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The evolution of complexity in social organization—A model using dominance-subordinate behavior in two social wasp species

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HIGHLIGHTS

- Varying complexities in two eusocial wasp species *R. marginata* and *R. cyathiformis*.
- Dominance patterns vary differently across species w.r.t. hierarchical ranks.
- A model suggesting a common interaction pattern with simple changes in strategies.
- The model could give rise to the observed patterns in both the species.
- A possible pathway for the evolution of complex societies from simpler ones.

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ABSTRACT

Dominance and subordinate behaviors are important ingredients in the social organizations of group living animals. Behavioral observations on the two eusocial species *Ropalidia marginata* and *Ropalidia cyathiformis* suggest varying complexities in their social systems. The queen of *R. cyathiformis* is an aggressive individual who usually holds the top position in the dominance hierarchy although she does not necessarily show the maximum number of acts of dominance, while the *R. marginata* queen rarely shows aggression and usually does not hold the top position in the dominance hierarchy of her colony. In *R. marginata*, more workers are involved in dominance-subordinate interactions as compared to *R. cyathiformis*. These differences are reflected in the distribution of dominance–subordinate interactions among the hierarchically ranked individuals in both the species. The percentage of dominance interactions decreases gradually with hierarchical ranks in *R. marginata* while in *R. cyathiformis* it first increases and then decreases. We use an agent-based model to investigate the underlying mechanism that could give rise to the observed patterns for both the species. The model assumes, besides some non-interacting individuals, the interaction probabilities of the agents depend on their pre-differentiated winning abilities. Our simulations show that if the queen takes up a strategy of being involved in a moderate number of dominance interactions, one could get the pattern similar to *R. cyathiformis*, while taking up the strategy of very low interactions by the queen could lead to the pattern of *R. marginata*. We infer that both the species follow a common interaction pattern, while the differences in their social organization are due to the slight changes in queen as well as worker strategies. These changes in strategies are expected to accompany the evolution of more complex societies from simpler ones.

1. Introduction

Group living animals display fascinating diversity in their social systems. Even within the class of the ‘truly’ social or eusocial species, there exists a considerable degree of variation in their social development. Eusociality, which is characterized by reproductive division of labor, cooperative brood care and overlap of generations, is mainly seen in ants, bees, wasps and termites (Wilson, 1971). The presence or absence of morphologically distinguishable reproductive and non-reproductive castes is used to further subdivide eusocial species into highly and primitively eusocial respectively (Wilson, 1971). Honeybees and many species of ants are examples of advanced or highly eusocial societies; their colonies are usually large, consisting of thousands of

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workers and one or a small subset of individuals who are queens. In typical highly eusocial species like the honeybees the queens use pheromones to maintain reproductive monopoly over their workers. The workers show well-defined division of labor, their activities are self-organized or regulated by the non-interactive queen through chemicals, rather than physical interactions. By contrast, the primitively eusocial species maintain comparatively smaller colonies with fewer workers, and the queens are generally highly interactive (Wilson, 1971). The primitively eusocial queen was previously believed to use aggression to suppress reproduction in the workers and maintain worker activities in the colony (Reeve and Gamboa, 1983; Reeve and Gamboa, 1987; Ito and Higashi, 1991; Ito, 1993; Monnin and Peeters, 1999) though the notion of work regulation using aggression has been challenged (Premnath et al., 1995; Jha et al., 2006). The presence of division of labor (Naug and Gadagkar, 1998) and queen pheromones (Sledge et al., 2001; Dapporto et al., 2007; Sumana et al., 2008; Bhadra et al., 2010) have been reported in some primitively eusocial species also, but it is still generally believed that, to successfully control the large number of workers in highly eusocial colonies, the non-interactive queens exhibit more complex control systems than their highly interactive primitively eusocial counterparts.

Interactions between individuals are critical in social organization, and dominance–subordinate interactions contribute largely to the total interactions observed in insect societies (Wilson, 1971). Social dominance hierarchy based on such agonistic interactions is a usual way of ranking individuals. Such dominance hierarchies have long been known to exist in group-living animals, for example in birds (Schjelderup-Ebbe, 1935), cattle (Schein and Fohrman, 1955), fish (Lowe, 1956), primates (Baldwin, 1971; Smuts, 1999; Sapolsky 1993) and in other beasts (Tyler, 1972; Clutton-Brock et al., 1982). As early as in the 1930s, some correlates of dominance were identified for the vertebrates and this made it possible to modify the existing social orders by experimental manipulations (Allee et al., 1939). Pardi showed that the very idea of dominance could be extended to the invertebrates also, and it is his pioneering work in the next decade that revealed the existence of a similar kind of social hierarchy in the primitively eusocial wasp *Polistes dominulus*, then known as *Polistes gallicus* (L.) (Pardi, 1948).

Ropalidia marginata is characterized as a primitively eusocial wasp species due to the absence of a morphologically distinguishable queen caste, but unlike in other such species, the queen is usually a meek and docile individual who rarely participates in any dominance interactions with any of her nestmates (Chandrashekara and Gadagkar, 1991; Gadagkar, 2001). As a result, she does not usually hold the top position in the dominance hierarchy of her colony (Sumana and Gadagkar, 2001). On the other hand, *Ropalidia cyathiformis* is another primitively eusocial species closely related to *R. marginata*, where the queen is aggressive, frequently indulges in dominance interactions with others and usually occupies the top position in the dominance hierarchy (Kardile and Gadagkar, 2002; Kardile and Gadagkar, 2003). The presence of a de-centralized work regulation mechanism, age polyethism, a non-aggressive queen who uses pheromones to regulate worker reproduction and a predetermined succession hierarchy makes the social organization of *R. marginata* more complex than most other primitively eusocial societies, including *R. cyathiformis* (Premnath et al., 1995; Naug and Gadagkar, 1998; Sumana et al., 2008; Bhadra et al., 2010; Bruyndonckx et al., 2006; Lamba et al., 2007; Bhadra et al., 2007; Bhadra and Gadagkar, 2008; Bang and Gadagkar, 2012). These two species together present an interesting scenario where it is possible to study differences in social organization in closely related species that might provide hints towards the evolution of complexity in social systems.

In this paper, we study the distribution of dominance and subordinate interactions among the hierarchically ranked individuals in *R. marginata* and *R. cyathiformis*. We focus on the differences in the dominance and subordinate patterns of the two species that might lead to their different levels of social complexity and thus hope to explore the underlying mechanisms that could delineate these patterns. How does the mechanism differ in these two species? Can we explain the differences between the two species in terms of simple changes in strategies of individual wasps? We use agent-based modeling to check if a common model could explain the behavioral patterns present in these species. Such an exercise could help us to trace the pathway for the evolution of more complex societies from simpler ones. Though the present study was stimulated by observations on these wasp species, the model we introduce and develop is not restricted only to the social insects; with further modifications and additional relevant parameters, we expect our model to be well applicable for even more complex societies including those of vertebrates.

2. The experimental data

2.1. Data collection

We used data from experiments conducted on nine colonies of *R. marginata* and *R. cyathiformis* each to investigate the patterns of dominance and subordinate behaviors in these species. The colony sizes ranged from 14 to 59 adults in *R. marginata*, and from 15 to 24 adults in *R. cyathiformis*. The adults on the nest were uniquely marked with spots of Testors® quick drying enamel paints prior to the observations. Behavioral observations consisted of randomly intermingled ‘instantaneous scans’ (in which a snapshopt of the behavioral state of each individual was recorded) and ‘all occurrences sessions’ (in which every occurrence of a set of chosen behaviors by any individual was recorded), each session lasting 5 min and followed by a break of 1 min between every session (Gadagkar, 2001). Such observations were made for 5 h each day in two separate blocks of 2 h 30 min each, over 6 consecutive days in *R. marginata*, yielding 30 h of data with 96 scans and 204 all occurrences sessions per nest. In case of *R. cyathiformis*, observations were made for 9 h in a single day in three separate blocks of 3 h each, consisting of 45 scans and 45 all occurrences sessions per nest. The queens were identified by observing the egg-laying behavior.

