

PREY ABUNDANCE AND THE EVOLUTION OF SOCIALITY
IN *ANELOSIMUS* (ARANEAE, THERIDIIDAE)

by
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Signed: Andy S. Powers

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ABSTRACT

Social spiders most likely evolved from subsocial-like ancestors, species in which siblings remain together for part of their life cycle but disperse prior to mating.

Understanding the ecological conditions that favor small colony sizes and periodic dispersal in subsocial species vs. large multigenerational colonies in the social species may provide insight into this evolutionary transition. The biogeography of these spiders and the ability of prey supplementation to delay dispersal in subsocial species implicate prey abundance as an important ecological factor influencing this process. I propose a conceptual framework in which environmental prey abundance determines the rate at which prey contact webs per unit web area, colony size determines web area and prey capture success, and per capita prey capture affects when spiders disperse. To further understand how prey abundance may have influenced the evolution of sociality, I have empirically explored aspects of this framework. Within the genus *Anelosimus*, I studied two social species inhabiting an Ecuadorian lowland rain forest, a subsocial species along the edge of an Ecuadorian cloud forest, and another subsocial species occupying a temperate riparian area of Arizona. In a comparative study examining relationships among sociality, prey availability, and prey capture rate across these species, the environments of social species tended to have relatively large prey and high overall prey

biomass, but not the highest numbers of prey items. Relationships among colony size, web size, and prey capture within three of these populations revealed significant foraging-related costs of increasing colony size that could be offset by the availability of high prey biomass in the form of large prey items. Finally, I conducted an experiment manipulating prey capture rate in a subsocial species that resulted in higher prey levels delaying dispersal within and among colonies. This effect often led to a single, relatively large individual remaining in nests of colonies that had been provided more prey. Overall, these findings indicate that, while the availability of high prey biomass may have allowed sociality to evolve, the concentration of prey biomass into large, but not necessarily more prey may have selected for the larger, longer-lived colonies characteristic of social species.

CHAPTER I: Introduction

Group living can benefit individuals by reducing their risk of predation (Alexander 1974; Caraco and Pulliam 1984; Tyler 1995), improving their access to resources (Giraldeau 1988), and/or increasing their inclusive fitness. At the same time, group living can increase parasitism and competition and lead to decreases in some aspects of individual fitness (Pulliam and Caraco 1984; Booth 1995). The net balance resulting from these benefits and costs depends largely on the environmental conditions in which groups exist. Particular social traits correlate with distinct ecological factors in several taxa. For example, group living in naked mole rats (Jarvis et al. 1994) and some cooperative breeding birds (Heinsohn 1992) is associated with harsh or unpredictable environmental conditions. Ecological explanations for the evolution of group living are typically complementary to, rather than exclusive of, explanations based on kin selection and reciprocity. For instance, if environmental conditions prohibit solitary individuals from successfully producing offspring (e.g. because resources are limited), their next most appealing option may be to help relatives produce offspring. I investigated how sociality is associated with a particular ecological factor – prey abundance – in social spiders.

Background

Sociality in spiders ranges from temporary colonies in subsocial spiders to permanent colonies sociality in social spiders. Social spiders remain in their parental colony for their entire lives with new generations replacing older ones within the nest. Consequently, social colonies grow to very large sizes and develop into reproductively isolated lineages with low genetic variability and female-biased sex ratios (Avilés 1997; Avilés et. al. 2000). Only at extremely large sizes, inseminated adult females may leave to establish new colonies. In contrast, subsocial spiders remain together in their parent's web only until their later juvenile and subadult stages when they disperse to build new, solitary webs in which females raise their offspring without the aid of others. Both social and subsocial spiders cooperate in web building, prey capture, and feeding, but only social females cooperate in brood care (Buskirk 1981; Christenson 1984; D'Andrea 1987; Avilés 1997). It is widely held that sociality arose from subsociality, and subsociality arose from solitary living (Kullman 1972; Krafft 1979). Thus, in addition to exhibiting an intermediate form of sociality, current subsocial species may resemble the ancestral subsocial species from which their social congeners originated.

Aspects of prey availability may have influenced the diversification of solitary ancestral species into descendant species exhibiting the social forms described above. As

web building spiders, all social spiders feed primarily on flying insects. Generally, in the New World, subsocial spiders occupy temperate and highland tropical environments, but social spiders only occupy lowland tropical environments. Because these environments differ in prey composition (Schoener & Janzen 1968; Barlow 1994; Hawkins & Lawton 1995), the geographic distribution of social spider forms suggests that prey availability is associated with the evolution of social species. Also, prey abundance can influence the amount of cooperation expressed within subsocial colonies (Ruttan 1990; Rypstra 1986; Leborgne et al. 1994; Lubin and Henshel 1996; Evans 1998).

