COOPERATION AND COLONY SIZE AS DRIVERS OF DIFFERENTIAL RESOURCE USE AMONG SYMPATRIC SOCIAL PREDATORS

by

GYAN HARWOOD

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Abstract:

Dietary differentiation is an integral component of species coexistence, and among solitary predators, body size differences allow each species to capture a different range of prey sizes. Social predators, however, are able to capture much larger prey than an individual, so prey size use is additionally influenced by group size and behavioural dynamics. To investigate this, we looked at cooperative hunting among three species of sympatric group-living spiders in Brazil that construct colonies of different sizes and are known to capture different sizes of prey. We performed feeding experiments to determine whether differential prey size use is produced by differences in group behaviour and group size. For each species we measured the level of cooperation and examined how colony size influenced group behaviour. We found that two of the species which live in equally large, multi-generational colonies displayed differences in their cooperation and prey size selectivity that are consistent with differences in prey size use previously observed: the species which captures larger prey in natural hunting scenarios showed higher levels of cooperation among hunters during the trials, and had more individuals participate when presented with large prey. The third species, which lives in smaller, temporary colonies, displayed the highest levels of cooperation and prey capture success, despite capturing the smallest prey on average in natural hunting scenarios. This disparity likely reflects the natural size distribution of colonies of this species, which is greatly dominated by solitary individuals that cannot capture the largest prey on their own. This study shows that behavioural differences among group-living predators, in addition to colony size differences, may be responsible for differential prey size use.

Preface:

The research project was designed by Gyan Harwood and Leticia Avilés. The field data were collected by Gyan Harwood in Brazil over two field seasons. Additional data were collected by Ruth Sharpe and Maxence Salomon, a PhD candidate and former post-doctoral fellow, respectively, in the Avilés lab. All analyses were conducted by Gyan Harwood.

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Dedication:

I dedicate this thesis to my cat, Chester, because I can.

Chapter 1: Introduction

Predation is a fundamental feature of biology and a major driver of both species evolution and ecological community structure (Holt 1977). As predators pick off the most susceptible members of a population, prey survival patterns result in the evolution of morphological and physiological adaptations such as limb-modification for increased running speed (Losos & Sinervo 1989, Bennett & Huey 1990, Bauwens et al 1995, Vanhooydonck et al 2006), cryptic colouration for camouflage (Ruxton et al 2004, Théry et al 2005, Stevens & Merilaita 2009), chemical production and secretion for deterrence (Eisner 1970, Rothschild 1972, Blum 1981, Roitberg & Isman 1992), as well as behavioural adaptations such as schooling or flocking (Kruuk 1964, Siegfried & Underhill 1975, Stinson 1980, Magurran 1990, Pitcher and Parish 1992, Fuiman & Magurran 1994), and shifting activity periods throughout the day (Nelson & Vance 1979, Metcalfe et al 1999, Wcislo et al 2004). Predators, in turn, have responded in kind with their own morphological and physiological adaptations, such as cryptic colouration (Théry et al 2004), high pursuit speeds (Harris & Steudel 1997), claws, teeth (Vermeij 2002), venom (Barlow et al 2009) and keen eyesight (Patterson et al 2011). Moreover, there have been group-level adaptations whose benefits extend beyond the individual, such as alarm calling in group-living prey species (Sherman 1977), information exchange (Ward & Zahavi 1973), and group hunting in predator species (Packer & Ruttan 1988).

At the community level, predators not only provide top-down control on prey population growth (Paine 1980, Pace et al 1999, Sinclair et al 2003, Baum & Worm 2009), but also promote stable co-existence among prey species via density-dependent predation (Paine 1966, Huston 1979, Chesson 2000). When a predator is removed, the emergence of a single

dominant competitor among the remaining prey species can result in a cascade of local extinctions. For example, when sea otters are removed from coastal habitats, sea urchins are freed from predation, and their unchecked herbivory in kelp forests destroys vital nursery habitat for many species of fish (Estes & Palmisano 1974).

While the occurrence of predators is certainly dependent on the distribution of their prey, predators must also contend with other predators in their habitat, and competition between them can affect which predators co-occur. A critical component of species coexistence is dietary differentiation. For multi-species co-occurrence it is important that diets among species do not completely overlap. The question is, how is dietary differentiation achieved? One possibility is that over many generations, character displacement may alter diets of co-occurring species overlapping in resource use in the presence of a competitor (Lack 1947, Schluter & Grant 1984, Dickman 1988, Grant & Grant 2006). Alternatively, the mechanism might be that communities are assembled from a non-random assortment of varying body sizes (Dayan & Simberloff 1998, Woodward et al 2005), whereby organisms that differ in body size also differ in diet. Current theories of community assembly, including the metabolic theory of ecology, demonstrate that body size increases as one moves up the trophic scale, resulting in fewer (both in species richness and population size), larger predators feeding on more abundant, smaller prey (Peters & Wassenberg 1983, Cohen et al 2003, Brown et al 2004, Woodward et al 2005). Typically, predatory species consume prey that are somewhere between 1 to 3 orders of magnitude smaller than themselves (Woodward & Hildrew 2002, Cohen et al 2003, Woodward et al 2005, Jonsson et al 2005). As the range of prey sizes available to a predator depends on its own body size, larger predators capture larger prey on average

than smaller predators (Shoener 1969, Bekoff et al 1984, Gittleman 1985, Losos et al 1989, Shine 1991, Marti et al 1993, Sinclair et al 2003, Radloff & Du Toit 2004, Hayward & Kerley 2008, Costa 2009). Thus, predators with different body sizes may be more likely to co-occur than predators with similar body sizes. This is most clearly illustrated in aquatic and marine food webs, where mouth gape size determines what an individual can consume. Fish and other animals will essentially be restricted to the size of prey that they can swallow, so larger, more mature individuals and also larger species, are able to capture larger prey (Unger & Lewis 1983, Dickman 1988, Marti et al 1993, Wainwright & Richard 1995, Scharf et al 2000, Costa 2009). Thus, variation among species in body size leads to dietary differentiation, which in turn facilitates species coexistence (Rosenzweig 1966, Woodward & Hildrew 2002). Coexisting predators with similar body sizes might have other mechanisms that prevent dietary overlap, such as being active at different times of the day (Schoener 1974, Marti et al 1993, Richards 2002, Kronfeld-Schor & Dayan 2003) or reaching maturity at different times throughout the year so they do not compete for the same prey at the same time (Werner & Gilliam 1984, Polis et al 1989).

There are, however, outlier species that do not adhere to these trophic body-size scaling patterns (Woodward et al 2005). The largest extant species are typically primary and secondary consumers, such as elephants and baleen whales, which have evolved large bodies while feeding on plants and microscopic animals. Another notable exception is pack-hunting animals, which work together to capture prey that may be many times larger than a single individual in the group. Therefore, the dietary breadth of group-living predators is not as strictly bound by the body size of its individual group members. Given this, what happens when multiple group-

living predators co-occur? What mechanisms prevent dietary overlap among them? Some studies (Vezina 1985, Radloff & Du Toit 2004) have looked at prey selection in rich carnivore communities, such as African savannahs, where many of the predator species are social. However, these studies have tended to focus on the relationships between predator and prey body sizes as a determining factor of prey size use, with little discussion of predator sociality other than that it allows those species to capture larger prey than solitary individuals. Other studies have compared social predator group sizes, either interspecifically (Gittleman 1989) or intraspecifically (Schaller 1972, Kruuk 1972, Kruuk 1975, Caraco & Wolf 1975, Bertram 1979, Bowen 1981, Gittleman 1989) and have shown that larger groups capture larger prey. While this may appear to answer how multiple group-living species capture different sizes of prey, these studies are incomplete because they do not address the interaction between group size and the individual and collective behaviours of group members. Some studies have examined the nonlinear relationship between group size and prey capture success in species where larger groups may suffer from increased freeloading by group members and are only marginally more successful than smaller groups (Caraco & Wolf 1975, Clark & Mangel 1986, Packer & Ruttan 1988, MacNulty 2012). What is needed is a comprehensive examination of how the interaction between group size and the behaviour of group members determines the size of prey that a species captures.

