

Notes on the ecology and behavior of a subsocial spider *Anelosimus baeza* (Araneae: Theridiidae) in Mexico

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Abstract. Subsocial spiders are located on the continuum between solitary species and social species and are characterized by extended maternal care, some cooperation in foraging and colony activities and dispersal in order to found new colonies. In the genus *Anelosimus* (Araneae: Theridiidae), up to nine species are thought to be subsocial. One of these spiders, *A. baeza* Agnarsson (2006), is distributed across a large geographical range from Mexico to southern Brazil, and potential differences in behavior in different populations are unknown. We studied the ecology and behavior of a population of *A. baeza* in a cloud forest habitat in Mexico. We tracked the population for ten months, analyzed the degree of cooperation and the presence of associated species, and explored the settling decisions made by dispersing spiders. We show that the breeding season for *A. baeza* in Mexico differs from other populations elsewhere in South America. Using a kinematic diagram, we recorded the sequence of behaviors involved in subduing and feeding on a model prey species. Larger colonies harbored more associated species. *Anelosimus baeza* prefers to settle in locations that already contain conspecifics or silk. Our study demonstrates that *A. baeza* is a viable candidate for research into sociality in spiders and its geographical correlates.

Keywords: Araneophagy, demography, foraging, kinematic diagram, sociality

Social spiders (i.e., non-territorial permanent social or cooperative spiders: Avilés 1997) are those in which adults of the same species share a communal colony and there is cooperative prey capture and feeding. Social spiders have evolved independently several times (at least 18 times: Agnarsson 2006), most notably in unrelated families such as Theridiidae, Eresidae and Dictynidae (Avilés 1997). Recent work suggests that despite having evolved independently several times, social spiders may be evolutionary dead-ends. If sociality ultimately results in dying out of the lineage, then it is important to understand the selective pressures that drive the evolution of sociality in the first place. Among the social spiders, one of the most studied genera has been *Anelosimus* (Family Theridiidae: Agnarsson et al 2007). In this genus, 14 species have been identified as having some characteristics of sociality (Tables I and II in Lubin & Bilde 2007).

A recent reconstruction of the genus revealed a wide ranging inter- and intracontinental dispersal (Agnarsson et al. 2006). Since the geographical distribution of *Anelosimus* can span a continent, we can expect substantial variation in behavior among the different populations of the same species. *Anelosimus* spiders disperse locally at short ranges — for example, a majority of *A. cf. jucundus* O.P. Cambridge 1896 showed a dispersal distance within a meter of origin (Powers & Avilés 2003). Though the genus *Anelosimus* is fairly widespread across the world, social *Anelosimus* are only known from the Americas, but this could be due to the relative lack of knowledge about *Anelosimus* spp. in Africa and Australasia (Agnarsson et al. 2006). Ecological and life history factors are thought to be the main drivers of the evolution of sociality in *Anelosimus*, with special emphasis on the web structure and the ability to capture large prey (Avilés 1997).

Located on the continuum between solitary spiders and social spiders, subsocial spiders are generally considered as precursors of sociality (Lubin & Bilde 2007). Subsocial spiders (non-territorial periodic social: Avilés 1997) are characterized

by the following: juvenile or subadult dispersal, extended maternal care and cooperation between siblings in the natal colony (Lubin & Bilde 2007). However, since extended maternal care is also seen in other nominally solitary species (e.g. *Theridion*: Agnarsson 2004), the emphasis on designating subsocial spiders is focused on the levels of cooperative foraging (Whitehouse & Lubin 2005). Subsocial spiders are also susceptible to variations in environmental pressures such as rainfall, altitude and predator pressure (Purcell & Avilés 2008). Some other factors that could constrain subsocial *Anelosimus* are competition for colony location, competition for prey and predation from associated species (Perkins et al. 2007).

