

Cooperation among unrelated individuals: the ant foundress case

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The vast majority of cooperating individuals are related to each other, as expected under kin selection¹. This makes those exceptional cases where cooperators are unrelated particularly interesting, because these groups should confer direct benefits, or a probability of direct benefits, on all their members, a condition which should have a great impact on the nature of their cooperation. Unrelated group members have been reported in kingfishers², manakins³, mongooses⁴, halictine bees⁵ and ant foundresses^{6,7}.

Here, we review the case of associations of unrelated ant queens during colony founding. Ant queens might begin nests with non-relatives because mass mating flights can make it impossible to locate relatives⁸. Where genetic relatedness has been measured directly, foundresses have been found to be unrelated (e.g. in *Messor pergandei*⁶, *Acromyrmex versicolor*⁶ and *Polyrhachis moesta*⁷). Even though they are unrelated, the foundresses must participate in costly tasks if they are to gain the cooperative benefits possible with grouping⁹, and these benefits must potentially apply to any one of the cofoundresses^{10,11}.

Ant foundress associations are an example of cooperation among non-kin. Across a dozen genera, queens able to found a colony alone often join unrelated queens, thereby enhancing worker production and colony survivorship. The benefits of joining other queens vary with group size and ecological conditions. However, after the first workers mature, the queens fight until only one survives. The presence of cofoundresses, and their relative fighting ability, also affects the extent of cooperative investment before worker emergence. This reveals previously overlooked early conflicts among queens, which reduce the mutualistic benefits of cooperation.

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Ant species with foundress associations share ecological characteristics rather than phylogenetic history. Cooperation occurs in three ant subfamilies, the Myrmicinae (e.g. *Solenopsis*, *Messor* and *Acromyrmex* spp.), the Dolichoderinae (*Azteca* and *Iridomyrmex* spp.) and the Formicinae (*Myrmecocystus*, *Lasius*, *Camponotus*, *Formica* and *Oecophylla* spp.)^{8,12}. Species with cooperative associations are territorial, and workers from mature colonies not only attack foragers but can completely destroy new nests (Table 1). Newly founded nests (Fig. 1a) also compete among themselves, with their first workers often stealing brood from neighboring nests (Fig. 1c). Colonies begun by more than one foundress produce more workers, and are more successful than solitary foundresses at defending themselves against other colonies (Table 2). This density-dependent competition among colonies might

even be the main force promoting foundress associations^{8,13}.

However, these associations are unstable because the advantage of having multiple foundresses ends with the emergence of adult workers^{14,15}. Queens in cooperative associations do not forage (the known exception is

Table 1. Natural variation in the number of queens per nest^a

Species	Group size ^b	Colonies with >1 queen	Effects of density or nest site characteristics	Evidence for choice of group size or choice of nestmate(s)	Refs
<i>Solenopsis invicta</i>	Range 1–17; mean 1.1–3.4 (7 mating flights) [†]	*48 ± 2.4% (n = 38–118 colonies)	Natural group size is associated with queen density. Mature colonies destroy new nests (F).	When queen density is experimentally manipulated, queens form larger groups in areas with high density. New nests are aggregated (F). No joiner–resident aggressive interactions observed (L).	19
<i>Myrmecocystus mimicus</i>	Range 1–9; mean 1.6–3.8* (3 surveys) ^{†††}	*20–89% (n = 88–165)	New nests aggregate away from mature colonies, which destroy new nests (F).	Repeated samples on the day of mating flight suggest that queens often join already dug nests. No joiner–resident aggressive interactions observed (F).	37
<i>Lasius niger</i>	Range 1–5; mean 1.3* (n not reported) ^{†††}	18% (n = 50)	Areas exposed to workers of mature colonies are avoided (L).	No significant preference for joining (n = 20) nor against heavier queens (n = 18; L).	15
<i>Lasius pallitarsis</i>	Not reported (3 sites; D = 5–7 km) ^{†††}	Not reported	Queens significantly aggregate when queen density is high (L).	Heavy queens prefer joining. Light queens are preferred by all, they are likely to leave when joined and more likely to join when fed (n = 58, L).	38
<i>Messor pergandei</i>	Range 1–6; mean 1.6* (1 site) ^{†††}	49% (n = 129)	New colonies aggregate close to mature colonies (F).	Six out of 128 marked foundresses moved to a different colony before eclosion of workers (F).	39
<i>Messor pergandei</i>	Range 1–28; mean 1.0–7.4 (19 sites; D = 4–45 km) [†]	*42–94% (n = 36–124)	Not reported.	In some sites there are only solitary queens (F). Queens, in particular from these sites, might behave aggressively towards joiners (L).	40
<i>Polyrhachis moesta</i>	Range 1–4; mean 1.8* (3 sites ; D>20 km) ^{††}	46% (n = 33)	Not reported.	Foundresses observed to reaggregate (K. Sasaki, pers. commun.; L).	7
<i>Acromyrmex versicolor</i>	Range 1–16; mean 2.5 (1 mating flight) ^{†††}	56% (n = 64)	New nests mostly under trees (F).	–	41