While little, if any, work has been done examining mechanisms for group-living species coexistence, one can posit several theories. We hypothesize that co-occurring group-living predators utilize different prey sizes as a result of differences in group size and the degree of cooperation displayed amongst group members in those species. Several studies have shown

that larger groups capture larger prey on average than smaller groups (Schaller 1972, Caraco & Wolfe 1975, Bowen 1981, Fanshawe & Fitzgibbon 1993, Creel & Creel 1995, Guevara et al 2011), and this may come about in two ways. First, larger groups may be more responsive to larger prey (or conversely, less responsive to smaller prey) as a more energetically efficient way to meet the metabolic needs of its members (Caraco & Wolf 1975, Nudds 1978, Packer 1986, Gittleman 1989). Alternatively, larger groups may not respond differently to any particular prey size, but by having more hunters, they will be more successful with the largest prey, and so the average size of prey they capture will be greater than that of a smaller group of hunters (Creel & Creel 1995). Either way, differences among social species in group size is analogous to differences among solitary predators in body size, as larger groups have more individuals available to work together to subdue large prey. However, larger groups will only realize their hunting potential if those individuals available to hunt actually participate in prey capture. Large groups that hunt a single large prey item may be more susceptible to freeloading if some of its group members are still able to feed despite not engaging in prey capture (Nudds 1978, Barnard & Sibley 1981, Packer & Ruttan 1988, Vickery et al 1991, Pruitt et al 2011). Thus, differences between species in the level of cooperation shown by their hunters can also drive differential prey size use. Hypothetically, two species may have similar sized groups but one might capture larger prey as a result of having a greater proportion of its group members participate in the hunt, while conversely, two species may differ in group size but ultimately utilize the same number of attackers and thus capture the same size of prey.

There are many challenges when it comes to empirical tests of the hypothesis that the interplay between individual and collective behaviours and group size that can lead to

differential prey size use among group-living predators. First, one must determine how to adequately quantify the effort a group invests in prey capture and how likely individuals are to participate in communal hunting. We recommend examining a suite of parameters to compare species. One can compare the size of the hunting parties, as groups may not utilize all their members for hunting. Since the size of the hunting party is limited by the size of the group, any comparison between species must include group size as a covariate in the analysis. Once variation in group size is accounted for, species with larger hunting parties can arguably be considered more cooperative, as a larger number of its group members are engaging in a communal activity. However, comparing the size of hunting parties may be limited if not all members participate. Some individuals may thus act as freeloaders that let other group members engage with a potentially dangerous prey. Therefore, a second variable to measure is the total number of individuals in the hunting party that actually participate in the hunt. Again, once variation in group size is accounted for, species with a greater number of attackers can arguably be considered more cooperative, since a greater number of its group members partake in a risky enterprise that will ultimately benefit the entire group. But like measuring hunting party size, measuring the total number of attackers is not sufficient for comparing levels of cooperation. Some group members that participate as attackers might only participate for limited periods before becoming freeloaders. Therefore, it is important to calculate the *average* number of attackers over the duration of the hunt and compare this with the average number of freeloaders. When comparing species, those whose hunting parties include a greater proportion of their individuals as attackers as opposed to freeloaders should be deemed more cooperative. Finally, if a hunting party has more members attacking certain prey sizes than

others, then this indicates variation in the level of group participation generated by different prey sizes.

The next major challenge with empirically testing this theory, that the range of prey sizes a social predator species can capture is determined by the size of its groups and the degree of cooperation among its group members, is finding an appropriate community of social predators. Such a community must contain multiple social predators that are observed to differ in prey size use, and they must display measurable differences in group size and level of cooperation of group members. Ideally, these species must be as close to one another as possible in body size, as a great size disparity between species will likely obscure the relative importance of different factors that determine prey size use. For example, at first, one might be inclined to examine well-known group hunters, like dolphins and porpoises. Orcas, however, are the only cetaceans known to capture prey larger than an individual, making it difficult to assess the axis along which prey specialization may happen. Alternatively, one might be inclined to examine African social carnivores, such as lions, hyenas and hunting dogs, but their large disparities in body size (Radloff & Du Toit 2004), as well as their different hunting strategies (ambush versus long-distance pursuit), further complicate analysis. Instead, one can look to the ever-reliable world of arthropods, in its endless diversity, to test these hypotheses.

Group-living spiders are an excellent system for understanding group dynamics relevant to prey capture. In social spiders, individuals live in colonies and work together to subdue a wide variety of prey that flies into their webs (Nentwig 1985, Uetz 1992, Avilés 1997, Lubin & Bilde 2007, Guevara et al 2011). Species in the cobweb spider family *Theridiidae* (Agnarsson et al 2006) are particularly valuable for comparative studies, and range in level of sociality from

solitary to fully social. Moreover, sociality has evolved independently several times in this family. These spiders comprise a set of close phylogenetic relatives with similar hunting methods, thus reducing confounding factors when examining prey size use. By observing spiders as they emerge from their refuges and tracking which ones attack prey and which ones do not, one can quantify the cooperative effort displayed by a colony, and also gauge the level of individual participation generated by different sizes of prey. Moreover, colony-members are totipotent, meaning that they can perform all tasks associated with group-living, and may thus essentially elect whether or not to participate in communal activities (Avilés 1997). This is in contrast to more well-studied social arthropods, such as eusocial hymenopterans and termites, where morphologically distinct castes may be constrained by their morphology to perform certain tasks (Wilson 1971, Michener 1974, Keller & Nonacs 1993, Seeley 2009).

Anelosimus is a cosmopolitan genus of cobweb spiders in the family *Theridiidae* whose member species display different levels of sociality. These social-types vary dramatically in life history and distributions of colony sizes (Avilés 1997, Lubin and Bilde 2007). Some species are solitary, as most arachnids are, and offspring disperse from their natal group shortly after hatching. Other species are termed subsocial, and offspring remain with their mother for an extended maternal care phase. As offspring grow and require more room, they participate in communal activities like building and expanding the size of the web and cooperatively capturing prey. As offspring near adulthood they lose their conspecific tolerance and so disperse to live the remainder of their lives solitarily. Thus, subsocial populations are composed of numerous solitary adults and single-family colonies containing between one and a few dozen juvenile siblings. Still other species are fully social and show extremely high levels of philopatry among

offspring (Avilés 1997). In these species, one or a few closely-related and inseminated females found a colony and the resulting offspring participate in communal activities as they mature. However, the vast majority of offspring forgo dispersal and remain in their natal colony their entire lives where they mate with close relatives. Colony members show high levels of conspecific tolerance and even help one another to raise offspring (Avilés 1997, Marques et al 1998, Samuk et al 2012). Dispersal is usually triggered when a colony reaches some critical population threshold or suffers some catastrophic event like destruction from a falling tree. Those that disperse usually mate before they leave (Jacson & Joseph 1973, Lubin & Robinson 1982, Vollrath 1988, Avilés 1992, Avilés 1997). Thus, populations of social species show a wide range of colony sizes, from single individuals up to hundreds or even thousands of individuals (Avilés 1997). Finally, there are other species that fall somewhere in between these discrete social-types (Avilés & Harwood 2012). For example, species that are intermediate subsocial-social display much higher levels of philopatry than subsocial species, but the level of conspecific tolerance and their repertoire of social behaviours are less than that of fully social species (Marques et al 1998, Agnarsson 2006).

The geographic distribution of these social-types tends to fall along latitudinal and elevational gradients, with more social species restricted to lower latitudes and elevations (Avilés et al 2007, Powers & Avilés 2007, Purcell & Avilés 2007, Purcell & Avilés 2008). However, there is range overlap among social species at mid-elevations and latitudes (Agnarsson 2006, Avilés et al 2007, Purcell et al 2012), where they are observed to capture prey of different sizes. Species with larger, more permanent colonies capture larger prey, on average, than species

with smaller, temporary colonies (Guevara et al 2011). The mechanisms responsible for these differences, however, are not clear.

