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Nonacs, Peter

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RESEARCH ARTICLE

Why do Hymenopteran workers drift to non-natal groups? Generalized reciprocity and the maximization of group and parental success

Peter Nonacs 🔘

Department of Ecology & Evolutionary Biology, University of California, Los Angeles, Los Angeles, California, USA

Correspondence
Peter Nonacs, Department of Ecology & Evolutionary Biology, University of California, Los Angeles, Los Angeles, CA 90024, USA.
Email: peter.nonacs@gmail.com

Abstract

Eusocial Hymenoptera are often characterized by having facultatively or obligately sterile worker castes. However, findings across an increasing number of species are that some workers are non-natal—they have 'drifted' away from where they were born and raised. Moreover, drifters are often indistinguishable from natal workers in the work and benefits provided to joined groups. This seems an evolutionary paradox of providing benefits to potentially unrelated individuals over close kin. Rather than being mistakes, drifting is proposed to be adaptive if joiners either gain inclusive fitness by preferentially moving to other kin groups or through generalized reciprocity in which exchanging workers across groups raises group-level genetic diversity and creates social heterosis. It is unclear, however, if reciprocity is unlikely because of a susceptibility to cheating. In resolving this question, a series of evolutionary simulations show: (1) Reciprocity can persist under a range of genetic assumptions and scenarios of cheating, (2) cheating almost always evolves, but can be expressed in a variety of ways that are not always predictable, (3) the inclusive fitness hypothesis is equally or more susceptible to cheating. Moreover, existing data in Hymenoptera (although not extensive) are more consistent with generalized reciprocity. This supports a hypothesis that drifting, as a phenomenon, may more often reflect maximization of group and parental fitness rather than fitness gains for the individual drifters.

KEYWORDS
drifting, Hymenoptera, inclusive fitness, reciprocity, simulation model, social heterosis

1 | INTRODUCTION

Cooperation between individuals is common across many species and taxonomic groups. As Darwin (1859) noted, the presence of cooperation creates an evolutionary conundrum when the cooperator does so at the cost of reducing their own reproductive output. Hamilton (1963) first provided an explicit solution—the loss of direct reproduction can be adaptive if that behaviour sufficiently benefits the reproduction of genetic kin. Hence, an individual's overall evolutionary fitness is inclusive of both its own reproduction and that gained by relatives due to being helped. Such kin-selected benefits may be strongly present in the evolution of eusociality in the Hymenoptera, which often involves individuals sacrificing some or all of their own reproduction in order to increase the reproductive

success of relatives. Consequently, in the majority of eusocial Hymenopteran species, a functioning group (i.e. a nest or colony) consists of one or multiple queens and their helpful daughter 'workers'. As an ideal, all the workers should be daughters of the queens. However, a growing list of species finds groups with individuals that are distantly or unrelated to any of the other group members, but in behaviour present no obvious difference from natal workers (Nonacs, 2017). Such individuals are known as 'drifters' and their existence seems to occur despite two apparent evolutionary costs: (1) Helping potentially competing genotypes reproduce; and (2) having closely related genetic kin lose that help.

Avoiding these two costs may be why most social insect species show varying degrees of nestmate recognition and nepotism (Wilson, 1971). Selectively across individuals, a recognition mechanism can make two kinds of errors: mistaking unrelated individuals as related or ejecting kin from the group as if unrelated (Reeve, 1989). Because minimizing one kind of error likely increases the occurrence of the other, nestmate and kin recognition may never be perfect. Thus, one explanation for drifters is they represent unavoidable errors built into any system of nestmate recognition. This 'mistake' hypothesis would predict that drifting should always be rare—which does not seem to be the general case (Nonacs, 2017). Drifting is a common phenomenon across a diversity of species and can reach high levels (e.g. 56% of females in *Polistes canadensis* move between nests; Sumner et al., 2007). This seems incompatible with drifting being a rare mistake and instead suggests there may be an adaptive and selectively advantageous basis. There are three such possible explanations.

First, drifters could be increasing their direct fitness. For example, direct gains could result from drifters entering groups to reproduce rather than to work, as in a clonal lineage of Cape honey bees. Drifting bees appear morphologically as workers, but lay their own eggs in invaded hives rather than work (Oldroyd, 2002). Nevertheless, most observations across multiple species find that drifters appear to behave no differently than natal workers (Sumner et al., 2007; Nonacs, 2017; Vickruck & Richards, 2021). Helpful drifters could still, through the death of higher ranked females, ascend to queen status (Leadbeater et al., 2011). The probability of rising through the ranks to become the queen, however, also appears often too low to reward joining nests of distantly or unrelated individuals (Nonacs et al., 2006). Hence, at best, direct fitness gains likely can account for only a fraction of the observations in nature.

Nonacs (2017) proposed a second possibility based on drifters increasing a group's genetic diversity and thus creating social heterosis that increases group-level survival or productivity (Nonacs & Kapheim, 2007). There is considerable evidence that genetic diversity can benefit groups in a variety of ways, such as resisting or decreasing disease transmission; improving homeostatic regulation; or diversifying task allocation and foraging strategies (Modlmeier et al., 2012; Nonacs & Kapheim, 2007; Oldroyd & Fewell, 2007). Therefore conceptually, drifting may operate as a cooperative network. Groups contribute some of their offspring to a shared pool of drifters, while simultaneously drawing their replacements from the same pool.