^aF, field study; L, laboratory study.

^bDeparture of group size distribution from random: †, $p < 0.05$; ††, $p \geq 0.05$; †††, not tested; *, estimated from histogram; D, distance between sites.

*A. versicolor*¹³). Instead, they seal themselves in a nest burrow to produce their first workers from their body reserves – fat, proteins, and glycogen obtained by digesting the wing muscles (Fig. 1b)¹⁶. These reserves are used to feed the developing workers, either by regurgitation or with trophic eggs (non-viable eggs produced specifically to feed the brood)^{16,17}. When workers emerge, they forage, which ends the stage when brood production is directly dependent on the body reserves of the queens. When this stage is reached, each queen no longer needs the others and can obtain an enormous fitness advantage if she can monopolize reproduction^{10,13}. At this point¹⁵, queens fight to the death in most species (Fig. 1d), whereas aggression is rarely observed before this time^{8,18}. Losers have zero fitness, thus when queens initially join the group they put their lives at risk, gambling that they will be the one to survive¹¹.

These ant foundress associations provide a simple system for investigating the ecological and behavioral factors that can promote cooperation in the absence of both relatedness and indirect fitness. In the past 16 years, the fire ant *Solenopsis invicta*^{9,18–27} has provided a particularly good model for the dynamics of cooperation and competition among unrelated foundresses.

Natural group sizes of ant foundress associations

Foundress groups form when the queens drop to the ground after their mating flight, but before completely sealing themselves away in a newly dug nest (Figs 1a and b). Group formation might occur by chance encounters, or by active searches for other queens or for already excavated nests.

In *S. invicta* and *Me. pergandei*, the natural distribution of group sizes has been shown to depart significantly from random (truncated Poisson distribution with no empty nests; Table 1), whereas in other species no significant departure was observed (possibly because of low statistical power). Nonrandom distribution of group sizes, in itself, does not demonstrate that group formation results from the queens' active choice, because it might also arise through spatial patchiness of suitable nest sites¹⁹. Spatial patchiness should be taken into account in field surveys. For instance, suitable nest sites are limited by temperature for *A. versicolor*, soil moisture for *Me. pergandei* and the occasional occurrence of floods for *S. invicta*^{8,13,19}. On the other hand, specific habitat requirements, resulting in nest clumping, can affect the intensity of competition among colonies and thus influence queen behavior during group formation.

A field experiment demonstrated that *S. invicta* queens form larger than expected groups under random encounters, in areas where higher densities of queens were released¹⁹. Larger groups form under high density, probably as an adaptive response to the expected intensity of competition. In areas of dense settlement, brood raiding (Fig. 1c) is more intense²², and larger groups have a greater probability of winning raids (Table 2). Clumping of queens and nests also occurs in *Myrmecocystus mimicus* (Table 2). Brood raiding and other pressures, for instance from mature colonies that destroy new nests, can act at the same time and influence optimal group size (Table 1). For instance, in *S. invicta* queen survival among group queens compared with solitary queens, was higher in two- but not in four-queen colonies when exposed to mature colonies²⁷ (Table 2), and in four- but not in two-queen colonies in experiments that simultaneously accounted for brood raiding and queen relocation (see next section)²². This suggests that optimal group size depends on several factors, and that groups might need to reach a certain minimum size before advantages accrue.

In *S. invicta*, queens cooperate in nest excavation and regularly return to the surface. Group size is only fixed after the nest entrance is closed¹⁹. In a field survey of *My. mimicus*, the average group size doubled between the end of the mating flight (mean = 1.6) and later the same day (mean = 2.9; Table 1), suggesting that, in this species, some queens join nests that are already being excavated. Before the entrances close, there might be conflict between residents and intruders because some group sizes provide greater benefits than others¹¹ (Table 2).

