

Article

## Cryptic successors unrevealed even by network analysis: A comparative study of two paper wasp species

Anindita Bhadra<sup>1</sup>, Ferenc Jordán<sup>2</sup>

<sup>1</sup>Behaviour and Ecology Lab, Department of Biological Sciences, Indian Institute of Science Education and Research - Kolkata, Mohanpur, India

<sup>2</sup>The Microsoft Research – University of Trento Centre for Computational and Systems Biology, Rovereto, Italy  
E-mail: jordan.ferenc@gmail.com

Received 2 April 2013; Accepted 30 April 2013; Published online 1 June 2013

### Abstract

Understanding queen succession could be a key contribution to the better understanding of the origins and evolution of eusociality. In order to investigate the nature of organizational changes during queen succession, we analyzed two closely related paper wasp species (*Ropalidia cyathiformis* and *Ropalidia marginata*). We compared the effects of in vivo and in silico queen removal on the structure of their interaction networks (the former resulting in queenless colonies with potential queens). We studied several structural measures. There is no major structural difference between full (queenright) and in silico queen-removed colonies but there are major differences between queenless and in silico queen-removed ones. This suggests that queen succession is accompanied by a major reorganization of the society, in Rm but not so much in Rc. We also analysed the centrality ranks of potential queens and found that their positional importance changes a lot during queen succession in *R. marginata*, as they are processed in the colony. In the queenright colonies of *R. marginata*, the direction of links is a better predictor of the identity of the potential queen than the strength of links.

**Keywords** centralization; small world; queen determination; behavioral caste.

<p>Network Biology ISSN 2220-8879 URL: <a href="http://www.iaees.org/publications/journals/nb/online-version.asp">http://www.iaees.org/publications/journals/nb/online-version.asp</a> RSS: <a href="http://www.iaees.org/publications/journals/nb/rss.xml">http://www.iaees.org/publications/journals/nb/rss.xml</a> E-mail: <a href="mailto:networkbiology@iaees.org">networkbiology@iaees.org</a> Editor-in-Chief: WenJun Zhang Publisher: International Academy of Ecology and Environmental Sciences</p>
---

### 1 Introduction

A major challenge in the study of primitive insect societies is to understand queen succession. In these species, individuals are not pre-destined to be queens or workers by genetics or development, as in highly eusocial species. Instead, social interactions play a major role in determining whether an individual can become a queen. When the queen is lost from a colony, one of the workers becomes the next queen. In most species, the identity of the next queen can be predicted, based on age, body size, aggression levels, ovarian condition or a combination of these factors. In *Polistes dominulus*, for example, the queen is always succeeded by the beta individual in the dominance hierarchy, while in the Stenogastrine wasps the oldest individual in the colony at the time of queen loss becomes the next queen. Thus the queen's successor can be predicted even in the

presence of the existing queen (Pardi, 1948; West-Eberhard, 1969; Cronin and Field, 2007; Cant et al., 2006; Röseler et al., 1986; Heinze et al., 1996; Ito and Higashi, 1991; Deshpande et al., 2006; Turillazzi, 1991).

This is the case also in *Ropalidia cyathiformis*, a primitively eusocial wasp where the queen's successor can be predicted, because the beta individual in the dominance hierarchy always succeeds the queen, who occupies the alpha position in the hierarchy, similar to *P. dominulus* (Deshpande et al., 2006). However, in *Ropalidia marginata* (a congeneric, sympatric species), the queen is a docile, non-interactive individual, who does not use aggression to maintain her reproductive monopoly. When the queen is lost from the colony, one of the workers becomes extremely aggressive within minutes, and develops her ovaries within a few days, to become the next queen. We designate this individual as the potential queen (PQ; Premnath et al., 1996; Kardile and Gadagkar, 2002; Sumana and Gadagkar, 2001; Gadagkar, 2001). Unlike in the case of *R. cyathiformis*, we cannot predict the queen's successor in *R. marginata*, because she seems to be an unspecialized individual with respect to her behaviour, age and ovarian condition (Deshpande et al., 2006; Chandrashekara and Gadagkar, 1992). But, like in *R. cyathiformis*, the potential queen is the most aggressive individual in the colony after queen removal. However, it is intriguing that the queen's successor, though cryptic to us in the presence of the queen, is "known" to other individuals in the colony (Bhadra and Gadagkar, 2008). In fact there is a pre-determined queue of at least five successors to the queen. Age is a significant but not perfect predictor of an individual's position in this queue (Bang and Gadagkar, 2012).

In an earlier study (Bhadra et al., 2009), we used data from behavioural experiments to characterize the social networks of *R. marginata* and *R. cyathiformis* based on dominance-subordinate interactions among individuals. Our preliminary analysis of the social networks of the two species corroborated our earlier behavioural results on both species. Experimental queen removal in both species leads to the emergence of a potential queen, and the resulting queen-less network (QL) is significantly different from the initial, queen-right one (QR). However, the queens in the two species are very different behaviourally, and also from the perspective of their position in the interaction network. While the queen in *R. cyathiformis* is a central node in the network, the node representing the queen in *R. marginata* is more peripheral (or isolated in 8 out of 12 colonies). Nevertheless, in all the 12 colonies, the interaction network underwent a drastic change after queen removal and the emergence of the potential queen. It is surprising from a structural perspective that removal of such a peripheral node (i.e. a non-significant individual) from the network can lead to such a drastic change in network structure. These results make it obvious that the queen in *R. marginata* is an important player in the colony, even though she does not stand out in the network of dominant-subordinate interactions (Bhadra et al., 2009). We note that these interactions represent only one, although evidently important type of interactions (considering networks representing several kinds of interactions is in preparation). Here we study whether (and how) we can predict the identity of the cryptic successor in *R. marginata* using network analysis. We explore several measures for network position and compare indices to see which one is the best predictor of the PQ's identity.

