



Kennedy, P., Sumner, S., Botha, P., Welton, N. J., Higginson, A. D., & Radford, A. N. (2021). Diminishing returns drive altruists to help extended family. *Nature Ecology and Evolution*, 5(4), 468-479.
<https://doi.org/10.1038/s41559-020-01382-z>

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Diminishing returns drive altruists to help extended family

Lay Summary:

Most social insects are highly aggressive to neighbour colonies, as expected by evolutionary theory. However, in a Central American wasp, workers are surprisingly generous to neighbours – providing food and helping to rear the young. Using mathematical modelling and field observations, we test the different hypotheses that biologists have proposed to explain this striking behaviour. Our field data show that workers face diminishing returns to helping effort on their home colonies. When this happens, switching colony to help more-distantly-related kin on neighbour nests can become the best way to promote the spread of a worker's genes in the population. Altruism to the neighbours can evolve when relatives live nearby and there are diminishing returns to staying at home.

Diminishing returns drive altruists to help extended family

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

Abstract:

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

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

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

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

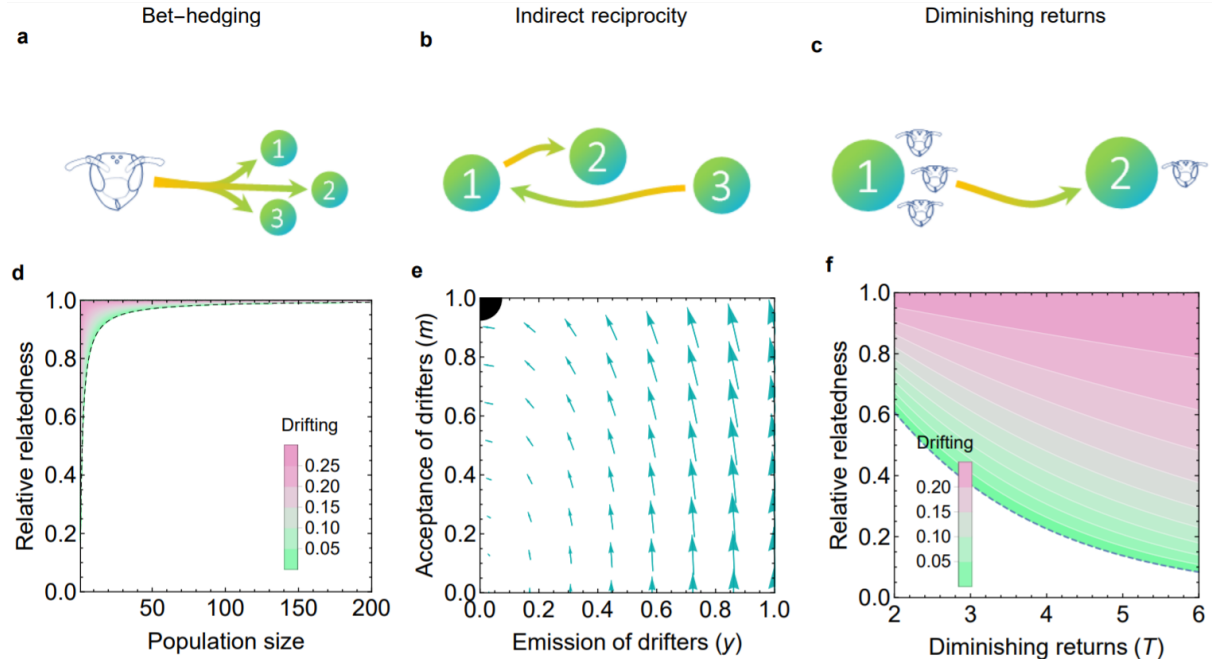


Fig. 1 | Three adaptive hypotheses have been proposed for cooperative drifting. (a) Bet-hedging. **(b)** Indirect reciprocity. **(c)** Diminishing returns. **(d)** Cooperative drifting is only favoured by bet-hedging (above dashed line) at extremely small population sizes and when recipients differ only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

Results

Selection for cooperative drifting

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

$$\begin{aligned} \max_{\mathbf{q}} \left\{ \mathbf{q}^{\dagger} \boldsymbol{\mu} - v \cdot \rho \sqrt{\mathbf{q}^{\dagger} \mathbf{C} \mathbf{q}} \right\} \\ \text{subject to} \quad \mathbf{q}^{\dagger} \mathbf{1} = 1 \end{aligned} \quad (1)$$

where the organism must choose the optimal weights (\mathbf{q}) to place on different investments, balancing the expectation ($\mathbf{q}^{\dagger} \boldsymbol{\mu}$, where \dagger denotes transpose) and variance ($\mathbf{q}^{\dagger} \mathbf{C} \mathbf{q}$) in absolute inclusive fitness