In this study we examine three sympatrically-occurring species of the spider genus *Anelosimus*: a subsocial species in its group-living phase, an intermediate social-subsocial species, and a fully social species. The latter two species build colonies that contain multiple adult females and their offspring, ranging from a few adults up to nearly a hundred individuals, but with the more social species forming more isolated and permanent colonies. The subsocial species, on the other hand, lives in single-family groups that range in size from one to a few dozen pre-adult siblings and their mother (Marques et al 1998, Agnarsson 2006, Purcell et al 2012). We performed feeding trials with various sizes of prey during which we tracked the number of individuals participating in prey capture and their responsiveness to different sizes of prey. We explored differences among species in the extent to which individuals participated in prey capture and whether the number of individuals participating as attackers increased as prey size increased. We tested the hypothesis that these differences, along with the spiders' characteristic colony sizes, explain the range of prey sizes they typically capture.

Chapter 2: Differences in degree of cooperation and group size likely lead to differential prey size use among sympatric social spiders

2.1 – Synopsis

To understand the behavioural and demographic mechanisms that allow for differential prey size use among sympatric social predators, we performed feeding trials on three co-occurring group-living spider species in southern Brazil. We presented three sizes of prey to a wide range of colony sizes for each spider species. We compared the level of cooperation displayed by each species by tracking the total number of spiders that respond to the prey, the average number of respondents that attack the prey at any time during the hunt compared to the average number of freeloading individuals, and the total number of respondents that participate over the duration of the hunt. Between the two species with higher levels of sociality, the one that captures on average larger prey in natural hunting scenarios also displayed higher levels of cooperation between individuals, suggesting that differences between species in cooperation can facilitate differential prey size use. The third species, which lives in smaller, temporary colonies, captures the smallest prey on average in natural hunting scenarios despite showing the highest levels of cooperation among the species, suggesting that group size places constraints on the range of prey sizes available to social predators.

2.2 - Materials and methods

    (a) *Study species and habitat*

The three species examined were *Anelosimus baeza* Agnarsson (subsocial), *Anelosimus jabaquara* Levi (intermediate social-subsocial), and *Anelosimus dubiosus* Keyserling (social),

which co-occur at Serra do Japi, a 354 km^2 semi-protected forest in São Paulo, Brazil (Purcell et al 2012). We tested 16, 29 and 32 colonies, respectively, and estimated the population of each by visually inspecting them at dusk when spiders are most active at repairing their web (Agnarsson 2006). The 16 colonies of the subsocial *A. baeza* and 32 colonies of the social *A. dubiosus* represent every colony that we located for these species, while the 29 colonies of *A. jabaquara* represent a subset of this more numerically abundant species. For this species, we purposely included the largest colony, while the remaining 28 colonies were randomly selected. We initially tested 32 colonies of *A. jabaquara* to match the number of colonies in *A. dubiosus*, but heavy rains destroyed several colonies before all trials could be completed. For the subsocial *A. baeza*, our study only included colonies containing multiple subadult spiders and excluded colonies containing solitary individuals. The reason for this is that we were primarily interested in the phenomenon of cooperation, so including solitary individuals in the analysis would have been inappropriate.

We presented each colony with small (3.9 ±0.16mm), medium (8.0 ±0.24mm) and large (14.2 ±0.37mm) prey, roughly corresponding to 1, 2 and 3-4 times the length of the largest spiders in the nests (older sub-adults in the first species, adult females in the latter two species). Prey consisted of live-captured flies and wasps that were propelled into the webs. We first measured the magnitude of each colony's response by tracking all the spiders that emerged from their refuges and surrounded the prey (i.e., *respondents).* Of these respondents, we calculated the average number of spiders attacking the prey (i.e., biting or ensnaring) at any time during the hunt vs. the average number merely observing they prey. By subtracting the latter from the former we obtained an *attackers-to-observers differential* as a measurement of

cooperation displayed by the species. Finally, we recorded the *total number of attackers* from each hunt to examine how group participation varies with prey size and colony size.

(b) *Analysis*

For a between-species comparison of *respondents* and *attackers-to-observers differential*, we constructed identical linear mixed-effects models with colony size, species, prey size-class, and their two and three-way interactions as factors, and with colony identity as a random factor to account for each colony being tested repeatedly with three prey items. To gauge any within-species variation in group participation for particular prey sizes, we performed separate ANCOVAs for each species to examine the effects of colony size, prey size and their interaction on the *total number of attackers*. All data were transformed ($\log_{10}[x +1]$) prior to analysis to ensure normality and to account for instances in which no spiders responded to the prey. Species differences were determined using planned orthogonal contrasts. All analyses were performed in R (2.15).

2.3 - Results

While all species employed a similar number of respondents for all prey sizes (figure 1) and all colony sizes (figure 3), the subsocial *A. baeza* maintained the highest attackers-to-observers differential across all prey (figure 2) and colony sizes (figure 4), followed by the social *A. dubiosus*, and then the intermediate social-subsocial *A. jabaquara* (figure 2). Whereas the subsocial and social species showed no correlation between colony size and the attackers-to-observers differential, the intermediate social-subsocial *A. jabaquara* had a significant negative

correlation (figure 4). That is, even though *A. jabaquara* increased the number of respondents with increasing colony size, most of these additional respondents did not actively engage with the prey.

The number of *respondents* per species as a function of prey size
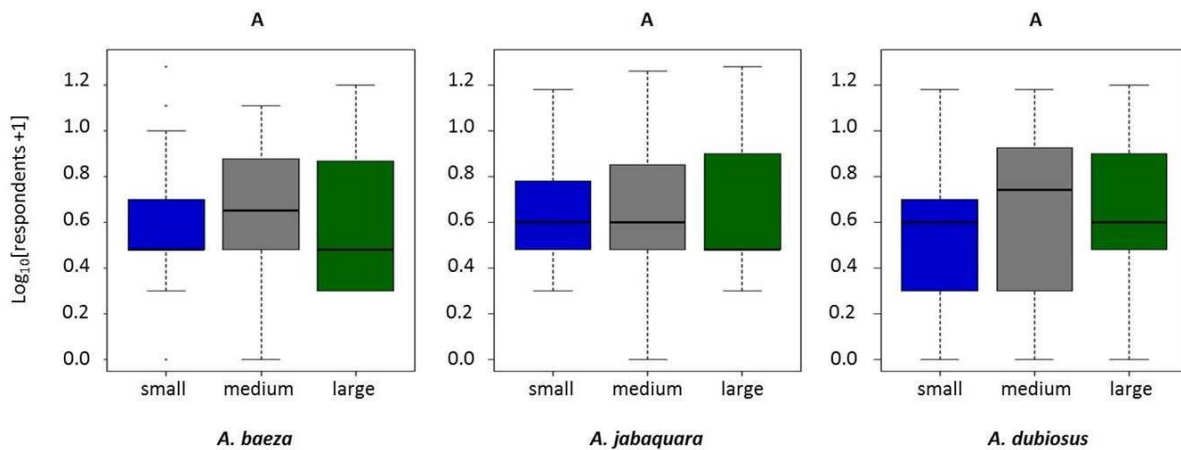

Figure 1: Log$_{10}$ transformed number of respondents for each species and prey sizes. There was no significant difference among species ($F_{2,71}$ = 1.70, p = 0.19), prey size ($F_{2,142}$ = 2.35, p = 0.10) or an interaction between the two ($F_{4,142}$ = 0.06, p = 0.99). Species with dissimilar letters above their boxplots are deemed significantly different via planned comparisons.

