

Programmed for gambling: *Polistes* wasps wager
current fitness for the possibility of increased future
fitness

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ABSTRACT

Cooperation by animals with non-relatives poses a challenge to kin selection theory unless direct fitness benefits are somehow obtained from the cooperative act. Several species of the Polistinae subfamily of wasps have helpers that are completely unrelated to the dominant female in the nest. Empirical studies indicate that these associations could be a result of nest inheritance by the subordinates, a very probable scenario in the species [28]. Further evidence suggests that subordinates in these cofoundress associations produce more direct offspring than lone foundresses mostly post nest inheritance, but sometimes even as subordinates [20]

This model examines the role of direct fitness in the evolution of such semisocial systems. Benefits of association are classified as survival and reproductive benefits and the effect of each on subordination is examined independent of the other. Results suggest that relatedness between the dominant and the subordinate in a nest is not necessary for such complex social systems to evolve. We also find evidence for increasing complexity in such systems in the form of helping tendency in brood 1 workers (eusociality) facilitating cofoundress associations (semisociality).

INTRODUCTION

In the past 50 years, eusociality has hogged the spotlight in the field of sociobiology. The phenomenon is expressed in many orders of insects [5, 19], especially in Hymenoptera where it has arisen at least 11 times independently [1]. [37] listed four defining characteristics shared by all eusocial species - the most discussed among them being reproductive division of labour. Adults are divided into two castes - reproductives (queens) and non-reproductives (workers). In a given nest, queen(s) monopolize(s) reproduction while the workers forage and care for the young. The paradox of how worker tendency would evolve without these individuals enjoying any reproductive success has long been regarded as a key challenge to evolution by natural selection [7, 16, 37]. In fact, the paradox is as old as the theory of evolution by natural selection itself and was identified by Darwin as potentially fatal to his theory [7].

"I . . . confine myself to one special difficulty, which at first appeared to me insuperable, and actually fatal to my whole theory. I allude to the neuters or sterile females in insect-communities: for these neuters often differ widely in instinct and in structure from both the males and fertile females, and yet, from being sterile, they cannot propagate their kind."

- Charles Darwin

Depending on how extreme caste differentiation in the concerned species is, there are multiple grades of eusociality. While referring to this problem, it appears that Darwin was addressing the most extreme grade - advanced eusociality where queens and workers are both morphologically and behaviourally distinct. Understanding these grades in combination with today's phylogenetic data could potentially give insights into the evolution of reproductive division of labour, the hallmark of eusociality.

GRADES OF EUSOCIALITY

There are three grades of eusociality - facultative, primitive and advanced. These grades are well established in the entomological literature. Understanding them along with phylogeny could help conceptual understanding of how life history strategies at one level could evolve from an existing ancestral life history [23, 6, 18].

Facultative eusociality

Facultative eusocial species do not have a clear distinction between reproductives and non-reproductives. All females are morphologically and behaviourally identical and possess the ability to reproduce independently. Worker tendency throughout lifetime is thought to result from death before reproduction rather than inability to reproduce [18].

Primitive eusociality

Primitively eusocial species are characterised by reproductive queens and nonreproductive workers. The castes are morphologically identical but behaviourally distinct. Unlike facultative eusocial species, reproductive status of a female is typically lifelong, although some workers could become queens via nest inheritance or queen replacement [6, 18]. These species provide essential testing grounds for theories of evolution of eusociality because helpers decide to not reproduce even though they possess the ability to do so.

Advanced eusociality

Advanced eusociality is characterised by morphologically and behaviourally distinct castes. Workers are typically sterile (incapable of reproducing) and smaller than queens. It is this extreme case that Darwin referred to in *The origin of species*. The solution he provided was based on group selection; that the whole colony is the unit of selection rather than individuals within the colony.

KIN SELECTION AND THE THEORY OF INCLUSIVE FITNESS

For a century later, there were very few parts of natural selection that were supported by mathematical models. Coming together of the sexes and parental care was the extent of social behaviour that these models could explain. In 1964 however, William Hamilton came up with his cornerstone paper on kin selection and the theory of inclusive fitness which has since been the predominant paradigm for explaining altruism and the evolution of worker caste [35, 32, 27, 17, 11]. Hamilton said that a trait would spread across a population if its inclusive fitness exceeds zero i.e. it must satisfy the condition:

$$rb - c > 0 \tag{1}$$

where b & $-c$ are the benefit of the act to the recipient and the cost to the actor respectively while r is a regression based relationship estimate between the actor and the recipient. Understanding that organisms attempt to maximize inclusive fitness rather than direct fitness is key to understanding evolution of self sacrificial and altruistic behaviours. Even though the worker caste has reduced reproductive success, these individuals spread their genes across the population by helping the queens raise offspring to whom they are related, thus increasing their indirect fitness gain.

From inequality (1), we see that relatedness is key to maximizing indirect fitness, and hence, for an inclusive fitness based explanation for altruism. [16] used combination of inclusive fitness and skewed relatedness in haplodiploid species to explain the statistical

dominance of eusociality by the Hymenoptera. It is worth mentioning here that relatedness is conceived as a regression coefficient of the actor's and the recipient's genotype. Hamilton pointed out that the appropriate relatedness coefficient would be the concentration of the actor's genes in the recipient, which in principle takes the form of a regression coefficient [15, 14, 13].

THE HAPLODIPLOIDY HYPOTHESIS

Haplodiploidy is a sex determination system prevalent in the insect order Hymenoptera. As the name suggests, males are haploid and develop from unfertilized eggs while females are diploid and develop from fertilized eggs. When compared with a diploid sex determination (as in humans), haplodiploidy is accompanied by many peculiarities. Key among these is the skewed relatedness among individuals in a nest which [16] used in combination with kin selection to explain altruism.

Females from a monogamous single-queen's brood are more related to each other ($r = 0.75$) than to their own offspring ($r = 0.5$). Hence, it is beneficial for these females to stay and help raise sisters in their mother's nest rather than leaving to found their own nest. However, [34] later pointed out that females (workers) are related to their brothers only by $r = 0.25$ which balances out any gain in indirect fitness from raising sisters. The only way haplodiploidy would favour worker tendency is if the queen produces a brood with a female biased sex ratio. Hence, the ability to create and exploit sex ratio asymmetry (female biased) is essential for the evolution of worker behaviour.

[31] describes two life-histories (female hibernation and larval diapause) commonly observed in social insects and how these conditions are crucial for evolution of stable sex ratio biases and hence, for evolution of eusociality in haplodiploid species. [29] later emphasize the use of realistic ecological and life history conditions and provide theoretical support for evolution of eusociality in species following a female hibernation life history.