Across the various categories of cooperation, such a network of exchanging workers may be best described as generalized reciprocity (Pfeiffer et al., 2005; Taborsky et al., 2016; van Doorn & Taborsky, 2012). This is where: 'Individuals decide to cooperate or not just dependent on whether they have been helped or not, irrespective of who has helped and who is there to be helped'. (van Doorn & Taborsky, 2012, p. 652). Generalized reciprocity networks are usually considered with regard to learning and facultative rules that allow the cooperation to persist (e.g. Barta et al., 2011). For example, a simple behavioural rule such as, 'help, if have received help'. In the context of a drifter network, this could be produce drifters, if having accepted drifters.

Generalized reciprocity could also increase individual-level fitness through drifting. From the queen's perspective, anything that increases her group's survival and reproductive output will also increase her direct fitness. If 'trading' workers does so, then it is to her advantage to have it happen—even, and perhaps especially, if the new workers are unrelated and contribute most to increasing group-level genetic diversity. In contrast, if an individual adds any positive benefit from working on its natal nest, it would likely suffer a decrease in their inclusive fitness by drifting into a group with unrelated individuals. Thus, the existence of drifting in a population could be an example of parent–offspring genetic conflict that parents are winning. Indeed, Nonacs (2017) proposed there may be no upper limit to how many offspring can drift, suggesting that populations can evolve to become equivalent to 'supercolonies' (Moffett, 2012), with little to no intraspecific aggression and all individuals freely mixing across all groups.

In a third possibility, Kennedy et al. (2021) recently modelled that drifting could be reconciled with sufficiently benefitting the drifter, if two conditions held. (1) Per capita gains in group productivity decline with group size (Nonacs, 1991), leading to equal amounts of work by an individual adding more to production in smaller groups than in larger ones. (2) Drifters preferentially join non-natal nests that are both smaller and have genetic relatives reproducing. Taken together, it is therefore possible for a drifter to gain more in indirect fitness by helping another smaller kin group than by remaining and helping its natal group. Using life-history parameters from an extant wasp population, Kennedy et al. (2021) showed such fitness gains are possible through drifting to smaller kin groups.

Although drifting could involve gains both through reciprocity and aiding kin, Kennedy et al. (2021) also argued that the former is likely to be unimportant. Should a cooperative drifter pool exist, it would be susceptible to a Tragedy of the Commons. Groups could cheat by drawing from the pool, while contributing no individuals from their group. This conclusion differed from previous modelling results where reciprocity networks are affected by cheating, but persist (Nonacs, 2017). Nonacs assumed (following Reeve 1989) kin recognition to be a general trait and ability; such that an individual's ability to differentiate between natal and non-natal nests is

the same as its ability to differentiate between a natal worker and a non-natal drifter (i.e. a single linked trait). Kennedy et al. (2021) confirmed these results, but found that if the traits are modelled as unlinked, reciprocity networks collapse. What evolves in place of reciprocity are individuals that never mistake a non-natal group for their natal one (i.e. they do not drift), and are willing to allow any non-groupmate to join them (see Kennedy et al. Figure 1e, p. 469). Beyond the linkage assumptions, however, the two models also had a number of other methodological difference that could have affected the predicted outcomes (Table 1).

The goal here is to resolve the differences between the two models and to more fully examine evolutionary hypotheses for drifting behaviour, by addressing four questions:

1. Kennedy et al. (2021) modelled drifting as a dyadic interaction between a cheater that accepts, but does not produce drifters, and a non-cheater that both accepts and produces. Would similar outcomes arise in an evolutionary simulation model with a larger number of interacting groups?

2. Can generalized reciprocity networks with unlinked traits persist when other forms of cheating can evolve (e.g. group strategic, individual strategic or spiteful: see Table 1)?

3. How do linked propensities to drift and accept drifters affect outcomes relative to (2)?

4. Is drifting to help kin in non-natal groups also susceptible to collapse when cheating can evolve as group strategic, individual strategic or spiteful behaviour?

2 | METHODS: EVOLUTIONARY SIMULATION MODELS

The simulated population consists of a constant population of 144 groups, each one headed by a single haplodiploid, monandrous 'queen'. The effects of multiple fathers are examined in Nonacs (2017). The queen is the mother of all offspring produced by the group (the father is one male mated to the queen). Each diploid individual has up to five loci that can evolve. Three loci determine drifting outcomes.
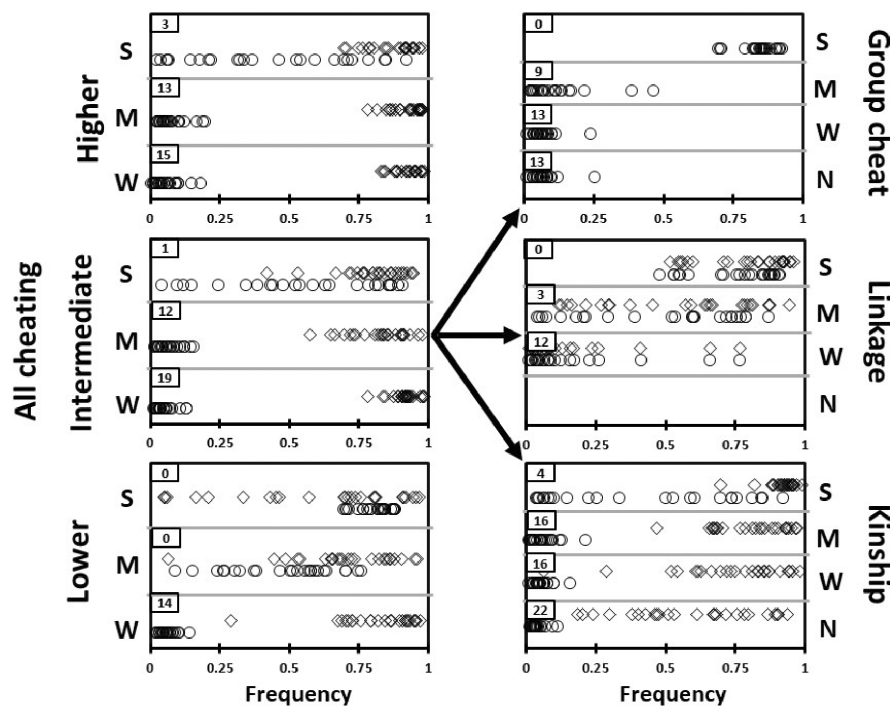