Anelosimus baeza Agnarsson (2006) is a subsocial spider found across parts of North, Central and South America (Avilés et al. 2001; Agnarsson 2006). *A. baeza* colonies are similar to solitary or small colonies of *A. eximius* Keyserling 1884 (Avilés et al. 2001). Their colonies are characterized by typical basket webs, with a capture area above and dried leaves incorporated into the colony. Since there is a lack of sex ratio bias, it has been speculated that there is outbreeding in this species; i.e., either male or female or both must leave the colony to seek mates (Agnarsson 2006). *Anelosimus baeza* is found at a range of altitudes from ca. 200 to 2500 m (Agnarsson 2006), but it is absent below 600 m in tropical rainforest (see Purcell & Avilés 2008).

Although there have been some studies on prey size and abundance, and environmental effects of predation pressure on colony survival in Ecuadorian populations of *A. baeza* (Powers & Avilés 2007; Purcell & Aviles 2008), little is known about the details of behavior seen during prey capture, preferences for founding colonies and how environmental factors affect the breeding season in other populations. Furthermore, *A. baeza* may show extreme variation in social behavior (L. Aviles, pers. comm. cited by Agnarsson 2006). Thus, basic details of ecology and behavior are needed from

different populations in order to come to a better understanding of subsociality in this species. Therefore, we designed a baseline study touching on several aspects of elemental ecology and behavior of *A. baeza* in Mexico. More specifically, we sought to determine the phenological pattern of this species. We recorded the presence of associated species (other spiders and insects) in the colonies. We studied foraging behavior in field and laboratory conditions to determine the level of cooperation between individuals. And, finally, we studied the settling decisions made by dispersing females in a greenhouse experiment.

METHODS

Study species and site.—A natural population of *A. baeza* colonies was surveyed in the Francisco Javier Clavijero Botanical Gardens, Xalapa, Mexico (19.514132°N, 96.936129°W; altitude: 1400 m). The colonies were found on the extremities of several trees. Observations on prey capture were made at the invertebrate biology laboratory in INBIOTEC, Universidad Veracruzana, Xalapa, Mexico. Spiders for the experiments were collected from trees in and around Xalapa.

Population structure.—Thirty-one colonies occupied by adult females and juveniles or females with egg sacs were marked with tags and surveyed twice a month from September 2010 to July 2011. We measured the colony volume (length $\times$ breadth $\times$ depth in cm) and recorded the number of individuals. In case of colony failure, we surveyed new ones. We recorded individuals in three categories: adult males, adult females and juveniles. The physical condition (hereafter 'status') of the colonies was scored by a single observer and separated into three categories: 1) webs with substantial damage and detritus; 2) webs with moderate damage and 3) webs with little or no damage and fresh appearance of the threads. These scores were later averaged over colonies and regressed against time elapsed since the beginning of monitoring. We analyzed the relationship between colony size (volume) and number of spiders with an ANCOVA, with date and colony number as covariates.

Associated species.—We recorded the number and presence of other associated organisms (i.e., other spiders and insects) in the colonies. Individuals were assigned to morphospecies. The Shannon-Wiener index, $H' = -\sum p_i \log(p_i)$, where p_i is the proportion of the i^{th} species (Magurran 2004), was calculated using the software Diversity (Version 1.6) to determine the diversity of associated species for each colony. We analyzed the relationship between colony size and diversity of associated species with a linear regression.

Cooperation during foraging.—Prey capture activities from eleven different colonies were observed under field conditions. As prey, a single Mexican fruit fly, *Anastrepha ludens* (Diptera: Tephritidae), was placed in the colony, the number of spiders participating in the capture was registered, and the total number of spiders feeding on the fly was recorded an hour later. This procedure was carried out 11 times (i.e., 11 colonies) between 11:00 and 16:00.

Fourteen colonies were collected from the field by removing the whole branch and placing it in a plastic container. Colonies were kept in the containers in the laboratory for 24 hours for acclimatization. Colonies were then removed from the container and clamped into position for filming.

