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LÚCIA CARVALHO NECO

Social terminology and the development of a metric of sociality: social networks
in spiders

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Dissertação apresentada ao Instituto de
Psicologia da Universidade de São Paulo
para obtenção do título de Mestre em
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Área de Concentração: Etologia

Orientador: Prof Dr. Nicolas Châline

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TRABALHO, POR QUALQUER MEIO CONVENCIONAL OU ELETRÔNICO,
PARA FINS DE ESTUDO E PESQUISA, DESDE QUE CITADA A FONTE.

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Aprovado em:

Banca Examinadora

Prof. Dr. Nicolas Châline

Instituição: Departamento de Psicologia Experimental, Universidade de São Paulo

Julgamento: _____

Assinatura: _____

Profa. Dra. Patricia Izar

Instituição: Departamento de Psicologia Experimental, Universidade de São Paulo

Julgamento: _____

Assinatura: _____

Dr. Danilo Muniz

Instituição: Departamento de Ecologia, Universidade de São Paulo

Julgamento: _____

Assinatura: _____

Prof. Dr. Benoit Jahyny

Instituição: Colegiado de Ciências Biológicas, Universidade Federal do Vale do São Francisco

Julgamento: _____

Assinatura: _____

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RESUMO

Neco, L. C. **Terminologia social e desenvolvimento de uma métrica de socialidade: redes sociais em aranhas**. 76f. Dissertação de Mestrado, Instituto de Psicologia, Universidade de São Paulo, São Paulo, 2017.

No livro *The Insect Societies*, Wilson propôs categorias de socialidade que foram consideradas uma unificação histórica da terminologia no estudo do comportamento social. Desde então, muitos novos padrões comportamentais foram descritos, mas não podiam ser encaixados em nenhuma das categorias disponíveis, prejudicando o consenso em torno dessa classificação bem estabelecida. Novas classificações gerais tentaram contornar as limitações mostradas pela categorização de Wilson, mas com pouco sucesso. Entre as proposições, algumas mantêm a forma de categorização discreta usando características consideradas importantes pelos autores que as propuseram; outros avançam em um modelo quantitativo de caracterização da socialidade. A análise de Carnap sobre os tipos de conceitos em ciência pode nos ajudar a avançar nesta discussão. Sua distinção entre conceitos qualitativos (classificatórios e comparativos) e conceitos quantitativos é usada aqui como base epistemológica para analisar o desenvolvimento das mudanças conceituais e classificações de socialidade propostas. A abordagem de Carnap reforça a proposta de superar a dicotomia entre espécies sociais e sociais a favor de um modelo de gradientes de socialidade. Concluímos que uma nova métrica de socialidade deve ser construída, usando características que não são arbitrárias, mas sim evolutivamente significativas e que permita a comparação entre o comportamento social de todas as espécies. Nesse sentido, a análise de redes sociais tem sido usada para descrever a estrutura de diferentes sociedades, características da estrutura das redes são comparáveis entre grupos e espécies. Aranhas sociais se constituem como um ótimo objeto de estudo, pois apresentam diferentes níveis de socialidade em diferentes níveis taxonômicos. Nós, portanto, desenvolvemos uma abordagem de redes sociais para quantificar a socialidade em colônias de *Anelosimus eximius* e descrever sua estrutura. Somado a isso, e considerando que a divisão do trabalho é uma característica importante das espécies eussociais, nós testamos se os indivíduos nas colônias se especializam em tarefas e se organizam em grupos em diferentes contextos sociais. Além disso, avaliamos quais os efeitos do tamanho de grupo nesta organização social. Indivíduos de *A. eximius* apresentam uma organização em grupos nos diferentes contextos sociais, e as colônias apresentam uma baixa, porém significativa, taxa de especialização em tarefas. Os grupos variam entre contextos, mas são frequentemente similares em contextos ativos. Em colônias menores, os indivíduos não apresentam grupos consistentes, todos os indivíduos parecem necessários para as tarefas. Complexidade social definida como especialização e formação de grupos dentro da colônia parece ser uma métrica útil de socialidade, permitindo a comparação de uma gama de espécies. O tamanho dos grupos tem que ser levado em conta, porque indivíduos aparentam ser sensíveis às necessidades da colônia.

Palavras-chave: métricas de socialidade, conceitos em ciência, aranhas sociais, divisão do trabalho

ABSTRACT

Neco, L. C. **Social terminology and the development of a metric of sociality: social networks in spiders.** 76p Dissertação de Mestrado, Instituto de Psicologia, Universidade de São Paulo, São Paulo, 2017.

In the book *The Insect Societies*, Wilson proposed categories of sociality that were considered a landmark unification of terminology in the study of social behavior. Since then, many new behavioral patterns were described, but they could not be fitted in any of the available categories, undermining the consensus around that well-established classification. New general classifications tried to circumvent the limitations shown by Wilson's categorization, but with little success. Among the propositions, some maintain the form of discrete categorization using features considered important by the authors who proposed them; others advance a quantitative model of characterization of sociality. Carnap's analysis of types of concepts can help moving forward in this discussion. His distinction between qualitative concepts (classificatory and comparative) and quantitative concepts is used here as an epistemological basis for analyzing the development of the proposed conceptual changes and classifications of sociality. Carnap's approach reinforces the proposal of overcoming the dichotomy between eusocial and social species in favor of a model of sociality gradients. We conclude that a new metric of sociality should be built, using characteristics that are non-arbitrary, evolutionarily meaningful, and amenable to comparing social behavior between all species. In this context, social network analysis is currently used as a means to describe social structures in animal systems, and the network structure characteristics can be compared across groups of different composition and species. Social spiders are good models to study social behavior because they present different levels of sociality in different taxonomic levels. We develop a social network approach to quantifying sociality in *Anelosimus eximius* colonies and describe its structure. In addition, since division of labor is an important feature of eusociality, we evaluated individual specialization in colony tasks and tested for the existence of groups of individuals through different social contexts. We also evaluated the effects of colony size on such organization. *A. eximius* present a organization in groups in different social contexts, and colonies exhibit a low, but significant, specialization rate in particular tasks. Group composition among spiders was flexible but frequently similar in active tasks. Individuals in smaller colonies did not form consistent groups; all individuals seem necessary to perform the tasks. The evaluation of social complexity in terms of specialization and group organization seems to be a useful metric, allowing the comparison of a wide range of species. Colony size should be an important qualifier of this metric, since individual behavior appears sensitive to colony needs.

Keywords: metric of sociality, scientific concepts, social spiders, division of labor

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1. GENERAL INTRODUCTION

Social life is challenging for the individuals because of the costs of living in groups. We can cite costs for reproduction (BILDE et al., 2007), the increase of disease transmission (BROWN; BROWN, 1986), and the larger chances of conflict between individuals (O'BRIEN, 1991) as examples. This challenge stimulated the development of many models balancing costs and benefits to explain the evolution of cooperation, one of the important features of social life. Among these, we find the models included in the theory of inclusive fitness (HAMILTON, 1964), models of direct (TRIVERS, 1971) and indirect reciprocity (ALEXANDER, 1987; NOWAK; SIGMUND, 1998), and group selection models (WILSON, 1975).

Although social behavior is much studied in vertebrates, such as birds (e.g. SLAGSVOLD; WIEBE, 2011), primates (e.g. KOENIG et al., 2013) and cetaceans (e.g. ESTEBAN et al., 2016), relevant knowledge about social complexity frequently comes from other animal models, such as some social invertebrates. The understanding of the processes involved in the emergence of complex interaction patterns coming from simple rules - such as trail formation in ants (CZACZKES et al., 2012), or the forms of collective prey capture connected to individual personalities in spiders (GRINSTED et al., 2013) - can help us to build more general models that assist in the study of the evolution of social systems.

One way of understanding the evolutionary processes responsible for the emergence of complex interactions between social organisms is comparing different species with similar levels of sociality. In 1969, Michener used the comparative method for classifying sociality in distinct types of association or evolutionary phases in order to compare different bee societies. The comparative method can identify behavioral patterns that could have evolved in response to similar environmental challenges (HARVEY; PAGEL, 1991). One way these behavioral similarities can be identified is through a metric that qualifies (in the form of categories) or quantifies the behaviors to be

analyzed. Therefore, we need a clear and objective metric of the complex and hard to classify phenomena of sociality.

A widely known and used categorization of levels of sociality was proposed by Wilson (1971), as a derivation from Michener's (1969) classification. He categorized social animals as communal, quasisocial, semisocial or eusocial in the so-called "parasocial sequence" or primitively subsocial, intermediate subsocial I, intermediate subsocial II or eusocial in the "subsocial sequence", intending to mirror the gradual steps in the evolutionary processes related to two different routes leading to the origin of eusociality.

Although this classification has been widely accepted, many new social species and behaviors were described after its elaboration, rendering its use increasingly more difficult. This is because many of the newly described social animals either fit in-between these categories, or present new interesting social features, undermining the consensus around the well-established classification (COSTA; FITZGERALD, 1996; LACEY; SHERMAN, 2005; COSTA, 2010).

One example of the limits of Wilson's categorization can be found in the classification of social spiders: *Anelosimus eximius* is a species with alloparental care and generation overlap (AVILES, 1997). It should be categorized as "intermediate subsocial II" in Wilson's "subsocial sequence", but it has been usually defined as quasisocial (BRACH, 1975; FOWLER, LEVI 1979), and, more recently, has been labeled as cooperatively social in a new classification restricted to spiders (AVILES, 1997).

The term "quasisocial" describes a species in which the evolution of sociality followed the "parasocial sequence". In other words, social behavior in the species evolved through the association of individuals from the same generation (WILSON, 1971). However, the most accepted view is that social spiders evolved by a subsocial pathway through delayed dispersal of the young (AVILES, 1997). The new classification from Aviles (1997) solves this problem but it is specifically limited to spiders.

Another example can be identified in the diversity of eusocial insects' organizations. In this regard, Crespi and Yanega (1995) point out that Michener-Wilson's eusocial category is based on a vague characteristic: "reproductive division of labor". But when we analyze this diversity, we can find examples of ants with no queens or hierarchy, bees with multiple or a single reproductive female, workers functionally and morphologically sterile (review in ANDERSON; MCSHEA, 2001), making it hard to discern what eusocial animals really are or where are the limits of this category. This is due to the multiple interpretations of reproductive division of labor as a characteristic of eusociality (CRESPI; YANEGA, 1995).

New general classifications (CRESPI; YANEGA, 1995; SHERMAN et al., 1995; COSTA; FITZGERALD, 1996; 2005; NONACS, 2001; LACEY; SHERMAN, 2005) tried to circumvent the confusion stemming from the use of Wilson's categorization, but with limited success (COSTA; FITZGERALD, 2005). They most often select characteristics considered relevant by their authors in relation to particular species, or for some theoretical approaches, but these characteristics are never sufficient to encompass the breadth of social complexity. Adding to that, some authors understand the evolution of sociality as gradual and hard to fit in simple categories, urging the need of a quantitative approach to this problem (SHERMAN et al., 1995).

Thus, there is a need to understand the development of different types of classifications of sociality and define metrics that enable the comparison between different levels of social complexity across different animal species, since there is confusion and misuse on the most generally accepted classification of sociality, and considering that there is no consensus on that matter. These metrics could allow the analysis of simpler cooperative species, without reproductive division of labor and with different levels of social complexity, which have traditionally been classified in relation to eusocial species, rather than in terms of their own characteristics (Costa, 2010). Because of this broad approach, they can represent an analytical tool for the study of the evolution of animal societies.

Among these species with simpler social organization, social spiders stand out as good model systems, because they present different levels of sociality in distinct taxonomic groups (UETZ; HIEBER, 1997; VIERA, 2011). Moreover, investigating the level of complexity of spider societies can teach us a lot about the steps in the evolution of sociality, because they lack reproductive division of labor, an allegedly important characteristic of eusociality (UETZ; HIEBER, 1997). In other words, we can analyze different levels of social organization in spiders that are not associated with reproductive skew (like in some other societies such as in mammals) and pay attention to other important characteristics of a society.

Considering the problems described above, it is useful to identify the best framework for useful metrics of sociality and proceed to test an approach that fits that framework. This dissertation addresses these problems. It is organized in two chapters. Chapter one is theoretical and aims at evaluating critically various conceptions of sociality, while providing new directions for the classification of social systems. In Chapter two we propose a metric of sociality based on the differentiation and organization between parts in a social system (specialization and division of groups) using social network analysis as a methodology. We then proceed to test a few hypotheses concerning these parts of the social system, using this methodology in the social spider *Anelosimus eximius*.