FIGURE 1 Individual simulation replicate means (*n* = 25) for the frequency of drifters in groups (circles) and the probability that groups would accept a drifter (diamonds), for each set of conditions. Note that allele frequencies for drifting and accepting are, respectively, almost identical to the frequency of drifters and the propensity to accept. Therefore, they are not displayed. The left column of panels displays nine results where all types of cheating could evolve (group- and individual-level strategic and spiteful). Colony productivity as a function of effective group size is either lower, intermediate or higher (Figure S1). Social heterosis could be weak (W), moderate (M) or strong (S). The right column of panels displays the effects of alternative assumptions about drifting, for the single condition of the intermediate group-size productivity function (i.e. for comparison to the middle left panel). In the top right panel, only group strategic cheating is possible and group behaviour is fixed to accept all drifters. This condition is also simulated under a condition where no (N) social heterosis is possible. In the middle right panel, the propensity to drift and to accept drifters is a single, linked trait. The bottom right panel assumes that drifters will only join groups where they have at least one allele in common (i.e. kinship) with the reproducing parents. Social heterosis ranges from none to strong. Under a 'baseline' condition of only group strategic cheating, no social heterosis and intermediate group productivity, the median outcome of the 25 replicates is 5.9% of group members are drifters (top right panel, N condition). The numbers shown with this and all the other conditions give the number of replicates where drifters are equal to or less than 5.9% of the group.

TABLE 1 Drifting favoured by generalized reciprocity as evaluated by previous studies and the current one.

Feature	Nonacs (2017)	Kennedy et al. (2021)	This study
Types of cheaters possible	1. Group strategic: Groups produce fewer drifters, while also being more accepting 2. Individual strategic: Drifters work less in non-natal groups than in the natal group 3. Spiteful: drifters sabotage non-natal groups and reduce their productivity	A variant of group strategic to find the optimal combination of propensities to drift and accept; individual strategic or spiteful not explicitly varied	All three are possible
Population	400 interacting groups, held constant	Dyadic interaction between two groups	144 interacting groups, held constant
Genotypes	Discrete values assigned that do not evolve	Genotypes evolve to optimal values	Genotypes evolve to stable values
Group size	Held in a small range across time	Not explicitly varied	Can grow from an initial size of 5–1000
Group productivity	Antagonistic functions of diversity and kin nepotism	Relative comparison of group size increase across dyad	Positive functions of diversity and group size effects for productivity and survival
Social structure	Monandry and polyandry	Monandry values	Monandry only

The first is a propensity to drift; ranging from 0 (*always remain in the natal group*) to 1 (*always try to drift*). Intermediate values may or may not drift (e.g. with a value of 0.5, an offspring is equally likely to drift or not). The second locus determines acceptance of drifters, with a range of values from zero to one. Acceptance is a group-level variable determined as the mean value of all the acceptance alleles across all natal workers present in the group. Larger values make it more likely a non-natal individual is allowed to join the group. Depending on the simulation, drifting and accepting are separate loci that can differ in value, or are linked such that both will be the same value. The third locus determines the helping effort a drifter provides in a non-natal group, ranging from −1 to 1. With a value of one, the drifter is as helpful in a non-natal group as it would be in its natal group (which always equals one). With a positive value, but less than one, the drifter exhibits 'individual strategic' behaviour and works less hard or efficiently in a non-natal group than it would at home. With allele values of <0, the drifter exhibits 'spiteful' behaviour that actually sabotages a non-natal group and reduces its productivity.

The fourth locus determines how genetic diversity enhances group productivity (social heterosis: Nonacs & Kapheim, 2007). There are 12 possible 'diversity' alleles in the population as a whole. However, if a group does not accept any drifters, its maximum possible genetic diversity would be three alleles: two from the diploid queen and one more from her haploid mate. This locus is meant as a proxy representing an individual's entire genome. Social heterosis is likely the result of diversity at multiple loci affected multiple phenotypic traits (Nonacs & Kapheim, 2007, 2008). Hence, the diversity locus in this model is not defined relative to any one specific trait or effect. It is just a measure for diversity, per se.

The final locus is neutral without any social heterosis. At the beginning of a simulation run, the alleles at this locus are set to be identical to those at the diversity locus. The purpose of this neutral locus is to be able to determine the degree to which social heterosis counters allele loss through random genetic drift.

The simulation proceeds through alternating bouts of growth (all groups produce individuals that either drift or remain as natal group workers), followed by a bout of reproduction (all produced offspring are either future queens or their mates). Drifters randomly encounter up to three other groups in the population they could join. They join if the group accepts them. If they fail to be accepted across the three encounters, they 'die' (i.e. are removed from the simulation). Note that a randomly mixing population without any internal spatial structure appears to be the least favourable arrangement for promoting reciprocity (Taborsky et al., 2021).

Overall group productivity is the sum of two functions reflecting effective group size and group-level social heterosis effects (see Supplement for mathematical relationships and details). Productivity is a positive but asymptoting function of effective group size. A scaling constant creates lower, intermediate or higher productivity levels due to effective group size. Effective group size is the sum of all workers' mean helpfulness allele value. The maximum value for effective group size is equal to the number of individuals (n), if all workers are equally beneficial. Admitting cheating drifters, however, produces a value of less than n and a group that has admitted many spiteful drifters could possibly have a less than zero value for this term. The social heterosis contribution to productivity is determined by a modified Shannon Diversity Index calculated from the frequencies of each of the diversity alleles. A scaling constant creates levels of social heterosis that are absent, weak, moderate or strong.