FEMALE HIBERNATION LIFE HISTORY

The female hibernation life history is followed by several social insects. It is prevalent in several bees, especially among bees of the subfamily Halictinae. For this reason, it is sometimes also referred to as the Halictine life history [31]. Nests are founded in the spring by mated overwintered females. Two broods are produced every year, of which, the second one consists of offspring and grand offspring of the foundresses. Females from the second brood mate and hibernate while the males die. Surviving females form the founding population of the subsequent generation [29]. 1 shows a schematic of the female hibernation life history.

The life history is also followed by several wasps of the Polistinae subfamily. However, these wasps have an added layer of complexity in their social system in the form of helpers or subordinates from the same generation as the queen. In this project, we used *Polistes dominulus* as a model species to examine life history followed by wasps of this subfamily and the added layer of social complexity in the system. A schematic of the *Polistes dominulus* life history with group founded nests is shown in 2.

***Polistes dominulus* life history**

Primitively eusocial wasps, *Polistes dominulus* found nests in spring. Nests are founded by solitary/lone foundresses or small groups of reproductive females that overwinter together as mated adults. Within each group, individuals have a dominance hierarchy set up which determines who the queen in the nest is. The dominant female/queen monopolizes reproduction, while the other females become subordinates and engage in foraging and brood care [30]. The dominant produces the first brood of the year (generation G1). Since the species is primitively eusocial, females from this spring brood can choose to stay and help her reproduce or leave and found their own nest. Foundress females and first brood reproductives then contribute to a second summer brood (generation G2). Females from the summer brood mate and overwinter to form the founding population of the subsequent year. Cofoundress associations are formed over winter between females that hibernate together. [28] however noticed that 35% subordinates engaged in these associations are completely unrelated to the dominant in the nest. Hence, kin selection fails to explain why these females would give up on reproduction in order to cooperate with an unrelated dominant.

[28] explanation for this was based on nest inheritance; that the subordinate inherits the nest and its entire worker force in case of dominant death mid-season. If one considers the small association sizes in these species and high queen mortality, nest inheritance, and hence, a direct fitness explanation seems highly probable. However, even with nest inheritance in place, wagering all current reproduction on the off-chance that the dominant might die seems like a huge gamble. Empirical evidence by [20] suggests that these apparently compulsive gamblers - the subordinates - are in fact successful investors who on average reap more direct benefits than their solitary/lone counterparts. Some subordinates produce more direct offspring than lone foundresses even without inheriting the nest.

KEY RESEARCH QUESTIONS

Based on this, we model the evolution of such semisocial associations in Polistinae subfamily of wasps. The model incorporates realistic life history as suggested by [31] and [29]. The aim of the model is to examine the relative importance of direct and indirect fitness in the evolution of cofoundress associations. Since 35% subordinates are unrelated to the

dominant in the nest, we also aim to examine under what conditions direct fitness benefits alone are sufficient to explain these associations.

Our hypothesis for formation of these associations is based on a direct fitness explanation and subordinate inheritance of the nest and its worker force. Therefore, it would also be interesting to infer if presence of eusociality (worker behaviour by females of the spring brood) facilitates semisociality (cofoundress associations between females from the same generation).

METHODS

In this project, we explicitly model (analytically and using simulations) the life history of *Polistes dominulus* and study the evolutionary dynamics of semisocial associations among females. Sociality is coded for by alleles at the 'S' locus. The phenotype of alleles at this locus determine whether successful cofoundress associations are established between two females. The trait is coded such that the probability of two females associating is modelled as the product of social tendencies of both females. Thus, the chances of a successful association is small even if one of the two females is disinterested in associating and hence, both females have a say in the association decision. It is worth noting here that there is only one 'S' locus coding for the dominant to accept the subordinate and the subordinate to join a dominant's nest. This means that whether sociality picks up in the population depends not on individual fitness gains to the dominant and subordinate but on the net fitness gained by both individuals. Once females engage in associations, they each possess a dominance tendency D , which determines who the dominant in the nest is. Dominance tendency D is defined as a sum of nest quality Q and some random environmental noise ϵ both of which come from normal distributions.

$$D = Q + \epsilon \quad (2)$$

Individuals were attributed another neutral trait 'N', which was used in the agent based model to estimate average relatedness between the dominant and the subordinate in social nests. A regression between the dominant and subordinate neutral trait is used as a relatedness estimate [13]. This is called the regression relatedness. A second relatedness estimate was calculated based on the probability that a female associates with a sister (pS), one of the parameters in our simulation model. This estimate is calculated as the sum of the relatedness with social partner times the the probability of associating with them. Since females are only provided with the option of associating with a full sister ($r = 0.75$) or a random female ($r = 0$), the probability based estimate was calculated as $r = 0.75 \times pS + 0.00 \times (1 - pS) = 0.75 \times pS$. It was ensured that the relatedness estimate from the two methods gave the same result.

MODEL ASSUMPTIONS

- N available nests at the start of every year - This assumption accounts for density regulation over winter and restores effective population size, N_e to N
- Nest Quality Q does not affect reproduction - Nests of the same size have the same number of offspring on average
- Additive trait expression - Trait phenotype is the average trait value expressed by both alleles at the concerned locus

- Estimate summer offspring of a foundress female is linearly related to the number of workers in the nest
- Maximum association size is limited to two - A simplifying assumption that social nests can only have one subordinate female
- One association attempt / female - Simplifying assumption that a failed attempt at associating means that a female can only found a nest solitarily
- Monogamy - Hymenoptera store sperm for life

ANALYTICAL MODEL

An adaptive dynamics based approach was used to model the evolution of cofoundress associations. There are two fundamental ideas of an adaptive dynamics:

1. That there is a resident population in dynamic equilibrium when a new mutant type appears
2. That the eventual fate of a mutant in a population depends on its initial growth rate (invasion fitness) when it is still rare compared to the resident type

In combination, these ideas amount to separation of short term population dynamics from long term evolutionary dynamics [3].

The first step in an adaptive dynamics approach is to identify evolving traits. Once this is done, a mathematical model of the demographic dynamics is established based on which we can calculate the invasion fitness. Invasion fitness of a rare mutant can be thought of as the fitness landscape the mutant experiences for the given resident trait. Importantly, the fitness landscape changes with each successful mutant invasion [3].

In our case, we started with a population of solitary individuals ($S = 0$). The demographic dynamics was modelled using a class structured matrix population model. The life history of the species was split into four stages - reproduction for first brood, survival of foundresses, reproduction for second brood and nest founding (refer 6). A transition matrix was made for each stage such that the contributing class of individuals were in the column and the receiving classes were in the rows. Multiplying all four matrices resulted in a transition matrix for the whole life history which was used to obtain class frequencies and reproductive values of the classes. This was further plugged into the direct fitness equation which was further used to arrive at the selection gradient. A positive selection gradient indicates higher mutant fitness than resident fitness which indicates that sociality would spread in the population. Further details regarding the analytical model are provided in .