2. CHAPTER ONE

From classificatory to quantitative concepts in the study of sociality in animals: An epistemological view¹

2.1. Introduction

Animal social systems have been studied long before Darwin (COSTA; FITZGERALD, 1996), but over the past few decades a debate has emerged over the classification of these systems (GADAGKAR, 1994; CRESPI; YANEGA, 1995; SHERMAN et al., 1995; WCISLO, 1997; COSTA; FITZGERALD, 1996, 2005; LACEY; SHERMAN, 2005; RAYOR; TAYLOR, 2006; WEST et al., 2007). In this chapter I will first present an overview of this debate and the issues associated with the use of some classificatory schemes. Secondly, I will introduce an epistemological approach drawing from Rudolph Carnap's arguments about the development of concepts in science, particularly his differentiation between classificatory, comparative, and quantitative concepts. Third, I will build upon this differentiation to discuss the problems with the contemporary classifications of social systems. After that, I will introduce a few criteria to a useful definition of sociality. Finally, I will propose future directions to the classification of social systems based on a quantitative, multi-dimensional approach to sociality.

2.2. Overview

In the book *The Insect Societies* (1971), E. O. Wilson proposed levels of sociality that are seen as a landmark in the unification of the terminology used in the study of social behavior. These levels (or categories), based on

¹ This paper was submitted to Biological Theory journal as a requirement of the Experimental Psychology Graduate Program.

Michener's (1969) work on bees, classified social animals according to three characteristics: (i) reproductive division of labor, (ii) generations overlap, and (iii) alloparental care. Species presenting all three characteristics were considered eusocial.

Until the mid-1980s, eusociality was restricted to some bees, ants, wasps, and termites. Since then, in many other species, new patterns of sociality were studied that did not fit perfectly in these categories (LACEY; SHERMAN, 2005).

One example of that is the case of tent caterpillars. They present big colonies in which individuals cooperate in capturing food and defense, but they are considered not much social because they lack division of labor and alloparental care, extremely important features of complex social behavior. A few other authors disagree with this position and argue that tent caterpillars are very much sophisticated in their social behavior and other characteristics must be considered in the comparison between species (COSTA; FITZGERALD, 1996). The discussions were about terminology and also the characteristics that lead the evolution of sociality.

More than that, the eusocial category seemed to expand hugely and encompass from shrimps (DUFFY et al., 2000) to naked-mole rats (JARVIS et al., 1994). A few authors argue that one of the three characteristics that defined animals as eusocial, the reproductive division of labor, is not clear (CRESPI; YANEGA, 1995).

As a result, the characterization of sociality was questioned and several reevaluations of social categories were presented. Some of these reevaluations maintain discrete categories while introducing new criteria (CRESPI; YANEGA, 1995; GADAGKAR, 1994), while others advance a classification based on quantitative criteria (SHERMAN et al., 1995; COSTA; FITZGERALD, 2005). Many of these proposals have failed to clarify the classification of social systems, and none have acquired wide acceptance (COSTA; FITZGERALD, 2005; RAYOR; TAYLOR, 2006).

In our view a clarification of the very concept of sociality and of the

characteristics that can be used as criteria for the classification of social behavior is important. Flawed classificatory schemes are problematic in the scientific practice, because concepts should delimit precisely and objectively the objects of study to create a qualified understanding about them (GERARD, 1958). To propose a proper classificatory scheme, it is important to ponder about the kinds of concepts we are using in developing it. In this work, we present such a reflection relying on the distinction between qualitative (classificatory and comparative) and quantitative concepts proposed by Carnap ([1966] 1995), and build on his approach to evaluate the conflict on how to classify forms of sociality from an epistemologically sound point of view. We will use Carnap's framework to analyze the evolution of the classifications of sociality, and to propose avenues for the development of a new classificatory scheme.

2.3. Carnap's analysis

A fruitful philosophical approach to analyze the historical changes in the classification of sociality is the typology of concepts put forward by Rudolf Carnap in 'On Explication' (1962). Carnap has been the most well-known philosopher among the logical positivist analytic tradition in philosophy, arising from the Vienna Circle, which criticized the "chair philosophy" full of scientifically non-informed discussions and stimulated empiricist methods and the use of logic (UEBEL, 2016).

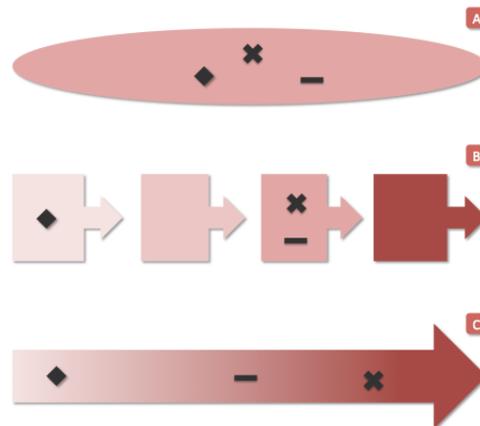
In Carnap's typology, three fundamental categories of concepts are presented: classificatory, comparative, and quantitative concepts. These three categories define concepts that are used in classification systems, objects that are blue can be of different shades of blue: sky blue, pure blue or cobalt blue. Because of that, we can relate them to the proposals of classifications of sociality. In each of these proposals, scientists have been trying to improve our knowledge about the differences between social systems using concepts available or new in the literature. In the same way, a social species can present different characteristics of sociality and be eusocial, subsocial or a certain degree social.

As Carnap (1962, [1966] 1995) discusses, classificatory concepts (Figure 1A) are related to classical categorization, according to which an object either belongs or not to a given class or set, in an all-or-nothing manner (CARNAP, [1966] 1995). These concepts usually result, though, in weak statements about the nature of the object and give little information about it, because only divide the domain in two possibilities (in or out), not observing differences in the objects included in the classes. They are widely used in prescientific conceptualization but are also extremely important to delimit big sets of scientific objects.

Comparative concepts provide more qualified information about the object in question, because, as the name says, they compare objects in a relationship scale (Figure 1B). In this comparison, an object can be harder than another one, for example. They can also organize objects in a row of intensity, building categories, e.g. cold, mild, and hot. (CARNAP, [1966] 1995). This way we can see the object not just by itself, but also in relation with other objects. From that, we can even build hypotheses about why they are related in a certain way.

Comparative concepts can finally give rise to quantitative concepts. Quantitative concepts characterize objects through numerical values that can be defined via measurements of the object or using indirect measures connected to the object (Figure 1C). In quantitative concepts, Carnap argues, there is more precision and fruitful amount of information about the object in question. They are the “most effective instruments of the scientific arsenal” (CARNAP, 1962, p. 9). For Carnap ([1966] 1995), the leap from comparative to quantitative concepts is important because it represents the shift from a qualitative language, restricted to names, to a numerical functional language, with more explanatory power.

Figure 1 - Schematic representation of classificatory (A), comparative (B), and quantitative (C) concepts.



Notes: “X”, “Minus” and “Diamond” are objects classified as the same category in (A). They all share a characteristic. “Diamond” is separated from “X” and “Minus” in B according to an order of intensity in this characteristic. The same objects are completely separate in C, because if this characteristic is measured, all three have different values in the continuum.

2.4. Application to sociality

Carnap’s typology can be applied to analyze the development of the classifications of sociality and also to point out to a more meaningful way to solve the conflict between classificatory schemes. In this section, I present examples of proposals in the field, how they can be connected with Carnap’s approach and discuss what should we be looking for based on that same approach.

Concepts of sociality that fit in the called “classificatory concepts” are used as a basis to build a more general understanding of the evolution of sociality in animals. They state the necessary conditions to classify an animal as social or not and, as said before, they give us very little information about the characteristics of each animal society.

An example of classificatory concept can be found in Wilson’s works. In *Sociobiology* (1975), he defines social animals as organisms from the same species that present, as an essential criterion, “reciprocal communication of a cooperative nature”. Michener (1953) is more restrictive,

defining organisms as social only if parents survive to cooperate with their offspring and there is division of labor. He is defining the “truly” social animals, considered later as eusocial animals. These are classificatory concepts because all organisms that present these characteristics will be considered social, despite other characteristics that could make their sociality different from one another.

In turn, comparative concepts are more frequently used in the literature, because of the information that is added to the concept of sociality, highlighting the differences in social systems. Examples of comparative concepts are found in the widely used classification from Wilson’s “The Insect Societies” (1971). Although the author discusses attributes of animal societies such as group size and cohesiveness, in addition to the time spent in social behavior, when it comes to his final classificatory scheme, Wilson (1971; 1975) uses only three characteristics (called qualities) to define sociality: generation overlap, reproductive division of labor, and alloparental care (Table 1). As eusocial animals show all three characteristics, eusociality becomes the reference for the categorization, that is, all other forms of sociality are described in relation to what they lack with regard to eusociality.

Moreover, he describes two different routes that would lead to the origin of eusociality (WILSON, 1971, 1975). In the so-called “parasocial route”, communal animals would be those who live together, but do not manifest any of the three features listed above, while animals are characterized as quasisocial when they display only alloparental care or semisocial when they present only alloparental care and reproductive division of labor. All social animals that are not eusocial can also be called “presocial”.

In the “subsocial sequence”, the close association between mother and the offspring are the leading vector for the evolution of eusociality. Then, animals considered primitively subsocial present extended parental care but the young disperse before reaching maturity. In turn, when the young animals stay until the adult phase and, consequently, there is overlap between generations, animals are classified as intermediate subsocial I. However, social animals that present alloparental care and generation overlap are

considered intermediate subsocial II. The next category will be eusocial, with all the three above-mentioned characteristics.

Table 1 - Wilson's classification of sociality and the qualities present in each category in the sequences of the evolution of social behavior (adapted from WILSON, 1975)

Degrees of sociality	Qualities of sociality		
	Cooperative brood care (alloparental care)	Reproductive castes (Reproductive division of labor)	Overlap between generations
Parasocial sequence			
Solitary	-	-	-
Communal	-	-	-
Quasisocial	+	-	-
Semisocial	+	+	-
Eusocial	+	+	+
Subsocial sequence			
Solitary	-	-	-
Primitively subsocial	-	-	-
Intermediate subsocial I	-	-	+
Intermediate subsocial II	+	-	+
Eusocial	+	+	+

Since this classification was based on insect societies, the majority of the studies using this categorization, and therefore discussing about the social terminology, focuses on eusocial animals (COSTA; FITZGERALD, 1996). Thus, many proposals tried to specify the differentiation between eusocial and presocial/communal animals, arguing for the important characteristics to the evolution of the “truly” social animals, as we will see in the following paragraphs. Much of the other categories from Wilson's classification, such as semisocial or quasisocial, are not frequently used (COSTA; FITZGERALD, 2005).

One of the proposals for revising the concept of eusociality, and consequently, how the classification of social animals is structured, is presented by Crespi and Yanega (1995). They argue that, as we have more information about social animals than Wilson had when he proposed his

classification (1971), categories of social behavior should be more detailed and unambiguous to reflect meaningful biological transitions between them. For these authors, the ideal criterion for the identification of eusociality would be the formation of castes in social animals. Castes are the consequence of the reproductive division of labor in a colony, where a few animals reproduce and there is a clear and irreversible division of functions inside the social group. In other words, for them, the reformulation of the concept of eusociality would be based merely on the reproductive altruism within a colony, as a result of the presence of castes that should be formed prior to reproductive maturity - in other words, morphological castes -, and not on all three characteristics indicated by Wilson (1971, 1975).

In the same paper, the terms “semisocial” and “quasisocial” are also redefined to constitute a bigger category called “cooperatively breeding societies” (CRESPI; YANEGA, 1995). Within this wider category, societies have individuals that reproduce while others help raise the offspring (alloparental care), but these behavioral strategies are reversible (they are not like castes), because they are not formed prior to maturity. The frequency distribution of lifetime reproductive success is what distinguishes “semisocial” (bimodal, a few individuals reproduce) and “quasisocial” (unimodal, many individuals reproduce) societies. Summarizing, this paper maintains eusocial, quasisocial and semisocial categories to classify social animals.

More recently, there was a proposal to extend the term “eusociality” to include family units (HARDISTY; CASSIL, 2010). These authors argue that polyphasic wake/sleep cycles, or in other words, the availability of individuals wake almost all day to perform colony activities, would be an additional trait that eusocial animals share. Another paper amplifies the term “division of labor”, arguing that humans should also be considered eusocial because of the number of females that cannot reproduce and help raise the offspring: the grandmothers (FOSTER; RATNIEKS, 2005). Again, these authors modify the eusocial category to include a new array of animals in the category, but maintain the categorical structure of sociality as a comparative concept.

In all these proposals, we have categories decomposing the general

concept of sociality. Eusocial animals are considered more social than other social animals in an order of complexity based on the characteristics presented by Wilson (1971), Crespi and Yanega (1995) and Hardisty and Cassil (2010). So, we are adding more information about the diversity included in the social phenomenon through comparisons between organisms. Nevertheless, there remains much diversity within these less inclusive sub-categories (e.g. subsocial, eusocial), such as the large differences in group size and organization between different bee species, which would nevertheless remain in the same (eusocial) category (MICHENER, 1974).

Another proposition to deal with comparative studies of social animals, which is very different from the proposal of discrete categories for sociality, was defended by Sherman et al. (1995) and later reaffirmed by the same authors (e.g. LACEY; SHERMAN, 2005). According to them, a eusociality continuum would unify the terminology in the field and facilitate the classification of new behaviors within the overarching concept of sociality. This is the first example of a truly quantitative concept, because the continuum would be the result of a measurement. The eusociality continuum, according to Sherman et al. (1995), would be built upon a metric of reproductive skew. The lifetime reproductive success (LRS) would be taken as an indicator of the level of sociality. The authors indicate possible already existing metrics to play this role in the continuum and measure LRS. It is important to make it clear that reproductive skew measures are usually based on the presence of reproductive altruism (or absence if skew = 0), as mentioned above.

