

1 **Diminishing returns drive altruists to help extended family**

2 P. Kennedy^{1*}, S. Sumner^{1†}, P. Botha¹, N. J. Welton², A. D. Higginson³ & A. N. Radford¹

3 ¹School of Biological Sciences, University of Bristol, 24 Tyndall Avenue, Bristol, BS8 1TQ, UK

4 ²Population Health Sciences, Bristol Medical School, University of Bristol, Canynge Hall, 39 Whatley Road,
5 Bristol, BS8 2PS, UK

6 ³Centre for Research in Animal Behaviour, University of Exeter, Exeter, EX4 4QG, UK

7 [†]**Current address:** Centre for Biodiversity and Environment Research (CBER), University College London,
8 Division of Biosciences, Gower Street, London, WC1E 6BT, UK

9 ^{*}**Correspondence:** *patrick.kennedy@bristol.ac.uk*

10 ^{*}**Corresponding author ORCID number:** 0000-0002-2524-6192

11
12 Supplementary files: (1) *Supplementary Information (modelling detail)*, (2) *dataset and statistical code*, (3) *simulation*
13 *code*, (4) *Extended Data (supplementary figures)*.

15 *Abstract:*

16 Altruism between close relatives can be easily explained. However, paradoxes arise when organisms
17 divert altruism towards more-distantly-related recipients. In some social insects, workers ‘drift’
18 extensively between colonies and help raise less-related foreign brood, seemingly reducing inclusive
19 fitness. Since being highlighted by W. D. Hamilton, three hypotheses (bet-hedging, indirect reciprocity,
20 and diminishing returns to cooperation) have been proposed for this surprising behaviour. Here we
21 show using inclusive fitness theory that bet-hedging and indirect reciprocity could only drive
22 cooperative drifting under improbable conditions. However, diminishing returns to cooperation create
23 a simple context in which sharing workers is adaptive. Using a longitudinal dataset comprising over a
24 quarter of a million nest-cell observations, we quantify cooperative payoffs in the Neotropical wasp
25 *Polistes canadensis*, where drifting occurs at high levels. As the worker-to-brood ratio rises in a worker’s
26 home colony, the predicted marginal benefit of a worker for expected colony productivity diminishes.
27 Helping on related colonies can allow effort to be focused on related brood that are more in need of
28 care. Finally, we use simulations to show that cooperative drifting evolves under diminishing returns
29 when dispersal is local, allowing altruists to focus their efforts on related recipients. Our results indicate
30 the power of nonlinear fitness effects to shape social organization, and suggest that models of eusocial
31 evolution should be extended to include neglected social interactions within colony networks.

32

33 Altruism – sacrifice of Darwinian fitness to increase that of a recipient – is easily explained when
34 occurring between close relatives¹, through an increase in the altruist’s inclusive fitness (success at
35 propagating copies of its genes in the population)^{2–4}. However, paradoxical forms of altruism arise when
36 individuals divert help from the closest relatives and towards more-distantly-related recipients^{5,6}. This
37 seemingly irrational behaviour appears to reduce inclusive fitness⁷.

38 Social insect colonies are often impenetrable ‘fortresses’⁸. However, in some (especially primitively-
39 eusocial) species, between-colony movement (‘drifting’) by both workers^{6,7,9–12} and foundresses¹³ can
40 be extensive. Often, opportunities for reproductive parasitism¹⁴ or nest inheritance¹³ provide clear
41 direct fitness motives. In other cases, drifters lack obvious opportunities for direct fitness^{7,11,12}, and help
42 more-distant relatives than recipients on their home colony. In some primitively-eusocial *Polistes* paper
43 wasps, the extreme extent of drifting by nonreproductive workers has become clear: in the tropics
44 (where *Polistes* originated), 56% of workers within a population were detected at multiple colonies¹².
45 Drifting workers perform standard cooperative tasks¹² (henceforth, ‘cooperative drifting’), creating
46 ‘extended kin groups’¹¹ (networks of cooperating colonies). However, despite primitively-eusocial
47 insects being long-standing models for understanding trajectories to complex eusociality¹⁵, the adaptive
48 function of cooperative drifting has not been identified.

49 Three hypotheses have been proposed to explain the evolution of cooperative drifting by non-
50 reproductive primitively-eusocial workers. The *bet-hedging* hypothesis¹² suggests that helping multiple
51 related colonies (‘1’, ‘2’, and ‘3’ in **Fig. 1a**) avoids the risk of investing in a single colony that could
52 succumb to chance failure or predation. By diversifying investments, workers accept reduced expected
53 inclusive fitness for the benefit of reduced variance in inclusive fitness. The *indirect reciprocity*
54 hypothesis⁵ suggests that helping in partner colonies (‘2’ in **Fig. 1b**) leads to other workers (‘3’ in **Fig.**
55 **1b**) – who may be nonrelatives – helping the home colony (‘1’ in **Fig. 1b**). For this to be beneficial, it is
56 assumed that help exchanged between neighbours is worth more than help from natal workers due to
57 ‘social heterosis’: a negative relationship between relatedness and ability to improve colony
58 productivity¹⁶. The *diminishing returns* hypothesis^{7,12} suggests that the marginal benefit provided by a
59 worker diminishes as the number of workers tending brood increases^{17,18} (‘1’ in **Fig. 1c**), an effect first
60 highlighted by Michener in 1964¹⁹, and helping on related colonies allows effort to be redirected
61 towards brood that are more in need of care (‘2’ in **Fig. 1c**). There has been no formal comparison of
62 these hypotheses, so we begin by using inclusive fitness theory to assess the plausibility of each.

63

64 **Results**

65 *Selection for cooperative drifting*

66 First, we show that, under normal conditions, bet-hedging¹² cannot select for cooperative drifting.
 67 We derive an explicit mean-risk trade-off for bet-hedging traits for an organism maximizing its inclusive
 68 fitness³ (*Methods 1*):

$$69 \quad \max_{\mathbf{q}} \left\{ \mathbf{q}^\dagger \boldsymbol{\mu} - v \cdot \rho \sqrt{\mathbf{q}^\dagger \mathbf{C} \mathbf{q}} \right\} \quad (1)$$

$$70 \quad \text{subject to} \quad \mathbf{q}^\dagger \mathbf{1} = 1$$

71 where the organism must choose the optimal weights (\mathbf{q}) to place on different investments, balancing
 72 the expectation ($\mathbf{q}^\dagger \boldsymbol{\mu}$, where \dagger denotes transpose) and variance ($\mathbf{q}^\dagger \mathbf{C} \mathbf{q}$) in absolute inclusive fitness
 73 returns, for particular values of risk-aversion (v) and the correlation (ρ) between the portfolio's return
 74 and whole-population average reproductive success (\bar{w}). The vector $\boldsymbol{\mu}$ contains the offspring
 75 production per unit invested (weighted by offspring relatedness), \mathbf{C} is the variance–covariance matrix
 76 for the investment payoff rates, and $\mathbf{1}$ is a vector of ones. A 'risky' portfolio has high variance. In
 77 *Methods 1*, we show that the value of risk aversion (v) that maximizes inclusive fitness is the coefficient
 78 of variation in \bar{w} . However, under demographic stochasticity – which is generated by random colony
 79 failures – meaningful fluctuations in \bar{w} will only occur if the population is extremely small (*Methods 1*),
 80 so $v \approx 0$. Moreover, in reasonably sized populations, fluctuations in \bar{w} that do happen due to random
 81 colony failure occur independently of fluctuations in the portfolio's returns, so $\rho \approx 0$. Since $v \approx 0$ (and
 82 $\rho \approx 0$), the second term of (1) is negligible, so workers should maximise only the expectation of
 83 inclusive fitness ($\mathbf{q}^\dagger \boldsymbol{\mu}$). The same logic underpins why bet-hedging against randomly occurring clutch
 84 failure is an unlikely explanation for birds distributing eggs over multiple nests²⁰ or parasitoids
 85 distributing eggs over multiple hosts²¹. In summary, the bet-hedging hypothesis for cooperative drifting
 86 is mathematically coherent (**Fig. 1d**) only in an extremely small population and/or in cases where
 87 drifting would lead to a very small reduction in expected inclusive fitness $\mathbf{q}^\dagger \boldsymbol{\mu}$, circumstances that only
 88 rarely arise in the natural world. One way, for instance, is if there were near-negligible differences in
 89 relatedness towards brood on home and neighbouring colonies, but *Polistes* drifters face falls in
 90 relatedness¹².

91 Second, we show that indirect reciprocity⁵ is unlikely to explain cooperative drifting. Using
 92 simulations, Nonacs⁵ has argued that drifters will automatically help only at colonies sharing indirect
 93 reciprocator alleles because these are the only colonies willing to accept them. However, there is no
 94 reason to expect pleiotropy between these two behaviours, so (unlike Ref.⁵) we allow the emission (y)
 95 and acceptance (m) of drifters to evolve independently in a kin-selection model (*Methods 2*). As in Ref.⁵,
 96 we find that when m is prevented from decreasing whilst y increases, drifting can evolve (*Methods 2*).
 97 But when this unjustified assumption is relaxed, indirect reciprocity collapses due to the invasion of

98 free-riding: colonies willingly accept foreign workers¹⁰ ($m = 1$) whilst none of their own workers drift
 99 ($y = 0$) (*Methods 2*; **Fig. 1e**).

100 Third, we show that diminishing returns^{7,12} can be a simple driver of cooperative drifting (*Methods 3*):
 101 as the effect of helping closely-related recipients declines, diversion of altruism towards more-distantly-
 102 related recipients can satisfy Hamilton's rule (increase in benefit b more than compensates for the
 103 decrease in relatedness r). In a kin-selection model using the framework of Davies *et al.*²², we let the
 104 probability of brood surviving to maturity (K) be determined by a simple diminishing returns function:
 105 $K = 1 - (1 - h)^T$, where $0 \leq h \leq 1$ is help received from workers. Higher values of T result in
 106 stronger diminishing returns. Help (h) received by each brood depends on the worker-to-brood ratio ψ
 107 in their colony, which may vary stochastically between and within colonies through time. For simplicity,
 108 we consider neighbouring colonies with equal brood numbers, lying at different points on a line of
 109 possible worker-to-brood ratios. Worker-to-brood ratios greater than $\psi = 1$ occur only on colonies in
 110 terminal decline, so we focus on $0 < \psi \leq 1$. Drifting reduces a worker's relatedness to the brood it
 111 cares for to the (nonzero) proportions $d_{\text{♀}}$ and $d_{\text{♂}}$ for female and male brood respectively, relative to
 112 raising siblings at home. When a home colony has worker-to-brood ratio ψ , selection favours a small
 113 increase in drifting (y) to a colony with a proportion g of the home colony's workforce when the
 114 improvement in indirect fitness from escaping diminishing returns (left-hand side) compensates for
 115 reductions in recipient relatedness (right-hand side):

$$116 \quad \frac{(1 - \psi x(1 - z)(g + y))^{T-1}}{(1 - \psi x(1 - z)(1 - y))^{T-1}} > \frac{4}{(3d_{\text{♀}} + d_{\text{♂}})} \quad (2)$$

117 where x is the proportion of females that are behaviourally sterile (not reproductive) and z is the
 118 proportion of offspring that are male, so $x(1 - z)$ is the proportion of offspring that are workers.

119 To find candidate evolutionarily stable strategies (ESS) for drifting level y , we set equal the left and
 120 right sides of Inequality 2 and rearrange for y . Letting consanguinity to male and female brood be
 121 devalued by the same amount ($d_{\text{♀}} = d_{\text{♂}} = d$), the ESS drifting level y^* occurs at:

$$122 \quad y^* = \frac{1}{1 + \sqrt[T-1]{d}} \left[1 - \sqrt[T-1]{d} g - \frac{1 - \sqrt[T-1]{d}}{\psi x(1 - z)} \right] \quad (3)$$

123 Given the possibility to drift to related colonies at sufficiently steeper points on an inclusive-fitness-
 124 returns curve, workers should tolerate a reduction in recipient relatedness (*Methods 3*; **Fig. 1f**;
 125 **Extended Data 1,2**). The ESS drifting level y^* increases whenever a gap in worker payoff increases
 126 between two related colonies: y^* increases with higher T (**Fig. 1f**), higher ψ and lower g , and for
 127 scenarios in which there is a larger workforce (lower z and higher x). For example, a worker may be

128 twice as related to brood on its home colony as to brood on a partner colony ($d = \frac{1}{2}$). Assume the
129 home colony (with $\psi = 1$) has twice as many workers as the partner colony ($g = \frac{1}{2}$). With diminishing
130 returns factor of $T = 4$, three-quarters of females developing as non-reproductive workers ($x = \frac{3}{4}$),
131 and a sex ratio of 3:1 female eggs to male eggs ($z = \frac{1}{4}$), the expected equilibrium level of cooperative
132 drifting from the home colony would be for 13.2% of worker effort to be divested to the less-related
133 partner colony ($y^* = 0.132$). As workers drift and group sizes consequently change, the marginal
134 payoff of staying on the home colony rises and the marginal payoff of helping on the partner colony
135 falls until $y = y^*$, where any further drifting would reduce inclusive fitness.