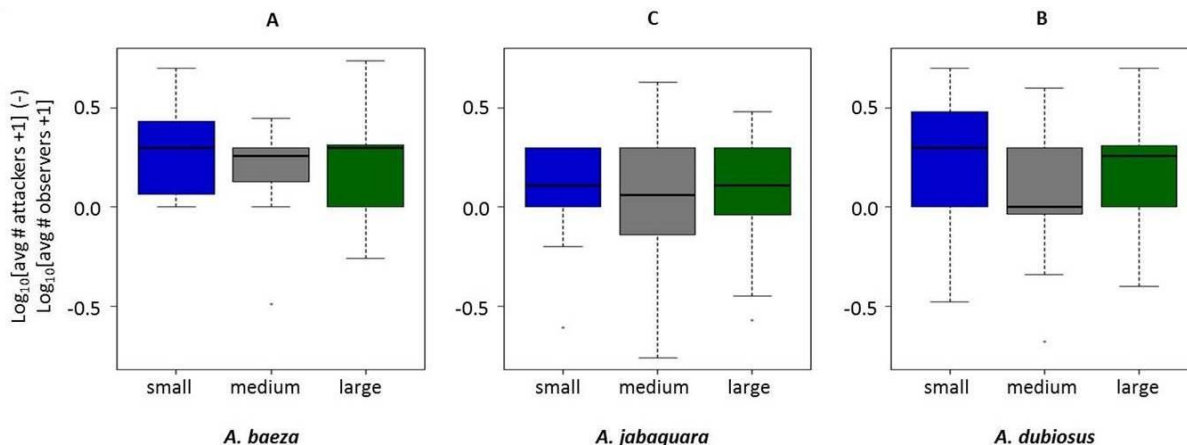The *attackers-to-observer differential* per species as a function of prey size

Figure 2: Log_{10} transformed attackers-to-observers differential for each species and prey sizes. There were significant differences among species ($F_{2,71}$ = 3.34, p = 0.04), but not among prey sizes ($F_{2,142}$ = 2.56, p = 0.08), and no significant interaction between species and prey size ($F_{4,142}$ = 0.32, p = 0.86). Species with dissimilar letters above their boxplots are deemed significantly different via planned comparisons.

The number of *respondents* per species as a function of colony size

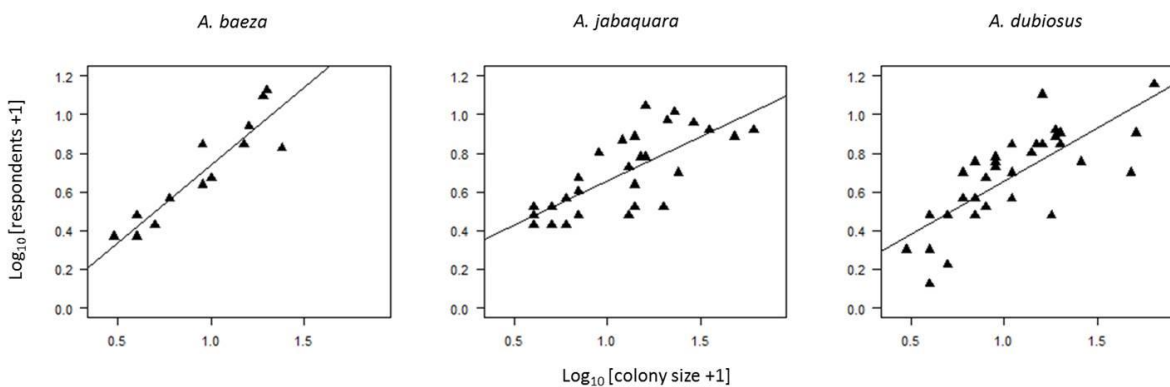**Figure 3**: Number of respondents as a function of colony size [CS]. All species increased their number of respondents as colony size increased, but *A. baeza* (respondents = 0.80*CS -0.07, r^2 = 0.85, p = <0.001) has a significantly steeper slope than *A. jabaquara* (respondents = 0.46*CS + 0.20, r^2 = 0.55, p = <0.001) and *A. dubiosus* (respondents = 0.55*CS, r^2 = 0.56, p = <0.001).

The *attackers-to-observers differential* per species as a function of colony size
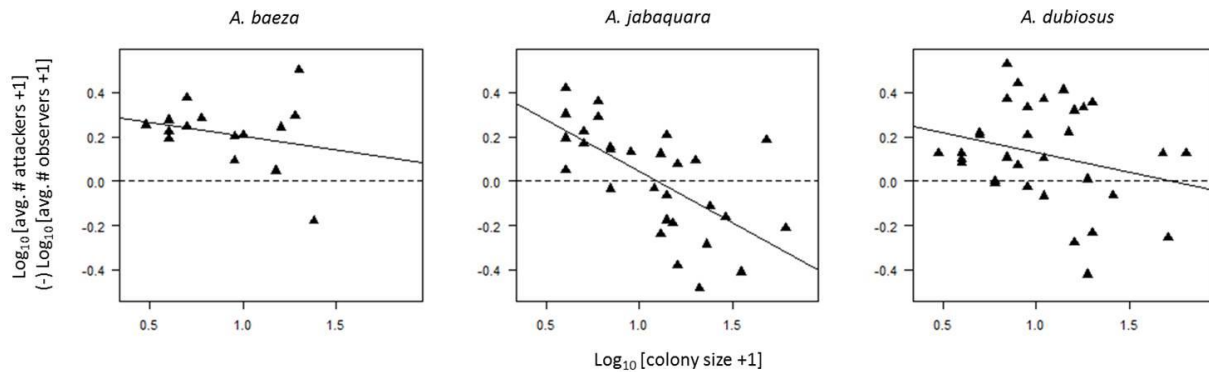
Figure 4: Attackers-to-observers differential as a function of colony size. Of the three species, only the intermediate social-subsocial *A. jabaquara* has a significant correlation: *A. baeza* differential = -0.13*CS + 0.33, r^2 = -0.001, p = 0.34; *A. jabaquara* differential = -0.46*CS + 0.51, r^2 = 0.40, p = <0.001; *A. dubiosus* differential = -0.18*CS + 0.30, r^2 = 0.04, p = 0.15. Each point represents one colony's response, averaged across all three prey sizes. Dashed line indicates an equal number of attackers and observers.

For *total attackers*, we found that the subsocial *A. baeza* increased its group participation as colony size increased for all prey sizes, while the two more social species had significant interactions between colony size and prey size: in the intermediate social-subsocial *A. jabaquara*, there was increased group participation for both large and medium prey, while for the more social *A. dubiosus* this increase was present for large prey only (figure 5).

The number of attackers per species as a function of prey size and colony size
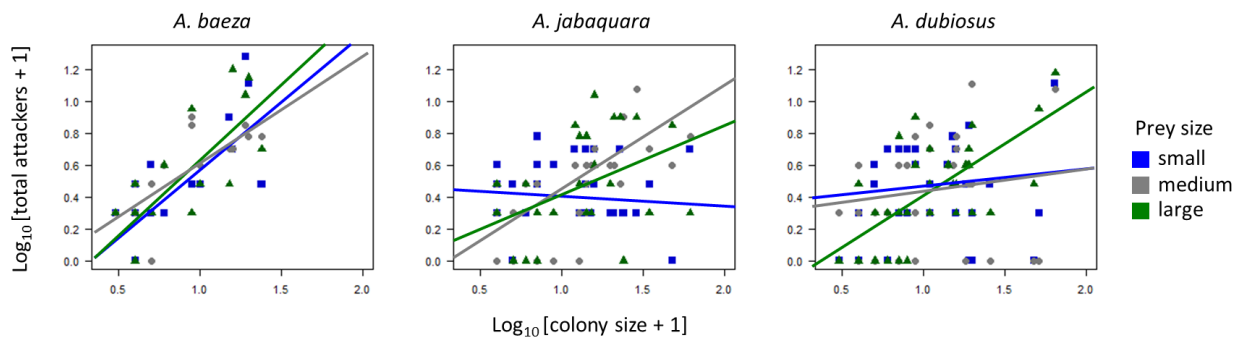
Figure 5: Total number of attackers for each species as a function of colony size for the three prey sizes. *Anelosimus baeza* showed no significant interaction between prey size and colony size ($F_{2,42}$ = 0.52, p = 0.60), but this was not the case for *A. jabaquara* ($F_{2,81}$ = 4.61, p = 0.01) and *A. dubiosus* ($F_{2,90}$ = 3.01, p = 0.05).

Table 1: Linear mixed-effects model with $\log_{10}$ [*NUMBER OF RESPONDENTS* +1] as the response variable.