## 2 Methods

### 2.1 Data

We used data from queen removal experiments each in *R. marginata* (Rm) and *R. cyathiformis* (Rc) collected for other experiments. Each data set consisted of the identifiers of the initiator and recipient individuals of pairwise dominant-subordinate interactions (directed graph), and the number of interactions between pairs of individuals (weighted graph). Data was available on the queen-right and queen-less conditions of each colony (we had 48 networks in total). Network analysis was performed using the software UCINET 6.0 (Borgatti et al., 2002), and statistical analysis was done using STATISTICA 7.0 and StatisticXL.

## 2.2 Network analysis: global properties

Social networks contain information on the relative position of individuals in networks, characterising part-to-whole (individual-to-group) relationships (for methodical background, see Wasserman and Faust, 1994). We have considered a few basic, structural properties of social networks (Croft et al., 2008, Wey et al., 2008).

We calculated the degree-based *network centralisation index* ( $NCP^D$ , Wasserman and Faust, 1994; Zhang, 2012b) for the unweighted and undirected versions of our networks, where *degree* ( $D$ ) is the number of adjacent nodes to a graph node (number of neighbours). Note that network centrality, expressed in percentages, is maximal (100%) if a central node is directly connected to all other nodes that are only linked to the central one (a perfect star), and minimal (0%) in a regular graph, where the positional importance of all nodes are equal (a lattice).

The *clustering coefficient* ( $CL$ ) of a graph node quantifies the frequency with which its neighbours are connected to each other. It can be averaged over the whole graph if one wants to provide a global network measure (we used its version weighted by the size of neighbourhood of each node).

The *average path length* ( $d$ ) of a graph is defined as the mean distance between pairs of nodes. For nodes  $i$  and  $j$ , distance is defined as the length of the shortest path between them (length meaning the number of edges connecting the two nodes). The average characterises the whole network (low average path length meaning easy and fast communication).

In regular graphs (where each node has exactly  $n$  neighbours, like on a lattice), both clustering coefficient ( $CL$ ) and average distance ( $d$ ) are high. In random networks, both measures are low. Small world networks are characterized as having mixed properties of the two, i.e. relatively high clustering but relatively low average distance (Zhang, 2012a). Thus, a high  $CL / d$  ratio (denoted by  $SW$ ) indicates that the given network is more “small world-like” (sensu Watts and Strogatz, 1998).

## 2.3 Network analysis: local properties

Beyond the global properties of the networks, we were also interested in the local indices characterising the particular positions of graph nodes in the networks. Positions of nodes in the social networks were quantified by three indices. Degree ( $D$ ) provides the simplest, unweighted and undirected measure of neighbourhood (Zhang, 2012b). Weighted degree ( $wD$ ) considers also the frequency of undirected interactions among individuals. Net status ( $ns$ ) is a directed but unweighted measure of positional importance in hierarchies (Harary, 1959): it is the summed distance from a given node  $i$  to all subordinates minus the same value calculated for the graph with reversed directions. Since these two indices consider either the direction or the weight of links, their comparison (to each other and to the unweighted and undirected case) may provide a key to understanding the mechanisms in the background of queen succession.

Based on these three measures, we calculated the ranks of all individuals in each colony. Then, we derived the relative ranks of the PQs (their actual rank over the number of individuals in the network): If the rank of individual  $i$  is  $k$  in a network of  $n$  individuals, its  $(k/n)_i$  relative rank tells how close it is to the leading alpha position (clearly, the rank  $k$  is not enough to characterise this: it does make a difference whether the third individual, with  $k=3$ , is the third in a colony of four or fifty wasps). If  $(k/n)_i$  is smaller, the individual is more central in the colony network, and in general, the alpha individual has a relative rank of  $1/n$ . We have analysed (1) which index gives the highest ranks to PQs (on average) and (2) which index gives the most consistent estimation for ranks of PQs (described by the coefficient of variation of the  $k/n$  values).

## 2.4 *In silico* queen removal experiments

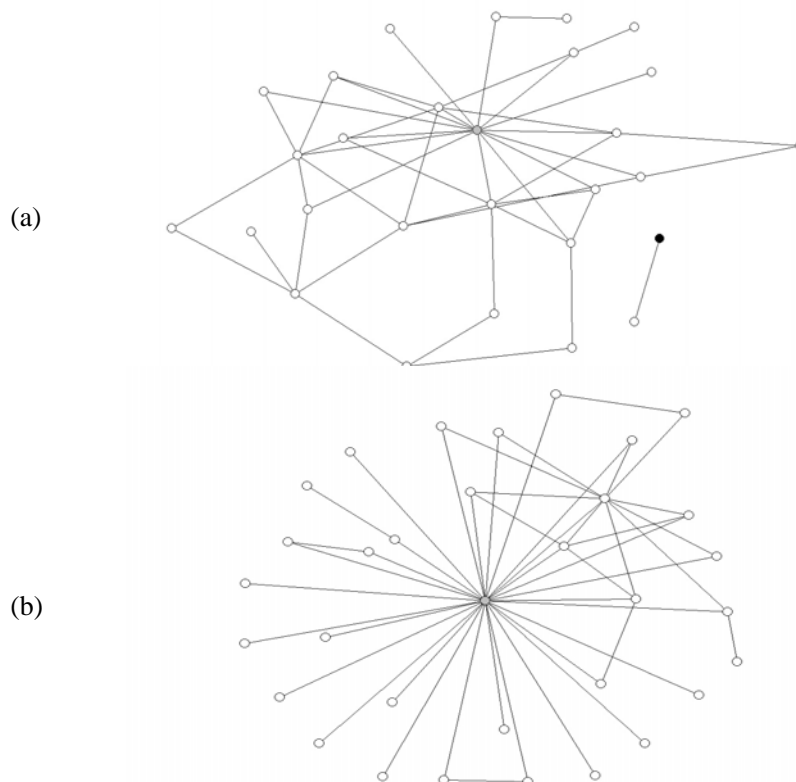
We carried out *in silico* queen removal experiments in the 24 queen-right networks: we removed the queen with all her interactions (both initiated and received) from the data set and constructed the “*in silico* queen removed” network. We also removed the PQ (identified from the experimental queen-less condition) and a