This metric aims at expanding the number of species taken as social and encompassing primarily all cooperative reproducers, including representatives of birds and mammals (SHERMAN et al., 1995). The authors understand that sociality and the evolution of reproductive altruism is a gradual phenomenon and this quantitative approach would enable the study of the selective pressures shared by the different animal societies.

A quantitative approach is also put forward by Costa and Fitzgerald (2005), who propose to abandon the terminology used in Wilson's

classification, with the exception of the term “eusocial”, which the authors limit to the classical eusocial insects: ants, bees, termites, wasps, and a few others. However, the hypothesis in focus in this work is that communication is a more appropriate criterion for sociality than reproductive skew. Costa and Fitzgerald (2005) also make clear that they are proposing the use of communication of a cooperative nature (based on the classificatory definition of sociality by WILSON, 1971), relevant for the social behavior, not all instances of communication.

The concept of reciprocal communication is evolutionarily meaningful; it focuses on character traits central to the organization of all societies. The evolution of communication for coordinated activity among conspecifics qualifies as an ‘evolutionary threshold’ (COSTA; FITZGERALD, 1996, p. 289)

For Costa and Fitzgerald (1996; 2005), the problem with reproductive skew as a sociality measure is that, first, focuses specific on reproductive effects of sociality as the most important characteristic of this phenomenon and give little attention to social systems with no reproductive altruism but exhibit complex communication and cooperative behaviors. Secondly, not only social, but any kind of behavior can theoretically be the cause of variations in reproductive success, such as “disease, host plant quality, climate, and so on” (COSTA; FITZGERALD, 1996, p.288). Thus, the concept of reproductive skew includes causes of variation that are not relevant for social behavior. This is different for communication, because the authors only focus on the cooperative instances of it, connecting their causes directly with important characteristics of sociality.

This classification aims at including organisms that do not have castes, but still present several cooperative behaviors. In the gall thrips *Anactinothrips gustaviae*, for instance, adults cooperate in the care of their young and share a colony site, but they do not have castes (KIESTER; STRATES, 1984). For the authors, cooperative communication could identify highly social animals like those even in the absence of reproductive division of labor (COSTA; FITZGERALD, 2005).

In these two examples of quantitative concepts, the authors use one characteristic of sociality to build their metrics. They can be called one-dimensional quantitative concepts. However, sociality can also be understood as a phenomenon composed by distinct components, such as the sociality attributes considered by Pollard and Blumstein (2012). In addition to the characteristics already mentioned in other proposals, such as castes and reproductive roles, these authors include group size and group substructure as relevant attributes to evaluate social complexity, without providing any quantitative metric to unify these characteristics.

Anderson and McShea (2001), in turn, divided the correlates of social complexity in four dimensions², which comports many attributes of social behavior, advocating for the quantitative measurement of them. The dimensions are: polyphenism, reproductive and behavioral totipotency, work organization, and communication. All of these but work organization had been considered before as important attributes to be measured in sociality. Work organization is related mainly with the foraging and defense strategies of the colonies.

Anderson and McShea (2001) show how quantitative concepts considering many attributes can bring more information about the objects than comparative concepts. They give examples of eusocial ant societies and show the incredible diversity of social organization they present. For instance, in the polyphenism dimension, some species are polymorphic, presenting a morphological and irreversible differentiation of castes, while some species do not have this morphological differentiation and sub-castes can be identified behaviorally. In the work organization dimension, some species forage individually, while others cooperate during foraging and even organize prey attack in groups. From these examples, we can understand how different can be species in the same category, and how these dimensions can

²Anderson and McShea (2001) refer to “categories”, but we chose to use the word “dimensions” to avoid confusion with social categories described earlier.

be continuous and should be measured quantitatively. Unfortunately the authors remain descriptive, and do not propose any measurement approach.

Most of the characteristics presented by Anderson and McShea (2001) were mentioned before: communication, reproductive polyphenism, and totipotency. Therefore, we understand that there is a confluence of some features that are considered important for the evolution of social behavior and can be taken into account in a complete approach in comparative studies of sociality. However, as mentioned before, although these proposals advocate for a quantitative metric, they do not present a proposal for an objective measurement of sociality.

In this context, an example of a recent multidimensional metric is found in Aviles and Hardwood (2012). Age at dispersal, the proportion of social groups vs. solitary individuals in the species, and the proportion of individuals that cooperate in the colony but do not reproduce, were the characteristics used in a quantitative metric that was applied to social spiders and naked mole-rat species. The first two characteristics relate to overlap between generations, while the last one is a measurement of reproductive skew. The authors consider this metric measurable in most social systems giving taxonomic unit to it. Nevertheless, it is blind to division of labor and communication, characteristics considered important for most of the previous authors mentioned.

In sum, we can see that the framework brought by Carnap can be applied to understand the development of the concepts of sociality. Actually, the development of these concepts follows closely the general trajectory for scientific concepts proposed by Carnap. Also, the adoption of a quantitative concept of sociality, as predicted in Carnap's general model, is reinforcing the abandonment of the dichotomy between eusocial and social organisms in favor of a model of sociality gradients. This model includes quantitative concepts based on attributes that can describe sociality in a more fine-grained comparative way.

2.5. Useful metric to sociality

In the previous section, we have showed how efforts to refine the conceptualization of sociality forms can be interpreted in terms of Carnap's approach to concepts, which envision a movement from classificatory and comparative to quantitative concepts as science advances. The next step, then, is to show how a quantitative concept of sociality can be useful to the investigation of this phenomenon. Finally, we can discuss how an appropriate metric can be proposed, in order to further develop a quantitative conceptual approach to sociality.

The first thing to consider, since we are dealing with an evolutionary phenomenon, is that the definition (and resultant metric) of sociality should be informative of which characteristics of organisms change when sociality evolves. In other words, features that compose social systems and are affected by their evolution (i.e. evolutionarily meaningful) are the best to include in a quantitative conceptual approach to sociality (COSTA; FITZGERALD, 2005), not arbitrary ones.

Adding to this first criterion, considering that this phenomenon evolved in many different taxa, the metric should be applicable to all animals. In this way, it would make it possible to compare which factors contributed to the evolution of the social organization under different selective pressures. This is a clear problem when we observe what Crespi and Choe (1997) called "polyphyletic origin of social lexicons", describing the frequent isolation between students of invertebrate and vertebrate sociality. This isolation, argue the authors, give rise to different terms of possible convergent patterns of social behavior.

An example that fits this criterion is Avilés and Hardwood's (2012) proposal. The authors not only propose a continuum that includes more than one attribute of sociality, but also discuss the need to choose features that are not specific to some social systems, to allow the metrics to be comparable between different species.

One relevant summary of these criteria to a useful definition for sociality were brought up by Crespi and Yanega (1995) (even though it is applied only to eusociality in their paper):

Our main criteria for a useful definition of eusociality are that the definition be *non-arbitrary* (categorizing societies by meaningful parameters), *universal* (applicable to all species), and *evolutionarily informative* in that it indicates differences between societies that differ in how natural selection affects behavioral interactions (CRESPI; YANEGA, 1995)

We are looking for a definition of sociality that is evolutionarily meaningful, reflecting differences and similarities in the evolution of social behavior, and can be applicable to all animals in order to allow comparative studies.

Besides being interesting to quantify the differences between societies of different species, the quantitative metric based on this concept of sociality can also be used in studies such as ecological comparisons, mechanistic models and phylogenetic analysis.

2.6. Conclusion

Using Carnap's typology of concepts we could compare the different approaches used by the authors who proposed ways to define and classify sociality in animals. If we follow Carnap, we will conclude that studies of social systems can be improved by using quantitative concepts, because they provide more information about these systems and allow meaningful comparisons between them. Recent work seems to go in that direction and advocate for a quantitative and multidimensional metric of sociality.

Many attributes of sociality have been proposed for a quantitative conceptual approach to this phenomenon and its evolution. Most of them, like division of labor (reproductive and organizational), appear very frequently in the literature, but there is no consensus on to how to measure them. Beyond that, we have to look for a useful metric for the study of this phenomenon. This metric should be build using characteristics that are non-arbitrary, evolutionarily meaningful, and that can be comparable between all animals.

3. CHAPTER TWO

Social networks as a metric of sociality in spiders

3.1. Introduction

Sociality encompasses such a wide range of social phenotypes and levels of complexity that the very possibility of comparisons within this diversity is challenging. In the book *The Insect Societies* (1971), Edward O. Wilson proposed categories (or levels) of sociality that turned into a landmark in the area, unifying the terminology in the study of social behavior. Wilson's categories were based on the presence of reproductive division of labor, generation overlap and alloparental care, which when all present defined eusocial species. As such, eusociality was restricted to some bees, ants, wasps and termites. However, reevaluations of Wilson's (1971) proposal have been put forward (e.g., CRESPI; YANEGA, 1995; SHERMAN et al., 1995; COSTA; FITZGERALD, 1996, 2005), and recently quantitative metrics of sociality have been proposed as an alternative (e.g., SHERMAN et al., 1995; ANDERSON; MCSHEA, 2001; AVILES; HARWOOD, 2012). These proposals stemmed from a debate over the characteristics that are important for the evolution of sociality and were mainly stimulated by the study, in many other species, of social patterns that did not fit into any of the available categories (COSTA; FITZGERALD, 2005). Indeed, quantitative metrics that take into account various characteristics of sociality and that are not restricted to some social systems and are evolutionarily meaningful would constitute more useful tools for comparative studies of social behavior (see Chapter 1).

Social complexity is being used in the literature to encompass many characteristics of social behavior (e.g., BLUMSTEIN; ARMITAGE, 1997; BOND et al., 2003; ANDERSON; MCSHEA, 2001), and social complexity metrics could be instrumental in the search of a more comprehensive way to compare different social systems. Nevertheless, even though it is intended as a general term, much of the literature mentioning social complexity is restricted to vertebrates and to characteristics such as boundedness, intelligence or culture, which are hardly applicable along the whole range of

social animals (e.g., DE WAAL; TYACK, 2009). A more integrative view of social complexity (FREEBERG; DUNBAR; ORD, 2012) should focus on the interacting individuals that compose the social system, considering the differentiation between those individuals (social roles) and how they are organized in the social system according to the nature and diversity of their interactions (group formation).

This approach to social complexity derives from Robert Hinde (1976)'s work. He proposes to describe sociality in terms of interactions (type and quality), relationships between group members through time, and the emerging structure (described by the dynamics of the relationships that converge into patterns, allowing for generalizations about social systems). In this way we can evaluate the importance of the interactions as essential to the social system, they are the "basic elements of social structure" (HINDE, 1976, p. 3).

Therefore, we will be looking for an approach to measure social complexity that could capture the general structure of interactions between individuals, reflecting patterns of differentiation between the individuals (social roles or specialization) and organization in the society (formation of groups). The approach used to measure these interactions should be applicable and comparable across different species.

A possible approach that fits in these requirements would be social network analysis (WEY et al., 2008). This type of analysis, derived from graph theory, studies the relationships (edges) between elements composing a network (nodes) and is used in many fields of science such as mathematics, economy and sociology. Recently it has been applied to the study of social animals, being used to evaluate different aspects of the structure of their societies based on the parts (individuals for example) of the social system (CROFT et al., 2008). Among these are studies on the cohesion within populations of dolphins (WISZNIEWSKI et al., 2009), stability in social roles of ants during time (JEANSON, 2012) and relationship between the structure of killer whales population and food availability (FOSTER et al., 2012). Most of these studies, like the latter, are connecting network measures with

environmental features.

Social network analysis intends to measure, according to Wey et al. (2008), the elements, in this case the interaction between organisms, which contribute and build the attributes of sociality. The attributes cited by Pollard and Blumstein (2012) (e.g., group size, social roles) are considered indirect measures of social complexity, because they emerge from these interactions (WEY et al., 2008). In this way, social network analysis has the potential to capture the richness of relations between individuals, which could be summarized by measures of the complexity of their interactions at more global levels, such as network structure measures.

Social network analysis has been mainly applied to analyze interactions in groups of vertebrates such as primates (TOKUDA et al., 2012) and marmots (WEY; BLUMSTEIN, 2010). Little has been developed in invertebrate organisms, although there are many more described social species and they are considered good model organisms, because they are smaller, often have larger group sizes and are easy to handle (KRAUSE et al., 2007).

Social spiders are good models to develop our proposal of using interactions to compare different social systems. Arachnids and insects were considered “the most useful database to analyze social evolution” (CRESPI; CHOE, 1997) because of the many and diverse occurrences of the evolution of social behavior. In addition, spiders have a large range of sociality levels (AVILES, 1997). Some species are organized in aggregations (connected individual webs with little cooperation), some are considered subsocial with a mix of social colonies and solitary individuals in the population and some are considered truly social or permanently social with stable colonies that have generation overlap (AVILES, 1997).

