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Kinship, parental manipulation and evolutionary origins of eusociality

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One of the hallmarks of eusociality is that workers forego their own reproduction to assist their mother in raising siblings. This seemingly altruistic behaviour may benefit workers if gains in indirect fitness from rearing siblings outweigh the loss of direct fitness. If worker presence is advantageous to mothers, however, eusociality may evolve without net benefits to workers. Indirect fitness benefits are often cited as evidence for the importance of inclusive fitness in eusociality, but have rarely been measured in natural populations. We compared inclusive fitness of alternative social strategies in the tropical sweat bee, *Megalopta genalis*, for which eusociality is optional. Our results show that workers have significantly lower inclusive fitness than females that found their own nests. In mathematical simulations based on *M. genalis* field data, eusociality cannot evolve with reduced intra-nest relatedness. The simulated distribution of alternative social strategies matched observed distributions of *M. genalis* social strategies when helping behaviour was simulated as the result of maternal manipulation, but not as worker altruism. Thus, eusociality in *M. genalis* is best explained through kin selection, but the underlying mechanism is likely maternal manipulation.

1. Introduction

In eusocial species, many offspring forego most or all direct reproduction to help their queen mother produce more siblings [1]. The predominant evolutionary explanation for this apparent altruism is that increased indirect fitness benefits from helping relatives outweigh losses in direct reproductive success [2]. This suggests that the phenotype that is targeted by selection in the evolution of eusociality is worker behaviour. Theory also predicts that maternal behaviour may drive eusocial evolution if queens gain fitness benefits through manipulating their daughters into helping [3–8]. If these fitness gains are sufficiently large, eusociality can theoretically evolve through maternal manipulation without any net inclusive fitness benefits to workers [4,6]. This is an important distinction, because understanding the mechanism underlying eusocial behaviour is necessary for understanding how it evolves [9]. Worker altruism and maternal manipulation are non-mutually exclusive mechanisms for eusocial evolution, and both are consistent with inclusive fitness theory [10]. However, some recent critics have argued that eusociality can evolve without significant relatedness between potential cooperators (i.e. in the absence of kin selection; [11], but see [12]). Resolving how relatedness, worker altruism and parental manipulation influence eusocial evolution requires calculating inclusive fitness across individuals that differ in social life histories, but the lack of appropriate life-history variation within most eusocial species generally precludes this fundamental test [12]. As a result, inclusive fitness estimates are typically based on assumed productivity and survival contributions among nest-mates [13].

We overcome this limitation by measuring inclusive fitness in a facultatively eusocial sweat bee (*Megalopta genalis*). Species with variable social behaviour

allow quantification of direct fitness costs to workers and benefits gained by queens as a result of eusociality, through comparisons with the fitness outcomes of non-social strategies. Eusocial and solitary nests of *M. genalis* co-occur throughout the dry season on Barro Colorado Island (BCI), Panama [14,15]. Eusocial nests are characterized by a strict division of labour: workers forage, feed their queens through trophallaxis, do not typically mate or lay eggs and have lower levels of juvenile hormone and the yolk precursor protein vitellogenin, which are associated with reproductive status [14,16–19]. Among successful foundresses, 34.5% produce only sons in their first brood, despite having mated, and remain solitary without workers. Foundresses that rear at least one daughter in their first brood may become queens of eusocial nests (46.9%), be superseded by a daughter (12.4%), or remain solitary if all daughters disappear without helping (i.e. 'failed eusocial', 6.2%) [14]. This variation in social organization allows for direct fitness comparisons of eusocial queens and workers with the presumed solitary ancestral life history. Such estimates of individual inclusive fitness are required to elucidate the mechanisms driving the expression of eusociality.

