

**ECOLOGICAL CORRELATES AND COMMUNITY-WIDE CONSEQUENCES OF
SPIDER SOCIALITY**

by

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Abstract

Understanding the suite of ecological conditions that favor sociality —the tendency of organisms to form groups and cooperate— is key to understanding the origin, maintenance and contribution of social groups to biodiversity. The ecological dynamics of sociality can in turn have many consequences that feed back to influence the way species use the available resources, interact with other species, and persist in nature. The causes and consequences of sociality thus arise from the interplay of organisms and ecological processes. My thesis includes three studies that provide insight into some of the ecological processes that influence sociality and in turn the consequences that sociality may have in resource use and community structure. In the first study (Chapter 2), I use ecological niche modeling to predict the geographical distribution of social and subsocial New World *Anelosimus* spiders and explore their ecological correlates across latitude and elevation. Using a comparative approach, I further show that elevational patterns are strongly associated with differences in climatic conditions between social systems. In the next study (Chapter 3), I explore the role of group living and cooperation in resource use in a natural community of *Anelosimus* spiders of similar body size, but with behaviors ranging from near-solitary to fully social. I conduct surveys of prey capture in four sympatric *Anelosimus* species in Brazil and find that level of sociality and cooperation greatly shape resource use and act to separate different species into different ecological niches. Finally, I conduct feeding experiments to analyze in more detail the emergent patterns of resource use in two sympatric spiders with similar level of sociality but different body size (Chapter 4). I find that differences in resource use arise through differences in foraging efficiency emerging from the interplay of sociality and individual traits (e.g. body size). My thesis highlights the importance of ecological processes in the broad-scale spatial distribution of sociality and its potential consequences in resource use, community structure and ultimately the maintenance of local diversity. These studies also emphasize the work that remains to be done in such exciting area of research.

Preface

Chapter 3 is modified from a publication in *Behavioural Ecology*, authored by myself, Marcelo O. Gonzaga, João Vasconcellos-Netto, and Leticia Avilés. I led the following stages of the research: developed the methods and collected the data, analyzed the results, and wrote the manuscript. M.O.G. and J.V.-N. contributed to data collection and editing of early versions of the manuscript. L.A. contributed with developing of methods, data collection, interpreting the results, and writing and editing the manuscript.

Chapter 4 is modified from a publication in *Functional Ecology*, authored by myself and Leticia Avilés. I led all stages of the research: developing the methods, carrying out the field experiments, analyzing the results and writing the manuscript. Leticia Avilés contributed with development of methods, interpreting the results, and editing the manuscript.

Publications related to thesis chapters:

Guevara, J., M.O. Gonzaga, J. Vasconcellos-Neto, and L. Avilés, 2011. Sociality and resource use: insights from a community of social spiders in Brazil. *Behav Ecol* 22:630-638. (Chapter 3)

Guevara, J. and L. Avilés, 2011. Influence of body size and level of cooperation on the prey capture efficiency of two sympatric social spiders exhibiting an included niche pattern. *Funct Ecol* 25:859-867. (Chapter 4).

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Dedication

To you, my darling Maya

Chapter 1: Introduction

1.1 Broad scale geographical patterns and the ecological correlates of spider sociality

Sociality—defined as the tendency of individuals of the same species to live in groups and display reciprocal, cooperative behavior (Wilson 1971, 1975)—is a widespread phenomenon in the animal kingdom, and as such, understanding of why individuals come together and cooperate remains an important question in biology. Historically, the most invoked explanations for the evolution of group living and cooperation have relied on principles of kin selection that emphasize cooperation evolving principally among relatives (Hamilton 1964, West-Eberhard 1975). Genetic relatedness, although critical in setting the stage for social interactions and cooperation (Boomsma 2007, Hughes et al. 2008, Hatchwell 2009), however is often not sufficient to explain the wide range of social diversity (Rubenstein and Lovette 2007, Jetz and Rubenstein 2011). As such, there has been increasing emphasis to incorporate into the existing theory alternate routes to the evolution of sociality, including ecological, life history, and demographic processes.

Ecological factors have been long recognized to shape animal social behavior (Lin and Michener 1972, Alexander 1974, Jarman 1974, West-Eberhard 1975) and can explain many of the observed interspecific differences in level of sociality (Emlen 1982, Komdeur 1992). The ecological theory of sociality posits that specific ecological conditions that make social living advantageous can represent strong selective pressures for group formation and cooperation. For instance, cooperative groups may evolve because they can be more effective at detecting and deterring predators in environments with strong predation pressure (i.e. Powel 1974, Siegfried and Underhill 1975, Kenwood 1978, Lazarus 1979, Treherne and Foster 1980, Godin et al. 1988, Cresswell 1994, Purcell and Avilés 2008, Zammit et al. 2008). Group formation and cooperative foraging may be also promoted in environments where food resources are widely spread and

elusive, or too large and dangerous, once found (Hector 1986, Bednarz 1988, Gese et al. 1988, Fanshawe and FitzGibbon 1993, Baird and Dill 1995, Creel and Creel 1995). The limitation of suitable habitat (Selander 1964, Komdeur 1992) as well as environmental factors, such as temperature and rainfall, may also facilitate or hinder group living and cooperation (Alexander 1974, Jarman 1974, Purcell and Avilés 2008). For instance, recent work in cooperatively breeding birds suggests the great role of climatic uncertainty resulting from unpredictable patterns of rainfall in shaping cooperatively breeding behaviors and the interspecific variation in sociality (Rubenstein and Lovette 2007, Jetz and Rubenstein 2011).

Although ecology is known to influence many aspects of animal group living and cooperation, the environmental predictors of animal sociality across broad geographical scales and potential emerging distribution patterns remain poorly understood (Hatchwell 2009). Because environmental factors often change with latitude and elevation, they can greatly influence the way social traits are distributed spatially at local and geographical scales. Broad-scale patterns of sociality likely associated with environmental gradients have been revealed in many social animals (i.e. Kaspari and Vargo 1995, Jetz and Rubenstein 2011, Purcell 2011). For instance, in social arthropods, greater levels of sociality have been either associated with lower latitudes and elevations (i.e. termites and social spiders; Wilson 1971, Avilés 1997, Porter and Hawkins 2001, Avilés et al. 2007, Guevara and Avilés 2007, Purcell and Avilés 2008, Purcell 2011), with higher latitudes and elevations (i.e. some social hymenoptera; Heinze 1993, Kaspari and Vargo 1995) or have been found to have no association at all (i.e. aphids; Stern and Foster 1997, Pike et al. 2007). While broad-scale distribution patterns have been described in the literature for many social groups, formal assessment of the ecological correlates of such broad-scale patterns remain scarce.

One way to visualize broad scale patterns of sociality and discern the role of ecological variables is to use ecological niche models that predict species distributions. Ecological niche models are based on the notion that the fundamental ecological niche of a species is a theoretical range of conditions a species can occupy (Hutchinson 1957, 1959), and as such it is an important determinant of its geographical distribution (MacArthur 1972, Holt 2003, Soberon and Peterson 2005). While only the realized niche can be observed in nature, —the niche space actually occupied given interactions with other species, such as competition and predation (Hutchinson 1957)— examining a species across its entire known geographical distribution reflecting a variety of environmental conditions permits visualization of the range of biotic and abiotic characteristics in

which a species is able to persist (Peterson et al. 1999, Peterson 2001, Peterson 2003 and references therein). Given that available data on a species occurrence rarely represent its entire distribution, approaches that integrate species locality data, GIS environmental data, and modeling algorithms (i.e. ecological niche models) have become increasingly popular to estimate a species' ecological niche and consequently to predict its potential geographic distribution and environmental correlates (e.g. Peterson 2001, Anderson et al. 2002, Raxworthy et al. 2003, Fortin et al. 2005, Rottenberry et al. 2006). Ecological niche models are a promising approach to predict species distributions (Illoldi-Rangel et al. 2004), to examine the evolution of ecological niches (i.e. Peterson and Holt 2003, Martinez-Meyer et al. 2004), spatial patterns of biodiversity, and to investigate speciation mechanisms (Graham et al. 2004).

As I will present later, I construct an ecological niche model to analyze and compare the spatial distribution of New World social spiders of the genus *Anelosimus*. Using the ecological niche modeling approach as well as comparative methods, I explore the environmental variables associated with differences in latitudinal/elevational distribution patterns of social and subsocial spiders. Linking ecological correlates to distribution patterns of spider sociality is key for explaining the spatial variation of social complexity in spiders and other social taxa, and in turn, it is essential for understanding the ecological route to the evolution of animal social behavior.

1.2 Foraging efficiency and patterns of resource use in communities of social spiders

Animal sociality is both a consequence and a determinant of its underlying ecology, and as such studying all parts of this loop is essential to understanding the origin and maintenance of social diversity. The ecological consequences of sociality have particularly received great attention in behavioral ecology research due to their importance for many aspects of an animal's life including its reproduction, predator protection, and foraging (Caraco 1979, Pulliam and Millikan 1982, Krebs and Davies 1996, Krause and Ruxton 2002). A wide range of literature exists specifically on the way social characteristics, such as group size and level of cooperation, shape the way animals engage in foraging activities and their ability to use the available resources. For instance, the general increase in foraging efficiency with group size is a well known general trend that has been widely studied and established in many social animals, including terrestrial and marine carnivores, birds, fish, and arthropods

(Rand 1954, Cody 1971, Krebs et al. 1972, Caraco and Wolf 1975, Nudds 1978, Buskirk 1982, Pitcher et al. 1982, Pitcher and Magurran 1983, Pulliam and Caraco 1984, Gittleman 1989, Baird and Dill 1996, Cerdá et al. 1998). This relationship arises because bigger groups may have a greater number of cooperating individuals that would allow them to detect and capture prey faster, use less energy during foraging, and increase the chances of successful prey capture (Creel and Creel 1995, Baird and Dill 1996, Krause and Ruxton 2002). Through increased cooperation, larger groups can be also more successful at capturing prey that are too elusive, too dangerous, or too large for solitary foragers or smaller groups to catch (Rand 1954, Kruuk 1966, Kleiman 1966, Caraco and Wolf 1975, Nudds 1978, Nentwig 1985, Hector 1986, Rypstra 1990, Creel and Creel 1995, Yip et al. 2008). Much evidence exists for the latter for many social taxa, but perhaps the best known example is the way cooperative hunting in social carnivores—i.e. African wild dogs, lions, wolves, and spotted hyenas—allows the capture of large and elusive prey otherwise unattainable by solitary foragers (Kruuk 1966, Caraco and Wolf 1975, Nudds 1978, Creel and Creel 1995). By its influence on the foraging ability of animals, sociality may thus expand the range of resources a species is able to exploit. This in turn may create differences in resource use between species that differ in level of sociality.

Numerous examples illustrating differences in patterns of resource use, namely differences in the range of prey size, as a function of hunting group size and level of cooperation have been identified for several social taxa (Lamprecht 1981, Hector 1986, Baird and Dill 1996, Holekamp et al. 1997, Yip et al. 2008). In social spiders, for instance, because species with more complex societies and bigger colonies are able to capture very large insects their range of prey body size use is much wider than that of less social species with smaller colonies (Guevara and Avilés 2007, Powers and Avilés 2007). All this general knowledge, however, comes from studies of populations of single species inhabiting separate environments (Lamprecht 1981, Hector 1986, Baird and Dill 1996, Holekamp et al. 1997, Yip et al. 2008). Thus, there is great need for further research on the foraging patterns of social animals that differ in social complexity but share the same habitat. Such work can shed light into the potential role of sociality in resource segregation and resource partitioning, a possibility that has not been considered in the literature. As I show later using a community of four social spiders with level of sociality ranging from almost-solitary to

very social, species capture prey sizes that reflect their level of sociality and as such, exhibit limited prey size overlap even among species contiguous along the sociality scale.

Understanding how sociality shapes resource use and acts to minimize the potential for food competition by separating sympatric species into different ecological niches is a required step to begin discerning the mechanisms that structure and maintain communities of social animals.

While many patterns of niche overlap may arise among sympatric species in nature, particularly relevant to communities of social animals are “included niche” patterns—i.e. the range of resources used by one species is included within the range of another species (Hutchinson 1957, Miller 1967, Schoener 1974*b*, Chase and Belovsky 1994). Included niche patterns may arise because less social species with smaller colonies may be exploiting a subset of the food resources exploited by more social species, which may form both large and small colonies. In such scenario, less social species with the included niche may be perceived to be at a disadvantage because they are always sharing their required resources with more social species. Unlike more social species, less social ones have no access to an exclusive set of resources, and thus they may be more vulnerable to competitive exclusion (Schoener 1974*b*). Explaining how species exhibiting included niches avoid exclusion can be problematic, yet necessary to our understanding of what drives and maintains the diversity of social organisms. Classic coexistence theory suggests that species with the included niche may be able to persist if they are superior foragers or more efficient at exploiting the shared resources (Hutchinson 1957, Miller 1967, Schoener 1974*b*). Experimental evidence of this theory comes largely from sympatric grasshoppers (Chase and Belovsky 1994, Chase 1996, Beckerman 2000) and has been only implied in other non-social taxa (e.g. Gilbert 1985, Bennett 1990). However, for the most part, this is an area of research that has received little attention in the literature.

Given the key role of sociality on the foraging efficiency of social animals, one way to approach the issue of the included niche in spite of underlying complexities is to consider how sociality may jointly allow for utilization of an exclusive range of resources in more social species while potentially contributing to increased efficiency on the shared resources in the less social species. In addition, one must also consider the possibility that differences in foraging efficiency can also arise from the interplay of sociality and other factors, including traits exhibited by individuals rather than the group as a whole. The effect of individual-level traits, particularly morphological (e.g. body size) and physiological on the foraging efficiency of animals in general has

been well studied in the literature (Peters 1983, Miles and Ricklets 1984, Douglas and Matthews 1992, Schluter 1993, Grant and Grant 2006, Herrel et al. 2006, Owen-Smith and Mills, 2008). For instance, it is well known that animals with large body sizes can generally handle larger food items more efficiently (Enders 1975, Wilson 1975), whereas smaller animals accelerate faster and enjoy greater maneuverability compared to their larger relatives (Taylor et al. 1972, Dial et al. 2008). Despite the obvious joint effect of individual- and group-level attributes on the foraging efficiency of social animals, research has focused on one or the other separately. Studying the combined effect of these factors is crucial to our ability to explain how differences in foraging efficiency arise in sympatric social organisms, what separates them into different ecological niches while minimizing the potential for competition, and in cases where included niche patterns are in place, how species coexistence is achieved.

1.3 Study system

The species I studied belong to the social spider genus *Anelosimus* Simon 1891 (Theridiidae). Here I provide a brief introduction to the relevant biology of *Anelosimus* spiders. Additional detail can be found in the relevant chapters.

Sociality is extremely rare amongst spiders as the vast majority of species are aggressive and solitary (Coddington and Levi 1991, Foelix 1996). The genus *Anelosimus* is thus considered exceptionally unique as most of its species, including all 43 described New World species, exhibit social behavior (Avilés 1997, Agnarsson 2006). *Anelosimus* spiders have been traditionally grouped into two broad social categories: (1) subsocial species, characterized by extended maternal care and in which cooperation amongst young siblings and sharing of the maternal nest is only temporary prior to dispersal of subadults, and (2) permanent social species (hereafter referred to as “social”), in which communal nests lasting for several generations consist of multiple cooperating adult spiders (Avilés 1997, Agnarsson 2006). With 7-8 social species and numerous subsocial ones, *Anelosimus* is the spider genus with the largest number of known social species, most of which occur in tropical and sub-tropical areas (Agnarsson 2006).

Anelosimus spiders build tri-dimensional webs in the shape of a basket with vertical prey capture threads for the interception of insects later subdued by the spiders (Nentwig

1985, Avilés 1997, Agnarsson 2006, Yip et al. 2008). Nests of subsocial spiders are usually occupied by single families and can contain between 20 and 100 spiders (Avilés 1997, Agnarsson 2006). In contrast, nests of social species are occupied by multiple females and their offspring and can contain thousands of spiders (Avilés 1997, Agnarsson 2006). Social and subsocial species (i.e. during their social phase prior to dispersal) cooperate in the construction and maintenance of the nest, defense, and prey capture and feeding (Kullmann 1972, Avilés 1997, Avilés et al. 2001). Social species may also cooperate in brood care (Avilés 1997). Amongst the well-known benefits of group living and cooperation in social spiders are higher rates of offspring survival (Avilés and Tufiño 1998), avoidance of dispersal costs (Uetz and Hieber 1997), and ability to capture large prey sizes otherwise unavailable to solitary spiders of the same size (Christenson 1984, Nentwig 1985, Nentwig and Christenson 1986).

Anelosimus spiders are ideal to examine broad scale patterns of sociality and its ecological correlates. The genus *Anelosimus* has a widespread distribution across the Americas and it is represented by multiple species in numerous areas containing a variety of habitats (Agnarsson 2006). At continental scales, one interesting feature about the geographic distribution of New World *Anelosimus* species is that social species appear to be restricted to tropical latitudes and low elevations whereas subsocial species tend to be absent in those areas, being notoriously distributed in more temperate areas and higher elevations (Avilés 1997, Agnarsson 2006). At certain sites of intermediate elevation there is overlap of social systems. Analyses of spatial variation in spider sociality suggest the importance of climatic variables in influencing their spatial distribution (Avilés et al. 2007, Purcell 2011).

Sympatric *Anelosimus* species found in areas of overlap offer an exciting opportunity to explore interspecific differences in prey-size use and the possibility of resource segregation based on differences in body or colony size, and/or differences in prey capture efficiency in cases where an included niche is in place. This would be possible because local communities often contain species that vary either in their level of sociality or in body size (Avilés 1997, Agnarsson 2006, Avilés et al. 2007). In addition, because social species form colonies containing dozens to thousands of spiders they may be able to capture larger prey than subsocial species with smaller colonies (Avilés 1997, Lubin and Bilde 2007). This would be due both to the greater size of their prey capture webs and the presence of more individuals that participate

in cooperative prey captures (Nentwig 1985, Rypstra 1990, Powers and Avilés 2007, Yip et al. 2008).

1.4 Overview of thesis

My thesis consists of three studies that address key questions about the ecological correlates (Chapter 2) and consequences (Chapters 3 and 4) of spider sociality.

1.4.1 Geographical patterns of spider sociality and the ecological correlates

In Chapter 2, I explore the differences in the geographical distribution of New World social and subsocial spiders and the ecological correlates associated with their occurrence. Specifically, using species presence data available for New World *Anelosimus* spiders, I develop ecological niche models to predict geographical patterns in the American distribution of social and subsocial *Anelosimus* species and evaluate the major environmental variables upon which they may depend. I perform similar analyses at a finer scale, focusing on *Anelosimus* species that occur along an elevation gradient on the eastern slopes of the Andes in Ecuador, and using a comparative approach I characterize differences in climatic variables associated with the elevational distribution of each social system. I find that the geographical patterns in spider sociality have strong climatic associations, but with notable differences in the relative importance of environmental variables between social systems. I show that social species occur most frequently at low latitudes and towards the Amazon region of central South America whereas subsocial species expand into higher latitudes reaching North America and towards the coastal edges of South America. In Ecuador, social species are most likely to occur in the lowland tropical rainforest and up to mid-elevation areas, whereas subsocial species are mostly restricted to mid and higher elevations. According to the ecological niche models, the occurrence of social species is defined by low temperature seasonality and high rainfall intensity across latitude and elevation. Subsocial species, on the other hand, exhibit opposite patterns with respect to latitude, and appear to be excluded from the lowland rainforest where warm temperatures and high rainfall intensity are common. The comparative analyses of elevational patterns of Ecuadorian species confirmed that there is indeed an elevational separation of social system.

Social species were found at lower elevations where they tend to experience climates with warmer temperatures, less seasonality, higher rainfall, and greater rainfall intensities. Subsocial species are found at higher elevations where they experience the opposite climate conditions. I show that social and subsocial spiders exhibit different environmental conditions and discuss these in relevance to various hypotheses explaining the patterns.

1.4.2 Patterns of resource use by sympatric social spiders exhibiting different levels of sociality

In chapter 3, I move from the broad geographical approach to local areas of overlap to gain insight into some of the ecological consequences of sociality. I explore the role of group living and cooperation in resource use in a natural community of four *Anelosimus* spiders of similar body size, but with behaviors ranging from near-solitary to fully social. I perform surveys of prey capture and find that the range of insect body sizes captured by each species reflects their nest and colony size. Thus, species with larger colonies and prey capture webs capture larger insects than less social species. Even among those species whose webs do not differ significantly in size—the two with the largest and the two with the smallest webs—one captures significantly larger insects than the other. This suggests a role of the extent to which nest mates cooperate in the capture of prey, as in only one of the species in each pair did the body size of the insects captured increase with colony size. The four species are thus packed along the spectrum of available insect body sizes from least to most social, with limited overlap between contiguous species. An analysis of niche overlap shows that this pattern of resource use is more over-dispersed than expected by chance, as would be expected if the species had been assembled or differentiated to avoid extensive dietary overlap. I consider alternative hypotheses to explain these patterns and suggest that group size and level of cooperation may play an important role in the dietary segregation of sympatric organisms.

1.4.3 The role of sociality and body size in the prey capture efficiency of social spiders

In Chapter 4, I analyze in more detail the emergent patterns of resource use by exploring how the interplay of sociality and individual traits shape foraging performance in two

sympatric spiders with similar level of sociality but different body size. I conduct foraging trials and show that given a five-fold difference in body size, the large species captures on average significantly larger insects than the small species. However, because the large species captures both small and large insects, its prey size range includes that of the small species, which is thus said to exhibit “an included niche”. Consistent with included niche theory, the small species is more efficient within the shared range as it is less likely to miss or ignore small prey than the large species. The small species also compensates for its small body size by having greater density of individuals within the nests, faster reaction times, and greater participation of individuals of all age classes in prey capture. As a result, the smaller species had a steeper increase in the body size of the insects it captured with increasing colony size than the larger species. I show that through its social attributes the small spider is a superior forager on the shared resources and thus compensates to some extent for the difference in body size between the species.

This result along with the other studies show the importance of considering ecology when analyzing the causes of sociality and gives insight into its role in the consequences of being social in the structure of local communities.

Chapter 2: Broad scale geographical patterns of spider sociality and the ecological correlates

2.1 Introduction

Many attributes of the environment, including resource availability, predation pressure, and climatic conditions, have been long recognized to shape many aspects of animal sociality (Kukuk et al. 1998, Hunt and Amdam 2005, Purcell and Avilés 2008, Yip et al. 2008, Zammit et al. 2008). Because these ecological conditions often change across latitude and elevation, they can greatly influence the way social groups are distributed spatially at local and geographical scales. Geographical patterns in the distribution of sociality potentially associated with environmental factors have been described in the literature for many social groups. For instance, greater levels of sociality appear to be linked to lower latitudes and elevations for a variety of social animals, including wasps and bees (Packer 1990, Reeve 1991, Eickwort et al. 1996, Richards 2000, Cronin and Schwarz 2001), thrips (Kranz et al. 2002), termites (Porter and Hawkins 2001), social spiders (Avilés et al. 2007, Purcell and Avilés 2008, Purcell 2011), and cooperative breeding birds (Brown 1987). Other social taxa may also exhibit either increased sociality at higher latitudes and elevations (e.g. some social hymenoptera; Heinze 1993, Kaspari and Vargo 1995) or no pattern at all (e.g. aphids; Stern and Foster 1997, Pike et al. 2007). For many social arthropods, such patterns appear to be largely influenced by aspects of the environment that may require group formation to ensure the chances of survival (e.g. high predation rates) or take advantage of resources that are too large or too difficult for single individuals to capture (e.g. the availability of very large prey; Jeanne 1979, Bridgman and Oliver 2006, Avilés et al. 2007, Powers and Avilés 2007, Purcell 2011). In cooperative breeding birds, greater levels of sociality are correlated with greater environmental variability in precipitation, probably due to increased risk of mortality (Jetz

and Rubenstein 2011). Although geographical patterns of sociality have been acknowledged for a variety of social taxa, studies performing formal assessments of their environmental correlates remain scarce.

Social spiders appear to provide one of the clearest cases for a correlation between geography and sociality and thus make great model systems. Among these, the spider genus *Anelosimus*, in particular, is an ideal case study because it has the largest number of social and subsocial species of any spider genera and a widespread geographical distribution comprising a variety of ecological conditions (Agnarsson 2006). The genus has also been extensively studied at continental and local (Ecuador) scales. At continental scales, New World *Anelosimus* species appear to follow a distribution pattern associated with latitude and elevation. The majority of species with higher levels of sociality (i.e. social species) seem to be restricted to relatively wet tropical forests, in particular low-elevation tropical rainforests. Less social species (i.e. subsocial species), on the other hand, appear to be common in temperate zones and, within the tropics, at elevations above 1,000 m (Avilés 1997, Agnarsson and Kuntner 2005, Agnarsson 2006, Avilés et al. 2007). At certain sites of intermediate elevation and latitude there is overlap of social systems. Thus, there are two apparent patterns that need to be explained: the dominance of social species in the low elevation tropical rainforest and the absence of subsocial species in these areas (Avilés et al. 2007).

Explanations for the apparent geographical patterns in the distribution of social and subsocial *Anelosimus* species in the Americas need to consider how climatic and ecological factors may influence costs and benefits of group living in the genus. For instance, the year-round aseasonal and warm climates of the tropics may contribute to the dominance of social species at low latitudes because it allows spider colonies to persist for several generations and grow very large, thus promoting permanent group living in social spiders (Avilés 1997). Their corresponding absence from higher elevations and latitudes, in turn, has been associated with potential latitudinal/elevational differences in food resources, such as the size of available prey (i.e. the *prey size* hypothesis; Avilés et al. 2007, Powers and Avilés 2007). The *prey size* hypothesis suggests that the formation of large colonies by social species requires habitats harboring great amounts of large insects in order to compensate for the scaling properties of their tri-dimensional webs (Yip et al. 2008). The absence of subsocial spiders from the lowland tropical rainforest, on the other hand, has been attributed to their

inability to establish in these areas due to high rates of spider mortality, web damage, and colony extinctions inflicted by seemingly extreme rainfall events and increased predation by ants (Avilés and Tufino 1998, Purcell and Avilés 2008). This is consistent with the *maternal survival* hypothesis that cooperative breeding should be selected for in environments with high probabilities of maternal death before the offspring can survive on their own (Avilés et al. 2007, Jones et al. 2007).