After the reproductive bout, each extant group has a 10–20% chance of dying, depending on its size (see Supplement for how probabilities decline with group size). Any group that has reached the maximum size (1000) is also eliminated from the population. All the removed groups are replaced to maintain a population of 144 groups. Replacement queens and their mates are randomly drawn from the reproductive pool. These new groups are also given a first cohort of five workers, all of which are offspring of the queen. The

genomes of the new queens and their mates can have mutated values (see Supplement for details).

All simulations run for 7500 cycles of growth and reproduction, under the following four variations (each variation is replicated 25 times):

1. At the beginning of each simulation run, drifting is at a low level with all alleles set equal to 0.1 (i.e. each offspring produced has a 10% chance to drift). All helping in non-natal groups alleles are set to a value of one, and never mutate. With drifters always behaving helpfully in non-natal groups, there is no reason to not accept them. Therefore, all acceptance alleles are also set to a value of one and do not mutate. Hence, the only way cheating can evolve is to not produce drifters. Social heterosis can be completely absent (i.e. no positive effect of increased genetic diversity), weak, moderate or strong. All 12 of the diversity alleles are distributed in equal numbers when the simulation run begins. Therefore, this simulation variant tests if the Kennedy et al. (2021) conclusions about the effects of group-level cheating hold in a larger evolving population.

2. Same as (1), but social heterosis is either weak, moderate or strong and acceptance alleles can evolve between 0 and 1, and helping alleles can evolve within a range from −1 to 1. At the beginning of a simulation run, all individuals are maximally accepting and helpful (allele values equal one). All loci are unlinked and can evolve independently. Therefore, this simulation variant tests if reciprocity can evolve and persist in the presence of multiple possible ways for cheating to occur (Table 1).

3. Same as (2), but drifting and accepting are a single, linked trait (as in Nonacs, 2017).

4. Same as (2), but drifters only are willing to join groups that contain 'kin' (i.e. at least one of the encountered group's queen or mate alleles is identical to at least one allele at the drifter's otherwise neutral locus). This variant is also simulated under a condition where no social heterosis is present.

At the conclusion of each simulation, one more cycle of worker production is replicated 10 times and the decisions and their outcomes recorded.

3 | RESULTS

3.1 | Reciprocity can persist with strong social heterosis in the presence of group-level cheating

When only group strategic cheating (Table 1) is possible and with no or weak social heterosis present, drifting is virtually absent (Figure 1, top right panel; Figure S2). Across the 25 replicated simulations, the median outcome with no social heterosis had 5.9% of its group's membership being drifters at the end of 7500 generations. The low levels that remain are likely due to rare 'mutants' the simulation introduces into the population, combined with weak selection

favouring no drifting over minimal drifting. Overall, the results from this one simulation (no social heterosis and only group strategic cheating) can be considered as the 'baseline' for comparison. Given that in this iteration, groups never pay any cost for admitting drifters, these results are consistent with Kennedy et al.'s (2021) findings—the presence of groups that accept but do not produce drifters causes mutually beneficial reciprocity networks to collapse.

As social heterosis increases to having moderate or strong effects on group productivity, however, drifting becomes more advantageous to the point that most of the group is composed of non-natal immigrants (Figure 1, top right panel; Figure S2). Most or all replications end with more that 5.9% of groups being drifters. This is consistent with Nonacs's (2017) finding that reciprocity can persist in the presence of cheaters, if group-level benefits from social heterosis are high enough.

At all levels of social heterosis, more than 50% of the moves to a non-natal group produced a per capita increase in group productivity relative to staying as a worker in the natal group (Figure 2, top panel). Although in the model all moves are random, a bias towards gains in productivity results from larger groups producing relatively more drifters, who by chance would encounter smaller groups where their work produces the greater gains, independent of whether or not they create more social heterosis.

3.2 | Reciprocity can persist with strong social heterosis in the presence of individual- and group-level cheating and spiteful cheating

When individual drifters can evolve to represent cheating strategies that either work less efficiently in, or sabotage non-natal groups, reciprocity network persistence continues to occur under conditions with strong social heterosis or with moderate levels if increasing group size by itself produces relatively low gains in productivity (Figure 1, left column). When comparing with a moderate group productivity function, the additional possibilities for how cheating can be expressed reduce the prevalence of reciprocity (i.e. compare left middle panel to top right one). Overall, the results suggest that a lowered level of reciprocity can be maintained, even with an added cost that cheaters that negatively affect productivity might also be accepted into groups.