136

137 *Diminishing payoffs in the wild*

138 To investigate plausible ranges within which diminishing returns to cooperation may exist, we used
139 longitudinal field tracking of brood development and worker numbers in a Neotropical paper wasp.
140 *Polistes canadensis* is a model species in which cooperative drifting is common and can reduce
141 relatedness to recipient brood considerably (e.g., $r = 0.56$ at home vs $r = 0.19$ on partner colonies)¹².
142 Colonies typically consist of a single queen and behaviourally nonreproductive daughter workers and
143 non-nestmate drifters¹². As workers emerge, colonies can grow in group size from fewer than 10
144 females to up to 200 females. In dominance hierarchies below the queen, a small number of high-
145 ranking wasps have an opportunity to inherit the nest on the death of the resident queen²³; most
146 subordinates perform helping behaviours (including foraging, nest hygiene, brood inspection, nest
147 building, and nest defense)^{12,24,25}. The lack of a covering nest envelope allows clear observation of
148 individual brood (**Fig. 2a**) and the opportunity to document whole-colony development through time²⁶.

149 We aimed to assess how a colony's success at producing new adults is associated with numbers of
150 workers and brood on the colony. Across 56 days, we made over a quarter-of-a-million observations of
151 more than 20,000 individually tracked brood cells on 91 wild post-worker-emergence colonies. The
152 stage of brood development in every cell in each colony was recorded repeatedly (*Methods 4*; **Extended**
153 **Data 3**) and treated as a state in a Markov model (**Fig. 2b,c**). The number of adults on the nest at night
154 (when all workers are present) was counted at intervals over the observation period. This resulted in a
155 dataset of 123,116 state-transitions involving live brood on 85 colonies in 471 colony-observations for
156 which worker number can be predicted by interpolation through the night censuses (*Methods 4*). To
157 investigate the extent to which there may be variation in payoffs within networks of colonies, we asked
158 how the number of workers correlated with colony success at different points of larval development.

159 Using between-colony variation in the number of workers and worker-to-brood ratio, whilst
160 controlling for within-colony variation and colony state (using the extent of brood-cell emptiness as a

161 proxy), a Bayesian hierarchical model predicts that colonies with higher worker-to-brood ratios and
162 worker numbers are associated with higher brood development pace and lower brood death. The
163 Markov model predicts that the expected time for a single egg-containing brood cell to produce an
164 adult successfully in colonies with different worker and brood numbers ('expected mean first passage
165 time', eMFPT) declines as more workers tend the brood (**Fig. 3a,b; Extended Data 4**). Multiplying
166 $1/\text{eMFPT}$ by brood number estimates the expected number of new adults that can be produced per
167 day (whole-colony productivity), which is highest in colonies with many workers and many brood (**Fig.**
168 **3c,d**). The slope of whole-colony productivity with respect to worker number (**Fig. 3e,f**) then provides
169 a prediction of the marginal increase in the daily number of brood successfully raised associated with
170 each additional worker (i.e., plausibility values for the payoff rate). The 'payoff' in **Fig. 3e,f** represents
171 an empirical estimate of the benefit b in Hamilton's rule from working on a colony of the given size. An
172 investment in a partner colony 2 is in the inclusive-fitness interest of a worker from a home colony 1 if
173 $r_2 b_2 > r_1 b_1$.

174 The difference in the predicted payoff from the model suggests that – within the main parameter
175 space occupied by colonies – workers are more valuable (lighter colours in **Fig. 3e**) at colonies with a
176 relatively 'understaffed' workforce faced with large brood-rearing challenges than at colonies with
177 fewer brood to rear. Future models that consider within-colony dynamics may further explain finer-
178 scale variation in brood development rates (see **Extended Data 5–8; SI Table S3**). However, the
179 prediction of variation in plausible payoff rates between colonies with different workforce sizes
180 suggests a context in which workers can increase indirect fitness by helping at less-closely-related
181 colonies.

182

183 *Scales of competition*

184 To explore the demographic conditions that can sustain cooperative drifting, we use agent-based
185 haplodiploid simulations (*Methods 5*) of a large population of monogynous colonies distributed over a
186 square lattice (where each colony has eight neighbours in a 'Moore neighbourhood'). To model simple
187 colony growth, we assume a 'unit' is a group of workers (e.g., 10 workers), and let colonies produce a
188 new unit every three time-steps (e.g., 3 weeks) until reaching a maximum of 10 units. We assume a
189 saturated environment in which each square on the lattice is occupied by one colony. At each time-
190 step, a randomly chosen 10% of colonies die and are replaced. The foundress of the replacement colony
191 is drawn either from lottery competition among the local eight colonies in the Moore neighbourhood
192 (when female philopatry is assumed) or globally from the whole population (when female philopatry is
193 relaxed). Males compete globally for mating with females in lottery competition. The number of

194 reproductively-destined offspring that colonies produce is a diminishing-returns function of the helper
195 effort h on the colony, $1 - (1 - h)^T$ as above. Colonies with more helpers therefore produce more
196 reproductively-destined females and males, and so have a greater chance in competition for nest sites
197 and mating, respectively. We evolve units' propensity to drift for workers on colonies with more than
198 five units, and show the results of competition by introducing mutant alleles to resident populations at
199 an initial frequency of 5%. After 1,000 time-steps, we record the mutant frequency and plot the average
200 change in frequency over three replicate simulations (*Methods 5*).

201 Under linear returns, drifting does not invade, regardless of demography (**Fig. 4a-c**). We then consider
202 moderate diminishing returns ($T = 3$) under three conditions: female philopatry and altruism directed
203 at local colonies in the Moore neighbourhood (**Fig. 4d**); female philopatry and altruism directed at
204 partner colonies whose queens are parents or daughters of their own queen (**Fig. 4e**); and female global
205 dispersal with altruism directed at local colonies in the Moore neighbourhood (**Fig. 4f**). (Female global
206 dispersal with altruism directed at the genealogically-close partner colonies is not considered, because
207 global female dispersal makes these pairings vanishingly rare.) Cooperative drifting can invade only
208 when we allow female philopatry and kin-directed altruism (**Fig. 4e**): under this scenario, neighbouring
209 nests develop genealogical links (spatial kin structure), and – when drifters are shared preferentially
210 within these links – cooperative drifting occurs at a more local scale than the spatial scale of
211 competition. *Polistes* wasps often form colony clusters within wider aggregations of tens to hundreds
212 of colonies^{11,12,27}, a context in which cooperative drifting can evolve by spatial selection under
213 diminishing returns.

214

215 **Discussion**

216 Established accounts of the evolution of eusociality assume actors must choose either to stay as
217 helpers or leave as reproductives^{8,28}. Our results suggest that diminishing returns may drive altruists to
218 diversify their help across recipients: workers in some primitively-eusocial societies may increase
219 inclusive fitness by providing altruism to recipients beyond their home colony. Under positive kinship,
220 spatial kin clustering, and diminishing returns^{17,29}, worker investments can evolve to become diffusible
221 public goods.

222 Our model predicts the conditions under which we expect cooperative drifting to have evolved
223 (**Equation 2, Fig. 1f**). Intuitively, drifting is more likely when there are stronger diminishing returns
224 (higher T), a larger difference in workforce between nests (smaller g), increased total workforce (higher
225 ψ), and a greater capacity to target kin (higher $d_{\text{♀}}$ and $d_{\text{♂}}$). For simplicity in **Equation 2**, we assume that
226 all colonies have the same sex ratio, but between-colony sex-ratio variation suggests an additional

227 factor: a colony producing mainly brothers has a reduced worker relatedness to the brood, at which
228 point switching colony may be rational for a worker. In short, drifting offers a simple route to boost
229 inclusive fitness when neighbouring colonies differ in parameters that determine the value of a worker.
230 Differences in worker and brood number arise easily among *P. canadensis* colonies (**Fig. 3a**), which are
231 subject to several sources of stochasticity. These include fluctuations in worker number due to the high
232 attrition rate of foraging workers¹², frequent loss of brood to parasitoids, presumed loss of brood due
233 to disease (based on workers' hygienic removal of larvae), episodes of queen replacement, and so on.
234 Fluctuations in brood cohort size translate into fluctuations in workforce size once the brood pupate.

235 Since Michener¹⁹ highlighted diminishing returns in hymenopteran societies in 1964, a number of
236 studies across ants, bees, and wasps have revealed declines in per-capita productivity with rising group
237 size (e.g.^{18,30–33}). This so-called 'reproductivity effect' has not proved universal (e.g.^{34–36}), but its frequent
238 occurrence leads to 'Michener's paradox': why do apparently partly-redundant helpers exist^{26,30}?
239 Previous tests of the reproductivity effect have used snapshots of per-capita productivity. By contrast,
240 we provide a prediction of plausible ranges for the payoffs of cooperation in a primitively-eusocial insect
241 using colony dynamics. Diminishing returns exist, but – through cooperative drifting – workers can
242 mitigate redundancy arising from stochastic variation in worker-to-brood ratios between colonies.

243 The extent of drifting across primitively-eusocial insects remains to be explored^{5,12}. However, the
244 relatively high levels of drifting observed in Neotropical species such as *P. canadensis* contrast with, for
245 example, the European wasp *P. dominula*, which also forms dense colony aggregations¹³ but shows high
246 aggression towards neighbours. This difference in social organization may be due to differences in the
247 intensity of diminishing returns (e.g., due to food availability or parasite density). Higher stochastic
248 predation of workers in some species may undermine workers' abilities to track need across nests.
249 Alternatively, drifting may be more likely in the tropics: unlike temperate species in which foundresses
250 establish nests synchronously in the spring, tropical species often establish nests throughout the year²⁵,
251 and so nests may be more likely to differ in worker-to-brood ratio. Tropical species may also experience
252 less uncertainty in neighbour relatedness, since nests are more commonly founded by local dispersal
253 from parent nests (simulated in **Fig. 4e**), although kin spatial structure can be reestablished in
254 temperate species by natal philopatry of spring foundresses³⁷. Direct comparisons between species
255 with and without cooperative drifting are needed.

256 Cooperative drifting has also emerged among complex eusocial species. Ant 'supercolonies' exist
257 when nests with multiple queens (polygyny) exchange workers (polydomy)^{6,38}. Supercoloniality results
258 in remarkably low-relatedness cooperation, and remains a theoretical challenge. The evolution of
259 supercoloniality is likely to involve informational constraints preventing nepotism⁶, although some

260 positive relatedness may be maintained by cryptic kin structure³⁹. Our results are relevant here: the
261 initial drivers of low-relatedness cooperation are unlikely to have been either bet-hedging by risk-
262 spreading at the expense of the expectation of inclusive fitness (**Equation 1; Fig. 1d**) or the reciprocity
263 scenario proposed by Ref.⁵ (**Fig. 1e**). In principle, diminishing returns may initially have favoured partial
264 diversion of altruism to more-distantly-related colonies. However, supercolony and primitively-
265 eusocial cooperative drifting are not completely analogous. Supercolony may have been a relatively
266 small step for ants that had already evolved high within-colony polygyny – and consequently reduced
267 relatedness⁴⁰ – for other reasons. Unlike primitively-eusocial wasps, the first step to explaining
268 cooperative drifting in ants is explaining polygyny⁴¹.

