



To leave or to stay: direct fitness through natural nest foundation in a primitively eusocial wasp

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Abstract

Dispersing from the natal nest to found new nests is an avenue for gaining direct fitness for workers in some primitively eusocial insects, especially in species with a perennial nesting cycle where males are present throughout the year. Such nest foundation is difficult to study in nature or in small laboratory cages. Hence, we have investigated the dynamics of nest foundation by workers of the primitively eusocial wasp *Ropalidia marginata* inside closed walk-in cages so that we could locate and observe every event of nest foundation. Starting with nine parent nests we observed the dispersal of female workers that initiated 9 single-foundress and 20 multiple-foundress nests. Wasps congregated outside their parent nests and engaged in dominance–subordinate interactions before initiating multiple foundress nests. The most dominant wasps of such aggregations became queens, and among the others, some joined the new nests as cofoundresses to become workers while the others remained in the parent nests. Solitary foundresses never participated in such off-nest aggregations. Solitary foundresses and future queens of multiple foundress nests engaged in self-feeding behaviour outside their parent nests, a behaviour not performed by wasps that did not initiate new nests. Queens of new nests gained immediate direct fitness. Although the cofoundresses continued to gain only indirect fitness, they are expected to have a higher probability of gaining direct fitness in the future as compared to the corresponding probability in their much larger parent nests. These findings underscore the importance of direct fitness in the evolution of cooperation in primitively eusocial insects.

Keywords Nest foundation · Direct fitness · Primitively eusocial wasp · *Ropalidia marginata* · Cooperation

Introduction

Cooperation among colony members, often involving reproductive altruism, is a hallmark of many insect societies. Kin selection is expected to favour the evolution of altruistic workers because they can gain indirect fitness by helping their colony members who are genetically related to them (Hamilton 1964a, b; Wilson 1971). In many advanced eusocial species such indirect fitness is the only

avenue of gaining fitness for workers (Holldobler and Wilson 1990; Crozier and Pamilo 1996; Bourke 2011). In many primitively eusocial species on the other hand, workers retain the ability to reproduce and may do so to some extent either in the presence or in the absence of their queens (West-Eberhard 1969a; Ross and Matthews 1991). Because indirect fitness was a novel concept in inclusive fitness theory, much empirical effort has gone into documenting how workers gain indirect fitness (Bourke 2011). On the other hand, much less effort has gone into investigating the possibility of workers, especially in primitively eusocial species, gaining direct fitness. Although we have studied the social biology of *Ropalidia marginata* over many years and although we know that workers can leave their natal nests and found their own new nests (Gadagkar 2001), we have little information about this phenomenon or the dynamics of nest foundation. The main reason for this is that departing foundresses are hard to follow in nature and typical laboratory cages do not provide adequate space for the coexistence of old and new nests.

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Hence, we have constructed large walk-in cages to enhance the chances of witnessing nest foundation. This paper contains the first report of such an effort involving the study of 29 newly initiated nests starting from nine parent nests.

The tropical primitively eusocial wasp *Ropalidia marginata*, the subject of this study, is an excellent species for investigating the behavioural dynamics of nest foundation. In each *R. marginata* colony, there is a queen who is the sole egg-layer of the colony, and several workers who do not lay eggs in presence of the queen although they can do so in the absence of the queen (Gadagkar 2001). It has a perennial nesting cycle; nests are initiated throughout the year by a solitary foundress or by small groups of female wasps (multiple foundress nests) in which one becomes the egg-layer and the rest function as workers and the latter are referred to as cofoundresses (Gadagkar 2001). And moreover, mating is not an essential requirement for nest foundation (Gadagkar et al. 1988) or to become the sole egg-layer of a colony despite the presence of other mated individuals (Chandrashekara and Gadagkar 1991); both virgin and mated females have equal chances of becoming the queen when paired under laboratory conditions (Shukla et al. 2013).