While the spider sociality cline has been long recognized in the literature, these patterns and their ecological correlates have not been analyzed systematically at large scales. Despite the acknowledgment that social behavior is tightly linked to ecological processes in various social animals (Lin and Michener 1972, West-Eberhard 1975, Emlen 1982, Rubenstein 1986, Evans 1996), there are only a few broad-scale comparative studies seeking to disentangle the ecological correlates of geographical patterns exhibited by species that live in groups and cooperate (Avilés et al. 2007, Jetz and Rubenstein 2011, Purcell 2011). Thus, a marked gap still exists in our knowledge of how and why patterns across social taxa vary geographically (Hatchwell 2009).

In order to fill this gap in our understanding, I characterize the geographical distribution of social and subsocial species at a continental scale and along an elevation gradient and evaluate the role of key environmental variables. Specifically, the goal of this study is two-fold. First, using species distribution data for New World *Anelosimus* spiders, I use ecological niche modeling to visualize geographical patterns in the distribution of social and subsocial *Anelosimus* species in the Americas, and along an elevation gradient on the eastern slopes of the Andes in Ecuador. Second, focusing on the Ecuadorian species, I use a comparative approach to analyze differences in key environmental conditions associated with level of sociality that may explain the elevation pattern and consider potential explanations for these patterns, including the *maternal death* and *prey size* hypotheses (Avilés et al. 2007).

2.2 Materials and methods

2.2.1 Species occurrence data

In the Americas, the range of occurrence of New World *Anelosimus* species extends between latitudes 41°33'N and 54°20'S and longitudes 102°18'W and 117°52'W comprising all of South America and parts of North America (Figure 2.1).

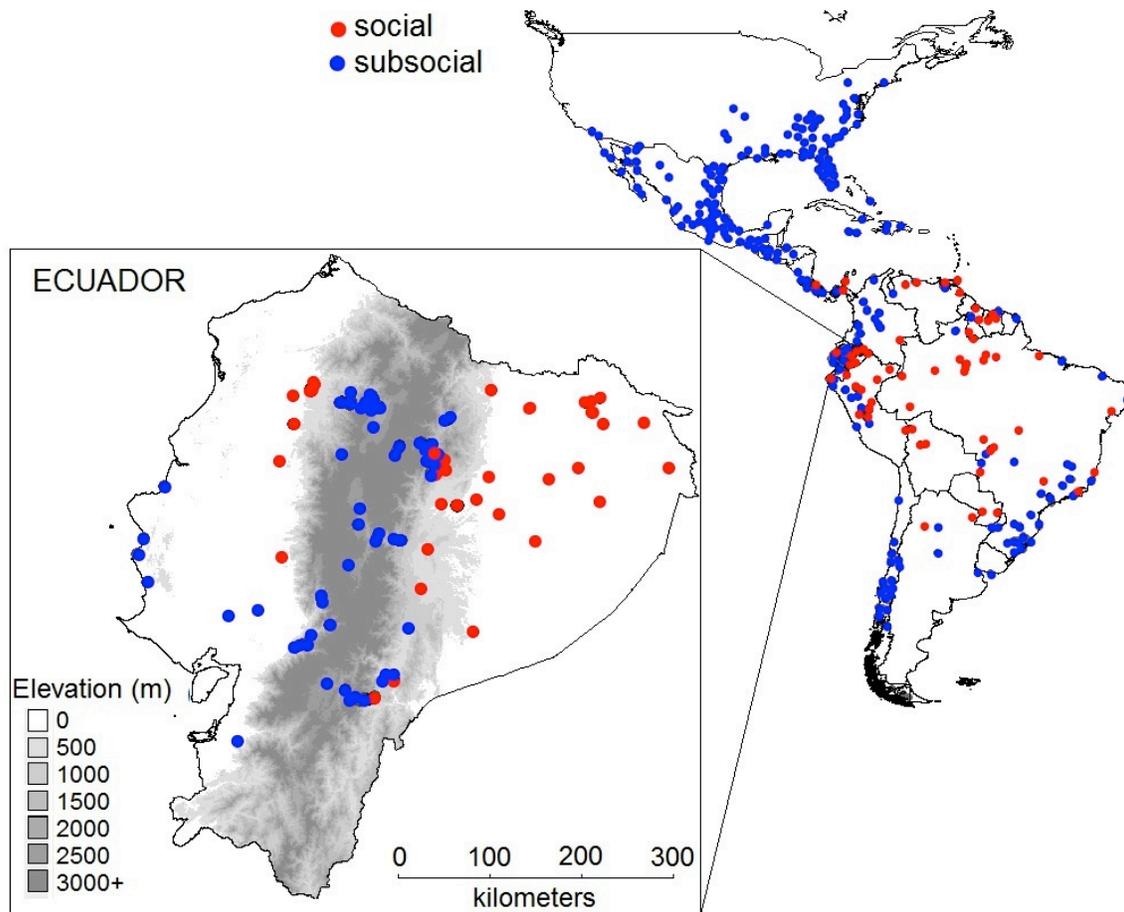


Figure 2.1 Location of the study area and distribution of presence data of social and subsocial spiders of the genus *Anelosimus* in the Americas and in Ecuador. For the Ecuador study, I focus my analyses on the eastern slopes of the Andes (Andes mountain ranges are shaded).

I compiled known occurrence points for New World *Anelosimus* species from our own fieldwork as well as from published studies (see Appendices 1 and 2 for a list of literature used and dataset processing). The final America dataset contained eight social ($n = 156$ records) and ~30 subsocial species ($n = 512$) of *Anelosimus*. The Ecuador subset consisted of five social ($n = 46$) and seven subsocial species ($n = 76$).

2.2.2 Level of sociality

I categorized species into two broad social categories, either social (i.e. permanent social) or subsocial (i.e. periodically social), based on the current knowledge of species ecology and behavior and using published literature (Avilés 1997, Agnarsson 2006). In general, subsocial species are characterized by extended maternal care and with cooperation amongst young siblings and sharing of the maternal nest being only temporary prior to dispersal of subadults. Social species are species with communal nests lasting for several generations and consisting of multiple cooperating adult spiders (Avilés 1997, Agnarsson 2006).

2.2.3 Environmental variables and data

I gathered a set of specific variables exclusively based on their ecological relevancy to the biology of *Anelosimus* spiders and their potential role in the spiders' geographical distribution. I chose six key variables for the Ecuador analysis (see Appendix 2 for data processing): Mean annual temperature ($^{\circ}\text{C}$), temperature seasonality (standard deviation), mean annual rainfall (mm), rainfall seasonality (coefficient of variation), mean rainfall intensity (mm/hr), and mean net primary productivity ($\text{gC}/\text{m}^2/\text{yr}$). For America, I excluded two variables, temperature and rainfall, as they were highly correlated with temperature seasonality and rainfall intensity, respectively (see Appendix 3 for methods).

The variables I chose, namely temperature, seasonality, and rainfall intensity, may directly limit the distribution of social and subsocial *Anelosimus* species (Avilés et al. 2007, Purcell and Avilés 2008, Purcell 2011). These variables, as well as others, such as primary productivity, may serve as proxies for biotic factors relevant to the distribution of social and subsocial *Anelosimus* for which GIS data are not available, such as insect body size and ant predation pressure (Avilés et al. 2007, Guevara and Avilés 2007, Powers and Avilés 2007, Purcell and Avilés 2008, Purcell 2011). Insect body size clines, for instance, may correlate

with temperature and time available for growth and reproduction (i.e. seasonality; Bidau and Martí 2007), net primary productivity, which reflects the abundance and quality of food resources and/or the habitat (Rosenzweig 1968, Hunter 1992, Ohgushi 1992), and predation risk (Damuth 1993), also associated with resource-rich tropical latitudes and warmer temperatures (Jeanne 1979, Menge and Lubchenco 1981, Sih et al. 1985). Thus, possible environmental predictors of insect body size clines may include seasonality, temperature, and net primary productivity. Similarly, predation pressure by ants has been associated with measures of energy available including net primary productivity and temperature (Jeanne 1979, Kaspari et al. 2000).

2.2.4 Species distribution models

Ecological niche modeling allows prediction of a species' geographical distribution based on known areas of occurrence and a combination of abiotic and/or biotic variables in the form of GIS layers (Peterson 2001, Peterson et al. 2002). I used the Maxent (version 3.3.3e; Phillips et al. 2006) algorithm to predict the distribution of social and subsocial *Anelosimus* spiders. The Maxent algorithm links georeferenced occurrence points with environmental variables at each point locality to determine the probability that the species will be found in any grid square along each variable axis. This information is then combined for all environmental variables to generate a model representing the relative probability of the species' distribution at each grid cell in the defined geographic space. A location with a high probability value indicates suitable environmental conditions for the species. I chose Maxent because it uses only presence (not absence) species occurrence data, performs well even with small sample sizes (Hernandez et al. 2006, Pearson et al. 2007, Wisz et al. 2008) and is known to perform better than other algorithms (Elith et al. 2006, Ortega-Huerta and Peterson 2008).

For the purpose of visualizing general latitudinal and elevational patterns in the distribution of spider sociality, I combined all American *Anelosimus* species belonging to the same level of sociality into a single dataset (i.e. either social or subsocial). For the elevational analysis, I used a subset containing social and subsocial species found in Ecuador. I ran models using the cross-validation method as well as all other default

parameters for Maxent, which are based on maximizing the results in a diverse set of modeling situations, as described by Phillips and Dudik (2008).

All final model outputs represent the average of 20 replicate models ran for each dataset. Model outputs were developed in the format of relative probabilities at each grid cell. Grid cells that are predicted as having optimal suitable conditions for the species have a relative probability value of 1, whereas grid cells with cumulative values close to 0 indicate unsuitable conditions (Phillips and Dudik 2008).

I used the area under the curve (AUC) of the receiver-operating characteristics (ROC) plot as a measure of the overall fit of the models (Liu et al. 2005, Elith et al. 2006). When the AUC is 0.5, the model is performing not better than random. Higher AUC values indicate better performance and optimal performance is a value of 1.0 (Hanley and McNeil 1982). I evaluated the importance of each environmental variable for explaining the distribution of social and subsocial species by its average percent contribution to the models and by jackknife analysis of the average gain for each variable.

2.2.5 Statistical analysis of *Anelosimus* species in Ecuador

I used comparative methods to further test statistically whether social and subsocial species differ in their elevational distribution and the effect of the environmental variables tested in the niche models while accounting for the possible effects of shared ancestry and statistical non-independence of species data points (Felsenstein 1985, Harvey and pagel 1991). Although elevation and climatic variables are not species traits, *per se*, and do not undergo evolution, it can be appropriate to treat them as continuous traits in a phylogenetic analysis to account for the possibility that closely related species may share similar ecological conditions, such as geographic distribution (Garland et al. 1992).

I fitted phylogenetic generalized least-squares (PGLS) models (Grafen 1989, Garland and Ives 2000, Rohlf 2001, Revell 2009) using the function “gls” implemented in the *nlme* and *ape* packages in R (Pinheiro et al. 2012). While ordinary least-squares (OLS) regressions assume that data points are independent, generalized least-squares methods consider phylogenetic relationships and incorporate the degree of non-independence between species into the error structure of the model. Thus, these models account for the possibility that closely-related species may be more similar to each other than to distantly related species

and for the possibility that the covariance between species may decline as their phylogenetic relatedness increases (Martins and Hansen 1997, Pagel 1999, Freckleton et al. 2002). I used maximum likelihood estimates of Pagel's λ (Freckleton et al. 2002, Revell 2009) to construct independent models in which level of sociality was the fixed factor and environmental values were independent variables. This estimate of λ avoids the errors associated with assuming complete phylogenetic independence ($\lambda = 0$, equivalent to ordinary least-squares analysis) or the overcorrecting caused by assuming complete phylogenetic covariance ($\lambda = 1$, equivalent to phylogenetic independent contrasts; Garland and Ives 2000).

In order to explore the effect of phylogeny and whether PGLS models improved model fit, I compared them with equivalent OLS models (i.e. without phylogenetic information, $\lambda = 0$). To compare PGLS vs. OLS models, I used the Akaike's information criteria method (AIC; Burnham and Anderson 2002). For this, I calculated the difference in AIC between fitted models (Δ AIC) and their corresponding Akaike weights. This method assumes that models with the lowest values of AIC are better models than those with high AIC values (i.e. the best models have a Δ AIC value of zero and the highest weight; Pagel 1997, Pinheiro and Bates 2000). To additionally discriminate between models, I used likelihood ratio tests against a X^2 distribution with 1 degree of freedom. For these tests, I used models obtained by maximum likelihood methods, whereas models obtained by restricted maximum likelihood (REML) were used for estimation of the model coefficients reported. Finally, to explore whether differences in sample sizes between species might influence my findings, I compared the best models (either OLS or PGLS) to corresponding models that incorporated sample size as a weighting factor. I used likelihood ratio tests and the Akaike information criteria procedure to compare unweighted vs. weighted models.

I conducted all the comparative analyses using the latest published version of the phylogenetic hypothesis for New World *Anelosimus* (Agnarsson et al. 2007). I used Mesquite v2.75 (Maddison and Maddison 2011) to re-draw the tree and drop tips of species not found in Ecuador (Figure 2.2). In the case of subsocial species, I combined *A. tungurahua* and its sister species *A. studiosus* into one single group as these species are currently believed to be the same species. I also combined *A. jucundus* and its sister species *A. octavius* into one group as the latter did not have a sample size suitable for statistical

analysis (Figure 2.2). As I did not have information on evolutionary tempo or distance among species (as measured by branch lengths), I set all branch lengths to 1 for the analyses.

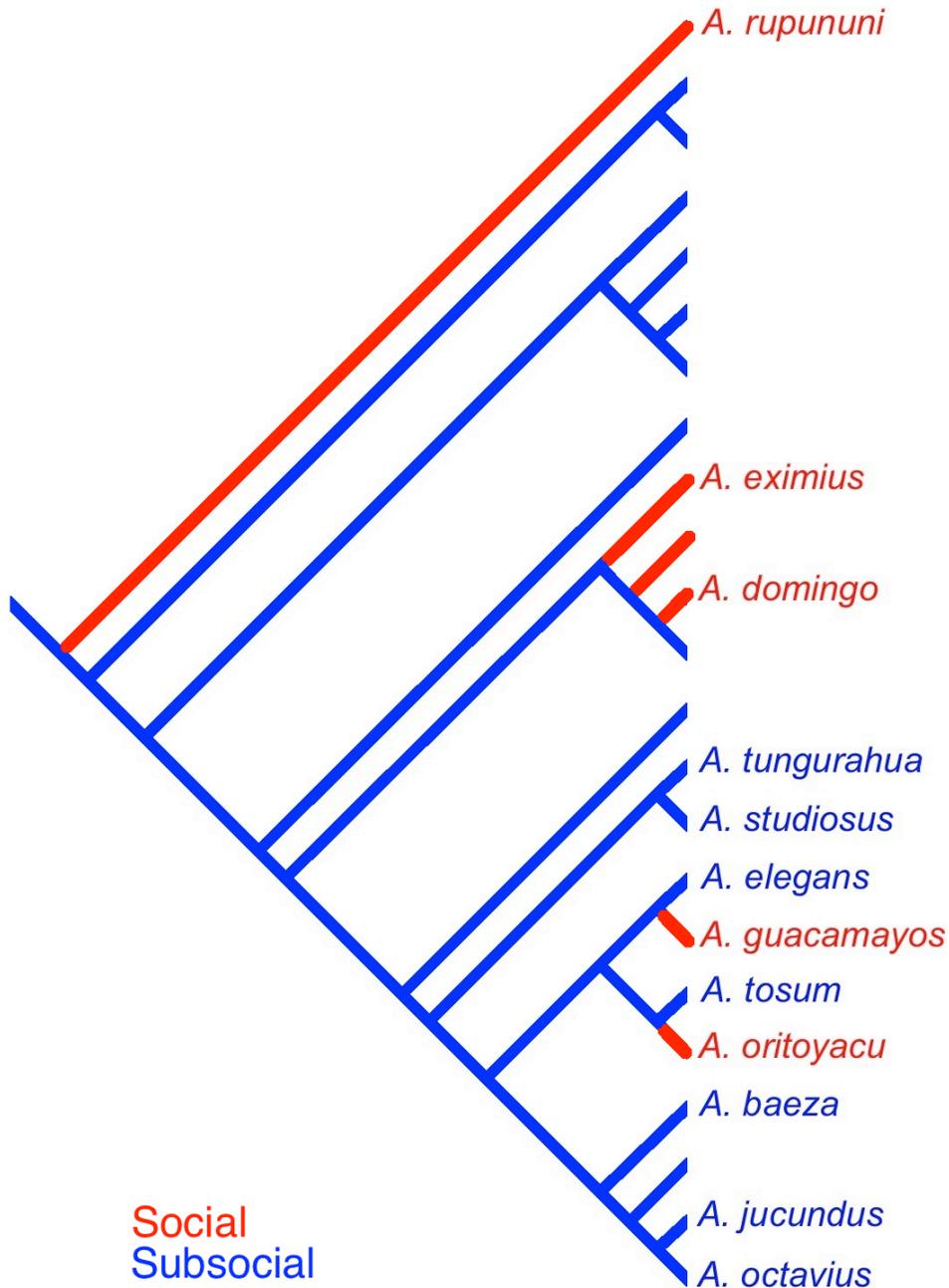


Figure 2.2 A phylogenetic tree for social spiders of the genus *Anelosimus* found in Ecuador. The tree was derived from Agnarsson et al. (2007). Branch lengths are set to 1.

I performed these analyses using a dataset consisting of point values extracted from the six GIS environmental layers corresponding to the known locality points for each species. In addition to the six environmental variables used in the Maxent model construction, I also ran models to formally test elevation differences. For dataset preparation I used the *dismo* and *maptools* packages implemented in R (Lewin-Koh et al. 2010, Hijmans et al. 2011).

In initial runs, I checked for outliers, examined scatterplots of tip data and values for standardized residuals from the phylogenetic regression models, and in the case of social species, I excluded one species (*A. oritoyacu*) from all subsequent analyses as it represented a significant outlier in the data. I report the results of the models as regression coefficients. All analyses were carried out using the statistical language R, v. 2.14.2 (R Development Core Team 2012).

2.3 Results

2.3.1 Latitudinal and elevational patterns of spider sociality (Maxent models)

Maxent prediction models revealed that social species were mainly located at low latitudes in the center of tropical South America whereas subsocial species spread into higher latitudes (southern North America) and near the edges and southern parts of South America (Figure 2.3). The most important contributors to the Maxent model for both social and subsocial species were temperature seasonality and rainfall intensity (Table 2.1). The corresponding AUC jackknife tests confirmed the importance of these variables to the models (Appendix 4). Response curves for these two environmental variables showed that, at continental scales (America), the probability of occurrence of social species greatly decreases in areas of high temperature seasonality whereas subsocial species occur less frequently in areas of high rainfall intensities (Figure 2.4). While response curves for the less important variables in the Maxent models did not show a particular pattern across the net primary productivity gradient for either social or subsocial species, they suggested that the probability of occurrence of social species greatly decreases in areas of high precipitation seasonality whereas subsocial ones are more tolerant to these conditions. Finally, Maxent models had high AUC values and small standard deviations (social 0.891 +/- 0.014,

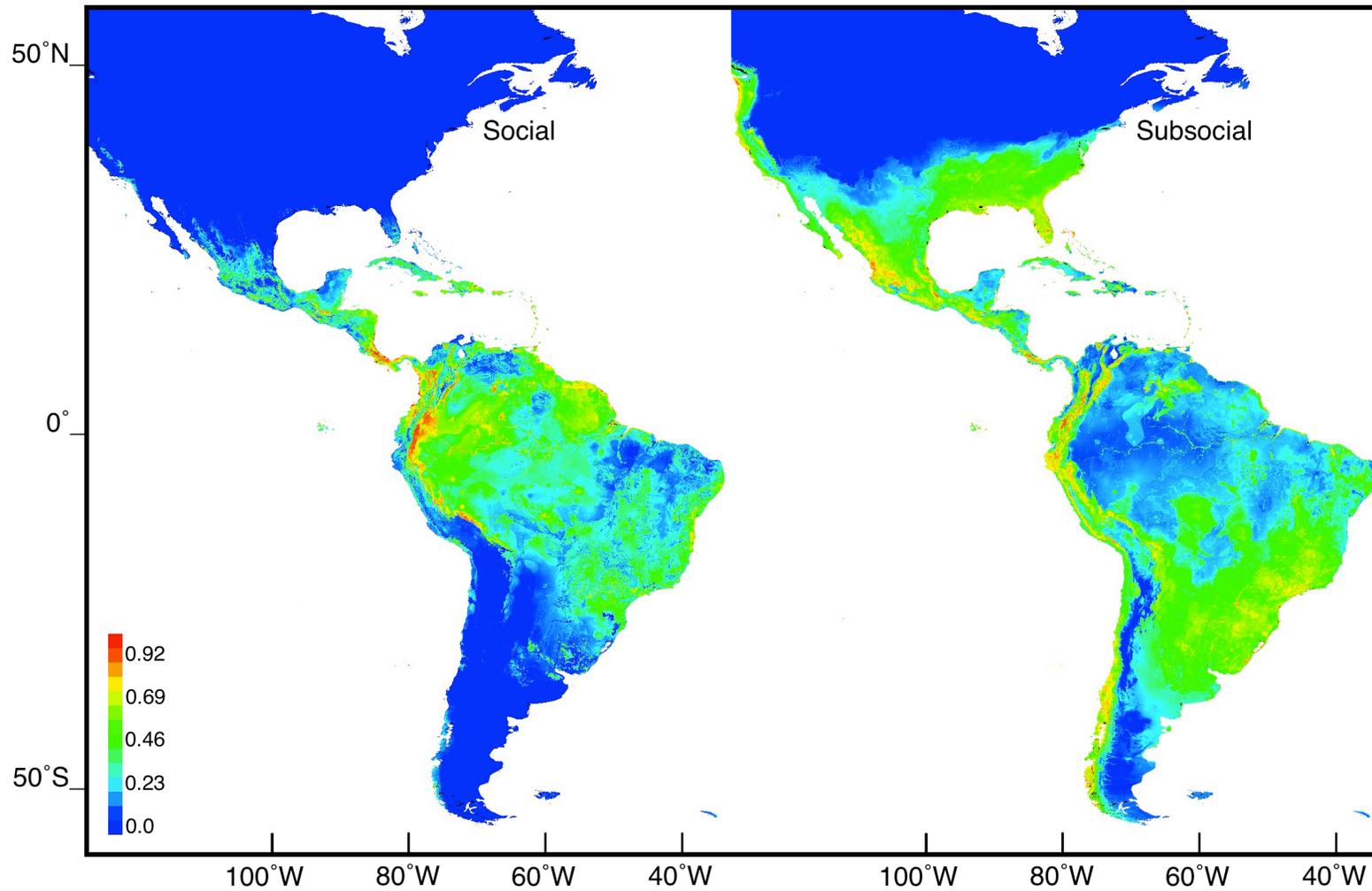


Figure 2.3 Maxent models showing the projected distribution of social and subsocial *Anelosimus* spiders in America. The scale on the left shows the probability of habitat suitability values (0 = lowest suitability; 1= highest suitability).

Table 2.1 Percent contribution of six environmental variables to Maxent distribution models for social and subsocial *Anelosimus* spiders in America and Ecuador. The most important variables given a jackknife analysis of variable importance shown with ** (Appendices 4 and 5).

Variable	America		Ecuador	
	Social	Subsocial	Social	Subsocial
Annual temperature	---	---	4.7	88.3**
Temperature seasonality	64.4**	70.1**	1.0	0.8
Annual rainfall	---	---	68**	2.6
Rainfall intensity	17.4**	13.4	13.1	3.5 **
Rainfall seasonality	6.1	4.8	3.3	2.4
Net primary productivity	12.1	11.7	9.9	2.5

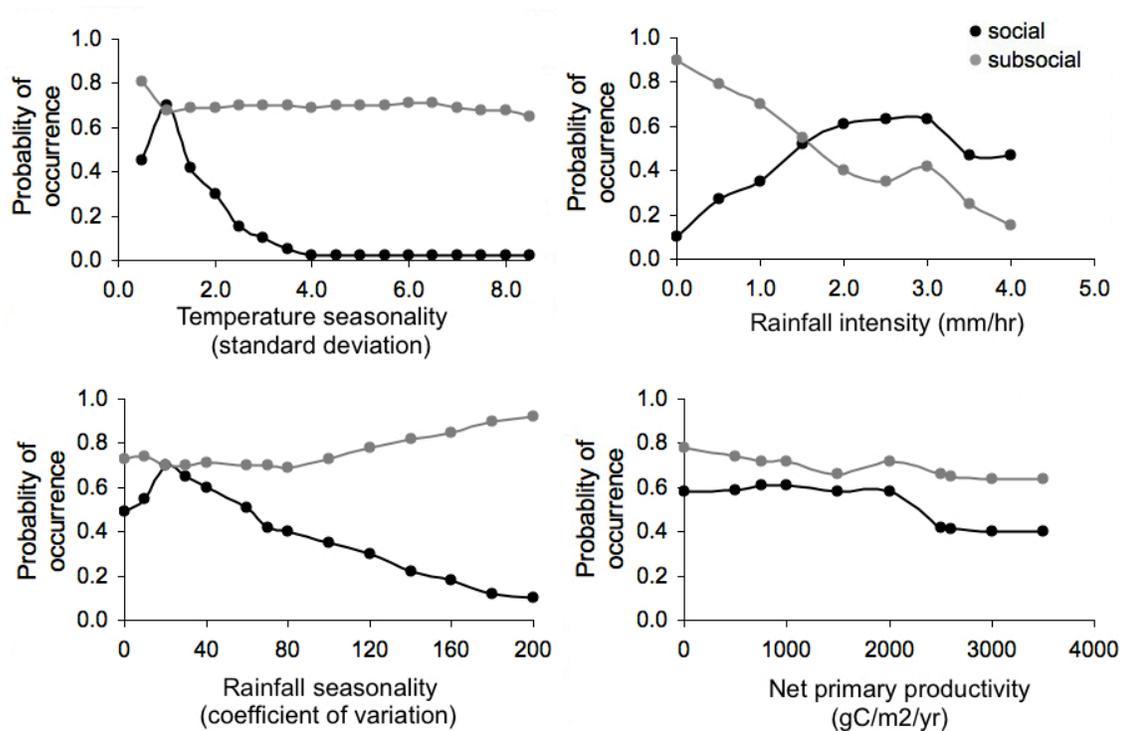


Figure 2.4 Probability of occurrence of social and subsocial *Anelosimus* spiders in America with respect to individual environmental gradients.

subsocial and 0.789 ± 0.015 ; Appendix 4) thus indicating overall good model performance and uniformity amongst replications.