2.2. The dominance patterns

All instances of nine different behaviors such as: attack, chase, nibble, peck, crash, sit over another individual, being offered food, aggressive biting and hold another individual by mouth (Chandrashekara and Gadagkar, 1991; Gadagkar, 2001) were pooled to calculate the dominance behavior shown by an individual. The recipient of each of these behaviors was given a score of 1 for computing rates of subordinate behavior. A dominance hierarchy for each nest was constructed using FDI (frequency based dominance index), which has been shown to be a good index for constructing dominance hierarchies in such wasp species (Bang et al., 2010). In a colony of n individuals, each individual is given an index of dominance (D) using the following formula:

$$D=\frac{\sum_{i=1}^{n} B_i+\sum_{j=1}^{m}\sum_{i=1}^{n} b_{ji}+1}{\sum_{i=1}^{n} L_i+\sum_{j=1}^{p}\sum_{i=1}^{n} l_{ji}+1}$$

where $\sum_i B_i$ denotes the rates at which the focal individual shows dominance behavior toward her colony members, $\sum_{ji} b_{ji}$ denotes the sum of the rates at which all individuals dominated by her show dominance behavior toward other colony members; 1 to *m* are thus individuals who have received aggression from the focal individual. Similarly, $\sum_i L_i$ denotes the rates at which the focal individual shows subordinate behavior toward her colony members, $\sum_{ji} l_{ji}$ denotes the sum of the rates at which all individuals who show aggression to the focal individual show subordinate behavior toward other colony members. Thus 1 to *p* are the individuals toward whom the focal individual shows subordinate behavior. Thus each individual including those who have not shown any dominance-subordinate interactions gets an index of dominance (D) and the individual with the highest D gets the top position in the dominance hierarchy (Premnath et al., 1990). Since this index takes into consideration both the indirect dominance and the indirect subordination shown by the individuals (by means of b_{ji} and l_{ji}), showing the most number of dominance behaviors does not guarantee that an individual would hold the topmost position in the hierarchy. We arrange all the individuals of the colony in decreasing order of their value of this FDI index and assign them ranks from one to *n*. Since the colonies have variable number of individuals, in order to pool the data we need to convert the ranks into normalized ranks. This is done by dividing each individual's rank by the total number of individuals in that colony. By doing so, the ranks of all the individuals are scaled between 0 and 1. We calculate the percentage of dominance-subordinate behavior shown by each individual for each colony and plot this against the individual's normalized rank. For this purpose we divide the scale of normalized ranks (0–1) into 14 bins of equal size. For instance, if the 10th ranked individual in a colony of 30 individuals shows 5 acts of dominance behavior where a total of 20 acts are recorded in the colony, then $(5/20)\times 100\% = 25\%$ would be added to the 5th bin, since the normalized rank $10/30 = 0.33$ lies between 4/14 and 5/14. Since the smallest colony had 14 individuals, in order to ensure that each bin has at least one individual for each nest, we used 14 bins. Thus in colonies of *R. marginata*, individuals who have normalized hierarchical ranks between 0 and 1/14 show 29.09% of the total dominance and 2.25% of the total subordination of the colony, those having ranks between 1/14 and 2/14 show 16.47% of the total dominance and 2.55% of the total subordination and so on (Table 1). We plotted this distribution in form of histogram in Fig. 1a, where black bars and gray bars represent the dominance and subordinate behaviors respectively. Similar analysis for the nine colonies of *R. cyathiformis* yielded the pattern observed in Fig. 1b; mean and variance for the bars are shown in Table 1.

2.3. *The comparison*

There are striking differences between the dominance–subordinate behaviors shown by the two species. While in all the nine colonies, the *R. cyathiformis* queen always held the top position in the dominance hierarchy, the *R. marginata* queen never held the top position in any of the nine colonies analyzed, her position being different in different colonies, ranging from 4 to 22. We compare the behavioral patterns shown by the two species (Fig. 1a and b) by means of Kolomogorov–Smirnov two sample test (Sokal and Rohlf, 1994). We perform the test for dominance as well as subordinate behaviors separately and found a significant difference at 95% confidence level for both the behaviors. We therefore conclude that the two species show dominance and subordinate patterns different from each other. The same conclusion could be drawn by using Cliff's delta (Cliff, 1993; Cliff, 1996), a measure of effect size, which represents the degree of overlap between two distributions. We calculated Cliff's delta of 0.58 for dominance and 0.10 for subordinate behaviors. We also compare each bar of one distribution with its corresponding bar in the other distribution by measuring Cohen's *d* index (Cohen, 1988), another measure of effect size and found high

Table 1
Mean and variance for the observed data and simulation results and the corresponding effect sizes.

Sl. no.	Normalized ranks	*R. marginata* (Fig. 1a)				*R. cyathiformis* (Fig. 1b)				Model results (Fig. 3a)				Model results (Fig. 3b)				Effect sizes: Cohen's *d*							
		DB		S		DB		S		DB		S		DB		S		1a. vs 1b.		3a. vs. 3b.		1a. vs. 3a.		1b. vs. 3b.	
		mean	*var*	*mean*	*var*	*mean*	*var*	*mean*	*var*	*mean*	*var*	*mean*	*var*	*mean*	*var*	*mean*	*var*	DB	S	DB	S	DB	S	DB	S
1	0–1/14	29.09	140.73	2.25	8.15	33.16	181.96	0.69	3.86	28.05	255.87	0.11	0.12	25.36	161.61	0.00	0.00	−0.32	0.63	0.18	0.45	0.07	1.05	0.59	0.50
2	1/14–2/14	16.47	51.15	2.55	4.41	50.72	212.97	8.95	26.58	20.48	329.07	2.96	20.46	52.23	248.56	10.55	46.01	−2.98	−1.63	−1.87	−1.32	−0.29	−0.12	−0.10	−0.26
3	2/14–3/14	14.47	51.27	7.12	23.77	4.45	25.95	0.77	4.70	12.47	112.55	5.40	40.88	6.10	99.77	4.70	70.05	1.61	1.68	0.62	0.09	0.22	0.30	−0.21	−0.64
4	3/14–4/14	5.42	7.89	2.68	9.23	0.46	1.72	0.23	0.43	7.26	56.65	3.93	26.26	0.40	4.82	0.32	4.20	2.26	1.11	1.24	0.92	−0.32	−0.30	0.03	−0.06
5	4/14–5/14	5.00	20.61	1.77	4.01	0.00	0.00	0.00	0.00	4.14	29.60	2.39	13.38	0.11	0.84	0.06	0.18	1.56	1.25	1.03	0.89	0.17	−0.21	−0.17	−0.20
6	5/14–6/14	4.94	20.72	4.67	41.47	0.00	0.00	0.00	0.00	4.11	24.24	3.69	27.19	0.45	6.29	0.46	6.73	1.53	1.03	0.94	0.78	0.17	0.17	−0.25	−0.25
7	6/14–7/14	3.57	32.61	2.91	25.65	1.32	6.32	2.85	13.06	3.69	17.91	3.95	26.45	0.50	5.45	1.04	21.62	0.51	0.02	0.93	0.59	−0.02	−0.20	0.34	0.43
8	7/14–8/14	1.59	4.30	2.50	11.53	1.56	5.88	4.52	35.81	4.05	18.77	5.08	26.33	0.73	7.04	1.78	35.31	0.01	−0.41	0.92	0.59	−0.72	−0.59	0.33	0.46
9	8/14–9/14	4.81	53.86	7.83	63.17	2.04	7.83	3.93	9.21	3.11	15.18	4.92	26.37	2.99	35.81	6.66	197.78	0.50	0.65	0.02	−0.16	0.29	0.43	−0.20	−0.27
10	9/14–10/14	3.74	11.47	8.66	12.44	1.90	3.23	8.16	64.70	3.03	11.45	6.54	41.19	3.02	27.24	8.73	163.98	0.68	0.08	0.00	−0.22	0.21	0.41	−0.29	−0.05
11	10/14–11/14	3.32	9.95	7.09	26.73	2.09	19.55	8.10	42.14	3.85	16.15	8.69	42.67	3.67	28.08	12.08	209.45	0.32	−0.17	0.04	−0.30	−0.14	−0.27	−0.32	−0.35
12	11/14–12/14	3.25	6.36	8.96	15.59	0.25	0.51	14.41	131.87	2.60	11.22	7.93	47.60	2.61	18.84	14.14	308.14	1.62	−0.63	0.00	−0.47	0.22	0.18	−0.76	0.02
13	12/14–13/14	2.53	5.41	14.02	31.93	1.24	3.12	15.81	118.17	3.16	16.95	13.46	84.83	1.81	23.11	12.30	185.41	0.62	−0.21	0.30	0.10	−0.19	0.07	−0.15	0.28
14	13/14–1	1.77	2.30	26.93	320.04	0.78	2.13	31.57	387.92	0.00	0.00	30.95	116.45	0.02	0.04	27.18	439.65	0.66	−0.25	−0.14	0.23	1.65	−0.27	0.73	0.22