Materials and methods

Experimental setup

We collected nine naturally occurring post-emergence colonies of *Ropalidia marginata* from Bangalore (12.97°N, 77.59°E), India and transplanted each nest inside a separate walk-in cage of dimension 2.13 m × 2.13 m × 2.13 m (Photo S1). The experiment was conducted in two phases. In the first phase, three nests were transplanted in December 2013 and the experiment was terminated in July 2014, and in the second phase, six nests were transplanted in February 2016 and the experiment was terminated in July 2016. After transplantation, we uniquely colour-coded all the wasps on the nest using Testors® quick-drying enamel paints and constructed a nest map, which is a record of composition and position of brood at any time point. We provided an *ad libitum* supply of larvae of the rice moth *Corcyra cephalonica* and dilute honey and water (replenished every day), and pieces of soft wood as building material in at least two arbitrarily changing places. Primitively eusocial wasps build nests on almost any substrate, and hence there was ample area for initiating nests inside each of the walk-in cages. For each parent nest, we identified the queen by observing egg-laying behaviour prior to quantitative behavioural observations.

Data collection

For each transplanted nest (henceforth: parent nest), we marked newly eclosed wasps every day and updated nest maps on alternate days until the nest was abandoned. We collected 5 h of behavioural data spread across 2 days per week for each nest. Not only did we record the behaviour of wasps present on the parent nests, but also all incidents of off-nest interactions and self-feeding behaviour. Behavioural observations consisted of randomly intermingled scans to record long-duration behaviour and all-occurrence sessions to record short-duration behaviour of wasps at any moment [for details of the behaviour, please see electronic supplementary material and (Gadagkar 2001)]. Each scan and all-occurrence session lasted for 5 minutes with a 1-minute break in between. We recorded a total of 50 scans and 50 all-occurrence sessions (AOS) per week for each nest. We also took census of the wasps for each nest once every night after 1930 h to record the presence or absence of any particular wasp on the parent nest and also the position of the wasps that rested outside their parent nests. We chose this particular time as we know from our previous observations that wasps return to their nests before it gets completely dark at night, and if a wasp is not present in the nest at this time, it does not return any time before the next morning. We collected the wasps which were found dead during the experiment, labelled them according to their individual as well as nest identity and stored them inside a –20 °C freezer. Following abandonment of a parent nest, we waited for the eclosion of at least one adult wasp from each of the new nests (henceforth: offspring nest) initiated inside the cage to record whether an offspring nest was successful or unsuccessful; an offspring nest was labelled ‘successful’ only when at least one adult individual had successfully eclosed from it. We terminated the experiment and collected all the wasps after the parent nest was abandoned or the offspring nests had produced at least one offspring each, which ever was later. Following this we collected all the wasps from all the offspring nests and stored them inside a –20 °C freezer. We define foundresses as wasps that participated in the new nest foundation and were present at the site of new nest initiation before the first egg was laid, whether it was a single-foundress nest or a multiple-foundress nest. In the multiple-foundress nests, cofoundresses were defined as those wasps among the foundresses that did not become egg-layers and that acted as workers in the newly initiated colony. We defined joiners as those wasps that joined newly initiated nests as workers after one or more eggs were laid.

Data analysis

We performed all data analysis using R studio (version 3.5.2) (RStudio Team 2015) (please see the electronic

supplementary material for details of the R-packages used and the details of the statistical models). We compared the behaviour of females that became foundresses and those who stayed back using data on behaviours performed both on the parent nests and in the off-nest aggregations, collected 2 weeks before each new nest was founded. We fitted a generalised linear mixed model with binomial error structure to identify the variables that significantly affected the probability of staying at the parent nest or leaving the parent nest to become a foundress. Using linear models, we compared the behaviour of the wasps that became the solitary foundresses, queens and cofoundresses of multiple foundress nests. We used a Mann–Whitney U test to compare the time taken for eclosion of the first adult wasp from solitary and multiple foundress nests. For computing the productivity of the nests on the day of eclosion of the first adult offspring, we measured the weighted sum of the total brood present. We assigned the different weights to varying stages of the brood to take into account the differential investment in producing eggs, larva, and pupa. We allocated the weights based on the index of productivity with each egg receiving a weight of 1, each larva receiving weight of 2, 3 or 4 according to the stages of development, and each pupa receiving a weight of 5 (Bang and Gadagkar 2012).