In Ecuador, Maxent models predicted social *Anelosimus* species to be most likely found towards the lowland Amazon rainforest, and subsocial species towards the Andean slopes at higher elevations (Figure 2.5). According to Maxent tests of a variable's percent contribution to the model and jackknife tests of variable importance, annual rainfall and rainfall intensity were the most important variables in the predicted distribution of social species (Table 2.1, Appendix 5). For subsocial species, average temperature and rainfall intensity were the most important variables to their distribution models (Table 2.1, Appendix 5). Response curves of these variables showed that the probability of occurrence of social species is highest in areas with high annual rainfall and rainfall intensity (Figure 2.6). The probability of occurrence of subsocial species, on the other hand, consistently decreases with increasing rainfall intensities as well as at warmer temperatures (Figure 2.6). Maxent models had high AUC values and small standard deviations (social 0.823 ± 0.036 , subsocial 0.919 ± 0.019 ; Appendix 5) thus indicating overall good model performance and uniformity amongst replications.

2.3.2 Comparative analyses of social and subsocial species along an elevation gradient in eastern Ecuador

Incorporating phylogenetic relationships fitted the data better (i.e. smaller AIC values and significant likelihood ratio tests) than the corresponding ordinary least-square analyses for five of six variables: annual rainfall, rainfall seasonality, rainfall intensity, annual temperature, and temperature seasonality (Table 2.2). For elevation, and the remaining variable, net primary productivity, models that included phylogenetic relationships did not make a difference in terms of model fit or the significance of the results, thus for consistency with the other variables I used the corresponding phylogenetic least square models for further analyses. In general, including a phylogeny in the models did not change the general findings obtained with ordinary least-square models. Both, phylogenetic and ordinary least-square models indicated that level of sociality in *Anelosimus* spiders was significantly associated with elevation, and individually with most climatic variables, except net primary

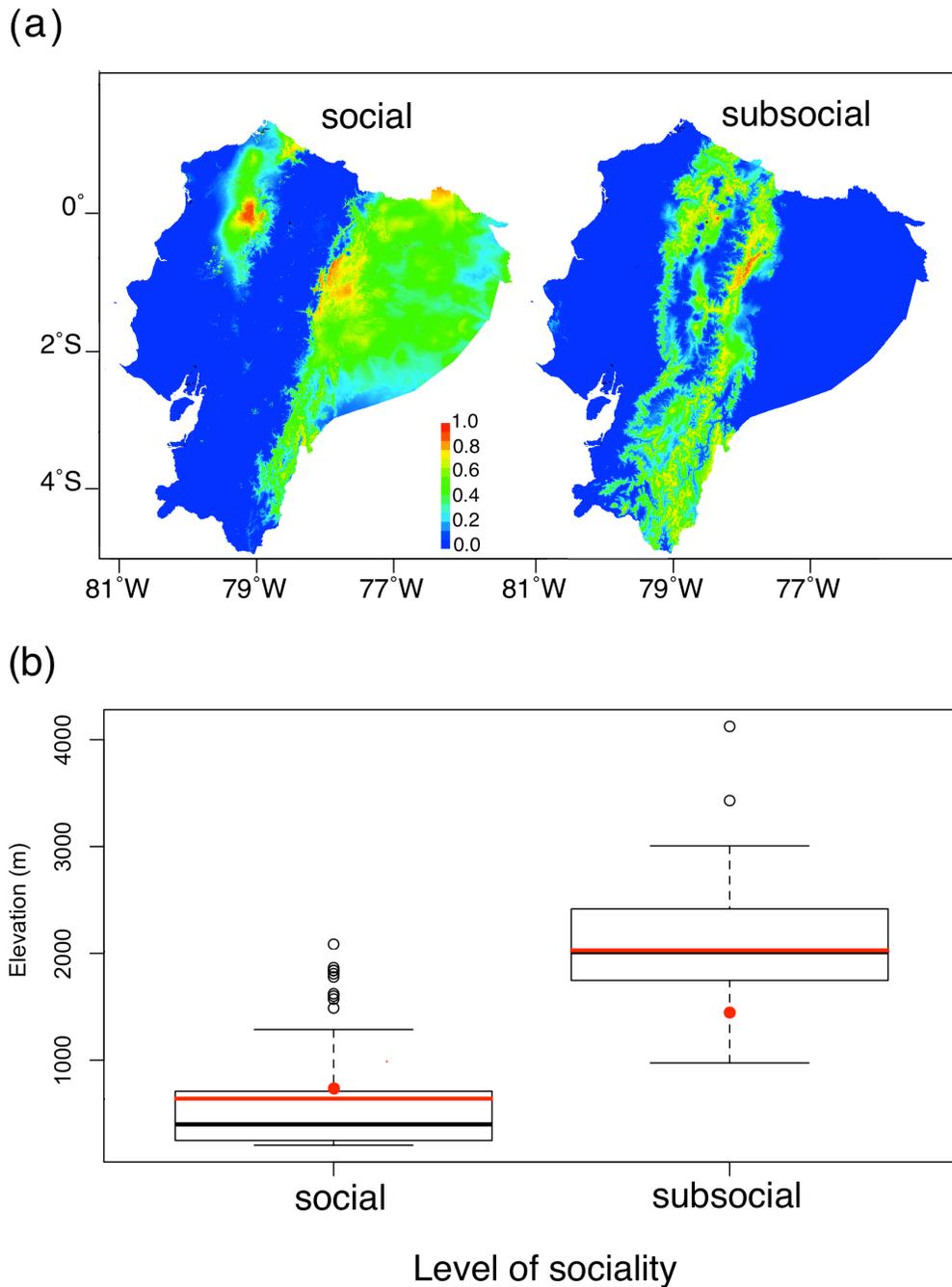


Figure 2.5 (a) Maxent models showing the projected distribution of social and subsocial *Anelosimus* spiders in Ecuador. The scale shows the relative probability of habitat suitability. (b) Corresponding differences in elevation. Box plots were constructed using the raw data of known occurrence. Boxplots show the median (*black line*), 25% and 75% (*black box*), 10% and 90% (*whiskers*) percentiles, and the corresponding mean (*red line*). The red dot indicates the phylogenetic corrected mean ($P = 0.023$; Table 2.3).

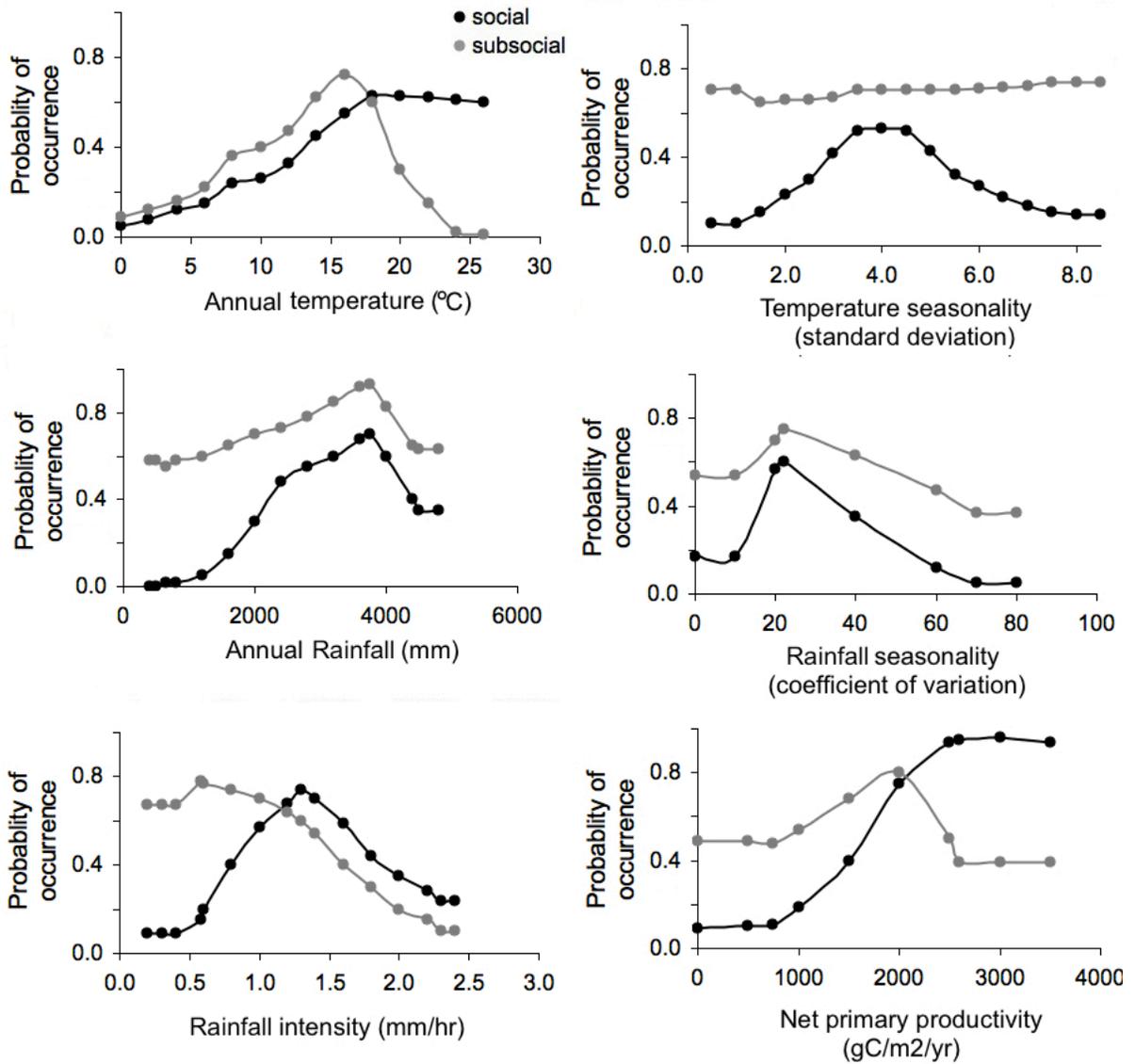


Figure 2.6 Probability of occurrence of social and subsocial *Anelosimus* spiders in Ecuador with respect to individual environmental gradients.

Table 2.2 Regression results and comparison of ordinary least-squares (O) and phylogenetic generalized least-squares (P) models explaining variation in various environmental variables between social and subsocial spiders ($n_{\text{social}} = 4$, $n_{\text{subsocial}} = 5$). The lowest Akaike Information Criterion (AIC) scores indicate the best model. Typically ΔAIC values of zero with the highest weight are the best models. LRT X^2 shows the likelihood ratio test distributed as X^2 and LRT P is the corresponding probability.

Variable		Coef.	s.e.	<i>t</i>	<i>P</i>	AIC	ΔAIC	weight	LRT X^2	LRT <i>P</i>
Elevation	O	1284.8	300.5	4.3	0.0037**	139.2	0	0.565	1.5	0.22
	P	619.8	262.2	2.4	0.049*	139.7	0.52	0.435		
Annual temperature	O	-6.0	1.3	-4.7	0.0023**	40.8	24.4	5.01e-06	26.4	<0.001***
	P	-4.2	1.4	-3.0	0.021*	16.4	0	9.999e-01		
Temperature seasonality	O	-1.4	0.6	-2.4	0.050·	26.5	4.25	0.107	6.3	0.0124*
	P	-1.2	0.4	-2.8	0.027*	22.2	0	0.893		
Annual rainfall	O	-1569.1	365.3	-4.3	0.0036**	117.1	4.24	0.107	6.2	0.013 *
	P	-1131.7	142.9	-7.9	<0.001***	112.8	0	0.893		
Rainfall intensity	O	-0.08	0.02	-3.9	0.0059**	-33.1	18.6	9.152e-05	20.6	<0.001***
	P	-0.08	0.01	-7.2	<0.001***	-51.7	0	9.999e-01		
Rainfall seasonality	O	15.6	9.5	1.7	0.14	65.9	2.40	0.231	4.4	0.036*
	P	9.0	5.6	1.6	0.15	63.5	0	0.769		
Net primary productivity	O	-157.1	169.7	-0.9	0.39	106.3	0	0.612	1.1	0.29
	P	26.0	111.5	0.2	0.82	107.2	0.91	0.389		

productivity and rainfall seasonality (Table 2.2). Weighted phylogenetic least square models did not change the findings obtained with the unweighted analyses, even in the two cases where it did improve model fit (i.e. elevation and temperature seasonality; Table 2.3). Since sampling biases did not affect my findings but improved model fit for two variables, for consistency I report patterns focusing on the weighted phylogenetic least square models for all variables.

Social species were associated with significantly lower elevations than subsocial species (PGLS (weighted) model: fitted means, social 716.6 m, subsocial mean 1426.8 m; $t = 2.9$, $P = 0.023$, Figure 2.5b). Phylogenetic generalized least square models (weighted) showed that social species are on average associated with higher temperatures (fitted means, social 22.9°C, subsocial 18.5°C; $t = -3.9$, $P = 0.0062$), lower seasonality (social 3.6, subsocial 5.0; $t = -3.0$, $P = 0.021$), higher annual rainfall (social 3361.4 mm, subsocial 1895.1 mm; $t = -5.3$, $P = 0.0011$), and higher rainfall intensities (social 0.167 mm/hr, subsocial 0.0789 mm/hr; $t = -7.8$, $P < 0.001$; Figure 2.7) than subsocial species. Unexpectedly, I did not find a significant difference in net primary productivity (social 1626.9 gC/m²/yr, subsocial 1631.1 gC/m²/yr; $t = 0.03$, $P = 0.97$) or rainfall seasonality (social 23.9, subsocial 40.7; $t = 2.4$, $P = 0.05$; Figure 2.7) between social and subsocial species in Ecuador. Collectively, these results indicate that, based on the *Anelosimus* populations in my sample from Ecuador, there is a separation of social level associated with elevation. Social species are found at lower elevations where they tend to experience climates with warmer temperatures, less seasonality, more rainfall, but greater rainfall intensities. Subsocial species are found at higher elevations where they experience the opposite climate conditions. A reassuring finding is that these results were consistent across models tested.

2.4 Discussion

Social spiders are typically concentrated in low elevation areas of the world's tropics (reviewed in Avilés 1997 and Avilés et al. 2001, Agnarsson 2006, Avilés et al. 2007). Consistent with this global pattern, Maxent distribution models showed two different latitudinal patterns for social and subsocial *Anelosimus* spiders: social species were concentrated at low latitudes, mostly in areas comprising the Amazon region, whereas the occurrence of subsocial species expanded to higher latitudes reaching North America and towards the drier or higher latitude coastal edges of South America. Social and subsocial spider Maxent distribution models across latitude (America) were mainly predicted by temperature seasonality and rainfall intensity. Social

Table 2.3 Regression results and comparison of unweighted phylogenetic generalized least-square models (U) against the corresponding weighted (W) models of the association between spider sociality ($n_{\text{social}} = 4$, $n_{\text{subsocial}} = 5$) and various environmental variables. The lowest Akaike Information Criterion (AIC) scores indicate the best model. Typically ΔAIC values of zero with the highest weight are the best models. LRT X^2 shows the likelihood ratio test distributed as X^2 and LRT P is the corresponding probability.

Variable		Coef.	s.e.	<i>t</i>	<i>P</i>	AIC	ΔAIC	weight	LRT X^2	LRT <i>P</i>
Elevation	U	619.8	262.2	2.4	0.049*	139.7	29.8	3.32e-07	29.8	<0.001***
	W	710.2	244.2	2.9	0.023*	109.8	0	9.99e-01		
Annual temperature	U	-4.2	1.4	-3.0	0.021*	16.4	0	9.99e-01	26.3	<0.001***
	W	-4.4	1.1	-3.9	0.0062**	42.6	26.3	1.96e-06		
Temperature seasonality	U	-1.2	0.4	-2.8	0.027*	26.2	14.2	0.001	14.2	<0.001***
	W	-1.4	0.5	-3.0	0.021*	8.0	0	0.999		
Annual rainfall	U	-1131.7	142.9	-7.9	<0.001***	112.8	0	0.905	4.5	0.034*
	W	-1466.3	275.0	-5.3	0.0011**	117.3	4.50	0.0955		
Rainfall intensity	U	-0.08	0.01	-7.2	<0.001***	-51.7	0	0.782	2.6	0.11
	W	-0.09	0.01	-7.8	<0.001***	-49.1	2.56	0.218		
Rainfall seasonality	U	9.0	5.6	1.6	0.15	63.5	0	0.642	1.2	0.28
	W	16.8	5.7	2.4	0.05	64.7	1.16	0.358		
Net primary productivity	U	26.0	111.5	0.2	0.82	107.2	0	0.799	2.7	0.0963
	W	4.2	136.7	0.03	0.97	110.0	2.7	0.201		

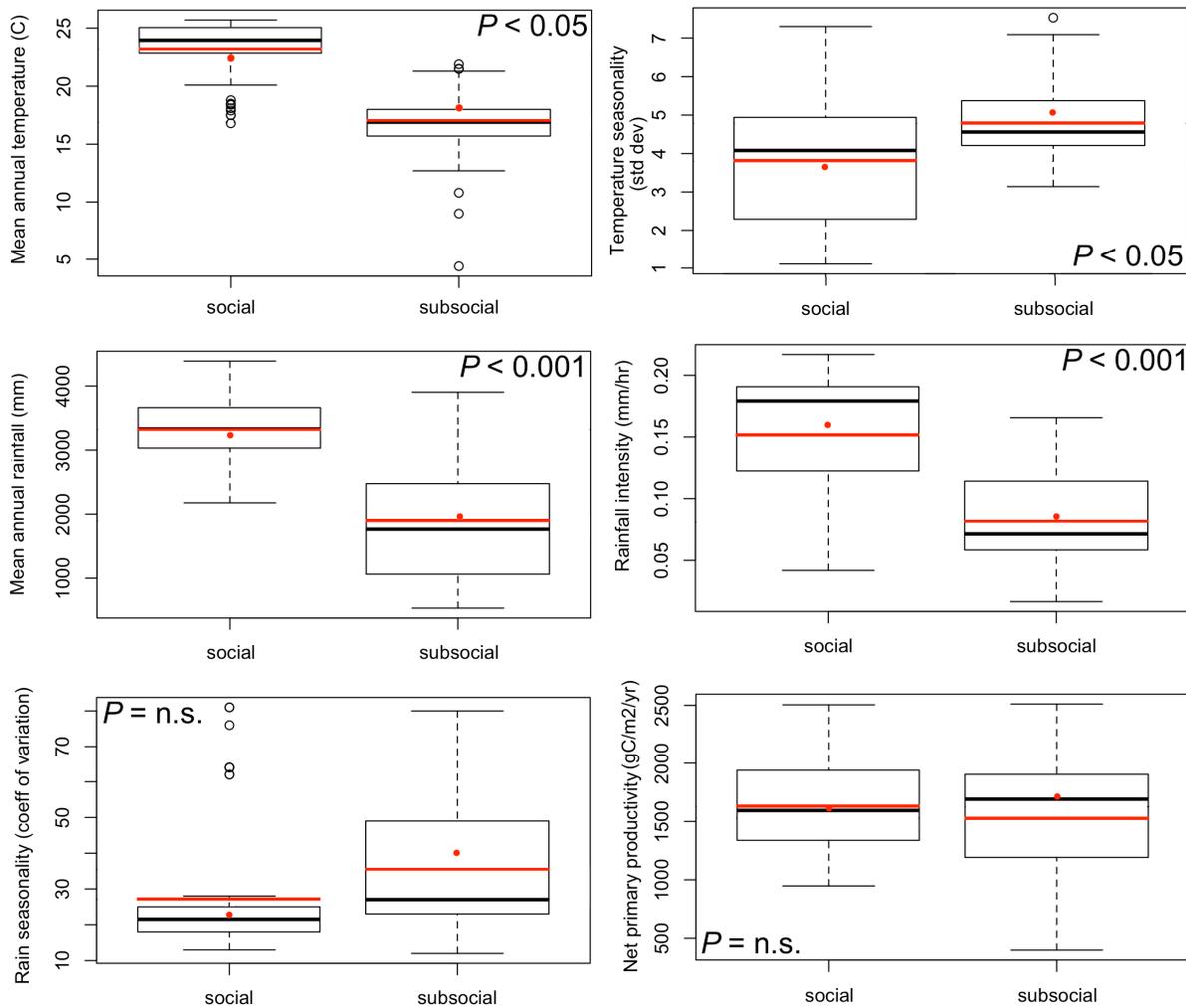


Figure 2.7 Environmental variables used to predict the distribution of four social and five subsocial *Anelosimus* spiders in Ecuador. Box plots were constructed using presence raw data. Box plots show the median (*black line*), 25% and 75% (*black box*), 10% and 90% (*whiskers*) percentiles, and the corresponding mean (*red line*). The *red dot* indicates the phylogenetic corrected mean, and the corresponding probability that two means are similar is given by *P* (Table 2.3).

species were absent from highly seasonal areas whereas subsocial species appeared to tolerate a wide range of temperature seasonality. Unlike social species, subsocial spiders were unlikely found in areas of high rainfall intensity. Within tropical latitudes (i.e. in Ecuador), social species were more likely to occur towards the lowland tropical rainforest whereas subsocial species were absent from these areas being found towards the slopes of the Andes. The

distribution of social species in Ecuador was mainly predicted by annual rainfall, with the lowest probability of occurrence in dry areas (low annual rainfall), thus explaining their absence from dry areas within tropical latitudes (e.g. in the coastal edges of Ecuador). The main environmental predictors of subsocial species in Ecuador were annual temperature and rainfall intensity, with the lowest probability of occurrence at higher temperatures and high rainfall rates.

Comparative analyses of Ecuadorian *Anelosimus* species confirmed patterns shown by the Maxent distribution models that social and subsocial species occupy different elevations and each social system is significantly associated with different environmental conditions. Amongst the most relevant findings, at low elevations, social species were significantly associated with warmer temperatures and greater rainfall at higher intensities. Subsocial species are associated with the opposite conditions at higher elevations. Contrary to my expectation that areas of higher net primary productivity may be associated with larger insect body sizes and thus with social *Anelosimus* species, I did not find a significant association between net primary productivity and social system.

There are several possible explanations as to how the variables tested could influence the two geographical patterns of spider sociality: the dominance of social *Anelosimus* spiders in the low-elevation tropical rainforest and the absence of subsocial species from these areas (Avilés et al. 2007). For example, subsocial spider colonies may be unable to colonize and persist in the lowland tropical rainforest because high rainfall intensities can cause severe and frequent web damage leading to extinctions of their typically small single-female colonies (Purcell and Avilés 2008). Since web damage repair requires costly silk production, social species with bigger colonies consisting of several females may fare better in these conditions as per capita expenditure in silk decreases with colony size (Riechert et al. 1986, Purcell and Avilés 2008). Thus, these conditions would favor *Anelosimus* species that form larger colonies and exhibit more advanced levels of sociality. This is consistent with the *maternal survival* hypothesis (Jones et al. 2007), that cooperative breeding should be favored in environments where single females have a greater probability of dying before her offspring can survive on their own (Avilés et al. 2007, Jones et al. 2007). Additional evidence for this idea comes from Purcell and Avilés (2008) who found that subsocial spider colonies transplanted to the lowland rainforest, as well as local social colonies, exhibited higher survival and better webbing when sheltered from the rain. In my study, rainfall intensity was accordingly one of the most important contributors to the Maxent distribution model of subsocial species in Ecuador (and across America), and a significant

variable separating out social from subsocial species in the comparative analyses. While social spiders were highly associated with areas of high annual rainfall and rainfall intensity both across latitude (i.e. Maxent model) and elevation (i.e. Ecuador Maxent model and comparative analysis), within tropical latitudes (Ecuador) they appeared to be absent from areas of very dry conditions (low annual rainfall). Interestingly, this pattern differs from that found by Purcell (2011) who showed that increased sociality (i.e. colony size) was negatively correlated with annual rainfall, thus suggesting opposite effects of annual rainfall and rain intensity during individual storms. While Purcell (2011) found this pattern using only one species of *Anelosimus* in Ecuador, it is clear that the role of annual rainfall deserves further study.

Another notable aspect of the lowland tropical rainforest consistent with the *maternal survival* hypothesis is potentially higher rates of predation, namely by ants (Purcell and Avilés 2008). Although ant abundance and predation rates are not parameters available through GIS data, they are positively correlated with net primary productivity and temperature (Kaspari et al. 2000, Kaspari and O'Donnell 2003). Ant abundance, in general, is known to be highest in lowland tropical rainforests (Jeanne 1979, Kaspari et al. 2000, Kaspari and O'Donnell 2003), which are warm and highly productive habitats. Contrary to my initial expectations, the effect of net primary productivity was not significant in either the distribution models or the comparative analysis. Temperature and temperature seasonality, however, were the most important contributors to the distribution of subsocial species across elevation and latitude (Maxent models), and were significant variables separating out the two social systems in the comparative analysis. Although temperature parameters alone, or in combination with productivity, cannot be used as reliable indicators of the incidence of ant predation, these patterns are consistent with previous observations in Ecuador showing that social spider nests in the lowland tropical rainforest (and the surrounding vegetation) contain greater numbers of ants than subsocial spider nests at higher elevations (Purcell and Avilés 2008, Guevara and Avilés 2009). This evidence, along with circumstantial observations of ant raids on social spider colonies in these areas (J. Guevara, personal observations) beg for a formal empirical study directly testing elevational differences in ant presence and their predation rates on spider colonies, and its association with the absence of subsocial spider colonies from these environments.

