



## Short report

Antecedents of behavioural and reproductive dominance in pairs of the primitively eusocial wasp *Ropalidia marginata*Alok Bang<sup>a,b,c,\*</sup><sup>a</sup> Indian Institute of Science, Bangalore, India<sup>b</sup> Indian Institute of Science Education and Research, Pune, India<sup>c</sup> Chetana-Vikas (Consciousness-Development), Wardha, India

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## ABSTRACT

What factors predispose some individuals to become reproductively dominant in a group where every member can reproduce? Antecedents of reproductive dominance have often been investigated in primitively eusocial species where reproductive skew exists despite adult reproductive potential displayed by every group-member, but such studies have rarely focused on small, incipient colonies. Here, I investigated antecedents of behavioural and reproductive dominance in pairs of the Indian paper wasp *Ropalidia marginata*. Common antecedents of behavioural dominance such as body size and age were inoperative in pairs of *R. marginata*. Moreover, age and behavioural dominance, but not body size, influenced reproductive dominance in pairs. These findings are not only different from other primitively eusocial insects, but also different from the colonies of *R. marginata*. It is likely that antecedents of reproductive dominance are different not only in different species, but also change with group size within a species, such that the role of behavioural dominance to achieve reproductive monopoly remains more effective in small groups such as pairs, and becomes less effective as the group size increases. These results require further investigations into the effect of group size on individual behaviour in group-living animals.

## 1. Introduction

Extreme reproductive skew arising due to monopolisation of reproduction by one or a few individuals in a group, despite retention of reproductive abilities by each group member, is a reason why determinants of reproductive dominance have been extensively studied in primitively eusocial insects (Michener, 1974; Wilson, 1971). Body size, age and behavioural dominance are reported as the most common antecedents of reproductive monopoly and reproductive dominance in social insects (Michener, 1974; Ross and Matthews, 1991).

With a few exceptions, all these studies have focussed on established colonies, thereby overlooking the founding phase of the colony. Although small group sizes are a common occurrence in the independent-founding primitively eusocial species such as the Indian paper wasp *Ropalidia marginata* (Gadagkar, 2001), information is lacking on the founding phase of the colony (for exceptions, see Michener et al., 1971; Arneson and Wcislo, 2003; Sibbald and Plowright, 2012). To address this lacuna, I investigated the antecedents of behavioural and reproductive dominance in pairs of *R. marginata*.

## 2. Methods

I performed experiments between April–October 2009 in Bangalore, India. I brought 12 *R. marginata* nests to the laboratory. To ensure behavioural naïveté of newly eclosed individuals, I removed all adults present on the nests at the time of collection. I isolated each newly eclosed female wasp within 24-h of her eclosion into an aerated plastic bottle and provided her with *ad libitum* food, water and nest-building material. Average relatedness between nestmates in *R. marginata* is low especially in the founding phase of the colony due to polyandry, serial polygyny, indeterminate nesting cycles, nest usurpation, nest adoption, and acceptance of foreign joiners. Previous work in *R. marginata* has also shown that nestmate pairs are not significantly different from non-nestmate pairs concerning their behaviour, survival and productivity (Gadagkar, 2001). Hence, I did not consider nest identity while pairing individuals.

I divided individuals to be paired into discrete binary categories as follows:

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## 2.1. Body size

I took fresh body weights of individuals at eclosion as a proxy of body size. Individuals showing a body weight difference of less than 5% were classified as having a similar body size, and those with a body weight difference of more than 15% were classified to be of different body sizes. In a subset of these experiments, ages of the paired individuals were controlled.

## 2.2. Age

I kept the age-window of experimental subjects within 10–20 days. Individuals born on the same day or born one day apart were considered to be of the same age, whereas, individuals showing a minimum of 5 days' age difference were considered to be of different ages. In a subset of these experiments, body sizes of the paired individuals were controlled.

## 2.3. Behavioural dominance

Each pair of individuals was observed during a 1-h contest, and all dominance-subordinate interactions were noted. Nine types of dominance behaviours are recognised in *R. marginata*. These are, 'aggressive bite', 'attack', 'chase', 'crash', 'hold in mouth', 'nibble', 'peck', 'sitting on another individual', and 'being offered liquid' (Gadagkar, 2001). An individual was designated as behaviourally dominant if she showed a minimum of 5 acts of dominance and more than twice the number shown by her partner during the same contest, and her partner was declared as behaviourally subordinate. Further details of these contests are described in Bang and Gadagkar (2016).

## 2.4. Reproductive dominance

Pairs of individuals were maintained together in aerated, transparent plastic bottles with *ad libitum* food, water and building material till one of the individuals laid an egg. In addition to egg-laying, I confirmed reproductive dominance by ovarian measurements of both individuals in the pair. The individual with a higher index of ovarian development, as calculated via subjecting different ovarian measurements to principal components analysis, was considered reproductively dominant of the pair (Gadagkar, 2001).

## Statistical analyses

Data in different binary variable categories were compared with the binomial test ( $\alpha = 0.05$ ) in R version 3.2.3.

## Ethics note

My experiments complied with the Association for the Study of Animal Behaviour/Animal Behavior Society Guidelines for the Use of Animals in Research, and with regulations of animal care in India.