Anastrepha ludens flies were placed in the webs, and foraging behavior was recorded with a digital camera (Sony DSC-HX1). Subsequently, the video recordings were analyzed with the event-recording software, Annotation (Version 1.0), to create a list of common behaviors observed from two spiders per colony during prey capture. We determined the transitional probabilities of the behaviors and constructed a kinematic diagram showing the most frequent transitions.

Settling decisions.—To determine the preference of dispersing spiders to settle on different substrates, we ran an additional experiment inside a small greenhouse (10 $\times$ 5 m). Three substrates for settlement were provided the dispersing spiders: (1) colonies consisting of web and spiders (WS, $n = 6$), (2) webs with no spiders in it (W, $n = 6$) and (3) a single branch free of web and spiders (C, $n = 6$). These settling substrates (separated by approximately 30 cm) were linked together in a grid (270 $\times$ 90 cm) with cotton thread. The order of the substrates was randomized. Spiders previously collected were held for one day, and marked with non-toxic paint on the abdomen with a fine paintbrush. The marked spiders ($n = 30$; six individuals per day for five days) were then released onto the grid along one edge at a distance of 40 cm from each other and left there for 24 hours. The location of marked spiders was registered after 24 hours. Settling preferences were analyzed with a chi-square test of goodness of fit.

Statistical Analyses.—All data were checked for normality before analysis. We used the statistical software GraphPad Prism (version 5) and JMP (Version 9) for all analyses.

RESULTS

Population structure.—*Anelosimus baeza* colonies were mostly found on the extremities of trees such as *Podocarpus* sp. (27% of colonies recorded) and *Citrus* spp. (39%), and a few colonies were also recorded on trees such as *Talauma mexicana* (17%), *Schefflera* sp. (7%), *Ficus* sp. (5%), as well as bamboo (5%). Especially in the citrus trees, colonies were sometimes located very close to each other on adjacent branches, and occasionally we observed silken connections between the colonies. Web construction activity was seen intermittently throughout the day. The webs of the colonies followed the typical pattern of *Anelosimus* webs with a basket or a sheet at the base, usually containing dry leaves and with capture threads extending upwards in a roughly pyramidal shape. Occasionally, small colonies (probably recently dispersed individuals) would build on a single leaf or a few leaves. Larger colonies had more individuals (ANCOVA: $F_{1,528} = 217.7$, $P < 0.0001$). We recorded 10 instances where the colonies became reduced in volume until there were no individuals left. Furthermore, we also observed two instances where previously defunct colonies were subsequently recolonized.

We monitored *A. baeza* colonies ($n = 41$) for 10 months and observed a decline in the number of individuals in the course of the year. Fig. 1 shows the decline in juveniles as the season changes. Females are present throughout the year with the possible exception of January, whereas males begin to appear in February and last till June. The period between February and June (possibly until July) is the breeding period, with juveniles appearing in August and September. We recorded