Results

Characteristics of parent nests and timeline of nest foundation events

After transplantation inside the walk-in cages, the nine parent nests used in this study contained 69.2 ± 30.5 (mean \pm SD) wasps (median = 64), 21.9 ± 6.9 pupae (median = 21), 69.7 ± 22.4 larvae (median = 64), 23.8 ± 5.7 eggs (median = 23) and 115.33 ± 31.81 cells (median = 103) (Table S1). The mean intervals between parent nest transplantation and initiation of first and last satellite nests were 53.1 ± 22.3 days (median = 50) and 85.0 ± 13.1 days (median = 91), respectively. Parent nests were abandoned between 113 and 186 days (mean \pm SD = 145.4 ± 27.7 ; median = 149) after transplantation. We observed a total of 29 new nests being initiated in the walk-in cages; the numbers of new nests per parent nests ranged from 1 to 7. A total of 76 wasps left their parent nests to become foundresses to initiate either solitary or multiple foundress nests. Among the 529 wasps that did not become foundresses, 138 became joiners in new nests and the remaining 391 stayed with their parent nests. As new nests were initiated, the parent nests began to decline with the reduction not only in the number of adults but also in the brood. We designated a parent nest as abandoned when there were no adult wasps left on it. After nearly all the workers had left or died, queens of parent nests

left their nests and sat in one of the corners of the cage and were found dead after 1–2 days; they never initiated new nests. In four nests queens were the last ones to leave the parent nests before it was abandoned. In the remaining five nests queens left their nests 2–5 days (Mean \pm SD = 3.0 ± 1.2) before the nest was finally abandoned. During the declining phase of the parent nests (when there were no pupae or larvae in them), all adults that eclosed left the nests and became joiners in one of the newly initiated nests, although some of them left their parent nests and became joiners even before it started declining. As only one parent nest was transplanted inside each walk-in cage, foundresses and joiners in each new nest initiated inside a walk-in cage, came from the same parent nest. The detailed timelines of events following transplantation of each of the nine parent nests into walk-in cages are given in Figs. S1–S9.

Characteristics of offspring nests

Of the 29 nests newly initiated from the 9 parent nests, 9 (31%) were solitary foundress nests and 20 (69%) were multiple foundress nests. The proportion of newly initiated multiple foundress nests was significantly greater than the proportion of newly initiated solitary foundress nests (Contingency Chi square, $\chi^2 = 8.345$, $p = 0.004$). Of all the wasps from nine parent nests, 1.48%, 3.31% and 7.77% became solitary foundresses, queens of multiple foundress nests and cofoundresses, respectively. The mean number of foundresses initiating multiple foundress nests was 3.4 ± 0.8 , with a range from 2 to 7. All nests that were initiated inside the walk-in cages were successful, i.e., at least one adult wasp eclosed from each nest. The time taken for eclosion of the first adult offspring from the solitary foundress nests (54.6 ± 2.6 days) was not different from the corresponding time for multiple foundress nests (53.1 ± 3.4 days) (Mann–Whitney U test, $U = 114.5$, $p = 0.253$; $N = 9$ and 20; Fig. S10 and Table S2). However, the productivity of nests on the respective days of eclosion of the first adult offspring was significantly greater for multiple foundress nests compared to solitary foundress nests (Mann–Whitney U test, $U = 173$, $p < 0.001$; $N = 20$ and 9; Fig. S10). Among the first eclosed wasps from the new nests, 6 were males and 23 were females; the proportion of females being significantly higher than that of the males (contingency Chi square, $\chi^2 = 19.931$, $p < 0.0001$).

Age of foundresses

Of the 76 foundresses, 70 eclosed after the parent nests were transplanted into the walk-in cages and therefore their ages were known exactly, while the exact ages of the remaining six foundresses were not known because they were from among the wasps brought from nature. On the day of each

new nest initiation ($N=29$), considering only the individuals eclosing in the walk-in cages, we found that there was no significant difference between the mean ages of individuals who stayed back (Mean \pm SD = 43.9 ± 10.8 days) in the parent nests and those that left (Mean \pm SD = 45.1 ± 9.4 days) to initiate a new nest (Wilcoxon matched-pair sign-rank test; $V=159$, $p=0.21$, $N=29$).