Fixed Effects	DF	F-value	p-value
Colony Size	1, 71	88.02	**<0.001**
Species	2, 71	1.70	0.19
Prey Size Class	2, 142	2.35	0.10
Species: Colony Size	2, 71	3.32	**0.04**
Colony Size: Prey Size Class	2, 142	2.73	0.07
Species: Prey Size Class	4, 142	0.06	0.993
Species: Colony Size: Prey Size Class	4, 142	0.68	0.61
Random Effects	Variance		
Colony Identity	0.002		
Residual	0.063		

Table 2: Linear mixed-effects model with $\log_{10}$ [*AVERAGE # ATTACKERS* +1] (-) $\log_{10}$ [*AVERAGE # OBSERVRS* +1] as the response variable (i.e., the attackers-to-observers differential).

Fixed Effects	DF	F-value	p-value
Colony Size	1, 71	11.96	**<0.001**
Species	2, 71	3.34	**0.04**
Prey Size Class	2, 142	2.56	0.08
Species: Colony Size	2, 71	2.58	0.08
Colony Size: Prey Size Class	2, 142	3.28	**0.04**
Species: Prey Size Class	4, 142	0.32	0.86
Species: Colony Size: Prey Size Class	4, 142	0.94	0.44
Random Effects	Variance		
Colony Identity	$5.68\ e^{-10}$		
Residual	$7.60\ e^{-2}$		

Table 3: Separate ANCOVAs for each species examining the influence of colony size and prey size on $\log_{10}$ [*TOTAL NUMBER OF ATTACKERS* +1].

A. baeza	DF	F-value	p-value
Colony Size	1	53.34	**<0.0001**
Prey Size Class	2	0.13	0.88
Colony Size : Prey Size Class	2	0.52	0.60
A. jabaquara			
Colony Size	1	15.34	**0.0002**
Prey Size Class	2	0.05	0.96
Colony Size : Prey Size Class	2	4.68	**0.01**
A. dubiosus			
Colony Size	1	22.05	**<0.0001**
Prey Size Class	2	0.01	0.99
Colony Size : Prey Size Class	2	2.93	**0.05**

2.4 - Discussion

Though it is known that co-occurring species of social spiders capture different sizes of prey (Guevara et al 2011), our study showed how two quantifiable traits, colony size and degree of cooperation among colony members, can play a role in determining this pattern. When species have similar group sizes, the species exhibiting greater cooperative tendencies should be able to capture larger prey. Thus, the more social *A. dubiosus* not only had more of its respondents attacking prey at a given time than the less social *A. jabaquara*, but its larger colonies increased their participation only when encountering the largest prey. High levels of cooperation, however, cannot make up for smaller group sizes. Though the least social species, *A. baeza*, displayed the highest levels of cooperation among colony members, it captures the smallest prey, likely because its colonies are not only significantly smaller than those of the other two species, but also because a large fraction of its population consists of solitary individuals who cannot subdue large prey (Guevara et al 2011). Thus, populations of this species as a whole capture small prey on average.

We also found that the two more social species, *A. jabaquara* and *A. dubiosus*, do not passively filter aerial prey, but instead actively increase their group participation for particular sizes of prey, perhaps to better exploit the most appropriate resources for their colony sizes. Yip et al (2008) found that growing spider colonies face a scaling predicament as the three dimensional volume of the refuge area increases more quickly than the two-dimensional surface of the prey-capture web, resulting in less capture area per individual. The spiders make up for the fewer insects caught per capita by capturing increasingly large ones as colony size increases (Yip et al 2008). Thus, species that form large colonies are only found in lowland

tropical and subtropical areas where there is a much greater abundance of large insects than at higher elevations or latitudes (Powers & Avilés 2007, Avilés et al 2007, Guevara & Avilés 2007, Purcell & Avilés 2007).

Serra do Japi is a uniquely situated mid-elevation and mid-latitude habitat that is suitable for *Anelosimus* species of different levels of sociality (Purcell et al 2012). Whether the dietary differentiation observed here is coincidental, or the product of mechanisms to prevent competition among these species, such as non-random species assemblage or character displacement, is yet to be determined. Perhaps selection on different behavioural strategies bestows each species with a particular range of colony sizes and a certain degree of cooperative behaviour, which in turn lead to dietary differentiation. Similar means of dietary differentiation may characterize other communities with otherwise potentially competing social predators (Hayward & Kerley 2008). Further studies of other social communities and of communities of other social predators are needed, however, before definite conclusions can be drawn.

The elevated levels of cooperation displayed by group-living *A. baeza* juveniles might seem contradictory to their solitary adult lifestyle, but as adults, these spiders must be self-sufficient to survive and reproduce. Thus, one might expect strong selection against passivity, as group-living juveniles with a tendency to hesitate to attack might not survive as adults. In contrast, individuals living in permanent multi-family colonies likely face relaxed selection for aggressive behaviour, as passive individuals can take advantage of prey captured by their more aggressive nest mates. Reduced aggression within social species has already been documented in the genus *Anelosimus*: females of less social species protect their egg-sacs more aggressively than females from more social cooperatively breeding species (Samuk et al 2012) and a closely

related species shows a positive correlation between group size and the frequency of individuals displaying a passive behavioural phenotype (Pruitt et al 2011).

Empirical and theoretical studies of group hunting predators tend to focus on group size as the variable expected to correlate with prey capture success and the size of prey caught (Caraco & Wolf 1975, Creel & Creel 1995). Here we show that whether the hunting potential of a given group size is realized will depend on the behaviour of its members. Thus, studies of group-hunting predators may need to be revisited with an eye to assess the degree to which hunting party members do, or do not, participate in the hunt.

Chapter 3: Conclusion

The aim of this research has been to better understand the behavioural and demographic mechanisms that allow different group-living predators to capture prey of different sizes. This, in turn, is a first step in a larger effort to understand how variation in the level of sociality affects coexistence among group-living organisms. There were three key findings in this research: (1) among species with equally large colonies, differences in collective and individual behaviours are consistent with differences in the size of the prey they capture; (2) species with a large range of colony sizes are subject to group-size-dependent variation in their group participation for different prey sizes, whereas species with a smaller range of colony sizes behave more or less consistently across all group sizes and prey sizes; and (3) small colony size constrains the maximum size of insects that can be captured.

Dietary differentiation is critically important for species coexistence, as a species whose diet overlaps entirely with that of another species can be outcompeted to extinction or be subject to character displacement (Dickman 1988, Dayan & Simblerloff 1998, Grant & Grant 2006). Among solitary predators, body size is likely the most important characteristic determining dietary breadth, as larger animals are privileged to a greater range of prey sizes, while small predators make do with a subset of prey sizes that may be within the range captured by larger predators (Shoener 1969, Peters & Wassenberg 1983, Bekoff et al 1984, Gittleman 1985, Losos et al 1989, Marti et al 1993, Woodward & Hildrew 2002, Cohen et al 2003, Sinclair et al 2003, Radloff & Du Toit 2004, Jonsson et al 2005, Hayward & Kerley 2008, Costa 2009). Thus, current theory contends that a non-random assortment of body sizes is fundamental to community assembly (Dayan & Simberloff 1998, Woodward et al 2005, Brown

et al 2004), as an assortment of differently sized predators will capture different sizes of prey and will promote coexistence in a single community. If several coexisting predators are roughly the same size, then other factors are expected to reinforce partitioning of niche space. For example, strong competitive interaction may steer evolution towards phenological differentiation so that species reach maturity at different times of the year (Werner & Gilliam 1984, Polis et al 1989), or towards diurnal shifts such that species are active at different times of the day (Schoener 1974, Marti et al 1993, Richards 2002, Kronfeld-Schor & Dayan 2003). By exploiting the environment in complementary ways, solitary predators can avoid direct competition for the same resources, which can facilitate coexistence with other species.