The absence of subsocial *Anelosimus* in areas of high rainfall intensity and factors (i.e. temperature parameters) that may correlate with high predator pressure is consistent with the notion that group living and cooperation may be a mechanism to occupy environments where individuals cannot

replace themselves, thus lending support to the *maternal survival* hypothesis (Avilés 1997, 1999, Avilés and Tufino 1998, Avilés et al. 2007, Jones et al. 2007). This idea is not restricted to social spiders. In cooperative breeding birds and mammals, for instance, more complex social behavior is predicted by harsh conditions where the fitness benefits of helping are most apparent (Rubenstein 2007, Jetz and Rubenstein 2011).

Furthermore, the dominance of social species in the lowland tropical rainforest has been previously attributed to the apparent abundance of large insect prey in these areas (i.e. *prey size* hypothesis; Avilés et al. 2007, Powers and Avilés 2007). The *prey size* hypothesis suggests that the formation of large colonies by social species requires habitats harboring large amounts of large insects in order for colonies to compensate for the scaling properties of their tri-dimensional webs (Yip et al. 2008) by capturing larger insects as colony size increases (Rypstra and Tirey 1991, Avilés 1997). This is because as colony size increases, the number of insect prey per spider declines in parallel with a decline in surface area to volume ratio of their tri-dimensional prey capture webs (Yip et al. 2008). In areas where large insects are abundant, as in the lowland tropical rainforests (Guevara and Avilés 2007, Powers and Avilés 2007), however, the spiders can make up for this decline by capturing increasingly large insects as the colony grows (Yip et al. 2008). It is the paucity of large insects at higher elevations and latitudes, therefore, that may prevent the formation of large colonies in those areas. As in the case of ant predation, I did not test directly the effect of insect body size. However, insect body size may in general obey to an association between climate and ecophysiological factors. Insect body size clines, for instance, may result from latitudinal/elevational variation in time available for growth and reproduction (Bidau and Martí 2007), which tends to decrease as latitude/elevation increases. Ectotherms, particularly insects, appear to generally follow converse Bergmannian clines more frequently than endotherms—i.e. body size of insects living in warmer areas tend to be larger than those inhabiting cooler climates (Brennan and Fairbairn 1995, Mousseau 1997, Blanckenhorn and Demont 2004, Bidau and Martí 2007). In addition, larger insect body sizes have been associated with high habitat productivity (i.e. through its effect on abundance and quality of the food resources and/or the quality of habitat; Rosenzweig 1968) as well as with high predation risk (Damuth 1993), also associated with resource-rich tropical latitudes and warmer temperatures (Jeanne 1979, Menge and Lubchenco 1981, Sih et al. 1985). Thus, possible environmental predictors of insect body size clines may include seasonality, temperature, and net primary productivity. Consistent with these, temperature seasonality was the main contributor to the

distribution models of social species across latitude, and was a significant variable separating social from subsocial species across elevation. I did not, however, find a significant effect of net primary productivity either across latitude or elevation. Again, not being direct measures of insect body size, the seemingly contradictory result associated with net primary productivity does not necessarily discard the relevance of the prey size hypothesis in the distribution of spider sociality. Ideally, the effect of prey size on the distribution of social spiders would be directly tested by sampling the insect body size available at each location where social and subsocial species are known to occur.

In addition to the *maternal survival* and the *prey size* hypotheses, other factors directly related to temperature and seasonality are likely to explain much of the geographical patterns exhibited by *Anelosimus* spiders. For instance, the year-round warm temperatures and typically aseasonal conditions of the tropics would allow the spider colonies to persist for several generations and grow very large, thus sustaining permanent group living in social spiders (Avilés 1997). This would partly explain the dominance of social species at low latitudes and, within those latitudes, low elevations. In contrast, increased seasonality of higher elevations and latitudes where subsocial species occur may promote early dispersal of subadults, thus constraining colony size and ultimately hindering permanent group living and the formation of large colonies in those areas. In accordance to this, subsocial species were significantly associated with increased seasonality and lower temperatures (i.e. mid and high elevations and latitudes). All of these factors may act in concert with other climatic and biotic factors in determining the distribution of *Anelosimus*. For example, while social spiders may be directly delimited at their upper range by biotic aspects of the habitat such as available prey size, they may also be directly influenced by climate. Climate, in turn, may also have direct effects on insect body size. Unfortunately, it is problematic to separate the relative contributions of biotic and abiotic factors due to their potential covariation and indirect effects (Gaston 2003), thus making these issues for further study. In general, the concentration of social species in tropical areas and low elevations appears not to be restricted to the genus *Anelosimus* as most other known social spiders in the Neotropics occur below 1,300 m (reviewed in Avilés et al. 2001). In addition, similar patterns in the distribution of social systems of different complexity have also been observed within species. For example, Purcell and Avilés (2007) showed a decrease in level of sociality (i.e. measured as colony size and proportion of nests containing solitary individuals) with increasing elevation in *A. eximius* in Ecuador.

Finally, particularly notorious was the smaller ranges of social species associated with relatively small suitable areas (i.e. mainly concentrated in parts of the Amazon basin) compared to the more widespread distribution of their subsocial counterparts. This suggests more specialized environmental requirements by this social system and potentially higher vulnerability to habitat destruction and to other known threats to tropical diversity. Exploring similar geographical patterns and assessing the relative importance of climatic variables across social taxa is key to our ability to predict the persistence of these populations in light of the habitat loss and climate change challenges faced by this unique group of spiders, as well as other social taxa.

Chapter 3: Sociality and resource use: insights from a community of social spiders in Brazil

3.1 Introduction

Group living in animals has well known consequences in many aspects of an animal's life including its reproduction, predator protection, and foraging (Caraco 1979, Pulliam and Millikan 1982, Krebs and Davies 1996, Krause and Ruxton 2002). Group characteristics, such as cooperativeness and group size, play crucial roles in the way social species engage in these activities and, in particular, in defining their foraging patterns and resource use. Bigger groups, for example, may detect prey faster (Baird and Dill 1996), use less energy and spend less time during prey capture (Creel and Creel 1995), and decrease variability in hunting success (Krause and Ruxton 2002). In addition, bigger groups may be more successful with specific prey types (Hector 1986, Creel and Creel 1995) and sizes (Caraco and Wolf 1975, Nudds 1978, Nentwig 1985, Rypstra 1990, Yip et al. 2008). For example, cooperative hunting in social carnivores—i.e. African wild dogs, lions, wolves, and spotted hyenas—allows the capture of prey otherwise unattainable by solitary foragers (Kruuk 1966, Caraco and Wolf 1975, Nudds 1978, Creel and Creel 1995). Sociality may thus play important roles not only in expanding the range of resources a species is capable of exploiting, but also in creating obvious differences in resource use between species that differ in level of sociality. However, although a wide range of literature has shown differences in prey size use as a function of sociality (i.e. hunting group size and level of cooperation) (Lamprecht 1981, Hector 1986, Baird and Dill 1996, Holekamp et al. 1997, Guevara and Avilés 2007, Powers and Avilés 2007, Yip et al. 2008), such studies have focused on populations of single species inhabiting separate environments. In such cases species comparisons are problematic as dietary differences could arise for reasons other than sociality if, for instance, the species occupy areas with marked differences in the size of the prey available (i.e. low vs. high elevations; Guevara and Avilés 2007). Comparative analyses of closely-related species that differ in relevant social traits (i.e. group size or level of

cooperation), but share the same habitat, can help disentangle the roles of sociality in creating differences in resource use among social organisms.

The social spider genus *Anelosimus* (Theridiidae) is ideal to examine the role of sociality in resource use as local communities often contain species that vary in their level of sociality (Avilés 1997, Agnarsson 2006, Avilés et al. 2007). In general, the more advanced social species (non-territorial permanent social, *sensu* Avilés 1997) form colonies containing dozens to thousands of spiders and may be able to capture larger prey than less social ones (i.e. subsocial or non-territorial periodic social) whose colonies contain single-family groups of at most a few dozen individuals (Avilés 1997, Lubin and Bilde 2007). This would be due both to the greater size of their prey capture webs and the presence of more individuals to participate in cooperative prey captures (Nentwig 1985, Rypstra 1990, Powers and Avilés 2007, Yip et al. 2008). Yip et al. (2008), for instance, have shown that the body size of insects captured by the Neotropical social spider *Anelosimus eximius* increases monotonically with colony size.

To contrast the association between sociality and prey size use amongst co-occurring social species, I studied a striking *Anelosimus* community containing at least five species with minimal body size differences (body lengths within 0.1 mm of one another), but with levels of sociality ranging from almost solitary to fully social. I tested the hypothesis that the ranges of insect body sizes captured by these sympatric spider species reflect their nest and colony sizes, as would be expected if larger nests are capable of intercepting larger insects and the presence of a greater number of individuals makes their cooperative capture possible. If level of sociality plays a role in the prey size captured, I predict that species with larger colonies and more developed cooperation will capture larger insects than less social species with smaller colonies. I then assess whether the various species capture prey selectively from the distribution of insect body sizes present in their environment. I finally test whether the pattern of resource use by this *Anelosimus* community is more over-dispersed than expected by chance and consider alternative hypotheses that might explain such a pattern. This community of closely-related *Anelosimus* spiders represents a unique opportunity to examine how sociality may shape resource use in sympatric species, and its potential role in resource segregation, a possibility not previously explored.

3.2 Materials and methods

3.2.1 Locality

Spider colonies and their prey capture patterns were studied in the protected reserve of Serra do Japi near Jundiá in the state of São Paulo, Brazil (23°12' - 23°22' S and 46°57' - 47°05' W and 650 – 1300 m elevation). This is a markedly-seasonal, semi-deciduous forest with leaf fall occurring especially during the dry and relatively cool autumn and winter seasons (from April to September). I conducted our prey capture surveys during the wet warm season (summer) in November to December 2005 (mean monthly rainfall > 100 mm) at three different sites within the reserve (Paraiso, Bauru, Bica), all located between 1000 – 1200 m elevation and covering about 3 km². At these sites, spider colonies occur sympatrically, mainly on shrubs and trees located both in the interior and forest edge. Although there are some differences among the species on the exact position they occupy on the plant substrate and relative to the forest edge (Purcel et al. 2012), nests of all species can be found in close proximity from one another in all areas, often as close as a few cm apart. In addition to studying the prey captured by the colonies, I used three sampling methods—no-kill malaise traps, knock-down sticky traps, and visual sampling—to assess the range of insect body sizes present in the environment in areas around the study colonies.

3.2.2 Species descriptions

The study community at Serra do Japi contained species representing the full spectrum of social behaviors present in the genus, including the nearly-solitary, *Anelosimus nigrescens* Keyserling; two subsocial species, *Anelosimus baeza* Agnarsson and *Anelosimus studiosus* Hentz; one species intermediate between social and subsocial, *Anelosimus jabaquara* Levi; and one social species, *Anelosimus dubiosus* Keyserling. *A. dubiosus* and *A. jabaquara* are close phylogenetic relatives, while the remaining three species belong to different subclades within the genus (Agnarsson 2006, Agnarsson et al. 2007). Geographically, *A. dubiosus* and *A. jabaquara* are known to occur only in Brazil at elevations of 600 to 1100 m (Agnarsson, 2006) where they are often found in sympatry (Gonzaga and Dos Santos 1999). The remaining species have a more widespread distribution in the Americas, occurring in a range of habitats except in lowland tropical rainforests (Agnarsson 2006, Avilés et al. 2007). Although relatively common throughout its range (Agnarsson, 2006), *A. studiosus* occurred at very low densities at

Serra do Japi. I thus only report on the characteristics of the nests and prey capture patterns of the two nests from which data were obtained (Table 3.1), but do not include this species in the analyses. Because of the strong seasonality of Serra do Japi (see above), the populations of any given species are synchronized in their phenology, with the reproductive season, which is slightly offset among species (Marques et al. 1998, Purcell et al. 2012), roughly coinciding with the warm-wet season.

My ranking from least to most highly social of *Anelosimus* species in this community is based on the instar at which individuals disperse from the natal nest. In the nearly solitary *A. nigrescens* spiderlings disperse early in their lifecycle so that nests contain mostly single females with an egg sac or with recently hatched spiderlings; beyond the second or third instar individuals live solitarily (this study, unpublished observations). In the subsocial *A. baeza* and *A. studiosus* colonies are also initiated by single females, but the offspring remain in their natal nest for several instars before dispersing (this study; see also Powers and Avilés 2007, for *A. baeza*, and Jones and Parker 2000 and Viera et al. 2007, for *A. studiosus*). At the time of this study, *A. baeza* colonies were in the midst of their social phase, as they contained mostly subadult individuals following the death of their mother, but prior to dispersal. While differences in the prey size utilized may exist at other phases of the phenology of this species (e.g. post-dispersal colonies containing single individuals), the timing of our study allowed us to observe the effects of group living and cooperation in prey capture patterns in this species, while assessing contemporaneous patterns of prey capture of the entire community. In *A. jabaquara* dispersal happens at the subadult to adult stages, but a fraction of females may remain in the natal nest to reproduce (Gonzaga and Vasconcellos-Netto 2001). In *A. dubiosus* females apparently mature and remain in the natal nest to breed and the establishment of new colonies may involve budding, in addition to the dispersal of solitary, possibly already inseminated, adult females (Marques et al. 1998). In *A. jabaquara* and *A. dubiosus*, therefore, a nest may be re-occupied by successive generations and colonies may contain up to a few dozen adult females. The life cycles of these two species are offset by a month, with *A. jabaquara* undergoing dispersal and producing egg sacs earlier than *A. dubiosus* (Marques et al. 1998). This study took place just prior to *A. jabaquara*'s dispersal period when its nests and colonies were close to their maximum size (Table 3.1).

Table 3.1 Summary of nests and prey captured by five sympatric social spider (*Anelosimus*) in Serra do Japi, Brazil. Daily observation periods (day or night) ranged from 2 to 8 h. D = day, N = night.

		Social	Intermediate	Subsocial	Subsocial	Almost solitary
		<i>A. dubiosus</i>	<i>A. jabaquara</i>	<i>A. baeza</i>	<i>A. studiosus</i>	<i>A. nigrescens</i>
Number of nests		23	27	25	2	46
Range of longest axis of nest (cm)		6 – 120	11 - 80	2 - 30	7 – 23	2 - 13
Range of nest cross section (cm ²)		12 – 5655	78 – 2727	2 – 426	22 – 106	3 – 79
Total number of prey (range)	D	1 – 19	1 – 20	1 – 10	1 – 5	1 – 4
recorded per colony	N	1 – 9	1 – 7	1 – 6	0	1 – 2
Total number of prey recorded	D	108	174	53	6	59
Per species	N	30	53	12	0	4
Range of prey size (body length	D	2 – 30	2 – 28	1 – 12	2 – 13	1 – 4
mm) recorded per species	N	4 – 24	2 – 30	1 – 10	0	1 – 4

3.2.3 Prey capture by spider colonies

I surveyed spider nests every 1 – 1.5 h during the daytime (08:00 and 18:30) from November 17 to December 02, 2005. Additionally, I surveyed a subset of the colonies during the night between 19:30 and 24:30 (Table 3.1). I performed night surveys under red light by placing a red filter over the flashlights to avoid disturbance and behavioral interference to the spiders and to prevent attracting insects to the nests. Sampling periods ranged from 2 to 8 h starting at different times each day and night. During each survey, I examined each nest for new insect prey naturally caught in the web and/or being consumed by the spiders. Insects were classified to order and whenever possible to family. Insect body length was measured to the nearest mm from the most anterior side of the head to the tip of the abdomen. Visually sampled specimens were assessed by eye to the nearest 5 mm. For consistency, all surveys were done by the same two observers.

3.2.4 Insect body size sampled from the environment

Concurrently with surveys of prey captured by the colonies I sampled flying and vegetation-dwelling insects that could potentially form part of the spider diets (1 mm in length or longer). I used three collecting techniques: no-kill malaise traps, knock-down sticky traps, and visual searching. Six no-kill malaise traps (1.2 m height, 1.2 m base) made of fine-mesh grey tulle and a superior collection bottle were set up at approximately 5 – 10 m away from existing spider colonies and at a minimum distance of 10 m from one another. A similar number of knock-down sticky traps (a double-sided sticky surface of 210 x 297 mm per side placed over two inferior sloping ramps that converged into a jar with alcohol) were set up equidistantly along each of the transects.

Specimens caught in the malaise and sticky traps were removed at the end of each observation period after 2 – 8 continuous hours of sampling (day 2 – 8 h, night 3 – 5 h) starting at different times each time. Each site was sampled at least three times in the day and once at night. All insects captured were taken to the laboratory for their identification and measurement. Visual searching was carried out at least three times during the day, and once or twice during night hours. It involved actively searching for five consecutive minutes insects and other arthropods flying or sitting on or under the surrounding vegetation at randomly selected points near the spider colonies. For all three collecting techniques, sampling bouts of identical

effort and procedure were used at all sites by the same observer. Insects were classified and measured as done above with the prey caught by the colonies.

3.2.5 Nest and colony size

Since nest size is correlated with the number of individuals present in a colony in all *Anelosimus* species studied (appendices in Powers and Avilés 2007, Purcell and Avilés 2007, Avilés et al. 2007), I used nest size (cross section of the nest at the widest part of the basket, as in Purcell and Avilés, 2007) as a surrogate for colony size. The length of the longest axis of *Anelosimus* nests ranged from 2 to 120 cm (surface area: 2 to 5655 cm²; Table 3.1).

3.2.6 Data analysis

I conducted a preliminary test of the effect of site (Paraiso, Bauru, Bica), time period (day or night), and sampling technique (colony, malaise, sticky, visual) on insect body length (natural log-transformed mm) using a mixed model ANOVA where colony/trap ID was treated as a random factor nested within site and technique. I found no effect of site ($F_{2,176} = 1.20$, $P = 0.3$) or site-technique interaction ($F_{2,3237} = 1.28$, $P = 0.3$) on insect body length, but significant effects of time period ($F_{1,3237} = 1.28$, $P < 0.0001$) and technique-time period interaction ($F_{3,3237} = 5.7$, $P = 0.0007$). I further found that differences in the size of the insects sampled during the day and night held for the sampling techniques (primarily for visual sampling), but not for the spider colonies (independent contrasts: colony day versus night $F_{1,3237} = 2.0$, $P = 0.2$). For comparisons of insect body length captured by the different spider species I thus combined day and night samples from all localities. Whenever sampling technique data were included in the analyses (i.e. selectivity and niche overlap analyses) I ran separate tests for day and night periods while combining samples from all localities. Although I found a significant effect of sampling technique ($F_{3,176} = 7.5$, $P < 0.0001$), I combined data from all techniques in analyses requiring an estimate of the entire range of insect body sizes available to the spiders.

I used a one-way analysis of variance, followed by Tukey-Kramer HSD tests (overall $\alpha = 0.05$), to compare the size of the nests (natural log-transformed cross section of the nest, in cm²) and the body sizes of the insects (natural log-transformed mean insect body length in mm) captured by the spider colonies. For the insect tests, I used as the response variable the average body size of insects captured per colony for the combined day and night samples, weighted by the number of insects entering in each estimate (Table 3.1). To assess the effect of colony size

on the average body size of the insects captured by the colonies, I first performed a linear regression for all species combined and then an analysis of covariance with species, colony size, and their interaction in the model. As a significant interaction between species and colony size was found, I finally performed separate regression analyses for each species.

To compare resource utilization in relation to resource availability for each of the species I calculated Jacobs' selectivity index D (Jacobs 1974), which standardizes the relationship between the proportion that each insect body size class (insect body size categories in mm) makes up of a species' diet and the relative abundance of that insect body size class in the combined environmental samples. The index ranges from -1 to +1. A positive value indicates that a given prey size is taken selectively whereas a negative value indicates that a prey size is avoided.

I calculated prey size overlap between species pairs using the Pianka (Pianka 1973) and the Czechanowski (Feinsinger et al. 1981) indices with values ranging from 0 (no overlap) to 1 (complete overlap). For this purpose I divided the insect body length data into 15 size classes to generate a data matrix of the number of prey items in each size class (in the columns) captured by each species (in the rows) as well as by the combination of sampling techniques. To assess whether the observed overlap values reflected a resource utilization pattern more over-dispersed than expected by chance I compared the observed data matrix with "pseudo-communities" generated by Monte Carlo simulations. I used primarily the RA2 randomization algorithm (Lawlor 1980), which relaxes the niche breadth for each species, but retains the zero structure of the matrix under the assumption that even in the absence of species interactions certain prey size classes may be unavailable for some species in the system. For the day data only, I also used RA4 (Lawlor 1980), a highly conservative algorithm that retains both niche breadth and zero structure. Although RA4 is not recommended for general use because of its proneness to type II error (failing to reject a null hypothesis that is false), patterns that are significant with this algorithm are expected to be "quite strong" (Winemiller and Pianka 1990, Gotelli and Entsminger 2009). In producing the null pseudo-communities both algorithms were run under the assumption that different insect body size categories were available to the spiders proportional to their frequency of occurrence in the environment, as assessed with the combination of sampling techniques. I performed 10000 Monte Carlo simulations of niche overlap for each species pair. Observed overlap values were then compared to these simulated null values.

All statistical tests were performed using the statistical software JMP IN (Windows NT Version 5.1). Monte Carlo simulations and overlap tests were conducted using the software EcoSim 7.72 (Gotelli and Entsminger 2009).

3.3 Results

There were significant differences in the size of the nests of the four *Anelosimus* species (mean area of the cross section of the nest \pm 95% CI in cm², back-transformed values: *A. dubiosus* 812.4 \pm 1.5, *A. jabaquara* 735.1 \pm 1.3, *A. baeza* 54.6 \pm 1.6, *A. nigrescens* 24.5 \pm 1.6; $F_{3,148} = 65.2$, $P < 0.0001$), with the two most social species having significantly larger nests than the two least social ones (Figure 3.1). Nest sizes of the social *A. dubiosus* and the intermediate social-subsocial *A. jabaquara*, or those of the subsocial *A. baeza* and the almost solitary *A. nigrescens*, however, were not significantly different from one another (Tukey-Kramer tests; Figure 3.1). Nonetheless, the four spider species differed in the insect body size they captured (mean insect body length \pm 95% CI in mm, back-transformed values: *A. dubiosus* 10.0 \pm 1.1, *A. jabaquara* 8.2 \pm 1.1, *A. baeza* 4.1 \pm 1.1, *A. nigrescens* 2.1 \pm 1.2; $F_{3,148} = 117.9$, $P < 0.0001$; Figure 3.1). The average body size of the insects caught increased with level of sociality, with all pairwise comparisons being significantly different from one another (Tukey-Kramer tests; Figure 3.1). The body size range of the prey captured by colonies of the four species is given in Table 3.1.

There was a positive relation between insect prey and nest size across all four species ($F_{1,28} = 79$, $P < 0.0001$; Figure 3.2), with no effect of time period or nest size-time period interaction on this pattern ($F_{1,28} = 0.05$, $P = 0.8$ and $F_{1,28} = 0.07$, $P = 0.8$, respectively). An ANCOVA revealed significant main effects of species groups ($F_{1,144} = 16.8$, $P < 0.0001$) and colony size ($F_{1,144} = 8.0$, $P = 0.005$). A significant interaction between species and colony size ($F_{3,144} = 2.8$, $P = 0.04$) indicated that the slopes of the relationship between prey body size and colony size differed among the species. Further regression analyses of individual species showed that the body size of the insect captured increased with nest size for *A. dubiosus* ($r^2 = 0.27$, $t = 3.2$, $P = 0.003$; Figure 3.3) and *A. baeza* ($r^2 = 0.25$, $t = 3.0$, $P = 0.005$; Figure 3.3), but not for *A. jabaquara* ($r^2 = 0.004$, $t = 0.4$, $P = 0.7$; Figure 3.3) or *A. nigrescens* ($r^2 = 0.0007$, $t = -0.2$, $P = 0.9$; Figure 3.3).