Multi-level framework and model

Prey abundance is likely to influence spider colonies according to processes occurring at the community, colony, and individual levels. At the community level, local prey density determines the frequency at which prey contact webs per unit web area. Colonies, of any given size, should experience higher prey capture rates, on average, in communities with higher prey densities compared to communities with lower prey densities. At the colony level, the number and sizes of spiders in a colony determine its prey capture rate via web size and prey capture success. At any given prey density, prey are likely to contact a web in proportion to its surface area (Buskirk 1975). Of the prey

that contact a web, the proportion that a colony captures is likely to depend on the number of spiders in the web (Buskirk 1975; Uetz 1989; Uetz 1992; Pasquet and Krafft 1992; Binford and Rypstra 1992); colonies with more spiders would have larger webs, making prey less likely to escape, and would be more likely to have spiders available for prey detection and capture when the opportunity arises, allowing them to capture larger prey. Concordantly with these ideas, colony size (number of spiders), web size, and prey capture are correlated for several social spiders (Buskirk 1975; Riechert et al. 1986; Ward 1986; Uetz 1988; Uetz and Hodge 1990). At the individual level, colony members require higher levels of prey intake as they grow larger. Support for this idea comes from the observation that when spiders within a colony grow larger while their prey intake remains constant, they become less likely to share prey (unpublished data; Fig. I.1). This may be due, in part, to a positive relationship between body size and metabolic rate in spiders (Greenstone and Bennett 1980; Anderson 1994). Individuals may decide whether or not to remain in colonies in response to their prey intake rates and prey requirements. For example, if at some point, an individual's requirements exceed its prey intake, it may disperse to a new location where its prey capture rate is higher (*sensu* Lubin 1993; Foelix 1996). Together, all three levels – community, colony, and individual – offer a fuller picture of what factors may determine prey capture rates and colony sizes in social

spiders. To further understand how such relationships might mediate an influence of prey abundance on sociality, I explored them in a mathematical model.

In this model, colonies consume prey mass at a rate, M_p/t , determined by their environmental prey abundance, web size, and ability to capture prey. Colonies exist in an environment with prey density R (mass of flying insects per area per time). Prey enter colonies by first contacting their webs at a rate assumed to be proportional to R and web area A_c , so prey abundance and web size determine the frequency at which prey contact webs, setting an upper limit to prey capture rate. Of the prey that contact a web, the proportion that the colony captures is referred to as its prey capture success S_c , which is estimated as the proportion of available prey that are smaller than or equal to the maximum prey size that a colony can capture. Thus overall, $M_p/t \propto R * A_c * S_c$. Because larger colonies can capture larger prey (Nentwig 1985; Rypstra and Tirey 1991; Uetz 1992), larger colonies can be expected to capture a larger proportion of the prey that contact their webs in environments where the mean prey size is relatively large. Given a Gaussian distribution of prey sizes available in the environment (Fig. 1.2a), the proportion of prey contacting the web that are subsequently captured by a colony can be described by a logistic equation,

$$S_c = 1 / (1 + ((1/a) - 1)(e^{-rMc})),$$

where a is the proportion of available prey that a solitary spider can capture, and r represents the rate at which S_c increases relative to M_c (Fig. I.2b). Both a and r are inversely correlated with the mean prey size available. In an environment with mainly small prey, even colonies containing low numbers of individuals will be able to capture most of the prey sizes that contact their webs. Also, with a larger proportion of prey being small in such environments, solitary spiders are likely to experience higher prey capture success rates than solitary spiders in environments offering mainly larger prey.

Web area, and therefore prey–web contact rate, is related to colony mass. Given a constant density ρ (spider mass/volume) distributed throughout the web, web volume V_c is proportional to spider mass M_c . More specifically, web volume is linearly related to colony mass with a slope of $1/\rho$: $M_c * 1/\rho = V_c$. This assumption is consistent with correlations found between web size and colony size in various spider species (Tietgen 1986; Leborgne et al. 1994; Ward 1996). Because $M_c = M_i * N$, where M_i is mean individual mass and N is the number of spiders in a colony, N can be substituted for M_c when M_i is similar among colony members. V_c is also related to A_c . Social spider colonies build three-dimensional asymmetrical webs (reviewed in Avilés 1997), so web shape is likely to scale geometrically (self-similarly), with surface area increasing nonlinearly with volume: $A_c \propto V_c^{2/3}$ (Fig. I.3). Therefore, the rate of increase for surface

area can be expected to decrease with increasing volume. The relationship between colony size and prey capture can then be defined by substituting these relationships for A_c and the logistic equation for S_c in the prey capture relationship defined above

$$(M_p/t) \propto (1/\rho * M_c)^{2/3} * R * 1 / (1 + ((1/a) - 1)(e^{-rM_c})) \text{ (Fig. I.4a).}$$

To approximate the relationship between per capita prey intake and colony size, this equation can be divided by M_c , which yields

$$(M_p/t)/M_c \propto (1/\rho)^{2/3} * M_c^{-1/3} * R * (1 / (1 + ((1/a) - 1)(e^{-rM_c}))) \text{ (Fig. I.4b).}$$

While the distribution of prey sizes available in the environment determines the shape of this curve, prey abundance R determines its height.