The family Theridiidae comprises representatives of social species with different levels of sociality (AVILES, 1997). *Anelosimus eximius* (Theridiidae) is one of the most studied species of social spiders and thus it is an adequate model to develop the first step of our approach on social

complexity using social network analysis. There are data available for this species on activity (e.g., CHRISTENSON, 1984), behavioral repertoire (e.g., VOLLRATH; ROHDE-ARNDT, 1983; CHRISTENSON, 1984) and phylogenetic relationships (e.g., AGNARSSON et al., 2006). This species is considered to be permanently social with stable colonies of as many as 10.000 spiders (AVILES, 1997). Thus, we expect this species to present high levels of social complexity in our approach. In other words, we expect to find certain differentiation among individuals (task specialization), and organization to perform different social tasks in the colony (formation of groups).

The idea of a behavioral specialization in the form of consistent individual differences between the members of the colony in spiders is currently being developed (EBERT, 1998; PRUITT et al., 2011, PRUITT et al., 2012). Other studies found a correlation between task participation and age and body weight (SETTEPANI et al., 2013; KEISER et al., 2014). Nevertheless, despite the available data on differentiation and organization in social spider's colonies, they are not yet considered a form of division of labor (UETZ; HIEBER, 1997) in the way we find in most social insects.

It is also important to understand how group size affects the stability of the organization and specialization in the colony. These crucial characteristics can change according to the number of individuals in the social group as a result of the necessities of the colonies (as we can see in some ants, ROBINSON, 1992) or the simple consequence of the number of relationships that could be established by the individuals (as in yellow-bellied marmots - MALDONADO-CHAPARRO et al., 2015). The effects of group size were also observed in social spiders shaping prey capture organization and prey type (HARWOOD; AVILES, 2013). The relationship between group size and group organization and specialization in the colony should be taken into account when we are analyzing social structure (ROBINSON, 1992), any metric of sociality should be able to deal with differently sized groups, and to evaluate social differences due to group size differences.

Considering that social interactions are a unifying characteristic that

seems to be shared by all social systems, and that many additional characteristics are based upon these interactions, this chapter proposes to take the first step in the development of a quantitative and multidimensional metric of sociality using social networks to analyze the interactions between individuals of the social system.

This first step's objectives are twofold: The first one is to investigate aspects of the social structure of *Anelosimus eximius* colonies that could reflect the social complexity based on the quantification of the association patterns between individuals in different social contexts and the evaluation of their organization in groups (or to which degree sets of individuals operate as distinct units in those contexts). Adding to that, we will also look at the pattern of specialization in the colony, or in which degree there is a differentiation of individuals performing different tasks.

To perform and guide this investigation, we address the following three questions: (i) *Are A. eximius colonies organized in groups? Is there a size threshold for group organization?* (ii) *Is this structure consistent across all social contexts?*; (iii) *Do A. eximius individuals specialize in tasks? Is this specialization affected by group size?*

We expect that *A. eximius* colonies will present organization based on groups in different social contexts and we also expect there will be a size threshold above which those groups begin to appear. However, we don't expect these groups to be the same in all of those contexts. Adding to that, we expect a specialization of groups in performing tasks, but not completely, like in social insects.

Our second objective is to discuss the role of these network analysis tools used here to investigate *A. eximius* behavior in the development of a quantitative and multidimensional metric of sociality.

3.2. Methodology

Biological material

Colonies of *Anelosimus eximius* were collected at the Michelin Forest Reserve, in Bahia, in July 2015, May 2016 and September 2016. In the laboratory, we housed the colonies in round plastic containers measuring 119 × 64.8 mm (diameter × height). The containers have perforations (n=20, 1mm diameter) in the lid for ventilation. The colonies were maintained at controlled temperature (between 25°C and 27°C) and humidity (60 – 75%), under natural light variation. Mealworm larvae (*Tenebrio molitor*) were offered each 3 to 5 days to the spiders and distilled water was sprayed into the containers at the same frequency.

Experiments

The experimental system consisted of acrylic boxes of 20×20×25cm (Figure 2). A net square separated the bottom 5 cm of the boxes to facilitate cleaning and web manipulation. The boxes contained a 3 cm (ratio) opening in one side protected by a removal copper net. This opening allowed manipulation of the colonies during the experiments.

Figure 2 - 3D draw from experimental box

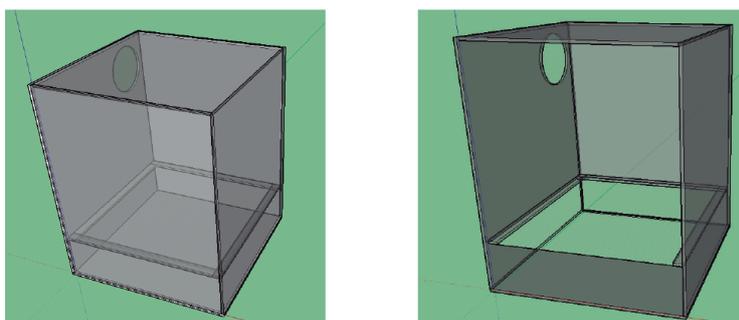
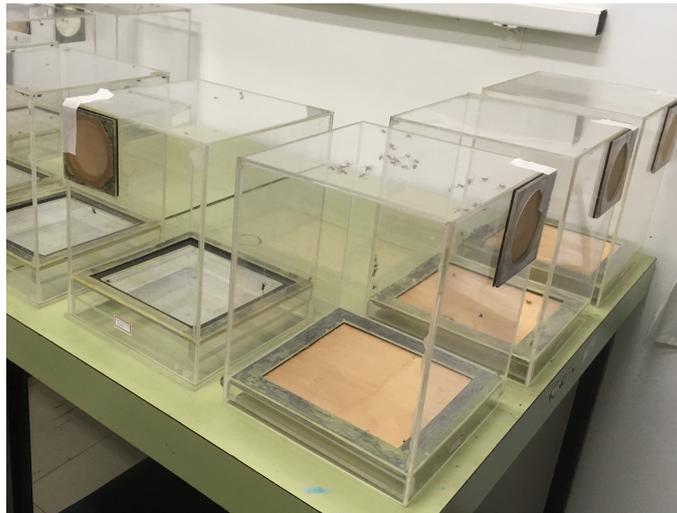


Figure 3 - Experimental boxes in the laboratory



Anelosimus eximius spiders have one peak of activity in the sunset (CHRISTENSON, 1984), so the observations of active behaviors (prey capture and web repair) took place between 1700 h and 1900 h. Fluorescent lights provided uniform illumination to the box during the experiments.

We built 27 samples of 36, 24 and 12 adult females (9 for each size), since adult females are responsible for most of the activity in colonies (CHRISTENSON, 1984). All spiders in a sample were from the same colony. Individual spiders were identified using a two-color mark on their abdomen (uni[®]PAINT marker) and entered into a database with a given identification number. The individuals were introduced in the box 5 days before the experiment began to allow for the building of a functional web.

Figure 4 - Two-color mark used to identify individual spiders



Two active social contexts in which interactions between spiders have been reported and partially described were observed: web repair (LUBIN; BILDE, 2007) and prey capture (PASQUET; KRAFFT, 1992). In those cases, we considered associations as a measure of interaction (WHITEHEAD, 1997). In addition, the spiders were also observed in what we called “resting hour” (out of the activity peak) to assess the pattern of associations between individuals out of activity. Here, interactions were measured by proximity.

We recorded the associations of all marked individuals in 10 samples of each context, in each colony, for the three sample sizes (36, 24 and 12 individuals) in order to capture patterns in these associations, not merely random interactions. To guarantee the independence between samples (allowing the individuals to rearrange in the colony), they were registered with an interval of 24 hours for resting, and 3 days for prey capture and web repair.

In the prey capture context, for each colony, we offered a mealworm (Size +3 cm) placed through the side opening of the acrylic box, 10 cm deep in the web as a prey. After 30 seconds of the arrival of the first individual to the prey, we started a scan every 3 minutes until the end of the capture. In each scan, we recorded which individuals actively participated in the capture together. We considered the capture finished when the prey stops moving for at least 5 minutes. The prey was offered each three days in each colony in a total of 10 samples per colony. All the individuals that participated (manipulating, biting or rolling the prey) at the same time in the prey capture were considered to be a group associating.

For the web repair procedure, we damaged the structure of the web in using a 10 cm long blade attached to a plastic handle heated with the help of a lighter. This blade were introduced into the side opening of the acrylic box and moved 1 cm to each side on the horizontal axis, which destroyed the threads present there. The damage was made each three days in each colony in a total of 10 samples. The web repair behavior of the individuals was observed for a total of 30 minutes since the first spider begin to move in

the web. Each 5 minutes we noted which individuals are depositing new threads on the web (web repair). All the individuals that participated at the same time in the web repair were noted as a group associating.

In the resting time, the associations between individuals were measured through proximity between individuals of the colony between 1400 h and 1500h (out of the activity peak) once a day during 10 days. Spiders were considered to be close if the distances between individuals are smaller than the first leg length (aprox. 1cm – AGNARSSON, 2006). This distance is arbitrary although it is based on a tactile recognition system already described in this species (PASQUET et al., 1997). All close individuals in a group will be considered associating.

Analysis

Before any analyses were done, we removed all individuals that did not participate in at least 50% of the trials in order to decrease error in the proportion of individuals participating in the social contexts. We removed zero to 17 individuals of the colonies. All analyses using group size directly were performed with the size of the colony after we dropped those individuals.

(i) *Are A. eximius colonies organized in groups? Is there a size threshold for group organization?*

For this question we standardized the number of observations of association in our experiments, because not all samples have the same effort. Next, we converted the standardized records of group association into a scale. Here, we used the “simple ratio index” (SRI), an unbiased estimate of the proportion of time the individuals spend together recommend by Ginsberg and Young (1992):

$$SRI_{ij} = x/(x+y_i+y_j)$$

where x = number of associations including both spider i and j in the same group; y_i = number of associations including spider i but not spider j in the same group; y_j = number of associations including spider j but not spider i in

the same group; and y_{ij} = number of associations including spider i and j in different groups at the same time (GINSBERG; YOUNG, 1992)

From this index, we built matrices of association between pairs of individuals (dyads) in each context. We had a total of 3 matrices (for the contexts: Web Repair, Prey Capture and Resting Time) for each colony.

In those matrices, individuals performing the same tasks or together all the time will present the maximum value (1) and individuals who are never seen together will present the minimum value (zero).

To investigate if individuals are organized in groups, we used Newman's eigenvector-based method of community division by modularity (NEWMAN, 2006). This method is validated by the modularity coefficient, Q (here I will call it Q_1), which is the sum of group associations for all dyads belonging to the same group minus its expected value if dyads associated in groups at random. The method maximizes the value of Q , allowing the best assessment of the community structure, even if all individuals belong to the same group (i.e. there's no division in groups).

According to Newman (2004), a Q -value greater than 0.3 is considered to be high enough to meaningful division of groups. Considering that we have small numbers of individuals within the experimental colonies, we decided not to use this simple rule ($Q > 0.3$). Instead, we tested for statistically significant associations between these individuals through a randomization test (i.e. a bootstrapping procedure). Bejder et al. (1998) suggest this kind of analysis. The procedure capture if the structural pattern was built by random interactions (null hypothesis) or not (alternative hypothesis).

The method consisted of constructing two null models (1000 randomizations) of the group positions of individuals in the population. Following Bejder et al. (1998), the full-restricted null model was composed by randomizations of individuals' positions maintaining the same number of groups and the same number of individual' participation in groups. The second null model, unrestricted, was composed by randomizations of

individuals' positions following no rules.

After the randomizations, we calculated the Q-value from each one of the new matrices of association. Then, we chose a 95% confidence interval for our observed Q-value to determine whether it was significant or not under both models.

These analyses were performed in R software v.3.2.2 (R CORE TEAM, 2015) using the packages "igraph" (CSARDI; NEPUSZ, 2006) and "vegan" (OKSANEN et al., 2017).

To investigate if these modularity values (Q) varied across the group sizes in each context, we fitted a linear model to our observed data of Q in all colonies and tested it using the analysis of variance (ANOVA). The analysis was performed in R software v.3.2.2 using the function *anova* from the package "stats" (R CORE TEAM, 2015). It uses the variance of the observed data to determine if a linear model can be applied to the observed data.

(ii) *Is this structure consistent across all social contexts?*

To access if this structure of association between individuals is consistent between the different contexts, we compare the matrices of association of the three contexts in each colonies. We used the same matrices that were built applying the "simple ratio index" (SRI).

We performed a Mantel's permutation test (MANTEL, 1967; MANLY, 1986) to evaluate the correlation between the contexts (with a total of 1000 permutations). The analyses were performed in R software v.3.2.2 (R CORE TEAM, 2015) using the *mantel.test* function of the package "ape" (PARADIS et al., 2004).

(iii) Do *A. eximius* individuals specialize in tasks? Is this specialization affected by group size?