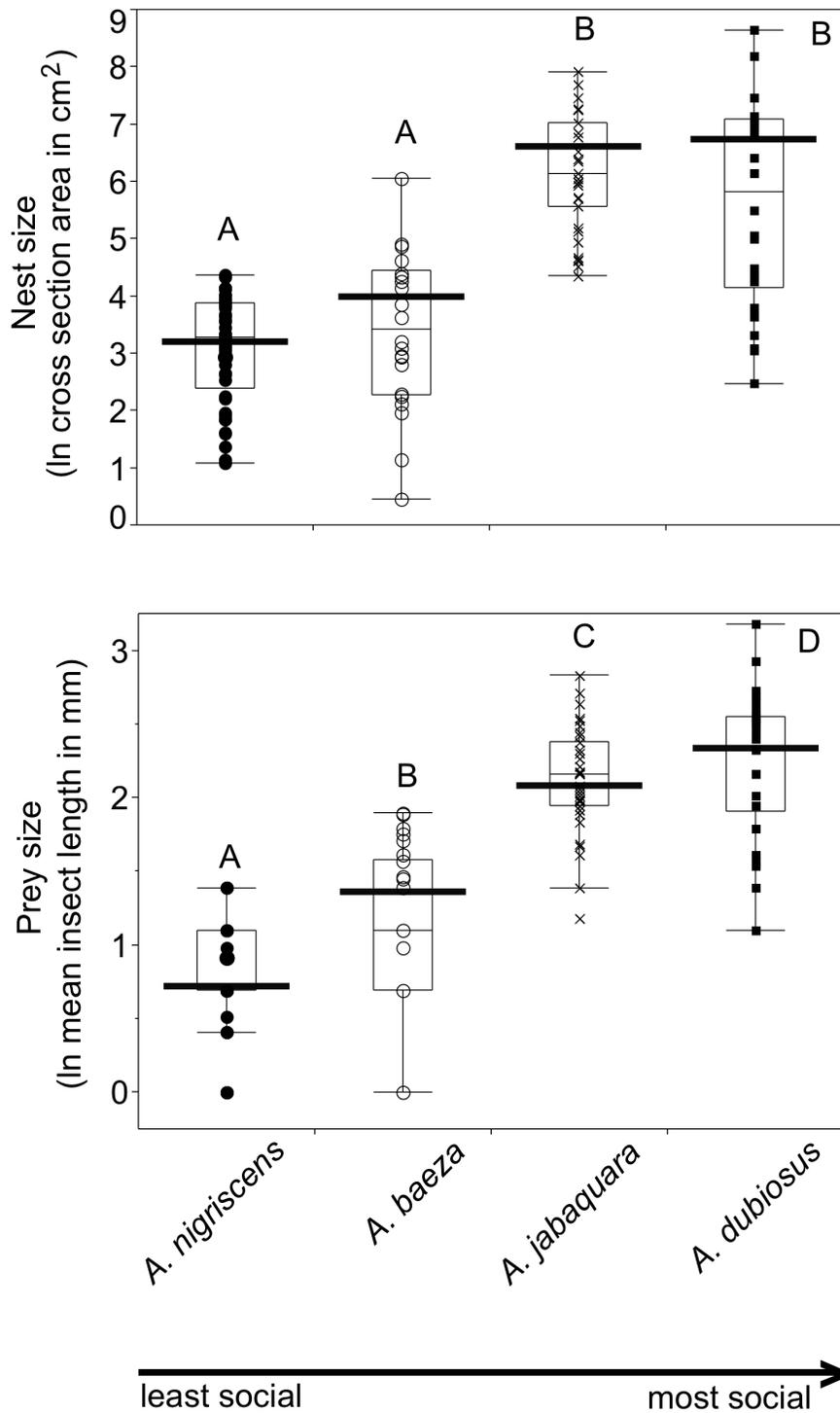


Figure 3.1 Quantile boxplots showing the distribution of nest sizes and the body size of insects captured by four sympatric *Anelosimus* spider species in Serra do Japi, Brazil (from least to most social: *A. nigriscens*, *A. baeza*, *A. jabaquara*, *A. dubiosus*). Diamonds represent the means and 95% confidence intervals. Non-significant differences are indicated by similar letters, as obtained by Tukey-Kramer HSD tests (overall alpha = 0.05).

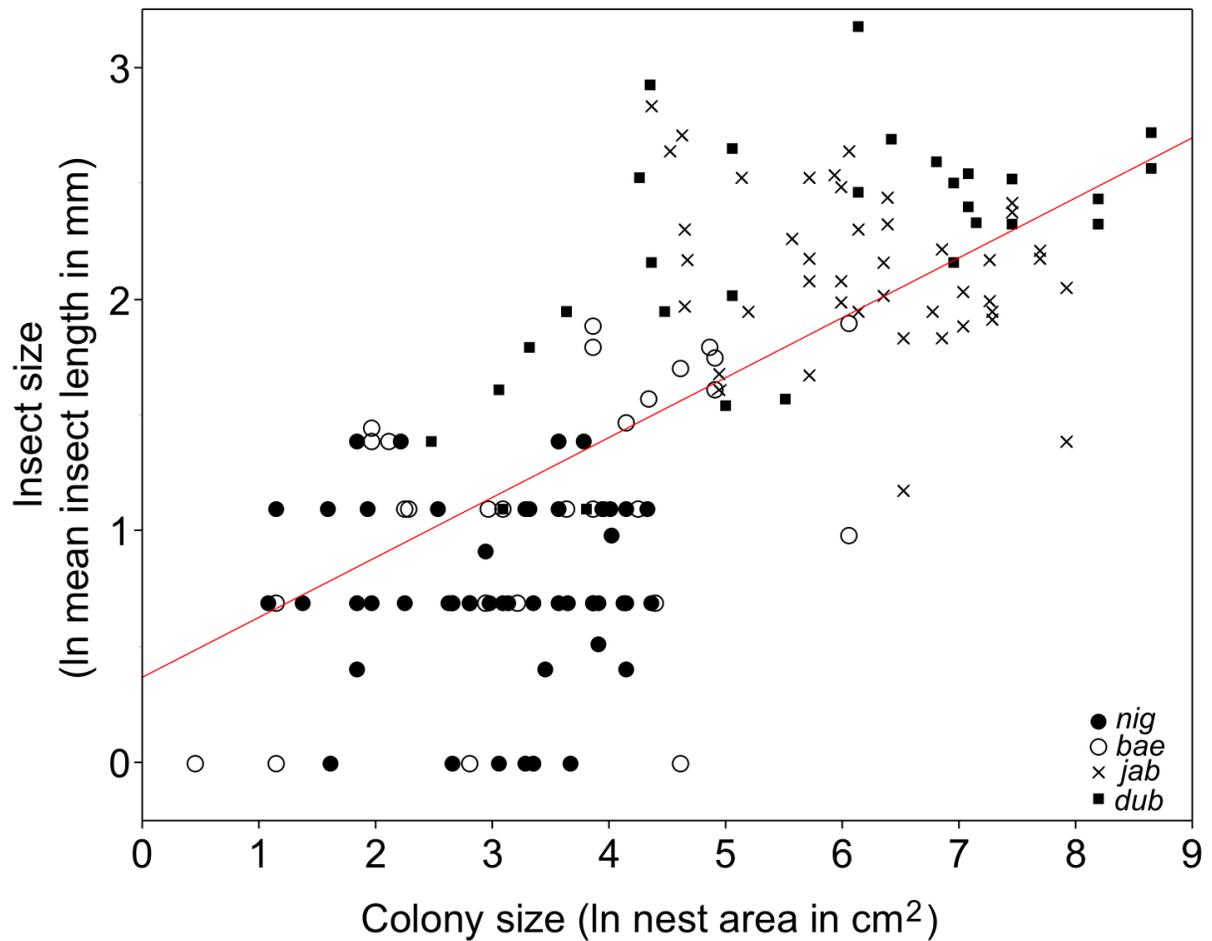


Figure 3.2 Regression of mean body size of the insects caught by a given colony (shown as the ln-transformed mean insect body length, in mm) on colony size (ln-transformed nest area in cm²) for the combined nests of four sympatric social and subsocial *Anelosimus* species (*dub* = *A. dubiosus*, *jab* = *A. jabaquara*, *bae* = *A. baeza*, *nig* = *A. nigrescens*) in Serra do Japi, Brazil (regression $r^2 = 0.54$, $t = 13.2$, $P < 0.0001$).

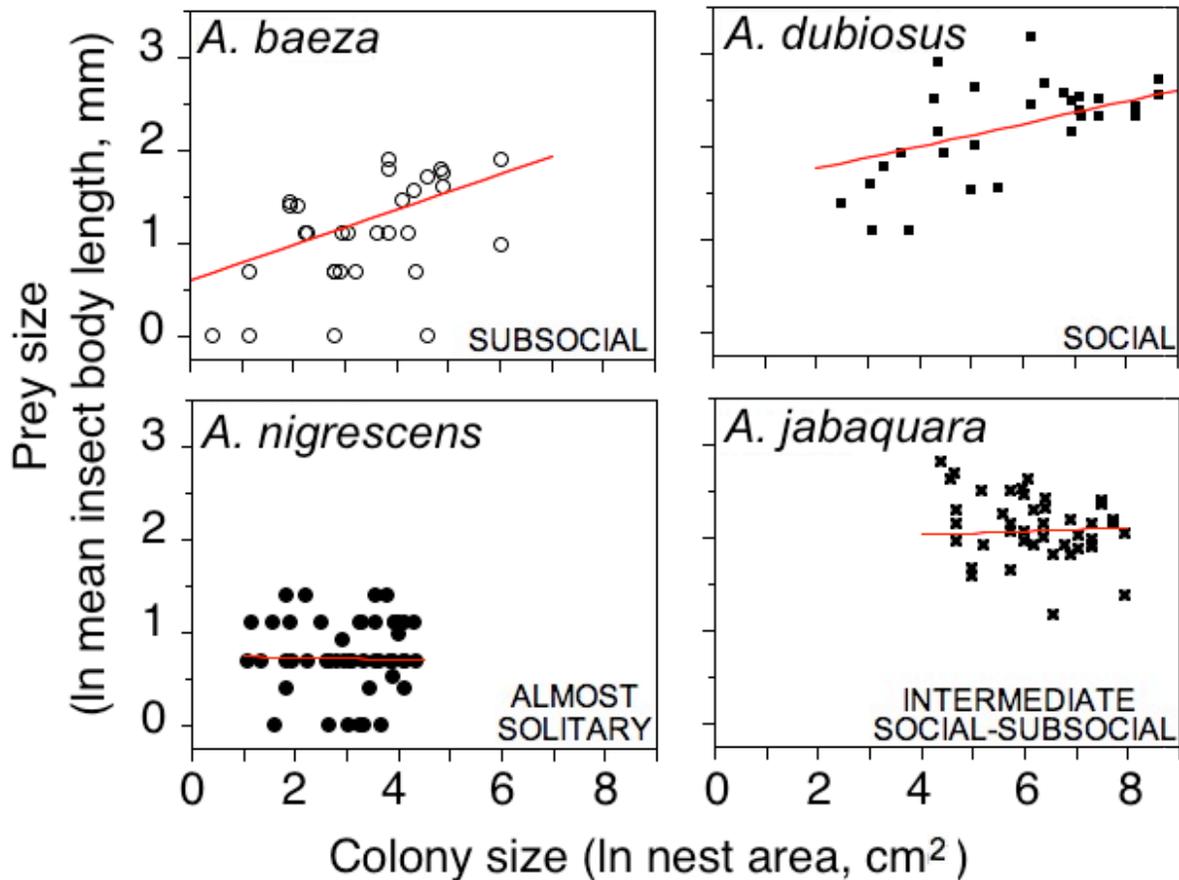


Figure 3.3 Regression of mean insect body size (given as the ln-transformed mean insect body length, in mm) on colony size (ln-transformed nest area in cm²) for nests of four sympatric species of *Anelosimus* in Serra do Japi, Brazil (regressions: *A. dubiosus* $r^2 = 0.27$, $t = 3.2$, $P = 0.003$; *A. jabaquara* $r^2 = 0.004$, $t = 0.4$, $P = 0.7$; *A. baeza* $r^2 = 0.25$, $t = 3.0$, $P = 0.005$; *A. nigrescens* $r^2 = 0.0007$, $t = -0.19$, $P = 0.9$).

Insects caught by the colonies ranged in body size from 1 to 30 mm (prey capture events $n = 400$ day, $n = 99$ night; Table 3.1). This range covered most of the spectrum of insect body sizes sampled from the environment, as only 4 out of 2931 insects obtained with the three sampling methods (day and night samples) were larger than 30 mm. The largest insect, seen by visual sampling, measured 43 mm. The range of insect body lengths obtained by the sampling techniques were 1 - 25, 1 - 26, and 1 - 43 mm for malaise traps ($n = 1695 + 126$), sticky traps ($n = 635$), and visual search ($n = 476$), respectively. Jacobs' indexes were positive for only small prey items for the two least social species (day samples only; Figure 3.4), indicating an apparent bias towards the capture of smaller prey relative to the insect body sizes available in

the environment. The two most social species had positive selectivity index values for larger prey sizes but not for smaller insect body sizes (day samples only; Figure 3.4) thus indicating segregated use of prey resources in relation to prey availability.

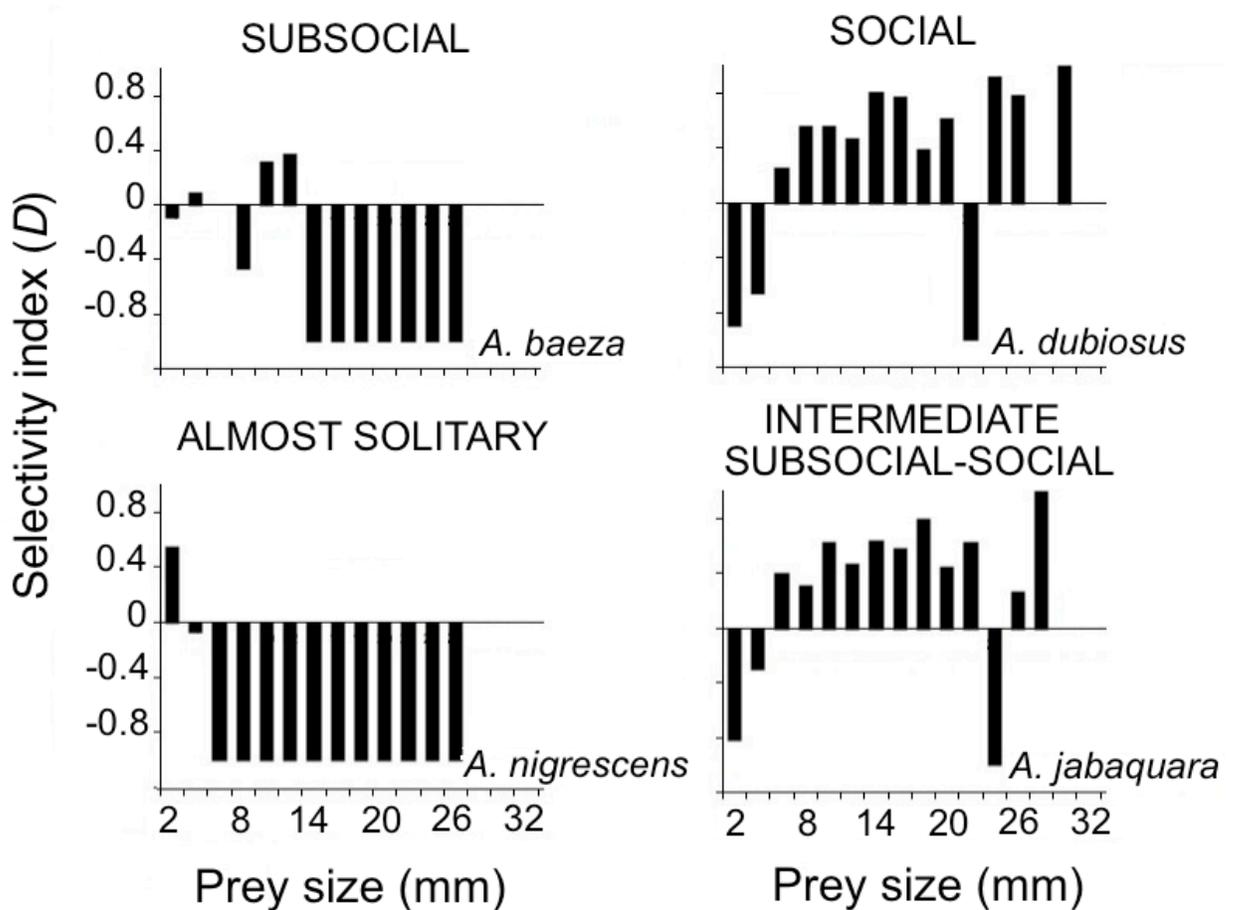


Figure 3.4 Comparison between the prey size utilized by four sympatric *Anelosimus* spider species and the distribution of insect body sizes sampled at Serra do Japi, Brazil using three sampling techniques (day samples only). Prey selectivity (D) is represented by Jacobs' index. Negative values indicate selectivity for the given prey size, and negative values indicate avoidance of a given prey size by the species.

Analysis of niche overlap with both the Pianka and Czechanowski indices and the RA2 algorithm showed overlap values significantly smaller than expected by chance in the range of prey sizes utilized by most species pairs, even for species contiguous in the sociality scale (Table 3.2, Figure 3.5). This general pattern held during the day and night, despite the smaller sample sizes of the latter. The only consistent exception was the *A. nigrescens* - *A. baeza* pair, for which overlap indices were non significantly different during both time periods. Comparable results were obtained with the conservative RA4 algorithm applied to day samples, with only two additional (and mixed) exceptions: *A. jabaquara* and *A. baeza* were not significantly different with the Pianka index and *A. dubiosus* and *A. jabaquara*, with the Czechanowski index. The distribution of prey sizes captured by the species was thus more overdispersed than expected by chance (overall RA2 for Pianka: day, observed = 0.13, expected = 0.46, $P_{\text{obs}} \leq P_{\text{sim}} < 0.0001$; night, observed = 0.18, expected = 0.45, $P_{\text{obs}} \leq P_{\text{sim}} < 0.0001$; for Czechanowski: day, observed = 0.14, expected = 0.33, $P_{\text{obs}} \leq P_{\text{sim}} < 0.0001$; night, observed = 0.18, expected = 0.34, $P_{\text{obs}} \leq P_{\text{sim}} < 0.0001$), consistent with a hypothesis of non-random patterns of resource use in this community.

3.4 Discussion

This study shows that interspecific differences in nest and colony size, for the most part, reflected differences in level of sociality in four sympatric spider species of the genus *Anelosimus*, with the two least social species having significantly smaller nests than the two most social ones (Figure 3.1). These differences, in turn, translated to differences in the size of the prey captured by the spiders. Interestingly, however, although the nests of the two least social and of the two most social species did not differ significantly from one another in size, the body size of the insects they captured did (Figure 3.1). Thus, the social *A. dubiosus* captured on average significantly larger insects than the intermediate social-subsocial *A. jabaquara* and the subsocial *A. baeza* captured on average significantly larger insects than the almost solitary *A. nigrescens* (Figure 3.1). Given that the two most social species are very similar in terms of nest structure and body size (Marques et al. 1998), and occupy the same microhabitat (Purcell et al. 2012), I propose that differences in the body size of insects captured may result from differences in the extent of cooperative prey capture in these two species, with *A. dubiosus*

Table 3.2 Values of Pianka (PK) and Czechanowski (CN) indices of overlap for the prey size used by four species of social spiders in Serra do Japi, Brazil. *P* represents the probability of observing, just by chance, the given niche overlap value or smaller using the randomization algorithm RA2. Above the diagonal values represent day patterns and below the diagonal, night patterns.

		<i>A. dubiosus</i>	<i>A. jabaquara</i>	<i>A. baeza</i>	<i>A. nigrescens</i>
<i>A. dubiosus</i>	PK	-----	0.0842, <i>P</i> < 0.0001	0.0550, <i>P</i> < 0.0001	0.0027, <i>P</i> = 0.0002
	CN		0.2666, <i>P</i> = 0.0001	0.0779, <i>P</i> = 0.0001	0.0026, <i>P</i> < 0.0001
<i>A. jabaquara</i>	PK	0.3616, <i>P</i> = 0.04		0.2443, <i>P</i> = 0.02	0.0219, <i>P</i> = 0.003
	CN	0.4760, <i>P</i> = 0.3	-----	0.2162, <i>P</i> = 0.02	0.0154, <i>P</i> = 0.005
<i>A. baeza</i>	PK	0.1131, <i>P</i> = 0.007	0.3645, <i>P</i> = 0.08		0.3933, <i>P</i> = 0.4
	CN	0.1128, <i>P</i> = 0.005	0.3131, <i>P</i> = 0.07	-----	0.2737, <i>P</i> = 0.4
<i>A. nigrescens</i>	PK	0.0021, <i>P</i> = 0.02	0.0287, <i>P</i> = 0.005	0.2253, <i>P</i> = 0.1	
	CN	0.0045, <i>P</i> = 0.02	0.0394, <i>P</i> = 0.01	0.1596, <i>P</i> = 0.07	-----

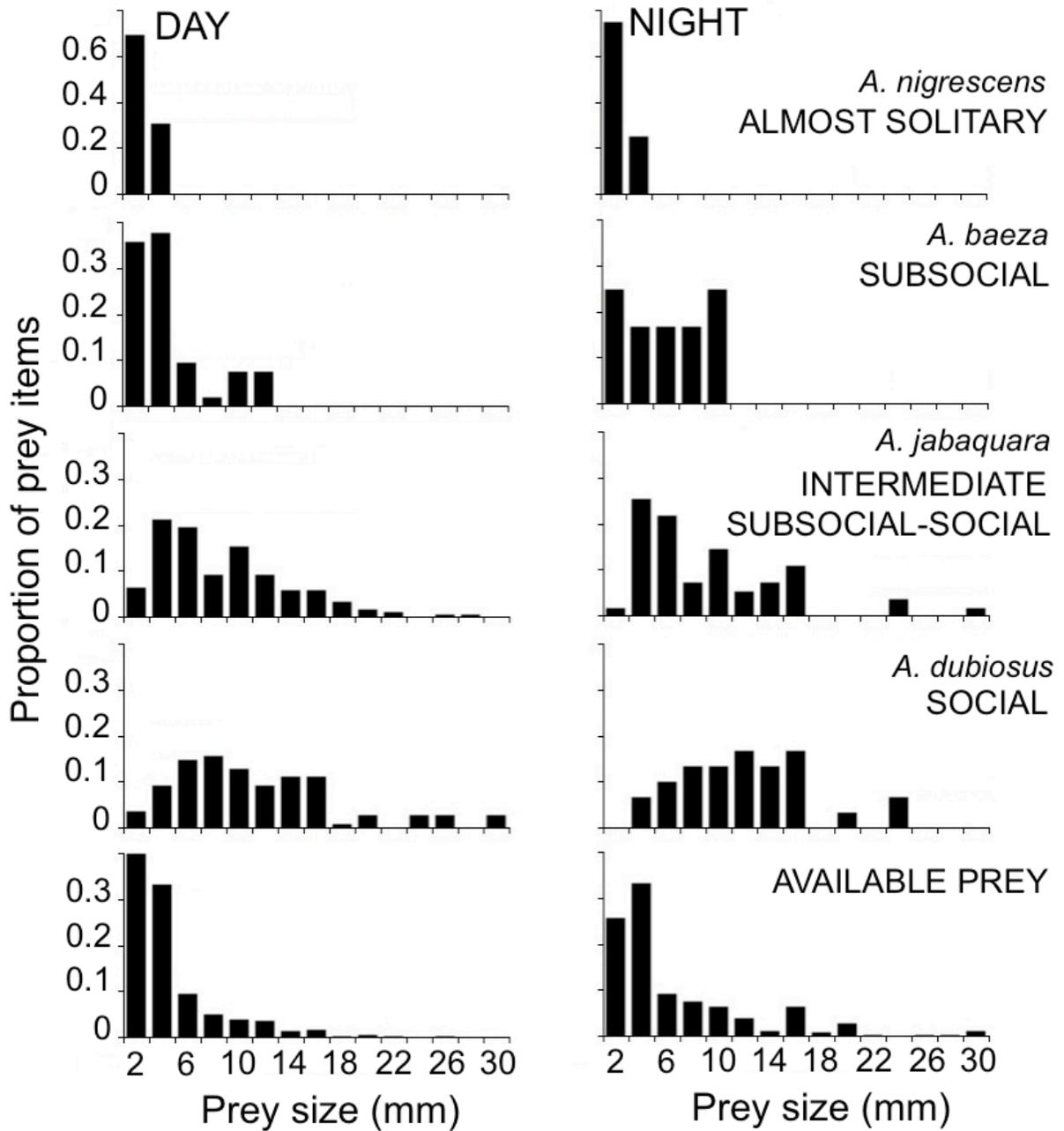


Figure 3.5 Resource utilization curves corresponding to day and night periods. Shown are the proportions of prey items of different size categories (in mm) consumed by four different sympatric species of *Anelosimus* spiders and the prey size sampled from the environment.

being more cooperative than *A. jabaquara*. This is suggested by the fact that the social *A. dubiosus* captured increasingly large insects as colony size increased, while the intermediate social-subsocial *A. jabaquara* did not (Figure 3.3). Such a pattern would arise if an increasing number of individuals participated in prey capture in larger *A. dubiosus*, but not in *A. jabaquara* colonies due to either differences in the density of individuals within nests and/or their degree of cooperativeness, hypotheses currently being investigated (G. Harwood and L. Avilés unpublished data). Earlier studies, in fact, suggest that *A. dubiosus* may be, in general, more cooperative than *A. jabaquara*. Marques et al. (1998), for instance, have shown that in *A. dubiosus*, young from different broods mix at a young age and appear to be fed by regurgitation by multiple females, whereas in *A. jabaquara* the brood of different females tend to remain in separate retreats until a relatively late instar. Along the same lines, compared to *A. jabaquara*, *A. dubiosus* is suggested to exhibit greater tolerance of conspecifics (Marques et al. 1998), a factor that is expected to be key in enabling higher levels of cooperation and more complex social behaviours in spiders, in general (Shear 1970, Kullmann 1972). Differences in the extent of cooperation may also underlie the different slopes for *A. baeza* and *A. nigrescens* (Figure 3.3), as nests of the latter species contained mostly single adult females, with or without a very young brood.

My findings also show that the four co-occurring species used resources differentially by capturing prey items towards the small or large end of the available range of insect body sizes as a function of their level of sociality (Figure 3.4). The small size of their nests and colonies may intuitively explain why large insects are not captured by the less social species. However, for more social species, given that their large colonies can capture both large and small prey, the apparent bias towards large prey deserves more attention. One possibility is that these large colonies ignore or reject potentially unprofitable small prey, concentrating instead on prey that can better fulfill the nutritional requirements of the colony. Increased sociality may thus confine the species to the large prey niche, leaving less social species with small colonies alone in exploiting small prey. Small insects may also be harder to detect in large nests (i.e. larger prey is more visible than small prey in large webs), thus having a greater opportunity to escape. Finally, as observed in other *Anelosimus* communities (M. Salomon, unpublished data), particular species may have greater density of silk in their webs, thus being better able to retain small prey. I note that these various possibilities are not necessarily mutually exclusive. On the other hand, I did not detect any differences in the body size of the insects available in the

different microhabitats occupied by the colonies, ruling out environmental differences as an explanation for the observed patterns.

An analysis of the overall pattern of prey usage by *Anelosimus* species in this spider community shows that it is more over-dispersed than expected by chance. Non-random prey size segregation was detected overall and between most species pairs when observed patterns were tested against a null model that randomizes niche breadth, but conserves prey size classes (the RA2 algorithm; Lawlor 1980) and, for day-time samples, a more conservative model that retains both niche breadth and prey size classes utilized (the RA4 algorithm; Lawlor 1980) (Table 3.2). Such non-random patterns of prey utilization as a function of level of sociality raise interesting questions regarding the mechanisms responsible for them. While the relatively high density of nests of the four most common *Anelosimus* species at Serra de Japi— an average of 0.1 nests per meter square in some areas (J Purcell, unpublished data), makes species interactions a plausible mechanism influencing at least some aspects of the space, time or dietary resource use by this community, it is unclear whether the observed patterns might reflect processes directly aimed at reducing dietary overlap or may be an indirect product of community assembly in response to factors other than diet.