Behaviour of foundresses

Before foundation of a multiple foundress nest, two-to-five female wasps aggregated outside the parent nests and engaged in dominance–subordinate interactions; solitary foundresses were never part of any such off-nest aggregations. There was always only one such aggregation before the initiation of any multiple foundress nest. There was no other kind of interaction among the participants of the aggregations apart from aggressive interactions, nor was there any other behaviour like bringing food from the feeder or sharing food among the participants of the aggregations. The most dominant individual of the aggregation always became the queen of the newly initiated multiple foundress nests, and a few others became cofoundresses. However, 23% of wasps (Mean \pm SD = 1.6 ± 1.5) from such aggregations did not become cofoundresses and stayed back in their parent nests. Such off-nest aggregations generally occurred during the day near the feeding areas inside the walk-in cages, and neither persisted for a long time nor during the night. The frequency per hour of dominance behaviour (i.e., dominance behaviour initiated by any individual) in the off-nest aggregations was the only significant predictor of becoming a foundress as opposed to staying back on a parent nest. Frequency per hour of self-feeding behaviour while on the parent nests, and the proportion of time spent outside the parent nests were not significant predictors (Table 1; to avoid clutter, here and elsewhere, we describe the results in words and refer the reader to the corresponding figures or tables for details of the statistical tests supporting the verbal statements). Wasps that became queens of multiple foundress nests exhibited significantly higher frequency of dominance behaviour in the off-nest aggregations compared to those that became cofoundresses (Fig. 1a). Wasps that became solitary foundresses did not participate in the off-nest aggregations. A small number of individuals showed off-nest self-feeding behaviour at the feeders provided. Analysing this behaviour separately we found that none of the 529 individuals who stayed back showed off-nest self-feeding behaviour, while among those that participated in new nest foundation, only the future egg-layers (i.e., solitary foundresses and queens of multiple foundress nests) exhibited off-nest self-feeding behaviour. There was no significant difference in frequency of off-nest self-feeding behaviour between solitary foundresses and queens of multiple foundress nests (Fig. 1b).

Table 1 Parameter estimates of generalised linear model for comparing wasps that stay back in the parent nests and those that leave the parent nests to become foundresses

Predictors	Estimate	z value	p value
DB_off	2.52	5.27	<0.00001***
FE_on	0.48	0.96	0.34
TSON	0.18	0.34	0.74

DB_off frequency per hour of dominance behaviour outside the parent nests, FE_on frequency per hour of self-feeding behaviour on the parent nests, TSON proportion of time spent outside parent nests. Three asterisks (***) signifies statistically significant difference at $\alpha=0.001$