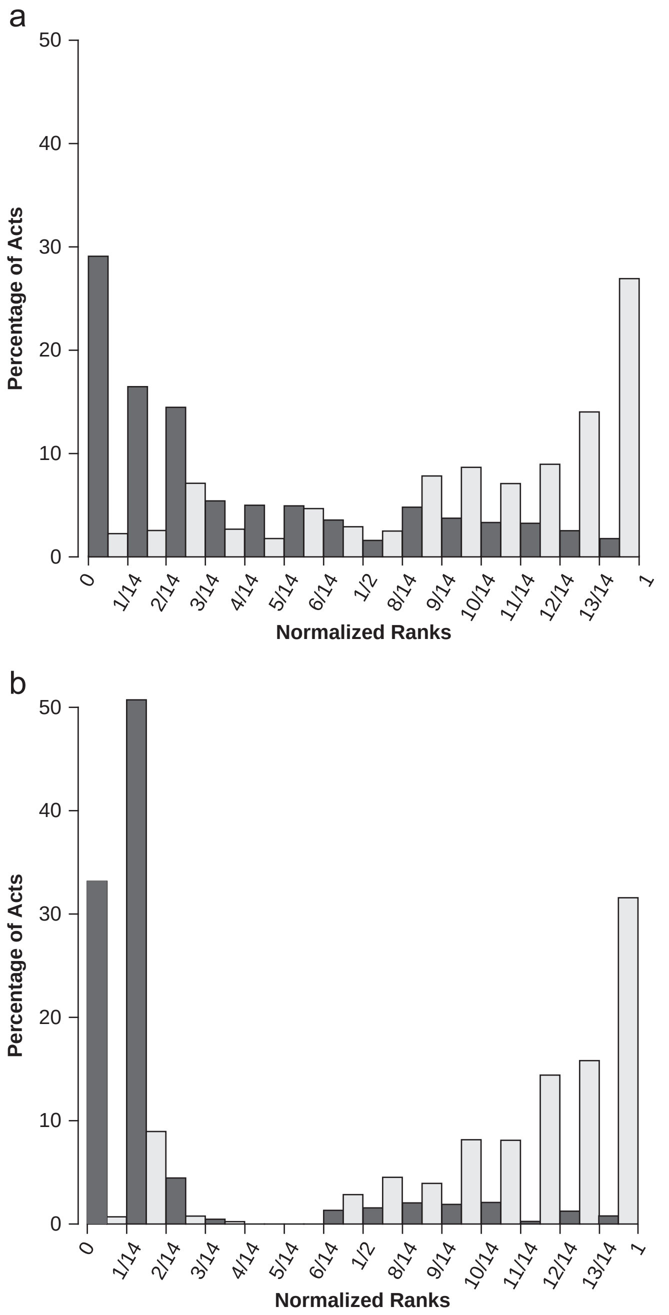

Fig. 1. Percentage of dominance acts (black bars) and subordinate acts (gray bars) plotted against the normalized ranks for (a) 9 colonies of *R. marginata* and (b) 9 colonies of *R. cyathiformis*.

effect sizes for many of the bars; all the details are presented in Table 1. Dominance in *R. marginata* is found to decrease almost consistently with the ranks for the higher ranks (black columns in Fig. 1a). Tukey multiple comparison test for proportion (Zar, 2009) confirms significant differences at 95% confidence level between column 1 and column 2, and also between column 3 and column 4, although the difference between column 2 and column 3 was insignificant. For *R. cyathiformis* however, it is very evident from the size of the black columns of Fig. 1b, that dominance behavior first increases and then decreases. Tukey test also shows significant difference at 95% confidence level between column 1 and 2, also between column 2 and 3. Since in all the nine colonies of *R. cyathiformis* the queen holds the top position in the hierarchy, this analysis suggests that she may not show maximum amount of dominance but there could be other individuals present in the colony who show more dominance than the queen. From the data we also found the acts of aggression shown by the individual holding the second position in the hierarchy to be numerically more than that of the queen in six out of nine colonies. Statistically, in all the nine colonies, the dominance shown by the second ranking individual is comparable with the queen (Tukey test, no significant difference at 95% confidence level). In both the species, the subordinate behaviors are not distributed equally among the workers, but gradually increase with their ranks for lower ranking individuals (gray bars). The two empty bins in the pattern of *R. cyathiformis* suggest the presence of more non-interacting workers in this species as compared to *R. marginata*.

3. The model

Can simple changes in strategies of the individuals explain the existing differences between the two species? We attempt to build a single model to explain the dynamics of the colonies that could give rise to these patterns. Existing models of dominance patterns can generally be classified into two categories. Self-organized models rely on a reinforcement mechanism that, depending on an individual's previous experiences, increases or decreases its ability to dominate others in an agonistic interaction (Hogeweg and Hosper, 1983; Jager and Segel, 1992; Theraulaz et al., 1995; Bonabeau et al., 1996). On the other hand, Correlational models assume pre-differentiated winning abilities in the individuals and further assume that their hierarchical ranks directly reflect their winning abilities (Chase, 1986; Bonabeau et al., 1999). Both the models are found to be equally capable of reproducing the dominance-subordinate patterns seen in *Polistes dominulus* (Bonabeau et al., 1999). Our model is closely related to the aforesaid correlational models, though the hierarchical ranks of the individuals do not always strictly follow the ordering of their winning abilities.

In our model each individual $\boldsymbol{i}$ is characterized by a strength function $\boldsymbol{x_i}$ which determines their winning abilities in an dominance interaction, i.e., if two individuals $\boldsymbol{i}$ and $\boldsymbol{j}$ meet, $\boldsymbol{i}$ will win over $\boldsymbol{j}$ if $\boldsymbol{x_i} > \boldsymbol{x_j}$, $\boldsymbol{j}$ will win over $\boldsymbol{i}$ if $\boldsymbol{x_j} > \boldsymbol{x_i}$, and if $\boldsymbol{x_i}=\boldsymbol{x_j}$, then both the individuals will have equal chances to win over the other. Let the individuals interact with an interaction probability $\boldsymbol{p_i}$. For a certain proportion of individuals, let's say for $\boldsymbol{w}$, we set $\boldsymbol{p_i}=0$, i.e., $\boldsymbol{w}$ proportion of individuals are non-interacting, and for the rest of the individuals, $\boldsymbol{p_i}$ is a function of their respective strengths $\boldsymbol{x_i}$. The functional relationship between them is expressed by

$$\boldsymbol{p_i} = f(\boldsymbol{x_i}) \sim |\boldsymbol{x_i}\text{-}\boldsymbol{\alpha}|^{\boldsymbol{\beta}}$$

where $\boldsymbol{\alpha}$ and $\boldsymbol{\beta}$ are parameters for monotonicity and homogeneity respectively (explained in the next section). We take $\boldsymbol{N=14}$ individuals, assign their strength $\boldsymbol{x_i}$ from a uniform random distribution ranging between 0 and 1, then determine their interaction probabilities $\boldsymbol{p_i}$ according to the functional relationship described above and with a specific value of $\boldsymbol{w}$, subjected to the normalization condition $\sum_i \boldsymbol{p_i=1}$. For each interaction, we choose two individuals at a time according to their $\boldsymbol{p_i}$'s and determine dominant and subordinate according to their $\boldsymbol{x_i}$'s. We allow 100 such interactions. The dominance hierarchy is then constructed by using FDI and percentage of interactions shown by each individual is also calculated. The whole process is repeated for 100 configurations. Then we bin the interaction data together for their respective normalized ranks as we did for the real data. We declare the individual with the highest $\boldsymbol{x_i}$ as the queen for each of the configurations and also track her position in the respective hierarchies.