269 Manipulating colony networks by adjusting worker-to-brood ratio (ψ) may offer tests of whether
270 wasps make strategic adjustments to investments (y). Empirical studies are needed to identify whether
271 host workers discern cooperative drifters and adjust acceptance thresholds (m) adaptively^{42,43}
272 according to need. Future theoretical work could assess the tension between selfish and cooperative
273 drifting in determining the acceptance of foreign workers. Wasps with high resource-holding potential
274 may exploit the relaxation of nest boundaries to drift for direct fitness (e.g., joining dominance
275 hierarchies on multiple nests to maximise chance of nest inheritance). Models of the mechanisms
276 individual workers might use to distribute their effort would be useful, potentially inspired by resource-
277 use models in foraging theory⁴⁴.

278 Nonlinear payoffs exert strong effects on social evolution: diminishing returns can limit the tragedy of
279 the commons⁴⁵, promote polymorphic equilibria⁴⁶, and increase sharing in reproductive skew games⁴⁷.
280 However, the extent to which diminishing returns shape investment patterns remains little quantified
281 – despite clear theoretical predictions. A tempting explanation for divestment across recipients is that
282 actors help different recipients in proportion to relatedness (an idea known as the ‘proportional
283 altruism’ model⁴⁸). This argument commits the ‘gamblers’ fallacy’⁴⁹: instead, it is always best to invest
284 in the single recipient who carries the highest inclusive fitness returns at any one time⁵⁰. To explain
285 altruism towards more-distant relatives, in the 1980s Altmann⁴⁹, Weigel¹⁷, and Schulman and
286 Rubenstein²⁹ highlighted diminishing returns to investment by a *single* individual. Here, we have
287 considered diminishing returns to investment by *multiple* individuals. In both cases, diminishing returns
288 provide a simple explanation for helping multiple recipients, which awaits empirical study in many
289 species. Our results indicate the power of nonlinear fitness effects to shape social organisation, and
290 suggest that models of eusocial evolution should be extended to include neglected social interactions
291 within colony networks.

292

293

294

295 **Author contributions.** PK, SS, and ANR planned field data collection, and PK and PB collected field data.
296 PK and ADH conducted modelling. PK, NJW, and ANR conducted statistical analysis, and PK, SS, and
297 ANR interpreted the results. PK drafted the manuscript and all authors contributed to its development.

298 **Data availability.** The transitions data for *P. canadensis* is available as supplementary information.

299 **Code availability.** The statistical code and individual-based simulation code are both available as
300 supplementary information.

301 **Competing interest statement.** The authors declare no competing interests.

302 **Acknowledgements.** We thank Christina Riehl, Petri Rautiala, and an anonymous reviewer for
303 constructive reviews during peer review. PK was funded by a Smithsonian Tropical Research Institute
304 (STRI) Short-Term Fellowship (hosted by Dr William Wcislo), the National Geographic Society (GEF-NE
305 145-15), and a European Research Council Grant to ANR (award no. 682253). SS was funded by the
306 Natural Environmental Research Council (NE/M012913/2). ADH was funded by the Natural
307 Environment Research Council (NE/L011921/1). ANR was funded by a European Research Council
308 Consolidator Grant (award no. 682253). Simulations were run on the University of Bristol's high-
309 performance computing facility, *BlueCrystal*. B. Wharam and A. C. Chadwick assisted with data entry. We
310 are very grateful for the support of the Panamanian authorities for this project; data were collected in
311 accordance with Panamanian law under a [Ministerio del Ambiente research permit \(SE/A-46-16\)](#) and
312 [Ministerio de Economía y Finanzas authorisation for field site access \(024-2016\)](#).

313 **Figure captions**

314 **Fig. 1 | Three adaptive hypotheses have been proposed for cooperative drifting. (a)** Bet-hedging. **(b)**
315 Indirect reciprocity. **(c)** Diminishing returns. **(d)** Cooperative drifting is only favoured by bet-hedging
316 (above dashed line) at extremely small population sizes and when recipients differ only slightly in
317 relatedness to the actor. Equilibrium divestment levels shown (*Methods 1*). **(e)** Cooperative drifting
318 cannot be explained by the indirect reciprocity hypothesis because free-riders invade ($y \rightarrow 0, m \rightarrow 1$).
319 Arrows show direction of selection. Black quarter-circle is the global attractor (*Methods 2*). **(f)**
320 Diminishing returns can select for cooperative drifting. Stronger diminishing returns and higher
321 relatedness favour more cooperative drifting (*Methods 3*). Relative relatedness is d in Equation 3 of
322 main text. For illustration, we plot equal reductions in relatedness for female and male brood ($d_{\text{♀}} =$
323 $d_{\text{♂}} = d$). $\psi = 1; g = 0.5; x = 0.75; z = 0.25$.

324 **Fig. 2 | Brood development in the Neotropical paper wasp *Polistes canadensis*. (a)** *P. canadensis*
325 colonies allow easy observation of individual brood cells. *Photograph: PK.* **(b)** Wasp development
326 involves states from egg (state 1) through larvae (2 to 6) to pupa (7) and finally a new adult (definitions
327 of states in **Extended Data 3**). This can be represented using a Markov model. **(c)** Baseline transition
328 probabilities between developmental states using an intercepts-only model (*Methods 4*). In using
329 developmental rates to produce a measure of colony productivity as a function of worker behaviour,
330 we set transitions to death as transitions back to egg (state 1), in order to exclude confounding effects
331 from between-queen variation in egg-laying rates.

332 **Fig. 3 | Brood-rearing rates in *Polistes canadensis*. (a)** Expected number of days for an idealised brood
333 cell successfully to produce an adult ('expected mean first passage time', eMFPT) predicted by
334 between-colony effects. Brood size denotes number of prepupal brood (states 1–6). Worker group
335 size denotes interpolated group size using night-time censuses. White dots denote colony
336 observations. To illustrate predictions in the main parameter space, we generated the prediction of
337 eMFPT for 1,000 simulated colonies inside the convex hull set by those colony observations with up
338 to 150 workers and over 40 brood (only 10 colony observations, from six colonies, in the dataset of
339 471 colony observations used to generate the model, lie outside this range). **(b)** 95% credible intervals
340 corresponding to *a*. **(c)** Predicted whole-colony productivity (daily expected number of new adults,
341 given the eMFPT values) is highest in colonies with many workers and many brood. **(d)** 95% credible
342 intervals corresponding to *c*. **(e)** Slope of predicted whole-colony productivity with respect to worker
343 group size, representing predicted effect of adding a new worker (the 'payoff' provided to the
344 recipients), an empirical estimate of the potential benefit *b* in Hamilton's rule. **(f)** 95% credible
345 intervals corresponding to *e*. See *Methods 4*.

346 **Fig. 4 | Evolution of cooperative drifting in a spatially explicit social haplodiploid simulation.** Results of
347 competition from agent-based simulations of the invasion of drifting. Red denotes mutants invading
348 from a starting frequency (p_{initial}) of 5% of the population; blue denotes mutants declining. White
349 denotes negligible change in frequency. Convergence-stable strategies are marked by asterisks.
350 Conditions were **(a–c)** no diminishing returns, $T = 1$, and **(d–f)** moderate diminishing returns, $T =$
351 3 ; **(a, d)** female philopatry and altruism directed at local colonies in the Moore neighbourhood, **(b, e)**
352 female philopatry and altruism directed at partner colonies with queens who are parents or daughters
353 of their own queen, **(c, f)** global female dispersal with altruism directed at local colonies in the Moore
354 neighbourhood. Nonlinear returns drive inter-colony cooperation only under both local female
355 dispersal and kin-directed altruism (panel **e**).

356

357 **References (Main text and Methods)**

- 358 1. Gardner, A., West, S. A. & Wild, G. The genetical theory of kin selection. *J. Evol. Biol.* **24**, 1020–
359 1043 (2011).
- 360 2. Gardner, A. The purpose of adaptation. *Interface Focus* **7**, 20170005 (2017).
- 361 3. Grafen, A. Optimization of inclusive fitness. *J. Theor. Biol.* **238**, 541–563 (2006).
- 362 4. Bourke, A. F. G. The validity and value of inclusive fitness theory. *Proc. R. Soc. B Biol. Sci.* **278**,
363 3313–3320 (2011).
- 364 5. Nonacs, P. Go high or go low? Adaptive evolution of high and low relatedness societies in social
365 Hymenoptera. *Front. Ecol. Evol.* **5**, 87 (2017).
- 366 6. Helanterä, H., Strassmann, J. E., Carrillo, J. & Queller, D. C. Uniclonal ants: where do they
367 come from, what are they and where are they going? *Trends Ecol. Evol.* **24**, 341–349 (2009).
- 368 7. Hamilton, W. D. The genetical evolution of social behaviour. II. *J. Theor. Biol.* **7**, 17–52 (1964).
- 369 8. Queller, D. C. & Strassmann, J. E. The many selves of social insects. *Science* **296**, 311–313 (2002).
- 370 9. Tsuchida, K. & Itô, Y. Internidal drifting and dominance behaviour in *Polistes jadvigae* Dalla Torre
371 workers (Hymenoptera: Vespidae). *J. Ethol.* **5**, 83–85 (1987).
- 372 10. Page, R., Post, D. & Metcalf, R. Satellite nests, early males, and plasticity of reproductive behavior
373 in a paper wasp. *Am. Nat.* **134**, 731–748 (1989).
- 374 11. Pickering, J. Sex ratio, social behaviour, and ecology in *Polistes* (Hymenoptera, Vespidae),
375 *Pachysomoides* (Hymenoptera, Ichneumonidae) and *Plasmodium* (Protozoa, Haemosporida). (PhD
376 Thesis: Harvard University, Cambridge, Massachusetts, 1980).
- 377 12. Sumner, S., Lucas, E., Barker, J. & Isaac, N. Radio-tagging technology reveals extreme nest-
378 drifting behavior in a eusocial insect. *Curr. Biol.* **17**, 140–145 (2007).
- 379 13. Grinsted, L. & Field, J. Market forces influence helping behaviour in cooperatively breeding paper
380 wasps. *Nat. Commun.* **8**, 1–8 (2017).
- 381 14. Beekman, M. & Oldroyd, B. P. When workers disunite: intraspecific parasitism by eusocial bees.
382 *Annu. Rev. Entomol.* **53**, 19–37 (2008).
- 383 15. Gadagkar, R. Origin and evolution of eusociality: a perspective from studying primitively eusocial
384 wasps. *J. Genet.* **69**, 113–125 (1990).
- 385 16. Nonacs, P. & Kapheim, K. M. Social heterosis and the maintenance of genetic diversity. *J. Evol.*
386 *Biol.* **20**, 2253–2265 (2007).
- 387 17. Weigel, R. M. The distribution of altruism among kin: a mathematical model. *Am. Nat.* **118**, 191–
388 201 (1981).
- 389 18. Grinsted, L. & Field, J. Predictors of nest growth: diminishing returns for subordinates in the
390 paper wasp *Polistes dominula*. *Behav. Ecol. Sociobiol.* **72**, (2018).
- 391 19. Michener, C. Reproductive efficiency in relation to colony size in Hymenopterous societies. *Insectes*
392 *Soc.* **11**, 317–341 (1964).
- 393 20. Bulmer, M. G. Risk avoidance and nesting strategies. *J. Theor. Biol.* **106**, 529–535 (1984).