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

Second, we show that indirect reciprocity⁵ is unlikely to explain cooperative drifting. Using simulations, Nonacs⁵ has argued that drifters will automatically help only at colonies sharing indirect reciprocator alleles because these are the only colonies willing to accept them. However, there is no reason to expect pleiotropy between these two behaviours, so (unlike Ref.⁵) we allow the emission (y) and acceptance (m) of drifters to evolve independently in a kin-selection model (*Methods 2*). As in Ref.⁵, we find that when m is prevented from decreasing whilst y increases, drifting can evolve (*Methods 2*). But when this unjustified assumption is relaxed, indirect reciprocity collapses due to the invasion of free-riding: colonies willingly accept foreign workers¹⁰ ($m = 1$) whilst none of their own workers drift ($y = 0$) (*Methods 2*; **Fig. 1e**).

Third, we show that diminishing returns^{7,12} can be a simple driver of cooperative drifting (*Methods 3*): as the effect of helping closely-related recipients declines, diversion of altruism towards more-distantly-related recipients can satisfy Hamilton's rule (increase in benefit b more than compensates for the decrease in relatedness r). In a kin-selection model using the framework of Davies *et al.*²², we let the probability of brood surviving to maturity (K) be determined by a simple diminishing returns function: $K = 1 - (1 - h)^T$, where $0 \leq h \leq 1$ is help received from workers. Higher values of T result in stronger diminishing returns. Help (h) received by each brood depends on the worker-to-brood ratio ψ

in their colony, which may vary stochastically between and within colonies through time. For simplicity, we consider neighbouring colonies with equal brood numbers, lying at different points on a line of possible worker-to-brood ratios. Worker-to-brood ratios greater than $\psi = 1$ occur only on colonies in terminal decline, so we focus on $0 < \psi \leq 1$. Drifting reduces a worker's relatedness to the brood it cares for to the (nonzero) proportions $d_{\text{♀}}$ and $d_{\text{♂}}$ for female and male brood respectively, relative to raising siblings at home. When a home colony has worker-to-brood ratio ψ , selection favours a small increase in drifting (y) to a colony with a proportion g of the home colony's workforce when the improvement in indirect fitness from escaping diminishing returns (left-hand side) compensates for reductions in recipient relatedness (right-hand side):

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

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

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

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

Given the possibility to drift to related colonies at sufficiently steeper points on an inclusive-fitness-returns curve, workers should tolerate a reduction in recipient relatedness (*Methods 3; Fig. 1f; Extended Data 1,2*). The ESS drifting level y^* increases whenever a gap in worker payoff increases between two related colonies: y^* increases with higher T (**Fig. 1f**), higher ψ and lower g , and for scenarios in which there is a larger workforce (lower z and higher x). For example, a worker may be twice as related to brood on its home colony as to brood on a partner colony ($d = 1/2$). Assume the home colony (with $\psi = 1$) has twice as many workers as the partner colony ($g = 1/2$). With diminishing returns factor of $T = 4$, three-quarters of females developing as non-reproductive workers ($x = 3/4$), and a sex ratio of 3:1 female eggs to male eggs ($z = 1/4$), the expected equilibrium level of cooperative drifting from the home colony would be for 13.2% of worker effort to be divested to the less-related partner colony ($y^* = 0.132$). As workers drift and group sizes consequently change, the marginal payoff of staying on the home colony rises and the marginal payoff of helping on the partner colony falls until $y = y^*$, where any further drifting would reduce inclusive fitness.

