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A comparative social network analysis of wasp colonies and classrooms: Linking network structure to functioning

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ABSTRACT

A major question in current network science is how to understand the relationship between structure and functioning of real networks. Here we present a comparative network analysis of 48 wasp and 36 human social networks. We have compared the centralisation and small world character of these interaction networks and have studied how these properties change over time. We compared the interaction networks of (1) two congeneric wasp species (*Ropalidia marginata* and *Ropalidia cyathiformis*), (2) the queen-right (with the queen) and queen-less (without the queen) networks of wasps, (3) the four network types obtained by combining (1) and (2) above, and (4) wasp networks with the social networks of children in 36 classrooms. We have found perfect (100%) centralisation in a queen-less wasp colony and nearly perfect centralisation in several other queen-less wasp colonies. Note that the perfectly centralised interaction network is quite unique in the literature of real-world networks. Differences between the interaction networks of the two wasp species are smaller than differences between the networks describing their different colony conditions. Also, the differences between different colony conditions are larger than the differences between wasp and children networks. For example, the structure of queen-right *R. marginata* colonies is more similar to children social networks than to that of their queen-less colonies. We conclude that network architecture depends more on the functioning of the particular community than on taxonomic differences (either between two wasp species or between wasps and humans).

1. Introduction

In recent years, network science has become an important tool for studying complex systems. Both the global topology of whole systems and the local patterns of interactions within them can be characterised by suitable network indices (Estrada, 2007; Scotti et al., 2007). In fact, holistic approaches are now more exact than ever before: we are able to quantify *to what extent* everything is connected to everything else, we have techniques for the identification of critically important nodes in networks and we can quantify and compare the topology ("shape") of different networks. Network properties help us to

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study the dynamics of complex systems and to make predictions about the behaviour of such systems and their components.

Recent studies on the topological characteristics of interaction networks in bottlenose dolphins (Lusseau, 2003) and guppies (Croft et al., 2004) have provided new insights into the behaviour of these animals: network analysis has acted as an interesting tool for answering questions regarding the behavioural repertoire and population structure of these species and others (Croft et al., 2008).

There is also an increasingly rich literature on comparative network analysis including social networks of animals (e.g. Faust and Skvoretz, 2002; Wey et al., 2008), reviving very old applications of network science in behavioural ecology (cf. Oster and Wilson, 1978). In this paper, we characterise the dominant-subordinate interaction networks of two social wasp species and friendship networks of children in classrooms and compare them. In order to ensure comparability, we only study the basic topology, excluding more system-specific information. We are particularly interested in two system-level properties of these networks: centralisation and small world character. An important question in network science is how structure is linked to function in complex systems, particularly how the topology and dynamics of networks are related. It has been demonstrated that dramatic changes of topology accompany major switches in functioning of some networks (an example is given by Krebs, 2002 for terrorist networks: large global changes precede local action). These large-scale, macroscopic properties give a general insight into the functioning of the system.

2. Materials and methods

We have studied the structural properties of 84 interaction networks described in 48 primitively eusocial wasp colonies (queen-right and queen-less stages of 12 colonies of *Ropalidia marginata* and 12 colonies of *Ropalidia cyathiformis*) and 36 classrooms (four classes in nine time steps). Fig. 1 shows three representative networks.

2.1. Wasp colonies

R. marginata and *R. cyathiformis* are two congeneric species of paper wasps that are found in peninsular India (Gadagkar, 2001). These wasps are primitively eusocial, i.e., they lack a morphologically distinct queen caste. Nevertheless, there is one individual in the colony who lays eggs and is designated as the queen, while the other individuals are workers who are responsible for colony maintenance. In both species, when the queen is dead or is experimentally removed from the colony, one of the workers becomes very aggressive, and if the queen is not replaced, she becomes the new queen of the colony within a few days. We call her the potential queen (PQ) (Premnath et al., 1996; Kardile and Gadagkar, 2002; Deshpande et al., 2006). We use data from 12 queen removal experiments carried out in Bangalore, India, on both species, to obtain 48 wasp social networks in queen-right and queen-less conditions. The data constitute dominance-subordinate interactions between pairs of individuals in the colonies.