2. Methods

(a) Observation nests

Our study design reduced variation in nest conditions, seasonal effects, local resource availability and other factors that may otherwise influence reproductive success or social behaviour. Each nest was constructed with a standardized piece of extra-light density balsa wood ($11 \times 76.2 \times 228.6$ mm) secured between two panes of transparent acrylic, covered with opaque fabric and hung under a plastic roof (see fig. 1 in the electronic supplementary material of reference [16]), which minimized variation in nest quality. Observation nests were hung in seven clusters of 10–15 nests throughout the 1500 ha forest on BCI; there were no differences among the clusters in any of the traits under study. This minimized variation in local environmental conditions and resource availability. Each observation nest was seeded throughout the reproductive dry season with a newly emerged female that we reared from the larval or pupal stage in tissue culture trays under ambient conditions, after collecting them from natural nests. This minimized seasonal variation and variation in early social experience among our foundresses. Nests were plugged with a piece of cotton for a few hours after females were introduced to the nests. After this initial adjustment period, females could leave and enter the nest freely. Observation nests were collected throughout the study period to preserve the individuals for genetic parentage analysis and physiological assays. (It is not possible to genotype *M. genalis* individuals non-destructively.) There were no significant differences in nest tenure or collection date among foundresses with different social outcomes, and social and solitary nests develop concomitantly and asynchronously throughout the dry season [14]. Differences in social behaviour are therefore unlikely to be driven primarily by environmental limitations. This pattern also ensures that our measurements of reproductive activity were not biased towards a particular social phenotype. Owing to our collection regime, we cannot be certain of the total reproductive success of each nest, but observed patterns of egg-laying in each subsequent brood indicate diminishing returns (see table 2 in [14]). Furthermore, the end of the study period coincided with the onset of the rainy season, which typically coincides with a marked reduction in reproductive activity [15]. This suggests that we captured the majority of the reproductive activity in most of our nests. Behaviour in these nests appears similar to behaviour of bees in natural nests. For additional details, see [14–16].

(b) Inclusive fitness calculations

We applied behavioural and genetic data to a general equation from Grafen to calculate inclusive fitness (I_F) on an individual basis ([20]; see electronic supplementary material, equations S1–S4):

$$I_F = (G_n \times r_o) + (G_s \times r_o) + (G_o \times r_r), \qquad (2.1)$$

where G_n is the fitness effects of each individual's genotype through non-social traits, G_s is the fitness effects of each individual's genotype through social traits and G_o is the fitness effects of each individual's genotype on the offspring of others. These fitness effects are weighted by relatedness to one's own offspring (r_o) and relatedness to the offspring of those receiving fitness effects (r_r). Filling in these variables requires assumptions about the genotypic mechanism underlying helping behaviour. For example, the extra offspring produced in eusocial nests may be counted as G_o and count toward worker I_F if helping behaviour is the result of worker altruism and is completely determined by daughter genotype. Conversely, if daughters' helping behaviour is the result of maternal manipulation, and is determined entirely by foundress genotype, then extra offspring produced as a result of help from workers would be counted as G_s, and would count toward foundress I_F. We made two estimates of I_F for each worker and foundress in the study—one assuming that all social interactions are the result of daughter genotypic effects and another assuming all social interactions are the result of foundress genotypic effects (see electronic supplementary material, equations S1–S4, figure S1 and table S1). This provides the extreme values of I_F, with the reality likely in between.

Estimating inclusive fitness also requires knowledge of how much fitness individuals in eusocial nests would have achieved if they had pursued a solitary lifestyle. We derive estimates of these fitness components based on productivity in solitary nests (i.e. the mean number of offspring produced by foundresses without workers; electronic supplementary material, table S1). To account for the variation in reproductive success among foundresses, we repeated each calculation using the lower and upper bounds of the 95% confidence interval for each constant included in each equation (electronic supplementary material, table S1). This level of accuracy is not possible in species for which all individuals follow a eusocial life history.