- 394 21. Hopper, K., Rosenheim, J., Prout, T. & Oppenheim, S. Within-generation bet hedging: a seductive
395 explanation? *Oikos* 219–222 (2003).
- 396 22. Davies, N. G., Ross, L. & Gardner, A. The ecology of sex explains patterns of helping in
397 arthropod societies. *Ecol. Lett.* **19**, 862–872 (2016).
- 398 23. Sumner, S., Kelstrup, H. & Fanelli, D. Reproductive constraints, direct fitness and indirect fitness
399 benefits explain helping behaviour in the primitively eusocial wasp, *Polistes canadensis*. *Proc. R. Soc. B*
400 **277**, 1721–1728 (2010).
- 401 24. Ferreira, P. G. *et al.* Transcriptome analyses of primitively eusocial wasps reveal novel insights into
402 the evolution of sociality and the origin of alternative phenotypes. *Genome Biol.* **14**, R20 (2013).
- 403 25. Southon, R. J. *et al.* High indirect fitness benefits for helpers across the nesting cycle in the tropical
404 paper wasp *Polistes canadensis*. *Mol. Ecol.* 1–6 (2019).
- 405 26. Wenzel, J. W. & Pickering, J. Cooperative foraging, productivity, and the central limit theorem.
406 *Proc. Natl. Acad. Sci.* **88**, 36–38 (1991).
- 407 27. Lengronne, T. *et al.* Little effect of seasonal constraints on population genetic structure in eusocial
408 paper wasps. *Ecol. Evol.* **2**, 2610–2619 (2012).
- 409 28. Davies, N. G. & Gardner, A. Monogamy promotes altruistic sterility in insect societies. *R. Soc.*
410 *Open Sci.* **5**, 172190 (2018).
- 411 29. Schulman, S. R. & Rubenstein, D. I. Kinship, need, and the distribution of altruism. *Am. Nat.* **121**,
412 776–788 (1983).
- 413 30. Kramer, B. H., Scharf, I. & Foitzik, S. The role of per-capita productivity in the evolution of small
414 colony sizes in ants. *Behav. Ecol. Sociobiol.* **68**, 41–53 (2014).
- 415 31. Tindo, M., Kenne, M. & Dejean, A. Advantages of multiple foundress colonies in *Belonogaster*
416 *juncea juncea* L.: greater survival and increased productivity. *Ecol. Entomol.* **33**, 293–297 (2008).
- 417 32. Naug, D. & Wenzel, J. Constraints on foraging success due to resource ecology limit colony
418 productivity in social insects. *Behav. Ecol. Sociobiol.* **60**, 62–68 (2006).
- 419 33. Clouse, R. Some effects of group size on the output of beginning nests of *Mischocyttarus mexicanus*
420 (Hymenoptera: Vespidae). *Florida Entomol.* **84**, 418–425 (2001).
- 421 34. Smith, A. R., Wcislo, W. T. & O’Donnell, S. Survival and productivity benefits to social
422 nesting in the sweat bee *Megalopta genalis* (Hymenoptera: Halictidae). *Behav. Ecol. Sociobiol.* **61**, 1111–
423 1120 (2007).
- 424 35. Bouwma, A. M., Nordheim, E. V. & Jeanne, R. L. Per-capita productivity in a social wasp: no
425 evidence for a negative effect of colony size. *Insectes Soc.* **53**, 412–419 (2006).
- 426 36. Shreeves, G. & Field, J. Group size and direct fitness in social queues. *Am. Nat.* **159**, 81–95 (2002).
- 427 37. Parsons, P. J., Grinsted, L. & Field, J. Partner choice correlates with fine scale kin structuring in
428 the paper wasp *Polistes dominula*. *PLoS One* **14**, 1–17 (2019).
- 429 38. Helanterä, H. Supercolonies of Ants. *Encycl. Soc. Insects* 1–3 (2020). doi:10.1007/978-3-319-90306-
430 4_121-1

- 431 39. Holzer, B., Keller, L. & Chapuisat, M. Genetic clusters and sex-biased gene flow in a unicolonial
432 *Formica* ant. *BMC Evol. Biol.* **9**, 1–11 (2009).
- 433 40. Boomsma, J. J., Huszár, D. B. & Pedersen, J. S. The evolution of multiqueen breeding in eusocial
434 lineages with permanent physically differentiated castes. *Anim. Behav.* **92**, 241–252 (2014).
- 435 41. Keller, L. Social life: the paradox of multiple-queen colonies. *Trends in Ecology & Evolution* **10**, 355–
436 360 (1995).
- 437 42. Mora-Kepfer, F. Context-dependent acceptance of non-nestmates in a primitively eusocial insect.
438 *Behav. Ecol. Sociobiol.* **68**, 363–371 (2013).
- 439 43. Couvillon, M. J. *et al.* En garde: rapid shifts in honeybee, *Apis mellifera*, guarding behaviour are
440 triggered by onslaught of conspecific intruders. *Anim. Behav.* **76**, 1653–1658 (2008).
- 441 44. McNamara, J. Optimal patch use in a stochastic environment. *Theor. Popul. Biol.* **21**, 269–288
442 (1982).
- 443 45. Foster, K. R. Diminishing returns in social evolution: The not-so-tragic commons. *J. Evol. Biol.* **17**,
444 1058–1072 (2004).
- 445 46. Sibly, R. M. & Curnow, R. N. Selfishness and altruism can coexist when help is subject to
446 diminishing returns. *Heredity (Edinb.)* **107**, 167–173 (2011).
- 447 47. Cant, M. A. A tale of two theories: Parent-offspring conflict and reproductive skew. *Anim. Behav.*
448 **71**, 255–263 (2006).
- 449 48. Dugatkin, L. A. *The Altruism Equation: Seven Scientists Search for the Origins of Goodness.* (Princeton
450 University Press, 2006).
- 451 49. Altmann, S. Altruistic behaviour: the fallacy of kin deployment. *Anim. Behav.* **27**, 958–962 (1979).
- 452 50. Dawkins, R. Twelve misunderstandings of kin selection. *Z. Tierpsychol.* **51**, 184–200 (1979).
- 453 51. Rice, S. H. The expected value of the ratio of correlated random variables. (2015). Available at:
454 <http://www.faculty.biol.ttu.edu/rice/ratio-derive.pdf>.
- 455 52. Zivot, E. Portfolio theory with matrix algebra. in *Introduction to Computational Finance and Financial*
456 *Econometrics, Econ. 424* (University of Washington, 2011).
- 457 53. Shpak, M. Evolution of variance in offspring number: The effects of population size and
458 migration. *Theory Biosci.* **124**, 65–85 (2005).
- 459 54. Starrfelt, J. & Kokko, H. Bet-hedging – a triple trade-off between means, variances and
460 correlations. *Biol. Rev.* **87**, 742–755 (2012).
- 461 55. Taylor, P. & Frank, S. How to make a kin selection model. *J. Theor. Biol.* **180**, 27–37 (1996).
- 462 56. Rice, S. H. A stochastic version of the Price equation reveals the interplay of deterministic and
463 stochastic processes in evolution. *BMC Evol. Biol.* **8**, 262 (2008).
- 464 57. Kemeny, J. G. & Snell, J. *Finite Markov Chains.* **40**, (Springer-Verlag, 1983).
- 465 58. Plummer, M. Package rjags. in *update* (2003).
- 466 59. Bell, A., Fairbrother, M. & Jones, K. Fixed and random effects models: making an informed
467 choice. *Qual. Quant.* **53**, 1051–1074 (2019).

- 468 60. Mundlak, Y. On the pooling of time series and cross section data. *Econometrica* **46**, 69–85 (1978).
- 469 61. Hooten, M. B. & Hobbs, N. T. A guide to Bayesian model selection for ecologists. *Ecol. Monogr.*
470 **85**, 3–28 (2015).
- 471 62. Ntzoufras, I. Gibbs variable selection using BUGS. *J. Stat. Softw.* **7**, 1–19 (2002).
- 472 63. Dias, S., Sutton, A. J., Ades, A. E. & Welton, N. J. Evidence synthesis for decision making 2: A
473 generalized linear modeling framework for pairwise and network meta-analysis of randomized
474 controlled trials. *Med. Decis. Mak.* **33**, 607–617 (2013).
- 475 64. Grinstead, C. M. & Snell, J. L. *Introduction to Probability*. (American Mathematical Society, 2006).
476 doi:10.1016/S1363-4127(97)81322-2
- 477
- 478
- 479
- 480

481

Methods

482 Tables of notation and supplementary detail on models are available in the **Supplementary Information**,
483 and supplementary figures are provided in the **Extended Data**.

484 1. Bet-hedging

485 We consider when an inclusive fitness maximising actor should divide its investments between separate
486 recipients to minimise the risk that its investments will be lost¹². Notation is summarized in **Table S1** (see
487 **Supplementary Information**). Following Grafen³, we start with the Price equation under uncertainty and
488 treat the target of selection as an individual maximand. The expected change in allele frequency due to
489 selection $\Delta\bar{G}$ – where average reproductive success for the population is \bar{w} , and I_i is absolute inclusive
490 fitness – is equal to the covariance over individuals i between the expectation of relative inclusive fitness
491 $\frac{I_i}{\bar{w}}$ and the individual's genotype G_i

$$492 \quad \mathbb{E}_\omega[\Delta\bar{G}] = \text{Cov}_i \left(G_i, \mathbb{E}_\omega \left[\frac{I_i}{\bar{w}} \right] \right) \quad (1.1)$$

493 where expectations \mathbb{E} are taken across possible states of the population $\omega \in \Omega$ that may occur. The
494 absolute inclusive fitness is the sum of all effects b_{ijt} of actor i on the absolute fitness of recipient j
495 (including the actor itself) across each role t (*i.e.*, $I_i = \sum_j^N r_{ij} b_{ijt}$). For derivation of Equation 1.1, see the
496 first term on the right-hand side of Eq. 6 in Grafen³. Under fitness additivity and frequency-independence,
497 the quantity $\mathbb{E}_\omega \left[\frac{I_i}{\bar{w}} \right]$ is considered to represent a maximand of organismal behaviour³: it is a target of
498 selection (as it covaries with genotype) that is under the control of the actor since I_i is composed of the
499 effects of the actor's behaviours.

500 The expectation of a ratio of random variables can be approximated by the Taylor series expansion. The
501 Taylor series is an acceptable approximation when \bar{w} does not rise to greater than $2\mathbb{E}_\omega[\bar{w}]$ ⁵¹. We expand
502 the maximand to the second order as follows:

$$503 \quad \mathbb{E}_\omega \left[\frac{I_i}{\bar{w}} \right] \approx \frac{1}{\mathbb{E}_\omega[\bar{w}]} \left(\mathbb{E}_\omega[I_i] - \frac{\sigma_\omega[\bar{w}]}{\mathbb{E}_\omega[\bar{w}]} \rho \sigma_\omega[I_i] \right) \quad (1.2)$$

504 where $\sigma_\omega[\cdot]$ denotes standard deviation over the states $\omega \in \Omega$, and ρ denotes the correlation between I_i
505 and \bar{w} . The division by $\mathbb{E}_\omega[\bar{w}]$ does not affect the optimal decision, and so we focus on the terms in the
506 brackets.

507 To make more explicit the quantity under a focal organism's control, we can describe as \mathbf{q} the vector of
508 investment weights (the proportions of its total resource) that the individual chooses to place on different
509 investments that affect the reproductive success of itself and other individuals. The expectation of the focal
510 individual's absolute inclusive fitness ($\mathbb{E}_\omega[I_i]$) is given by $\mathbf{q}^\dagger \boldsymbol{\mu}$, where $\boldsymbol{\mu}$ is the vector of expected inclusive

511 fitness payoffs from the different potential options (the expectation over the different states $\omega \in \Omega$). By
 512 convention, \dagger denotes transpose. Likewise, the standard deviation of a focal individual's absolute inclusive
 513 fitness appearing in Equation 1.2 ($\sigma_\omega[I_i]$) is given by $\sqrt{\mathbf{q}^\dagger \mathbf{C} \mathbf{q}}$, where \mathbf{C} is the variance-covariance matrix of
 514 the payoffs over the states $\omega \in \Omega$, and $\mathbf{q}^\dagger \mathbf{C} \mathbf{q}$ gives the variance (over the states $\omega \in \Omega$) of the individual's
 515 absolute inclusive fitness.

516 The aim for the organism can then be expressed using the following maximand (echoing financial
 517 portfolios⁵²):

$$518 \quad \max_{\mathbf{q}} \left\{ \mathbf{q}^\dagger \boldsymbol{\mu} - v \cdot \rho \cdot \sqrt{\mathbf{q}^\dagger \mathbf{C} \mathbf{q}} \right\} \quad (1.3)$$

519 where the sum of \mathbf{q} is one. The coefficient of variation in population average reproductive success (v) is
 520 not affected by the organism's choice of \mathbf{q} . Whereas in economics, individuals have subjective risk
 521 aversions, 'risk aversion' in biology is imposed by the environment: a higher v makes individuals more
 522 averse to having an inclusive fitness investment portfolio that has correlated fluctuations with population
 523 average reproductive success. An environment can have high v or low v , and this is imposed on the
 524 organism. The bet-hedging hypothesis implies that an optimisation trade-off exists within \mathbf{q} , balancing the
 525 expectation and the variance in inclusive fitness profit (measured in the absolute number of offspring-
 526 equivalents produced).