To answer this question, we wanted to investigate interactions between two classes: individuals and tasks. An existing and relevant tool to achieve this objective in social network analysis is the bipartite graphs. They

are commonly used to describe patterns in ecological webs (where classes can be pollinators and plants, for example) (DORMANN et al., 2008), and one of these important patterns is specialization. The use of this type of network to investigate specialization of individuals on tasks was proposed by Charbonneau et al. (2013) and developed by Jeanson (unpublished paper).

We prepared a matrix of individual participation in the two active social contexts (called here tasks) for each colony. After that, we built a bipartite weighted graph of social contexts and individuals, when connections represent how many times individuals participated in a task. We had results that, not only investigated if individuals separated themselves into different tasks, but how much specialized they were to each task or how much the colony had specialized individuals.

We calculated the indexes H'_2 and d'_{task} , both suggested by Blüthgen et al. (2006) to access the specialization rate in the colony. H'_2 , or standardized two-dimensional Shannon entropy, is an index of specialization of the entire network (BLÜTHGEN et al., 2006; DORMANN, 2011). d' quantifies specialization at the individual (d'_{indiv}) or task (d'_{task}) level. The d' index is derived from Kulback-Leibler (1951) distance, and compares the individual participation in each task considering all tasks available (BLÜTHGEN et al., 2006; DORMANN et al., 2009). Both indexes vary from 0 (no specialization) to 1 (complete specialization).

After that, we computed modules of participation in tasks by applying Newman's (2004) modularity measure (Q) in a bipartite weighted version to it using the algorithm provided by Stephen Beckett (2016). This measure can divide the bipartite network into groups of individuals that more frequently engage in each task.

To test for a statistically significant pattern of interactions between individuals and tasks in network-level analyses, we also performed a randomization test. The method used Patefield's (1981) algorithm to randomize the links between individuals and tasks. This algorithm preserves the marginal sums, in other words, each individual performs the same

number of interactions than in the observed network and each task receives the same number of interactions.

After the randomizations, we calculated the H'_2 and Q values from each one of the new networks. Then, we conclude our observed values to be significant if they lie outside a 95% confidence interval from the null model data. All the above analyses were performed in R software v.3.2.2 (R CORE TEAM, 2015) using the package “bipartite” (DORMANN et al., 2008).

In addition, to assist in the discussion of the results, we also compared the rate of specialization of tasks performing a T Test using d'_{task} values.

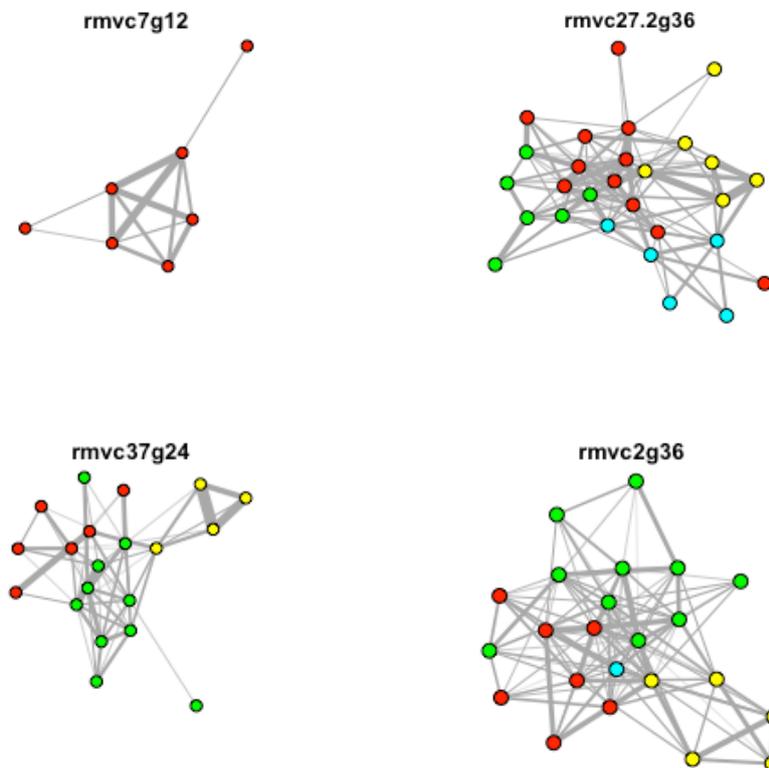
To investigate if the H'_2 and Q values varied across the group size, we fitted a linear model to our observed data in all colonies and test it using the analysis of variance (ANOVA). The approach was performed in R software v.3.2.2 using the function *anova* from the package “stats” (R CORE TEAM, 2015).

3.3. Results

(i) Do *A. eximius* colonies present a structure organized in groups across different social contexts? Is there a size threshold for the colony to be organized in groups?

For the Prey Capture context, almost all colonies formed modules (except for “rmvc7g12”). They ranged from 2 to 5 groups. Nevertheless, experimental modularity values (Q_1) varied from almost zero to more than 0.3 (Figure 5).

Figure 5 - Examples of networks in Prey Capture context and their modules



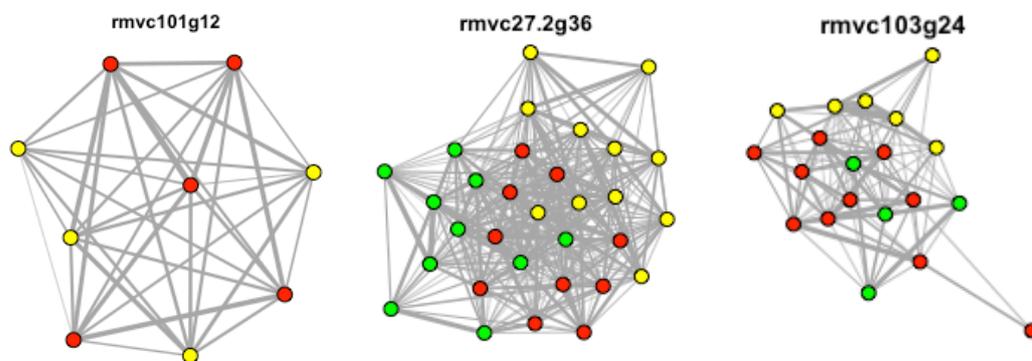
Notes: Each color corresponds to one experimental module in the network. $Q_1 = 0.00; 0.23; 0.38; 0.18$, respectively.

From all 28 experimental colonies, 10 colonies presented modularity values that differ significantly from the unrestricted null model and 6 of those colonies also presented modularity values that differ significantly from the full-restricted null model (Table S1). Those were colonies with the formation of association groups performing activities together in the prey capture context.

The majority of the significant colonies (5) had 36 individuals. The remaining 18 colonies' networks resembled the networks produced by the nulls models, resulting in no significant groups.

All colonies in Web Repair context presented modules (Figure 6). They ranged from 2 to 4 modules and experimental modularity values (Q_1) varied from almost zero to more than 0.3 (Figure 6). In spite of that, many colonies had low modularity values. In consequence, the topology of their networks was very connected, with few clear groups. The null models helped us to identify groups that were not random.

Figure 6 - Examples of networks in Web Repair context and their modules



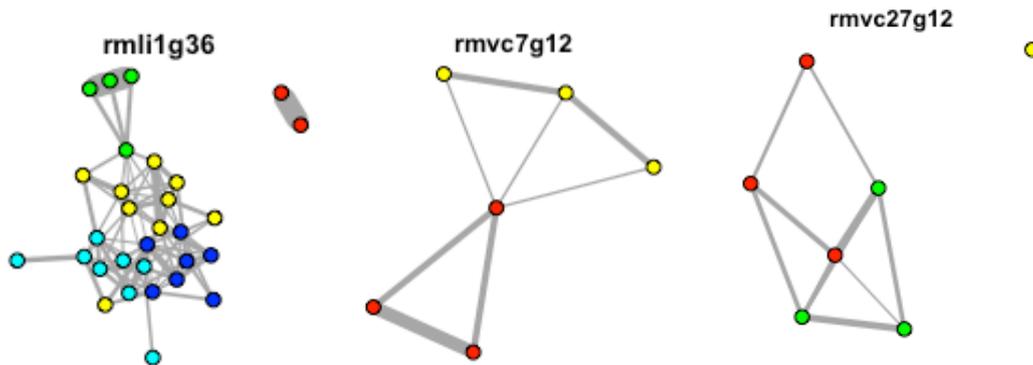
Notes: Each color corresponds to one experimental module in the network. $Q_1 = 0.01$; 0.13 ; 0.21 , respectively.

In this social context, 12 colonies presented modularity values that differ significantly from the unrestricted null model and 4 of those colonies also presented modularity values that differ significantly from the full-restricted null model (Table S2). These colonies had significant groups of individuals performing web repair together.

From the 12 significant colonies on the unrestricted model, the majority had 36 individuals. From the 4 colonies significant on the full-restricted model, 2 had 36 individuals and 2 had 24 individuals. The remaining 16 colonies presented results that resembled the networks produced by the nulls models, resulting in no significant groups.

All colonies in Resting Time context presented modules (Figure 7). They ranged from 2 to 6 modules. Experimental modularity values (Q_1) varied from 0.02 to 0.5. Only 5 colonies presented modularity values that differ significantly from the unrestricted null model, and 4 of them also differ from the full-restricted null model (Table S3). 23 colonies' networks do not differ from the networks produced by the nulls models, resulting in no significant groups.

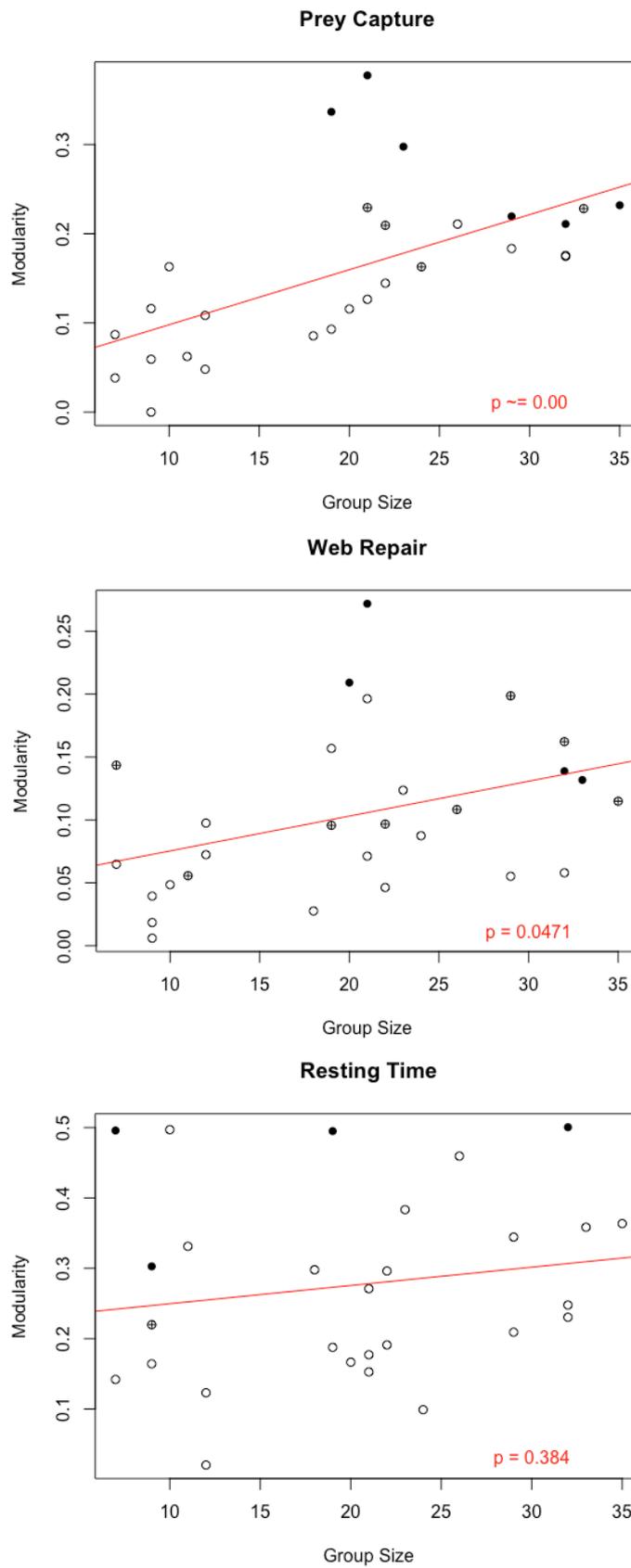
Figure 7 - Examples of networks in Resting Time context and their modules



Notes: Each color corresponds to one experimental module in the network. $Q_1 = 0.50$; 0.30 ; 0.02 , respectively.

Adding to that, the values of modularity in the Prey Capture context seem to increase with group size (ANOVA: F value = 14.5814, Pr ($>F$) = 0.0007). The same result can be seen in the Web Repair context (ANOVA: F value = 4.3431, Pr ($>F$) = 0.0471). In contrast, the modularity values in the Resting Time context do not present any linear correlation with group size (ANOVA: F value = 0.7850, Pr ($>F$) = 0.3837) (Figure 8).