Whether insects could plausibly be a limiting factor for *Anelosimus* spider species in Sierra do Japi has yet to be determined. There is evidence, however, that prey availability and the body size distribution of insects in the environment influence the range of colony sizes that can be sustained in particular habitats (Guevara and Avilés 2007, Powers and Avilés 2007). Thus, *Anelosimus* species with large colonies are only sustainable in areas such as the lowland rainforest where large insects are abundant (Guevara and Avilés 2007, Powers and Avilés 2007, Yip et al. 2008). A paucity of large insects at Serra do Japi, where only 0.54% of the insects were larger than 25 mm (this study; compared to 8.5% of the insects in the lowland rainforest, data from Guevara and Avilés 2007), may limit not only the size, but also the number of large colonies that can be sustained in this habitat. It is more difficult to envision how small insects, which are much more abundant, could be a limiting factor for small colonies. However, considering that small colonies occur at greater densities and tend to be clustered (following dispersal, all five species produce small daughter colonies in the vicinity of their source colony) (e.g. Vollrath 1982, Avilés and Gelsey 1998, Powers and Avilés 2003), the occurrence of interference competition for available insects among nearby nests is plausible. Evidence for food competition in spiders is mixed (Wise 1984, 1993, Horton and Wise 1983, Riechert and

Cady 1983, Fasola 1999), but has been demonstrated experimentally in some cases (e.g. Brown 1981, Spiller 1984, Herberstein 1998).

Alternatively, the observed dietary segregation as a function of level of sociality may be an indirect product of community assemblage in response to factors other than food resources. For example, patterns of microhabitat use by social and subsocial *Anelosimus* species at Serra do Japi (Purcell et al. 2012) suggest that substrate requirements, dictated by species differences in nest sizes, as well as competition for nesting sites within microhabitats, may influence the numbers and types of species present in this habitat, indirectly leading to the observed diet segregation patterns.

I should note that the diet-segregation and substrate-requirements/competition hypotheses need not be mutually exclusive. It is possible, for instance, that once the species with greater and lower levels of sociality came to primarily occupy the forest interior and the forest edge, respectively (Purcell et al. 2012), additional processes may have acted to further separate the species along spatial, temporal, or dietary axes within each of these microhabitats. Further studies, however, are needed to establish the likelihood that species interactions may be or could have been an organizing factor in this community and the extent to which such interactions may have involved competition for nesting sites vs. available prey. A test of the hypothesis that prey is a limiting factor for *Anelosimus* species in this community, for instance, could involve artificially increasing the density of nests in some areas and decreasing it in others to determine whether prey intake, and thus growth and survival of individuals and colonies in manipulated vs. control areas, is affected in the expected manner. A test of the competition-for-nesting-sites hypothesis, on the other hand, could involve selectively removing the nests of one of the species in some areas to determine if those substrate locations are subsequently colonized by colonies of the remaining species.

Evidence for the role of sociality in the prey size use of social organisms is robust (Nudds 1978, Lamprecht 1981, Nentwig 1985, Hector 1986, Gittleman 1989, Rypstra 1990, Creel and Creel 1995, Baird and Dill 1996, Yip et al. 2007). In particular, the ability of larger hunting groups with increased cooperation to utilize larger food sizes than smaller groups or solitary individuals has been demonstrated in many social taxa. In spotted hyenas (*Crocuta crocuta*), for example, although a single individual can capture prey up to three times its body weight, group hunting is required to capture larger prey such as zebra or buffalo (Cooper 1990, Holekamp et al. 1997, Trinkel 2010). Similarly, in pale chanting goshawk (*Melierax canorus*)

social hunts allow capture of large prey (rodents) whereas only smaller prey (lizards and birds) can be subdued during solitary hunts (Malan 1998).

The potential role of sociality as an organizing factor in communities of co-occurring organisms, on the other hand, has received little attention. Nonetheless, there is evidence that in sympatry group size differences may lead to differential exploitation of resources in Mediterranean scavenger ant communities, where species that recruit large foraging groups are more successful at exploiting larger prey than species that recruit small groups (Cerdá et al. 1998). In addition, an effect of group-level attributes on species competition has been suggested in acacia ant communities where colony size increases a species position in the competitive hierarchy, with competitive interactions taking the form of wars of attrition with ~1:1 mortality (Palmer 2003, 2004). While these studies did not analyze systematically the direct role of sociality in the context of prey size use and niche segregation, they point to the potential importance of sociality as an organizing factor in the assemblage of these communities.

Chapter 4: Prey capture efficiency in two sympatric social spiders in Ecuador: influence of body size and level of cooperation

4.1 Introduction

Exploring how phenotypic traits shape the ecology of organisms is a key approach to community ecology (e.g. McGill et al. 2006, Petchey and Gaston 2006, Webb et al. 2010). In particular, understanding how morphological, physiological, and behavioral traits influence animal performance in ecologically relevant tasks, and thus determine a species' abilities to exploit resources, is paramount to assessing what structures and maintains animal communities (e.g. Wainwright 1996, Webb et al. 2010, Irschick et al. 2007). Because morphological and physiological traits are specially notorious for directly influencing many aspects of performance, a vast number of studies have focused in demonstrating their importance in the location, capture, and handling of different resources (Peters 1983, Miles and Ricklets 1984, Douglas and Matthews 1992, Schluter 1993, Grant and Grant 2006, Herrel et al. 2006, Owen-Smith and Mills, 2008). In African seed-eating birds, for example, the food handling performance of individuals is associated with beak size, with large-beaked individuals being able to crush harder seeds than individuals with smaller beaks (Smith 1993). In general, animals with large body sizes can handle larger food items (Enders 1975, Wilson 1975), whereas smaller animals accelerate faster and enjoy greater maneuverability compared to their larger relatives (Taylor et al. 1972, Dial et al. 2008).

Behavioral traits, which are key for animals that live and forage in groups, however, have been generally less explored in the context of animal performance (Dial et al. 2008). In addition to individual-level traits, in group-living animals relevant traits emerging from their social behavior—such as group size and level of cooperation—may also be key influences on performance, thus further shaping resource use by a species. Overall foraging efficiency, for instance, increases with foraging group size in several social taxa, including terrestrial and

marine carnivores (Caraco and Wolf 1975, Nudds 1978, Pulliam and Caraco 1984, Gittleman 1989, Baird and Dill 1996), birds (Rand 1954, Cody 1971, Krebs et al. 1972), fish (Pitcher et al. 1982, Pitcher and Magurran 1983), and arthropods (Cerdá et al. 1998, Buskirk 1982). Through increased cooperation, larger groups are able to catch larger prey than solitary individuals or groups with less cooperation (Rand 1954, Kruuk 1966, Kleiman 1966, Nudds 1978, Nentwig 1985, Rypstra 1990, Yip et al. 2007). The obvious relationship between individual- and group-level attributes in jointly influencing a species' performance (i.e. prey capture efficiency), and thus shaping resource use, however, received little attention in studies of social animals. Finally, the majority of foraging performance studies have focused exclusively on single species, most of which pertain to vertebrate groups (Irschick et al. 2007). This severe lack of multi-species data, particularly that dealing with invertebrates (Irschick et al. 2007), hinders our ability to understand emerging patterns of resource use at the community level.

In the social spider genus *Anelosimus* Simon (Araneae: Theridiidae) species capture prey sizes in accordance to their social attributes. For instance, species that form bigger colonies and build larger webs are able to capture larger prey (Guevara and Avilés 2007, Powers and Avilés 2007, Yip et al. 2007, Guevara et al. 2011). This is because larger groups allow for more individuals to participate in prey capture and build larger webs for the interception of larger prey (Nentwig 1985, Rypstra 1990, Guevara and Avilés 2007, Lubin and Bilde 2007). In this study, I explored the roles of individual- and group-level characteristics by simultaneously studying two sympatric and closely related social spiders —*Anelosimus eximius* Keyserling and *Anelosimus domingo* Levi (Figure 4.1). The species seem to have very similar social systems, prey capture webs, and behaviors (Rypstra and Tirey 1989, Avilés 1997, Agnarsson 2006), but exhibit a dramatic difference in size, with *A. eximius* being close to five times larger in body weight than *A. domingo* (Powers and Avilés 2007).

The dramatic difference in body size of these sympatric species opens up some intriguing questions and possibilities: (1) Is the insect body size caught by the two species directly proportional to their own body size or can the smaller spider somehow compensate for its smaller body size by increasing individual or group level performance? If the latter, I then ask what mechanisms may be responsible for such increased performance, including having a greater number of individuals cooperating in prey capture and/or by having faster reaction times. (2) Since the large species forms both large and small colonies, to the extent that the body size of the insects captured may be a function of colony size (e.g. Yip et al. 2007), the large species can potentially utilize insects that overlap in size with those utilized by the small

species. In such a case, the small species would have its food niche (i.e. small insects) completely included within the niche of the large species (i.e. small to large insects). This possibility is interesting on two accounts: First, although included niche patterns have been described for some taxa (e.g. Miller 1967, 1968, Cameron 1971, Colwell and Fuentes 1975), only a few studies have quantitatively demonstrated them in natural populations (Chase and Belovsky 1994, Chase 1996, Beckerman

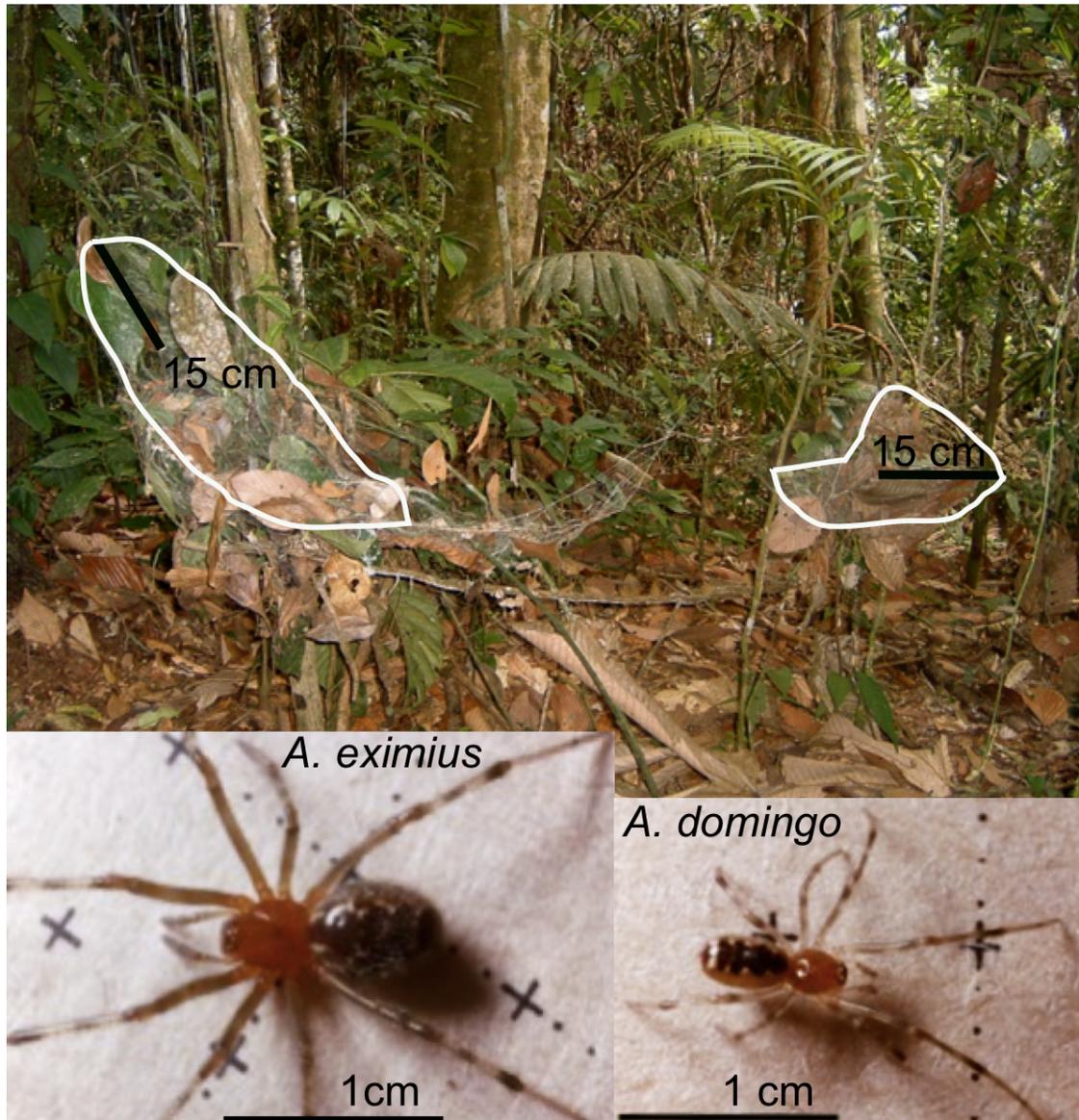


Figure 4.1 Adult females and basket-shaped nests of the two sympatric species of social spiders in eastern Ecuador, *A. eximius* and *A. domingo*. White lines delineate the cross-section area of the baskets.

2000). Thus, their prevalence and the conditions under which they may occur in nature remain largely unexplored. Second, were the two species to be in competition with one another, a prediction of included niche theory is that the small species should be more efficient at utilizing resources in the shared range (Miller 1967, Schoener 1974). This is because while the species with the broader food niche can exploit an exclusive prey size range the species with the included niche must always share its resources and thus it may be more vulnerable to exclusion.

Here I first studied the natural prey capture patterns of the small and large sympatric social *Anelosimus* spider species to determine whether and to what extent the niche of the small species is included within the niche of large one. I then carried out performance experiments to (1) examine whether the small spider is able to compensate to some extent for its small size through individual- or emerging group-level traits, and (2) test the prediction of included niche theory that the small species should be more efficient at utilizing the resources in the shared range (small prey).

4.2 Materials and methods

4.2.1 Study site

I studied the sympatric social species *A. eximius* and *A. domingo* at a lowland tropical rainforest part of the Estación Biológica Jatun Sacha (1°42'N, 77°36'W; elevation: 385 – 410 m; annual mean temperature 25°C) in the Amazon basin in eastern Ecuador. The reserve has an area of ~2500 ha of which 70% consists of primary rainforest, with the remainder being regenerated secondary rainforest. At the site, I found nests of *A. eximius* and *A. domingo* along trails in the forest understory and near the station facilities. I conducted prey capture observations during June (six observation days) and August (seven observation days) 2005 and in July 2006 (four observation days). I carried out foraging efficiency experiments during November and December 2007.

4.2.2 Species descriptions

Anelosimus eximius and *A. domingo* are both Neotropical permanent social species usually found in lowland rainforests, up to an elevation of 1100 and 1000 m respectively (Levi 1963, review in Avilés 1997, Agnarsson 2006, Avilés et al. 2007). Nests of both species may contain from a single solitary female and her brood to approximately 2000 individuals for *A. domingo*,

and up to tens of thousands of individuals for *A. eximius*, which is the species with largest colonies of any social spider species (Rypstra and Tirey 1989, Avilés 1997, Avilés et al. 2001). In Jatun Sacha, *A. eximius* nests can be found either in the forest understory or along edges (Purcell and Avilés 2007) whereas *A. domingo* nests are restricted to the forest understory (Avilés et al. 2001, Agnarsson 2006). In this area of co-occurrence, *A. eximius* nests are typically much smaller than nests found at the forest/river edges or tree tops (Purcell and Avilés 2007), thus often being similar in size as *A. domingo* nests. *A. domingo* nests, however, contain a greater density of individuals of all age classes (L. Avilés, unpublished data). Nests of both species are also similarly shaped as a basket interwoven with dead leaves and twigs, and projecting long aerial threads into the superior vegetation (Figure 4.1) (Brach 1975, Christenson 1984, Avilés et al. 2001, Agnarsson 2006, Purcell and Avilés 2007).

These species, although similar in appearance, differ in body size. In Ecuador populations, the body size of *A. eximius* adult females can range from 4.4 to 5.0 mm in length (median = 4.7 mm, $n = 5$), whereas that of *A. domingo* females can range from 3.0 to 3.9 mm in length (median = 3.2 mm, $n = 5$) (Avilés et al. 2001). Average weights for adult females of each species are 11.82 ± 0.44 and 2.55 ± 0.76 wet mg, respectively (LSM \pm SE, for $n = 48$ and 19 *A. eximius* and *A. domingo* adult females from one and four colonies, respectively; K.S. Powers and L. Avilés, unpublished data).

4.2.3 Nest and colony size estimations

For both of these species, nest size is correlated with the number of spiders present in a colony (appendices in Powers and Avilés 2007, Purcell and Avilés 2007), with *A. domingo*, the smaller species, having a greater density of individuals within the nests (L. Avilés, unpublished data). I thus used the species-specific equations given in Powers and Avilés (2007, online supplementary materials) to infer the total number of individuals contained in the colonies of the two species from the size of their nests (area of the cross section of the nest at the widest part of the basket, as shown in Purcell and Avilés 2007; Figure 4.1). The length of the longest axis of *A. domingo* nests included in the natural prey capture surveys ranged from 6 to 65 cm (surface area: 14 to 2553 cm²), whereas those of *A. eximius* ranged from 4.5 to 90 cm (surface area: 11 to 5655 cm²). For the foraging experiments, the length of the longest axis ranged from 13 to 82 cm (surface area: 102 to 3542 cm²), for *A. domingo*, and from 16 to 103 cm (surface area: 107 to 8090 cm²), for *A. eximius*.

4.2.4 Surveys of natural prey capture by spider colonies

For the natural prey capture observations I surveyed all 22 *A. domingo* and 25 *A. eximius* nests every 1.5 - 2 h between 07:30 and 17:30. To account for possible differences in available prey over the course of a day, I started the surveys at different times each day, reversing the order in which the nests were visited every other day. During each survey, I examined the nests for new insect prey naturally caught in the web and/or being consumed by the spiders. To avoid counting the same prey twice, I carefully noted the prey already present in the nests, and in some occasions removed the prey with long forceps taking care in minimizing web damage. In cases where two prey items were naturally caught in the same nests at the same time, I treated them as independent samples. This was done because the goal of the prey capture observations was to estimate the body size of insects utilized by each species rather than, for example, the number of spiders participating in prey capture which I measured during the prey capture performance experiments (see below). In the case of the latter, since the simultaneous presence of two prey items would have been problematic I ensured that foraging trials involved only one insect each time.

I classified all insect prey to order and measured body length (mm) from the most anterior side of the head to the tip of the abdomen. The number of prey captured daily by the individual colonies ranged from 0 to 8 for *A. domingo* and 0 to 12 for *A. eximius*. Overall, in over 102 hours of observation in 2005 and 26 hours in 2006 I recorded 160 prey capture events for 25 *A. eximius* colonies and 130 for 22 *A. domingo* ones, reflecting the natural prey capture rates of the observed colonies of both species.

4.2.5 Experiments of prey capture performance

I conducted a foraging experiment to measure the relative efficiency with which each species captures the shared and exclusive prey size range and the behaviors that may be responsible for any differences observed. I used naturally occurring nests of both species to conduct feeding trials where colonies were supplied each time with insect prey of different body sizes. For each species, I selected three experimental nests roughly belonging to each of three nest size categories (length of the longest axis across the nest: small: < 20 cm; medium: 20 – 40 cm; large: > 40 cm) for a total of nine nests per species. To test for differences in capture efficiency of the shared prey size range, I used insects of 4, 8, 16, 25, and 36 mm, in line with the previously determined resource utilization curves of these two species (see Results section). I used two additional

insect body sizes—49 and 64 mm—consumed solely by the bigger species, *A. eximius*, to measure efficiency in the exclusive size range. I used insects of the six insect orders—Coleoptera, Hymenoptera, Diptera, Homoptera, Lepidoptera, Orthoptera—most commonly utilized by these spiders (Guevara and Avilés 2008).

During each feeding trial, two different observers supplied more or less simultaneously an insect randomly chosen from the seven size classes to nests of similar size of the two species. This was done for all nests and insect body sizes in random order and by the same two observers. Each time, I chose the taxonomic order for a given insect body size randomly from the six insect categories. Whenever not all insect categories were available for a particular size class (i.e. Hymenoptera for the 49 and 64 mm size class), I chose randomly the insect order from the remaining categories. Each time, I either handled the insect with forceps or threw it into the nest directly from the vial. I supplied each nest with a total of 12 prey items corresponding to each of the size classes 4 and 8 mm, 6 prey items for each of 16, 25 and 36 mm size classes, and 3 prey items for size classes 49 and 64 mm (Table 4.1). I did not supply small colonies of either species with large prey (49 and 64 mm) to avoid damaging their webs. Thus, for the entire experiment, I had a total of 828 feeding trials (Table 4.1).

I recorded the time the prey hit the web, time of approach/attack by the spiders, time until the prey was subdued and killed (if the capture was successful), the number and age of the spiders participating in the capture event, and the proportion of prey successfully caught by the colonies (prey capture success). Since insects were artificially introduced in the webs, I did not assess the probability that an insect of a given body size was successfully intercepted by the webs.

Table 4.1 Experimental design for feeding trials corresponding to five different size classes of insects and three colony sizes. This experiment was applied simultaneously to nests of two sympatric social spiders that had close to a 5-fold difference in body size (biomass).

	Insect body length (mm)							
	4	8	16	25	36	49	64	
Small nests $n = 3$	12	12	6	6	6	0	0	$N_{insects} = 42/\text{nest}$
Medium nests $n = 3$	12	12	6	6	6	3	3	$N_{insects} = 48/\text{nest}$
Large nests $n = 3$	12	12	6	6	6	3	3	$N_{insects} = 48/\text{nest}$

4.2.6 Data analysis

4.2.6.1 Surveys of natural prey capture by colonies

Differences in average insect body size caught by each species were tested using a two factor ANOVA where the response variable was the log10-transformed mean insect body length captured by each of the spider colonies weighted by the number of insects in each sample (the total number of insects for each colony), and the factors were “species”, log10-transformed “colony size”, and “species x colony size” interaction, with “colony size” being an estimate of the total number of spiders in a colony based on the size of its nest (see above).

4.2.6.2 Foraging performance trials

To test for differences between the species in degree of cooperation among colony members I fitted a factorial mixed-model ANOVA where the response variable was, for each colony and insect body size class, the median of the total number of spiders attacking the prey, weighted by the number of prey items in each estimate. The factors were “species”, square root-transformed surface area of the nest “nest size”, prey size “length”, and the interactions of the factors. For the analyses, prey size was treated as a continuous variable. Further, I tested for differences between species in the number of individuals from different age classes participating in prey capture events. For this, I fitted a nominal logistic model where the response variable was “age class” with associated frequencies for each colony and the factor was “species.”

I tested for differences in reaction time (from the moment the prey hit the web until attack begun) by fitting a factorial mixed-model ANOVA where the response variable was median reaction time (min) by spiders in each colony weighed by the number of prey capture events entering each estimate, and the factors were “species,” prey size “length” and species x length interaction. A similar model was used to test for species differences in median time to subdue the prey from the moment the prey hit the web until it was killed by the spiders.

I used nominal logistic regression to test for differences between species in the probability that insects of different body sizes were ignored (or not detected) by the spiders. The response variable was the prey categories “ignored/not ignored” and the factors were “species” and prey size “length” treated as a continuous factor. Since samples taken from the same colonies were not independent from one another, I included colony identity as a random

effect. A similar nominal logistic model was used to test for differences in prey capture success, defined as the proportion of insects introduced that were successfully captured by colonies of each species. The response variable was “prey capture success” (captured/not captured), and the factors were “species”, prey size “length”, square root-transformed-nest surface area “nest size”, and the interactions species x length and length x nest size. Again, colony identity was included in the model as a random effect.

All statistical tests were performed using the statistical software JMP (Windows NT Version 5.1).

4.3 Results

4.3.1 Natural prey capture surveys

There were no differences in the average size of the *A. domingo* and *A. eximius* nests and colonies found at the time of the study in the forest understory ($F_{(1,45)} = 0.9, P = 0.3$; $F_{(1,45)} = 1.33, P = 0.25$), although *A. domingo* individuals occurred in significantly greater densities within the nests ($F_{(1,19)} = 6.7, P = 0.03$). As expected based on body size differences, colonies of *A. eximius*, the larger species, captured on average larger prey than colonies of the smaller *A. domingo* ($F_{(1,43)} = 44.3, P < 0.0001$; Figure 4.2). However, while the size of the prey captured by both species increased with colony size, the slope of this relationship was steeper for the smaller than the larger species (interaction term $F_{(1,43)} = 6.9, P = 0.01$; Figure 4.2), thus indicating an acceleration of effort as colony size increased in the smaller species relative to the larger one.

Overall, the smaller species captured a narrower range of insect body sizes (2 – 25 mm), which was included within the range utilized by the larger species (2 to 46 mm; Figure 4.3). *A. domingo* thus exhibited an included niche relative to *A. eximius*. In addition, most of the prey biomass consumed by *A. eximius* came from its exclusive insect body size range (large sized prey; Figure 4.3).