527 Equation 1.4 highlights that variance in inclusive fitness ($\mathbf{q}^\dagger \mathbf{C} \mathbf{q}$) only matters when the level of stochasticity
 528 v (i.e., the coefficient of variation in population average reproductive success \bar{w}) and the correlation ρ are
 529 non-negligible. This is generally only true when there is environmental stochasticity that makes a genotype's
 530 total reproductive success fluctuate in a correlated fashion between environmental states. For instance,
 531 there may be some distinct environmental states when one type of colony does worse, such as big colonies
 532 fail when there is a drought. However, this would require a genotype starting from a position of
 533 overinvesting workers in one type of colony, such that it may then be able to reduce its variance by diverting
 534 some effort towards a different type of colony that doesn't fail in that environmental state.

535 The bet-hedging hypothesis proposed by Sumner et al.¹² is based on hedging against individual risks to
 536 colonies: demographic stochasticity. In general, demographic stochasticity can only generate meaningful
 537 fluctuations in \bar{w} when population (or deme) size is very small^{53,54}. Next, we illustrate the effect of
 538 population size, which we then plot in **Fig. 1d** of the main text.

539 To illustrate the bet-hedging hypothesis in a specific example, we switch to a neighbour-modulated
 540 perspective⁵⁵. Notation is summarised in **Table S2**. We focus on the effects experienced by recipients due
 541 to the actions of related actors. Thus, instead of focusing on the expected relative inclusive fitness $\mathbb{E}_\omega \left[\frac{I_i}{\bar{w}} \right]$
 542 of an actor i , we focus on the expected relative fitness $\mathbb{E}_\omega \left[\frac{w_j}{\bar{w}} \right]$ of a recipient j . The Taylor approximation

543 allows us to write the condition for selection of a trait of interest in a population undergoing pure
 544 demographic stochasticity as:

$$\begin{aligned}
 545 \quad & \text{Cov}_j \left(G_j, \frac{1}{\mathbb{E}_\omega[\bar{w}]} \left(\mathbb{E}_\omega[w_j] - \frac{\text{Cov}_\omega[w_j, \bar{w}]}{\mathbb{E}_\omega[\bar{w}]} \right) \right) > 0 \\
 546 \quad & \therefore \text{Cov}_j \left(G_j, \mathbb{E}_\omega[w_j] - \frac{\text{Var}_\omega[w_j]}{N\mathbb{E}_\omega[\bar{w}]} \right) > 0 \tag{1.4}
 \end{aligned}$$

547 since $\text{Cov}_\omega[w_j, \bar{w}] = \rho_{w_j, \bar{w}} \text{Var}_\omega[w_j]$ and under pure demographic stochasticity⁵⁶ $\rho_{w_j, \bar{w}} = \frac{1}{N}$.

548 We consider the following scenario. Workers invest in colony reproductive success (where w_j is the
 549 reproductive success of the colony's queen) with linear returns $w_j = An_j$, where n_j is the number of
 550 workers helping at queen j 's colony and A is a constant. After this investment period, queens are exposed
 551 to random catastrophe (such as a predation of the nest) with independent probability θ which reduces their
 552 reproductive success to a proportion k of its value. Workers must decide during the investment period
 553 whether to invest solely in their home colony, where the queen is the closest related queen, or divest some
 554 of their investment to neighbour colonies.

555 We assume that there are two sizes of colony with equal numbers of brood: colony type 1 and colony
 556 type 2. Type 1 and type 2 colonies have a high (n_1) and low (n_2 , where $0 < n_2 < n_1$) number of workers,
 557 respectively. For each genotype we let half the colonies be type 1 and half be type 2, and pair each type 1
 558 colony with a type 2 colony. For simplicity, we assume a haploid asexual population (i.e., workers share
 559 their queen's allele for the trait of interest). We ask whether workers on a type 1 colony should divest part
 560 of their investments to a type 2 colony in order to hedge against the risk of their investments on the home
 561 nest being lost to random colony failure. If workers divest from a type 1 colony, they are paired with a
 562 foreign queen on a type 2 colony identical at the focal locus with probability α or a random queen (who
 563 may or may not be identical at the focal locus) on a type 2 colony with probability $1 - \alpha$. A mutant worker
 564 from a type 1 colony with divestment level y will expend a proportion y of its effort on the neighbouring
 565 type 2 colony and a proportion $1 - y$ on its own colony. We assume a population monomorphic for a
 566 resident strategy \bar{y} .

567 The absolute fitness w_2 of a queen on an n_2 colony carrying a mutant allele y if no catastrophe occurs is:

$$568 \quad w_2 = A\{n_2 + n_1(\alpha y + (1 - \alpha)[Py + (1 - P)\bar{y}])\} \tag{1.5}$$

569 where P is the frequency of mutant allele in the population. The absolute fitness w_1 of a queen on an n_1
 570 colony carrying the mutant allele is as follows if no catastrophe occurs:

$$571 \quad w_1 = An_1(1 - y) \tag{1.6}$$

572 There are then four outcomes for any given queen:

	Starts with few workers (n_2)	Starts with many workers (n_1)
No catastrophe occurs	w_2	w_1
Catastrophe occurs	kw_2	kw_1

573

574 The probability of each outcome is:

	Starts with few workers (n_2)	Starts with many workers (n_1)
No catastrophe occurs	$\frac{1-\theta}{2}$	$\frac{1-\theta}{2}$
Catastrophe occurs	$\frac{\theta}{2}$	$\frac{\theta}{2}$

575

576 Accordingly, the variance of w over population states ω is:

$$577 \quad \text{Var}_\omega[w] = \frac{1}{2} \left((1-\theta)((w_2 - \mathbb{E}_\omega[w])^2 + (w_1 - \mathbb{E}_\omega[w])^2) + \theta((kw_2 - \mathbb{E}_\omega[w])^2 + (kw_1 - \mathbb{E}_\omega[w])^2) \right) \quad (1.7)$$

578 where:

$$579 \quad \mathbb{E}_\omega[w] = \frac{1-\theta}{2}(w_1 + w_2) + \frac{\theta}{2}k(w_1 + w_2) \quad (1.8)$$

580 To ask if a small increase in the level of altruism divested to relatives ($y - \bar{y}$) can invade, we evaluate the
 581 derivative of the approximation of expected relative fitness (which covaries with genetic value in Equation
 582 1.5). We set this to equal to zero to find the candidate equilibria y^* :

$$583 \quad \left. \frac{\partial \left(\mathbb{E}_\omega[w_j] - \frac{\text{Var}_\omega[w_j]}{N\mathbb{E}_\omega[\bar{w}]} \right)}{\partial y} \right|_{y=\bar{y}} = 0 \quad (1.9)$$

584 As y^* is too complex to give intuition, we plot y^* for a range of population sizes (N) and differences in
 585 relatedness between the home and partner colony in **Fig. 1d** of the main text (i.e., when ‘relative relatedness’
 586 is one, there is no difference between a worker’s relatedness to the home colony and the partner colony).
 587 The region in which divestment to multiple relatives is favoured is very narrow.

588

589 2. Indirect reciprocity

590 In this section and the diminishing returns section below, we apply the Taylor-Frank method⁵⁵ to a
 591 haplodiploid population, using the framework of Davies *et al.*²², where x is level of altruistic sterility, z is
 592 the sex ratio (proportion male), y is probability of drifting, and m is probability of accepting incoming
 593 drifters. An overview and further detail is given in Section 2 of the **Supplementary Information**, with
 594 notation in **Table S1** and the consanguinity values for haplodiploids in **Table S2**.

595 We model the indirect reciprocity hypothesis for drifting between unrelated colonies proposed by Ref.⁵
 596 in a haplodiploid population. Ref.⁵ argues that a colony's '*willingness to accept drifters*' (m) is an honest signal
 597 of its cooperative willingness to emit drifters, allowing the evolution of drifting in the absence of
 598 genealogical kinship. We follow Nonacs⁵ in letting m be the 'tag' used passively to determine whether to
 599 drift to a target colony: if the colony will let the worker in, it enters. Accordingly, we look for evolutionarily
 600 stable strategy, y^* and m^* .

601 We randomly match each colony with a local unrelated recipient colony. Capital letters denote the mean
 602 value of the trait in a social group. We assume that the probability with which females develop as sterile
 603 helpers is the same on all colonies (x). The following events occur:

- 604 1. Of helper females on a focal ('home') colony, a proportion Y_f will be emitted to a recipient colony
 605 as drifters (i.e., Y_f is the mean value of the drifting trait in the home colony). Of these, a proportion
 606 M_r are on average accepted (since M_r is the average level of willingness to accept drifters among
 607 members of the recipient colony that receives drifters from the focal colony). Any workers that
 608 attempt to drift but are rejected by the neighbour colony return to their home colony and work
 609 there.
- 610 2. Of helper females on a donor colony to the 'home' colony, a proportion Y_d will be emitted to the
 611 home colony as drifters. Of these, a proportion M_f are accepted.

612 To include 'social heterosis', we let help have the effect u on an unrelated partner colony and the effect
 613 a on the home colony. When $u > a$, workers can make a bigger contribution on an unrelated partner
 614 colony (having unrelated genotypes in the workforce amplifies productivity). When $u < a$, workers can
 615 make a bigger contribution on their own home colony (having unrelated genotypes in the workforce impairs
 616 productivity).

617 Brood developing on the home colony receive h units of help:

$$618 \quad h = [a(1 - M_r Y_f) + u M_f Y_d] x \quad (2.1)$$

619 In this section, we assume linear returns to cooperation, such that $K = h$, where K is a brood member's
 620 probability of successfully developing and h is the help received during its development (see
 621 **Supplementary Information** for table of notation).

622 In Case A, we show that the result of Ref.⁵ can be recovered in the improbable scenario where workers
 623 that accept incoming drifters are unable to stop themselves from drifting in turn. In Case B, we show that
 624 cooperative drifting does not invade when this constraint is removed.

625 **2.1 Case A: Constrained pleiotropy between emission and acceptance of drifters**

626 Here, we force m and y into pleiotropy, so that an increase in the trait value of one is accompanied by an
 627 increase in the trait value of the other. We assume $M_f = \beta Y_f$, $M_r = \beta Y_r$, and $\bar{m} = \beta \bar{y}$, where β is a constant
 628 ($\beta > 0$). Substituted into Equation 2.1:

$$629 \quad h = [a(1 - \beta Y_r Y_f) + u\beta Y_f Y_d]x \quad (2.2)$$

630 In the Supplementary Information, we provide the background to the relative fitness functions. The
 631 relative fitness of both male and female brood is:

$$632 \quad W_\delta = W_\varnothing = \frac{x}{K} (\beta u Y_f Y_d + a(1 - \beta Y_r Y_f)) \quad (2.3)$$

633 In the absence of kinship between colonies (as assumed by Ref.⁵), selection favours a small increase in
 634 drifting y when it increases the fitness of the home brood (sisters and brothers on the home colony), which
 635 occurs when:

$$636 \quad c_\varnothing \frac{\partial W_\varnothing}{\partial Y_f} p_{\text{sis}} + c_\delta \frac{\partial W_\delta}{\partial Y_f} p_{\text{bro}} > 0 \quad (2.4)$$

637 where c_\varnothing is the class reproductive value for females, which for haplodiploids is $\frac{2}{3}$, and c_δ is the class
 638 reproductive value for males, which for haplodiploids is $\frac{1}{3}$. The terms p_{sis} and p_{bro} are haplodiploid
 639 consanguinities to sisters and brothers, respectively, which are $\frac{3}{8}$ and $\frac{1}{4}$. Evaluating with both Y_f and Y_r at
 640 the population average drifting level \bar{y} , the effect on the fitness of female and male brood in the home nest
 641 due to a small increase in drifting by workers from the home nest is:

$$642 \quad \left. \frac{\partial W_\varnothing}{\partial Y_f} \right|_{Y_f=\bar{y}} = \left. \frac{\partial W_\delta}{\partial Y_f} \right|_{Y_f=\bar{y}} = (u - a) \frac{x\beta\bar{y}}{K} \quad (2.5)$$

643 Substituting the relevant consanguinities (p_{sis} and p_{bro}) and Equation 2.5 into the condition for selection
 644 on drifting (Equation 2.4) gives:

$$645 \quad (u - a) \frac{x\beta\bar{y}}{3K} > 0 \quad (2.6)$$

646 Since $\frac{x\beta\bar{y}}{3K}$ has a positive real value, drifting is favoured in this scenario if:

$$647 \quad u > a \quad (2.7)$$

648 Accordingly, cooperative drifting can invade under the hypothesis proposed by Ref.⁵ when increasing the
 649 emission of drifters ($y > 0$) to non-relatives is the unavoidable price of increasing the acceptance of drifters
 650 ($m > 0$) from non-relatives. Due to a constraint forcing pleiotropy between the traits (β), it is worth paying
 651 the price of losing home workers when the incoming non-relatives increase the colony's productivity more
 652 than home workers (through social heterosis, $u > a$).