Figure 8 - ANOVA results on regression between group size and modularity (Q_7) in each of the contexts



Notes: Circles are representative of the observed data. Crossed circles are modularity values that differ from the unrestricted null model. Filled circles are modularity values that also differ from the full-restricted model.

(ii) *Is this structure consistent across all social contexts?*

Most correlations were not significant (Table 2), implying that the individuals form groups with different composition in different social contexts. In other words, in each context, individuals are associating in a different way with others.

The majority of significant results were present in the relationship between the Prey Capture and Web Repair contexts. In those contexts, individuals frequently associate with the same partners, and thus the groups, which emerge from the association matrices, are similar.

Table 2 - Results of Mantel tests between different social contexts

COLONY	PC X RT		PC X WR		WR X RT	
	p value	z stat	p value	z stat	p value	z stat
rmli1g12	0.515	0.3037	0.263	0.3712	0.549	0.6067
rmvc5g12	0.013	0.3595	0.813	0.2022	0.659	0.1799
rmvc7g12	0.413	0.4691	0.057	0.6099	0.339	0.3868
rmvc26g12	0.383	0.2500	0.743	0.3678	0.511	0.4996
rmvc27g12	0.569	0.1910	0.081	0.1571	0.399	0.1444
rmvc36g12	0.833	0.5093	0.015	0.5658	0.061	0.3938
rmvc101g12	0.637	0.7715	0.067	0.4557	0.783	0.6887
rmvc102g12	0.241	0.2066	0.743	0.3065	0.929	0.2754
rmvc103g12	0.143	0.3683	0.067	0.4557	0.783	0.6887
rmvc27g24	0.725	0.8552	0.105	0.8042	0.111	0.9884
rmvc7g24	0.111	0.5797	0.907	0.5130	0.801	0.5403
rmvc103g24	0.801	1.1654	0.401	1.0648	0.023	0.7779
rmvc37g24	0.015	1.1748	0.019	0.7886	0.091	1.0470
rmvc101g24	0.297	1.4372	0.033	1.4206	0.237	2.3683
rmvc27.2g24	0.319	1.1174	0.133	2.1108	0.989	1.9579
rmvc5g24	0.785	0.4688	0.027	1.3176	0.537	0.8672
rmvc10g24	0.725	0.6413	0.549	2.8630	0.345	1.2591
rmli1g24	0.381	0.4784	0.383	1.0583	0.333	1.1050
rmvc7g36	0.751	1.2595	0.659	1.2802	0.177	1.6685
rmvc27g36	0.429	0.4181	0.001	1.1320	0.065	0.8582
rmvc2.2g36	0.229	0.7315	0.001	2.7094	0.693	1.4345

COLONY	PC X RT		PC X WR		WR X RT	
	p value	z stat	p value	z stat	p value	z stat
rmvc37g36	0.683	0.4008	0.237	0.8027	0.681	0.6092
rml1.2g36	0.399	0.7573	0.223	2.8346	0.079	1.8468
rmvc5g36	0.339	1.5380	0.241	2.4693	0.039	3.0818
rmc1g36	0.913	0.3573	0.135	1.2034	0.903	0.6293
rml1g36	0.495	1.0628	0.249	2.0837	0.251	1.1213
rmvc27.2g36	0.263	0.4209	0.001	1.9698	0.153	1.2452
rmvc2g36	0.107	0.1971	0.117	1.2198	0.859	0.5330

Notes: "PC"- Prey Capture, "RT"- Resting Time, "WR" – Web Repair. Dark red values are those significant on 95% confidence interval and light red values are significant under a 90% confidence interval.

(iii) Do *A. eximius* individuals specialize in tasks? Is this specialization affected by group size?

To identify the specialization rate of the colonies, we used the H'_2 index. The values ranged from 0.022 to 0.198, which indicate an existent but low rate of specialization of the colonies (Table 3). Reaffirming the presence of a degree of specialization, almost all colonies presented values of H'_2 that differed from the null model. The structure of the interactions between individuals and task seem to emerge non-randomly.

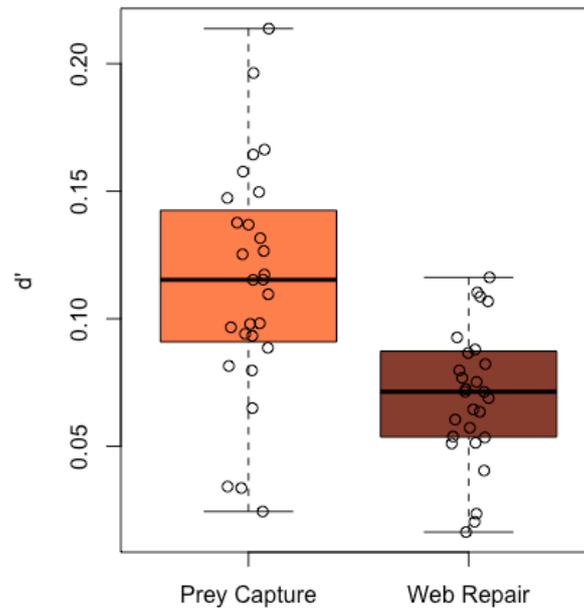
Table 3 - Specialization rate and confidence interval from Bipartite networks

COLONY	H'_2	Mean H'_2 Null	Null 2.5.CI	Null 97.5.CI
rml1g12	0.167	0.034	0.010	0.069
rmvc5g12	0.101	0.033	0.010	0.069
rmvc7g12	0.029	0.027	0.005	0.061
rmvc26g12	0.095	0.026	0.006	0.060
rmvc27g12	0.106	0.029	0.003	0.075
rmvc36g12	0.080	0.027	0.009	0.055
rmvc101g12	0.022	0.025	0.006	0.058
rmvc102g12	0.029	0.026	0.006	0.059
rmvc103g12	0.092	0.028	0.008	0.059
rmvc27g24	0.067	0.035	0.014	0.064
rmvc7g24	0.198	0.043	0.019	0.075
rmvc103g24	0.086	0.041	0.019	0.075
rmvc37g24	0.123	0.045	0.021	0.078
rmvc101g24	0.088	0.032	0.014	0.057
rmvc27.2g24	0.064	0.033	0.015	0.058
rmvc5g24	0.072	0.039	0.017	0.066
rmvc10g24	0.068	0.021	0.008	0.038
rml1g24	0.118	0.037	0.016	0.065
rmvc7g36	0.122	0.045	0.024	0.071
rmvc27g36	0.075	0.042	0.016	0.072
rmvc2.2g36	0.107	0.041	0.022	0.063
rmvc37g36	0.121	0.045	0.021	0.082
rml1.2g36	0.170	0.031	0.016	0.052
rmvc5g36	0.102	0.035	0.017	0.058
rmc1g36	0.077	0.032	0.013	0.059
rml1g36	0.088	0.048	0.023	0.078
rmvc27.2g36	0.125	0.048	0.025	0.078
rmvc2g36	0.123	0.055	0.027	0.088

Notes: " H'_2 " – Specialization index at the network level; "CI" – Confidence Interval. Red values are those that differ from the null model (significant).

Adding to that, we used d'_{task} to look at the specialization at the task level. The values for Prey Capture ranged from 0.02 to 0.21. Values of Web repair varied from 0.01 to 0.11 with one outlier of 0.22. Prey Capture is a more specialized task than web repair (Figure 9), i.e., it is performed by more specialized individuals (T Test = 15.177, df = 55, p-value < 2.2e-16).

Figure 9 - Boxplot of specialization rate of tasks (d'_{task})



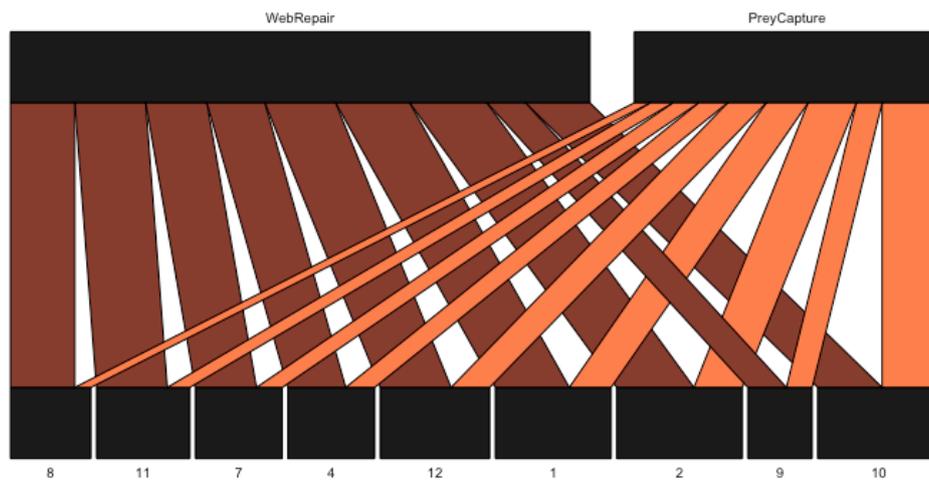
We used the modularity approach to identify groups specialized in tasks and test them using a null model. The values of modularity ranged from 0.060 to 0.17. Despite low values, almost all colonies presented modularity values that differ from the null model (in a 95% confidence interval) (Table 4). In other words, those colonies presented groups that were more specialized in performing a specific task. The only 4 (four) colonies with no significant values had 12 individuals. Figure 10 and Figure 11 are examples of colonies' bipartite networks which show individuals' participation in the two tasks observed.

Table 4 - Modularity values and confidence interval from Bipartite networks

COLONY	Q	Mean Q Null	Null 2.5.CI	Null 97.5.CI
rmli1g12	0.164	0.075	0.044	0.110
rmvc5g12	0.153	0.078	0.042	0.123
rmvc7g12	0.067	0.065	0.029	0.109
rmvc26g12	0.122	0.066	0.035	0.104
rmvc27g12	0.150	0.071	0.030	0.125
rmvc36g12	0.113	0.072	0.042	0.108
rmvc101g12	0.060	0.065	0.035	0.101
rmvc102g12	0.075	0.068	0.038	0.106
rmvc103g12	0.099	0.077	0.045	0.118
rmvc27g24	0.123	0.082	0.055	0.113
rmvc7g24	0.191	0.088	0.059	0.120
rmvc103g24	0.127	0.094	0.064	0.127
rmvc37g24	0.162	0.096	0.063	0.129
rmvc101g24	0.116	0.081	0.057	0.108
rmvc27.2g24	0.100	0.072	0.051	0.098
rmvc5g24	0.113	0.078	0.053	0.105
rmvc10g24	0.118	0.062	0.041	0.086
rmli1g24	0.133	0.081	0.056	0.110
rmvc7g36	0.156	0.097	0.073	0.125
rmvc27g36	0.112	0.082	0.053	0.111
rmvc2.2g36	0.132	0.089	0.066	0.112
rmvc37g36	0.133	0.088	0.060	0.118
rmli1.2g36	0.170	0.072	0.054	0.094
rmvc5g36	0.135	0.075	0.055	0.099
rmc1g36	0.113	0.075	0.050	0.102
rmli1g36	0.126	0.095	0.071	0.121
rmvc27.2g36	0.152	0.090	0.067	0.114
rmvc2g36	0.150	0.102	0.072	0.130

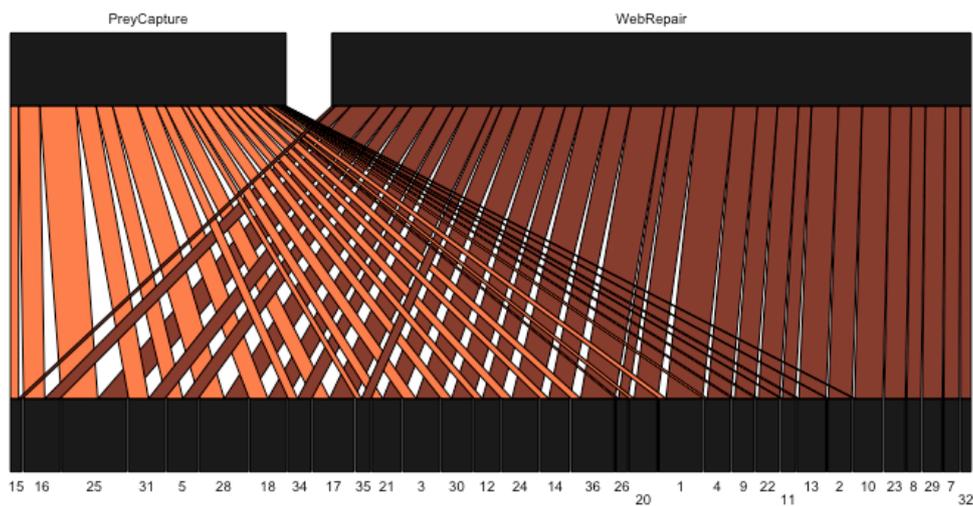
Notes: "Q" – Modularity; "CI" – Confidence Interval. Red values are those that differ from the null model (significant).