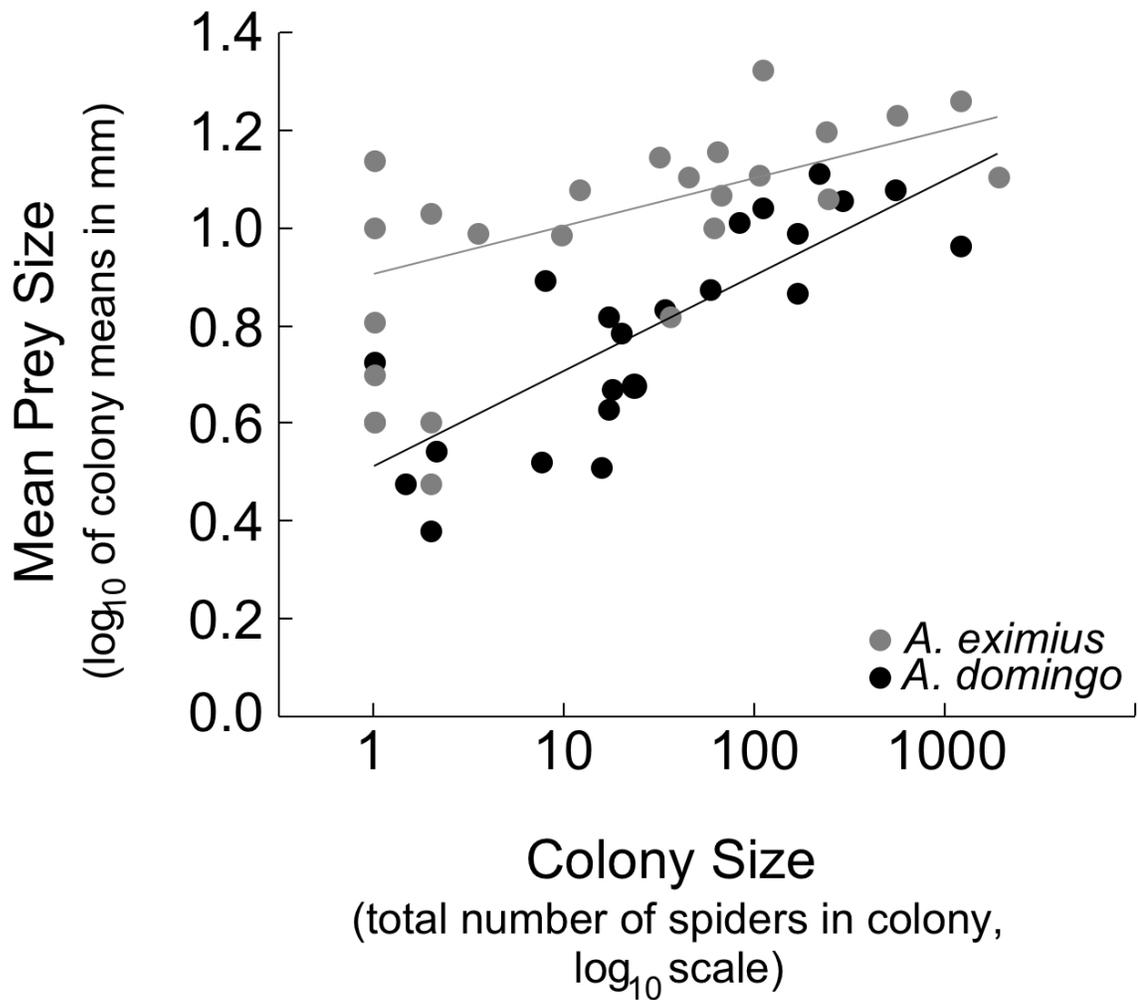


Figure 4.2 Relationship between prey size (log₁₀-transformed insect body length, mm) and nest size (log₁₀-transformed total number of spiders in a colony, as inferred from the area of the cross section of the nest) for colonies of two sympatric social spiders of the genus *Anelosimus* exhibiting a close to five-fold difference in body size (biomass), with *A. eximius* being the larger species.

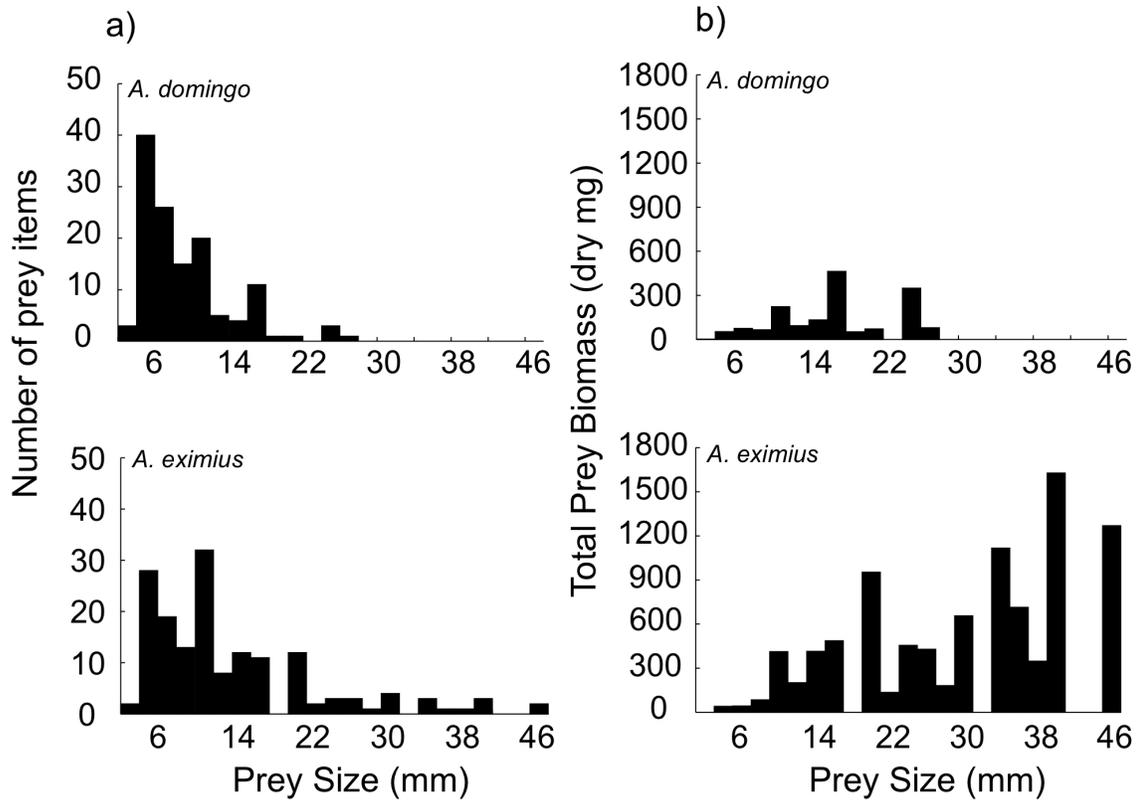


Figure 4.3 (a) Resource utilization curves showing the distribution of prey size (insect body length in mm) by total number of prey items captured by two sympatric social spiders of the genus *Anelosimus*. *A. domingo*, a species close to five times smaller in body size (biomass), exhibits a prey size range included within the range of the larger *A. eximius*. (b) Total biomass of prey captured corresponding to different prey sizes. Most of the prey biomass captured by *A. eximius* comes from large insects.

4.3.2 Foraging performance experiments

The total number of spiders attacking increased with prey size for both species (*A. domingo* $r^2 = 0.70$, $t = 11.3$, $P < 0.0001$; *A. eximius* $r^2 = 0.57$, $t = 8.5$, $P < 0.0001$; Figure 4.4), but for insects of all body sizes, more spiders attacked in the smaller *A. domingo* than in the larger *A. eximius* ($F_{(1,110)} = 25$, $P < 0.0001$; Figure 4.4). For *A. domingo*, more age classes, including juveniles, were involved during prey capture events, whereas for *A. eximius* participating individuals were mostly adult and subadult females ($Wald-\chi^2 = 50.2$, $P < 0.0001$; Figure 4.4). In general, I found that *A. domingo* had faster reaction times when prey of any size landed in their webs than did *A. eximius* ($F_{(1,95)} = 23.2$, $P < 0.0001$; Figure 4.4). With both reaction and killing time considered,

both species took longer to subdue larger prey (*A. domingo* $r^2 = 0.83$, $t = 11.1$, $P < 0.0001$; *A. eximius* $r^2 = 0.47$, $t = 5.1$, $P < 0.0001$; Figure 4.4), but in general *A. domingo* subdued small prey faster than *A. eximius*, whereas the latter was faster than the former at subduing large prey (species x prey size interaction $F_{(1,95)} = 50.1$, $P < 0.0001$; Figure 4.4).

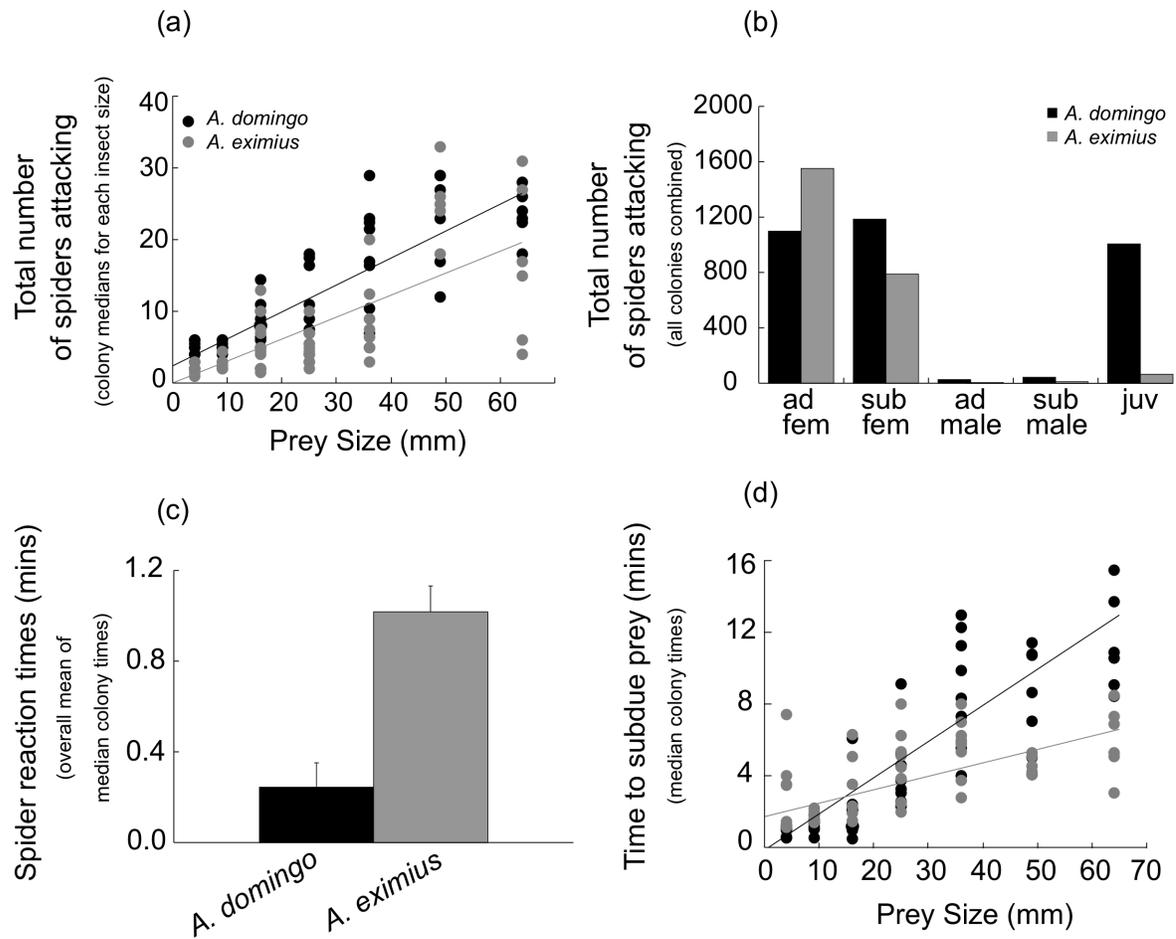


Figure 4.4 Potential mechanisms allowing a small-sized social spider (*A. domingo*) to capture small prey more efficiently than the larger-sized social spider, *A. eximius*: (a) cooperative effort: relationship between number of spiders attacking the prey (median) and prey size (insect body length, mm), (b) cooperative effort: total number of spiders belonging to five age/gender classes involved in attacking the prey (ad fem = adult female, sub fem = subadult female, ad male = adult male, sub male = subadult male, juv = juveniles), (c) reaction/detection time: mean (+SE) of median time (min), (d) prey subdue time: relationship between time to subdue prey (reaction + killing time) (median, min) and prey size (insect body length, mm).

I found that there was a difference between the species in whether or not they initiated an attack on prey of different sizes (species x prey size interaction: $Wald-\chi^2 = 23.8, P < 0.0001$). While insect body size did not have a significant effect on whether it was attacked by *A. domingo* ($\chi^2 = 2.03, P = 0.2$; Figure 4.5), *A. eximius* was more likely to “ignore” or not detect small insects ($\chi^2 = 22.6, P < 0.0001$; Figure 4.5). The species also differed in how likely they were to succeed at subduing insects of different body sizes (species x prey size interaction: $Wald-\chi^2 = 39.7, P < 0.0001$; Figure 4.5). While prey capture success declined with insect body size for *A. domingo* ($\chi^2 = 39.3, P < 0.0001$; Figure 4.5), the opposite held for *A. eximius* ($\chi^2 = 6.3, P = 0.01$; Figure 4.5).

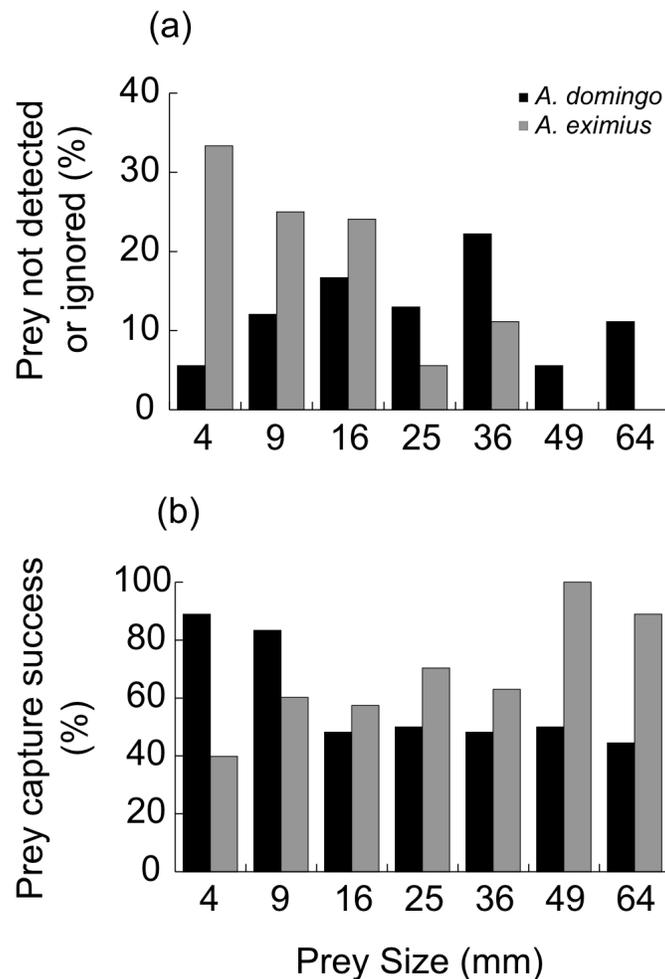


Figure 4.5 Foraging efficiency (given as a %) for different prey sizes (mm) by colonies of two sympatric social spiders of the genus *Anelosimus* (a) prey not detected and/or ignored, (b) success in prey capture.

4.4 Discussion

By virtue of their morphological, physiological, or behavioral traits co-occurring species can differ in their foraging performance and thus the resources they utilize—e.g. bill size in Galapagos finches (Grant and Grant 2006), body form in sticklebacks (Schluter 1995), body size in sparrows and sunfishes (Werner and Hall 1974, Pulliam 1985). For species that live and forage in groups, resource use can be further shaped by traits exhibited by the group as a whole (i.e. group size and cooperation). Here, I explored the simultaneous effect of individual- and group-level traits on patterns of prey size use and prey capture performance in two sympatric social spiders. Given a close to a five-fold difference in body size, I found that on average the large species captured larger insects than the small species. Moreover, consistent with the included-niche hypothesis, I found that the small species captured a prey size range (small prey) included within the range of the large species (ranging from small to large prey). The small species, however, had a steeper increase in the body size of the insects captured with increasing colony size than the large species (Figure 4.2). Furthermore, foraging performance trials showed that colonies of the small species were less likely to miss or ignore small prey and were, in general, more efficient foragers on the shared range (small prey) compared to the large species. Colonies of the large species were, on the other hand, more successful at capturing prey towards and above the upper end of the overlapping range (Figures 4.3 and 4.5).

The ability of the small species to compensate, to some extent, for its smaller size was associated with overall faster reaction times and the involvement of a greater number of individuals and age classes in the capture of insects of all body sizes (Figure 4.4). These patterns may have reflected in part the greater density of individuals within *A. domingo* nests, which would place a greater number of individuals in a position to detect and respond to struggling prey (Clark 1986). However, the fact that in the large species foraging individuals were restricted mostly to adult and subadult females, whereas in the small species more age classes, including juveniles, were involved in attacking and subduing prey does suggest that the small species invests more resources in prey capture and is thus, in a sense, more cooperative than the large species. Foraging group size is also correlated to food detection times in fish (Pitcher et al. 1982) and birds (Krebs et al. 1972). Having more individuals participating increases the chances that other group members are alerted to the presence of prey, thus reducing the number of prey that escapes (Clark 1986). Eventually, however, the small species was unable to keep up with increasingly large insects, and could not capture the large size

classes utilized exclusively by the large species. This suggests that there is a limit to the extent to which greater cooperation can compensate for differences in body size.

That the smaller species had its niche fully included within the niche of the larger species is of particular interest as included niche patterns are expected to be rare in nature given the apparent disadvantage of the species without access to exclusive resources (Miller 1967, Schoener 1974). Such patterns may be sustainable, however, if the species with the included niche were more efficient at exploiting resources in the shared range (Miller 1967, Schoener 1974), a pattern that, as I discuss below, may or may not arise as a result of species competition. Whether the species I studied are, or have been in the past, in competition with each other is still an open question. They do live sympatrically in the forest understory where nests of both species may be found in the same or neighboring plants (L. Avilés personal observation) where interference competition for flying insects is plausible. While such competition could be avoided by relocating the nests to unoccupied areas in the forest, nest relocation is likely to be costly. Thus the ability of these species to preferentially derive energy from insects towards the two ends of the spectrum of available insect body sizes may facilitate to some extent their co-occurrence in their shared environment. In addition to differences in body size, included niche patterns may arise when species differ in their level of sociality. Such appears to be the case at Serra do Japi, Brazil, where four *Anelosimus* species with similar body size, but ranging in level of sociality from nearly solitary to fully social co-occur (Guevara et al. 2011). In this case, less social species, which only form small colonies, utilize a resource range that is included within the broader range utilized by more social species, which form both small and large colonies.

Nevertheless, while included niche dynamics may be driven by interspecific competition (Chase and Belovsky 1994, Chase 1996), they need not be (Beckerman 2000). Thus, the greater efficiency of *A. domingo* spiders in the shared prey size range (i.e. small insects) may simply be a reflection of the small size of the spiders or a result of mechanisms to optimize energy intake on the part of both species. Small size, for instance, may allow the spiders greater acceleration to pursue prey and greater ability to manipulate small prey than bigger individuals (Bonner 2006, Dial et al. 2008). More efficient use of the small insects may also be a mechanism to meet potentially higher energetic demands per unit biomass of *A. domingo* colonies given higher metabolic rates associated with small body sizes (Glazier 2005). Increased activity within the colonies resulting from faster reaction times may be also associated with higher metabolic rates and thus greater food requirements (Stephens and Krebs

1986). Density manipulations on ant colonies (*Temnothorax rugatulus*), for instance, showed that more crowded nests expended more energy than nests of the same size with fewer individuals (Cao and Dornhaus 2008). Thus, the small species may be required to take advantage of all small prey available, whereas the large species, having access to large prey items, can afford to ignore small prey.

The greater efficiency of *A. domingo* on small prey is straightforward to explain given its small body size and associated ability to manipulate and chase small prey, greater metabolic demands, and inability to capture large prey. That *A. eximius* is less likely to respond and successfully capture small prey is more puzzling, as large animals may still be capable of overpowering small prey with similar, if not greater, ability than smaller ones (e.g. Wilson 1975, Grant et al. 1976, Pulliam 1985, Herrel and O'Reilly 2006). This finding may thus reflect either inability of the spiders or their webs to detect or retain small prey or a tendency of the spiders to ignore them. Field observations suggest that nests of these species differ in silk density (M. Salomon, unpublished data), with *A. domingo* having greater density of fibers that may prevent small prey from escaping compared to the less dense nests of *A. eximius*. Also, given the greater exoskeleton to biomass ratio of small insects, small prey may be considered relatively unprofitable for the larger bodied *A. eximius* and thus ignored by the spiders. While small animals with higher metabolic rates require more food relative to their body weight (Glazier 2005, Chown et al. 2007), large animals generally require more total energy to maintain their bodies (Peters 1983, Bonner 2006). Thus due to greater total energetic demands, *A. eximius* may concentrate its foraging efforts on more profitable large prey. Rypstra (1993) showed that few large prey items are indeed more profitable for reproduction in social spider colonies compared to an equal mass of small prey. The difference in performance between my study species may thus reflect mechanisms on the part of both species to better meet their own energetic requirements.

Chapter 5: Conclusion

Understanding the ecological conditions that promote group living and cooperation is critical to our ability to explain the origin of social diversity and interpret the associated patterns observed in nature. Moreover, being able to predict how such social diversity is maintained in nature requires an understanding of the ways sociality may in turn affect the ecology of an animal's life such as its ability to exploit the available resources, reproduce, and ultimately persist in the environment. In the preceding chapters, I have addressed questions about the ecological causes and consequences of sociality using observational, experimental, comparative, and ecological niche modeling approaches. In this concluding chapter, I summarize some of the most important findings of my work and attempt to synthesize the implications and potential goals for future research.

5.1 Geographical patterns of spider sociality and the ecological correlates

One approach to understanding the origin of social complexity and the patterns observed in nature is to discern the suite of ecological conditions that make group-living beneficial and influence the presence and persistence of social taxa in some areas but not in others.

Characterization of the overall environmental niche of a species (i.e. the set of environmental conditions where it can persist) followed by understanding which environmental variable is most important in limiting its distribution is an important step in understanding any emerging patterns in a species geographical distribution (Soberón and Peterson 2005).

In Chapter 2, I used ecological niche modeling and comparative methods to explore the latitudinal and elevational patterns in the distribution of *Anelosimus* spider sociality in the Americas and their association with specific climatic variables. Among the most important findings from my study is that social species occurred most frequently at low latitudes, and within those latitudes, low elevation and exhibited overall a smaller geographical range than subsocial species. The range of subsocial species, on the other hand, expanded into higher

latitudes but was restricted to mid and higher elevations. The latitudinal occurrence of social species was significantly associated with areas of low seasonality and high rainfall intensity, whereas the opposite pattern was true for subsocial species. Across the elevation gradient, social species were significantly associated with low elevation areas characterized by warmer temperatures, low seasonality, greater annual rainfall and rainfall intensities. Subsocial species were restricted to higher elevations with conditions opposite to social species. These results show that social and subsocial spiders occupy different environmental niches that appear to be associated with specific ecological requirements by each social system. The climatic conditions of lowland tropical rainforests, for example, may allow for greater proportions of large insect sizes compared to more seasonal, less tropical, habitats (e.g. higher elevations and latitudes). Group formation may be promoted in these areas as successful capture of larger prey may be required to address scaling properties of the spider's tri-dimensional nests. Thus, large prey sizes would be required by social spiders in order to meet the nutritional demands of their large colonies (Yip et al. 2008). In eastern Ecuador, the lowland tropical rainforest harbors larger insect sizes than habitats at higher elevations and it is thus correlated with higher levels of sociality (Avilés 2007, Guevara and Avilés 2007, Powers and Avilés 2007). The absence of subsocial species from the tropical lowlands, on the other hand, may be associated by potentially high extinction rates of colonies inflicted by heavy precipitation in these areas (Purcell and Avilés 2008). Temperature parameters, however, because they are often correlated with other biotic and abiotic variables, are less straightforward to pinpoint their main (either direct or indirect) role in the distribution of sociality and thus merit further research. Adaptation to different temperatures, for instance, may only secondarily explain why species with different levels of sociality occur in given areas. The fact that subsocial spiders may not do well at higher temperatures does not necessarily explain why a species with that level of sociality does not occur in the lowland rainforest. Given that they are prevented from living in the rainforest for whatever reason may not be an indication that they are not adapted to higher temperatures. Experimentally testing for the direct effect of temperature on the physiological tolerance of social spiders should be relatively straightforward given the ease of collecting and setting up *Anelosimus* colonies in the laboratory. Experimentally testing the climatic limitations of *Anelosimus* would also act as useful validation for the ecological niche models developed in this study.

While my study shows that the distribution of sociality is generally associated with environmental factors, which may directly (e.g. rainfall intensity) or indirectly (e.g.

temperature, predation) act upon the species, the complete picture of the processes controlling latitudinal and elevational variation in level of sociality is still poorly understood. To fully understand what drives the biogeography of sociality it is important to consider other key factors that limit species distributions, such as the dispersal abilities of individuals or groups, potential barriers to dispersal including topographic and ecological conditions, the physiological tolerances of the species, evolutionary changes, and stochastic events. Therefore, predictive distribution models developed with environmental variables alone cannot be exhaustive and need to be interpreted in consideration of these other factors.

As shown by my study, ecological niche modeling in combination with comparative methods are promising tools for predicting species distributions and identifying factors that have contributed to distribution patterns at continental scales. With the increasingly popularity of ecological niche model software and the wide availability of high-resolution digital GIS databases, there has been a growing interest in the past few years to uncovering broad-scale patterns of species distributions, for both past and present. Showing the existence of broad-scale latitudinal and elevational patterns in the distribution of species and their biological traits, including their social behavior, is a required starting point to formulate hypotheses about the processes regulating spatial patterns of diversity. However, despite major conceptual advances and the availability of large amounts of data, our ability to predict these patterns still rests on the quality of species locality data. Thus, it is worth mentioning that a concern in identifying patterns in species distributions using ecological niche models is the difficulty in determining if such patterns indeed reflect the entire range of the species under study or result from biases or insufficient sampling effort. For instance, based on my own collecting experience, I believe that there may have been some bias in collecting effort towards *Anelosimus* species inhabiting some areas, say in Ecuador, compared to the rest of the continent. This suggests that there may be many unreported ecological conditions for the species in other areas in the Americas that have not been taken into account in the models. Further refinement of spatial species distribution data is thus important and should be encouraged.