Social predators are fundamentally different from solitary predators in that their cooperative lifestyle allows them to capture much larger prey than an individual. Thus, body size differences among social predator species do not sufficently explain patterns of dietary differentiation, and ultimately coexistence. Instead, differences in group size and cooperative behaviour of individuals may play a larger role in determining the size of prey captured. As initially hypothesized, this research showed that, among species with similar group sizes, those that capture larger prey in natural hunting scenarios also show higher levels of cooperation. When spiders from the more social *A. dubiosus* respond to a prey, at any given time, a greater number of individuals are involved as attackers rather than freeloaders compared to the intermediate social-subsocial *A. jabaquara*. Moreover, the attackers-to-observers differential was not correlated with colony size in *A. dubiosus*, whereas it was negatively correlated with colony size in *A. jabaquara*, indicating that larger colonies of *A. jabaquara* experienced greater levels of freeloading among respondents. Finally, increasingly large colonies of *A. dubiosus* have

higher levels of group participation (i.e., the total number of attackers) for large prey only, whereas increasingly large colonies of *A. jabaquara* had higher levels of group participation for both large and medium prey. This greater appeal to large prey in particular, coupled with the higher levels of cooperation in its largest colonies, likely allows *A. dubiosus* to capture larger prey on average than *A. jabaquara*. However, the distribution of different group sizes within a species may play an even greater role in determining prey size use than cooperation. In our feeding trials, the subsocial *A. baeza* showed high levels of cooperation and was highly successful in capturing all sizes of prey, but this was at odds with the fact that in natural populations, it captures the smallest prey among all tested species (Guevara et al 2011). This most likely has to do with the colony size distribution of this particular species, as the population is dominated by solitary individuals, which cannot capture large prey on their own, while group-living family groups are less abundant (Purcell et al 2012). In contrast, the other two species, and the more social *A. dubiosus*, in particular, form colonies from which individuals are less likely to disperse so that their populations are dominated by a greater number of nests containing multiple adults and fewer with solitary individuals. A greater abundance of larger colonies in these species allow them to capture larger prey on average.

Although a comparison between three species is not sufficient for drawing general conclusions, this study provides a first step to better understand the mechanisms that may lead to dietary differentiation among social predators, which in turn points to the importance of level of sociality as a mechanism of coexistence in natural communities. Just as communities of solitary predators may be composed of a non-random assortment of body sizes, communities of group-living predators may be composed of a non-random assortment of species with

different levels of sociality. The differing philopatric tendencies of individuals of various species lead to different distributions in their group sizes, while the differing levels of conspecific tolerance might affect how well individuals in those groups work together. Furthermore, colony size appears to be associated with the type of plant substrate that the various species require for nest-building, thus further differentiating species in the way they exploit their environment (Purcell et al 2012). Social species like *A. dubiosus* have low dispersal rates and female-biased sex ratios, which allow colonies to rapidly grow to an adequate size (Avilés 1997). These species tend to construct webs centrally on plants where there is greater structural support for their larger and longer lived nests. They also tend to occupy the forest interior instead of the forest edge, where vegetation is more robust and longer lived. In contrast, less social species, such as *A. jabaquara* have higher dispersal rates and individuals are more likely to live solitarily. The species tends to build its webs at the distal ends of branches, perhaps because its colonies do not grow as large and are not as long lasting than those of *A. dubiosus*. Nevertheless, they still occupy the forest interior where there is greater structural support than at the forest edge. Subsocial species like *A. baeza* are obligatorily solitary as adults and thus do not require sturdy plants for structural support of their small nests. These types of species can thus build their webs on smaller plants in open areas, which may be less adequate for the more social species. Ultimately, the life history traits of each species determine both the size distribution of their colonies and the way in which its individuals interact with one another. The distribution of colony sizes, in turn, determines the structural requirements for nest-site location, while the interplay between the distribution of colony sizes and the extent to which individuals cooperate in prey capture further determine the average size of prey that a species captures. The

combination of these two factors may then create sufficiently large differences to reduce dietary overlap between species, thus facilitating coexistence.

This research provides key information that has been absent from most discussions of community assembly, namely, the factors that may allow multiple group-living predators to co-exist. One strength of this study is that the close phylogenetic relationships among the species considered implies that they exhibit minimal differences in morphology and body size that may influence the size of the prey they capture, making group behaviour and colony size differences the more prominent factors of differentiation. A second strength of this study is that it teases apart the mechanisms that may be responsible for dietary differentiation in a group of social predators, including the cooperative tendencies of individuals, colony size, and their interaction. What is still lacking is an accurate way to quantify the relative importance of body size, group behaviour and the distribution of group sizes in determining a species' diet. We know that larger bodied predators benefit from a greater dietary breadth, and we have shown that the distribution of group sizes can potentially play a larger role in determining prey size than the level of cooperation among individuals. The relative importance of these three factors, however, has not been assessed. This would require an expansion of our study to include not only species of various group sizes, but also of varying body sizes. Unfortunately, sociality is rare among predators, constituting only 10-15% of carnivore species (Bekoff et al 1984, Gittleman 1984), so we are unlikely to find a community with a sufficiently large number of congeneric species that vary both in body and colony size. Alternatively, theoretical models could shed light on these issues. The work laid out in this thesis could be used in setting the parameter values for such theoretical models.

In conclusion, the factors determining community assembly may be different for solitary and group-living predators. Among solitary predators, body size is likely a key factor, as it limits the size of prey that a species can capture. When several coexisting solitary predator species are similar in size, they often differ in other life-history traits to exploit their environment at different times of the year or day thus avoiding dietary overlap. For group-living predators, body size is less of a factor since cooperative individuals can capture prey many times larger than themselves. As shown here, differences in group size and collective behaviours may play a major role in determining the size of the prey captured and thus the community in which a species can persist.

Bibliography:

Agnarsson, I., 2006. A revision of the New World eximius lineage of Anelosimus (Araneae, Theridiidae) and a phylogenetic analysis using worldwide exemplars. Zoological Journal of the Linnean Society 146, 453–593.

Agnarsson, I., Avilés, L., Coddington, J.A., Maddison, W.P., 2006. Sociality in Theridiid Spiders: Repeated Origins of an Evolutionary Dead End. Evolution 60, 2342–2351.

Avilés, L., 1992. Metapopulation biology, levels of selection and sex ratio evolution in social spiders. Doctoral dissertation. Harvard University, Cambridge, Massachusetts.

Avilés, L., 1993. Interdemic Selection and the Sex Ratio: A Social Spider Perspective. The American Naturalist 142, 320–345.

Avilés, L., 1997. The Causes and Consequences of Cooperation and Permanent-Sociality in Spiders, in: Choe, J.C., Crespi, B.J. (eds.), The Evolution of Social Behaviour in Insects and Arachnids. Cambridge: Cambridge University Press, pp. 476-498.

Avilés, L., Agnarsson, I., Salazar, P.A., Purcell, J., Iturralde, G., Yip, E.C., Powers, K.S., Bukowski, T.C., 2007. Altitudinal Patterns of Spider Sociality and the Biology of a New Midelevation Social Anelosimus Species in Ecuador. The American Naturalist 170, 783–792.

Avilés, L., Harwood, G., 2012. A Quantitative Index of Sociality and its Application to Group-Living Spiders and Other Social Organisms. Ethology, 118, 1219-1229.

Barlow, A., Pook, C.E., Harrison, R.A., Wüster, W., 2009. Coevolution of diet and prey-specific venom activity supports the role of selection in snake venom evolution. Proceedings of the Royal Society B 276, 2443–2449.

Barnard, C.J., Sibly, R.M., 1981. Producers and scroungers: A general model and its application to captive flocks of house sparrows. Animal Behaviour 29, 543–550.

Baum, J.K., Worm, B., 2009. Cascading top-down effects of changing oceanic predator abundances. Journal of Animal Ecology 78, 699–714.

Bauwens, D., Garland, T., Castilla, A.M., Damme, R.V., 1995. Evolution of Sprint Speed in Lacertid Lizards: Morphological, Physiological and Behavioral Covariation. Evolution 49, 848–863.

Bekoff, M., Daniels, T.J., Gittleman, J.L., 1984. Life History Patterns and the Comparative Social Ecology of Carnivores. Annual Review of Ecology and Systematics 15, 191–232.