We estimated inclusive fitness for each of 180 foundresses that at least built an entrance collar in observation nests. Building an entrance collar is the first step in nest initiation, and thus indicates the intent of these females to begin nesting [15]. Many ($n = 67$) of these foundresses disappeared before their first brood of offspring emerged. In these cases, foundress inclusive fitness is zero, because unguarded nests are quickly destroyed by predators [21]. We calculated inclusive fitness for a single worker in each of 56 nests with at least one worker (53 eusocial nests, three superseded nests), and divided this equally across each worker in the 20 nests that had more than one worker. All empirical values are from reference [14]. Some components of fitness estimates are based on arithmetic means, rather than based on geometric ones [22] because we did not measure changes across generations, and there was thus no difference in scale to account for.

(c) Computer simulation

We modelled the evolution of eusociality based on field-derived data for *M. genalis*. All simulations assume a stable haplodiploid population where 1000 singly mated foundresses initiate nests each generation. Based on field data from *M. genalis* on BCI [14], 63% of initiating foundresses survive to successfully raise their first brood (113 of 180 initiated nests). Of those 113, 39 were classified as solitary as they only laid male eggs in the first brood [14]. Survival rate for solitary foundresses to successfully raise a second brood is 13 of 23 (57% of nests left to attempt

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a second brood). Sixteen nests were collected at this stage and, therefore, it is unknown if they would have survived to make later broods. Nests were collected randomly with respect to sociality, however, so this was not likely to introduce a bias in survival and reproductive estimates. Survival rate to successfully raise a third brood is 50% (one out of two, with the other 11 collected before attempting a third brood). Mean productivity for solitary foundresses from field data is 3.64 offspring in the first brood (142 offspring per 39 nests), 2.00 offspring in the second brood (26/13) and 2.00 offspring in the third (2/1). Nests in which queens lay female eggs in the first brood can become 'eusocial' by retaining a daughter as a worker. Of the 74 nests in which the queen raised at least one female offspring, 53 became eusocial (both queen and worker survived) and 97% (34 of 35; 18 nests were collected at this stage) successfully raised a second brood. In 14 nests, the queen disappeared before her daughter (a supersedure), and five of these superseding daughters survived to successfully raise a second brood. Seven nests were classified as failed eusocial (no first brood daughters stayed as workers). Of these, three survived to raise a second brood. None of the nests in these latter categories was collected at this stage. Only some eusocial nests successfully raised a third brood (3/6; the remaining 28 were collected before attempting a third brood). None of the superseded or failed eusocial nests produced a third brood. The study period did not extend beyond a third brood for any nest. Mean productivity from field data across all nests that raised females is 3.64 offspring in the first brood (269/74), 3.00 offspring in the second brood of successful nests (126/42) and 1.33 offspring in the third brood of successful nests (4/3). The productivity values for these nests include both females that became workers and the offspring from superseding daughters. The simulation model takes both factors into account by removing workers from the dispersing pool of females, and having superseding females produce their own genetic daughters and sons (i.e. superseding workers mate and reproduce, as observed in *M. genalis* [14]).

At the start of a simulation, all nests are solitary and no daughter will assume a worker role. Offspring are raised in brood sets, no nest survives past raising a third brood cohort, and any given offspring has an equal probability of being female or male (i.e. genetically, all foundresses are equally likely to lay female or male eggs for each reproductive event). All offspring disperse into a common mating pool. Every female mates with one randomly chosen male. Thus, males can potentially mate with more than one female. Each generation, 1000 mated females are randomly picked from this pool to initiate new nests. The remaining females are discarded, and thus represent females that dispersed from their natal nest, but did not successfully found a nest. Thus, dispersal mortality is modelled as a constant and will not differentially favour any strategy.

For the first 5000 generations, only sex ratios are allowed to evolve. There are two sex ratio loci: one determines the sex ratio in the first brood, and the second determines sex ratio in subsequent brood cohorts. Thus, it is possible for protandry or protogyny to evolve. The initial population has 100% alleles for a 50:50 sex ratio at both loci. Mutation randomly introduces sex-biasing alleles producing ratios that range from 0:100 to 100:0, at 5% intervals. Mutation rate is initially set at 0.01 per locus to introduce a variety of alleles over the first 2500 generations. Thereafter, it is reduced to 0.001 per locus, allowing directional selection to be more effective. Sex ratios are additive in effect: heterozygous foundresses produce the mean value across their two alleles. For example, a foundress with alleles for 25% and 75% male bias, will produce female and male eggs with equal likelihood.