Diminishing payoffs in the wild

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

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

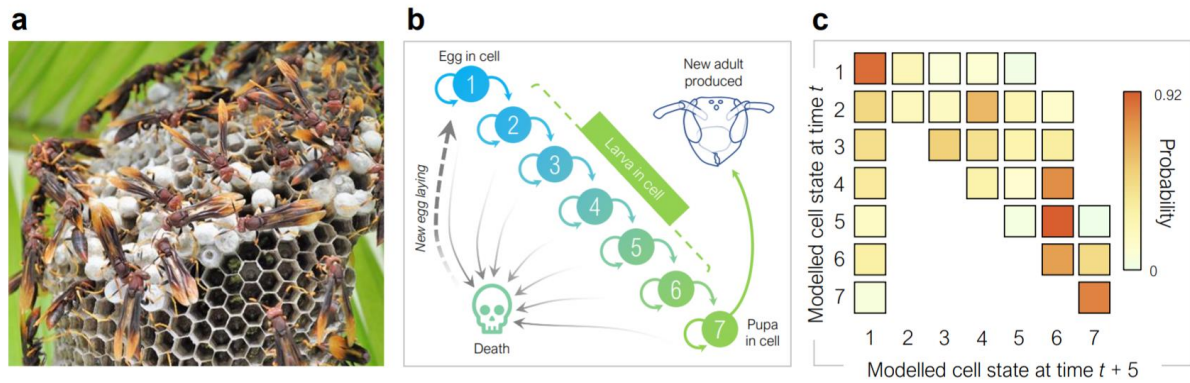


Fig. 2 | Brood development in the Neotropical paper wasp *Polistes canadensis*. (a) *P. canadensis* colonies allow easy observation of individual brood cells. *Photograph: PK.* (b) Wasp development involves states from egg (state 1) through larvae (2 to 6) to pupa (7) and finally a new adult (definitions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

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

The difference in the predicted payoff from the model suggests that – within the main parameter space occupied by colonies – workers are more valuable (lighter colours in **Fig. 3e**) at colonies with a relatively 'understaffed' workforce faced with large brood-rearing challenges than at colonies with

fewer brood to rear. Future models that consider within-colony dynamics may further explain finer-scale variation in brood development rates (see **Extended Data 5–8**; **SI Table S3**). However, the prediction of variation in plausible payoff rates between colonies with different workforce sizes suggests a context in which workers can increase indirect fitness by helping at less-closely-related colonies.

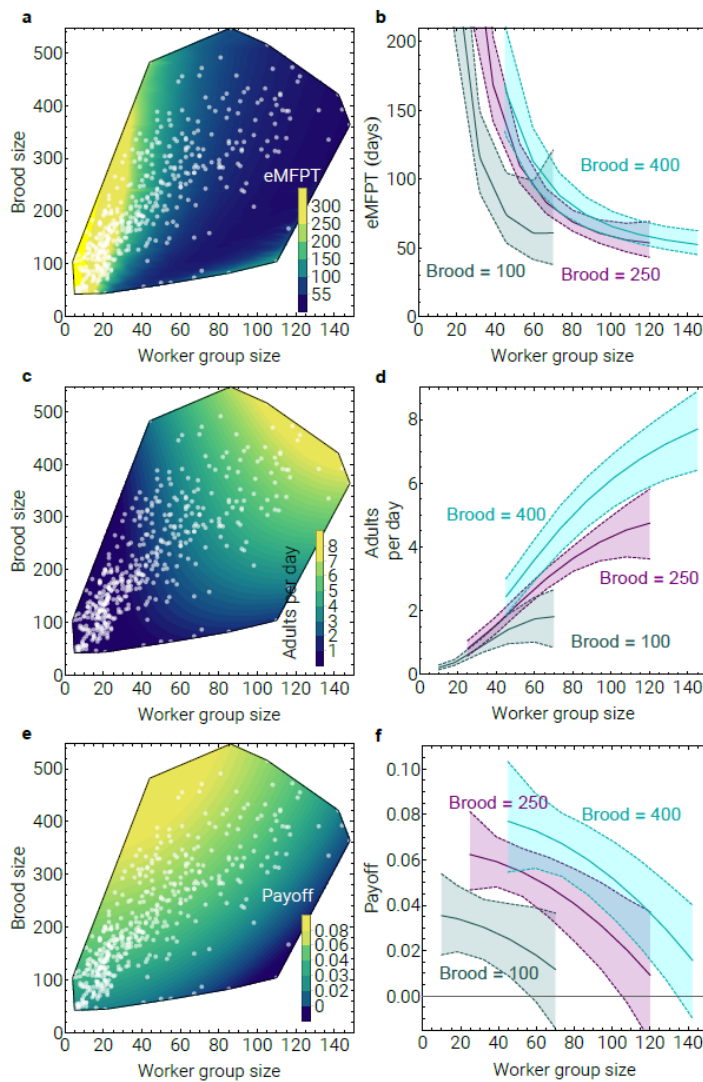


Fig. 3 | Brood-rearing rates in *Polistes canadensis*. (a) Expected number of days for an idealised brood cell successfully to produce an adult ('expected mean first passage time', eMFPT) predicted by between-colony effects. Brood size denotes number of prepupal brood (states 1–6). Worker group size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