AGENT BASED MODEL

Individual-based simulations were also used to analyse the evolutionary dynamics. The life history of these Polistinae wasps was explicitly coded on C++.

Initially, the population is assumed to be monomorphic for the social trait ($S = 0$). During the density regulation phase after both reproduction bouts, females attempt associations based on their social tendencies. A parameter determining the probability of associating with a sister is used to introduce sibling bias during formation of associations. Thus, it is possible to determine what fraction of individuals engage in cofoundress associations with sisters rather than random females. If a female wants to associate with a sister but there is no sister around, she remains solitary. After associations are formed, individuals are allowed to disperse and find nesting sites available for occupation. Both solitary and associated females are equally likely to find nests. Once all N nests are occupied, the remaining females die. Surviving females are queens (and subordinates) of nests in the subsequent year.

During reproduction, mutations occur on each allele with a probability μ_m . Each mutation changes the allelic value by an amount drawn from a normal distribution with mean 0 and standard deviation σ_m (mutational step). Parameter values chosen for the mutational process do not affect the qualitative outcome of the simulations. The phenotypic effect of allelic values smaller than 0 or larger than 1 is 0 and 1, respectively.

An average of ten replicate runs was used to obtain sociality value for a given combination of parameters.

RESULTS

Social females experience two kinds of benefits. Empirical evidence suggests that larger nests tend to fail less often due to predation or foundress death [20]. Hence, females in a social nest were provided a survival benefit. Mortality of social females was set to lower values compared to their solitary counterpart. Apart from these benefits, social females also experience higher reproduction due to presence of a subordinate. This in turn results in a larger size of worker force from their first brood. We examined the effect of both survival and reproductive benefits on the evolution of social tendency. Apart from this, in order to compare relative importance of direct and indirect fitness, we also varied the relatedness parameter and the probability of females attempting associations with sisters. The model consisted of many other parameters that were left static through the simulations. Refer to 1 for the list of static parameters along with the value they took across simulations. Other parameters were varied depending on what we were looking for. The range of values these variable parameters took is given in 2. Before diving into the results, it is worth taking a look at 1 and 2 in order to familiarize oneself with the notations.

EFFECT OF SURVIVAL BENEFIT

Empirical evidence from [20] suggests that larger nests (more cofoundresses) are less prone to failure by predation or foundress death. Thus, females engaged in social associations enjoy a higher survival rate. In our model, survival benefit is provided to social females by setting parameters $D_d, D_s < D_l$.

where, D_d , D_s and D_l represent mortality rates of the dominant, subordinate and lone foundress respectively.

4 shows the effect of survival benefit on the evolution of social tendency. Reproductive benefits were kept constant in these simulations at $b_s = 0.8$ and $b_w = 0.5$. Mortality of the dominant and the subordinate was varied relative to mortality of the lone foundress (which was fixed at 0.5). Results show that semisociality evolves more often with higher dominant and subordinate survival. In fact, current benefit values are too low for these cofoundress associations to evolve in the absence of a survival benefit.

EFFECT OF RELATEDNESS AND SIZE OF WORKER-FORCE

Each panel in 4 is an f vs. pS plot and shows that sociality evolves more easily when strength of worker force in the nest is high (or when fewer females leave their parental nest). What is also as per expectation is the easier evolution of sociality with higher indirect benefits (higher pS). However, a plateau is observed in the heatplot which means

that relatedness does not facilitate crossing of the zero selection gradient barrier (3). This compares well with the analytical results shown in .

EFFECT OF REPRODUCTIVE BENEFIT

Visualizing evolution of social tendency by varying parameters b_s and b_w gives us the effect of increased reproductive benefit (that social females experience) on evolution of co-foundress associations. Each panel in 5 depicts effect of subordinate and worker benefits for varied death probabilities and worker force strength. In each case, the dominant, subordinate and lone foundress mortalities (D_d , D_s and D_l) were set to the same value to ensure zero survival benefits. By varying subordinate and worker benefits, it was observed that the minimal requirement for the evolution of sociality was $b_s, b_w \geq 1.0$. Adjacent panels depict benefit requirements depending on what foundress mortality is set to. It is observed that increase in foundress mortality increases the ease of evolution of social tendency, S . The probability of attempting associations with a sister (pS) is fixed in this scenario at 0.5 since mean foundress – cofoundress relatedness was estimated at 0.53 ± 0.52 by [20].

DISCUSSIONS

The main aim of this study was to examine evolution of the complex social system observed in the Polistinae subfamily of wasps and determine how ecological and life history characteristics affect social structure. In order to understand evolution of semisocial associations observed in these species, it is important to note the two fold gamble social females engage in. Attempting to associate with another female post winter is a gamble in itself. When females attempt associations, they have an identical chance of ending up as either dominant or subordinate. Once associations are formed, the subordinate is invariably invested in the dominant's death which would result in nest inheritance and hence, increased fitness benefits to her. As mentioned above, social females experience different kinds of benefits. Biological explanations to observed trends are provided below.

EFFECT OF SURVIVAL BENEFIT

Figure 4 shows the effect of varied mortality rates in social females on the evolution of semisociality. It is observed that lower mortality of the dominant and the subordinate facilitates evolution of cofoundress associations. This might seem counter intuitive if one considers lower nest inheritance that accompanies dominant survival. However, considering social tendency is governed by alleles at a single locus and that females stand a 50% chance of ending up as the dominant female in the nest, investing in a social trait must be beneficial as long as the average fitness of females engaged in the association exceeds solitary females. In case of low dominant mortality, increased lifetime fitness of the dominant compensates for higher fitness costs of associations to the subordinate.

EFFECT OF RELATEDNESS AND SIZE OF WORKER-FORCE

In the strict definition of eusociality, workers are offspring of the queen in the nest. However, in the Polistinae wasps, there is an additional layer of complexity in the social system in the form of semisocial associations between females from the same generation. 3 shows how evolution of eusociality (first brood workers) facilitates evolution of semisociality in these species. We already know that a female hibernation life history facilitates evolution of worker tendency in brood 1 females [29]. Considering Polistinae wasps follow this life history and the evidence for increasingly complex social systems provided by our model, evolution of semisociality seems like a probable follow up to worker tendency in the offspring generation. Thus, presence of eusociality - the highest form of social organisation in animal societies leads to an added layer of complexity in the social system of these wasps. 3 also shows that relatedness between associating females increases the rate of evolution of semisociality. However, this on its own is not sufficient to explain evolution of these

associations. This is puzzling considering the increased indirect fitness benefits provided to the subordinate due to higher relatedness with the dominant. However, the symmetry in the model i.e. identical chances for individuals to be dominant or subordinate and the fact that sociality is coded for by single locus makes relatedness irrelevant, at least w.r.t. facilitating cofoundress associations. This particular result is clearer from the analytical model presented in . Thus, direct fitness explanations are not merely sufficient, but essential to explain semisocial associations in Polistinae wasps. This result could explain why 35% subordinates may be completely unrelated to the dominant in the nest.