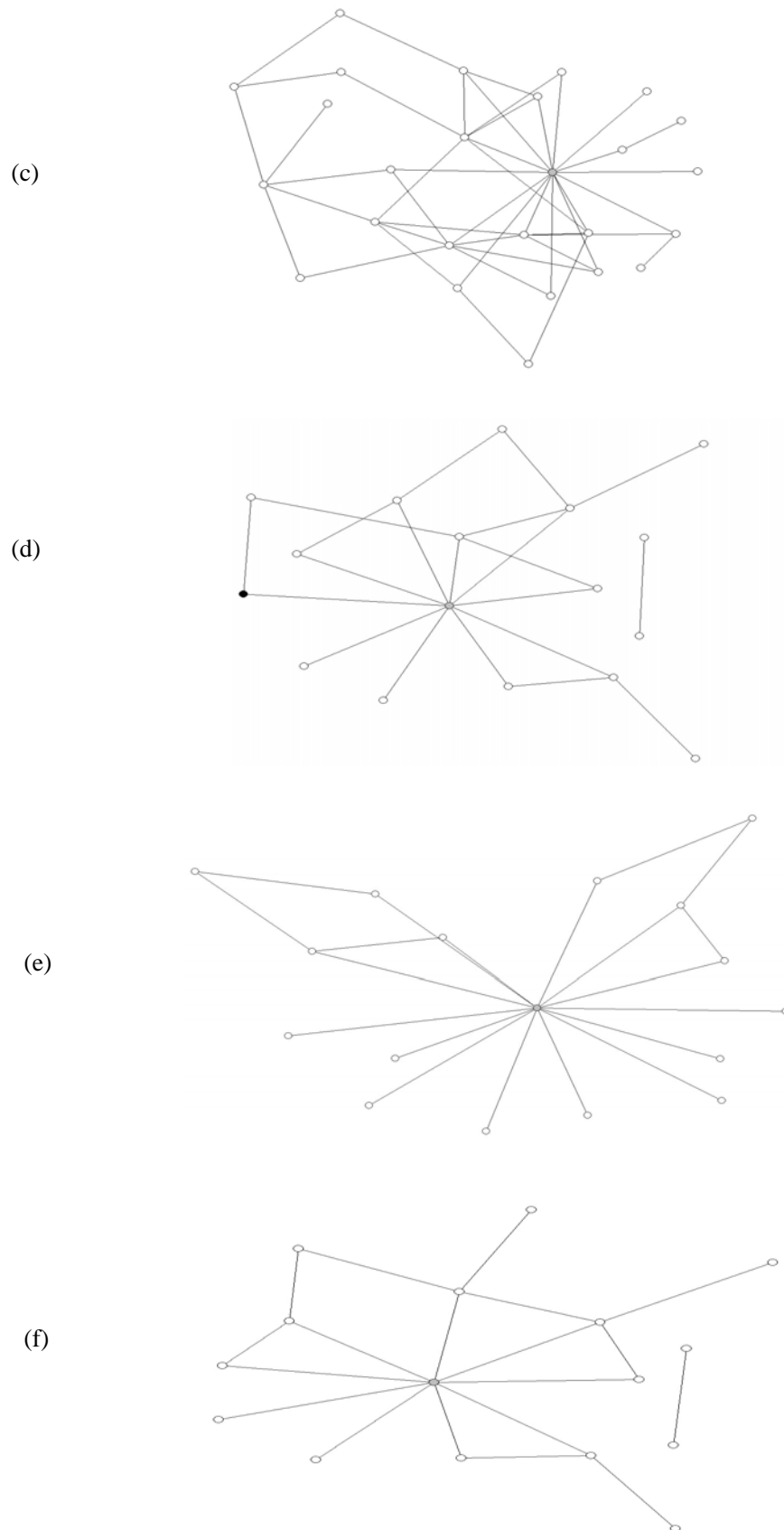
random worker from the QR data and generated “*in silico* PQ-removed” and “*in silico* worker-removed” networks, respectively. The five types of networks (QR, QL and the three removals) were then compared using a Mann-Whitney U test for global network properties ( $NCP^D$ ,  $d$ ,  $SW$ ). We investigated also the local indices for queens and PQs in the *in silico* queen removed networks of *R. marginata*.