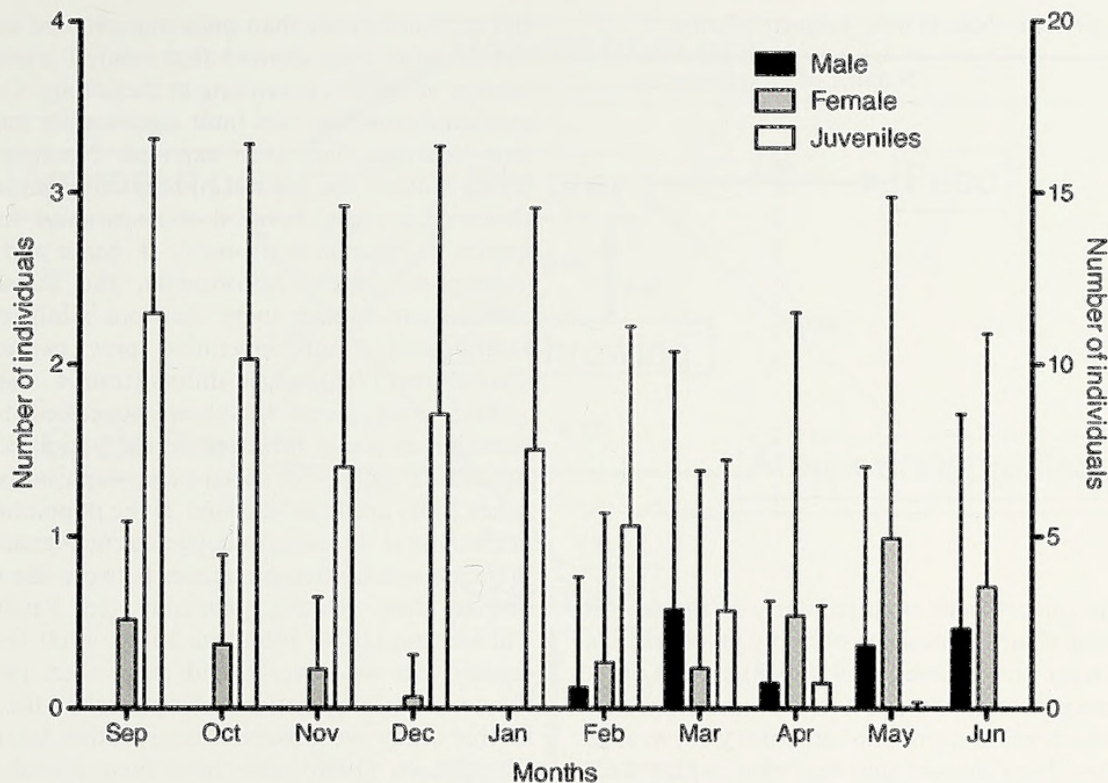


Figure 1.—Phenology of *A. baeza* colonies over a period of ten months, showing abundance of adult males, females and juveniles. The secondary y-axis gives the number of juveniles.

more than one adult female in the same colony (but separated spatially), suggesting some level of tolerance toward conspecific females. The average status of the colony declined over time (linear regression, $R^2 = 0.9$, $n = 15$, $P < 0.0001$).

Associated species.—Colonies harbored different heterospecific species, including potential prey, that were sheltered in the colonies, though not in direct contact with the capture web (Table 1). Diversity of associated species significantly increased with the average volume of the colony (Fig. 2; linear regression, $R^2 = 0.18$, $n = 40$, $P < 0.01$).

Cooperation in foraging.—*Anelosimus baeza* shows broad cooperation in prey capture: both males and females, as well as juveniles, attacked the prey together. Experimentally placed model prey (*Anastrepha ludens*) were attacked collectively by most members of the colony in both field and laboratory conditions. In field conditions, we estimated that approximately 60% of the spiders participated in the hunt, and there was a significant positive relationship between the number of spiders attacking and the number of spiders in the colony ($R^2 = 0.48$, $n = 11$, $P = 0.0176$). From preliminary observations, we identified and codified a list of units of behavior observed during foraging. The most frequent transitions were Retreat from prey → Approach prey, Silk throwing → Bite prey, and Retreat from conspecific → Stand still (Fig. 3).

Even though the spiders cooperate in hunting prey, we observed frequent fights among conspecifics. Fights were most common between females. The process from approach prey to feeding is very dynamic and involves a series of steps (Fig. 3). We did not observe any synchronization in movements between colony members or periodic immobility as seen in *A. eximius* (sensu Krafft and Pasquet 1991; see discussion).

Settling decisions.—Spiders significantly preferred to settle in locations already containing spiders (50%, 15 individuals) and webs, followed by webs only (13.3%, 4 individuals) ($\chi^2 = 14$, $df = 2$, $P < 0.001$). Control branches (without spiders or webs) were very rarely (6.6%, 2 individuals) chosen as substrates. Thirty per cent (9 individuals) of the spiders disappeared and were not recovered.