Scales of competition

To explore the demographic conditions that can sustain cooperative drifting, we use agent-based haplodiploid simulations (*Methods 5*) of a large population of monogynous colonies distributed over a square lattice (where each colony has eight neighbours in a ‘Moore neighbourhood’). To model simple colony growth, we assume a ‘unit’ is a group of workers (e.g., 10 workers), and let colonies produce a new unit every three time-steps (e.g., 3 weeks) until reaching a maximum of 10 units. We assume a saturated environment in which each square on the lattice is occupied by one colony. At each time-step, a randomly chosen 10% of colonies die and are replaced. The foundress of the replacement colony is drawn either from lottery competition among the local eight colonies in the Moore neighbourhood (when female philopatry is assumed) or globally from the whole population (when female philopatry is relaxed). Males compete globally for mating with females in lottery competition. The number of reproductively-destined offspring that colonies produce is a diminishing-returns function of the helper effort h on the colony, $1 - (1 - h)^T$ as above. Colonies with more helpers therefore produce more reproductively-destined females and males, and so have a greater chance in competition for nest sites and mating, respectively. We evolve units’ propensity to drift for workers on colonies with more than five units, and show the results of competition by introducing mutant alleles to resident populations at an initial frequency of 5%. After 1,000 time-steps, we record the mutant frequency and plot the average change in frequency over three replicate simulations (*Methods 5*).

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

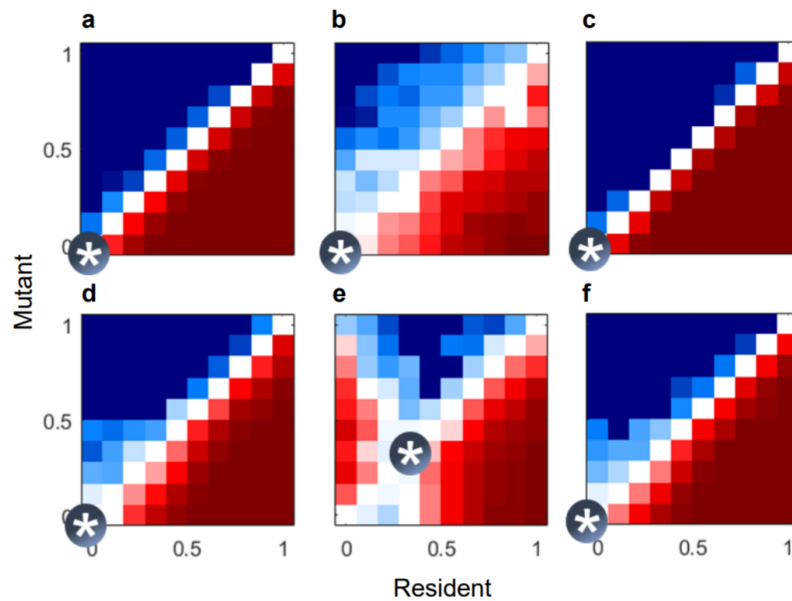


Fig. 4 | Evolution of cooperative drifting in a spatially explicit social haplodiploid simulation. Results of competition from agent-based simulations of the invasion of drifting. Red denotes mutants invading from a starting frequency (p_{initial}) of 5% of the population; blue denotes mutants declining.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

Discussion

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

Our model predicts the conditions under which we expect cooperative drifting to have evolved (Equation 2, Fig. 1f). Intuitively, drifting is more likely when there are stronger diminishing returns (higher T), a larger difference in workforce between nests (smaller g), increased total workforce (higher ψ), and a greater capacity to target kin (higher d_{φ} and d_{δ}). For simplicity in Equation 2, we assume that all colonies have the same sex ratio, but between-colony sex-ratio variation suggests an additional factor: a colony producing mainly brothers has a reduced worker relatedness to the brood, at which

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

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

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

Cooperative drifting has also emerged among complex eusocial species. Ant 'supercolonies' exist when nests with multiple queens (polygyny) exchange workers (polydomy)^{6,38}. Supercoloniality results in remarkably low-relatedness cooperation, and remains a theoretical challenge. The evolution of supercoloniality is likely to involve informational constraints preventing nepotism⁶, although some positive relatedness may be maintained by cryptic kin structure³⁹. Our results are relevant here: the

initial drivers of low-relatedness cooperation are unlikely to have been either bet-hedging by risk-spreading at the expense of the expectation of inclusive fitness (**Equation 1; Fig. 1d**) or the reciprocity scenario proposed by Ref.⁵ (**Fig. 1e**). In principle, diminishing returns may initially have favoured partial diversion of altruism to more-distantly-related colonies. However, supercoloniality and primitively-eusocial cooperative drifting are not completely analogous. Supercoloniality may have been a relatively small step for ants that had already evolved high within-colony polygyny – and consequently reduced relatedness⁴⁰ – for other reasons. Unlike primitively-eusocial wasps, the first step to explaining cooperative drifting in ants is explaining polygyny⁴¹.

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

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

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

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

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

Competing interest statement. The authors declare no competing interests.

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

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