Figure 10 - Bipartite network of colony "rm101g12"



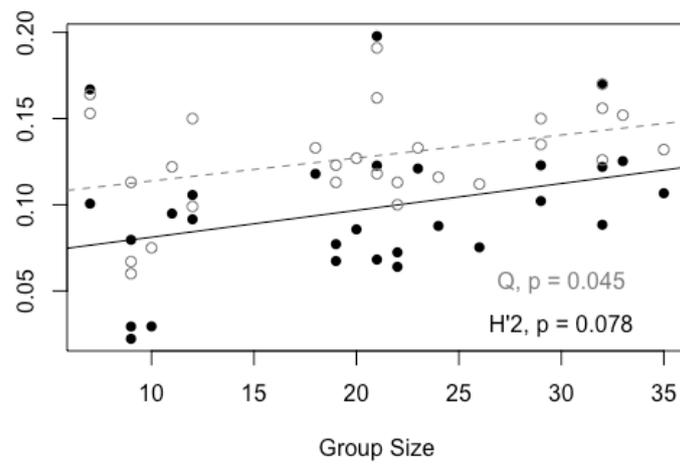
Notes: Q = 0.06

Figure 11 - Bipartite network of colony "rm1.2g36"



Notes: Q = 0.17

Adding to that, the values of values of modularity (Q) seem to increase when the group size increase (ANOVA: F value = 4.44, Pr ($>F$) = 0.045). In contrast, the specialization of the colony (H'_2) only presented a marginally significant result (ANOVA: F value = 3.36, Pr ($>F$) = 0.0784) (Figure 12).

Figure 12 - Influence of group size in Specialization rate (H'_2) and Modularity (Q)

Notes: Circles are representative of the observed data. Filled black circles are Specialization values and Grey circles are Modularity values. Solid line is H'_2 linear model and dashed line is Q linear model.

3.4. Discussion

From the perspective of social complexity we are advocating, the best way to characterize sociality for comparative purposes is looking at the nature of interactions between individuals in the colonies. Here, we studied colonies of the social spider *Anelosimus eximius* and tested for the formation of groups of preferred association during social contexts (Prey Capture, Web Repair and Resting Time), the stability of these associations across contexts and the patterns of specializations of individuals performing tasks (Prey Capture and Web Repair) using social network metrics. More than that, we investigated the influence of group size in those metrics.

Our first question investigates one important aspect of social structure: the formation of groups, also called compartmentalization or modularity in networks (WHITEHEAD, 1997) in which some individuals interact more with specific others during social contexts. This approach is specially used for the identification of groups in species with fission-fusion structure, such as primates (e.g., TOKUDA et al., 2012), bats (KERTH et al., 2011), fishes (CROFT et al., 2006) and elephants (WITTEMYER et al., 2005) and nearly constant social units as in sperm whales (WHITEHEAD, 2003).

Here, we found an interesting structure in the social spiders. They formed associated groups of individuals during all social contexts, despite low values of modularity (Q_1). These groups were mostly significant in larger colonies. Considering that larger colonies have been observed to live longer and have more success (VOLLRATH, 1982; CHRISTENSON, 1984; AVILES; TUFÍÑO, 1998; PASQUET; KRAFFT, 1992), modular association could be increasing task efficiency and survival of the colony. Adding to that, variations in group size is known to affect social structure in other animals (e.g. GRIFFITHS; MAGURRAN, 1997; MALDONADO-CHAPARRO et al., 2015).

Ebert (1998) linked the degree of participation in prey capture and web repair to the level of food deprivation of the animals or their body condition. This could result in the formation of temporary groups of “hungry” individuals, but the stability of those groups would not be strong, since all

individuals would feed at some point. However, feeding in spiders is somewhat disconnected from prey capture, since large prey can accommodate feeding spiders long after the prey is subdued.

A. eximius individuals are considered to be totipotent; they can perform any activity in the colony (AVILES, 1997). Considering the major stability of groups in larger colonies, *A. eximius* probably respond to the necessities of the colony and the external stimuli, as in insect societies (ROBINSON, 1992). Smaller colonies will need more, or even all, individuals performing important activities at the same time, such as capture of larger prey items. Because of that, we did not observed consistent groups being formed.

Vibratory communication can play a role in this social organization. Vibratory signals are usually sent through the web and influence social spacing (measurement of density) of spiders. They can “organize” collective activities in the colony such as prey capture behavior (BURGESS; UETZ, 1982; KRAFFT; COOKSON, 2012) and, because of that, can possibly cause the formation of groups. In *A. eximius*, the path of the spider to the prey is interspersed with brief pauses that contribute to its guidance. Synchronization of these pauses may allow the participation of other individuals in the capture (KRAFFT; PASQUET, 1991). This type of behavioral group component could allow a better location of prey, because it isolates the noise produced by the moving group (PASQUET; KRAFFT, 1992), but can also allow the sending of vibratory signals between individuals (VAKANAS; KRAFFT, 2001). The role of these phenomena as recruitment mechanism has however not yet been established, not even the possible different responses of individuals to the signals that could lead to this organization.

On average, the social contexts are all equally modular but the effect of group size on modularity (Q_1) increase from Resting Time, where there is no effect, to Web Repair and Prey Capture. This points out to an interesting qualitative difference between those contexts: the level of proximity association doesn't change with the size of group, but the occurrence of an activity implies the formation of groups of individuals that frequently do the

activity together, that we can call “task forces”, possibly coordinated by the own dynamics of each activity. Following the last results, the coordination of individuals in larger colonies is known to affect the capture success (PASQUET; KRAFFT, 1992). The formation of groups in those colonies could maximize this coordination and allows the individuals to have more success in killing prey.

Broadening our discussion, organization in groups or substructure could also have implications for parasite transmission (COUZIN, 2006). Keiser et al. (2016) observed that networks of social spiders *Stegodiphus dumicola* during rest were disassortative; individuals associate with others that were different in terms of their personality. They also observed that parasite transmission is more likely to occur when individuals have different personality indices, resulting in possible rapid and devastating spread of harmful microbes. The modular structure of the individuals’ association during Resting Time could avoid this rapid transmission. If this is true, we expect no relation with group size, because all sizes of the colony need this protection. Since we did not measure personality, we cannot affirm disassortative association, but the structure we found here could help slow down this transmission.

In our second question, we wished to investigate if individuals associate similarly in different contexts. The composition of the groups is mostly different in each context, but more frequently similar between the active social contexts or tasks (Prey Capture and Web Repair). This result can also support the idea of an organization of “task forces”, or groups of individuals that are most likely to perform the tasks in groups. It does not show us anything about how active these individuals are in each task, they just associate with the same individuals while performing different social tasks.

The behavioral asymmetry of activity between individual spiders has recently been studied by the field of animal personality. There is evidence that some individuals are consistently more active and aggressive towards prey than others (PRUITT et al. 2011). Those active individuals can be the

first ones to get to the prey and start to repair a damaged web. Consequently, they would be more likely to associate, while less active individuals would form other groups. The relationship between group composition and individual personality in this species still need to be broadly studied.

Often the organization in groups emerge due to various and probably species-specific physiological and ecological factors, such as resource availability (CHAPMAN, 1990) and cognitive constraints (MALDONADO-CHAPARRO et al., 2015), result of social structure dynamics (discussion in COUZIN, 2006). But the mere existence of a structuration of the relationships can be understood as a condition to sociality, because they are “a prerequisite for the evolution of reciprocally altruistic behaviors” (COUZIN, 2006). As sociality always involves cooperation (WILSON, 1975), preferred associations could serve as a threshold for social behavior.

Another dimension of sociality that we investigated here was task specialization. In social animals, differences in the propensity to perform behavior of individuals can lead to differential participation in the activities of the colony (BESHERS; FEWELL, 2001). This structure of distinctive participation can increase the performance of the colony if it improves the efficiency of the individual (OSTER; WILSON, 1978; ROBINSON, 1992; LICHTENSTEIN et al., 2016). When this individual variation in task participation is stable, it is called division of labor (OSTER; WILSON, 1978). However, task specialization can vary from a slight variation in participation to the stability observed in many social insect societies' castes (ROBINSON, 1992; SETTEPANI et al., 2012). The question if social spiders colonies are structured with a division of labor similar to eusocial insects stimulated many studies of their behavior. At first and until very recently, no task specialization seemed to be observed, and spiders associations were considered egalitarian (WHITEHOUSE; LUBIN, 2005). Although social spiders lack morphological castes, later developments on this question showed individual variation in performing tasks in different species of spiders (e.g., RYPSTRA, 1993; EBERT, 1998; PRUITT et al., 2012). Its predictors were diverse and

variable according to the study: age, personality, body size or condition, among others (review in KEISER et al., 2014). In this study, we found colonies of *A. eximius* to have specialist individuals. Almost all colonies present a significant structure of specialization, even with low values of H'_2 and Q. Therefore, individuals of *A. eximius* have different task participation and can be separated (using Q) in two groups, each one more frequently participating in one of the contexts.

Specific models to understand the mechanisms that cause task participation in spiders still need to be developed, but some possibilities may be inferred from the many existing in insect societies, as reviewed by Beshers and Fewell (2001). The proposed models use internal and external factors to explain the variation in participation in the different tasks. A few models can be better applied in the organization of social spiders. An example is the class of response threshold models. They are constituted by the assumption that individuals (workers in insects) respond to task stimuli according to internal thresholds, the variation in these thresholds between individuals causes the division of labor (ROBINSON; PAGE, 1989). If these models were transposed to *A. eximius* colonies here, they would fit really well with our results. Other possibility includes the influence of experience molding task participation (RAVARY et al., 2007); individuals that were successful in performing one task, would have a greater propensity to perform it again.

The research about social spiders could benefit from our study. Most of the studies on task participation in spiders were done in other genera. Previous results in *A. eximius* (EBERT, 1998; SETTEPANI et al., 2012; PRUITT et al., 2012) did not identify task participation in the way we found here, even considering the apparent complexity of their colonies. Ebert (1998) observed a greater propensity of smaller individuals to perform active tasks in the colony, while Settepani et al. (2012) observed that adults perform more prey capture than others. Pruitt et al. (2012) found that aggressive and active individuals perform more prey capture and that the diversity in behavioral types is correlated with colony success. Here, we could identify individuals more frequently participating in one of the tasks, evidencing a consistent

behavioral asymmetry between two tasks. It appears that the methodology and analyses used in our study are sensitive to the organization of *A. eximius*. It also brought new information to the existing studies on task participation in this species.

Ecological constraints could be preventing the evolution of more specialized individuals such as the risk of death in costly activities or the colony funding by sociotomy. Social spider colonies can be founded by two forms, sociotomy and emigration, similar to insect societies (VOLLRATH, 1982). The most successful founding mechanism is sociotomy (emigration has a extremely low establishment success – AVILES; TUFIÑO, 1998), a process of colony fission also referred to as budding, hesmosis, and swarming (HÖLLDOBLER; WILSON, 1977). In spiders, it happens frequently through physical catastrophes, such as a falling branch, which separate the colony in two (VOLLRATH, 1982). If organisms are too specialized, this could be a downfall for the newborn colony if lacks specialists from one task.

Prey capture was the task with greater values of specialization (d'_{task}). In other words, this task had more specialized individuals than Web Repair. Considering the ability to catch large prey as important to the evolution of sociality in spiders (NENTWIG, 1985) specialization could be a factor that helps this species to improve success at subduing prey, when specific individuals are more focused on this activity. More than that, prey capture is considered as a costly activity (unlike web repair), which involves a lot of energy, coordination and risks (VOLLRATH; ROHDE-ARNDT, 1983). Again, active and aggressive individuals (PRUITT et al. 2011) would have a greater propensity to perform this task.

The specialization rate (H'_2) and modularity (Q) in *A. eximius*, similar to the results on the formation of groups, increase with group size (with marginally significant results for H'_2). As we have small experimental colonies, compared to how large they can be in the field (up to 10.000 individuals), we can hypothesize that future research could probably observe this effect more strongly in larger colonies.

We can draw a comparison between colony development in many social insects to what is happening to our social spiders. In solitary founding, for example, social insects' queens keep a large behavioral repertoire and only shift to exclusive reproduction when colony size increases. In wasps (O'DONNELL, 1996), in particular, this is even more visible. When group size increases, workers specialize more in fewer activities and interactions are responsible for the development of parallel processing, where many activities happened at the same time (KARSAI; WENZEL, 1998). Individuals of *A. eximius* also seem to perceive information about the necessities of the colony and act according to it.

All these results combined are also very important to the development of a new metric of sociality. If we have more sensitive results to identify patterns of organization and specialization in this spider, probably we will have promissory results in others animals. For example, this metric could allow the comparison and maybe approximate forms of organization in social spiders and insect societies. Considering the amount of variation in the organization of division of labor in insect workers (ANDERSON; MCSHEA, 2001), a few of them could be facing similar ecological problems than we see in spiders. Adding to that, applying the same idea of social complexity to vertebrates, we can compare observations and methodologies on the formation of groups studying fission-fusion dynamics (e.g. AURELI et al. 2008); differentiation among individuals can be investigated by, for example, social skew (e.g. WANG et al., 2009), dominance hierarchy and the diversity of relationships between individuals (e.g., FISCHER et al, 2017).