2.2. Children in classrooms

We use data from a longitudinal social network survey made in four classrooms of three Budapest secondary schools in nine time steps covering roughly 3 years. A survey (anonymous questionnaire with closed answers) was made. Individual networks are signed and directed graphs containing information about strong positive and negative links between students (weak positive and negative links have been used for filtering noise in the information provided: they were collected but not considered). Here, we use the undirected, unsigned form of each graph, for comparative purposes. Note that more specific information is still available for comparing human social networks, but only very basic, limited information can be used for interdisciplinary (wasp and children) comparisons. Children were aged either 10 (two classes) or 14 (two classes) at the beginning of the survey.

2.3. Network analysis

Social networks contain a great deal of information about their nodes and links (for example the sign, direction and weight of edges, or some quality of nodes). While sophisticated methods are available for characterising any single network, only very simple network properties are useful for between-system, multidisciplinary comparisons. Here we focus on the general topology of the wasp and children networks (for a wider methodical background, see Wasserman and Faust, 1994).

2.4. Small world (SW) character

The *clustering coefficient* (*CL*) of a graph node quantifies how densely its direct neighbours are connected to each other. In other words, it is the number of links between its neighbours divided by the maximum number of links between them. It can be averaged over the whole graph if one wants to provide a global network measure. Also, if given for the whole graph, it can be weighted by the size of neighbourhood of each node; we used this "weighted overall" version (see UCINET, Borgatti et al., 2002).

The *average path length* (*d*) of a graph is defined as the mean distance between pairs of nodes. For nodes *i* and *j*, their 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.

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 characterised as having mixed properties of the two, i.e. relatively high clustering but relatively low average distance. Thus, a high *CL*/*d* ratio (denoted by *SW*) indicates that the given network is more "small world-like", sensu Watts and Strogatz (1998).

2.5. Centralisation (NCI^D)

We calculated the degree-based *network centrality index* (NCI^D) for unweighted and undirected networks, where *degree* (*D*) is the number of direct neighbours of a graph