In an earlier experiment, we tested the cryptic successor hypothesis in *R. marginata* (Bhadra and Gadagkar, 2008). In five of the eight colonies used, we had two potential queens, one of which was the successor (PQ2), and the other we designated here as the loser (PQ1). In the remaining three experiments, we had only the successor (PQ1). We used data on dominant-subordinate interactions from the queen-right colony to construct a degree-based hierarchy for the colony. We also constructed a similar hierarchy based on all paired interactions observed in the QR colony. In both kinds of hierarchies, we looked for the ranks of the eight successors (5 PQ2's and 3 PQ1's) and the losers (5 PQ1's).

### 3 Results

We have shown previously that the *R. marginata* QR and QL networks are at the two extremes of centrality, with some QL *R. marginata* networks achieving 100% centrality (i.e. a perfect “star” topology). The *R. cyathiformis* QR networks are more centralized than the *R. marginata* ones, while the QL networks of *R. cyathiformis* are also highly but much less centralized than the QL networks of *R. marginata* (Bhadra et al., 2009). We removed particular individuals, *in silico*, from the QR networks; (we could remove the queen *in silico* only from four of the 12 *R. marginata* networks; in the remaining eight, queens were isolated network nodes). We could remove the PQ in silico from 11 of the 12 networks in *R. marginata*. Both the queen and the PQ could be removed similarly from all the *R. cyathiformis* networks. Fig. 1 shows the QR, QL and queen-removed (Qrem) networks of a typical colony in both species. The Qrem networks of both species were similar to their own QR networks, and they were significantly different from the QL networks in their centrality measures. The queen-removed, PQ-removed and worker-removed networks were similar within a species (Fig. 2). All the comparisons were made by Mann-Whitney U test, with alpha set to 0.007, after Bonferroni correction.

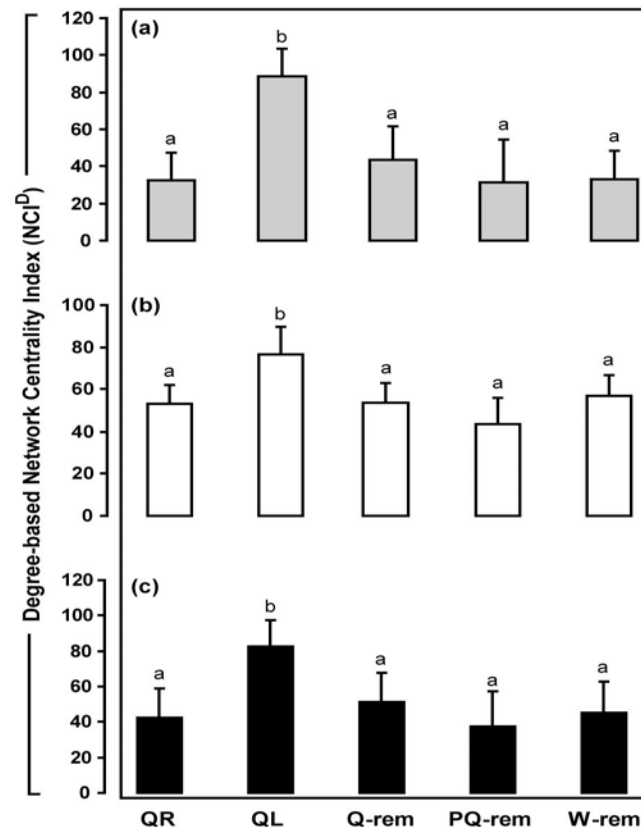




**Fig. 1** The queen-right (a: V269 QR), queen-less (b: V269 QL) and *in silico* queen removed (c: V269 Qrem) networks of a *R. marginata* colony constructed using dominance-subordinate interactions. The similarly constructed queen-right (d: C08 QR), queen-less (e: C08 QL) and *in silico* queen removed (f: C08 Qrem) networks of a *R. cyathiformis* colony. Black, gray and white

nodes show the queen (Q), the potential queen (PQ) and the workers, respectively.

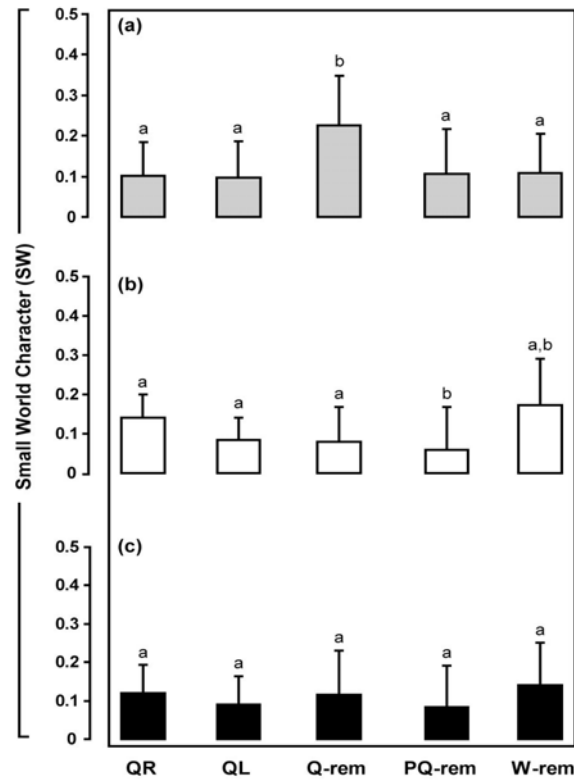
In *R. marginata*, the Qrem networks were more small-world-like than all the other networks. In *R. cyathiformis*, the PQrem networks were the least small-world-like, and were significantly different only from the Qrem networks (Fig. 3). All the comparisons were made by Mann-Whitney U test, with alpha set to 0.007, after Bonferroni correction.