4. Results

4.1. The effects of parameters

The effect of the parameters on the model can be seen by the following. We first examine the response of the model for varying values of the homogeneity parameter $\boldsymbol{\beta}$ with $\boldsymbol{\alpha}=0$ and $\boldsymbol{w}=0$. When $\boldsymbol{\beta}$ is **0**, all $\boldsymbol{p_i}$ s become equal, all individuals have equal probability to interact with all others. So the dominance-subordinate pattern reflects only their winning abilities (Fig. 2a). The inhomogeneity within the interaction probabilities increases as $\boldsymbol{\beta}$ differs from zero. The scenarios are depicted in Fig. 2b with $\boldsymbol{\beta}=\mathbf{0.5}$, in Fig. 2c with $\boldsymbol{\beta}=\mathbf{1.0}$ and in Fig. 2d with $\boldsymbol{\beta}=\mathbf{2.0}$. In all cases, the queen happens to be the top ranked

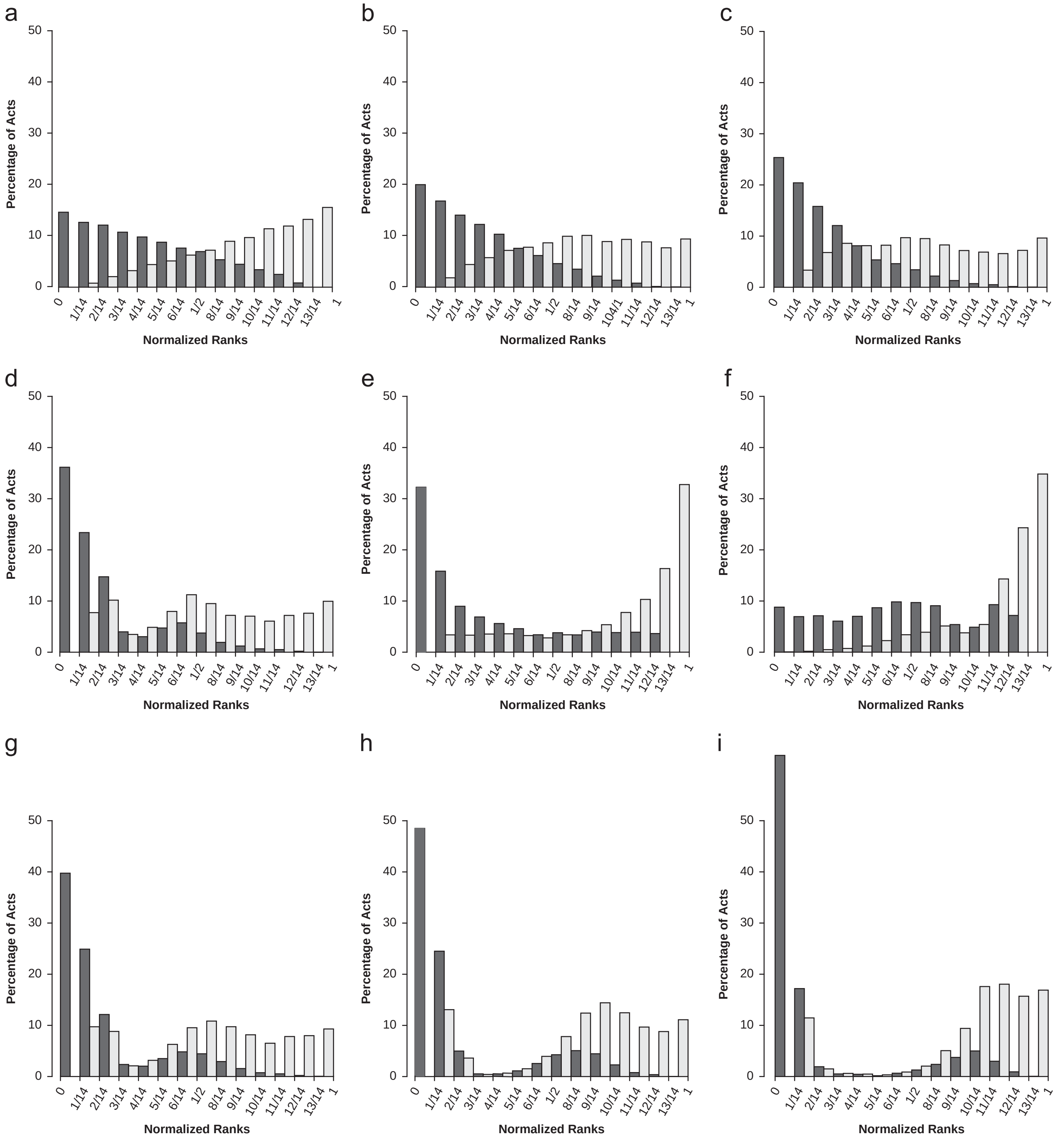

Fig. 2. Percentage of dominance acts (black bars) and subordinate acts (gray bars) plotted against the normalized ranks obtained by averaging over 100 configurations of 100 interactions with parameters (a) $\boldsymbol{w}=0$, $\boldsymbol{\alpha}=0$, $\boldsymbol{\beta}=0$, (b) $\boldsymbol{w}=0$, $\boldsymbol{\alpha}=0$, $\boldsymbol{\beta}=0.5$, (c) $\boldsymbol{w}=0$, $\boldsymbol{\alpha}=0$, $\boldsymbol{\beta}=1$, (d) $\boldsymbol{w}=0$, $\boldsymbol{\alpha}=0$, $\boldsymbol{\beta}=2$, (e) $\boldsymbol{w}=0$, $\boldsymbol{\alpha}=0.5$, $\boldsymbol{\beta}=2$, (f) $\boldsymbol{w}=0$, $\boldsymbol{\alpha}=1.0$, $\boldsymbol{\beta}=2$, (g) $\boldsymbol{w}=10$, $\boldsymbol{\alpha}=0$, $\boldsymbol{\beta}=2$, (h) $\boldsymbol{w}=30$, $\boldsymbol{\alpha}=0$, $\boldsymbol{\beta}=2$ and (i) $\boldsymbol{w}=50$, $\boldsymbol{\alpha}=0$, $\boldsymbol{\beta}=2$.

individual in each of the 100 configurations. As from our data set it is evident that the interaction probabilities are heterogeneous in nature, we expect a non-zero value of $\boldsymbol{\beta}$ for our species. As $\boldsymbol{\beta}$ increases gradually from $\mathbf{0}$, the individuals with higher winning abilities tend to interact more often with the others and the percentage of dominance in the first columns gradually increase from 14% for $\boldsymbol{\beta}=\mathbf{0}$ to reach 36% for $\boldsymbol{\beta}=\mathbf{2.0}$. Since for both the *R. marginata* and *R. cyathiformis*, the first column of dominance percentage is around 30%, we expect our desired $\boldsymbol{\beta}$ would be around $\mathbf{2}$, so we keep $\boldsymbol{\beta}=\mathbf{2.0}$ for the rest of the variation.