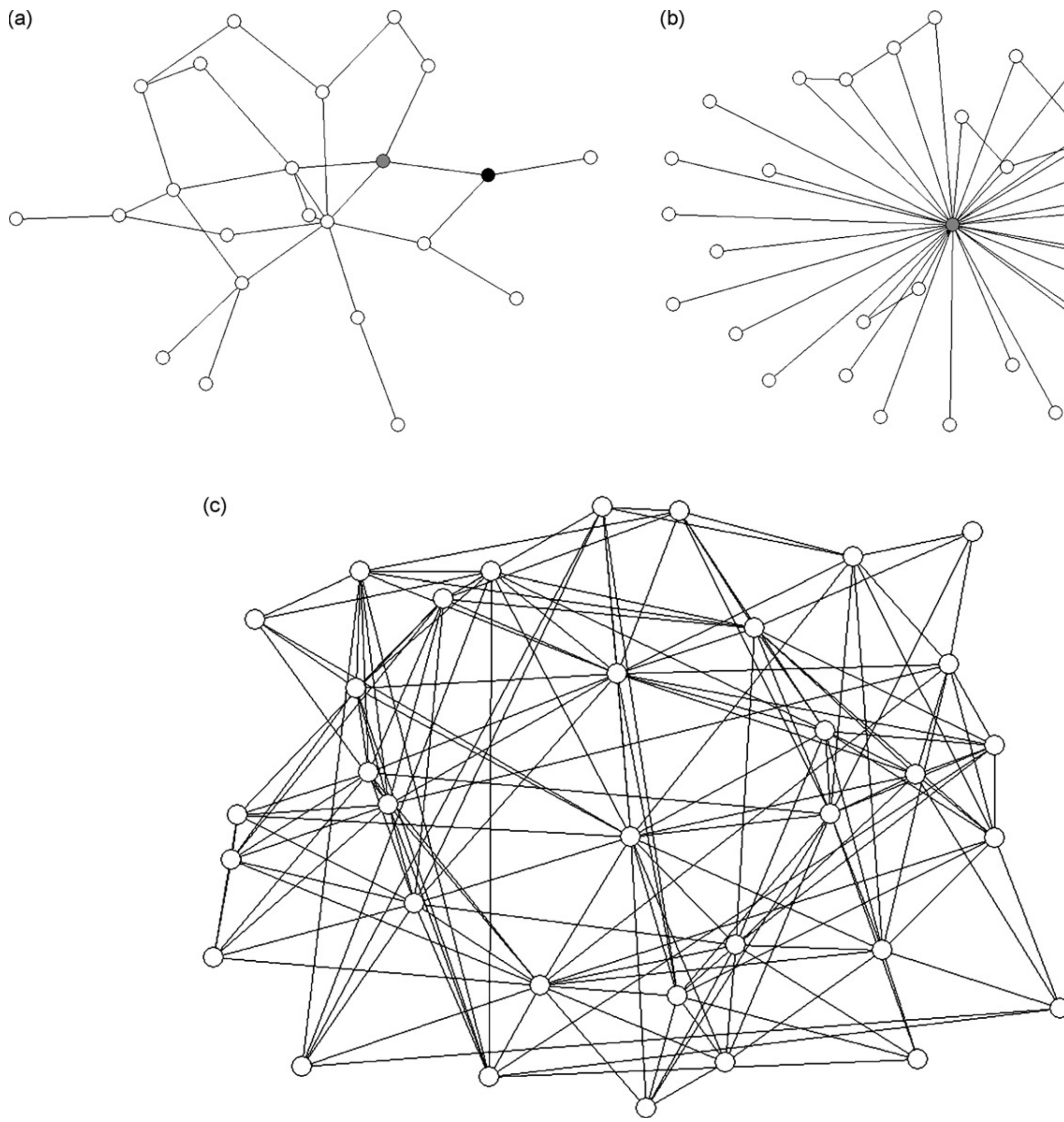

Fig. 1 – Human and animal social networks. (a) A typical *Ropalidia marginata* colony with queen (RmQR; colony number v272r; queen is black, potential queen is grey, NCI^D = 26.84, SW = 0.027), (b) is the queen-less form of the same colony (the new queen is in grey; she was the postqueen in (a), NCI^D = 97.73, SW = 0.033), and (c) is a class of students (class coded AG, NCI^D = 26.55, SW = 0.251). See explanation in text. Figure drawn by UCINET (Borgatti et al., 2002).

node. Note that network centrality, expressed in percentages, is maximal (100%) if a central node is directly connected to all other nodes (see Fig. 2). We have our networks with the *SW* data of a published dolphin network (Lusseau, 2003), although we cannot calculate the NCI^D of the latter (see Appendix).

3. Results

Here we study global network properties such as centrality (NCI^D) and small world-like character (*SW*) of the wasp and children networks (see Appendix for results), while local network properties characterising the position of individual nodes will be discussed elsewhere (Bhadra et al., in preparation).

3.1. Comparison of wasp species (Rc vs. Rm)

The average *SW* and NCI^D values are 0.0988 and 60.22, respectively, for Rm and 0.1124 and 64.62, respectively, for Rc colonies (pooled average for a total of 24 networks for both species). Based on both *SW* (Mann–Whitney *U*-test, $p = 0.273$) and NCI^D (Mann–Whitney *U*-test, $p = 0.721$), there are no species-specific differences in the architecture of the social networks. Thus, colonies of *R. marginata* (Rm) and *R. cyathiformis* (Rc) are not characterised by significantly different social interaction networks.

3.2. Comparison of colony stages (QR vs. QL)

The average *SW* and NCI^D values are 0.1205 and 42.54, respectively, for QR and 0.0907 and 82.30, respectively, for