In sum, we describe a useful methodology to identify, quantify and qualify the formation of groups and the patterns of specialization in spiders based on the interactions of individuals during social contexts. The analyses were sensitive enough to show patterns that add interesting information about the organization of this species. This points out to a great first step to continue with the proposition of a metric of sociality that fits the criteria of being general, meaningful and not hierarchical when comparing a wide range of species. We hope further developments on the subject will improve this

proposal.

4. GENERAL DISCUSSION

The objectives of this dissertation were to identify the best framework for a useful metric of sociality and take the first step in testing an approach that fits that framework. In Chapter 1, we compared different proposals to define and classify sociality in animals using the typology of concepts developed by Rudolph Carnap (1962). We understood that studies of social systems could be improved by using quantitative concepts, because they provide more information about these systems and allow meaningful comparisons between them. Finally, we conclude that a new metric of sociality should be built, using characteristics that are non-arbitrary, evolutionarily meaningful, and amenable to comparing social behavior among all animals. Following these results, we argued that social complexity defined in terms of organization and specialization of interactions in the colony could be the best way to compare different societies and tested a few questions using *Anelosimus eximius* as a model.

For social spiders, this is a new way to look at their organization, considered egalitarian until recently (WHITEHOUSE; LUBIN, 2005). However, these results are well connected with studies in this species (e.g., PRUITT et al., 2012) and of other social spiders, which found, for example, many predictors for task participation (KEISER et al., 2014). It seems that we did not have sensitive methodologies to perceive aspects of social spiders organization as the ones available in the recent literature. Our results open more doors to the study of social structure in spiders.

Indeed, many questions still have to be studied in spiders. It is necessary to expand the amount of tasks observed, including the care of egg sacs and defense of the colony. Moreover, the inclusion of reproduction in this list of tasks is very important, adding more possibilities of comparison of one important aspect of the evolution of sociality. Studies already found interesting results in *A. eximius* such as a relationship between feeding and reproduction (VOLLRATH; ROHDE-ARNDT, 1983) and a negative relation between active task participation and reproduction (RYPSTRA, 1993).

As we pointed out, this development is just a first step in the direction of a metric that could be useful to compare different social animals in similar aspects. We proposed to look at two aspects that could reflect social complexity, based on Freeberg et al. (2012)'s definition: organization and differentiation among individuals, here measured by the formation of groups and specialization. Both of them are quantifiable in all animals and flexible to different social structures.

The metric we are developing is based on the assumption that sociality is an emergent property of the interactions between individuals in a social system (BLUMSTEIN, 2013). While many classifications that we examined focused on complex characteristics of sociality such as reproductive aspects in eusocial insects and cognitive abilities in vertebrate societies, this proposal is looking to the structure that is affected by them in a bottom-up rather than a top-down way. As Hinde (1976) proposed and much of the literature of social network analysis confirmed, interactions are affected by differences in sociality and could be used to expose them in a global manner. Be it a source or a consequence of sociality, we expect that they will correlate to the aspects of sociality we wish to compare between social animals.

There are two arguments that could make a metric proposed by following this first step very useful. First, it can be used in all species, evidencing characteristics that influence social species success, and second, it can include an important aspect of eusocial animals, reproductive division of labor, without losing sensitivity in analyzing other aspects of division of labor.

The evaluation of social complexity in terms of specialization and group organization seems to be a useful metric, allowing the comparison of a wide range of species. Colony size should be an important qualifier of this metric in spiders, since individuals appear sensitive to colony needs. In our study, we indeed show a fine gradation according to group size, which also points out to the proposed method being useful for intraspecific as well as interspecific comparisons.

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APÊNDICE A - SUPPLEMENTARY MATERIAL

Table S 1 – Results of Modularity (Q_1) in Prey Capture and confidence intervals from both null models

Colonies	Modules	Q_1	NullU Modules	NullU 2.5.CI	NullU 97.5.CI	NullF Modules	NullF 2.5.CI	NullF 97.5.CI
rml1g12	2	0.038	2.065	0.004	0.145	2.246	0.019	0.217
rmvc5g12	2	0.087	2.089	0.000	0.130	2.238	0.008	0.181
rmvc7g12	1	0.000	1.825	0.000	0.112	1.238	0.000	0.317
rmvc26g12	2	0.062	1.979	0.000	0.127	2.107	0.008	0.161
rmvc27g12	2	0.048	1.217	0.000	0.068	1.403	0.000	0.107
rmvc36g12	3	0.116	2.331	0.036	0.146	2.457	0.042	0.178
rmvc101g12	2	0.059	2.032	0.000	0.109	2.096	0.001	0.137
rmvc102g12	2	0.163	2.162	0.017	0.173	2.319	0.047	0.237
rmvc103g12	2	0.108	2.084	0.001	0.121	2.129	0.010	0.145
rmvc27g24	5	0.093	2.577	0.053	0.127	2.777	0.062	0.144
rmvc7g24	4	0.126	2.740	0.063	0.139	3.016	0.064	0.196
rmvc103g24	4	0.116	2.648	0.063	0.148	2.673	0.059	0.146
rmvc37g24**	3	0.377	2.947	0.096	0.197	3.388	0.110	0.278
rmvc101g24*	4	0.163	2.803	0.066	0.139	3.222	0.078	0.187
rmvc27.2g24	3	0.145	2.981	0.092	0.197	3.031	0.090	0.208
rmvc5g24*	4	0.209	2.884	0.091	0.191	3.320	0.098	0.255
rmvcli1g24*	2	0.229	2.812	0.088	0.189	3.168	0.104	0.240
rmvc10g24	2	0.085	2.449	0.042	0.112	2.611	0.045	0.121
rmvc7g36	3	0.175	3.196	0.098	0.176	3.554	0.111	0.202
rmvc27g36	3	0.211	3.027	0.107	0.231	3.353	0.124	0.271
rmvc2.2g36**	5	0.232	3.414	0.113	0.190	3.894	0.122	0.226
rmvc37g36**	3	0.298	2.938	0.101	0.218	3.269	0.113	0.287
rml1.2g36**	3	0.211	3.096	0.088	0.157	3.570	0.094	0.204
rmvc5g36**	3	0.219	3.226	0.108	0.192	3.371	0.114	0.210
rmc1g36**	3	0.337	2.839	0.084	0.181	3.418	0.109	0.287
rml1g36	4	0.176	3.298	0.117	0.201	3.599	0.131	0.226
rmvc27.2g36*	4	0.228	3.309	0.121	0.209	3.838	0.145	0.272
rmvc2g36	4	0.183	3.050	0.095	0.189	3.365	0.120	0.232

Notes: Q_1 – Modularity; * - Modularity values that differ from the unrestricted null model; ** - Modularity values that also differ from the full-restricted model; NullU – Unrestricted null model; NullF - Full-restricted model; CI – Confidence interval.

Table S 2 - Results of Modularity (Q_1) in Web Repair and confidence intervals from both null models

Web Repair	Modules	Q_1	NullU Modules	NullU 2.5.CI	NullU 97.5.CI	NullF Modules	NullF 2.5.CI	NullF 97.5.CI
rml1g12	2	0.065	2.166	0.010	0.098	2.254	0.020	0.113
rmvc5g12*	2	0.144	2.205	0.021	0.138	2.405	0.040	0.202
rmvc7g12	2	0.018	1.465	0.000	0.054	1.445	0.000	0.063
rmvc26g12*	2	0.056	1.700	0.000	0.051	1.810	0.000	0.063
rmvc27g12	2	0.072	1.770	0.000	0.101	2.014	0.000	0.198
rmvc36g12	3	0.039	2.175	0.013	0.093	2.314	0.021	0.122
rmvc101g12	2	0.006	1.445	0.000	0.035	1.376	0.000	0.030
rmvc102g12	2	0.048	1.852	0.000	0.074	1.843	0.000	0.073
rmvc103g12	2	0.098	2.206	0.017	0.117	2.280	0.021	0.125
rmvc27g24	3	0.157	2.766	0.075	0.168	2.888	0.081	0.187
rmvc7g24	4	0.196	2.934	0.103	0.225	3.063	0.110	0.255
rmvc103g24**	3	0.209	2.798	0.083	0.176	2.953	0.088	0.184
rmvc37g24**	3	0.272	2.978	0.092	0.186	3.289	0.117	0.217
rmvc101g24	3	0.087	2.629	0.047	0.105	2.743	0.050	0.109
rmvc27.2g24	2	0.046	2.442	0.029	0.073	2.483	0.029	0.072
rmvc5g24*	3	0.097	2.472	0.039	0.093	2.651	0.043	0.101
rmvcli1g24	3	0.071	2.470	0.037	0.090	2.548	0.041	0.095
rmvc10g24	2	0.028	2.148	0.011	0.048	2.200	0.006	0.044
rmvc7g36*	3	0.162	3.208	0.092	0.160	3.526	0.103	0.180
rmvc27g36*	3	0.108	2.695	0.054	0.113	2.903	0.060	0.135
rmvc2.2g36*	3	0.115	3.018	0.066	0.111	3.128	0.070	0.118
rmvc37g36	4	0.124	2.791	0.069	0.134	3.124	0.079	0.164
rml1.2g36	3	0.058	2.538	0.031	0.061	2.574	0.033	0.061
rmvc5g36	2	0.055	2.627	0.039	0.076	2.692	0.038	0.077
rmc1g36*	3	0.096	2.445	0.034	0.093	2.481	0.040	0.101
rml1g36**	3	0.139	3.059	0.074	0.126	3.254	0.077	0.136
rmvc27.2g36**	3	0.132	2.912	0.062	0.115	3.135	0.069	0.121
rmvc2g36*	3	0.199	3.282	0.101	0.177	3.616	0.115	0.208

Notes: Q_1 – Modularity; * - Modularity values that differ from the unrestricted null model; ** - Modularity values that also differ from the full-restricted model; NullU – Unrestricted null model; NullF - Full-restricted model; CI – Confidence interval.

Table S 3 - Results of Modularity (Q_1) in Resting Time and confidence intervals from both null models

Resting Time	Modules	Q_1	NullU Modules	NullU 2.5.CI	NullU 97.5.CI	NullF Modules	NullF 2.5.CI	NullF 97.5.CI
rml1g12**	3	0.496	2.470	0.073	0.298	2.824	0.128	0.397
rmvc5g12	2	0.142	2.146	0.020	0.285	2.336	0.084	0.330
rmvc7g12**	2	0.303	1.847	0.000	0.229	1.978	0.000	0.291
rmvc26g12	2	0.331	2.141	0.003	0.359	2.577	0.143	0.448
rmvc27g12	3	0.020	2.046	0.000	0.232	2.121	0.031	0.287
rmvc36g12	2	0.164	2.455	0.069	0.287	2.630	0.086	0.276
rmvc101g12*	3	0.220	2.176	0.027	0.219	2.209	0.029	0.225
rmvc102g12	3	0.497	2.078	0.000	0.553	2.856	0.333	0.667
rmvc103g12	2	0.123	2.305	0.048	0.198	2.336	0.052	0.201
rmvc27g24	3	0.188	2.950	0.115	0.254	2.998	0.122	0.270
rmvc7g24	4	0.153	3.104	0.131	0.277	3.298	0.148	0.290
rmvc103g24	3	0.167	3.047	0.118	0.244	2.940	0.109	0.230
rmvc37g24	3	0.177	3.064	0.115	0.231	3.116	0.110	0.238
rmvc101g24	3	0.099	2.975	0.096	0.191	2.794	0.086	0.176
rmvc27.2g24	3	0.191	3.108	0.115	0.238	3.084	0.115	0.242
rmvc5g24	4	0.296	3.262	0.156	0.336	3.685	0.206	0.386
rmvcli1g24	3	0.271	3.271	0.138	0.274	3.594	0.179	0.322
rmvc10g24	4	0.298	3.046	0.155	0.371	3.656	0.225	0.460
rmvc7g36	3	0.230	3.481	0.144	0.256	3.512	0.150	0.260
rmvc27g36	6	0.459	3.690	0.223	0.467	4.204	0.309	0.517
rmvc2.2g36	4	0.364	4.420	0.249	0.412	5.128	0.304	0.468
rmvc37g36	5	0.383	3.830	0.224	0.456	4.402	0.307	0.515
rml1.2g36	5	0.248	3.854	0.176	0.304	4.230	0.213	0.341
rmvc5g36	5	0.209	3.414	0.140	0.243	3.433	0.139	0.242
rmc1g36**	4	0.495	3.406	0.174	0.396	3.939	0.242	0.480
rml1g36**	5	0.501	4.070	0.226	0.395	4.758	0.282	0.454
rmvc27.2g36	3	0.358	4.233	0.238	0.395	4.752	0.288	0.453
rmvc2g36	6	0.344	3.785	0.209	0.402	4.404	0.295	0.473

Notes: Q_1 – Modularity; * - Modularity values that differ from the unrestricted null model; ** - Modularity values that also differ from the full-restricted model; NullU – Unrestricted null model; NullF - Full-restricted model; CI – Confidence interval.