Benefits of cooperation: increased colony survival

The main benefit of cooperation – higher success at brood raiding after entrances are opened by foraging workers (Fig. 1c, Table 2) – is directly attributable to the presence of extra queens. This is because the queens draw on their limited body reserves to produce the workers¹⁶; multiple queens that contribute to egg-laying^{15,28} produce more workers^{13–15} and, in some cases, produce them

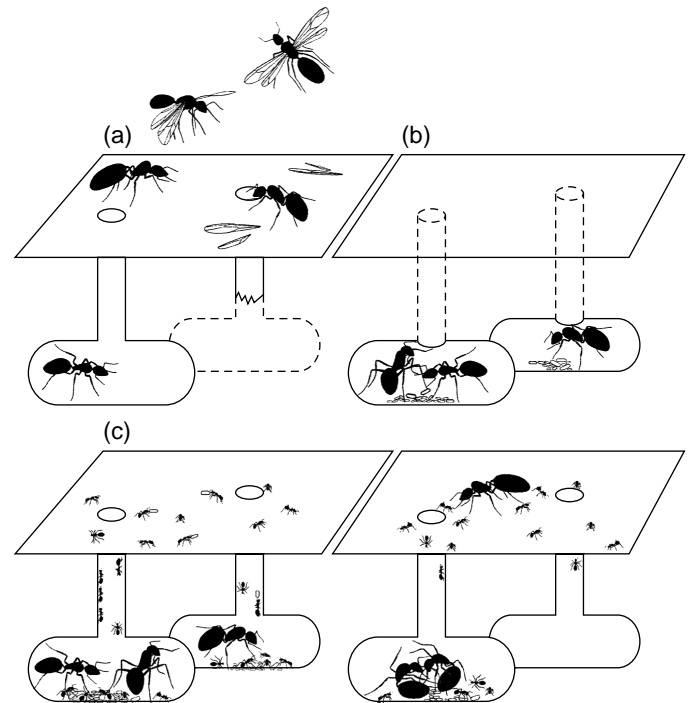


Fig. 1. Colony development and queen behavior during the founding stage. (a) Mating flight. After alighting, queens shed their wings, search for a nest site and dig a nest burrow alone or with other queens. (b) Claustral phase. Queens seal themselves in a burrow, lay eggs from their body reserves, and feed the larvae with trophic eggs and secretions. (c) Adult workers hatch. Workers open the nest and start foraging, providing energy from the outside. Brood raiding: workers of neighboring colonies steal brood mutually. (d) Queens fight until only one survives. Queens from raided nests might attempt usurpation of neighboring nests.

earlier^{14,15}. The number of first workers directly determines colony success at brood raiding, as shown in an experiment in which adding workers to one-queen colonies shortly before brood raiding increases their success²⁹.

Table 2. Evidence of cooperative benefits shared equally among group members^a

Species	Colony development	Colony survival and defense
<i>Solenopsis invicta</i>	Queens cooperate at nest excavation (F) ¹⁹ . Multiple-queen colonies produce more workers than solitary foundresses (L) ¹⁹ . Colonies founded by ten-queen associations produce sexuals 60% earlier than colonies started by one queen, in spite of no significant difference in colony size at maturity (L) ⁴³ .	Multiple-queen colonies are more successful at brood raiding. Increasing the number of workers enhances the probability of winning a raid (F) ^{22,42} . Three-queen colonies survive worker attacks better than lone queens (L). Two- but not four-queen colonies have higher per-queen survival up to worker emergence (F) ²⁷ . Usurping queens are less successful when entering a three-queen than a one-queen colony, independently of the number of workers present (L) ²⁶ .
<i>Myrmecocystus mimicus</i>	Queens cooperate at nest excavation (F) ³⁷ . Multiple-queen colonies produce more workers than solitary queens ³⁷ .	Multiple-queen colonies are more successful at brood raiding than solitary queens (L) ³⁷ .
<i>Lasius niger</i>	Two-queen colonies produce more workers in less time than solitary foundresses (L) ¹⁵ .	Two-queen colonies are more successful at brood raiding than solitary queens (L) ¹⁵ .
<i>Messor pergandei</i>	Queens all contribute to nest excavation (with queens differing in their contribution in some nests), to oviposition (no significant differences), and to egg tending (with significant differences among queens, L) ²⁸ .	Multiple-queen colonies are more successful at brood raiding than solitary queens (L) ¹⁴ . Increasing the number of workers enhances the probability of winning a raid (L ²⁹ , but see F ³⁹). Colonies started by multiple queens open nine days earlier than colonies started by solitary queens (L) ¹⁴ .
<i>Oecophylla smaragdina</i>	Multiple queens cooperate to build a nest when there are silk-producing larvae and they shelter the brood beforehand (F) ³⁰ .	–