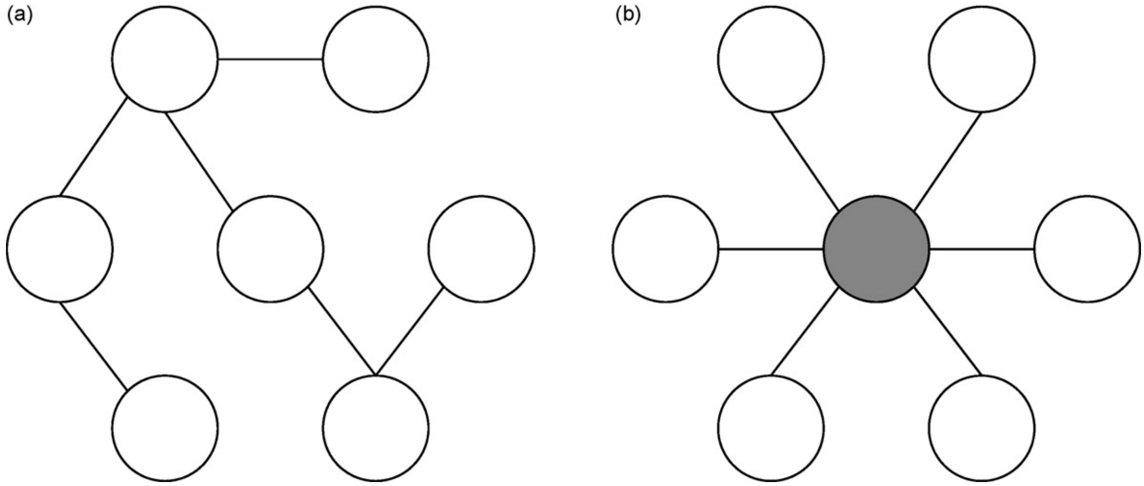

Fig. 2 – Two simple, hypothetical networks. Both consist of seven nodes and six links, but while (a) is not really centralised (*NCI^D* = 30), (b) is perfectly centralised (*NCI^D* = 100).

QL colonies (pooled average for a total of 24, 12 Rc and 12 Rm colonies in case of both stages). The difference between queen-right (QR) and queen-less (QL) stages of wasp colonies is significant only for NCI^D (Mann–Whitney *U*-test, $p = 0.000$; for *SW*, $p = 0.089$). QL colonies are significantly more centralised than QR colonies (Fig. 3a), although there is no statistically significant difference in their *SW* characters (Fig. 3b).

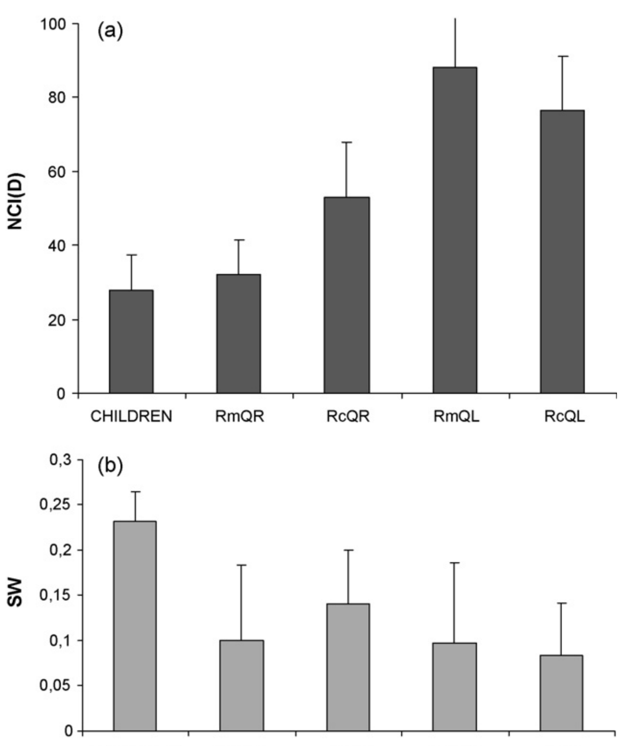

Fig. 3 – Centrality and small world character. The average values of *NCI^D* (a) and *SW* (b) for classroom networks and the queen-less (QL) and queen-right (QR) forms of *Ropalidia marginata* (Rm) and *Ropalidia cyathiformis* (Rc). Standard deviation is also shown.

3.3. *Comparison of species-specific colony conditions (RcQR, RmQR, RcQL and RmQL)*

The pairwise comparison of the four combinations of wasp species and stages always shows significant differences for NCI^D (Mann–Whitney *U*-test: $p = 0.0011$ for RcQR vs. RmQR; $p = 0.0009$ for RcQR vs. RcQL; $p = 0.000001$ for RmQR vs. RmQL; $p = 0.000003$ for RmQL vs. RcQL) but never for *SW* (Mann–Whitney *U*-test: $p = 0.1135$ for RcQR vs. RmQR; $p = 0.0284$ for RcQR vs. RcQL; $p = 0.7553$ for RmQR vs. RmQL; $p = 0.9774$ for RmQL vs. RcQL). Based on NCI^D values, the difference between QL and QR is much larger in Rm than in Rc (Fig. 3a). If the combination of *SW* and NCI^D values is considered, the four types of networks are clearly separated on the (Fig. 4).