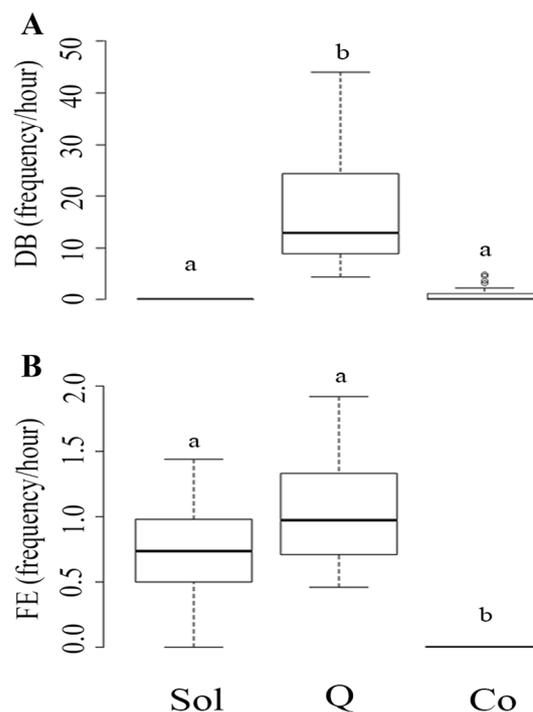


Fig. 1 Comparison of off-nest behaviour of wasps that left the parent nests to become foundresses. Sol=solitary foundresses, Q=queens of multiple foundress nests, Co=cofoundresses of multiple foundress nests. All comparisons were done using linear models at $\alpha=0.05$; bars carrying different letters are significantly different from each other. **a** frequency per hour of dominance behaviour (DB) of foundresses outside the parent nests; Sol v/s Q (linear model; estimate = -17.12 , $t=-4.46$, $p=0.0003$); Sol v/s Co (linear model; estimate = -0.77 , $t=-1.81$, $p=0.08$); Q v/s Co (linear model; estimate = 16.35 , $t=9.79$, $p<0.0001$), **b** frequency per hour of self-feeding (FE) behaviour of foundresses outside the parent nests; Sol v/s Q (linear model; estimate = -0.31 , $t=-1.75$, $p=0.09$); Sol v/s Co (linear model; estimate = 0.07 , $t=12.73$, $p<0.0001$); Q v/s Co (linear model; estimate = 1.07 , $t=16.55$, $p<0.0001$)

Joiners in offspring nests

A total of 138 wasps that initially had stayed back in their parent nests, then joined the 29 newly initiated nests after

eggs had already been laid in them. Joiners were never part of the off-nest aggregations prior to nest foundation. Solitary foundress nests received 1–2 joiners (mean \pm SD = 1.2 ± 0.5), which was significantly less than the 3–10 joiners (mean \pm SD = 6.2 ± 1.9) received by the multiple foundress nests (Mann–Whitney U test; $U = 152$, $p < 0.001$). However, when the number of joiners received per resident wasp was considered, there was no significant difference between solitary foundress nests and multiple foundress nests (Mann–Whitney U test, $U = 70.5$, $p = 0.36$). Joiners were 6–46 days old (mean \pm SD = 14.1 ± 8.2 days) on the day of joining a new nest; ages of joiners in the solitary foundress nests were not significantly different from ages of joiners in multiple foundress nests (Mann–Whitney U test, $U = 1192$, $p = 0.06$; $N = 15$ and 123 ; Table S4). However, joiners were significantly younger than the foundresses (Mann–Whitney U test, $U = 10274$, $p < 0.0001$, $N = 138$ and 76).

Drifting behaviour

Nine out of the 47 cofoundresses of multiple foundress nests were seen to revisit their parent nests from time to time (we refer to them as drifters); none of the queens of multiple foundress nests, nor any of the solitary foundresses did so. Also, we did not observe any drifting between two newly initiated nests inside a walk-in cage. Eight of the nine drifters were observed to bring food to their respective parent nests both before becoming cofoundresses and after they had become cofoundresses. Drifters maintained the same frequency per hour of bringing food to their new nests as they had been doing in their parent nests (Fig. 2) although they significantly reduced the rates of bring food to the parent nests after they became cofoundresses (Fig. 2). Eight out of the nine drifters eventually remained in their cofounded nests after 7–19 days (mean \pm SD = 13.6 ± 4.1 days) of drifting, while one returned to its parent nest after 11 days of drifting and eventually became the queen of the parent nest.

Discussion

Transplanting naturally occurring nests of *R. marginata* into large walk-in cages has permitted us to document the process of new nest foundation, a process that permits workers from the parent nests to enhance their chances of obtaining direct fitness. Having observed 29 new nest foundations from nine parent nests and comparing the behaviour of wasps who stayed back and those who left to found new nests, and comparing the behaviours of egg-layers, cofoundresses and joiners, we are now able to understand the dynamics of new nest foundation and the interplay between direct and indirect fitness. We have previously studied new nest foundation in nature documenting that 35% of newly initiated