Next we examine the behavior of the model for various values of the monotonicity parameter $\boldsymbol{\alpha}$, keeping $\boldsymbol{\beta}=\mathbf{2.0}$ and $\boldsymbol{w}=\mathbf{0}$. For three different values $\boldsymbol{\alpha}=\mathbf{0.0}$, $\boldsymbol{\alpha}=\mathbf{0.5}$ and $\boldsymbol{\alpha}=\mathbf{1.0}$, the results we get are depicted in the Fig. 2d, e and f. In Fig. 2d, for $\boldsymbol{\alpha}=\mathbf{0.0}$, following the line of Fig. 2c, most of the dominance behavior is shown by the top ranked individual who is also the queen in all of the 100 configurations. Here the interaction probabilities of the individuals are monotonically connected with their strengths; higher strengths lead to higher interactions. As we increase the value of $\boldsymbol{\alpha}$ from 0, this monotonic relationship breaks and the probability of the existence of individuals with low strength but higher interaction increases. For $\boldsymbol{\alpha}=\mathbf{0.5}$ (Fig. 2e), we get some low ranked individuals who show more subordinate behavior than others, a characteristic that we have observed in our study species. Therefore we expect for our species, the value of $\boldsymbol{\alpha}$ would be around 0.5. But in this case also, in 97 out of 100 configurations, the queen retains the top position in the hierarchy. For $\boldsymbol{\alpha}=\mathbf{1.0}$ (Fig. 2f), we get an inverse monotonous relationship between strength and interaction probabilities, where higher strengths lead to lower interaction probabilities. We get almost a mirror image of the pattern in Fig. 2d; the lowest individual in the hierarchy shows most of the subordinate behavior, dominance behavior is shared among all the individuals almost equally except for the lowest individual, and only in 1 out of 100 cases, the queen retains the top position. Since the $\boldsymbol{\alpha}$ values are subtracted from the strength function $\boldsymbol{x_i}$ whose range is between 0 and 1, we vary $\boldsymbol{\alpha}$ also from 0 to 1. In both the ends of the scale, i.e., for $\boldsymbol{\alpha}=\mathbf{0.0}$ and $\boldsymbol{\alpha}=\mathbf{1.0}$, we get a monotonous relationship between $\boldsymbol{x_i}$ and $\boldsymbol{p_i}$; in between these extremities, the monotonicity breaks.

The effect of non-interacting individuals on the model is shown in the next three figures. Here we keep $\boldsymbol{\alpha}=\mathbf{0}$ and $\boldsymbol{\beta}=\mathbf{2}$ fixed for all three cases and vary $\boldsymbol{w}$. As we keep on increasing the percentage of non-interacting individuals to 10%, 30% and 50%, the total dominance–subordinate interactions are shared by the remaining individuals, so the percentage of interactions for at least one of them also increases. We can see the effect clearly in the first dominance bin (Fig. 2g, h and i). The percentage of cases where the queen holds the top position also decreases gradually as 90, 67 and 49 respectively, since the chance that the queen becomes a non-interacting individual also increases gradually. Table 2. summarizes different combinations of parameter values used in the shown figures.

Table 2
List of parameters, fixed or varied in different figures.

Parameters kept fixed	Parameters varied	Figures
$\alpha=0.0$, $w=0\%$	$\beta=0.0$	2a
	$\beta=0.5$	2b
	$\beta=1.0$	2c
	$\beta=2.0$	2d
$\beta=2.0$, $w=0\%$	$\alpha=0.0$	2d
	$\alpha=0.5$	2e
	$\alpha=1.0$	2f
$\alpha=0.0$, $\beta=2.0$	$w=0\%$	2d
	$w=10\%$	2g
	$w=30\%$	2h
	$w=50\%$	2i

4.2. The two different strategies

What will happen if the queen changes her strategy slightly? To investigate this situation, we change by hand the $\boldsymbol{p_i}$ of the individual with highest $\boldsymbol{x_i}$, i.e., of the queen, to a small value, say $\boldsymbol{p_Q=av(p_i)/N}$ where $\boldsymbol{av(p_i)}=(\sum\boldsymbol{p_i})/\boldsymbol{N}$. For $\boldsymbol{\beta}=\mathbf{2}$, $\boldsymbol{\alpha}=\mathbf{0.50}$ and $\boldsymbol{w}=\mathbf{0}\%$, we obtain a pattern qualitatively very similar to Fig. 1a where like *R. marginata*, in most of the cases the queen does not hold the top position in the hierarchy. The value we set for $\boldsymbol{p_Q}$ is arbitrarily chosen to be very close to 0 ($\sim$ or <0.01), so that the queen becomes almost non-interacting in terms of dominance behavior, a feature which is common in *R. marginata*. As we take the value of $\boldsymbol{p_Q}$ away from 0, the queen's interactions increase and her chance of holding the top position in the hierarchy also increases in turn. If we keep the value of $\boldsymbol{p_Q}$ at such a small but non-zero value, that the queen gets involved in a moderate number of interactions, for example $\boldsymbol{p_Q=av(p_i)}$, (>0.01 and <0.1, all other parameters being the same), we get a pattern qualitatively similar to Fig. 1b. Here, the queen does not always show maximum dominance interactions but mostly holds the top position in the hierarchy, the feature that is common in *R. cyathiformis*. The differences in patterns introduced by the change in queen's strategy are in general similar in nature for all parameter values.

We search through the parameter space for quantitative similarity with statistical significance. For $\boldsymbol{\beta}=\mathbf{2}$, $\boldsymbol{\alpha}=\mathbf{0.43}$, $\boldsymbol{w}=\mathbf{4}\%$ and $\boldsymbol{p_Q=av(p_i)/N}$, we obtain the pattern seen in Fig. 3a. We get a different pattern with $\boldsymbol{p_Q=av(p_i)}$, $\boldsymbol{\beta}=\mathbf{2}$, $\boldsymbol{\alpha}=\mathbf{0.31}$ and $\boldsymbol{w}=\mathbf{50}\%$ (Fig. 3b). The differences between Fig. 3a and b for both the dominance and subordinate patterns are found to be significant at 95% confidence level by Kolomogorov-Smirnov two-sample test. The effect sizes (Cliff's delta) of 0.44 and 0.05 were measured for dominance and subordinate behaviors respectively and all the Cohen's *d* indices are furnished in Table 1. In the first case we find that in 23 out of 100 cases the queen holds the top rank in the hierarchy (Fig. 3a). We use the Kolomogrov–Smirnov test for goodness of fit (Sokal and Rohlf, 1994) and find that the differences between Figs. 3a and 1a for both the dominance and subordinate patterns are non-significant at 95% confidence level (Cliff's delta for dominance and subordinate behaviors are 0.04 and –0.03 respectively, Cohen's indices are shown in Table 1). It is also worth noting that in the *R. marginata* data set 14% of the total individuals were non-interacting and from a different analysis of 100 colonies of *R. marginata*, we know that in 16 colonies the queen was the top ranked individual (Bhadra et al., in preparation). In the second case we find that in 99 out of 100 cases the queen holds the top position in the hierarchy (Fig. 3b). We again use the Kolomogrov–Smirnov test for goodness of fit and find that the differences of the patterns in Figs. 3b and 1b are both non-significant at 95% confidence level (Cliff's delta for dominance and subordinate behaviors are -0.10 and –0.04 respectively, Cohen's indices are shown in Table 1). In the *R. cyathiformis* data set, there were 40% non-interacting individuals and in 100% colonies, i.e., 9 out of 9, queens were at the top position of the hierarchy.

Our thorough investigation of the parameter space reveals that, for a range of combinations of the three parameters $\boldsymbol{\alpha}$, $\boldsymbol{\beta}$ and $\boldsymbol{w}$, we get the non-significant difference between our model results and the real data. We show the regions where we get $p>0.05$ in Kolomogorov–Smirnov test for goodness of fit in Fig. 4a for *R. marginata* and in Fig. 4b for *R. cyathiformis*.