3.4. *Comparison of wasps and children*

The average *SW* and NCI^D values of classroom networks are 0.2322 and 27.96, respectively. Social networks in classrooms significantly differ from wasp colony networks in 17 out of 18 possible comparisons. The *SW* character is different in the most general case (i.e. 36 classrooms vs. 48 wasp networks, Mann–Whitney *U*-test: $p = 0$), in case of comparing classrooms to either species-specific or stage-specific networks (Mann–Whitney *U*-test: $p = 0$ for classroom vs. Rc; $p = 0$ for classroom vs. Rm; $p = 0$ for classroom vs. QR; $p = 0$ for classroom vs. QL), and also in case of comparing classrooms to the four combinations of species and stages (Mann–Whitney *U*-test: $p = 0$ for classroom vs. RcQR; $p = 0$ for classroom vs. RmQR; $p = 0$ for classroom vs. RcQL; $p = 0$ for classroom vs. RmQL). For NCI^D, except for comparing classrooms to RmQR colonies (Mann–Whitney *U*-test: $p = 0.14$), all other comparisons show significant differences (Mann–Whitney *U*-test: $p = 0$ for 36 classrooms vs. 48 colonies; $p = 0$ for classroom vs. Rc; $p = 0$ for classroom vs. Rm; $p = 0$ for classroom vs. QR; $p = 0$ for classroom vs. QL; $p = 0$ for classroom vs. RcQR; $p = 0$ for classroom vs. RcQL; $p = 0$ for classroom vs. RmQL). Fig. 3a and b illustrate the low centrality and high SW character of classrooms, the latter is also shown

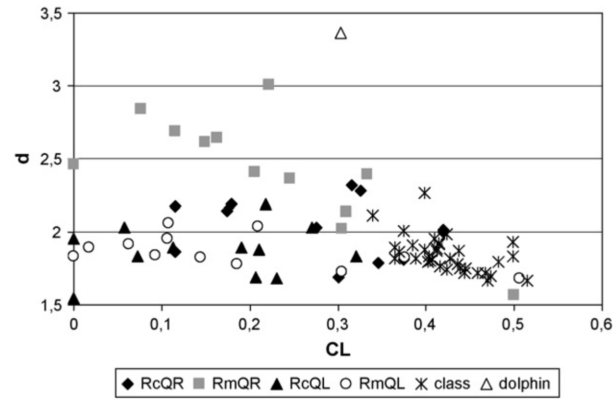

Fig. 4 – Clustering and distance. The *CL* and *d* values of the 84 studied networks and a dolphin network taken from literature for comparison (Lusseau, 2003). Regular-like (high *CL*, high *d*; dolphin), random-like (low *CL*, low *d*; queen-less wasps) and small world-like networks (high *CL*, low *d*; classrooms) can be localised on this plane.

in Fig. 4 (high clustering, low distance). Classroom networks are not as variable in their architecture as wasp colonies, as shown in Fig. 5.

4. Discussion

We have compared 84 social networks describing the interaction systems of 48 wasp dominance networks and 36 friendship networks of children. We have found that social networks in classrooms clearly differ from wasp colonies, based on both centrality and the small world character. However, in some cases one of the wasp species has an interaction network more similar to human social networks than to the networks of the other species. For example, based on centralisation, RmQR networks are closer to classroom networks than to RcQR networks (Fig. 3a). This suggests that *R. marginata* colonies and the communities of children in classrooms are similar from the viewpoint of being more homogeneous (more democratic?), while *R. cyathiformis* colonies are governed by one or a few key individuals. We find that network centrality was maximal (100%) in case of a *R. marginata* QL colony: here the PQ is directly connected to every other member of the colony (this seems to be quite unique in real networks, see Faust and Skvoretz, 2002, for comparison). So our results regarding the high centrality values for the queen-right *R. cyathiformis* colonies and the queen-less colonies of both species, as compared to the queen-right *R. marginata* colonies are in concert with behavioural observations described above. In *R. cyathiformis*, the queen is the most aggressive individual in the colony, and the potential queen is the second most aggressive individual, who further steps up her aggression to levels similar to that of the queen. This is typical of primitively eusocial wasp species. However, in *R. marginata*, the queen is a docile individual who does not show much aggression towards her workers (Premnath et al., 1996; Kardile and Gadagkar, 2002; Sumana and Gadagkar, 2003). If the queen is removed, one individual becomes extremely aggressive within minutes, and eventually becomes the new queen of the colony. However, unlike in the case of *R. cyathiformis*, this individual, also designated as the potential queen, does not seem to occupy any special position in the dominance hierarchy in the presence of the queen (Deshpande et al., 2006).