Bennett, A.F., Huey, R.B., 1990. Studying the evolution of physiological performance. Oxford Surveys in Evolutionary Biology *7*, 251-284.

Bertram, B.C.R., 1979. Serengeti Predators and their Social Systems, in: Sinclair, A.R.E (Ed.), Serengeti: Dynamics of an Ecosystem. Chicago: University of Chicago Press, pp. 221-248.

Blum, M.S. (Ed.), 1981. Chemical defenses of arthropods. New York: Academic Press.

Bowen, W.D., 1981. Variation in coyote social organization: the influence of prey size. Canadian Journal of Zoology 59, 639–652.

Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M., West, G.B., 2004. Toward a metabolic theory of ecology. Ecology 85, 1771–1789.

Caraco, T., Wolf, L.L., 1975. Ecological Determinants of Group Sizes of Foraging Lions. The American Naturalist 109, 343–352.

Chesson, P., 2000. Mechanisms of Maintenance of Species Diversity. Annual Review of Ecology and Systematics 31, 343–366.

Clark, C.W., Mangel, M., 1986. The evolutionary advantages of group foraging. Theoretical Population Biology 30, 45–75.

Cohen, J.E., Jonsson, T., Carpenter, S.R., 2003. Ecological community description using the food web, species abundance, and body size. Proceedings of the National Academy of Science 100, 1781–1786.

Costa, G.C., 2009. Predator size, prey size, and dietary niche breadth relationships in marine predators. Ecology 90, 2014–2019.

Creel, S., Creel, N.M., 1995. Communal hunting and pack size in African wild dogs, Lycaon pictus. Animal Behaviour 50, 1325–1339.

Dayan, T., Simberloff, D., 1998. Size patterns among competitors: ecological character displacement and character release in mammals, with special reference to island populations. Mammal Review 28, 99–124.

Dickman, C.R., 1988. Body size, prey size, and community structure in insectivorous mammals. Ecology 69, 569–580.

Eisner, T., 1970. Chemical defense against predation in arthropods. Chemical Ecology, 157-217.

Estes, J.A., Palmisano, J.F., 1974. Sea otters: their role in structuring nearshore communities. Science 185, 1058–1060.

Fanshawe, J.H., Fitzgibbon, C.D., 1993. Factors influencing the hunting success of an African wild dog pack. Animal Behaviour 45, 479–490.

Fuiman, L.A., Magurran, A.E., 1994. Development of predator defences in fishes. Reviews in Fish Biology and Fisheries 4, 145–183.

Gittleman, J.L., 1985. Carnivore body size: Ecological and taxonomic correlates. Oecologia 67, 540–554.

Gittleman, J.L., 1989. Carnivore Group Living: Comparative Trends, in: Gittleman, J.L. (Ed.), Carnivore Behavior, Ecology, and Evolution. Ithaca: Cornell University Press, pp. 183–207.

Grant, P.R., Grant, B.R., 2006. Evolution of Character Displacement in Darwin's Finches. Science 313, 224–226.

Guevara, J., Avilés, L., 2007. Multiple techniques confirm elevational differences in insect size that may influence spider sociality. Ecology 88, 2015–2023.

Guevara, J., Gonzaga, M.O., Vasconcellos-Neto, J., Avilés, L., 2011. Sociality and resource use: insights from a community of social spiders in Brazil. Behavioral Ecology 22, 630–638.

Harris, M.A., Steudel, K., 1997. Ecological correlates of hind-limb length in the Carnivora. Journal of Zoology 241, 381–408.

Hayward, M.W., Kerley, G.I.H., 2008. Prey preferences and dietary overlap amongst Africa's large predators. South African Journal of Wildlife Research 38, 93–108.

Holt, R.D., 1977. Predation, apparent competition, and the structure of prey communities. Theoretical Population Biology 12, 197–229.

Huston, M., 1979. A General Hypothesis of Species Diversity. The American Naturalist 113, 81–101.

Jacson, C.C., Joseph, K.J., 1973. Life-history, bionomics and behaviour of the social spider Stegodyphus sarasinorum Karsch. Insects Sociaux 20, 189–203.

Jonsson, T., Cohen, J.E., Carpenter, S.R., 2005. Food Webs, Body Size, and Species Abundance in Ecological Community Description. Advances in Ecological Research 5, 1–84.

Keller, L., Nonacs, P., 1993. The role of queen pheromones in social insects: queen control or queen signal? Animal Behaviour 45, 787–794.

Kronfeld-Schor, N., Dayan, T., 2003. Partitioning of Time as an Ecological Resource. Annual Review of Ecology, Evolution, and Systematics 34, 153–181.

Kruuk, H., 1964. Predators and Anti-Predator Behaviour of the Black-Headed Gull (Larus Ridibundus L.). Behaviour. Supplement III–129.

Kruuk, H. (Ed.), 1972. The spotted hyena: a study of predation and social behavior. Chicago: University of Chicago Press.

Kruuk, H., 1975. The Function Aspects of Social Hunting by Carnivores, in: Beer, C., Manning, A. (Eds.), Function and Evolution of Behaviour. Oxford: Clarendon Press, pp. 119-141.

Lack, D. (Ed.), 1947. Darwin's Finches. Cambridge: Cambridge University Press.

Losos, J.B., Naeem, S., Colwell, R.K., 1989. Hutchinsonian Ratios and Statistical Power. Evolution 43, 1820–1826.

Losos, J.B., Sinervo, B., 1989. The Effects of Morphology and Perch Diameter on Sprint Performance of Anolis Lizards. Journal of Experimental Biology 145, 23–30.

Lubin, Y., Bilde, T., 2007. The Evolution of Sociality in Spiders, in: H. Jane Brockmann, T.J.R. (Ed.), Advances in the Study of Behavior 37, 83–145.

Lubin, Y.D., Robinson, M.H., 1982. Dispersal by Swarming in a Social Spider. Science 216, 319–321.

MacNulty, D.R., Smith, D.W., Mech, L.D., Vucetich, J.A., Packer, C., 2012. Nonlinear effects of group size on the success of wolves hunting elk. Behavioral Ecology 23, 75–82.

Magurran, A.E., 1990. The adaptive significance of schooling as an anti-predator defense in fish. Annales Zoologici Fennici 27, 51–66.

Marques, E.S.A., Vasconcelos-Neto, J., Mello, M.B. de, 1998. Life History and Social Behavior of Anelosimus jabaquara and Anelosimus dubiosus (Araneae, Theridiidae). Journal of Arachnology 26, 227–237.

Marti, C.D., Steenhof, K., Kochert, M.N., Marks, J.S., 1993. Community Trophic Structure: The Roles of Diet, Body Size, and Activity Time in Vertebrate Predators. Oikos 67, 6–18.

Metcalfe, N.B., Fraser, N.H.C., Burns, M.D., 1999. Food availability and the nocturnal vs. diurnal foraging trade-off in juvenile salmon. Journal of Animal Ecology 68, 371–381.

Michener, C.D. (Ed.), 1974. The Social Behavior of the Bees: A Comparative Study. Cambridge: Harvard University Press.

Nelson, B.V., Vance, R.R., 1979. Diel foraging patterns of the sea urchin Centrostephanus coronatus as a predator avoidance strategy. Marine Biology 51, 251–258.

Nentwig, W., 1985. Social spiders catch larger prey: a study of Anelosimus eximius (Araneae: Theridiidae). Behavioral Ecology and Sociobiology 17, 79–85.

Nudds, T.D., 1978. Convergence of Group Size Strategies by Mammalian Social Carnivores. The American Naturalist 112, 957–960.

Pace, M.L., Cole, J.J., Carpenter, S.R., Kitchell, J.F., 1999. Trophic cascades revealed in diverse ecosystems. Trends in Ecology & Evolution 14, 483–488.

Packer, C., 1986. The Ecology of Sociality in Felids, in: Rubenstein, D.I., Wrangham, R.W. (Eds.) Ecological Aspects of Social Evolution. Princeton: Princeton University Press, 425-451.