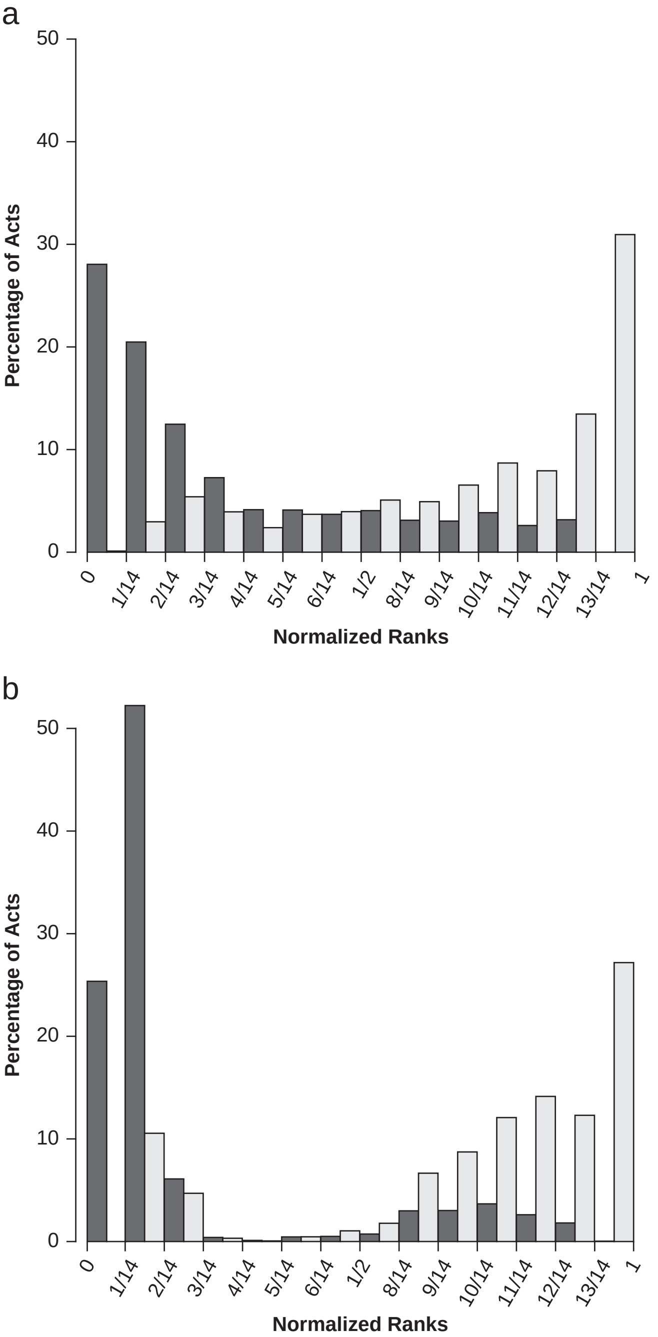

Fig. 3. Percentage of dominance acts (black bars) and subordinate acts (gray bars) plotted against the normalized ranks obtained by averaging over 100 configurations of 100 interactions with parameters (a) $\beta=2$, $w=4$, $\alpha=0.43$ and $p_Q=av(p_i)/N$ and (b) $\beta=2$, $w=50$, $\alpha=0.31$ and $p_Q=av(p_i)$.

We found that, near the observed values of w (14% for *R. marginata* and 40% for *R. cyathisformis*) and the approximately estimated values of β (explained in the next section), there is a range of non-zero α values for which the model holds. We investigate the sensitivity of the parameters of the model using effect sizes also. We show the regions where we get a very small mismatch between the model results and the observed data ($|$Cliff's delta$| < 0.1$) in Fig. 4c for *R. marginata* and in Fig. 4d for *R. cyathiformis*. We observe that, by using the effect size, we get bigger regions of validity those are supersets of the regions indicated by the Kolomogorov-Smirnov test.

4.3. The distributions of interaction probabilities

What could be the significance of the functional relationship of the strength x_i and interaction probabilities p_i? In other words, having the above-mentioned relationship between x_i and p_i, what could we predict about the interaction probabilities p_i? Since x_i's are taken from a uniform random distribution, the probability density function $P(x)$=constant. And since we have considered p_i as a function of x_i and for $\beta=2$, $p_i \sim (x_i-\alpha)^2$, one could write $x_i \sim p_i^{1/2}$, therefore:

$$P(p)\mathrm{dp} = P(x)\mathrm{dx}$$

$$or,\ P(p) = (\mathrm{dx}/\mathrm{dp})P(x)$$

$$or,\ P(p) \sim \mathrm{dx}/\mathrm{dp} = (1/2)p^{(1/2-1)}$$

$$or,\ P(p) \sim p^{-0.5}$$

So, one could expect that the density function for the interaction probability $P(\mathrm{p})$ should fall as a power-law with an exponent of $-\mathbf{0.5}$. We constructed the distributions of interaction probabilities for both the species from the data (Fig. 5). We tried to fit a non-linear regression function $y=Ax^{-B}$ to the plots. In Fig. 5a, for *R. marginata*, we get $A=\mathbf{0.94}$ and $B=\mathbf{0.69}$, both A and B are significant at 95% confidence level (analysis of variance test using F-statistics (Zar, 2009)). In Fig. 5b, for *R. cyathiformis*, we get $A=\mathbf{0.84}$ and $B=\mathbf{0.70}$, where B is significant at 95% level, but A is not. These results qualitatively give justification for our assumptions about the functional relationship between the strength function and the interaction probability. The power–law distribution in interaction probability suggests that one can get smaller values (very close to zero) with a greater probability and higher values (in this case, close to 0.5) with a small but finite probability.

4.4. Polistes dominulus

The social organization of the temperate paper wasp *P. dominulus* has been studied in detail over many years. It is considered as a typical primitively eusocial wasp species, lacking morphological distinction between the queen and worker castes. The queen in *P. dominulus* holds the topmost rank in the dominance hierarchy, as in *R. cyathiformis*. But unlike in *R. cyathiformis*, the *P. dominulus* queen always shows most of the dominance behavior and all the other individuals share the subordinate behaviors almost equally (Pardi, 1948; Theraulaz et al., 1989; Theraulaz et al., 1992). High ranked individuals other than the queen usually indulge in nest building and brood care while the others take up the job of foraging (Theraulaz et al., 1992; Theraulaz et al., 1990). The dominance hierarchy is therefore coupled with the organization of labor in the colony, which is generally regarded as an important factor in the evolution of eusociality (Oster and Wilson, 1978). We were interested in checking if slight changes in individual strategies in our model could also give rise to the patterns similar to those seen in the social interactions of *P. dominulus*, which are different from those observed in *R. marginata* and *R. cyathiformis*.