DISCUSSION

Our investigation of the basic ecology and behavior of *A. baeza* showed that the breeding season occurs from February to June. There is a significant relationship between the size of the colony and the presence of associated species, suggesting that as the colony grows larger, more niches are available for heterospecific species and also there is an increase in potential predation pressure. Most colonies contain a maximum of two adult females, which is similar to another subsocial spider, *A. viera* Agnarsson 2012 (ex cf *studious*: Viera et al 2007; Agnarsson 2012). Our analysis of the foraging behavior of the species suggests that though there is cooperative hunting, it is fairly individualistic with frequent aggressive interactions between conspecifics, and as such can be described as 'hunting in the presence of a companion' (sensu Whitehouse & Lubin 2005). Females preferred to settle in locations with pre-existing colonies rather than establishing a new colony in a vacant space, a common behavior seen in other colonial araneids (e.g., Rao & Lubin 2010).

Prey size and abundance were previously studied in an Ecuadorian population of *A. baeza* (Powers & Avilés 2007). This study showed that prey capture rate is low, and *A. baeza* captures smaller prey than social *Anelosimus*. Larger prey

Table 1.—Other species associated with *A. baeza* colonies.

Taxa	Number of morphospecies
Arachnids	
Clubionidae	2
Tetragnathidae	1
Salticidae	3
Theridiidae	4
Thomisidae	1
Mimetidae	1
Araneidae	1
Opiliones	1
Insects	
Coccidae	2
Dermaptera	1
Lepidoptera	1

(relative size to the spider) were captured early in the season than later, suggesting that the presence of many juveniles aids in the capture of larger prey. Purcell et al. (2008) carried out a transplant experiment to test the effect of different levels of altitude, rainfall and predation pressure on colony survival in *A. baeza* in Ecuador. They showed that the colonies that were transplanted to lower altitudes (from 2100 m to 1000 m and

400 m) failed faster than ones transplanted to higher altitudes. Furthermore they showed that rainfall intensity affected the number of spiders remaining in the colony. Colonies that were protected from the rain built significantly more web material than colonies that were exposed. Nentwig & Christenson (1986) studied the natural history of *A. jucundus* in Panama. However, a recent revision of *Anelosimus* suggested that the species in Panama is probably *A. baeza* and not *A. jucundus* (Agnarsson 2006). Accordingly, the Panamanian species' colonies can contain more than one adult female in the web and possibly non-cooperative prey capture (Nentwig & Christenson 1986), which differs from *A. baeza* in Ecuador.

Anelosimus baeza has been suggested to have a large variation in social behavior across populations (L. Aviles in Agnarsson 2006), but social polymorphism (sensu Riechert & Jones 2008) needs to be tested. If the population of *A. jucundus* in Panama is *A. baeza*, as suggested by Agnarsson (2006), then there are substantial differences between the two populations, despite their relative proximity. In Panama Nentwig & Christenson (1986) found up to six adult females in a single colony, but we never found more than two. Furthermore, there was no cooperative feeding between the females, whereas in this study we observed cooperative hunting. Nentwig & Christenson (1986) also base their speculation of lack of cooperation on the fact that adult females seemed to be