For the next 5000 generations, maternal manipulation alleles are allowed to mutate into the population at a rate of 0.01 for the next 2500 generations and 0.001 thereafter. The manipulation 'effectiveness' of alleles ranges from 0% to 100%, at 5% intervals. Maternal manipulation allows a foundress to potentially force one daughter from the first brood (if a female egg has been laid) to become a worker. The effect is additive. For example, a foundress with alleles for 25% and 75% manipulation strength will have a 50% chance of converting any given daughter into a worker. Females from later broods never become workers, as is observed in the field. In our simulation, no more than one daughter becomes a worker on any nest. (The median and arithmetic mean $\pm$ standard deviation number of workers observed in eusocial nests in the field are 1.0 and 1.45 ± 0.64, respectively.) Sex ratios can continue to evolve over time, along with allele frequencies for producing workers. Mortality rates between broods for the queen and her worker are conservatively assumed to be equal. Sex ratios and the frequencies of nest types are recorded after the 10 000th generation. All simulations are replicated 50 times.

We included two other factors into the models that are consistent with *M. genalis* life history. The first is that males are likely to be short-lived [23,24], such that first-cohort males should have little chance of mating with late-cohort females, which has been demonstrated theoretically [25], but is untested for *M. genalis*. We added a 95% mortality rate between cohorts for males. This means that, relative to a second-cohort male, the average male from the first cohort has only a 5% chance of mating a second-cohort female. The first-cohort male has only a 0.25% relative chance to mate a third-cohort female. Nevertheless, first-cohort males still have the advantage over later-cohort males in that they can potentially compete across three cohorts of females. If males outnumber females in a given cohort, all the females mate within that cohort. If, however, females outnumber males, their chances of mating within the cohort were set equal to (m_i/f_i), where m and f are the number of males and females in cohort i. The probability of mating in a later cohort was therefore equal to $(1 - m_i/f_i)$. Note that if $i > 1$, then the population of males would be the sum of those born in that cohort, plus the survivors from previous cohorts.

The second factor is the advantage that nests with a worker can be continually occupied, which potentially reduces the opportunity for unrelated females to enter unguarded nests and lay eggs [21]. Therefore, we added a 5% rate of social parasitism for the first brood of all nests. If a nest became eusocial after the first brood, this rate was reduced to zero for the subsequent broods. Social parasitism remained at 5% for solitary nests. This resulted in relatedness being slightly higher in eusocial nests than solitary nests because they became less susceptible to parasitism by unrelated females. We also reversed this effect of relatedness by making eusocial nests be more susceptible (e.g. at a 40% rate).

We repeated the simulations under conditions where the alleles influence expression of worker behaviour in the daughters, rather than expression of manipulation by foundresses. The effect of the alleles was still additive and independent of the maternal genotype. We also repeated simulations with an assumption that environmentally stochastic events arbitrarily decreased a given daughter's chance to succeed as a foundress. Such individuals became more likely to remain as workers. This effectively tests the effect of dispersal limitation on inclusive fitness gains associated with worker behaviour. Adding environmental variation in such a way had no effect on the model outcomes (see the electronic supplementary material).