EFFECT OF REPRODUCTIVE BENEFIT

Increasing foundress productivity due to presence of subordinates and workers eases the evolution of semisociality. This seems rather intuitive. However, what is rather interesting is that semisociality evolves even with the subordinate adding fewer offspring to the dominants offspring count than she would've added to her own count, had she reproduced independently ($b_s, b_w < 1$). As mentioned in the results section, mortalities of solitary and social females was equated in this case to eliminate any survival benefits social females experience.

Adjacent panels in 5 show that lower benefits are required for evolution of sociality when likelihood of female mortality is higher. Even though mortality for individuals is set to the same value, the fact that a semisocial nest potentially has two queens means that these nests enjoy assured fitness returns i.e. the chances of a nest perishing due to foundress death is lower in these nests. The trend of increasing sociality with increase in foundress mortality is observed because the benefit of these assured fitness returns is higher with higher foundress mortality.

FUTURE DIRECTIONS

The next step in this project would be to code sociality using alleles at two separate loci; S_1 and S_2 . Alleles at S_1 would code for the dominant's tendency to accept a subordinate whereas S_2 would code for the subordinate's tendency to join a dominant. In such a model, the trait would spread across the population only with increased fitness benefits to both individuals engaged in forming associations relative to solitary females. Thus, the subordinate would have to independently gain higher fitness than her solitary counterpart which is what [20] observed empirically.

Further, we could also gain insights into the evolution of polygyny by varying degree of reproductive skew between the dominant and subordinate (allowing subordinates to reproduce) while producing the first brood. Reducing reproductive skew might reduce tension

among cofoundresses, but it will also reduce relatedness within the nest thus affecting worker tendency of brood 1 females. It would be interesting to allow altruism in brood 1 females and subordinates to evolve simultaneously along with reduced reproductive skew in group founding nests. Once we allow helping tendency to evolve, we could test how new genetic background introduced by the subordinate (now dominant) post nest inheritance affects worker tendency to stay in those nests and help the new dominant. This in turn would affect altruism in subordinates. Evolution of polygynous nests in such a scenario would be in agreement with what is observed in nature. Phylogeny of the subfamily Polistinae reveals close links between independent nest founding (as observed in *Polistes dominulus*) and swarm founding life histories of social wasps [2]. Considering that a life history switch might be possible with change in one model parameter indicates this could potentially be the route these species took towards evolution of a polygynous life history.

APPENDIX A1

Polistes dominulus is a sexually reproducing haplodiploid species that follows a female hibernation life history (described in the methods section). Here, we split the life history into four stages - (i) Reproduction for first brood (ii) Survival of nest foundresses (iii) Reproduction for second brood and (iv) Founding nests the subsequent year (Refer 6 for a schematic). Transition among stages is modelled by transition matrices B , C , D and E . Males do not affect the social trait. They merely mate and transmit their genes to the future generations. Therefore, existence of males is ignored in this analytical model.

DEMOGRAPHY

In the first stage, foundresses in solitary and social nests contribute to first brood females - reproductives and workers. Here, we classify reproductives as one class of individuals while workers are split into two classes - workers from social and asocial nests. Columns in the transition matrix indicate the contributing classes - Lone foundress (L), dominant/foundress (D) and subordinate/cofoundress (C) while the rows represent the receiving classes - which consist of workers in a lone foundresses nest (W_L), reproductives ($G1$) and workers in a social nest (W_S) in addition to L , D and C as the first three rows. Each element in the matrix represents contribution of the classes in the column to the classes in the rows after the first reproductive bout in the season. In the matrix below, fecundities of the solitary and social foundresses is denoted as F_1 and F_2 respectively while the fraction of helpers in the offspring generation is denoted by h .

$$B = \begin{pmatrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & 1 \\ F_1 h & 0 & 0 \\ F_1 \tilde{h} & F_2 \tilde{h} & 0 \\ 0 & F_2 h & 0 \end{pmatrix}$$

This is followed by the second survival stage where nest foundresses survive with a certain probability. Hence, this is a square matrix with the above mentioned six classes along the rows and the columns. Mortalities of the solitary and social (dominant and subordinate/cofoundress) are represented in the matrix as D_l , D_d and D_c respectively. It is important to note that the sequence of classes along the rows and columns matter since we would eventually like to arrive at one 3×3 matrix that represents the entire life history [25].

$$C = \begin{pmatrix} 1-D_l & 0 & 0 & D_L \frac{1}{F_1 h} & 0 & 0 \\ 0 & 1-D_d & D_c(1-D_l) & 0 & 0 & D_d D_c \frac{1}{F_2 h} \\ 0 & 0 & (1-D_d)(1-D_c) & 0 & 0 & 0 \\ 0 & 0 & 0 & 1-D_l + D_l \frac{(F_1 h - 1)}{F_1 h} & 0 & 0 \\ 0 & 0 & 0 & 0 & 1-D_l & 0 \\ 0 & 0 & 0 & 0 & 0 & 1-D_d D_c + D_d D_c \frac{(F_2 h - 1)}{F_2 h} \end{pmatrix}$$

The second reproductive bout in the year results in all reproductive females. Hence, this would result in a 1×6 transition matrix where all six classes mentioned above result in one class of reproductive autumn females. In the below matrix, fecundities of the lone foundress, dominant and the first brood reproductives during the second reproductive bout is denoted as F_l , F_d and F_{g1} respectively.

$$D = (F_l \quad F_d \quad 0 \quad 0 \quad F_{g1} \quad 0)$$

These second generation reproductives then hibernate and form the founding population the subsequent year. This is where density regulation occurs where the population is restored to its initial size. A density regulation term α is introduced here in order to do so.

$$E = \begin{pmatrix} \alpha(1 - S\bar{S}) \\ \alpha \frac{S\bar{S}}{2} \\ \alpha \frac{S\bar{S}}{2} \end{pmatrix}$$

Once transition matrices for all four stages were obtained, we multiply them to obtain one 3×3 matrix that represented the entire life history (A). This is a method adopted from [25]. The obtained transition matrix was then used to obtain class frequencies and reproductive values of concerned class of individuals. $A = EDCB$