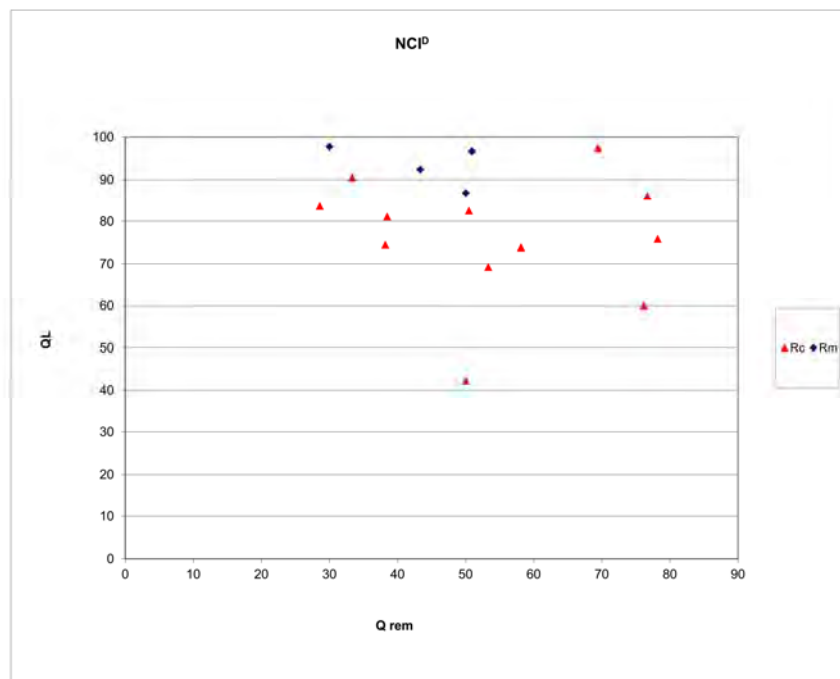
**Fig. 2** Mean and standard deviation of the degree-based network centrality index ( $NCI^D$ ) for the queen-right, queen-less, queen-removed, PQ-removed and worker-removed networks in (a) *R. marginata* and (b) *R. cyathiformis* and (c) for pooled data. Bars carrying different letters are significantly different from each other (Mann Whitney U-test, alpha set to 0.007 after Bonferroni correction).

It is an important finding that the difference between the QL and Qrem versions of the same networks is larger in *R. marginata* than in *R. cyathiformis*. This suggests that the loss of the queen is followed by serious network reorganisation especially in *R. marginata* (Fig. 4).

For illustration, we present the actual ranks of relevant individuals in the colonies (based on their degree values), while relative ranks will be used below for comparing indices to each other. *R. cyathiformis* potential queens were the top-ranking nodes in both the QL and the Qrem networks, and both the queens and the potential queens had high ranks in the QR networks (Table 1). However, the potential queens did not rank high in the Qrem networks of *R. marginata*, though they always had rank 1 in the QL networks (Table 2). In the QR networks of *R. marginata*, neither the queens nor the potential queens had high ranks (Table 2).



**Fig. 3** Mean and standard deviation of the small world character (SW) for the queen-right, queen-less, queen-removed, PQ-removed and worker-removed networks in (a) *R. marginata* and (b) *R. cyathiformis* and (c) for pooled data. Bars carrying different letters are significantly different from each other (Mann Whitney U-test, alpha set to 0.007 after Bonferroni correction).



**Fig. 4** The plots show the pairs of  $NCP^D$  values for QL and Qrem versions of the same network. Values are calculate for the 12 Rc and 4 Rm colonies where *in silico* queen removal was possible. If the loss of the queen was not more than deleting a node from the network,  $NCP^D$  values would equal for a pair of networks. Thus, the larger the difference between the pairs, the more important the reorganisation of the colony network after queen loss is.

**Table 1** Degree-based ranks of the queens in the queen-right, as well as PQs in the queen-right, QL and queen removed networks of *R. cyathiformis*. The PQ's are ranked 1 in most of the QL and queen removed networks. Note that there is a single network (C86) where neither the queen nor the PQ are most central in QR.

Nest	QR		QL	Qrem
	Q	PQ	PQ	PQ
<b>C01</b>	2	1	1	1
<b>C03</b>	4	1.5	1	1.5
<b>C07</b>	2	1	1	1
<b>C08</b>	8.5	1	1	1
<b>C33</b>	1	2	1	1
<b>C34</b>	2	1	1	1
<b>C38</b>	1	2	1	1
<b>C50</b>	2.5	1	1	1
<b>C58</b>	5	1	1	1
<b>C59</b>	1	2.5	11	1
<b>C60</b>	4	1	1	1
<b>C86</b>	2.5	2.5	1	2

**Table 2** Degree-based ranks of the queens in the QR, as well as PQ's in the QR, QL and Qrem networks of *R. marginata*. The PQ's do not have unique ranks in the queen removed networks, but they are ranked 1 in all QL networks.