The majority of moves by drifters are towards smaller groups (Figure 3, top panel), but with weak social heterosis only a minority of these moves result in producing higher per capita productivity. Across all levels of social heterosis, a percentage of moves actually reduces the productivity of the joined group, likely because of accepting sabotaging drifters. This follows from groups producing a variety of drifters, ranging from being helpful in non-natal groups to actively sabotaging such groups. Interestingly, under all model conditions, there was tremendous variation in behaviour when in a non-natal group, ranging from most drifters being very helpful to most actively sabotage the joined group (Figure 4). Across all the model variations, there are no significant correlations between helping
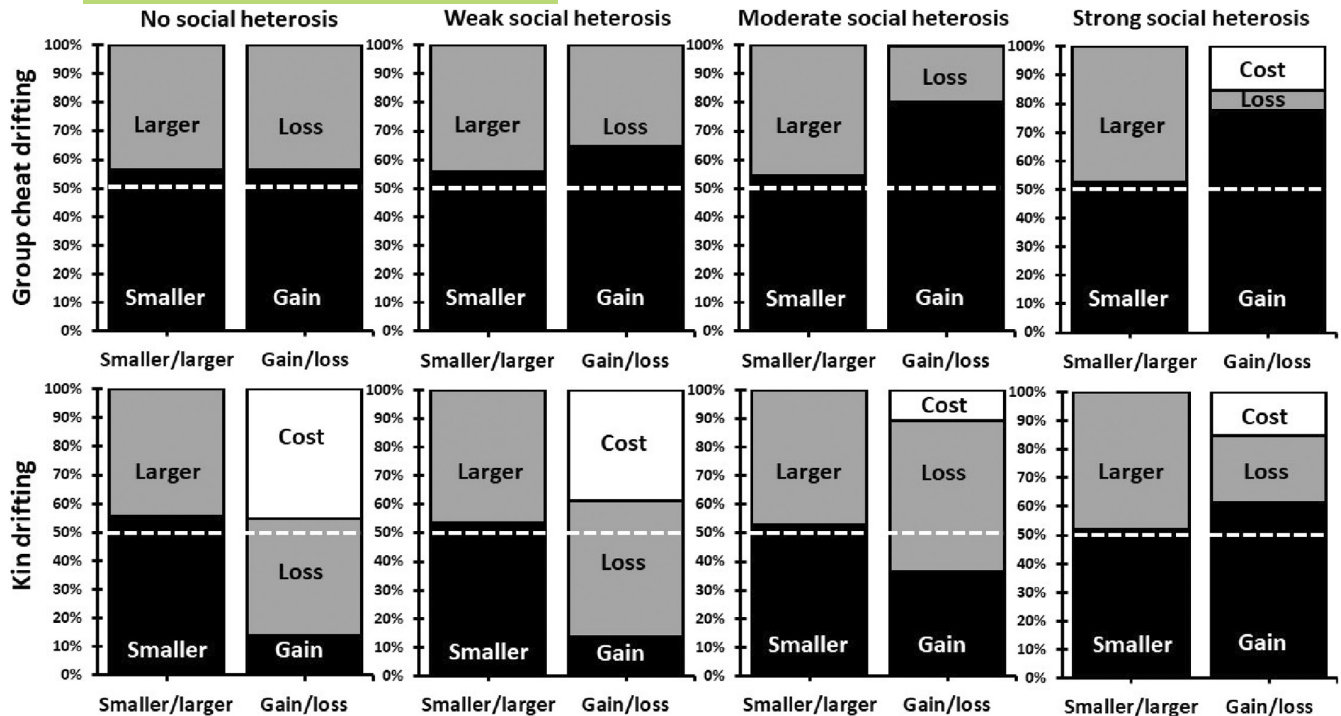
FIGURE 2 Frequencies of joining smaller or larger groups, and whether the move was fitness enhancing. The first column shows the frequency of moves that joined either smaller groups than the natal one, or groups equal or larger in size. The second column shows where moves result in more production (i.e. a gain) than if the drifter had stayed in the natal group, increased production but not as much as staying would have (i.e. a loss) or actually decreased productivity in the joined groups (i.e. imposed a cost on the joined group). The top panel is for the variant where only group strategic cheating is possible. The bottom panel is where drifters only join kin groups.

allele values and drifting allele values. Selection on the propensity to drift is the main determinate of frequency of drifters in nests, and the level of helpfulness (or not) expressed by those individuals is almost immaterial. The genetic diversity effects that any drifter provides may suffice to offset negativity in helpfulness.

3.3 | Propensities to drift and accept drifters as one general trait increases the persistence of reciprocity

The main effect of these two traits being linked is that more individuals drift, especially with moderate levels of social heterosis (Figure 1). Drifting with linked traits is more likely to gain in productivity with weak social heterosis then if they are unlinked, but the relationship reverses as social heterosis becomes stronger (Figure 3). As above, the propensity to drift (now identical to the propensity of accepting) determines the proportion of drifters in groups, while helping allele values vary widely (Figure 4, Figures S3–S5).

3.4 | Drifting in search of kin groups is also susceptible to cheaters

When drifters are only willing to join groups that have alleles in common (i.e. are kin), drifting becomes common only with strong social

heterosis (Figure 1 bottom right panel). Spiteful cheating evolves even when drifters are only willing to join kin groups (Figures 3 and 4). Such spiteful drifting implies that reducing the productivity of less related individuals will feedback to help the more related individuals in the natal group dominate a shared offspring pool. Also, in the kin simulations, the willingness of nests to accept drifters tends to be lower than under the other sets of conditions when social heterosis is weak (i.e. Figure 1: compare left middle panel to bottom right one). This may be the effect of spiteful drifters being present in the population.