For a stable population, the dominant eigenvalue λ was set to 1 and the right eigenvector was used to calculate class frequencies of the three concerned class of females - solitary foundress, dominant and subordinate. Class frequency of u_1 of the solitary foundress was set to 1 and the matrix was solved to obtain the other two class frequencies and the winter scaling factor α relative to u_1 . The solutions to these class frequencies at demographic equilibrium are:

$$u_1 = 1 \tag{3}$$

$$u_2 = \frac{S\bar{S}}{2(1 - S\bar{S})} \tag{4}$$

$$u_3 = \frac{S\bar{S}}{2(1 - S\bar{S})} \tag{5}$$

The fraction of females that survive winter (at the density regulation stage) is given by

$$\alpha = \frac{2}{2F_l + 2\tilde{h}(1 - D_l)F_1F_{g1} + S\bar{S}(F_d + \tilde{h}(1 - D_l)(F_2 - 2F_1)F_{g1} - 2F_l)} \quad (6)$$

REPRODUCTIVE VALUES

Once class frequencies were obtained, the transition matrix A was also used to calculate class specific reproductive values. This is defined as the long term genetic contribution of individuals to future generations [10]. These reproductive values were obtained from by calculating the left eigenvector for transition matrix A when the population is stable ($\lambda = 1$). Again, long term genetic contribution of the lone foundress was set to 1 and reproductive values of the other classes were calculated relative to this.

$$v_1 = 1 \quad (7)$$

$$v_2 = \frac{-2 + 2\alpha\tilde{h}(1 - D_l)F_1F_{g1} + \alpha S\bar{S}(D_d(1 - D_c)F_d - 2\tilde{h}(1 - D_l)F_1F_{g1} - 2F_l) + 2\alpha F_l}{\alpha S\bar{S}(\tilde{h}(-1 + D_l)F_1F_{g1} - F_l)} \quad (8)$$

$$v_3 = \frac{D_d(1 - D_c)F_d}{\tilde{h}(1 - D_l)F_1F_{g1} + F_l} \quad (9)$$

Equations 3 - 9 can now be plugged into an inclusive fitness or direct fitness equation to eventually arrive at the selection gradient. Both inclusive fitness and direct fitness approaches are equivalent and are different ways of looking at the same process. [33] shows how these two approaches are computationally equivalent and why one of them might be easier depending on the situation. 7 shows an intuitive schematic comparison between the two approaches (adaptation of West et al., 2007). In our model, we used the direct fitness or the neighbour modulated fitness approach. However, a brief outline of both approaches is provided below.

INCLUSIVE FITNESS APPROACH

Inclusive fitness was an idea introduced by [16] and is an actor-centred approach. It accounts for fitness effects on a number of recipients due to the action of a focal actor. This approach adds up behavioural effect of the focal individual on all recipients as the indirect fitness component whereas the direct fitness component is its own offspring stripped off of any additional offspring it has due to help from others.

DIRECT FITNESS APPROACH

In contrast, the direct fitness (also known as the neighbour modulated fitness) approach is a recipient-centred approach. This approach accounts for the behavioural effects of all actors on one focal recipient [33]. In the recent years, direct fitness has emerged as the preferred method of modelling kin selection [12, 26, 8, 21, 22, 36, 24] and this is the approach we will use in our model as well. A direct fitness equation is first formulated from analysing the life history and including individuals from all classes that affect the trait of interest.

$$W_{S,\bar{S}} = u_1v_1 + u_2v_2 + u_3v_3 = (1 - S\bar{S})v_1 + \frac{S\bar{S}}{2}(v_2 + v_3) \quad (10)$$

SELECTION GRADIENT

Once the direct fitness equation is obtained, we further calculate the selection differential (W_{dir}) w.r.t. the trait of interest (S in our case). The sign of the selection gradient determines whether the trait will spread across the population. The relationship between the two is provided by the canonical equation of adaptive dynamics which under standard adaptive dynamics assumptions is given by [9] (Also see [4]).

$$W_{dir} = \frac{\partial W}{\partial S} + \frac{\partial W}{\partial \bar{S}} \times \frac{d\bar{S}}{dS} = \frac{(rS + \bar{S})(F_d + \tilde{h}(1 - D_l)(F_2 - 2F_1)F_{g1} - 2F_l)}{2\tilde{h}(1 - D_l)F_1F_{g1} + 2F_l} \quad (11)$$

The numerator of the selection gradient equation is split into two parts here. The sign of the selection gradient exclusively depends on the second part of the equation. Since the relatedness term lies in the first part of the equation, it is evident that it cannot facilitate semisociality by itself. However, once direct fitness benefits facilitate formation of such associations, indirect benefits can speed up the process of evolution of cofoundress associations. This is perfectly in agreement with results from the agent based model.

FIGURES

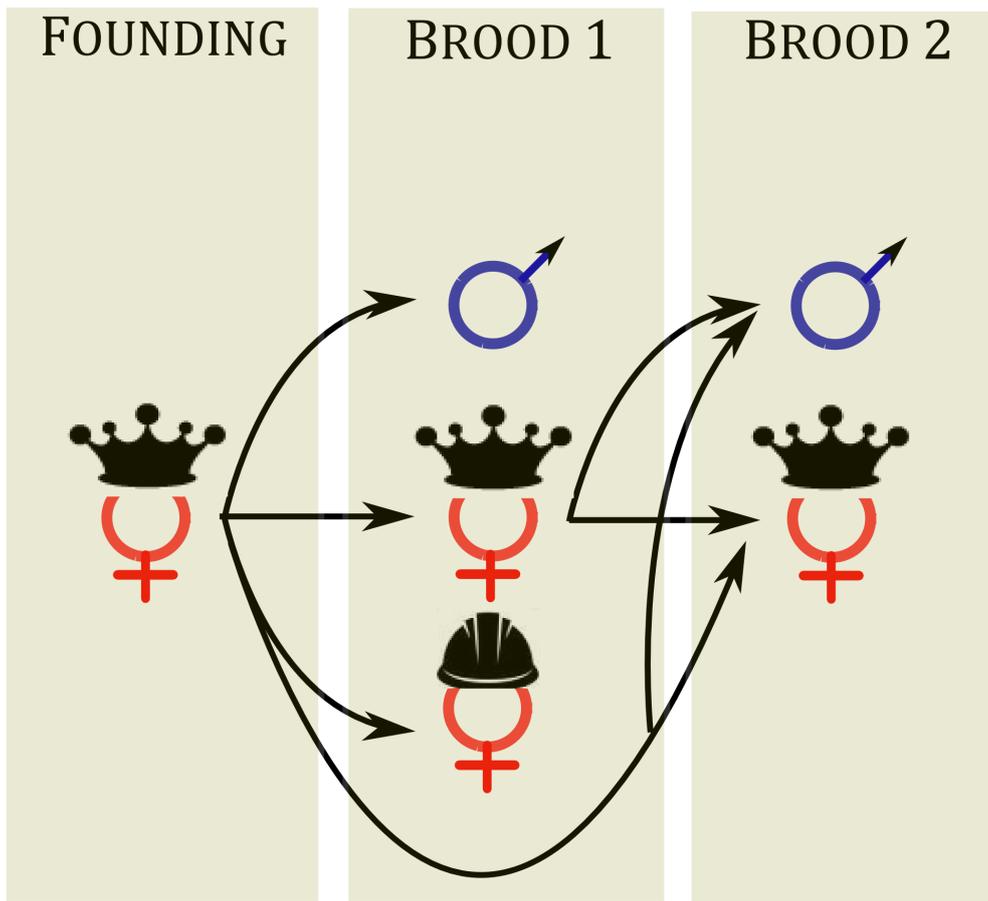


Figure 1: Partially bivoltine female hibernation life history considered by [31] and [29]. Nests are founded by mated overwintered females in spring. 1 depicts solitary founding as is observed in Halictine bees and many other social insects