Nest	QR		QL	Qrem
	Q	PQ	PQ	PQ
<b>V262</b>	6	7	1	6
<b>V269</b>	25	1	1	1
<b>V272</b>	8	4	1	6.5
<b>V277</b>	12.5	2	1	2
<b>V519</b>	0	4.5	1	1.5
<b>V532</b>	12	1	1	0
<b>V614</b>	33.5	25	1	2
<b>V638</b>	15	1.5	1	10.5
<b>V657</b>	18	2	1	1
<b>V800</b>	2.5	16.5	1	9

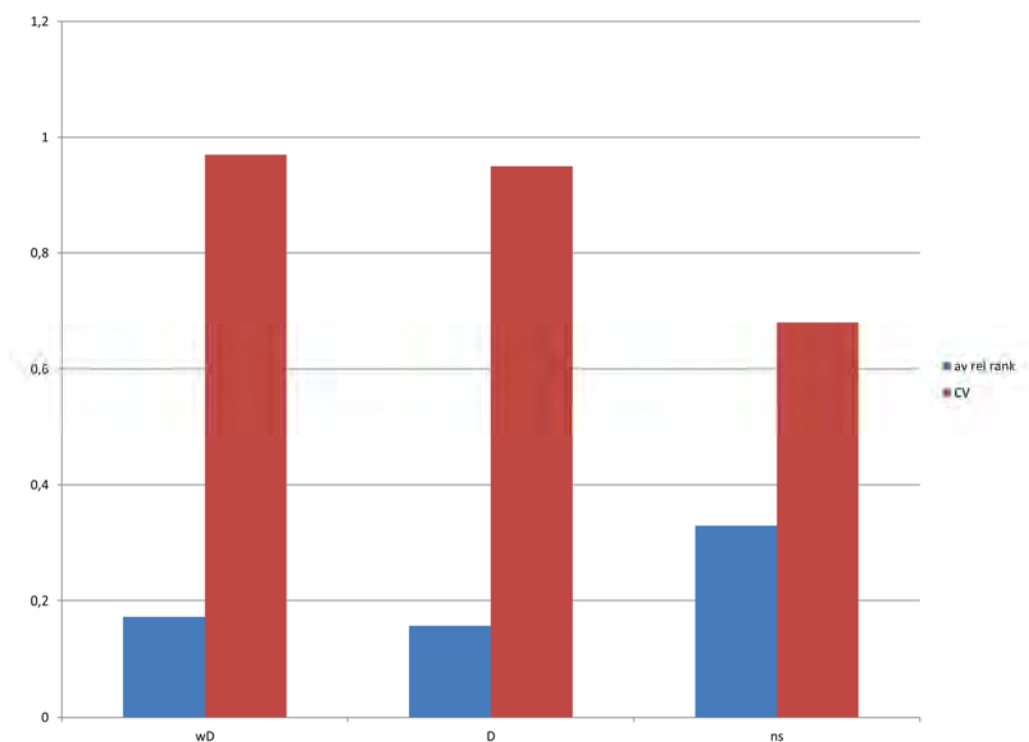
It is not easy to predict the potential queens on the basis on their degree-based rank, and the choice of the centrality index to be used is a key question: whether the unweighted and undirected measure of degree is suitable, or whether it should be a weighted or directed index. For this comparison, we have used the  $k/n$  relative ranks. Our findings suggest that weighted degree ( $wD$ ) gives better ranks for PQs than the directed net status index ( $ns$ ), but  $ns$  may provide more consistent prediction on the identity of the PQ (Table 3, see also



Fig. 5). We suggest that an index consistently predicting a lower rank has higher predictive power than another one predicting higher rank but in a less consistent way.

**Table 3** The relative ranks for the PQ's in *Rm* networks, based on three indices ( $wD$ ,  $D$ , and  $ns$ ). We also show the number of individuals in the colonies ( $N$ ). On the right, the average ( $av$ ), standard deviation ( $std$ ) and coefficient of variation ( $CV$ ) of relative ranks are shown.

Colony	v262r	v269r	v272r	v277r	V519	V532	V586	V614	V638	V621	V657	V800	av	std	CV
N	10	28	23	13	17	8	17	28	31	40	16	44			
wD (PQ)	0.15	0.04	0.17	0.19	0.06	0.56	0.06	0.05	0.06	0.03	0.38	0.33	0.17	0.17	0.97
D (PQ)	0.15	0.04	0.17	0.15	0.09	0.56	0.06	0.07	0.06	0.03	0.28	0.23	0.16	0.15	0.95
ns (PQ)	0.20	0.25	0.09	0.15	0.76	0.31	0.06	0.75	0.34	0.40	0.34	0.31	0.33	0.23	0.68



**Fig. 5** The average relative rank and its coefficient of variation ( $CV$ ) for PQ individuals in the Rm QR, based on three network metrics, degree ( $D$ ), weighted degree ( $wD$ ) and directed net status ( $ns$ ).

In the experiments used to test the cryptic successor hypothesis, neither the cryptic successors nor the losers had high ranks in the hierarchies of their colonies, and there was no consistent pattern observed in the rank order of the queen and the two potential queens in a colony (Table 4). Since we know that the queen in *R. marginata* is non-aggressive, as opposed to the queen of *R. cyathiformis*, and that we cannot identify the queen's successor in the QR colony of *R. marginata* by her position in the dominance hierarchy, we considered it prudent to consider the network of all paired interactions that take place in the QR colony to

attempt prediction of the queen's successor. However, even considering all interactions we could not predict the identity of the queen's successor in the QR colony (Table 5).

**Table 4** Ranks of the queens, cryptic successors and losers in the QR networks of *R. marginata* based on all dominance-subordinate interactions. The PQs do not have unique ranks in the networks.