^aF, field study; L, laboratory study.

Table 3. Evidence of early queen–queen conflict and competition^a

Species	Effect of social environment on individual investment	Unequal investment (mass loss or maternity share) of cofoundresses and occurrence of oophagy	Mortality or aggression before worker emergence
<i>Solenopsis invicta</i>	Optimum curve of colony productivity with group size (F) ²¹ . Queens given a nestmate lose less mass than solitary queens, independently of brood size (n = 86, L) ⁹ .	Queens in associations eat eggs (L) ²¹ , solitary queens do not (L) ¹⁷ . Differential mass loss of initially equally heavy cofoundresses (L) ²³ is predicted by size difference, which in turn predicts fighting ability (L) ⁹ . The most likely survivor has lost less mass and has more workers (L) ²⁵ (but see L ²⁴).	Early queen mortality is higher in four- than in one-queen colonies, and in four-queen colonies increases with queen initial mass (L) ¹⁸ . This is not consistent with queens dying of starvation, but rather with phenotype-dependent early aggression (L) ¹⁸ .
<i>Myrmecocystus mimicus</i>	Optimum curve of colony productivity with group size (L) ³⁷ .	Queens in associations eat eggs (L) ³⁷ .	Early queen mortality occurs and has a minimum at the population-average group size (L) ³⁷ .
<i>Lasius</i> spp.	Optimum curve of colony productivity with group size (L) ¹⁵ .	Queens of initially same mass differ significantly after 25 days; egg laying is not equally distributed in 12 out of 15 two-queen <i>L. niger</i> colonies (L) ¹⁵ .	Early queen mortality is higher in <i>L. pallitarsis</i> non-kin queen pairs than for solitary queens (L) ³² .
<i>Messor</i> spp.	Optimum curve of colony productivity with group size in <i>Me. aciculatum</i> (L) ³⁵ .	In <i>Me. pergandei</i> , no significant differences among queens in egg laying, but significant differences in egg tending (L) ^{14,28} .	In <i>Me. pergandei</i> , mortality occurs before worker emergence (L) ¹⁴ , e.g. in 84% of experimental multiple-queen colonies (F) ³⁹ .
<i>Camponotus ferrugineus</i> ^b	Not recorded	Queens stand over their own eggs and displace each other; queens eat eggs (L) ⁴⁴ .	Aggressive behavior observed (L) ⁴⁴ .
<i>Formica podzolica</i>	Optimum curve of colony productivity with group size (L) ³⁴ .	Queens in associations eat eggs (L) ³⁴ .	Lethal early queen fights observed (L) ³⁴ .

^aF, field study; L, laboratory study.

^bIn one field-collected association.

Brood raiding can eliminate >90% of the nests long before any one colony produces sexual progeny²⁰. Benefits of cooperation in the face of brood raiding have been documented for *S. invicta*, *My. mimicus*, *Lasius niger* and *Me. pergandei* (Table 2). Cooperative colony founding can also increase the odds of successful defense against usurpation. Queens who have lost all of their brood because of raiding might try to usurp neighboring colonies²⁰. In laboratory experiments on fire ants, three-queen associations were able to resist usurpation more successfully than solitary foundresses²⁶. Additional benefits to group nesting occur in species requiring symbionts that might not be carried by all newly mated queens (fungus-growing ants⁸), or in those with complex nest architecture. The arboreal ant *Oecophylla smaragdina* builds nests by weaving leaves with the silk produced by larvae: multiple queens can cooperate to position leaves but solitary queens can only weave leaves that already overlap³⁰ (Table 2).

Who should queens join?