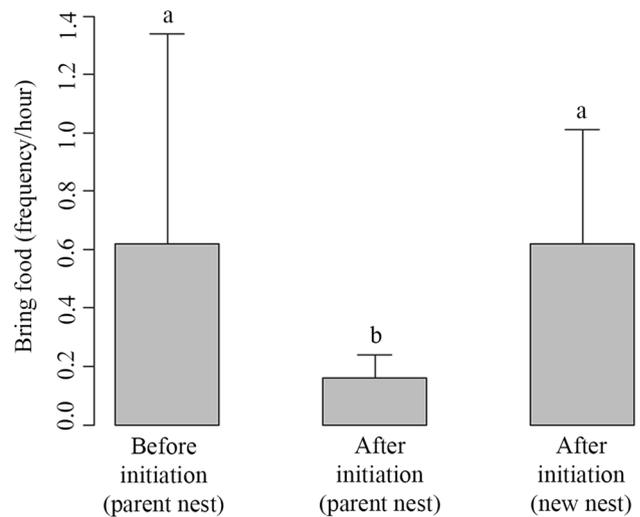


Fig. 2 Comparisons between frequencies per hour of bring food behaviour (BF) by drifters to parent nests and new nests before and after nest foundation. All comparisons were done using generalised linear model at $\alpha = 0.05$; bars carrying different alphabets are significantly different from each other. Frequency per hour of BF to parent nests significantly different before and after nest foundation (generalised linear model; estimate = 4.059, $t = 3.048$, $p = 0.006$); no significant difference in frequency per hour of BF to parent nests before nest foundation and new nests after nest foundation (generalised linear model; estimate = 0.033, $t = 0.073$, $p = 0.94$). Frequency per hour of BF to parent nest significantly less compared to new nest after nest foundation (generalised linear model; estimate = 4.026, $t = 0.821$, $p = 0.0002$)

nests are solitary foundress nests (Shakarad and Gadagkar 1995), consistent with the 31% solitary foundress nests in this study. However, this study conducted in walk-in cages, has permitted us to discover several previously unknown features of new nest foundation, such as off-nest aggregations, self-feeding behaviour by future egg-layers outside the parent nests (at the feeders), behavioural predictors of future foundresses, drifting of wasps that for a time bring food to more than one nests and joining behaviour by wasps that seem to wait until a new nest is successfully built before opting to leave the parent nest.

Perhaps our most interesting observation is that prior to every event of multiple foundress nest initiation, future foundresses as well as some wasps that did not eventually become cofoundresses, aggregated from time to time outside their parent nests, during about a week before nest foundation. We observed dominance–subordinate interactions in these off-nest aggregations. These interactions were decisive because in each case the most dominant individual in the aggregation became the egg-layer of the new nest. This means that the decision of who would be the egg-layer and who would be subordinate cofoundresses was made before nest building began. This is consistent with a previous study where we showed that when nestmate wasps of same age are

enclosed in small plastic boxes, they interact to form a dominance hierarchy before nest foundation, with the most dominant always become the egg-layer in the new nest (Brahma et al. 2018a). We have also shown previously that when experimenters knock down parent nests of *R. marginata* and remove the queens, the remaining individuals form groups of various sizes and in each group one wasp becomes dominant and subsequently becomes the queen of the new nest (Premnath et al. 1996). In our study, it is especially interesting that some of the participants in the off-nest aggregations (which incidentally were towards the lower end of the dominance hierarchy in the off-nest aggregations) stayed in the parent nests and did not become cofoundresses. It thus appears that the wasps assess their fitness options in the parent nest and in the new nest before making a decision, as also observed in *Polistes dominula* (Grinsted and Field 2017a, b). In our study, we see that even if a wasp apparently makes a wrong decision at this time, there is yet another option for correction. Some cofoundresses whom we called drifters continued to divide their loyalty between the parent and new nests, bringing food to both and in some cases returning back to the parent nests for good, as also seen in some *Polistes canadensis* (Sumner et al. 2007) and *Bombus terrestris* (Blacher et al. 2013). At least in one case a returning wasp became the new sole egg-layer of the parent nest to which she had returned. Conversely, wasps that do not become cofoundresses in the beginning can change their strategy and become joiners of the new nests after it has been successfully established.