3. Results

(a) Field data

We calculated two measures of I_F for 260 individual *M. genalis* females to reflect the extreme ends of a social control spectrum.
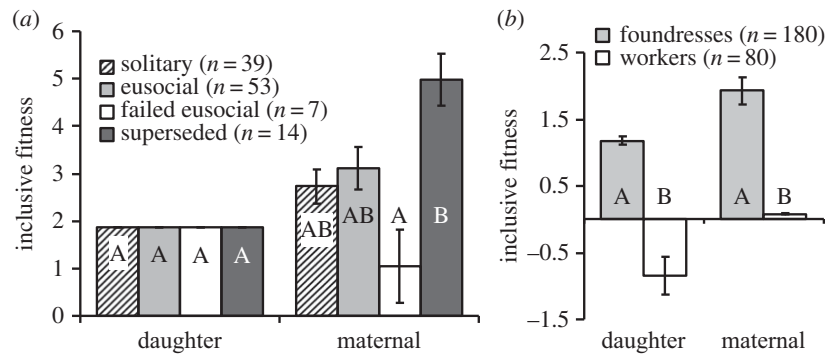
Figure 1. Comparisons of mean inclusive fitness across individuals $\pm$ s.d. Summary and test statistics are in tables 1 and 2. Letters indicate significant differences ($p < 0.05$). (a) Inclusive fitness of females that successfully reared at least one offspring but had different social outcomes, calculated under the assumption that social outcomes are regulated by daughter genotypes and maternal genotypes; Kruskal–Wallis test followed by pairwise Schaich and Hamerle *post hoc* tests. (b) Inclusive fitness of foundresses and workers under the assumption that social outcomes are regulated by daughter genotypes and maternal genotypes (*t*-test). Groups with statistically significant ($p < 0.05$) differences are indicated by the letters A and B.

Table 1. Inclusive fitness estimates for reproductive females. Inclusive fitness estimates for foundresses that successfully reared at least one offspring with different social outcomes under the assumption of daughter genotypic effects and maternal genotypic effects underlying the social interactions within each nest. Values represent the mean $\pm$ 1 standard deviation. χ^2 is from a Kruskal–Wallis test.

model	solitary ($n = 39$)	eusocial ($n = 53$)	failed social ($n = 7$)	superseded ($n = 14$)	χ^2 (without ties)	p
daughter genotype	1.87 ± 0	1.87 ± 0	1.87 ± 0	1.87 ± 0	—	—
maternal genotype	2.73 ± 2.23	3.10 ± 3.26	1.04 ± 2.04	4.97 ± 2.06	11.91	0.008

Table 2. Inclusive fitness estimates for all foundresses and all workers. Inclusive fitness estimates for foundresses and workers under the assumption of daughter genotypic effects and maternal genotypic effects underlying the social interactions within each nest. Values represent the mean $\pm$ 1 s.d. *t* and *p* are from a *t*-test.

model	all foundresses ($n = 180$)	all workers ($n = 80$)	t	p
daughter genotype	1.18 ± 0.91	-0.84 ± 2.56	9.35	<0.001
maternal genotype	1.93 ± 2.70	0.08 ± 0.07	6.11	<0.001

Estimates based on daughter genotype assume that daughters are entirely in control of whether they stay in the nest as workers. The 'extra brood' produced in a eusocial nest beyond what is produced in the average solitary nest ($\pm$ 95% confidence intervals) is thus assigned to the inclusive fitness of the daughter or the mother, depending on which genotype is controlling the social organization of the nest. At the other extreme, this decision is assumed to be regulated as an indirect genetic effect of the maternal genotype. For foundresses that successfully reared at least one brood of offspring, I_F estimates based on daughter genotype are the average expected reproductive success of all foundresses without workers, and were thus equal whether they remained solitary, became queens of eusocial nests, were superseded, or failed to keep workers (figure 1a and table 1). When I_F estimates are based on maternal genotypic control, superseded foundresses have significantly higher I_F than those whose daughters disappeared without helping, but queens and solitary foundresses have equal I_F (figure 1a and table 1). This supports previous results that

M. genalis foundresses that attempt to recruit workers have similar reproductive success to those who remain solitary [14].