If queens can choose, they should always join a queen they can beat in the eventual fight for sole control of the colony³¹. Because queens vary in fighting ability^{9,18,23–25,32}, poor competitors should only join an association if their odds of success as a solitary foundress are even more dismal⁹. A model that incorporates survival chances (while searching for nest sites) and variable benefits of cofounding (Table 2), predicts that ant queens should join any nest if the odds that they will die before joining a nest are high, but that otherwise they should discriminate by competitive ability³¹. Kinship is not a factor because the chance of encountering relatives is so low. In laboratory experiments with *Lasius pallitarsis* (Table 1), the joining decision depends on the phenotype of potential cofoundresses, which supports the model's prediction that variance in competitive ability might favor conditional joining behavior. It is in the best interests of individual queens to sort into groups by competitive ability, such as size⁹ or body mass^{23,24}, where they cannot tell who

will win. In *S. invicta*, initially heavier queens are more likely to survive fights after worker emergence in two-queen colonies^{23,24}. Aggressive interactions before worker emergence might also be less common in associations with queens of equal or similar competitive ability, because evenly matched competitors will not challenge each other as readily¹⁸. Though we know the impact of joining similar- and different-sized queens, we do not yet know whether queens favor like-sized individuals in the field. Whether the costs of rejecting a possible nest, or nestmate, are too great for such discrimination should be resolved with future studies.

Competition among foundresses in the same group

As foundresses are unrelated, they are expected to compete. Once in a group, cofoundresses might face a trade-off. Increased individual investment in laying eggs, which serve both as new workers and as food for the workers during their larval stage, enhances worker production, colony survival and growth. However, increased investment might be costly to the individual queen, reducing her probability of surviving fights if her condition, when fighting occurs, is directly associated with fighting ability³³. Other costs might arise, for example, if the workers preferentially feed the queen in better condition (which might increase her survival) or if increased early egg laying decreases the later fecundity of the surviving queen⁹.

For several species, there is evidence that queens produce fewer per capita first worker-brood when initiating colonies with cofoundresses than when alone^{9,15,21,34,35} (Table 3). It follows that *S. invicta* queens within associations lose less mass before worker emergence than solitary queens^{9,21}. An experiment, in which per capita brood number and the presence of a nestmate queen were manipulated independently of each other, demonstrated that lower mass loss is a response to the presence of nestmates and not to different brood care demands⁹. Lower individual mass loss probably reflects competition among the queens

– either the queens selfishly limit their mass loss, and/or they influence each other's investment and condition.

In *S. invicta*²¹ and *Formica podzolica*³⁴, competition takes the form of cofounding queens eating eggs. In very large groups, colony productivity can even drop below that of solitary queens: this has been shown to occur in a field experiment with *S. invicta*, where ten-queen associations were observed to produce fewer workers overall than solitary queens²¹. Results from five species in different genera (*S. invicta*, *My. mimicus*, *L. niger*, *Messor aciculatum*, *F. podzolica*; Table 3) suggest that a colony's overall worker production reaches a maximum at intermediate queen numbers and declines in larger groups. This suggests that once a given worker brood is produced, queens parasitize their nestmates' investment, often by eating their eggs.

In associations of *S. invicta*, the queen that loses the least mass is the most likely to survive^{23,24}, as would be predicted if losing less mass in the presence of other queens, and maintaining a better condition than the cofoundresses, grants a direct benefit in fights³³. Similar results have been obtained for *L. pallitarsis*³². This correlation might also arise indirectly if fighting ability is not determined by relative body mass at the time of fights, but by some other phenotypic trait (e.g. size) that affects both the outcome of fights and the ability of queens to influence how much they each invest in worker production. Evidence for *S. invicta* is consistent with this hypothesis. Experimental manipulations of queen investment through differential feeding and exposure to different social environments do not result in an increased survival probability of the queen having lost least mass, indicating that differential mass loss does not directly affect the outcome of fights⁹. Instead, the relative and combined mass loss of cofoundresses reflects physical size differences between them, measured as head width⁹. The greater the size difference between queens, the less mass the larger queen loses and the lower the combined mass loss of both queens⁹. Larger queens are also more likely to win the fights⁹. This lower mass loss by the larger queen is probably the selfish response of a better competitor in the presence of a cofoundress. Indeed, for solitary queens there is no significant correlation between physical size and mass loss⁹.