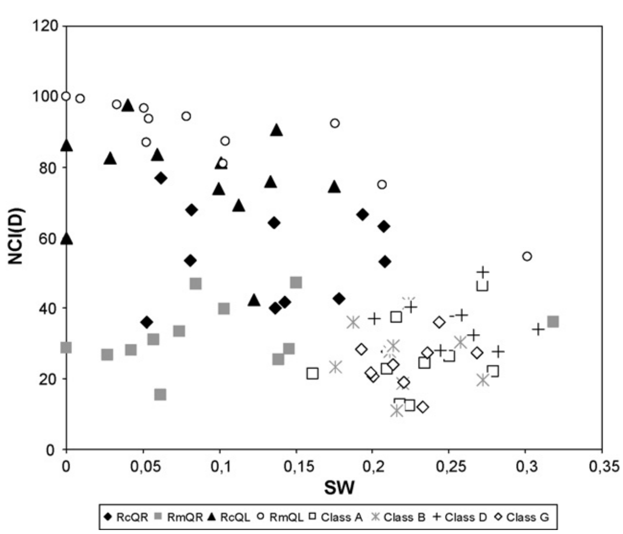

Fig. 5 – Combinations of topological properties. The combination of NCI^D and *SW* clearly separates certain kinds of networks and shows the higher temporal plasticity of wasp networks. Classroom networks are more constant in their structural properties, even if individuals can join and leave the class. Wasp networks are, on the contrary, dramatically reorganised after removing or loosing the queen.

Classroom networks do not change too much in time. Though individuals can either join or leave classes, the general architecture is much more robust to these changes as compared to the removal of queens from wasp colonies. The transition from the queen-right to the queen-less state in *R. marginata* is more fascinating from the perspective of longitudinal network analysis, because the de-centralised network suddenly becomes absolutely centralised, with the PQ emerging as the central node, while she does not necessarily occupy a very important position in the queen-right network. Moreover, this transition is caused by the removal of the queen, who hardly features as an important node in the queen-right de-centralised system. A seemingly parallel phenomenon in the human society might be a shift from a democracy to a dictatorship or autocracy. This is a well-documented and understandable example for the strong relationship between the structure and the dynamics of interaction networks. Even more interesting is the fact that in *R. marginata*, the extremely centralised queen-less network is a mere step in the transition process from one de-centralised queen-right network to another: as the network regains its original de-centralised nature, the PQ, now the queen, becomes a docile individual, hardly visible in the network from being the focal point of the queen-less network (and eventually she can become an isolated node in the network of dominance interactions).

Particular structural indices may give valuable information on networks, and their combinations can refine our understanding of network architecture and help in identifying network types. For example, the *SW* character is a ratio of *CL* to *d*, but if *CL* and *d* are considered separately, their combination turns out to be unique (consider the dolphin network: top-middle in Fig. 4 reflecting high clustering and large distance). These dolphin networks are the most regular-like networks. Similarly, classroom networks are the most small world-like networks (bottom-right corner in Fig. 4: large clustering, small distance) and queen-less wasp networks are the most random-like networks (top-left corner in Fig. 4: small clustering, large distance). Note that having the typical topology of random networks does not guarantee that a network was made randomly.

Major changes happen in wasp colonies if the queen is removed or lost. The difference between queen-right and queen-less colonies is significant, contrary to the difference between the interaction networks of different wasp species. Moreover, human interaction networks can be more similar to wasp networks than wasp networks to each other. This suggests that community organisation is driven more by functionality than by taxonomy.

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Appendix A. The codes and studied properties (*CL*, *d*, *SW*, NCI^D) of the studied networks (for the dolphin network no NCID data was published in Lusseau, 2003).