3.5 | Results across all model variations

From the same starting conditions, multiple combinations of drifting, accepting and helping behaviour can evolve. Conditions that generally favour the persistence of reciprocity in the presence of cheaters do not converge on a single and predictable frequency of drifters within groups. Also, the helping locus exhibits the complete range of values in all conditions; from equally helpful in non-natal groups, to maximally spiteful (Figures S3–S5). Values never converge on a single level of helpfulness. This suggests that two populations that have the same functional relations for group size productivity and social heterosis effects could evolve very different levels of drifting, with drifters markedly differing in their behaviour within non-natal groups.
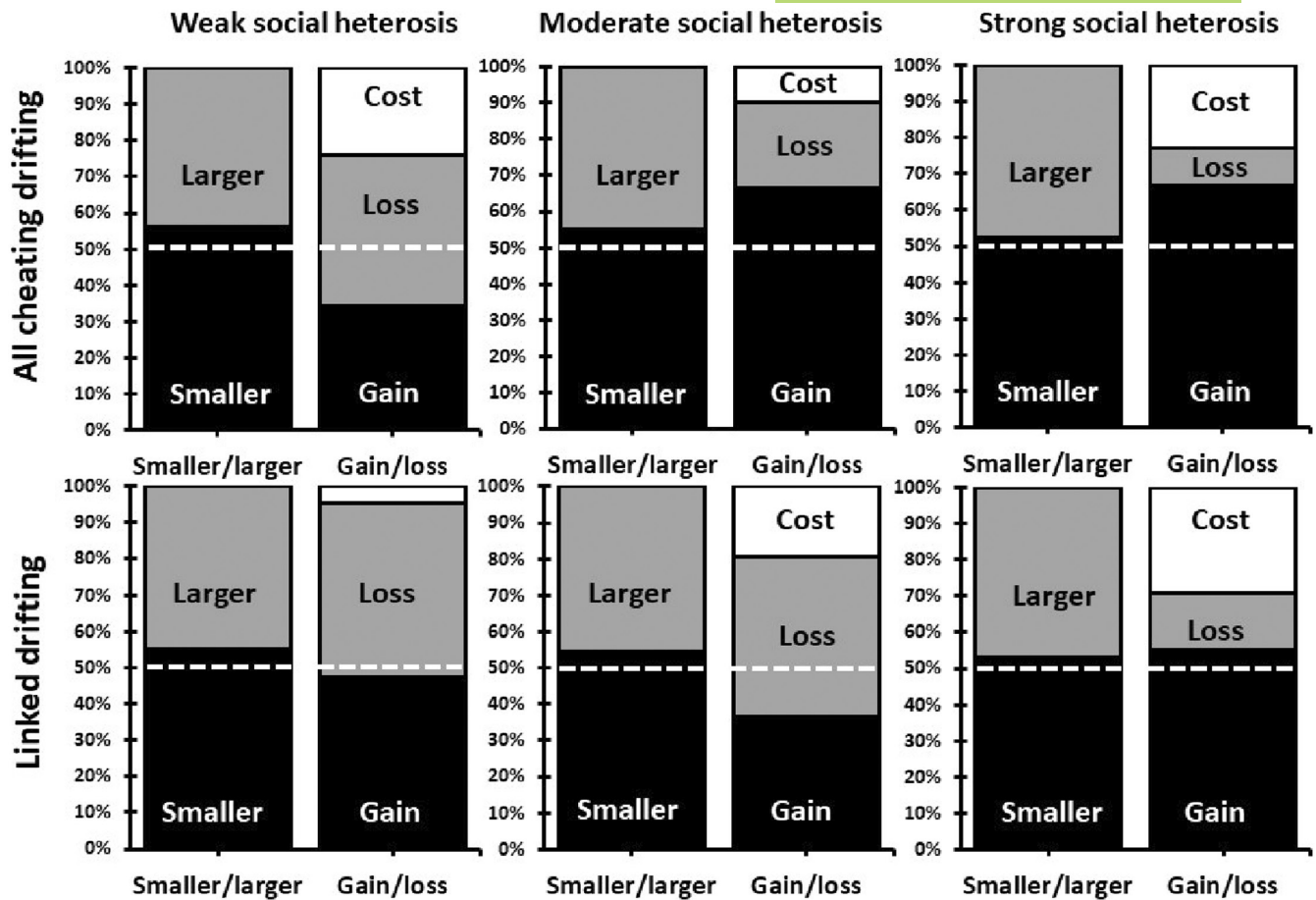
FIGURE 3 Description is the same as for Figure 2. The top panel is for the variant where all three cheating strategies are possible. The bottom panel is where drifting and accepting is also one, linked trait.
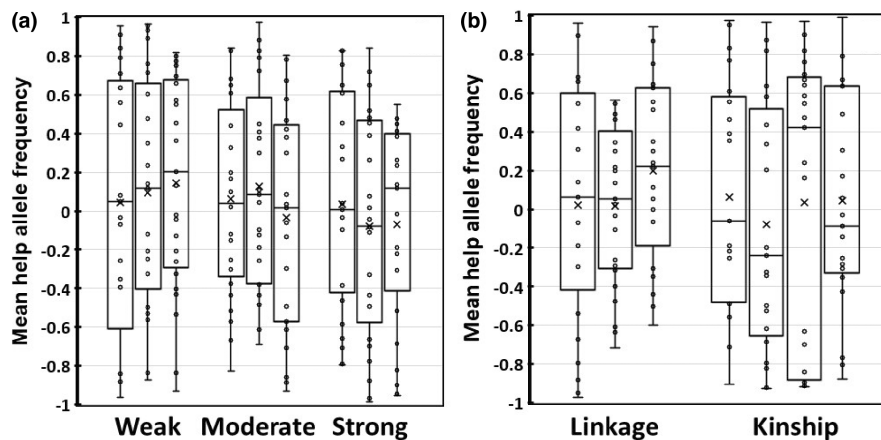

FIGURE 4 Mean allele frequencies for helping behaviour across simulation replicates (*N*=25). Horizontal lines show the median value, with X being the distribution mean. (a) Nine variations where all types of cheating can evolve. Each set of three represents a level of group productivity from lower to higher. Within each set, social heterosis varies, left to right, from weak to strong. (b) The left set shows values where drifting and accepting are a single, linked trait. The right set shows values where drifters will only join related groups. For all, group productivity is intermediate and social heterosis varies from either weak (left set) or absent (right set) to strong.