653 2.2 Case B: Absence of pleiotropy between emission and acceptance of drifters

654 We now remove the assumption of pleiotropy, so that m and y are treated independently. Again assuming
 655 that drifters would be unrelated to brood they care for on partner nests as in Ref.⁵, the condition for
 656 selection to favour a small increase in drifting is the same as Equation 2.4. The relative fitness of male and
 657 female brood is now:

$$658 \quad W_{\delta} = W_{\varnothing} = \frac{x}{K} (M_f u Y_d + a(1 - M_r Y_f)) \quad (2.8)$$

659 Evaluating again with both Y_f and Y_r at the population average drifting level \bar{y} , and with M_f and M_r at
 660 the population average acceptance level \bar{m} , the effect on the fitness of female and male brood in the home
 661 nest due to a small increase in drifting by workers on the home nest is:

$$662 \quad \left. \frac{\partial W_{\varnothing}}{\partial Y_f} \right|_{Y_f=\bar{y}} = \left. \frac{\partial W_{\delta}}{\partial Y_f} \right|_{Y_f=\bar{y}} = -a \frac{\bar{m}x}{K} \quad (2.9)$$

663 As long as a recipient colony does not reject incoming drifters ($\bar{m} > 0$), a small increase in drifting by
 664 workers leads to a loss in relative fitness for their sibling brood. Again substituting the relevant
 665 consanguinities (p_{sis} and p_{bro}) and Equation 2.9 into the condition for selection on drifting (Equation 2.4)
 666 gives:

$$667 \quad a \frac{\bar{m}x}{3K} < 0 \quad (2.10)$$

668 Since $\frac{\bar{m}x}{3K}$ has a positive real value, drifting is favoured if:

$$669 \quad a < 0 \quad (2.11)$$

670 That is, if home workers are actively deleterious to the home colony's productivity. Thus if workers
 671 provide any benefit to their home colony ($a > 0$), they should not be emitted as drifters to unrelated
 672 colonies.

673 Selection favours an increase in acceptance (m) of any incoming drifters from other colonies when:

$$674 \quad c_{\varnothing} \frac{\partial W_{\varnothing}}{\partial M_f} p_{\text{sis}} + c_{\delta} \frac{\partial W_{\delta}}{\partial M_f} p_{\text{bro}} > 0 \quad (2.12)$$

675 A small increase by workers in acceptance to the home nest of incoming drifters increases the relative
 676 fitness of their brother and sister brood on the home nest:

$$677 \quad \left. \frac{\partial W_{\text{♀}}}{\partial M_{\text{f}}} \right|_{M_{\text{f}}=\bar{m}} = \left. \frac{\partial W_{\text{♂}}}{\partial M_{\text{f}}} \right|_{M_{\text{f}}=\bar{m}} = u \frac{x\bar{y}}{\bar{K}} \quad (2.13)$$

678 Substituting Equation 2.13 into Equation 2.12 gives the condition for an increase in acceptance (m):

$$679 \quad \bar{y} \frac{ux}{3\bar{K}} > 0 \quad (2.14)$$

680 Assuming incoming drifters would contribute positively to productivity ($u > 0$), $\frac{ux}{3\bar{K}}$ has a positive real
 681 value, and acceptance is favoured if:

$$682 \quad \bar{y} > 0 \quad (2.15)$$

683 Selection favours acceptance ($m > 0$) whenever drifters are being emitted by other colonies ($\bar{y} > 0$).
 684 Whilst selection favours the minimisation of drifting to unrelated colonies in all circumstances in which
 685 workers are helpful (Equation 2.15), it favours maximum acceptance m of foreign cooperative drifters (i.e.,
 686 free-riding) (Equation 2.11). Accordingly, willingness to accept drifters (higher m) is not an honest signal
 687 of willingness to emit drifters (higher y). In the absence of complex and implausible social insect colony
 688 versions of the stabilising mechanisms known to sustain indirect reciprocity (including between-colony
 689 monitoring of whole-colony reputation, uncheatable physical greenbeards, or punishment of free-riding
 690 colonies by cooperative colonies), the proposed effect of indirect reciprocity⁵ cannot drive drifting. We plot
 691 the direction of selection in **Fig. 1e** of the main text.

692 Finally, we note that in principle ‘social heterosis’ ($u > a$) between *related* nests could drive drifting by kin
 693 selection, rather than by indirect reciprocity: a large benefit that could be provided to distant kin would
 694 compensate for their more distant relatedness, and so satisfy Hamilton’s rule. However, this would require
 695 acutely strong social heterosis at levels unknown in any social insect: high synergies between genotypes
 696 would need to ensure that halving relatedness to recipients would more than double the benefit a worker
 697 can provide.

698

699 3. Diminishing returns

700 We consider a situation in which colonies differ in their worker-to-brood ratio ψ , in the range $0 < \psi \leq$
 701 1. For simplicity, we consider neighbour colonies with equal absolute brood numbers. Variation in worker-
 702 to-brood ratio can arise for any reason. For instance, *Polistes canadensis* colonies show considerable variation
 703 in worker number for a given brood size (as shown in the horizontal range of the scatter-points of **Fig. 3**
 704 in the main text), often through chance worker mortality (estimated at 7% per day¹²). We ask when workers

705 on a home colony with ψ should invest in a partner colony that has a proportion $g < 1$ of worker-to-
706 brood ratio of the home colony. The diminishing returns hypothesis predicts that workers should not invest
707 in other colonies, despite ψ variation, when the returns from cooperation are linear: the increment in the
708 payoffs of altruism is the same regardless of ψ . When there are diminishing returns to cooperation,
709 however, a worker on a home colony with high ψ may experience weaker indirect fitness returns on its
710 home colony than on a neighbour colony.

711 We assume that ψ variation between colonies occurs unpredictably from the perspective of an individual.
712 Accordingly, wasps are blind to their colony type when deciding whether to pursue altruistic sterility (worker
713 phenotype) or reproduction. Let the sex ratio (z) and proportion of females that are sterile altruists (x) be
714 common to all nests. We assume that the partner colony will emit no drifters and ask what the equilibrium
715 level of drifting will be from the home colony to the partner colony. The average level of drifting y from
716 the home colony to the partner colony is Y . Both y and Y are evaluated at population average value \bar{y} .

717 We consider the extent of drifting that should evolve between two types of nest ('1' and '2'), which differ
718 in their worker-to-brood ratio (ψ). Using the framework of Davies *et al.*²² (described in the Supplementary
719 Information), we let the absolute fitnesses of focal female brood on the home type 1 colony (subscript '1')
720 and the partner type 2 colony (subscript '2') respectively be:

$$721 \quad w_{\varphi,1} = (1 - x)K_1 \quad (3.1)$$

$$722 \quad w_{\varphi,2} = (1 - x)K_2 \quad (3.2)$$

723 The rate of producing reproductives on a home colony of type s is $K_s = 1 - (1 - h_s)^T$ (see
724 **Supplementary Information** for details). The total help received by brood on each colony type is:

$$725 \quad h_1 = x(1 - z)\psi(1 - Y) \quad (3.3)$$

$$726 \quad h_2 = x(1 - z)\psi(g + Y) \quad (3.4)$$

727 The population average levels of help on colonies of each type in the population:

$$728 \quad \bar{h}_1 = x(1 - z)\psi(1 - \bar{y}) \quad (3.5)$$

$$729 \quad \bar{h}_2 = x(1 - z)\psi(g + \bar{y}) \quad (3.6)$$

730 The population average relative fitnesses on each nest type, for both male and female brood, assuming
731 colony types 1 and 2 are equally frequent in the population, are (**Supplementary Information**):

$$732 \quad W_{\sigma,1} = W_{\varphi,1} = \frac{2K_1}{\bar{K}_1 + \bar{K}_2} \quad (3.7)$$

$$733 \quad W_{\sigma,2} = W_{\varphi,2} = \frac{2K_2}{\bar{K}_1 + \bar{K}_2} \quad (3.8)$$

734 where \bar{K}_s is the population average value of K_s for colonies of type s .

735 As above (Equation 2.4), let $c_{\text{♀}}$ be the class reproductive value for females ($\frac{2}{3}$). Let $c_{\text{♂}}$ be the class
 736 reproductive value for males ($\frac{1}{3}$). Selection favours an increase in cooperative drifting from nest type 1 to
 737 nest type 2 (y) when the net effect on all potentially-affected parties (sisters, brothers, partner-colony female
 738 brood, and partner-colony male brood) leads to an expected increase in the success of a mutant allele for
 739 drifting (we assume no effect on self fitness, since drifters are already committed to being behaviourally-
 740 sterile helpers):

$$741 \quad c_{\text{♀}} \left(\frac{\partial W_{\text{♀},1}}{\partial Y} p_{\text{sis}} + \frac{\partial W_{\text{♀},2}}{\partial Y} d_{\text{♀}} p_{\text{sis}} \right) + c_{\text{♂}} \left(\frac{\partial W_{\text{♂},1}}{\partial Y} p_{\text{bro}} + \frac{\partial W_{\text{♂},2}}{\partial Y} d_{\text{♂}} p_{\text{bro}} \right) > 0 \quad (3.9)$$

742 with traits evaluated at their population average values ($y = Y = \bar{y}$), and where $d_{\text{♀}}$ is the devaluation in
 743 consanguinity to female brood on the partner colony (relative to sisters on the home colony) and $d_{\text{♂}}$ is the
 744 devaluation in consanguinity to male brood on the partner colony (relative to brothers on the home colony).
 745 Although we are focusing on scenarios in which a worker's consanguinity to brood is lower on the partner
 746 colony than on the home colony, and hence 'devalued' ($d_{\text{♀}}, d_{\text{♂}} < 1$), there can also be scenarios in which
 747 a worker is more consanguineous with brood on the partner colony, which may only apply to one sex. For
 748 instance, nephews are more consanguineous to a female than brothers are ($p_{\text{nephew}} = \frac{3}{8}$ but $p_{\text{bro}} = \frac{1}{4}$). If
 749 the partner-colony male brood are nephews, $d_{\text{♂}}$ would be greater than 1. If the partner-colony female
 750 brood are nieces, $d_{\text{♀}}$ remains below 1 (since $p_{\text{niece}} = \frac{3}{16}$ but $p_{\text{sis}} = \frac{3}{8}$).

751 A small increase in drifting (Y) by workers from the home type 1 nest leads to a loss of relative fitness for
 752 the workers' sibling brood on their home nest:

$$753 \quad \left. \frac{\partial W_{\text{♀},1}}{\partial Y} \right|_{Y=\bar{y}} = \left. \frac{\partial W_{\text{♂},1}}{\partial Y} \right|_{Y=\bar{y}} = - \frac{2\psi T x (1-z) (1 - \psi x (1-z) (1 - \bar{y}))^{T-1}}{\bar{K}_1 + \bar{K}_2} \quad (3.10)$$

754 A small increase in drifting (Y) by workers from the home type 1 nest leads to an increase in relative
 755 fitness for the related brood on the partner type 2 nest to which they drift:

$$756 \quad \left. \frac{\partial W_{\text{♀},2}}{\partial Y} \right|_{Y=\bar{y}} = \left. \frac{\partial W_{\text{♂},2}}{\partial Y} \right|_{Y=\bar{y}} = \frac{2\psi T x (1-z) (1 - \psi x (1-z) (g + \bar{y}))^{T-1}}{\bar{K}_1 + \bar{K}_2} \quad (3.11)$$

757 Substituting Equations 3.10 and 3.11 into Inequality 3.9, and dividing both sides by $\frac{\psi T x (1-z)}{6(\bar{K}_1 + \bar{K}_2)}$, gives the
 758 condition for selection to favour a small increase in drifting:

$$759 \quad \frac{(1 - \psi x (1-z) (g + y))^{T-1}}{(1 - \psi x (1-z) (1 - y))^{T-1}} > \frac{4}{(3d_{\text{♀}} + d_{\text{♂}})} \quad (3.12)$$

760 which is Inequality 2 in the main text.