Packer, C., Ruttan, L., 1988. The Evolution of Cooperative Hunting. The American Naturalist 132, 159–198.

Paine, R.T., 1966. Food Web Complexity and Species Diversity. The American Naturalist 100, 65–75.

Paine, R.T., 1980. Food Webs: Linkage, Interaction Strength and Community Infrastructure. Journal of Animal Ecology 49, 667–685.

Paterson, J.R., García-Bellido, D.C., Lee, M.S.Y., Brock, G.A., Jago, J.B., Edgecombe, G.D., 2011. Acute vision in the giant Cambrian predator Anomalocaris and the origin of compound eyes. Nature 480, 237–240.

Peters, R.H., Wassenberg, K., 1983. The effect of body size on animal abundance. Oecologia 60, 89–96.

Pitcher, T.J., Parish, J.K, 1992. Functions of Shoaling Behaviour in Teleosts, in: Pitcher, T.J. (ed.) Behaviour of Teleost fishes. London: Chapman & Hall, pp. 363-427.

Polis, G.A., Myers, C.A., Holt, R.D., 1989. The Ecology and Evolution of Intraguild Predation: Potential Competitors That Eat Each Other. Annual Review of Ecology and Systematics 20, 297–330.

Powers, K.S., Avilés, L., 2007. The role of prey size and abundance in the geographical distribution of spider sociality. Journal of Animal Ecology 76, 995–1003.

Pruitt, J.N., Iturralde, G., Avilés, L., Riechert, S.E., 2011. Amazonian social spiders share similar within-colony behavioural variation and behavioural syndromes. Animal Behaviour 82, 1449–1455.

Purcell, J., Avilés, L., 2007. Smaller colonies and more solitary living mark higher elevation populations of a social spider. Journal of Animal Ecology 76, 590–597.

Purcell, J., Avilés, L., 2008. Gradients of precipitation and ant abundance may contribute to the altitudinal range limit of subsocial spiders: insights from a transplant experiment. Proceedings of the Royal Society B 275, 2617–2625.

Purcell, J., Vasconcellos-Neto, J., Gonzaga, M.O., Fletcher, J.A., Avilés, L., 2012. Spatio-Temporal Differentiation and Sociality in Spiders. PLoS ONE 7, e34592.

Radloff, F.G.T., Du Toit, J.T., 2004. Large predators and their prey in a southern African savanna: a predator's size determines its prey size range. Journal of Animal Ecology 73, 410–423.

Richards, S.A., 2002. Temporal partitioning and aggression among foragers: modeling the effects of stochasticity and individual state. Behavioral Ecology 13, 427-438.

Roitberg, B.D., Isman, M.B. (Eds.), 1992. Insect Chemical Ecology: An Evolutionary Approach. New York: Chapman & Hall.

Rosenzweig, M.L., 1966. Community Structure in Sympatric Carnivora. Journal of Mammalogy 47, 602.

Rothschild, M., 1972. Secondary plant substances and warning colouration in insects. Symposium of the Royal Entomological Society of London 6, 59-83.

Ruxton, G.D., Sherratt, T.N., Speed, M.P. (Eds.), 2004. Avoiding attack: the evolutionary ecology of crypsis, warning signals, and mimicry (Vol. 249). Oxford: Oxford University Press.

Samuk, K.M., LeDue, E.E., Avilés, L., 2012. Sister clade comparisons reveal reduced maternal care behavior in social cobweb spiders. Behavioral Ecology 23, 35–43.

Schaller, G.B. (Ed.), 1972. The Serengeti lion: a study of predator–prey relations. Chicago: Chicago University Press.

Scharf, F.S., Juanes, F., Rountree, R.A., 2000. Predator size-prey size relationships of marine fish predators: interspecific variation and effects of ontogeny and body size on trophic-niche breadth. Marine Ecology Progress Series 208, 229-248.

Schluter, D., Grant, P.R., 1984. Determinants of Morphological Patterns in Communities of Darwin's Finches. The American Naturalist 123, 175–196.

Schoener, T.W., 1969. Models of Optimal Size for Solitary Predators. The American Naturalist 103, 277–313.

Schoener, T.W., 1974. Resource partitioning in ecological communities. Science 185, 27-39.

Seeley, T. D., 2009. The wisdom of the hive: the social physiology of honey bee colonies. Cambridge: Harvard University Press.

Sherman, P. W. (1977). Nepotism and the evolution of alarm calls. Science, 197, 1246-1253.

Shine, R., 1991. Why do Larger Snakes Eat Larger Prey Items? Functional Ecology 5, 493.

Siegfried, W.R., Underhill, L.G., 1975. Flocking as an anti-predator strategy in doves. Animal Behaviour 23, 504–508.

Sinclair, A.R.E., Mduma, S., Brashares, J.S., 2003. Patterns of predation in a diverse predator–prey system. Nature 425, 288–290.

Stevens, M., Merilaita, S., 2009. Animal camouflage: current issues and new perspectives. Philosophical Transactions of the Royal Society B 364, 423–427.

Stinson, C.H., 1980. Flocking and Predator Avoidance: Models of Flocking and Observations on the Spatial Dispersion of Foraging Winter Shorebirds (Charadrii). Oikos 34, 35–43.

Théry, M., Debut, M., Gomez, D., Casas, J., 2005. Specific color sensitivities of prey and predator explain camouflage in different visual systems. Behavioral Ecology 16, 25–29.

Uetz, G.W., 1992. Foraging strategies of spiders. Trends in Ecology & Evolution 7, 155–159.

Unger, P.A., Lewis, W.M., 1983. Selective Predation with Respect to Body Size in a Population of the Fish Xenomelaniris Venezuelae (Atherinidae). Ecology 64, 1136.

Vanhooydonck, B., Herrel, A., Damme, R.V., Irschick, D.J., 2006. The Quick and the Fast: The Evolution of Acceleration Capacity in Anolis Lizards. Evolution 60, 2137–2147.

Vermeij, G. J., 2002. Evolution in the consumer age: predators and the history of life. Paleontological Society Papers, 8, 375-394.

Vézina, A.F., 1985. Empirical relationships between predator and prey size among terrestrial vertebrate predators. Oecologia 67, 555–565.

Vickery, W.L., Giraldeau, L.-A., Templeton, J.J., Kramer, D.L., Chapman, C.A., 1991. Producers, Scroungers, and Group Foraging. The American Naturalist 137, 847–863.

Vollrath, F., 1982. Colony Foundation in a Social Spider. Zeitschrift für Tierpsychologie 60, 313–324.

Wainwright, P.C., Richard, B.A., 1995. Predicting patterns of prey use from morphology of fishes. Environmental Biology of Fishes 44, 97–113.

Ward, P., Zahavi, A., 1973. The Importance of Certain Assemblages of Birds as "information-Centres" for Food-Finding. Ibis 115, 517–534.

Wcislo, W.T., Arneson, L., Roesch, K., Gonzalez, V., Smith, A., Fernández, H., 2004. The evolution of nocturnal behaviour in sweat bees, Megalopta genalis and M. ecuadoria (Hymenoptera: Halictidae): an escape from competitors and enemies? Biological Journal of the Linnean Society 83, 377–387.

Werner, E.E., Gilliam, J.F., 1984. The Ontogenetic Niche and Species Interactions in Size-Structured Populations. Annual Review of Ecology and Systematics 15, 393–425.

Wilson, E.O. (Ed.), 1971. The Insect Societies. Cambridge: Belknap

Woodward, G., Ebenman, B., Emmerson, M., Montoya, J.M., Olesen, J.M., Valido, A., Warren, P.H., 2005. Body size in ecological networks. Trends in Ecology & Evolution 20, 402–409.

Woodward, G., Hildrew, A.G., 2002. Body-size determinants of niche overlap and intraguild predation within a complex food web. Journal of Animal Ecology 71, 1063–1074.

Yip, E.C., Powers, K.S., Avilés, L., 2008. Cooperative capture of large prey solves scaling challenge faced by spider societies. Proceedings of the National Academy of Science 105, 11818–11822.