One consistent result is that conditions where drifting evolves also have more diversity at the social heterosis locus than at neutral locus where genetic drift reduces diversity (Figures S6–S9). This implicates social heterosis as a contributing factor for persistence of reciprocity.

4 | DISCUSSION

Across species in the social Hymenoptera, a colony may contain multiple hard-working, but functionally sterile, individuals that were born

and initially raised elsewhere (Nonacs, 2017; Sumner et al., 2007). On the face of it, leaving one's natal group to join and help another seems maladaptive for the drifting worker. Nevertheless, Nonacs (2017) in a simulation model found that drifting behaviour could be adaptive and is best described as a form of generalized reciprocity (Taborsky et al., 2016, 2021; van Doorn & Taborsky, 2012). Figuratively, offspring are commodities that can be exchanged in order to increase group-level genetic diversity that leads to greater productivity (i.e. social heterosis). Proposing that drifting operates as a case of generalized reciprocity differs from previous considerations, in that drifting decisions are not facultative and do not evolve in response to experience (e.g. Hamilton & Taborsky, 2005). Instead, but analogously in this case, genotypes determine behavioural propensities and it is allele frequencies that evolve in response to outcomes.

Alternatively, Kennedy et al. (2021) propose that drifters can increase their inclusive fitness by joining genetic kin in smaller groups, where a worker's help would have a relatively larger effect. They further argue that reciprocity is unlikely and will collapse due to cheating as long as becoming or accepting drifters are two independently evolving traits. Kennedy et al. (2021) framed their model as an interaction between an altruist (that both produces and accepts drifters) and a cheater (that accepts drifters, but retains its own offspring). It is no surprise that cheater genotypes produce the larger and more productive groups—and eventually drive altruism from the population. The same outcome is found here with many interacting groups, if within-group genetic diversity has no or relatively small benefits. Increasingly stronger effects of social heterosis, however, can create situations where both drifter producing altruism and cheating coexist (Figure 1 top right panel; Figure S2). Expanding the evolutionary simulations to consider the entire range of potential cheating tactics (Table 1) requires relatively stronger social heterosis for drifting to persist. Nonetheless, the overall results contradict a conclusion that reciprocity is always unstable if drifting and accepting drifters are two separate traits.

Furthermore, drifters are relatively more common in populations when drifting and accepting are one, general expression of kin recognition (Figure 1; compare middle panels). One point in favour of drifting and accepting being linked is that in nature potential drifters are more often observed being rejected than being admitted (Reeve, 1989; Wilson, 1971). In the simulations here, linking of traits has the most negative effect on drifter acceptance. Thus, while it may be unrealistic to assume that the two traits have exactly identical propensities, it may be equally unrealistic to assume that no correlation exists between them. It is unknown in nature if the rate at which individuals try to move between groups correlates with acceptance rate.

Interestingly, Kennedy et al. (2021) did not test whether their model of drifting for inclusive fitness benefits was similarly susceptible to cheating. The results here suggest that it may be more susceptible to cheating (Figure 1, bottom right panel). Many moves produce less in fitness gain than remaining in the natal group, or reduce the productivity of the joined kin group (Figure 2). Only an additional benefit gained through strong social heterosis makes drifting to kin

have a fitness-enhancing payoff more than 50% of the time. Thus, it appears the same argument that questions the possibility of reciprocity between unrelated groups also applies to drifting for inclusive fitness gains. As a thought problem, consider two interacting cousin kin groups, one an altruist and the other a cheater. Which cousin's genotype would dominate reproduction?

The results here are consistent in one other aspect with Nonacs' (2017) findings. Even when evolutionary simulations have the exact same starting conditions, they rarely converge to one set of values for drifting, accepting, helping or in the frequencies of non-natal groupmates Figure 1). Such results suggest that drifting may be quite variable and stochastic across species or different populations despite the underlying environmental conditions being relatively similar.

In every set of conditions where cheating could evolve, it did. Furthermore, every possible type of cheating would be present: Groups produced fewer drifters (group strategic, through the drift locus); drifters worked less efficiently in non-natal groups (individual strategic, through the help locus); and some drifters negatively affected productivity (spiteful, again through the help locus). However, the prevalence of each type of cheating also varied greatly across all replicates in each condition (Figure 4, Figures S3–S5). This suggests that the presence of any type of cheating is what affects the networks of cooperation, rather than one type specifically having a larger effect than the others.

Finally, the models here all assume random search that results in joining any group willing to accept a drifter. This results in an abundance of 'poor' drifter decisions where they would have gained more by not drifting (Figures 2 and 3; although the average decision in a number of situations had a positive payoff). Obviously, drifting could be more fitness enhancing if specific other groups were preferentially targeted (Garcia-Ruiz et al. 2022)—especially if the smallest groups were sought out, or those with closest kinship. For instance, Lengronne et al. (2021) observed in *P. canadensis* that most wasps drift locally, where the neighbouring groups are most likely to be kin. Also, on average, wasps join smaller groups. However, any discriminating search based on size or kinship would also likely quickly lose its advantages. Consider if drifters search out smaller groups and join them. This would make small groups rare (i.e. small groups attracting joiners would soon no longer be small). Once the population has little variation in the desired characteristic, then the only possible benefit remaining for drifting would be generalized reciprocity and the continued exchange of genetic variation.

The various points raised above also illustrate an important caveat. Generalized reciprocity is plausible, and not impossible or improbable as claimed. Yet, it is also likely that different assumptions about the magnitude of social heterosis, group size productivity relationships, group survival or searching strategies could predict greater reciprocity networks or their complete absence. Similarly, inclusive fitness gains are possible and plausible, but how often do they occur? To date, drifting has not been extensively enough studied across the eusocial Hymenoptera to definitively support or refute either hypothesis. However, some inferences are possible.