In addition, in my view, a true understanding of the processes underlying the observed sociality patterns, as well of species diversity patterns in general, requires better information on various aspects of species biology and geographic variation in these characters, not just on species locality data. Incorporating information on morphology, functional characteristics, behavioral traits, and phylogenetic affinities of species in GIS datasets is not only technological feasible, but a necessity in order to explore patterns that are more representative of nature's

diversity. For the social spiders in my study, for instance, using *social* and *subsocial* terminology as the main measure of sociality does not adequately capture the complexity of social variation in the genus *Anelosimus*, as sociality varies in a more continuous matter than the currently recognized discrete categories. Thus, further modeling incorporating other variables reflecting a species level of sociality, such as colony size or level of cooperation, should give more detailed insight into social behavior distribution patterns and their ecological correlates. Ideally, using a standardized metric describing in more detail a species level of sociality would allow comparison of patterns across a range of social taxa, and the associated common ecological conditions that shape their distribution.

Along the same lines, ecological niche models generate at best *potential* distributions based on the environmental variables provided by the user and thus will not accurately predict aspects of a distribution that are influenced by biotic and abiotic factors not included in the model. For instance, my models may over-predict the range of social spiders if the climatic conditions in an area are suitable, but there is some external factor that prevents colonization, such as the presence of competitors, absence of large prey sizes, or physical barrier such as a mountain range. I envision future research increasingly incorporating data describing these additional variables into the models.

Understanding whether and how species distribution patterns change with latitude and other environmental gradients is additionally becoming an increasingly important tool in light of climate change and other important threats to biodiversity. This is particularly true for arthropods in general as they are highly sensitive to temperature (Dobson 1996, Speight et al. 1999) and climate change is expected to have a great effect on their behavior, population dynamics, interactions with other species, and geographical ranges (Harrington et al. 1999, Harrington et al. 2001, Bale et al. 2002, Beaumont and Hughes 2002). In the unique group of social spiders I studied, the distribution of species with more advanced levels of sociality is closely linked to the use of lowland tropical rainforest habitats, known to be increasingly threatened by logging, agriculture, and urban development pressures. Thus, documenting the spatial patterns of sociality is a necessary first step to our ability to predict changes in population sizes associated with such threats to tropical biodiversity and set up adequate conservation plans.

5.2 Resource use by social spiders exhibiting different levels of sociality

Just as the way the surrounding environment plays a primordial role in promoting animal sociality, there is a feedback of the latter that in turn shapes important ecological aspects of an animal's life. In Chapters 3 and 4 I have specifically focused on the ways sociality may create community-wide patterns of resource use by its influence on the way groups exploit and utilize food resources.

In Chapter 3, I surveyed the prey size captured by colonies of four sympatric social spiders (*Anelosimus*) in Brazil to explore the effect of sociality on community-wide patterns of prey capture, and its potential role in resource partitioning. The main finding of this study is that interspecific differences in group size and level of cooperation creates differences in the prey size utilized by sympatric social spiders. I showed that species with more advanced levels of sociality and larger nest and colony sizes captured distinctly larger average prey sizes than less social species with smaller nests and colonies. These differences were greater than expected by chance even for those species contiguous in the sociality scale that overlapped in the size of their nests. For the latter cases (i.e. species with similar nest sizes), I propose that differences in prey size may be the result of potential differences in level of cooperation. These results are consistent with the idea that differences in group characteristics, such as colony size and degree of cooperation, can potentially create significant differences in resource use in co-occurring closely-related species, and thus may play important roles on resource partitioning and facilitate the coexistence of social animals.

Unfortunately, I am unable to compare and generalize these findings because there is a tremendous lack of data in this field of research. Studies exploring the role of sociality on patterns of resource use have had a long history of focusing on social species inhabiting different environments. In such cases, species comparisons are problematic as dietary differences could arise for reasons other than sociality if, for instance, the species occupy areas with marked differences in the size of the prey available (i.e. social spiders inhabiting low vs. high elevations, Guevara and Avilés 2007). I thus stress the need for further observational comparative analyses of closely-related species that differ in relevant social traits (i.e. group size or level of cooperation), but share the same habitat. Having replicate communities allows for comparison across different environmental conditions and social taxa. This is important because many communities may either not comply with our predictions or, if they do, they may

not necessarily rule out other alternative hypothesis for the patterns exhibited (i.e. patterns are due to chance). Because observational data on prey size use can be obtained easily for most social animals, the generality of this pattern could be easily tested in a wide range of social taxa.

In addition, extending the scope of these studies to explore how sociality may act to separate species in their use of other resource and niche variables, including habitat choice and size, spatial distribution, and time, may yield insights into the interaction of different niche axes along which the species may be separated from one another as a function of their social behavior. For example, related studies (Purcell et al. 2012) conducted on the community of *Anelosimus* spiders in Brazil have shown that in addition to prey size, sociality acts to separate spiders also in their phenology and the microhabitat they occupy. Incorporating more than one niche variable is critical to our ability to make a coherent contribution to our understanding of patterns at the community level. So far, most studies of resource use by social animals have paid disproportionate attention to prey type and size and thus a clear association between sociality and many other resource variables remains to be discovered in general.

While my study provides with observational evidence of non-random resource segregation as a function of sociality (i.e. colony size and possibly differences in level of cooperation), it does not completely pinpoint the mechanism responsible for this pattern. Competition for insect prey is a compelling explanation for the patterns observed, especially since the trait involved (i.e. colony size) is known to greatly influence prey size exploitation in our system (Powers and Avilés 2007, Yip et al. 2008) and colonies in this area were found in high densities, at least during the time this study was carried out. Although it is not possible to rule out the possibility that resource-partitioning-like patterns are the outcome of other mechanisms such as stochastic species colonization, one reassuring finding was that patterns were not random as the species were more over-dispersed along the prey size niche than expected by chance. I envision further research incorporating experimental field tests of resource competition in order to give insight into competition as a driving force of these patterns. Such tests should also be conducted on taxa from different trophic levels as the role of competition may be more evident for, say, social vertebrate carnivores at the top of the food chain. Making efforts to experimentally reveal the underlying mechanisms is extremely important as it represents a big gap in our understanding of the observed patterns. The potential role of sociality in separating sympatric species into different ecological niches, minimizing resource competition, and potentially facilitating their coexistence is an exciting and previously

overlooked possibility deserving deeper empirical investigation in this and other animal social systems.

Another important implication of this study is the potential for character displacement (divergence and/or convergence) in group-level traits and its role in the coexistence of social species. For example, if the sympatric species were in competition with one another for insect prey, species differences in characteristics affecting prey capture (i.e. colony size and/or level of cooperation) would develop giving rise to the observed differences in prey size. Unfortunately, this is only suggestive as I lack formal observations of colony size and patterns of resource use in allopatric populations of this community, a required piece of evidence for character displacement. I must mention, however, that it would be interesting to explore the possibility for character displacement in the sympatric social spiders, *A. eximius* and *A. domingo*, which both exhibit advanced levels of sociality, similar nest structures and prey capture behaviors, and generally similar ecological requirements. In Ecuador, *A. eximius* populations found in the interior of the tropical rainforest, where it occurs sympatrically with *A. domingo*, exhibits smaller colony sizes than allopatric populations found at the forest edges. Although the co-occurring species appear to converge in nest size, they differ in the extent the individuals cooperate during prey capture (i.e. *A. eximius* is “less cooperative” than *A. domingo*) and thus differ in their efficiency when capturing prey of different sizes. I believe these two social spiders represent an exciting opportunity to explore the potential for character displacement in group-level traits —i.e. convergence (Abrams 1986, 1996) in nest and/or colony size, and divergence in level of cooperation. In addition, allopatric populations of *A. eximius* found in the range edge (i.e. at higher elevations) also show different colony sizes and potentially different prey capture patterns than populations in the lowland rainforest (Purcell and Avilés 2007). While differences in environmental conditions and resource availability may play greater roles in these cases, it is nevertheless worthwhile to explore the interplay between environmental variation and resource competition in these cases. Either way, the potential for character displacement in group-level traits is an interesting idea that deserves further attention.

5.3 Prey capture efficiency: the role of body size and level of sociality

Furthermore, although sociality may directly influence foraging efficiency, it is well known that other factors such as individual –level traits, including body size, play a primordial role on an individual and/or groups’ ability to forage. In Chapter 4, using two sympatric social spiders in Ecuador, I conducted foraging efficiency experiments to explore in more detail how the observed differences in resource use may emerge via the effect of sociality on the ability of species to utilize food resources. Because the species under study exhibited interspecific differences in body size, a trait known to directly influence the foraging efficiency of many animals, I examined simultaneously the relative contribution of both sociality and body size to their ability to capture prey of different sizes. I also explored how the resulting differences in foraging efficiency may minimize the potential for food competition in cases where one species has its prey size niche completely included within the niche of the other species.

The main finding of importance in this study is that increased levels of cooperation played an important role in the ability of the species with small body size to forage more efficiently on the shared resources (i.e. small prey sizes), and thus to compensate, to some extent, for body size differences while decreasing the potential for competition. The other species, on the other hand, was a better forager on larger prey sizes as a result of its larger body size and social foraging. I recommend future research to focus on understanding in more detail the relative contributions of each, individual and social traits, to observed patterns of resource use. For example, social and individual traits may each influence foraging directly or via an interaction where the relative strength of each varies in some way. It is also possible that in a social setting individual traits may not directly affect foraging efficiency but indirectly through their effect on social traits, which in turn influence foraging efficiency. For example, species with bigger body sizes may form smaller groups to avoid overcrowding.

My study is the first attempt to examine the simultaneous role of individual traits (i.e. body size) and group characteristics in foraging performance and thus contributes to our understanding of how they jointly interact to shape resource use in communities of social organisms. Despite the obvious importance of group living and cooperation in influencing the foraging efficiency of social animals, resource use in communities of social species have been mainly related to individual-level traits in the literature (e.g. Owen-Smith and Mills 2008; but see Cerdá et al. 1998). The majority of studies that have a looked at the effect of sociality on

foraging efficiency have focused exclusively on single species, most of which pertain to vertebrate groups (Irschick et al. 2007). This severe lack of multi-species data, particularly that dealing with invertebrates (Irschick et al. 2007), hinders our ability to understand emerging patterns of resource use at the community level.

Finally, the three studies in my thesis further our understanding of how environmental factors facilitate group living while shaping the geographical distribution of social animals, and how group living and cooperation may in turn affect the way species partitioning their resources when part of the same community. Mainly, this study suggests the need for further research exploring the generality of the observed broad-scale as well as community-wide patterns. The ecological niche modeling approach is a valuable method to discern broad-scale patterns and I stress it should be used more frequently to explore the ecological correlates of sociality and the generalities across social taxa. Also, the study of resource segregation as a consequence of sociality should be studied deeper in natural communities of other social animals since, likely, there are many undocumented cases illustrating the role of sociality in resource partitioning, and potentially in species coexistence. In these cases, because of the underlying complexities of social living and the simultaneous processes operating at the individual and group levels, I suggest caution when exploring the roles of each separately. In any case, while my research has shown the importance of sociality in creating differences in resource use in sympatric social animals, it seems clear that there remain many unanswered questions for the role of sociality at the community level. Exploring in more detail this new and exciting area of research will help us understand the mechanisms that facilitate the coexistence of social animals and structure their natural communities. This in turn is essential to our ability to predict the maintenance of social animal diversity and their contribution to overall global biodiversity.

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Appendix 1

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Appendix 2

Pre-processing of species presence and environmental datasets

To assemble the species locality dataset, when available I used published locality coordinates (Appendix 1) and, for localities for which only descriptions were available, I approximated point localities using the online georeferencing application Biogeomancer Workbench (<http://www.biogeomancer.org>). I investigated the validity of outlier data points and eliminated those that appeared not valid (i.e. points falling outside the continental boundaries). To minimize the effects of spatial autocorrelation on the analysis, I trimmed the number of data points to one per grid cell for the America ($\sim 5 \text{ km}^2$) and Ecuador datasets ($\sim 1 \text{ km}^2$).

I accessed a set of temperature and rainfall layers (mean annual temperature, temperature seasonality, annual rainfall, rainfall seasonality) from the WORLDCLIM V1.4 database (Hijmans et al. 2006; <http://worldclim.org>) corresponding to 0.25 arc-min ($\sim 5 \text{ km}^2$ per pixel) and 30 arc-sec ($\sim 1 \text{ km}^2$) resolution for the areas comprising the Americas and Ecuador respectively. I also obtained satellite-borne monthly precipitation intensity data (mm/hr) for America (0.25 arc-min) and Ecuador (30 arc-sec) for the 2000 – 2005 period from the Tropical Rainfall Measuring Mission Project, TRMM (Huffman et al. 2004; data product TRMM-3B43v6, <http://disc.gsfc.nasa.gov>).

For the America range, I accessed net primary productivity data (mean annual npp, $\sim 5 \text{ km}^2$ per pixel) from the Global Production Efficiency Model (GloPEM) dataset derived from high-resolution radiometer images (Prince and Small 2003; www.landcover.org). For the Ecuador range, I accessed net primary productivity data derived from satellite-borne remote sensors (NASA-MODIS Terra datasets) at $\sim 1 \text{ km}^2$ resolution through the Data Pool at the NASA Land Processes Distributed Active Archive Center (LP DAAC;

http://lpdaac.usgs.gov/get_data). For this study area, I obtained four tiles of the MODIS data (h09v08, h09v09, h10v08, h10v09; MOD17A3) corresponding to yearly net primary productivity for six years (2000 - 2005)

I reprojected all layers to a geographic projection (Lat/Lon, World Geodetic System 1984-WGS84) and resampled them to a final pixel resolution of either 0.0417 degrees for the Americas, or 0.00833 degrees for Ecuador. For this, I used bilinear interpolation which is appropriate for continuous data. When necessary, I interpolated data into gaps of no-data generated when mosaicking tiles together. For multi-year datasets, I calculated the average cell value to obtain a single layer for that variable (six 1-year MOD17 layers, and 6 sets of monthly rainfall rate TRMM data). I created mask layers for all datasets and clipped them to final area bounded by 124°57'W and 57°25'S for the Americas, and 81°0'W and 5°5'S for Ecuador.

I used the MODIS Reprojection Tool 4.1 (LP DAAC, https://lpdaac.usgs.gov/lpdaac/tools/modis_reprojection_tool) to export all the original HDF-formatted MODIS datasets, create mosaics, and reproject them. I used ArcGIS v10 (ESRI 2010) and its Spatial Analyst extension for all other spatial calculations and processing of datasets.

Appendix 3

Correlations for environmental variables

	Temperature	Temperature Seasonality	Rainfall	Rainfall Seasonality	Rainfall Intensity	NPP
Temperature	0	-0.869	0.578	0.312	0.566	-0.520
Temperature Seasonality	-0.276	0	-0.596	-0.336	-0.541	-0.655
Rainfall	0.599	-0.023	0	-0.132	0.854	0.562
Rainfall Seasonality	0.185	0.574	-0.111	0	-0.217	0.203
Rainfall Intensity	0.367	0.356	0.592	-0.584	0	0.558
NPP	0.190	-0.274	0.344	-0.441	0.550	0

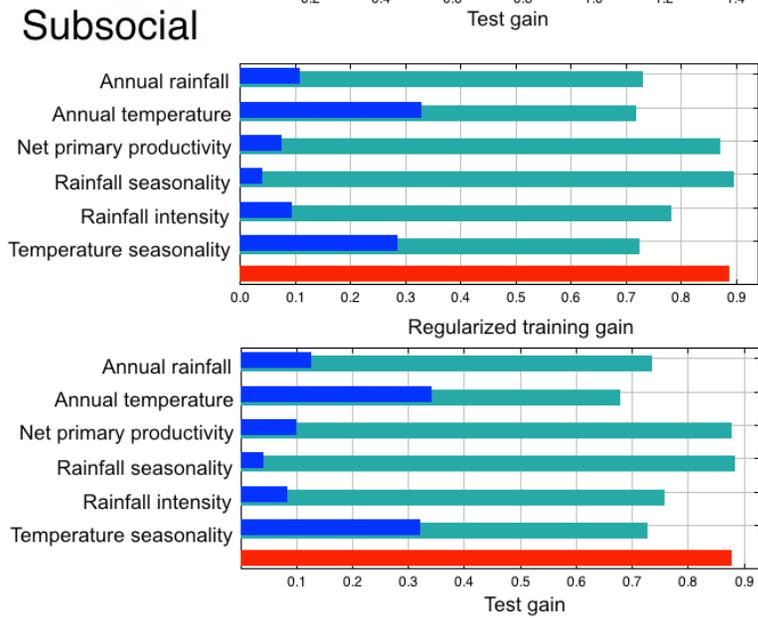
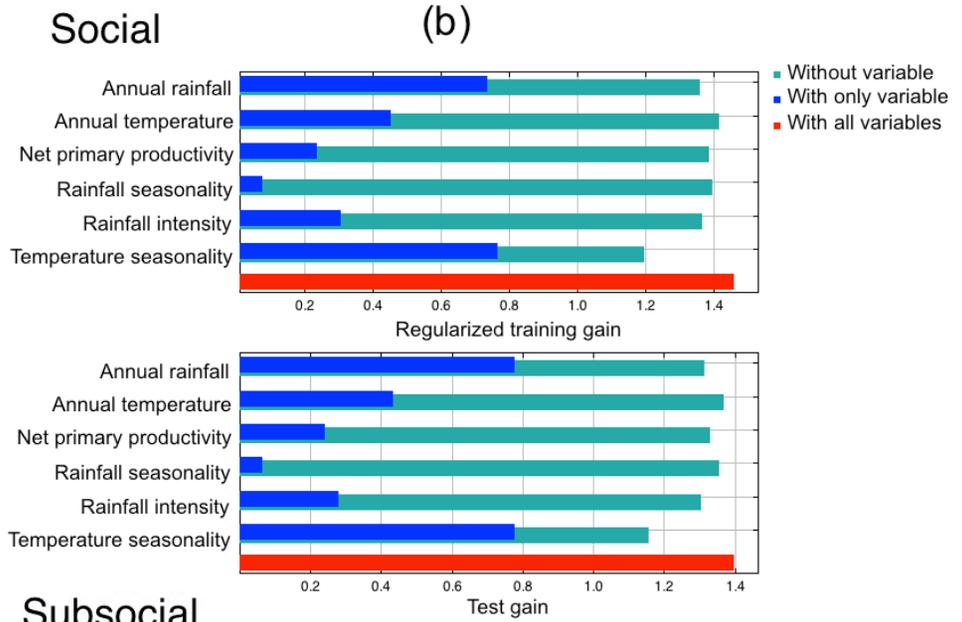
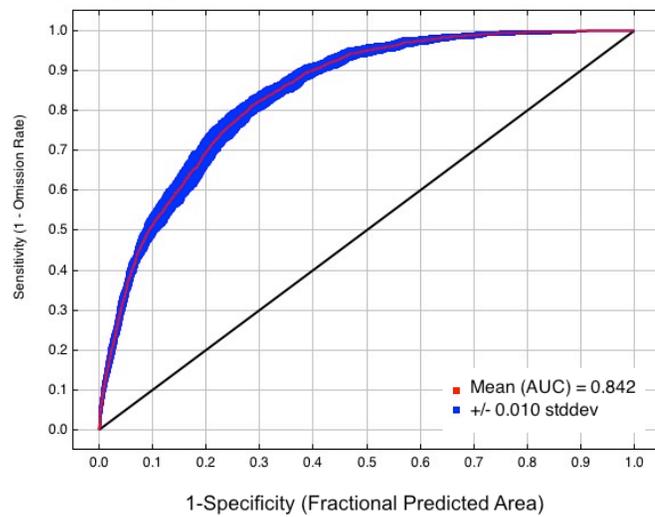
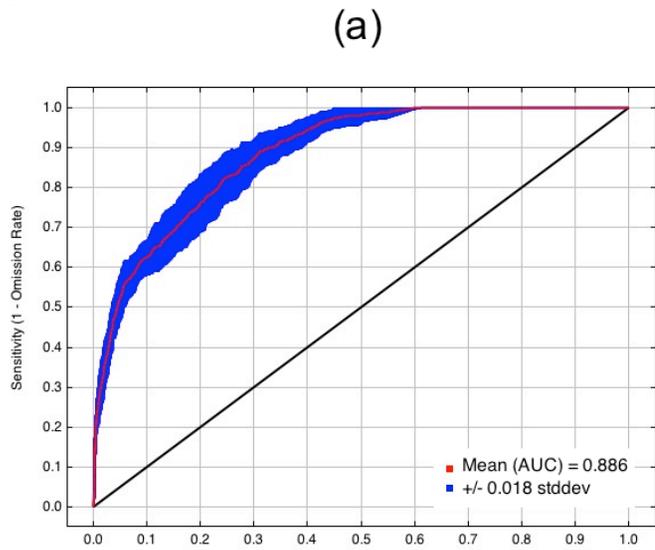
Although I chose the environmental variables exclusively based on their relevancy to the biology of *Anelosimus* spiders, I further tested that the chosen variables were not highly correlated with each other in order to minimize problems with multi-collinearity. One useful approach is to use PCA axes (Principal Component Analysis) as variables, however, this method made interpretability of the ecology of my species increasingly difficult given the goal of my study and the specific variables I wished to test (and keep) in the analysis. I thus used Pearson correlation coefficients (i.e. implemented in ENMTools, <http://enmtools.blogspot.ca/>) for each pair of variables at both spatial scales, America and Ecuador. At the spatial scale of Ecuador (~1 km² per pixel) all pairs of variables were not highly correlated ($r < \sim 0.699$; Table above: correlation coefficients for America shown in the upper right part of the table above the diagonal zeroes, and for Ecuador in the lower left below the zeroes), thus I retained them all for the construction of distribution model. At the spatial scale of America (~5 km² per pixel), two

pairs of variables were highly correlated ($r > 0.85$, Table above, in bold), temperature versus temperature seasonality, annual rainfall versus rainfall intensity). I retained temperature seasonality and rainfall intensity for model construction as they are key variables to my study.

Appendix 4

Maxent model performance (America)

The figure below shows (a) Averaged area under the curve (AUC) of the receiver-operating characteristics (ROC) plot for 20 replicate Maxent runs using the combined dataset of social and subsocial spiders in America. If $AUC = 0.5$, the model is performing not better than random. $AUC \sim 1.0$ indicates optimum performance (Hanley and McNeil 1982). (b) Jackknife tests of variable importance for the corresponding Maxent models. The variables with highest gain when used in isolation (i.e. contain the most useful information by themselves) are annual rainfall and temperature seasonality for social species, and annual temperature and temperature seasonality for subsocial species. The variable that decreases the gain the most when omitted (i.e. contains the most information that is not present in other variables) is temperature seasonality, for both social and subsocial species.

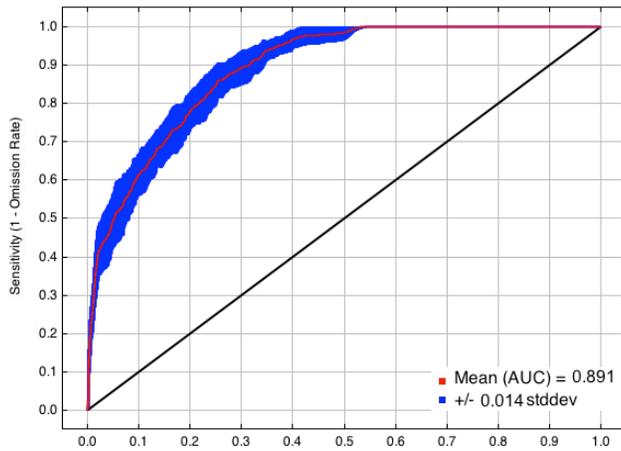


Appendix 5

Maxent model performance (Ecuador)

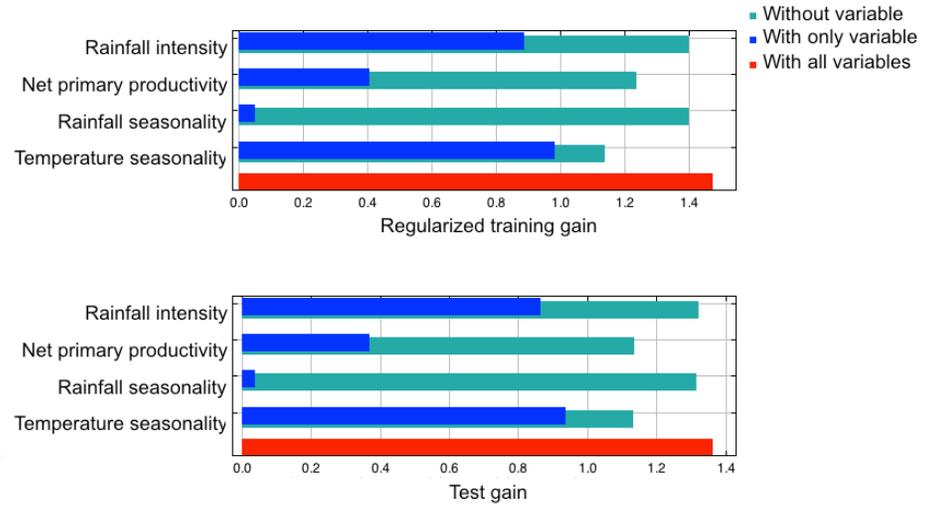
The figures below show (a) Averaged area under the curve (AUC) of the receiver-operating characteristics (ROC) plot for 20 replicate Maxent runs using the combined dataset of social and subsocial *Anelosimus* spiders in Ecuador. When $AUC = 0.5$, the model is performing not better than random. AUC values close to 1.0 indicate optimum performance (Hanley and McNeil 1982). (b) Jackknife tests of variable importance for corresponding Maxent prediction models. For social species, temperature seasonality (and rainfall intensity) was the variable with the most gain when used in isolation (i.e. contains the most useful information by itself) and with the most decrease in gain when omitted (i.e. contains the most information that is not present in other variables). For subsocial species, temperature seasonality had the most information.

(a)



Social

(b)



Subsocial