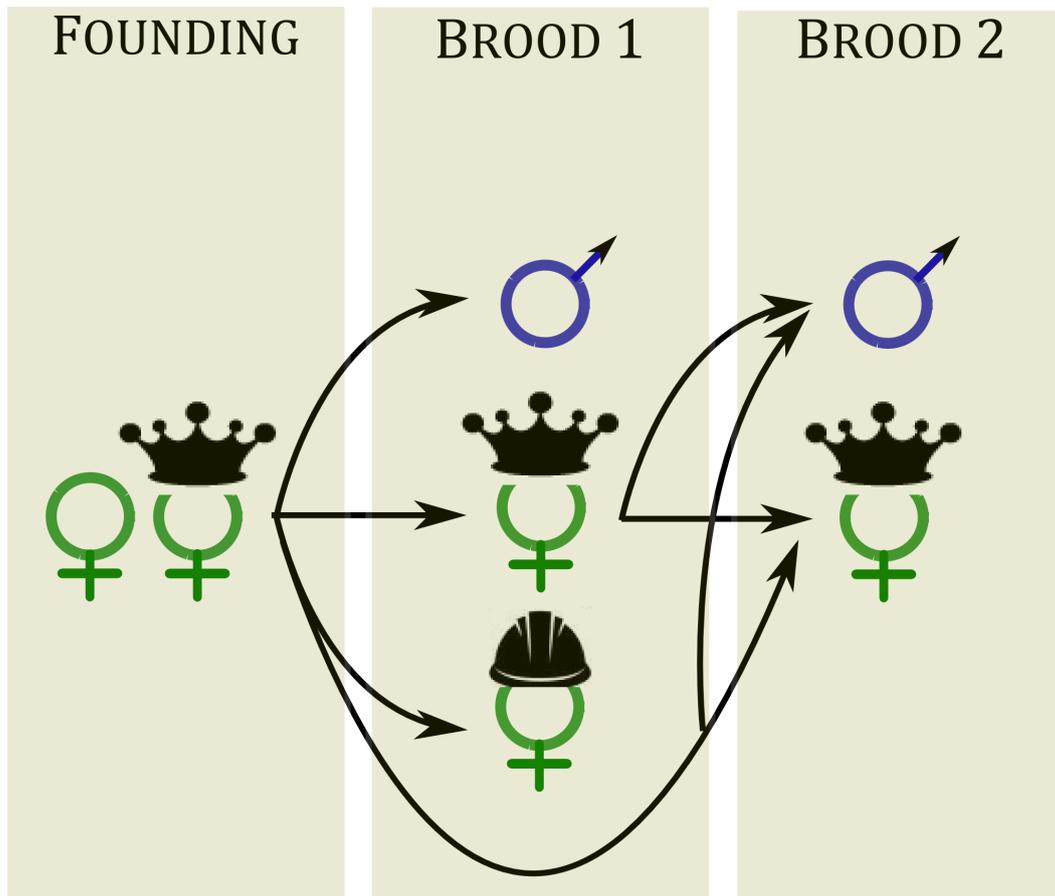


Figure 2: 2 differs from 1 in that the nests are founded by groups of individuals with a dominance hierarchy set up among them. The dominant female (queen) monopolizes reproduction while the subordinates engage in foraging and brood care. It is evolution of these cofoundress associations that we are interested in

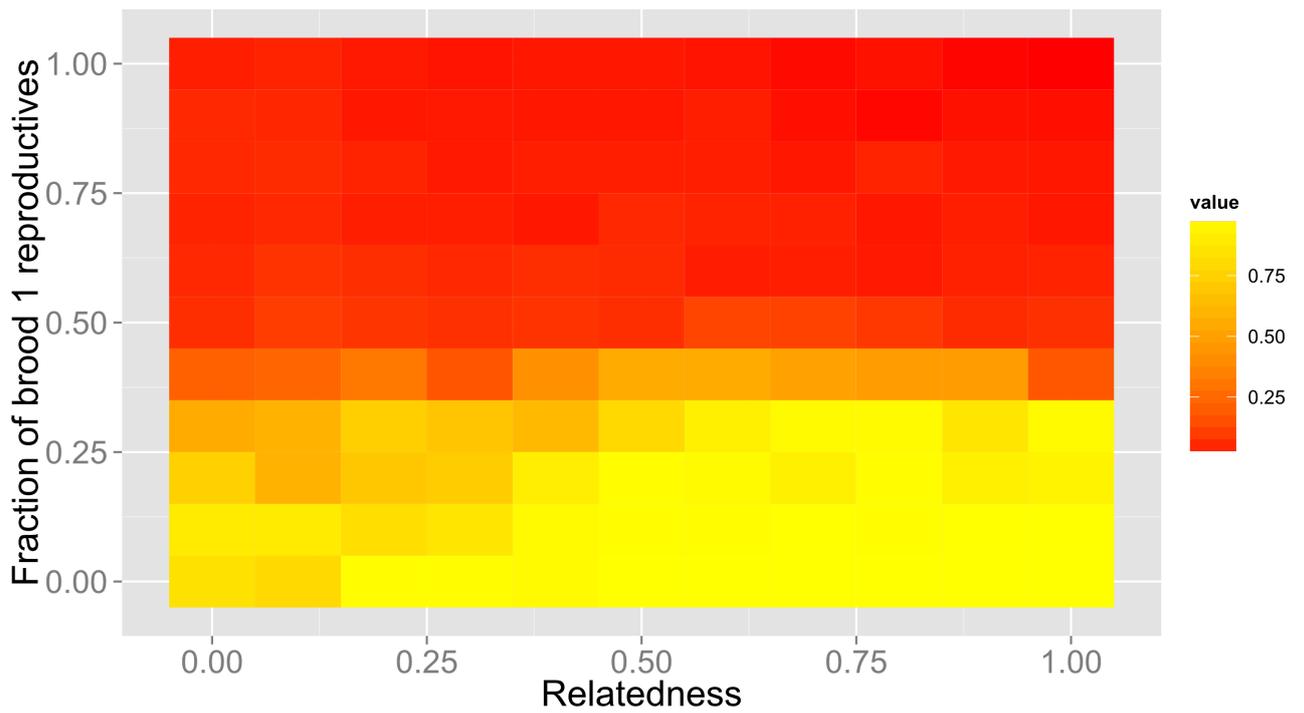


Figure 3: Effect of relatedness and size of worker force on evolution of semisociality. Larger worker force from the first brood is seen to facilitate semisociality. Relatedness between the dominant and subordinate has a marginal effect as well. However, it is evident that increase in relatedness cannot facilitate crossing of the 0 selection gradient line which is seen as a plateau in this graph