The queen within a group that loses least mass should have a smaller share of maternity among workers, especially if nestmate queens are of the same initial mass, because queens draw on their body reserves to produce workers. Paradoxically, genetic analysis²⁵ of the first worker-brood in *S. invicta* two-queen colonies, in which initial queen mass was controlled, revealed that the queen losing least mass (and the most likely to survive) had a significantly larger share of maternity among larval and adult workers. This pattern is consistent with the ability of the queens to affect each other's condition and investment through differences in their competitiveness. Either the queen who is the stronger competitor is able to contribute disproportionately to viable eggs that become workers, or the poorer competitor regurgitates more or contributes disproportionately to the trophic eggs.

The relative phenotype of cofoundresses thus modifies the extent of cooperative benefits of foundress associations. The association between relative fighting ability and the extent of cooperative investment (estimated as queen mass loss)^{9,25}, with the ensuing costs to colony productivity, reveals selfish interactions in spite of the apparent peacefulness of queen behaviors before worker eclosion^{8,13}. These peaceful interactions range from grooming to occasional food exchange [e.g. *P. moesta*, *Lasius flavus*, *Camponotus vicinius*, *Iridomyrmex purpureus*⁷ and *S. invicta* (E. Vargo, pers. commun.)⁹] and the contribution of all

queens to egg laying and brood care (Table 2). The occurrence of early conflicts and the possibility that queen–queen competition regulates individual contribution to costly tasks (Table 3), suggest that group selection need not be invoked to account for the apparently altruistic behavior of unrelated ant cofoundresses (see Ref. 9 for references).

Do workers influence the outcome of queen fights?

When adult workers emerge, aggression among queens intensifies and escalates to fatal fights^{10,15}. Because workers are present when queens fight, the workers might influence which queen survives. In cooperative associations, workers might be expected to favor their mother over unrelated queens; however, there is little evidence that workers attack queens. In *S. invicta*, queen fights are conspicuous, although sometimes workers have been observed to attack already injured queens^{9,23,24}, and queens that had been experimentally prevented access to the brood pile²⁴. Genetic analyses of two-queen colonies have revealed that in most colonies the survivor is the mother of most of the workers²⁵. This result does not necessarily imply that workers affect the outcome of fights because of the previously discussed correlation between maternity shares, mass loss and fighting ability. In another study, with a smaller sample size and initial mass differences between cofoundresses, there was no significant association between maternity and queen survival²⁴, and manipulating the queens' share of maternity among the worker brood in *S. invicta* did not affect queen survival significantly^{23,24}. In *My. mimicus*, worker aggression could also be directed against queens that have injured themselves in fights¹⁴.

Even in the absence of within-colony kin recognition, it is possible that workers might attempt to bias the outcome of queen competition, for instance, by favoring the most fecund queen³⁶. Laboratory studies of *L. niger* reveal that queens differ significantly in egg-laying rates and that workers preferentially feed the queens with the higher egg-laying rates¹⁵. This suggests that queens that maintain good condition up until worker emergence might signal their fecundity to workers⁹.

Conclusions

Grouping can be favored even among unrelated individuals if, by joining, a group member achieves higher fitness than she could have as a solitary female, and if the final jackpot winner cannot be entirely predicted when the group forms. As long as group members are needed, conflict is mild and hard to detect, but it becomes overt as group members jockey for the best position in the final fights. As soon as the presence of other group members is no longer advantageous, the group falls apart as members fight to the death for sole control. Workers appear to have a little role in these conflicts, possibly because of the lack of within-colony kin discrimination. Important directions for future work include extending experiments conducted on fire ants to other species. There are gaps in at least three areas. First, we need data on the process of group formation and nestmate choice under field conditions. Second, we need detailed behavioral and physiological analyses of how the cooperating, and at the same time competing, queens allocate their resources to parental investment (worker production and care), to clarify further the potential trade-off between individual- and colony-level investment optima. Third, we need to know whether queens can monitor, or even influence, each other's contribution to cooperative benefits. Together with the available evidence, filling these gaps should soon allow, for the first time, a

synthesis of costs and benefits at the individual and colony level in a cooperative system.

Acknowledgements

We thank Laurent Keller, David Queller, Lotta Sundström and the referees for their comments, Esther Schreier for drawing Fig. 1, and the Swiss federal program for academic recruitment (no. 409) and NSF grant number IBN 9808809 for partial financial support.

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