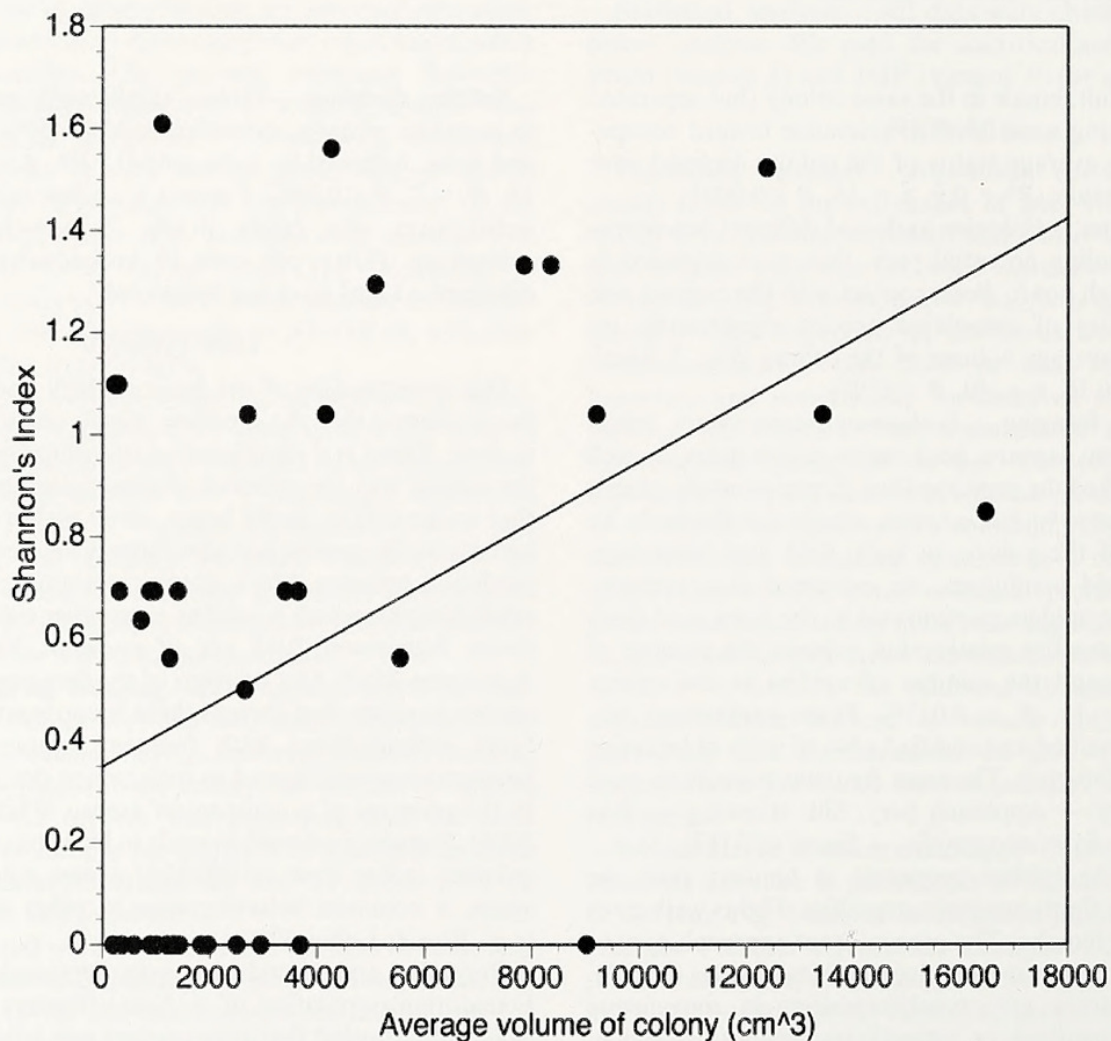


Figure 2.—Diversity of associated species found in *A. baeza* colonies increased with the volume of the colony ($R^2 = 0.18$, $n = 40$, $P < 0.01$).