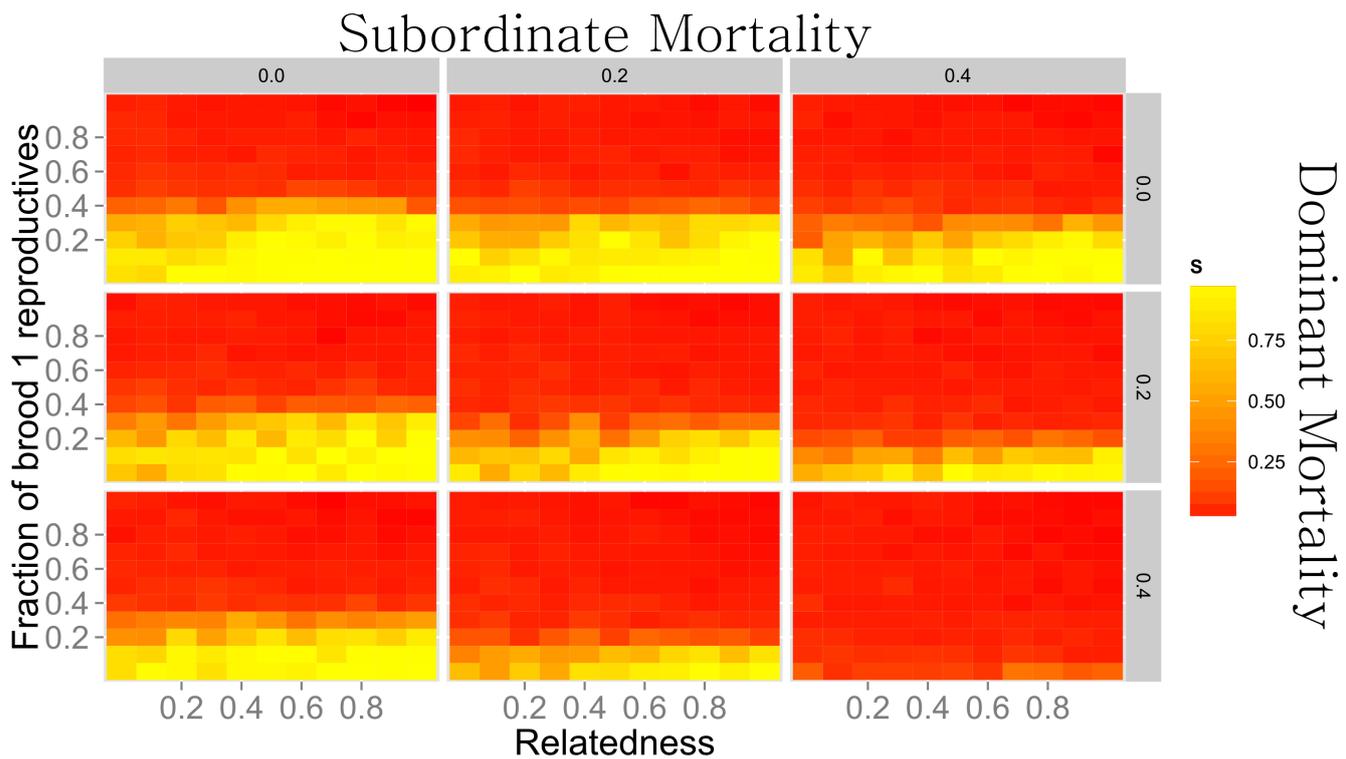


Figure 4: Effect of survival benefit on evolution of semisociality. Empirical evidence suggests lesser failure of larger nests. Here, mortality of solitary females is fixed at 0.5 and mortality of social females is varied from 0 - 0.4 thus providing them with a survival benefit. Each graph in the above panel is a $1 - h$ vs. r graph as depicted in 3

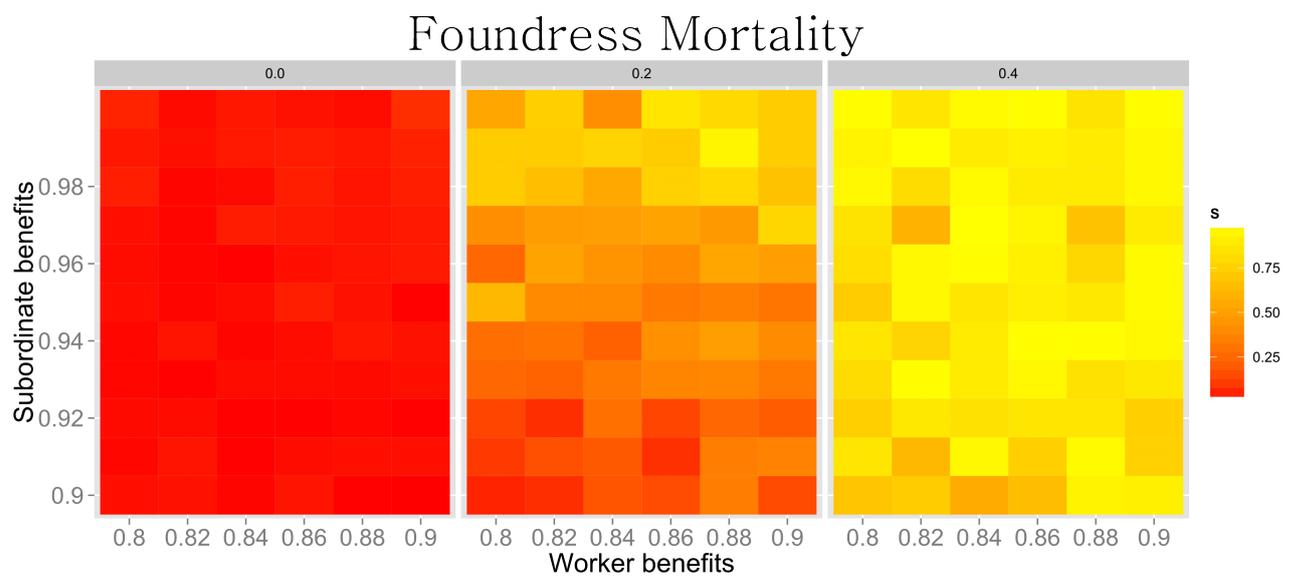


Figure 5: Effect of reproductive benefits on evolution of semisociality. Social nests also have subordinate helpers. Each panel in this figure is a graph of subordinate benefits vs. worker benefits. To eliminate any survival benefit, mortalities of all three classes of females was equated. A look at adjacent graphs in the panel above suggests social nests enjoy assured fitness returns whose benefit increases when chances of nest perishing increases