761 To find candidate evolutionarily stable strategies (ESS) for drifting (y^*), we set the left and right sides of
762 Inequality 3.12 equal to one another, and rearrange for y . The ESS level of drifting is given by:

$$763 \quad y^* = \frac{1}{1 + \sqrt[T]{\left(\frac{3}{4}d_{\text{♀}} + \frac{1}{4}d_{\text{♂}}\right)}} \left[1 - \sqrt[T]{\left(\frac{3}{4}d_{\text{♀}} + \frac{1}{4}d_{\text{♂}}\right)} g - \frac{1 - \sqrt[T]{\left(\frac{3}{4}d_{\text{♀}} + \frac{1}{4}d_{\text{♂}}\right)}}{\psi x(1-z)} \right] \quad (3.13)$$

764 which is Equation 3 in the main text (where, for simplicity, we assume that consanguinity to male and
765 female brood is devalued by the same proportion; $d_{\text{♀}} = d_{\text{♂}} = d$). Higher levels of relatedness (higher $d_{\text{♀}}$
766 and $d_{\text{♂}}$) and stronger diminishing returns (higher T) select for higher levels of drifting y^* at equilibrium
767 (**Extended Data 1**). We plot the equilibria at illustrative values in **Fig. 2f** of the main text. In **Extended**
768 **Data 2**, we plot the candidate equilibria at different values of sex ratio z and female helping x .

769

770 4. *Polistes canadensis* payoffs

771 To obtain empirical measures of productivity in *Polistes canadensis*, we tracked a cohort of developing brood
772 on 91 free-living post-emergence colonies over a 56-day period (from 14th June to 8th August 2016).
773 Colonies were clustered in six aggregations on the north coast of Panama (15.2 ± 7.7 colonies per
774 aggregation, mean \pm S.D.). Five aggregations were in clearings between lowland tropical forest and the
775 Panama Canal (former US Army Base Fort Sherman, San Lorenzo National Park, Colón Province) and one
776 aggregation was in a clearing in a mangrove swamp (Galeta Point, Colón Province). We use an observational
777 approach to quantify productivity. Key parameters of brood-rearing can be quantified effectively in
778 unmanipulated colonies, including natural rates of stochastic failure, predation, parasitism, queen turnover,
779 workforce fluctuations, and male production. Associations between brood transition rates and workforce
780 size are correlational, and so we view our results as plausible ranges within which causal effects can exist.

781 To measure the impact of workers at different developmental states, we split brood into stereotypical
782 categories in a sequence. Each category, and its notation, is listed in **Extended Data 3**. We examined each
783 brood cell at 5-day intervals, using a ladder to access colonies and a flashlight to illuminate each cell. A small
784 number of observations were made on the following morning due to issues with field site access. The
785 current classification of the brood cell was dictated to a second observer, who recorded it on a hexagonal
786 grid of the nest. Accordingly, brood classification was done by a single observer blind to the previous state
787 of the cell.

788 We censused adult group size by recording total adult numbers at night (8 pm–11 pm, 6–7 censuses per
789 colony across the monitoring period). We used a red light (which wasps are unable to see) to avoid
790 disturbance. Nests that were difficult to observe were counted multiply on a given night and averages taken.

791 A small number of males emerged and stayed on nests. Adult males observed in daylight surveys during the
792 brood counts on 5-day intervals were used to interpolate male number through time; otherwise, males were
793 assumed to be absent. Female number (henceforth, ‘group size’) during each 5-day interval was defined as
794 interpolated total number of adults minus interpolated male number. We assumed that any changes in group
795 size between night-censuses occur gradually without sudden jumps, to avoid imposing artificial step changes
796 in the model. We therefore estimated group size during each interval as the mean (across 5 days) of the
797 fitted group sizes generate by a cubic spline interpolation through the night-censuses. For 5-day brood-
798 observation intervals in which the first night census occurred within 1 day of the beginning of the interval,
799 we allowed a limited extrapolation of 1 day in order to approximate mean group size over the 5-day interval.
800 All intervals that would require any other extrapolation of group size were excluded from the analysis below
801 in which group size is used as a predictor. To obtain estimates of the payoff rates, we fit a Markov model
802 (shown in **Fig. 3**) to the brood development data, asking how colony productivity changes in association
803 with different worker and brood numbers.

804 **4.1 Statistical methods**

805 The (relatedness-weighted) marginal effect of a worker on the development time of a larva is an
806 incomplete measure of indirect fitness payoff. This is because *Polistes* nests experience considerable
807 individual brood death¹², which returns the cell to the start of the developmental process (once the queen
808 has redeposited an egg). A worker’s major contribution might be to prevent inefficiency by minimising the
809 rate of brood death. To accommodate both effects, we therefore analysed brood development as a Markov
810 model, where the target parameter for inference is the expected time for a brood cell to produce a new
811 adult (‘time to absorption’ of the Markov model⁵⁷). The cell may cycle through repeat deaths before finally
812 producing an adult. We treated the Markov transition matrix as a function of the predictor variables worker
813 number, worker-to-brood ratio, brood-cell emptiness, and interactions. To estimate the transition matrix,
814 we used Bayesian mixed models with colony as a random effect. Using the resulting estimate of the ‘time
815 to absorption’ for *P. canadensis* colonies of different worker and brood sizes, we then obtained the predicted
816 colony productivity rate, defined as the expected number of new adults produced per unit time. Because
817 we are interested in the marginal effect of each additional worker on brood production, we took as an
818 estimate of Hamiltonian benefit B the partial derivative of this rate with respect to worker number,
819 evaluated at the point in demographic parameter space characterising any focal colony.

820 In principle, workers absconding due to a colony entering the declining phase and productivity falling
821 might generate the appearance of a decline in worker number causing a decline in productivity, whilst in
822 reality the decline in productivity caused the decline in worker number. To mitigate this as far as is possible,
823 we include brood-cell emptiness as a measure of colony state and allow for its interactions.

824 Because (1) brood states are categorical and (2) longitudinal data were collected in discrete time steps, we
825 give a multinomial likelihood for the number of transitions observed from each development state i into
826 each state j , which provides information on the probability π_{ij} of a brood transition from developmental
827 state i to state j . We model the number of transitions $\phi_{i \rightarrow j}$ (defined over a 5-day interval) where the self-
828 transition $i \rightarrow i$ provides the reference category ($\phi_{i \rightarrow i} = 1$) and all other transitions are described by log-
829 linear functions of the predictors \mathbf{x}_p in the vector \mathbf{x} (i.e., $\ln(\phi_{i \rightarrow (j \neq i)}) = \alpha_{ij} + \boldsymbol{\beta}_{ij,p} \cdot \mathbf{x}_p$):

$$830 \quad \pi_{ij} = \frac{\phi_{i \rightarrow j}}{1 + \sum_{j \neq i}^J \phi_{i \rightarrow j}} = \frac{e^{(\alpha_{ij} + \boldsymbol{\beta}_{ij,p} \cdot \mathbf{x}_p)}}{1 + \sum_{j \neq i}^J e^{(\alpha_{ij} + \boldsymbol{\beta}_{ij,p} \cdot \mathbf{x}_p)}} \quad (4.1)$$

831 The predictors include random effects for colony ID (defined below, Equation 4.3). The $\phi_{i \rightarrow j}$ transitions
832 are the entries in the following matrix:

$$833 \quad \Phi = \begin{bmatrix} 1 & \phi_{1 \rightarrow 2} & \phi_{1 \rightarrow 3} & \phi_{1 \rightarrow 4} & \phi_{1 \rightarrow 5} & - & - & - & \phi_{1 \rightarrow 9} \\ - & 1 & \phi_{2 \rightarrow 3} & \phi_{2 \rightarrow 4} & \phi_{2 \rightarrow 5} & \phi_{2 \rightarrow 6} & - & - & \phi_{2 \rightarrow 9} \\ - & - & 1 & \phi_{3 \rightarrow 4} & \phi_{3 \rightarrow 5} & \phi_{3 \rightarrow 6} & - & - & \phi_{3 \rightarrow 9} \\ - & - & - & 1 & \phi_{4 \rightarrow 5} & \phi_{4 \rightarrow 6} & - & - & \phi_{4 \rightarrow 9} \\ - & - & - & - & 1 & \phi_{5 \rightarrow 6} & \phi_{5 \rightarrow 7} & - & \phi_{5 \rightarrow 9} \\ - & - & - & - & - & 1 & \phi_{6 \rightarrow 7} & - & \phi_{6 \rightarrow 9} \\ - & - & - & - & - & - & 1 & \phi_{7 \rightarrow 8} & \phi_{7 \rightarrow 9} \\ - & - & - & - & - & - & - & 1 & - \\ - & - & - & - & - & - & - & - & 1 \end{bmatrix} \quad (4.2)$$

834 State 1 is egg, states 2-6 are larval states, state 7 is pupa, state 8 is adult (successful pupation), and state 9
835 is death during development. The final two rows, adulthood (8) and death (9), are absorbing.

836 The model is solved in discrete time because brood were observed at intervals. Accordingly, brood are
837 free to transition from one state to a state further downstream than the next step in the sequence; they have
838 passed through the transitional states during the 5-day window. Some transitions are not biologically
839 possible during a 5-day window (such as 1 to 6 or 3 to 7), so are not permitted in the Markov transition
840 matrix (represented by a dash). We present two models with increasing complexity. ‘Model 1’ focuses on
841 the baseline transition rates (i.e., intercepts and random effects only) for the complete dataset of observed
842 transitions between live-brood-containing cells, which allows us to estimate the baseline productivity rate
843 of *P. canadensis* colonies (Fig. 2c of the main text).

844 Next, we present an indicator-variable-selection model (‘Model 2’) to identify the marginal change in
845 productivity associated with each additional worker at different points in the parameter space typifying *P.*
846 *canadensis* colonies. We exclude all colony-observations lying outside of the night-census range, and a small
847 number of colony observations with fewer than 10 (2-to-6 state) larvae. These steps focus the payoff model
848 onto a core dataset of 471 colony observations on 85 colonies, comprising 123,116 observed brood
849 transitions (from the total dataset of 168,811 observed brood transitions on 1,027 colony observations on
850 91 colonies). The model parameters were estimated using a Bayesian approach computed using Markov

851 chain Monte Carlo (MCMC) simulation in JAGS (using `tjAGS`⁵⁸ in R). We confirmed MCMC convergence
 852 using potential scale reduction factors (PSRF; \hat{R}) for five chains ($\hat{R} < 1.1$ for the large majority of
 853 parameters). After an adaptation phase of 5,000 iterations and a burn-in of 1,000 iterations, we sampled
 854 parameter slope values for 15,000 iterations with a thinning of 4. For the posterior predictive model
 855 (described below) to generate the inference about payoff rates using simulated input values for colony
 856 worker and brood numbers, we continued running MCMC sampling for a further 10,000 iterations with a
 857 thinning of 10.

858 4.2 Within and between effects

859 We use a ‘within-between’ formulation⁵⁹, which follows the ‘de-meaning’ procedure suggested by
 860 Mundlak⁶⁰. We split each time-varying predictor (i.e., predictors whose values can differ between different
 861 colony-observations within the same colony) into a ‘between-colony’ component and a ‘within-colony’
 862 component. The between-colony component is the mean value \bar{x}_C of the relevant predictor for the focal
 863 colony C (across its colony-observations). The within-colony component is the deviation from this mean
 864 in any one colony-observation.

