields the recursions:

$$Q_1 = \left((1-m)^2 \left(\frac{1}{n} + \frac{n-1}{n} Q_1 \right) + (1 - (1-m)^2) Q_2^p \right) (1-w)^2 \quad (\text{B.2})$$

$$Q_2 = \left((1-m)^2 Q_2 + (1 - (1-m)^2) Q_2^p \right) (1-w)^2, \quad (\text{B.3})$$

479 where, w is the mutation rate. We solve eqs. (B.1) to (B.3) simultaneously
480 and evaluate at the limit of low mutation rate ($w \rightarrow 0$), recovering:

$$Q_1 = 1 - 2dnu, \quad (\text{B.4})$$

$$Q_2 = 1 + \left(\frac{2d(m-1)^2}{(m-2)m} - 2dn \right) u, \quad (\text{B.5})$$

$$Q_2^p = 1 + \frac{2(d(1 - (m-2)m(n-1)) - 1)}{(m-2)m} u. \quad (\text{B.6})$$

481 These are used in eqs. (8) and (10) of the main text. Therefore in our case
482 the appropriate relatedness would be:

$$R_1 = \frac{Q_1 - Q_2}{1 - Q_2} = \frac{(1-m)^2}{1 + m(2-m)(n-1)} \quad (\text{B.7})$$