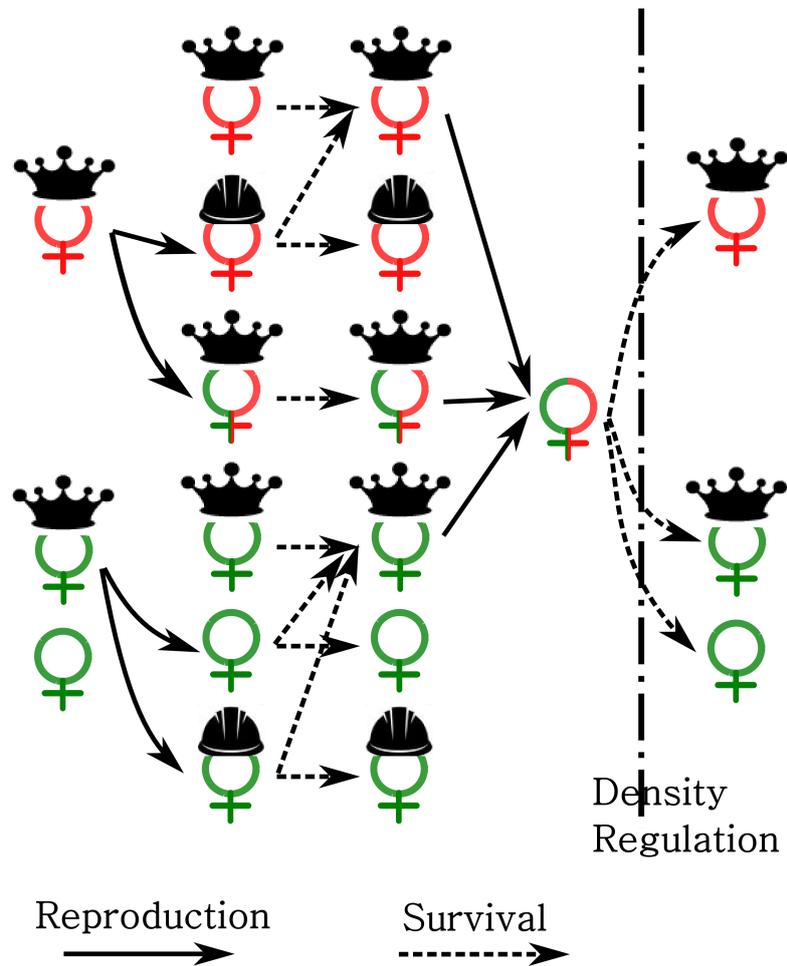


Figure 6: Female hibernation life history followed by the Polistinae wasps split into four stages (i) Reproduction for brood 1 (ii) Survival of nest foundresses (iii) Reproduction for brood 2 and (iv) Founding nests the subsequent year. These stages are used to build separate transition matrices and hence make progress with the analytical model easier

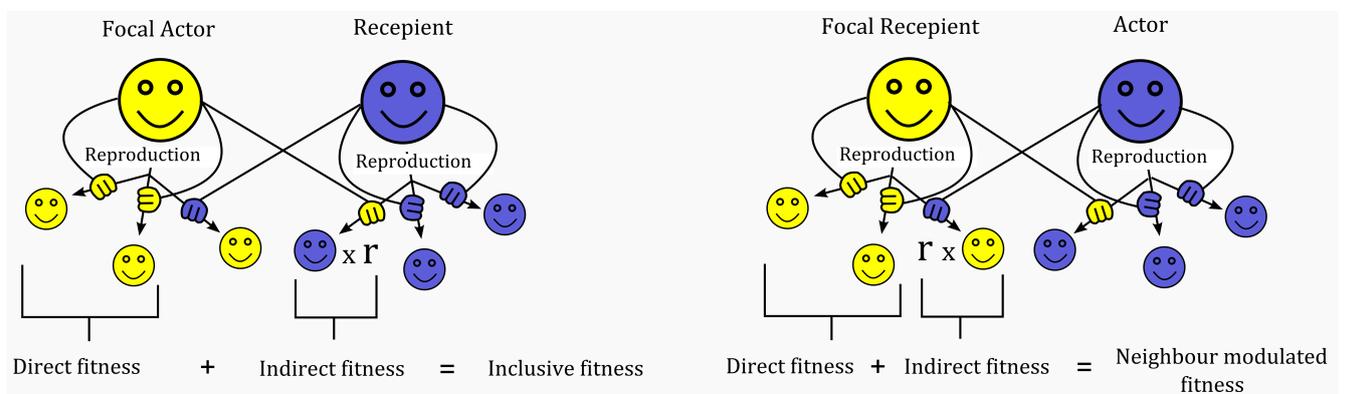


Figure 7: Comparison between the inclusive fitness (actor-centred) approach and direct fitness or neighbour modulated fitness (recipient-centred) approach. Inclusive fitness accounts for fitness effects on a number of recipients due to the action of a focal actor as opposed to neighbour modulated fitness, which accounts for the behavioural effects of all actors on one focal recipient

TABLES

Table 1: Summary of static model paramters with the value each took through simulations

Static Parameters List		
Symbol	Meaning	Value
μ_m	Mutation rate	1×10^{-4}
σ_m	Mutation step size	0.2
μ_q	Mean nest quality	0.25
σ_q	standard deviation in nest quality	0.125
μ_e	Mean environmental noise	0.25
σ_e	standard deviation in environmental	0.125
F_1	Poisson parameter to pick number of offspring a solitary foundress has	10
z	Sex ratio	0.5

Table 2: Summary of manipulated model paramters with the range of values each took through simulations

Dynamic Parameters List		
Symbol	Meaning	Value
b_s	Additional number of queen offspring/queen offspring due to presence of a subordinate in the nest	0.8, 0.9 - 1
b_w	Additional number of queen offspring/queen offspring due to presence of a worker in the nest	0.5, 0.8 - 0.9
$f = 1 - h$	Fraction of brood 1 females that are reproductives	0 - 1
r	Relatedness between the dominant and the subordinate in the nest (Coded as the probability of attempting associations with a sister in this model)	0 - 1
D_d	Dominant mortality rate	0 - 1
D_c	Subordinate/cofoundress mortality rate	0 - 1
D_l	Lone foundress mortality rate	0 - 1

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