Future direct fitness options for workers depend, among other things, on the competition they have to face from other contenders to the position of sole egg-layer in the parent nest or in the new nest. For some wasps, direct fitness options in the parent nest may be poor on account of a large number of competitors while it may be certain and immediate if they become solitary foundresses or, better still if they become queens of multiple foundress nests. For other wasps, although direct fitness may not be possible immediately in the new nests, chances in the future may be higher in the new nests with fewer competitors compared to the parent nests with more competitors. Perhaps in some cases, their chances in the parent nests may unexpectedly change because of the eclosion, death or departure of some of the competitors, leading to the behaviour of joining new nests as late comers or drifting and reversing their original decision of staying back or becoming cofoundresses, as the case may be. In *Polistes dominula*, subordinate wasps adjust their work as per their nest inheritance ranks (Cant and Field 2001), and also produce more offspring after nest inheritance as compared to becoming a solitary foundress (Leadbeater et al. 2011). The off-nest aggregations observed in our study are reminiscent of pre- or post-hibernation aggregations in *Polistes* sp. (West 1967; West-Eberhard 1969b; Gamboa and Dropkin 1979; Strassmann 1981; Röseler 1991; Ito 1993;

Dapporto et al. 2005, 2006), although there would not be any opportunities for reversing their decision and returning to the old nests in their temperate environment for these wasps.

Another interesting observation is that queens of multiple foundress nests and solitary foundresses fed themselves with *Corcyra cephalonica* larvae when they were away from the parent nests, usually at the feeding sites. This observation is interesting because such off-nest feeding has not been observed in wild colonies or colonies inside small cages, and such behaviour was restricted to those wasps who immediately laid eggs in the new nests. Such selective behaviour that is expected to enhance egg-laying capacity (Keeley 1985; Wheeler 1994), prior to new nest foundation, but only by future egg-layers, lends credence to the idea that new nest foundation is a strategy for altering the fitness trajectories of the wasps based on their own assessment of their options (Shakarad and Gadagkar 1997).

Throughout the experiment newly initiated multiple-foundress nests received significantly greater number of joiners compared to solitary-foundress nests. One advantage of joining multiple foundress nests rather than solitary foundress nests is an increased probability of success (i.e., production of at least one adult offspring) in the former compared to the latter (Shakarad and Gadagkar 1995); thus, making it highly profitable from the perspective of the joiners. On the contrary, joining a solitary foundress nest provides opportunities of remaining higher up in the reproductive hierarchy of the colony compared to that in multiple foundress nests, and thus joiners in the former have greater chances of gaining direct fitness benefits in future through nest inheritance (Cant and Field 2001; Leadbeater et al. 2010, 2011; Seppä et al. 2012; Grinsted and Field 2017a, b). Interestingly the joiners in newly initiated nests of *R. marginata* were significantly younger than the nest foundresses; this is because during the declining phase of a parent nest, the newly eclosed females left the nests and became joiners in one of the newly eclosed nests inside the walk-in cage.

We observed the eclosion of both male and female wasps from the nests initiated inside the walk-in cages, and in most of the cases, the first eclosed offspring was a female. As all the queens of nests initiated inside the cages were eclosed after parent nest transplantation, it is evident that they mated inside the walk-in cages with males that eclosed from their respective parent nests. Studies related to mating biology of *R. marginata* are always done in small plastic boxes (22 cm × 11 cm × 11 cm), and before the current study we have not witnessed mating in nature or in larger enclosures compared to the plastic boxes.

Our study suggests that direct fitness through new nest foundation is a significant component of the lifetime inclusive fitness of workers of *R. marginata*. We have recently demonstrated that gaining indirect fitness by working in their natal nests in the beginning of their lives does not

significantly reduce their chances of gaining direct fitness later in life (Brahma et al. 2018b). Such an ability to combine indirect and direct fitness is expected to promote the evolution of social behaviour in a more powerful way. Moreover, the behavioural strategies associated with new nest foundation that we have documented provide opportunities for understanding how and why some workers but not others are able to combine direct and indirect fitness.

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Authors' contribution AB and RG designed study, AB and SM conducted study, AB analysed the data, and AB and RG co-wrote the paper.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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