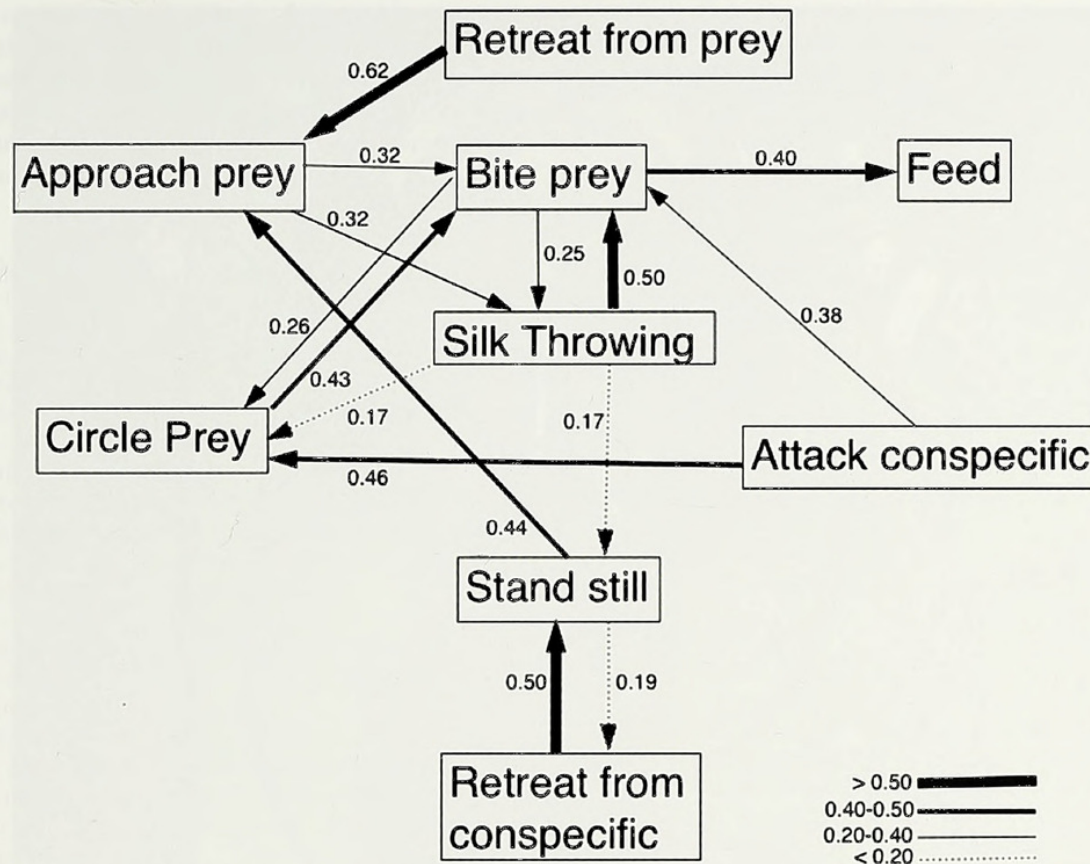


Figure 3.—Kinematic diagram showing the transitional probabilities of common behaviors during foraging. Less common behaviors, namely Move prey and Cutting threads are not shown.

spatially separated from one another, as they were located under different leaves of the same Compositaceae plant. In our study, all colonies were located in the extremities of trees, with no distinct stratification.

Anelosimus baeza in Mexico also seems to follow a different phenology than populations in Ecuador and Panama. For example, egg sacs are seen from December to February in Ecuador (Powers & Avilés 2007) and from February to April in Panama (Nentwig & Christenson 1986), whereas in this study egg sacs were observed as early as October and throughout December in Mexico. Variation in phenology may be related to differences between populations in altitude, latitude and rainfall.

If there are differences in social behavior, there may be population level differences in foraging behavior as well. The kinematic diagram shows that biting the prey does not always lead to feeding on the prey. Between colonies, individuals show considerable variation in their behavior, attacking other conspecifics and circling prey. These aggressive interactions suggest that although the spiders are hunting the same prey, they are not necessarily hunting together. This interpretation is further strengthened by the fact that not all individuals participate in the hunt. In any cooperative hunting species, there are bound to be a few free riders, resulting in hunting success decreasing with group size after group size reaches some optimal level (e.g., in wolves: MacNulty et al. 2011). We noted that silk throwing, wherein the spider quickly drew silk from the spinnerets and flung it at the prey in order to immobilize it, was frequently followed by biting the prey. This suggests that cooperation in hunting is most obvious at this

stage; i.e., immobilization of the prey. Therefore larger prey should lead to more cooperation, as seen in *A. eximius* (Souza et al. 2007). Feeding occurs directly on the prey in *A. baeza*, unlike in social spiders such as *Stegodyphus sarasinorum* Karsch 1891, where parts of the prey are transported back to the central parts of the colony (D. Rao pers. obs.).