Nest	Q	CS	LO	n
V519	15	1.5		17
V532	4.5	0	4.5	8
V586	0	4.5	1	17
V614	18	2		28
V621	0	18	18	40
V638	25	11	6.5	25
V657	12	1	3	20
V800	2.5	16.5		47

**Table 5** Ranks of the queens, cryptic successors and losers in the QR networks of *R. marginata* based on all paired interactions. The PQs do not have unique ranks in the networks.

Nest	Q	CS	LO	n
V519	12.5	2		20
V532	5	7	10	19
V586	21	10	1	34
V614	14	2		50
V621	50.5	9.5	9.5	56
V638	33.5	25	8	34
V657	12	1	3	20
V800	2.5	16.5		47

#### 4 Discussion

*R. marginata* and *R. cyathiformis* together present a highly exciting scenario for studying the evolution of eusociality. While *R. marginata* is known to display certain characteristics of highly evolved societies, *R. cyathiformis* is a typical primitively eusocial species. This dichotomy between the two closely related species is most obvious in the behaviour of their queens. While on the one hand, the queen of *R. marginata* is a non-aggressive, non-interactive individual who seems to use pheromones rather than aggression to maintain reproductive monopoly in her colony, the queen of *R. cyathiformis* occupies the alpha position in the dominance hierarchy of her colony, and acts as the central "pacemaker" of the colony (Kardile and Gadagkar, 2003). The behavioural contrast between these species is also reflected in their social networks.

Based on the number of neighbours in the QR network, predicting the identity of the new queen (PQ) is quite easy in *R. cyathiformis* but is much harder in *R. marginata*. Even when we use weighted networks (i.e. information on the frequency of interactions, measured by  $wD$ ), the situation does not alter. However, if we

consider the direction of the links (*ns*), the average relative rank of PQs is larger (further away from the alpha-position) but the results are more consistent: the PQ is around the one-third mark of the individual ranks. Though there is a lot of variation even in this, of the three indices used, *ns* has the least CV (0.68), which is still quite high on an absolute scale. Thus we have to accept that network analysis does not take us any closer to predicting the identity of the PQ in the queen-right colony of *R. marginata* (Deshpande et al., 2006; Chandrashekara and Gadagkar, 1992; Bhadra and Gadagkar, 2008).

The *in silico* removals of the potential queen and a random worker affected network centrality in none of these species. This was surprising for *R. cyathiformis*, because the potential queen is in quite an important position even in the QR network (perhaps the presence of the queen reduced the effect of removing the potential queen). It was not surprising that these targeted removals did not affect the *R. marginata* colonies. From the biological perspective, the fact that the removal of the potential queen from the queen-right network does not affect the colony is important as it means that though there is a designated successor to the queen, the colony also has a back-up mechanism. If the queen dies, the potential queen would take up the responsibility of the queen, but if the designated successor is missing, there would be another to take up her place. This is consistent with the fact that there is actually a queue of successors present in the colony at any time, at least in *R. marginata* (Bang and Gadagkar, 2012). However, the result that the centrality measure does not change when the queen is removed *in silico* from *R. cyathiformis* colonies is very surprising. A closer look at the *R. cyathiformis* QR networks reveals that the queen usually interacts directly with the potential queen and a few other individuals, and the network is dense. Hence, the removal of the queen might not cause great alterations in the centrality of the network. Interestingly, *in silico* queen removed networks of *R. marginata* are more small-world-like than the QR or QL networks. This is probably because the queens show very few interactions, and the removal of these nodes increases the clustering coefficient of the networks. Generally, larger difference in a network measure between the QL and Qrem versions of the same colony indicates more important reorganisation after queen loss (Fig. 4). This result is also interesting in the light of recent work carried out on these two species with respect to the mechanism of the evolution of complexity in the social wasps. It has been demonstrated that by tweaking with the queen and worker interaction strategies in the relatively more primitive *R. cyathiformis*, a social organization like that of the more socially complex *R. marginata* can be easily achieved theoretically (Nandi et al., 2013).

We have also demonstrated that neither the potential queens in the dominance-subordinate interaction networks from the queen removal experiments, nor the cryptic successors and losers in both the dominance-subordinate and all interactions networks from the Q-PQ exchange experiment ranked high in the degree-based hierarchies. These results help us to conclude with more confidence that the queen's successor cannot be identified in *R. marginata* as long as the queen is present, using all the social network analysis methods by which we can identify her in *R. cyathiformis*. Since *R. marginata* seems to have acquired certain characteristics of more evolved societies, the presence of a designated successor to the queen who is acceptable to all other individuals in the colony, but cannot be perceived by behavioural or apparent anatomical and physiological differences is another aspect of the more evolved eusociality of *R. marginata*. Since the queen of *R. marginata* is known to produce a pheromone that she applies on the nest material, which the workers can perceive just by being on the nest (Bhadra et al., 2010, Mitra et al., 2011), it is possible that they use some similar subtle cues to identify their successor in the presence of the queen. Such perception would not necessarily involve active interactions between the potential queen and other workers and this might be the reason why she does not rank high in the centrality rank of the dominance network, unlike in the QL condition, when the PQ directs aggression actively towards her nestmates in order to step up the process of her own ovarian development (Lamba et al., 2007).