We have seen in Fig. 2d that, with $\alpha=0.0$, $\beta=2.0$ and $w=0$, the queen shows the most dominance behavior (36.1%) and also holds the top position in the hierarchy in each of the 100 configurations. Subordinate behaviors are shared almost equally by all the individuals except the queen. This is the qualitative pattern of dominance in *P. dominulus* colonies reported by Pardi (1948) and Theraulaz et al. (1995). However, it should be noted that a different dominance index was used by these authors, and all the data were from observations of pre-emergence nests while ours are of post-emergence nests. We believe that our

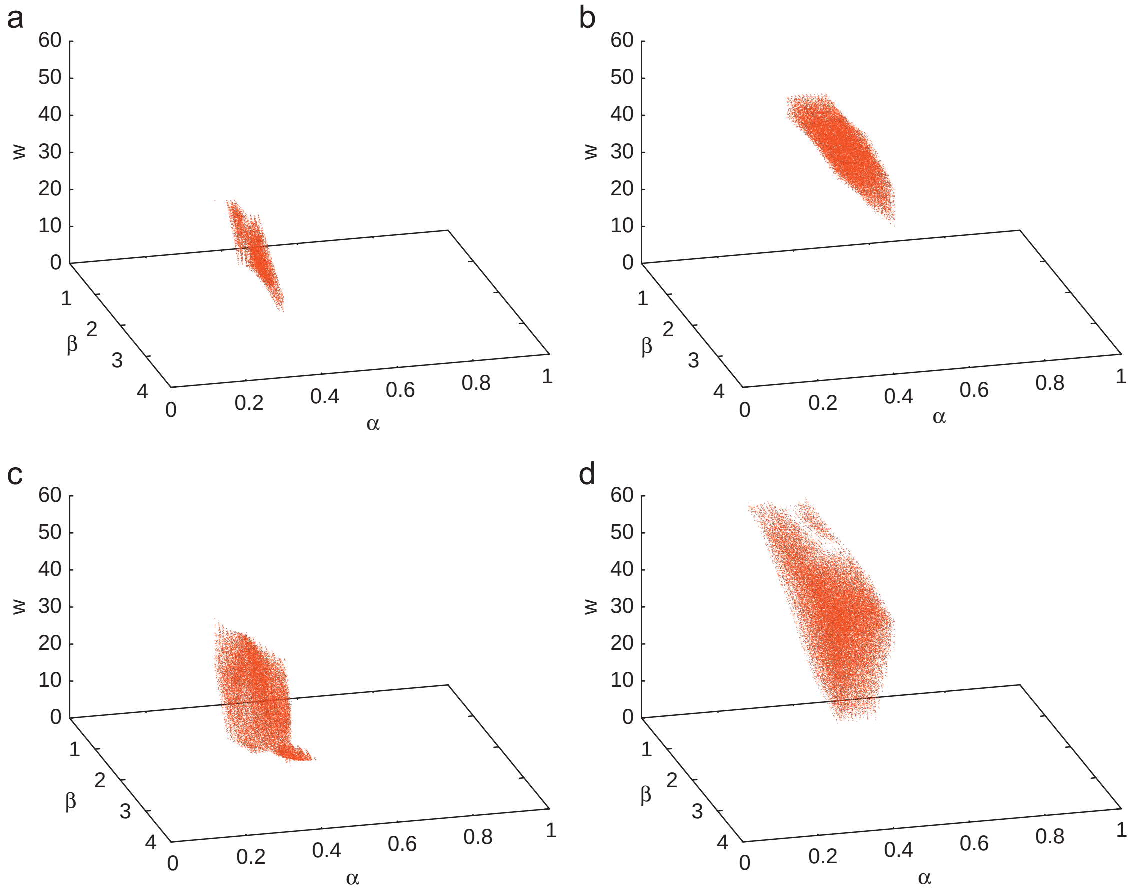

Fig. 4. The sensitivity analysis for the parameters of the proposed model. The regions indicate the combination of parameters for which the model results are indistinguishable from the observed data. The criteria used for testing the validity: $p > 0.05$ in Kolomogorov–Smirnov test for goodness of fit, (a) *R. marginata*, (b) R. cyathiformis. Also: $|\text{Cliff's delta}| < 0.1$ as a measure of effect size, (c) *R. marginata*, and (d) *R. cyathiformis*.

model would also be applicable for post-emergence nests of *P. dominulus*.

5. Discussion

5.1. *Strategies in R. cyathiformis*

Our analysis suggests that from a typical primitively eusocial species, where the queen holds the top position in the dominance hierarchy and also shows the most dominance behavior, more complex societies could evolve by changing the queen's as well as the workers' strategies. The queen could slow down her interaction rate to a moderate value but still remain at the top position of the hierarchy if she directs some of her aggression towards a single individual, the second in rank, who in turn would dominate the others in the colony. In case of loss of the queen, the individual who was second in rank and who is also the second strongest individual (in terms of $\boldsymbol{x}_i$), could become the new queen and later eventually slow down her aggression. This strategy is likely to be observed in *R. cyathiformis*, where the queen holds the topmost rank in the dominance hierarchy of the colony but the second ranked individual often shows a considerable amount of dominance, sometimes more than the queen. When the queen dies or is experimentally removed, the second ranking individual steps up her aggression and becomes the potential queen of the colony, which is reminiscent of similar situations in *R. marginata* (Kardile and Gadagkar, 2003). Hence it is likely that the potential queen in *R. cyathiformis* eventually becomes the new queen of the colony, a situation that we have not yet demonstrated experimentally.

5.2. *Strategies in R. marginata*

In *R. marginata* colonies, no attempts at egg-laying by the workers has ever been recorded and all workers have much poorly developed ovaries as compared to the queen (Chandrashekara and Gadagkar, 1991; Gadagkar, 2001). However, in *R. cyathiformis* colonies, the queen is not always the sole egg layer, occasional egg-laying by one or a few workers has been recorded (Gadagkar, 2001). Thus the reproductive threat to the queen is likely to be low in *R. marginata* as compared to *R. cyathiformis*, a condition which has definitely been achieved through a more advanced and efficient control system. The queen in *R. marginata* is actually known to use pheromones to regulate worker reproduction (Sumana et al., 2008; Bhadra et al., 2010), while such a pheromone is not yet known in *R. cyathiformis*. It is possible that the *R. marginata* queen has adopted the strategy of slowing down her dominance interaction rate to an even lower value as compared to *R. cyathiformis*. Since the *R. marginata* queen does not require to expend energy in dominance interactions, she can use more energy for reproduction as well as for production of pheromones. However, though the *R. marginata* queen does not occupy the topmost position in the dominance hierarchy, she does not lose the ability to be aggressive, and continues to be the strongest individual (in terms of $\boldsymbol{x}_i$). She can resort back to aggression if required for maintaining her status in the colony (Saha et al., 2012). If the *R. marginata* queen is lost or removed from the colony, the second strongest individual, who probably was also using the less-interaction strategy, takes up the queen's job. We observe one of the workers to become extremely aggressive on death or removal of the queen, but within a few

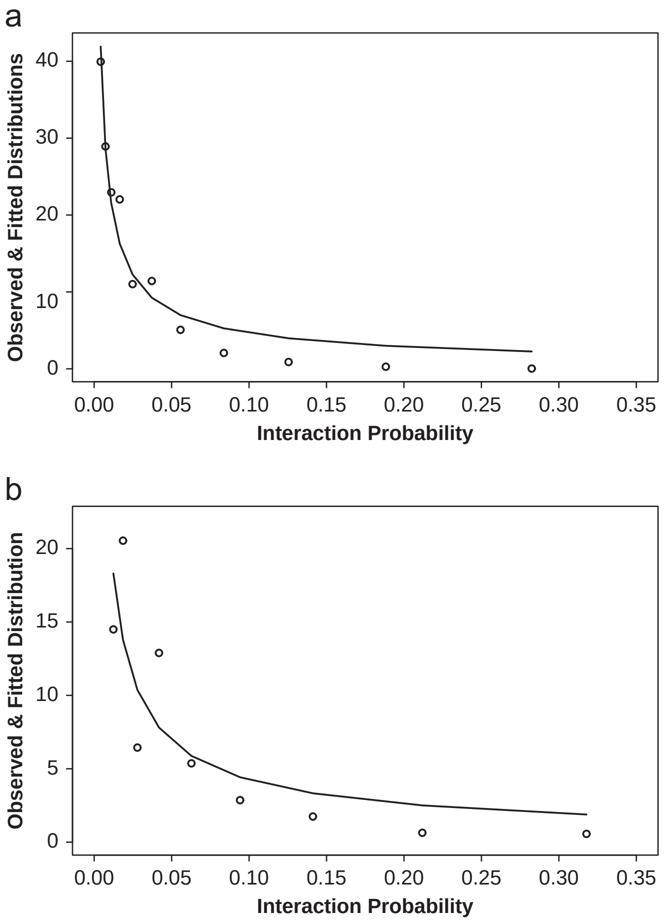

Fig. 5. Probability density distribution (open circles) for the interaction probabilities for 9 colonies of (a) *R. marginata* and (b) *R. cyathiformis*. The solid curve signifies the fitted distributions of the form $y = Ax^{-B}$.

days she develops her ovaries and begins egg-laying (Premnath et al., 1996; Sumana and Gadagkar, 2003). During this period she also gradually reduces her aggression and eventually becomes a meek and docile queen, channeling her energy towards reproduction.