We did not observe any synchronization between individuals as seen in *A. eximius* (Krafft & Pasquet 1991), where spiders exhibit periodic states of motion and immobility. Kraft & Pasquet (1991) suggested that this pattern of synchronization and stillness enhances prey localization by eliminating potentially confounding vibrations generated by the spiders themselves. However, *A. baeza* webs are very small compared to those of *A. eximius*, and hence there may not be a need to develop specific patterns of intra-individual communication. Furthermore, the number of spiders that attack a prey is determined by the size of the prey (Souza et al. 2007). In our study, we used a single model prey species and thus did not determine differences in levels of cooperation due to prey size.

Since the colonies of *Anelosimus* spiders accumulate dead leaves and are fairly stable in time and space, they create a new microhabitat that is subsequently exploited by other organisms (Viera et al. 2007). Interest in associated species has focused on either kleptoparasitic spiders (Nentwig & Christenson 1986) or araneophagic spiders (Perkins et al. 2007). Araenophagic predators of *Anelosimus* have been recorded from the following spider families: Anyphaenidae, Agelenidae, Salticidae, Pholcidae (Jackson & Rowe 1987; Jackson 2000; Perkins et al. 2007; Viera et al. 2007). We also observed kleptoparasitic and araneophagic spiders, and our results



Figure 4.—First record of predation of *A. baeza* by an araneophagic spider (Araneae: Mimetidae).

suggest that as colony size increases, *A. baeza* has the potential to harbor more species. Furthermore, the probability of colony failure is also linked to the number of associated species, but it is unclear from our study whether poorly defended colonies are invaded more often or whether invasion causes the colony to fail. A similar finding was reported in *A. studiosus*, where there was a close correspondence between the rate of loss of colonies over time and the association rate of anyphaenids and agelenids (Perkins et al. 2007).

Furthermore, we observed direct predation by a mimetid species (Fig. 4) on *Anelosimus* for the first time. We suggest that, in accordance with Purcell and Avilés' findings (Purcell & Avilés 2008), salticids primarily use *Anelosimus* colonies as a refuge rather than for predation, though they might capture *Anelosimus* facultatively. We also recorded a few insect species within the colony (Table 1), but since they did not come into contact with the capture threads, they may not be treated as prey.

Predation by ants is considered to be a major factor influencing the distribution of subsocial *Anelosimus* in Ecuador, as there was a greater abundance of ants in areas where the relatively small colonies of *A. baeza* suffered colony failure (Purcell & Avilés 2008). We did not note any significant incidence of ants in the colonies in our study site.

Dispersing *Anelosimus* tend to settle very close to the 'natal' colony (e.g., *A. jucundus*: Powers & Avilés 2003). In the present study we observed, but did not measure, short inter-colony distances. We also observed silken threads connecting closely spaced colonies, and these connections disappeared

after heavy rains, only to reappear later, similar to that seen in *A. viera* (Viera et al 2007). The pattern of joining and disconnecting colonies is reminiscent of fission-fusion dynamics seen in other cooperative species and suggests that temporary breakdown of connection may be better for continued survival of the colony than a permanent disconnect between areas of the colony (Kerth 2010). These observations are in concordance with our experiments with settling decisions, where spiders preferred to settle in pre-existing colonies. This preference may be because (1) spiders show high levels of sericophily, (2) spiders treat the presence of a pre-existent colony as an indication that the site is profitable, (3) it is a strategy to avoid predation pressure due to traveling or (4) spiders avoid lost opportunity costs by settling in proven sites (Lubin et al. 1993; Jakob et al. 2001). Sericophily may be a general predisposition in spiders across different levels of sociality, since a similar pattern was seen in a colonial spider *Cyrtophora citricola* Forsskal 1775 (Rao & Lubin 2010).

A. baeza is a continent-spanning subsocial spider and as such is a promising candidate for testing different hypotheses ranging from the evolution of sociality to the influence of geography on behavior. Our study represents a baseline view of several components of the ecology and behavior of this species. Further research will focus on comparative parallel experiments on widely separated populations.

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