The most detailed study of drifting under natural conditions is the multiyear observations of *P. canadensis* (Lengronne et al., 2021; Sumner et al., 2007), and these populations provide the parameters in Kennedy et al.'s (2021) inclusive fitness model. Nevertheless, the patterns of *P. canadensis* behaviour fit more predictions that are consistent with generalized reciprocity (Table 2). Other studies have measured the consequences of drifting in more limited contexts. For example, in another wasp species (*Polistes dominula*), groups larger than about eight females gain little from adding another adult (Grinsted & Field, 2018), and while being on a multifoundress nest likely has higher fitness than attempting to nest alone, switching between nests does not consistently increase fitness (Grinsted & Field, 2017). This suggests *P. dominula* often find themselves with options across

TABLE 2 Observed behaviour in populations of *Polistes canadensis*, across multiyear studies.

Observations consistent with maximization of indirect inclusive fitness
Non-natal nests visited by drifters, on average, contain genetic kin (mean $r = 0.12$–0.19 acrossLengronne et al., 2021; Sumner et al., 2007)
Drifters move more often (but not exclusively) from larger to smaller nests where their working is likely to produce greater per capita benefit (Lengronne et al., 2021)
No evidence that drifters are selfish and laying eggs in non-natal nests or otherwise cheating by not working (Sumner et al., 2007)
Observations more consistent with benefits gained through generalized reciprocity
Drifting is extremely common, with estimates that over 90% of the nests might have either received drifters, produced them or both (Sumner et al., 2007; Lengronne et al., 2021)
Drifters do move to unrelated nests and this is not exceedingly rare. Although drifting within a local group of nests is the most common occurrence, likely unrelated wasps from far away groups do disperse into local populations (Lengronne et al., 2021)
Size of a nest is not significantly predictive as to whether or not it accepts drifters (Lengronne et al., 2021)
Manipulations of nest size and worker to brood ratios either have small or no significant effects on the remaining workers drifting patterns (Lengronne et al., 2021)
Individual nests are highly variable in relatedness (± 2SD around the mean: 0.39–0.59; Sumner et al., 2007)
Mean nest sizes are large (19.6 workers; Lengronne et al., 2021), which means that the per capita added direct productivity from the work that a drifter provides is likely to be quite small (Nonacs, 1991)
Across the studies, ratios of natal to joined nest brood relatedness values vary from $0.59/0.19 = 2.95$ to $0.56/0.17 = 3.29$. Thus, a drifter needs to create approximately $3\times$ more productivity in a non-natal nest to have greater fitness. This seems unlikely, and Sumner et al. (2007) concluded that indirect fitness gains alone could not explain the high rate of drifting
Sumner et al. (2007) found that drifting does not diminish with age. Therefore, the natural populations seem closer to approximating supercolonies (Moffett, 2012), where individuals freely traverse across nests with minimal aggression.

nests varying little in terms of inclusive fitness payoffs. Finally, drifting occurs in a number of *Apis* species (reviewed in Nonacs, 2017) and also in a stingless bee species (64% of followed workers drifted in *Melipona fasciculata*: Oliveira et al., 2021). As these nests are composed of hundreds to thousands of workers, it is unlikely that any worker switches groups based primarily on inclusive fitness considerations.

Although the current data with Hymenoptera are more favourable towards generalized reciprocity, more work is needed to better understand the phenomenon of drifting (see Taborsky et al. (2021), table 4.1 for multiple examples of reciprocity between unrelated individuals across a wide variety of taxa). Future studies can focus on testing several specific predictions. First, the two overarching questions of: Are genetically more diverse groups significantly more productive; and do drifters strongly prefer to join smaller kin groups where the productivity gains could maximize fitness? Kennedy et al. (2021) showed that in their *P. canadensis* population, this was possible, but did not report how often such moves occurred or how much was gained. Other more specific predictions would be: (1) If traits are linked, then there should be an across-group positive correlation between producing offspring that drift and the acceptance of non-natal individuals; (2) generalized reciprocity could evolve with random joining leading to no correlation between group size and the probability of accepting a drifter, while for inclusive fitness maximization should create a negative correlation with group size; and (3) for generalized reciprocity, many or most accepted drifters should be distantly or unrelated, while for inclusive fitness, they should be rare.

5 | CONCLUSION

In the present study, drifting evolves even if many joining decisions result in lower productivity gain than not drifting would have produced (Figures 2 and 3). Tellingly, spiteful drifting that reduces productivity of joined groups can also evolve. Sabotaging another group instead of remaining and gaining inclusive fitness by raising more kin is difficult to reconcile with that individual maximizing its own fitness. However, from the point of view of the drifter's parents in reproductive competition against other parents, a sabotage strategy that sacrifices some of their offspring appears to be advantageous. Similarly, from a parental perspective (and also that of the non-drifting siblings) 'trading' genetic kin workers for helpful unrelated ones is a fitness-increasing decision—if there is a net gain in group productivity. Consequently, the outcomes generated here make sense only when considered as a group level effect that is equivalent to maximizing parental fitness. Drifters are the individuals that make the behavioural decisions, but the selective forces that created them reside and act through their parents. Thus, drifters are an extension of their parents' genomes, with their evolution through generalized reciprocity being definitely plausible. How often reciprocity might actually promote drifting in nature is a fascinating question that begs to be answered with more data.

AUTHOR CONTRIBUTIONS

Peter Nonacs is responsible for alL aspects of the paper.

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CONFLICT OF INTEREST STATEMENT

None.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

There are no data and the modeling results are presented in the paper. The annotated computer code is in the supplement.

ORCID

Peter Nonacs ⬥ https://orcid.org/0000-0003-3010-0777

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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