5.3. Non-interacting workers

Considering different percentages of individuals who do not take part in any dominance-subordinate interactions, we obtained two distinct patterns (Fig. 3), with 4% and 50% non-interacting individuals respectively. In the *R. marginata* colonies, we find that 14% of the individuals did not interact, while in *R. cyathiformis* this value was 40% (difference is significant at 95% confidence level, 2-proportion Z test). We speculate that the *R. cyathiformis* queen, being the strongest individual in the colony, uses some of her aggression towards the second strongest individual, who might use her aggression to directly recruit workers for foraging and other colony maintenance activities. Hence the interactions are limited among the few individuals who are directly involved in work regulation. In *R. marginata*, dominance behavior is used by the workers to regulate each others' foraging activities; the frequency of dominance behavior in the colony decreases with decreased hunger levels, and increases with increased hunger levels in the colony (Bruyndonckx et al., 2006; Lamba et al., 2007). Workers in *R. marginata* can be differentiated into three behavioral castes—sitters, fighters and foragers. While the foragers are involved in foraging activities, the fighters are the ones showing maximum aggression, and the sitters typically belong to the non-interacting group (Gadagkar 2001; Gadagkar and Joshi, 1983). Since work regulation is achieved through a decentralized system of recruitment, colony maintenance activities are performed through a two-tiered system in which some individuals use aggression to make others work, so that interactions are not limited to only a few individuals, as in *R. cyathiformis* (Kardile and Gadagkar, 2002). Hence the low percentage of non-interacting individuals is explained by the change in the strategy of work regulation.

5.4. Conclusions

Through our model, we have proposed a common mechanism, with simple changes which could give rise to the observed dominance-subordinate patterns in both the primitively eusocial species *R. cyathiformis* and *R. marginata*. At one end of the model we have *Polistes*-like patterns, where the queen holds the top position in the hierarchy and also shows most of the dominance interactions. A simple reduction in the queen's interaction allows the evolution of a hierarchical control system where the queen still holds the top position in the hierarchy but does not necessarily show most of the aggression in the colony. She directs some of her aggression towards the second ranking individual, who in turn helps her to control worker activities in the colony. These changes could lead to the evolution of a social system like *R. cyathiformis*. A further reduction of the queen's interaction turns the control system towards a more decentralized one, where worker activities are controlled by the workers themselves; while the queen, who also evolves a pheromone to signal her presence to her workers, does not hold the top position in the hierarchy any longer. These changes lead to the evolution of a social organization like that of *R. marginata*. The changes required to go from an *R. cyathiformis*-like system to an *R. marginata*-like system may be harder to achieve than the changes required to go from a *Polistes*-like system to an *R. cyathiformis*-like system, given that the former necessitates the physiological changes required for the production and perception of pheromones. But once achieved, it would allow the colony to increase its size by producing more workers and also allow the queen to channel most of her physical energy to reproduction, eventually becoming a morphologically large egg-laying machine, as in the highly eusocial species like ants and the honeybees. Using our model, we have traced out a plausible evolutionary pathway through which more complexities in social organization could have evolved (Fig. 6).

5.5. Future directions

Although our model is fundamentally similar to the correlational models discussed in Section 3, there are some important differences. We have used a mathematical relationship by which the strengths of the individuals are connected to the probabilities through which they interact. The predictions about the interaction probabilities are consistent with the experimental observations for the concerned two species. It would be interesting to know if the knowledge of interaction probabilities could lead to the formation of the expected dominance-subordinate pattern, i.e., if a correct prediction is possible for the dominance-subordinate pattern from the distribution of interaction probabilities. Existing dominance data from other group-living species could be re-examined along this line. A successful prediction would certainly substantiate the model to a large degree. Another important aspect is the strategy of the individual with highest strength, a change in which could vary the dominance profile a lot. It would be very interesting to examine the effect of such

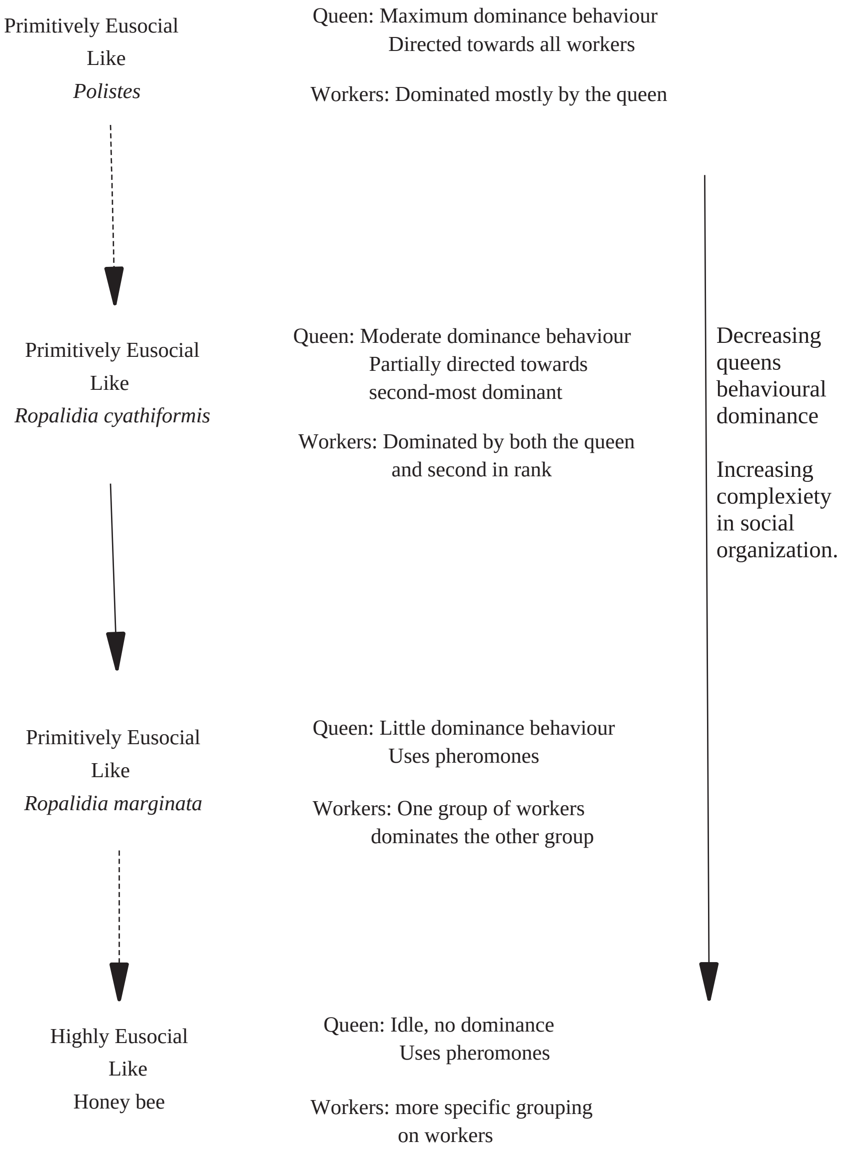

Fig. 6. Schematic diagram tracing the plausible evolutionary pathway.

changes in animal societies of higher complexities where other complicated factors could be present. We are also encouraged by the successful predictions made by the self-organized models in case of *P. dominulus* (Bonabeau et al., 1999). Our lab has recently carried out some experiments to validate the assumptions of self-organized models and we are now trying to verify the results in terms of reinforcement of dominance abilities.

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