## 3. Results

### 3.1. Behavioural dominance

Body size did not affect behavioural dominance, even when controlled for age (Table 1). Similarly, age did not affect behavioural dominance, even when controlled for body size (Table 1).

### 3.2. Reproductive dominance

Body size did not affect which individual in the pair became the egg-layer, even when controlled for age (Table 1). Age, on the other hand, influenced reproductive dominance in *R. marginata* such that the older

individuals had a higher probability of becoming the egg-layer, even when controlled for body size (Table 1).

Behavioural dominance influenced reproductive dominance such that behaviourally more dominant individuals had a higher probability of becoming the egg-layer in the pair (Table 1).

## 4. Discussion

### 4.1. Behavioural dominance

A closer inspection of constituent behaviours of behavioural dominance shows that all instances of behavioural dominance in the paired contests consisted of a single behaviour 'peck' (Bang, 2010). 'Peck' is one of the least engaging and least harmful dominance behaviours in *R. marginata* (Bang et al., 2010; Gadagkar, 2001). The unimportance of body size as an antecedent of behavioural dominance is expected in species where contests consist of ritualised dominance behaviours, thereby not requiring higher body fat reserves to prevail during contests. Additionally, the existence of extrinsic determinants of behavioural dominance such as winner-loser effects in *R. marginata* (Bang and Gadagkar, 2016) could explain relative unimportance of contribution of intrinsic traits such as age and body size to influence behavioural dominance.

### 4.2. Reproductive dominance

A rewarding result of this study was to find the role of behavioural dominance in reproduction in pairs of *R. marginata*. This result is not surprising if we consider other eusocial wasps and insects (Hölldobler and Wilson, 1990; Michener, 1974; Ross and Matthews, 1991). However, it is surprising considering the colonies of *R. marginata* where behavioural dominance plays no role in determining the queen or her successors (Bang and Gadagkar, 2012). The importance of behavioural dominance in pairs but not in colonies of *R. marginata* might be due to decreasing efficiency of behavioural dominance to achieve reproductive monopoly as the group size increases.

Similar to other eusocial wasps (Ross and Matthews, 1991) and *R. marginata* colonies, reproductive dominance in pairs of *R. marginata* was also influenced by age, such that older individuals displayed a higher probability to become egg-layers. Age of an individual might be taken as a proxy for her ability to survive and reproduce, and hence, it may be a good predictor of an individual's reproductive maturity and reproductive dominance. An important difference that lies between *R. marginata* and several other primitively eusocial species is that the positive tripartite association between age, dominance behaviour and reproductive dominance that is commonplace in other primitively eusocial species (Michener, 1974; Ross and Matthews, 1991), is missing in *R. marginata*. While in colonies of *R. marginata*, behavioural dominance plays no role, this study shows that in pairs of *R. marginata*, age and behavioural dominance independently influence reproductive dominance without any association between them. These results are indicative of two independent pathways to achieve reproductive dominance in smaller groups of *R. marginata*, either by being older or by being behaviourally dominant.

## 5. Conclusions

The existing theory about reproductive control in eusocial species proposes a change from physical control by the queen in primitively eusocial species with smaller colonies, to non-physical control by the queen in highly eusocial species with larger colonies (Hölldobler and Wilson, 1990; Michener, 1974; Ross and Matthews, 1991; Wilson, 1971). Although this suggests an association between group size and mechanism of reproductive control, investigations into group-size mediated changes in reproductive control within the same species have rarely been, if at all, studied. It is hence, interesting to find evidence for

**Table 1**Effect of body size and age on behavioural dominance, and effect of body size, age and behavioural dominance on reproductive dominance (binomial test,  $\alpha = 0.05$ ).

Response variable	Explanatory variable	N (Pairs)	Behavioural/Reproductive Dominance shown by each category of explanatory variable	P-value
Behavioural dominance	Body size	29	13 Large : 16 Small	0.71
	Body size (age controlled)	20	11 Large : 9 Small	0.82
	Age	19	10 Old : 9 Young	> 0.99
	Age (body size controlled)	12	6 Old : 6 Young	> 0.99
Reproductive dominance	Body size	38	18 Large : 20 Small	0.87
	Body size (age controlled)	27	16 Large : 10 Small	0.33
	Age	26	20 Old : 6 Young	<b>0.009</b>
	Age (body size controlled)	20	16 Old : 4 Young	<b>0.01</b>
	Behavioural dominance	27	22 Behaviourally Dominant : 5 Subordinate	<b>0.002</b>

the coexistence of these two hitherto non-overlapping traits (physical and non-physical control over reproduction) associated with two evolutionarily distinct groups (primitively and highly eusocial species) within a single species. Although *R. marginata* may seem unique in this regard, it is possible that there are other primitively eusocial species displaying similar group size mediated changes in behavioural and reproductive strategies. This study calls for more focused efforts on founding stages of primitively eusocial species, where a natural variation in group size exists, making this group ideal for investigating effects of group size on behaviour, life-history traits and evolution of sociality.

#### Conflict of interest

The author declares no conflict of interest.

#### Data availability

The datasets generated during the current study are available from the author on reasonable request.

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