## Acknowledgements

The work on wasps was supported by grants from the Department of Science and Technology, Department of Biotechnology and the Ministry of Environment and Forests, Government of India (to RG) and a CSIR Senior Research Fellowship to AB. We are thankful to Dr. Annagiri Sumana and Dr. Sujata A. Deshpande for allowing us to use their data on *R. marginata* and *R. cyathiformis* respectively for the analysis of this paper. Behavioural observations on wasps for the cryptic successor experiment were carried out by AB. Data analysis was performed by AB and FJ. We gratefully acknowledge the inputs provided on this work by Prof. Raghavendra Gadagkar, which have enriched the manuscript greatly. AB and FJ co-wrote the paper. Our experiments comply with regulations for animal care in India.

## References

- Bang A, Gadagkar R. 2012. Reproductive queue without overt conflict in the primitively eusocial wasp *Ropalidia marginata*. Proceedings of the National Academy of Sciences of USA, 109: 14494-14499
- Bhadra A, Gadagkar R. 2008. We know that the wasps “know”: Cryptic successors to the queen in *Ropalidia marginata*. Biology Letters, 4: 634-637
- Bhadra A, Jordán F, Sumana A, et al. 2009. A comparative social network analysis of wasp colonies and classrooms: linking network structure to functioning. Ecological Complexity, 6: 48-55
- Bhadra A, Mitra M, Deshpande S, et al. 2010. Regulation of reproduction in the primitively eusocial wasp *Ropalidia marginata*: On the trail of the Queen pheromone. Journal of Chemical Ecology, 36: 424-431
- Borgatti SP, Everett MG, Freeman LC. 2002. Ucinet for Windows: Software for Social Network Analysis. Analytic Technologies, Harford, USA
- Cant MA, Llop JB, Field J. 2006. Individual variation in social aggression and the probability of inheritance: Theory and a field test. American Naturalist, 167: 837-852
- Chandrashekhara K, Gadagkar R. 1992. Queen succession in the primitively eusocial tropical wasp *Ropalidia Marginata* (lep.) (Hymenoptera: Vespidae). Journal of Insect Behavior, 5: 193-209
- Croft DP, James R, Krause J. 2008. Exploring Animal Social Networks. Princeton University Press, Chicago, USA
- Cronin AL, Field J. 2007. Social aggression in an age-dependent dominance hierarchy. Behaviour, 144: 753-765
- Deshpande SA, Sumana A, Surbeck M, et al. 2006. Wasp who would be queen: A comparative study of two primitively eusocial species. Current Science, 91: 332-336
- Gadagkar R. 2001. The Social Biology of *Ropalidia marginata*. Harvard University Press, Cambridge, MA, USA
- Harary F. 1959. Status and contrastatus. Sociometry, 22: 23-43
- Heinze J, Trunzer B, Oliveira PS, et al. 1996. Regulation of reproduction in the ponerine ant, *Pachycondyla villosa*. Journal of Insect Behavior, 9: 441-450
- Ito F, Higashi S. 1991. A linear dominance hierarchy regulating reproduction and polyethism of the queenless ant *Pachycondyla sublaevis*. Naturwissenschaften, 78: 80-82
- Kardile S, Gadagkar R. 2002. Docile sitters and active fighters in paper wasps: a tale of two queens. Naturwissenschaften, 89: 176-179
- Lamba S, Kazi YC, Deshpande S, et al. 2007. A possible novel function of dominance behaviour in queen-less colonies of the primitively eusocial wasp *Ropalidia marginata*. Behavioural Processes, 74: 351-356
- Mitra A, Saha P, Chaoulideer ME, et al. 2011. Chemical communication in *Ropalidia marginata*: Dufour's

- gland contains queen signal that is perceived across colonies and does not contain colony signal. *Journal of Insect Physiology*, 57: 280-284
- Nandi AK, Bhadra A, Sumana A, et al. 2013. The evolution of complexity in social organization – a model using dominance-subordinate behaviour in two social wasp species. *Journal of Theoretical Biology* (in press)
- Pardi L. 1948. Dominance order in *Polistes* wasps. *Physiological Zoology*, 21: 1-13
- Premnath S, Sinha A, Gadagkar R. 1996. Dominance relationships in the establishment of reproductive division of labour in a primitively eusocial wasp (*Ropalidia marginata*). *Behavioral Ecology and Sociobiology*, 39: 125-132
- Röseler PF, Röseler I, Strambi A. 1986. Studies of the dominance hierarchy in the paper wasp, *Polistes gallicus* (L.). *Monitore Zoologico Italiano*, 20: 283-290
- Sumana A, Gadagkar R. 2001. The structure of dominance hierarchies in the primitively eusocial wasp *Ropalidia marginata*. *Ethology, Ecology and Evolution*, 13: 273-281
- Turillazzi S. 1991. The Stenogastrinae. In: *The Social Biology of Wasps* (Ross KG, Matthews RW, eds). Comstock, Ithaca, New York, USA
- Wasserman S, Faust K. 1994. *Social Network Analysis: Methods and Applications*. Cambridge University Press, USA
- Watts DJ, Strogatz SH. 1998. Collective dynamics of 'small-world' networks. *Nature*, 393: 440-442
- West-Eberhard MJ. 1969. The social biology of polistine wasps. *Miscellaneous Publications Museum of Zoology University of Michigan*, 140: 1-101
- Wey T, Blumstein D, Shen W, et al. 2008. Social network analysis of animal behaviour: a promising tool for the study of sociality. *Animal Behaviour*, 75: 333-344
- Zhang WJ. 2012a. *Computational Ecology: Graphs, Networks and Agent-based Modeling*. World Scientific, Singapore
- Zhang WJ. 2012b. Several mathematical methods for identifying crucial nodes in networks. *Network Biology*, 2(4): 121-126