Megalopta genalis workers have significantly lower I_F than females that found nests, including those that fail to raise any brood, when estimates are based on daughter genotype control (figure 1b and table 2). In some cases, workers have negative average I_F, because some eusocial nests have lower productivity than the average solitary nest. Worker I_F is also lower than foundress I_F when estimates are based on maternal genotype control, but is positive on average (figure 1b and table 2). These results were robust within the 95% confidence intervals of field-derived measures of foundress and solitary female fitness (electronic supplementary material, tables S2 and S3). This comparison illustrates that working is least deleterious, and therefore less strongly selected against in daughters, when the effects result from maternal genotype. Overall, our results support previous findings that females do not achieve higher fitness by helping, relative to nest founding [26–28], and suggest the
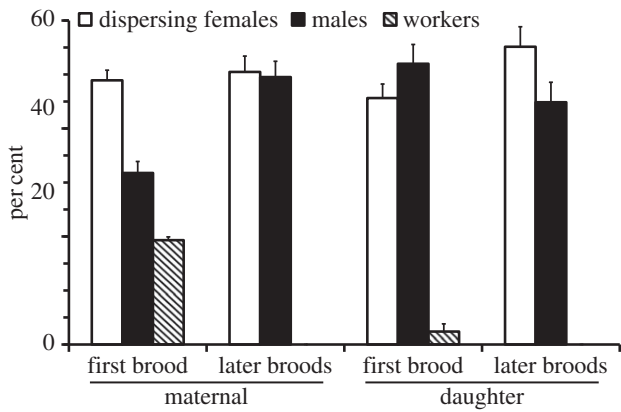
Figure 2. The mean (+1 s.d.) percentages of offspring that became dispersing females, males and workers in the first and later broods (second and third broods combined) in the mathematical simulations. All females born in later broods were assumed to disperse. Helping is determined either by the mother's or daughter's genotype.

evolution of eusociality is more likely to be commensurate with maternal inclusive fitness gains [5,29].

(b) Simulation models

We simulated conditions under which maternal and worker behaviour leads to eusociality based on field data from *M. genalis* [14], and two parameters that are typical for bees, but are assumed for this species: (i) males are short-lived and those produced early in the season are unlikely to mate with late-season females [23,24]; (ii) solitary nests are not as well guarded, and thus more likely susceptible to brood mortality [21]. The results match two observed natural patterns: (i) female-biased emergence occurs early in the season, followed by increased male production (figure 2) and (ii) both solitary and eusocial nests co-occur in populations, although a better quantitative fit was achieved by increasing our estimate of eusocial nest mortality between first and second broods from our field estimate of 3% to 25% (figure 3).

We used this model to further explore two fundamental questions regarding the evolution of eusociality: (i) the importance of relatedness among workers and the siblings they help to raise [11], and (ii) the likelihood of eusociality evolving through maternal effects versus facultative offspring helping behaviour [3–8]. First, eusociality is uncommon when within-nest relatedness is simulated as lower in social than solitary nests (figure 3). This result is consistent with empirical data suggesting that kin selection is an important factor in the evolution of eusociality [12], but is in stark contrast to a recent model based on unrealistic survival and productivity benefits [11] that suggested eusociality evolves independent of relatedness.

Second, when modelled as a daughter-based decision to behave altruistically (or as a conditional response to environmental constraints), results are inconsistent with field-observed data. Under these conditions, simulated nests are male-biased in first broods (figure 2) and failed eusocial nests dominate at equilibrium (figure 3), meaning that daughters with genotypic control of social interactions leave the nest rather than remain as workers. Eusocial nests become more common than solitary nests only if solitary nest mortality is reduced from field estimates by 50%, but failed eusocial nests remain the most

frequent. Thus, although eusociality can theoretically evolve through either manipulation or altruism by maximizing the inclusive fitness of the individual in which the gene has its effects, manipulation requires less restrictive conditions.

4. Discussion

A defining feature of eusociality is cooperation among overlapping generations of mothers and daughters [1]. Thus, understanding the relative influence of maternal and filial behaviour as mechanisms promoting cooperation across generations is critical. Our conclusion that helping behaviour can evolve and be maintained without net inclusive fitness gains to workers is based on empirically derived estimates of the relative contribution of each female in a nest, as well as consideration of the mechanisms underlying these life-history strategies and their associated fitness payoffs.