865 We denote the slope dealing with a between-colony component with the subscript ‘b’ (e.g., $\beta_{ij,workers|b}$)
 866 and the slope dealing with a within-colony component with the subscript ‘w’ (e.g., $\beta_{ij,workers|w}$). We also
 867 permit $x_{workers}$ to interact with the two other predictors: $\beta_{ij,empty,workers}$ denotes an interaction between
 868 x_{empty} and $x_{workers}$, and $\beta_{ij,ratio,workers}$ denotes an interaction between x_{ratio} and $x_{workers}$. We allow
 869 these interactions at both the between-colony and within-colony levels. The random intercept for the
 870 transition $i \rightarrow j$ for colony C is $\beta_{ij,C}$. Thus, the fully saturated model for the transition from state i to state
 871 j (subject to pruning of variables during the indicator-variable-selection process detailed in the next section)
 872 is:

$$\begin{aligned}
 873 \quad \ln(\phi_{i \rightarrow (j \neq i)}) &= \alpha_{ij} + \beta_{ij,C} + \beta_{ij,empty|w}(x_{empty} - \bar{x}_{empty,C}) + \beta_{ij,empty|b}\bar{x}_{empty,C} \\
 874 &\quad + \beta_{ij,workers|w}(x_{workers} - \bar{x}_{workers,C}) + \beta_{ij,workers|b}\bar{x}_{workers,C} \\
 875 &\quad + \beta_{ij,ratio|w}(x_{ratio} - \bar{x}_{ratio,C}) + \beta_{ij,ratio|b}\bar{x}_{ratio,C} \\
 876 &\quad + \beta_{ij,empty,workers|w} \left((x_{empty} - \bar{x}_{empty,C})(x_{workers} - \bar{x}_{workers,C}) \right) \\
 877 &\quad + \beta_{ij,empty,workers|b} (\bar{x}_{empty,C}\bar{x}_{workers,C}) \\
 878 &\quad + \beta_{ij,ratio,workers|w} \left((x_{ratio} - \bar{x}_{ratio,C})(x_{workers} - \bar{x}_{workers,C}) \right) \\
 879 &\quad + \beta_{ij,ratio,workers|b} (\bar{x}_{ratio,C}\bar{x}_{workers,C}) \\
 880 & \tag{4.3}
 \end{aligned}$$

881 The random effect of colony ID is:

882
$$\beta_{ij,c} \sim \mathcal{N}\left(0, \frac{1}{\tau_{ij}}\right) \quad (4.4)$$

883 where the precision τ is drawn from a gamma distribution:

884
$$\tau_{ij} \sim \text{Gamma}(0.001, 0.001) \quad (4.5)$$

885

886 **4.3 Model averaging**

887 In an indicator-variable-selection procedure, we construct the saturated model (Equation 4.3), and
 888 introduce a series of binary indicator variables that ‘switch on’ or ‘switch off’ each predictor throughout
 889 MCMC⁶¹. The duration of MCMC time with each coefficient switched on is proportional to the coefficient’s
 890 marginal likelihood of contribution. For each predictor p ’s regression slope $\beta_{ij,p}$ (within the vector $\beta_{ij,p}$
 891 in Equation 4.1), we can therefore annex a binary coefficient $g_{ij,p}$ that switches between 0 and 1, and then
 892 track the mean of the posterior distribution for $g_{ij,p}$. The closer this mean is to 1, the more frequently the
 893 corresponding regression slope $\beta_{ij,p}$ is retained in the model.

894 For the random effects, we used independent Bernoulli priors for $g_{ij,p}$ to allow the MCMC sampler to
 895 turn the specific random effect on or off directly. For other predictors, we used a product of the
 896 independent priors for $g_{ij,p}$ and $\beta_{ij,p}$ ⁶²:

897
$$f(\beta_{ij,p} | g_{ij,p}) = g_{ij,p} f(\beta_{ij,p} | g_{ij,p} = 1) + (1 - g_{ij,p}) f(\beta_{ij,p} | g_{ij,p} = 0) \quad (4.6)$$

898 Following Ref.⁶², we used normal priors for the conditional distribution of $\beta_{ij,p}$ given $g_{ij,p}$.

899 $\beta_{ij,p}$ is indistinguishable from zero when $g_{ij,p}$ switches the predictor off. We model the indicators as
 900 Bernoulli random variables with a 50:50 prior ($g_{ij,p} \sim \text{Bernoulli}(0.5)$), representing our starting point of
 901 indifference between either including or dropping the slope $\beta_{ij,p}$. For interactions, we set a prior of
 902 $\text{Bernoulli}(0.2)$. To accommodate the within-between formulation, we apply the indicator variables to the
 903 whole fixed effect predictor: the predictor cannot be turned on for one component (e.g., the between-
 904 colony component) and switched off for the other component (e.g., the within-colony component).

905 The effects on the transition probabilities whose 95% credible intervals do not overlap zero are shown
 906 in **Extended Data 3**.

907

908 **4.4 Model checking: residual deviance**

909 The residual deviances D_i for each multinomial model corresponding to the seven initial states i are given
 910 by summing over the residual deviance contributions for each colony-observation k , where E_{kij} is the

911 observed number of transitions from state i to state j for colony-observation k and \hat{E}_{kij} is the
 912 corresponding expected number of transitions from the fitted model⁶³:

$$913 \quad D_i = \sum_k 2 \left(\sum_j E_{kij} \log \left(\frac{E_{kij}}{\hat{E}_{kij}} \right) \right) \quad (4.7)$$

914 The deviance explained by the fixed effects is presented in **Extended Data Fig. S6**.

915 In **Extended Data 6–8**, we plot residual deviance contributions for each colony-observation against
 916 predictors. There is no evidence of structure in the plots: most colony-observations fit relatively well, but
 917 some colony-observations exhibit very high deviance. In **Supplementary Information Table S3**, we
 918 provide the mean residual deviances for each of the seven starting state models (residual deviances divided
 919 by $471n_i$, where n_i is the number of states into which a cell can transition from starting state i , and 471
 920 is the number of colony-observations. The models for starting states 1 and 6 have high mean residual
 921 deviances. Inspection of potential outlier colony-observations (colony-observations with unusually high
 922 residual deviance contributions) suggests that these high residual deviances may be partly reflective of
 923 episodes of unusually high mortality on colonies, with substantial death of large larvae (starting state 6)
 924 and substantial cannibalism of eggs (starting state 1). Future models focusing on predictors of severe
 925 mortality episodes and other on-colony dynamics may be required to reduce residual deviance in these
 926 scenarios.

927

928 4.5 Expected time to adulthood

929 To calculate the worker effect on the transition matrix, controlling for oviposition rate, we submit all
 930 estimated transition-to-death probabilities ($\phi_{i \rightarrow 9} \forall i$) to the prediction matrices as transitions to new eggs.
 931 This isolates the potential effect of workers (as opposed to the egg-layer) to obtain per-cell efficiency
 932 without the confounding effect of variation between queens in the rate at which replacement eggs are laid
 933 following the death of larvae.

934 The expected time to absorption ('expected mean first passage time' in **Fig. 3a** of the main text), in which
 935 a brood cell transitions from egg to adulthood ($\hat{m}_{1 \rightarrow 8}$) via intermediate states, can be obtained using the
 936 linear algebra for a discrete Markov process via the 'fundamental matrix' method of Kemeny and Snell⁵⁷.
 937 Following Grinstead & Snell⁶⁴, we obtain the fundamental matrix \mathbf{N} by inverting the matrix $\mathbf{I}_t - \mathbf{Q}$, where
 938 \mathbf{I}_t is the identity matrix for the transient states and \mathbf{Q} is a square matrix of transition probabilities between
 939 each transient brood state with length equal to the number of transient states (i.e., all states apart from
 940 adulthood and death). Accordingly:

$$941 \quad \mathbf{N} = (\mathbf{I}_t - \mathbf{Q})^{-1} \quad (4.8)$$

942 We solve for \mathbf{N} for each of the recorded iterations in MCMC separately, in order to sample the posterior
 943 predictive distribution using simulated colonies across the parameter space of worker and brood number,
 944 with the number of empty cells set to the population-average value. The element $n_{i,j}$ in \mathbf{N} is the frequency
 945 with which the brood cell is expected to visit state j given a current state i . The vector \mathbf{t} of times to
 946 absorption (using the values at any one recorded iteration of MCMC) is then:

$$947 \quad \mathbf{t} = \mathbf{N}\mathbf{1} \quad (4.9)$$

948 where $\mathbf{1}$ is a column vector of 1s. The i th element of \mathbf{t} is the duration (in step numbers) from state i to
 949 successful production of a new adult.

950 To obtain the $\mathbf{I}_t - \mathbf{Q}$ matrix within MCMC, we employ the between-colony effects, which provide a
 951 measure of the quantities of interest (workforce size and worker-to-brood ratio) that abstracts away
 952 extraneous between-colony variation (in the random intercepts terms $\beta_{ij,c}$) and within-colony variation
 953 that is likely to be confounded by colony ageing (in the within-colony effects). We then derive the predicted
 954 whole-colony rate of brood production by converting the per-cell time to absorption to a productivity rate
 955 per unit time and scaling this rate by the brood cohort size on each colony (using the total number of eggs
 956 to large larvae, states 1–6, a measure of cohort size).

957 In the main text, we plot the expected mean first passage time in **Fig. 3a** and the estimated whole-colony
 958 productivity in **Fig. 3c**.

959

960 **4.6 Indirect fitness payoff calculation**

961 Extracting predictions at the population mean level of cell emptiness (**Extended Data 9**), we plot the
 962 posterior predictive distribution for whole-colony productivity using the 1,000 simulated points (in
 963 *Mathematica*). That is, to extract the shape of the posterior predictive distribution, we fit the smooth
 964 interpolation to 1,000 closely-packed samples monitored in MCMC.

965 The diminishing returns hypothesis predicts that a worker can maximise inclusive fitness by shifting from
 966 a home colony 1 with worker-to-brood ratio ψ_1 and brood number t_1 (where she is related to the brood
 967 by r_1) to a partner colony 2 with worker-to-brood ratio ψ_2 and brood number t_2 (where she is related to
 968 the brood by r_2):

$$969 \quad r_2 \left. \frac{\partial w(\psi, t)}{\partial \psi} \right|_{\substack{\psi=\psi_1 \\ t=t_1}} > r_1 \left. \frac{\partial w(\psi, t)}{\partial \psi} \right|_{\substack{\psi=\psi_2 \\ t=t_2}} \quad (4.10)$$

970 where she has a larger effect on the production rate w of offspring-equivalents by changing ψ_2 on 2 than
 971 she would have by changing ψ_1 on 1. The end result of the Markov model is a model of these partial

972 derivatives (estimates of the payoffs driving the benefit term in Hamilton’s rule) for colonies of different
973 worker numbers and brood numbers (**Fig. 3e** in the main text).

974

975 **5. Individual-based simulation**

976 To simulate the spatial invasion of cooperative drifting under nonlinear returns to cooperation, we
977 consider the evolution of a decision rule in a haplodiploid population on a square lattice in a spatially explicit
978 individual-based simulation. Nodes represent colony sites. Each colony has a single monogamous
979 reproductive pair of a diploid queen and haploid drone. We simulate a death–birth updating process: each
980 time-step, 10% of nodes are selected, and their resident colonies die. A new colony at each updating node
981 is then founded by a new queen drawn from within the dispersal range for females, with probabilities
982 proportional to the payoffs of each of the surrounding eight colonies. We consider two discrete conditions
983 for the female dispersal range: (1) female philopatry (local dispersal within the Moore neighbourhood [the
984 surrounding eight nodes]); and (2) global female dispersal (dispersal from any distance on the lattice with
985 equal probability).

986 Drones are selected from anywhere in the lattice⁵⁷, with probabilities proportional to the queen’s fitness
987 at each colony on the lattice. Colonies produce female workers as they age: every three time-steps, they gain
988 a unit of workers, until reaching a maximum number of units (set to 10 in the main text results; **Fig. 4**).
989 Queen fitness w (production of reproductively destined brood) is determined by:

$$990 \quad w = 1 - (1 - h)^T \quad (5.1)$$

991 where h is the total worker effort received by the colony rescaled between 0 (no workers) and 1 (maximum
992 number of workers possible). We consider two discrete conditions for diminishing returns: no diminishing
993 returns ($T = 1$) and moderate diminishing returns ($T = 3$).

994 Each worker has a finite amount of help to distribute. We consider selection on a single locus y , which is
995 the probability of drifting by workers on colonies above a threshold worker number (5 in **Fig. 4**). Drifter
996 help is distributed at random within each worker’s local helping window. We consider two discrete
997 conditions for the size of the helping window: (1) workers help indiscriminately within the local Moore
998 neighbourhood; (2) workers restrict the helping window only to colonies with immediate genealogical ties
999 to the home colony (defined as the parent colony from which the mother queen came or a daughter colony
1000 on which a sister is queen).

1001 Main Text **Fig. 4** summarises the role of local cooperation.

1002

1003 **Additional information**

1004 Additional detail on methods is provided in the **Supplementary Information**, and statistical and
1005 simulation code is provided in the electronic material. Additional figures are provided in **Extended Data**.