Network type	Network ID	*CL*	*d*	*SW*	*NCI*(*D*)
R. cyathiformis queen-right	c01r	0.346	1.786	0.194	66.67
	c03r	0.419	2.012	0.208	53.27
	c07r	0.300	1.688	0.178	42.86
	c08r	0.174	2.142	0.081	53.33
	c33r	0.276	2.033	0.136	64.10
	c34r	0.179	2.187	0.082	67.95
	c38r	0.375	1.810	0.207	63.33
	c50r	0.316	2.316	0.136	40.11
	c58r	0.326	2.282	0.143	41.67
	c59r	0.115	2.178	0.053	36.11
	c60r	0.115	1.861	0.062	76.79
	c86r	0.419	2.000	0.210	27.78
R. marginata queen-right	v248r	0.245	2.363	0.104	39.74
	v260r	0.163	2.642	0.062	15.42
	v262Ar	0.500	1.571	0.318	36.11
	v262r	0.310	2.133	0.145	28.57
	v267r	0.000	2.459	0.000	28.89
	v268r	0.222	3.006	0.074	33.33
	v269r	0.205	2.408	0.085	46.72
	v270r	0.115	2.692	0.043	28.03
	v272r	0.077	2.838	0.027	26.84
	v273r	0.149	2.615	0.057	30.95
	v276r	0.333	2.394	0.139	25.45
	v277r	0.304	2.026	0.150	46.97
R. cyathiformis queen-less	c01l	0.000	1.956	0.000	86.11
	c03l	0.218	2.186	0.100	73.81
	c07l	0.207	1.692	0.122	42.31
	c08l	0.058	2.029	0.029	82.50
	c33l	0.073	1.835	0.040	97.44
	c34l	0.271	2.029	0.134	75.83
	c38l	0.231	1.679	0.138	90.48
	c50l	0.191	1.891	0.101	81.11
	c58l	0.321	1.836	0.175	74.44
	c59l	0.211	1.881	0.112	69.23

Appendix A. (*Continued*)

Network type	Network ID	*CL*	*d*	SW	*NCI*(*D*)
	c60l	0.000	1.545	0.000	60.00
	c86l	0.113	1.894	0.060	83.64
R. marginata queen-less	v248l	0.144	1.825	0.079	94.29
	v260l	0.376	1.823	0.206	74.88
	v262Al	0.304	1.727	0.176	92.42
	v262l	0.185	1.782	0.104	87.27
	v267l	0.000	1.833	0.000	100.00
	v268l	0.209	2.040	0.102	80.77
	v269l	0.108	2.057	0.053	86.79
	v270l	0.017	1.895	0.009	99.42
	v272l	0.063	1.920	0.033	97.73
	v273l	0.106	1.953	0.054	93.53
	v276l	0.506	1.679	0.301	54.55
	v277l	0.093	1.838	0.051	96.70
Class A	aa	0.340	2.114	0.161	21.51
	ab	0.427	1.821	0.234	24.37
	ac	0.474	1.699	0.279	21.98
	ad	0.467	1.718	0.272	46.47
	ae	0.402	1.795	0.224	12.41
	af	0.410	1.956	0.210	22.88
	ag	0.439	1.751	0.251	26.55
	ah	0.412	1.887	0.218	12.80
	ai	0.415	1.925	0.216	37.42
Class B	ba	0.398	2.267	0.176	23.49
	bb	0.403	1.836	0.219	18.56
	bc	0.414	1.917	0.216	11.14
	bd	0.499	1.833	0.272	19.56
	be	0.398	1.881	0.212	27.72
	bf	0.404	1.806	0.224	41.29
	bg	0.498	1.932	0.258	30.44
	bh	0.388	1.820	0.213	29.44
	bi	0.375	2.004	0.187	36.09
Class D	da	0.384	1.910	0.201	37.24
	db	0.436	1.783	0.245	27.93
	dc	0.498	1.830	0.272	50.00
	dd	0.445	1.751	0.254	37.61
	de	0.458	1.722	0.266	32.48
	df	0.407	1.807	0.225	40.46
	dg	0.443	1.717	0.258	38.18
	dh	0.515	1.669	0.309	34.19
	di	0.470	1.667	0.282	27.64
Class G	ga	0.365	1.894	0.193	28.44
	gb	0.416	1.766	0.236	27.25
	gc	0.424	1.743	0.243	36.21
	gd	0.437	1.874	0.233	11.95
	ge	0.365	1.821	0.200	20.69
	gf	0.370	1.862	0.199	21.65
	gg	0.412	1.869	0.220	19.18
	gh	0.482	1.798	0.268	27.34
	gi	0.424	1.984	0.214	24.09
Dolphin group	dolphin	0.303	3.360	0.090	–

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