Inclusive fitness disparities between *M. genalis* reproductive females and workers are consistent with differences in their physiology, and together help elucidate the mechanisms underlying eusocial behaviour in this species. *M. genalis* females do not become workers because they are less fecund, as workers mate and lay eggs at similar rates to queens when the latter are removed [17]. *M. genalis* workers are generally smaller than dispersing females and queens, and solitary reproductive females are smaller than queens [16]. Small size does not inherently preclude functioning as a reproductive, however, as size is unrelated to fecundity, and we do not find evidence of a trade-off between offspring size and offspring number [14,16,17]. Small body size may instead be disadvantageous for females in dispersing or within-nest social competition. Size-based life-history decisions are consistent with maternal manipulation because, as in other Hymenoptera [30], *M. genalis* foundresses determine offspring size through larval nutrition [31]. A small daughter may be making the best of a bad situation by helping, but her expected inclusive fitness is lower than for most of her nest-founding sisters (figure 1*b*). Given that helping and dispersing females are temporally and spatially concomitant, it is unlikely that ecological constraints are the sole factor in shaping this decision. These empirical observations are consistent with the maternal manipulation model of eusocial evolution, but additional work is needed to experimentally demonstrate the role of maternal manipulation.

A key result in our simulations is that alternative life histories (i.e. both eusocial and solitary reproductive strategies) coexist at equilibrium in the same population, thus matching the natural history of *M. genalis* and potentially explaining the maintenance of behavioural polymorphisms more generally. This result differs from most kin selection models of cooperative breeding based on maximizing inclusive fitness, which tend to predict that populations should either be all solitary or all eusocial [32] or predict stable coexistence only at estimates of dispersal and colony size far beyond what are observed in nature (as in [11]).

Our results reconcile claims made by supporters and critics of kin selection by demonstrating that relatedness is an essential component of eusocial evolution, but that helpers do not necessarily improve their inclusive fitness by foregoing reproduction (see also [33]). These findings suggest the earliest evolutionary steps towards eusociality are most favoured if mediated through maternal manipulation.
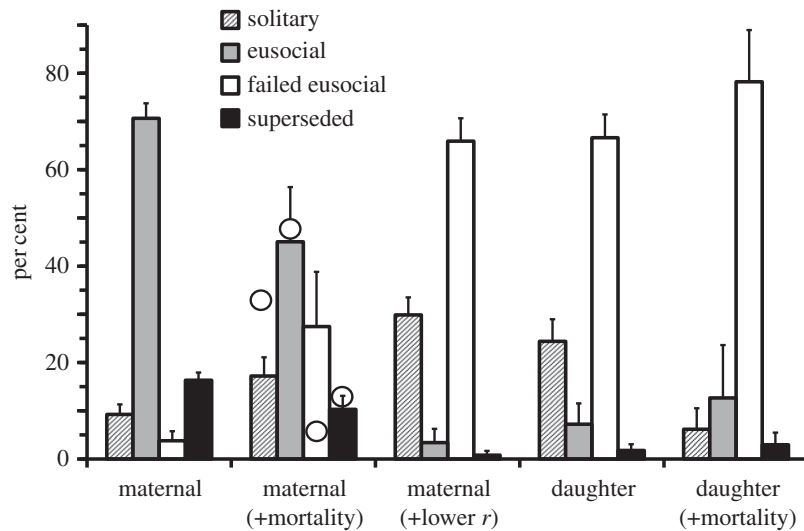
Figure 3. The mean (+1 s.d.) percentages of nests that are eusocial, superseded, failed eusocial and solitary compared across simulation variants. Variants include maternal: helping is modelled as an effect of maternal genotype (survival and productivity parameters are from field data); maternal (+mortality): survival between first and second brood is reduced to 75% for eusocial nests; maternal (+lower r): relatedness between foundress and offspring is lower in eusocial nests than solitary nests; daughter: helping is modelled as an effect of daughter genotype (survival and productivity parameters are from field data); daughter (+mortality): survival between first and second brood is reduced to 35.5% for solitary nests. Overlaid white dots represent frequency of nest types observed in the field.

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