To represent individuals' prey requirements, let there be a minimum threshold for energy intake per unit colony mass $(M_p^{min}/t)/M_c$. This value remains constant and independent of the numbers of spiders in a colony. Eventually, a colony may reach a mass at which prey capture drops to $(M_p^{min}/t)/M_c$, thus limiting colony mass (Fig. I.5a). At maximum colony mass M_c^* , no further individuals can be added to the colony and the growth of existing members becomes restricted. Dispersal and reductions in colony size (through colony fission events for example) can allow continued growth and reproduction for individuals in these conditions. Each time an individual disperses, colony biomass decreases thereby increasing per capita prey capture for the remaining colony members.

Factors such as size and competitive ability may determine which individual disperses from the colony at such a time.

In an environment with many small prey available to colonies, per capita prey capture will decrease with colony size. Dispersing individuals may experience higher prey intake rates foraging solitarily than in a colony at its maximum size. However, per capita prey capture may not reach its minimum level until extremely large colony sizes if available prey biomass is sufficiently high enough (Fig. I.5a). In an environment with generally large insects, per capita prey capture will begin at a lower level and then increase before gradually decreasing. Intermediate-sized colonies will experience the highest per capita prey capture rates in this type of environment, but colonies may still reach very large sizes before ever reaching minimum prey capture rates or even rates comparable to that of dispersed, solitary spiders (Fig. I.5b). Such spiders may benefit more by staying in large colonies even as per capita prey capture decreases rather than dispersing and foraging solitarily.

In addition to predicting colony energetics, this model provides evolutionary insights. For colonies to reach M_c^* , increasing colony size must yield a fitness advantage to colony members (e.g. due to greater predator protection or avoiding dispersal costs). Alternatively, if increasing prey capture rate provides a greater fitness advantage, then colonies should be considerably smaller than M_c^* . Comparing natural colony sizes to those predicted in the model may shed light into the factors that have selected for current

colony sizes. Avilés & Tufino (1999), for example, found fitness to be highest at intermediate colony sizes in the social spider *Anelosimus eximius*, possibly due to greater juvenile survival caused by high per capita prey capture rates. This finding would indicate that high per capita prey capture has selected for intermediate colony sizes in this environment. It is likely that several factors influence the effect of colony size on fitness however, so no single selective pressure may account for current colony sizes. Given a fitness advantage conferred by remaining in natal colonies, exposure of subsocial species to relatively high prey capture rates over evolutionary time could give rise to lineages with delayed dispersal, thereby setting the stage for greater colony sizes and increased cooperation to evolve.

Research

In the following chapters, I explore hypotheses and predictions derived from this energetic framework in the spider genus *Anelosimus*. Originally an Old World genus, most *Anelosimus* currently occupy New World environments. This genus provides an appropriate system for questions regarding the evolution of sociality, as it contains three social species and several subsocial species (Levi 1963; Levi 1972; L. Avilés, personal comm.). The most recent phylogeny of this genus indicates a basal subsocial condition with sociality arising at least twice (Varas 1998; I. Agnarsson, personal comm.).

Chapter II presents a comparative study characterizing prey availability and capture rates in social and subsocial species. It examines the expectation that available and captured prey biomass is higher for social spiders than for subsocial spiders due to larger and/or more abundant prey. In Chapter III, I explore the hypothesis that per capita prey capture changes with colony size within species but differently between social and subsocial species by studying relationships among colony size, web size, and prey capture within three *Anelosimus* species. In terms of the energetic model presented above, this hypothesis makes four predictions in which N is substituted for M_c by maintaining constant individual masses within colonies: (1) across environments, N should be directly proportional to R , and high R correlates with larger N^* ; (2) V_c/N is constant, $A_c \propto V_c^{2/3}$, and $A_c/N \propto N^{-1/3}$ (Fig. I.3); (3) in environments with large prey, larger colonies capture larger prey; and (4) $(M_p/t)/N$ is related to colony mass differently across prey environments such that in environments with mainly small prey, $(M_p/t)/N$ is related to colony mass by a negative function with slope close to $-1/3$, while in environments with larger prey, $(M_p/t)/N$ increases with colony mass before decreasing (Fig. I.4). Lastly, Chapter IV presents an experiment testing the effect of prey level on dispersal timing in the subsocial species *A. arizona* to investigate the hypothesis that spiders disperse when they can no longer reach their prey requirements in their natal colony. This chapter tests the

prediction from the energetic model that, given constant prey size, individuals in high R environments disperse later than individuals in low R environments.

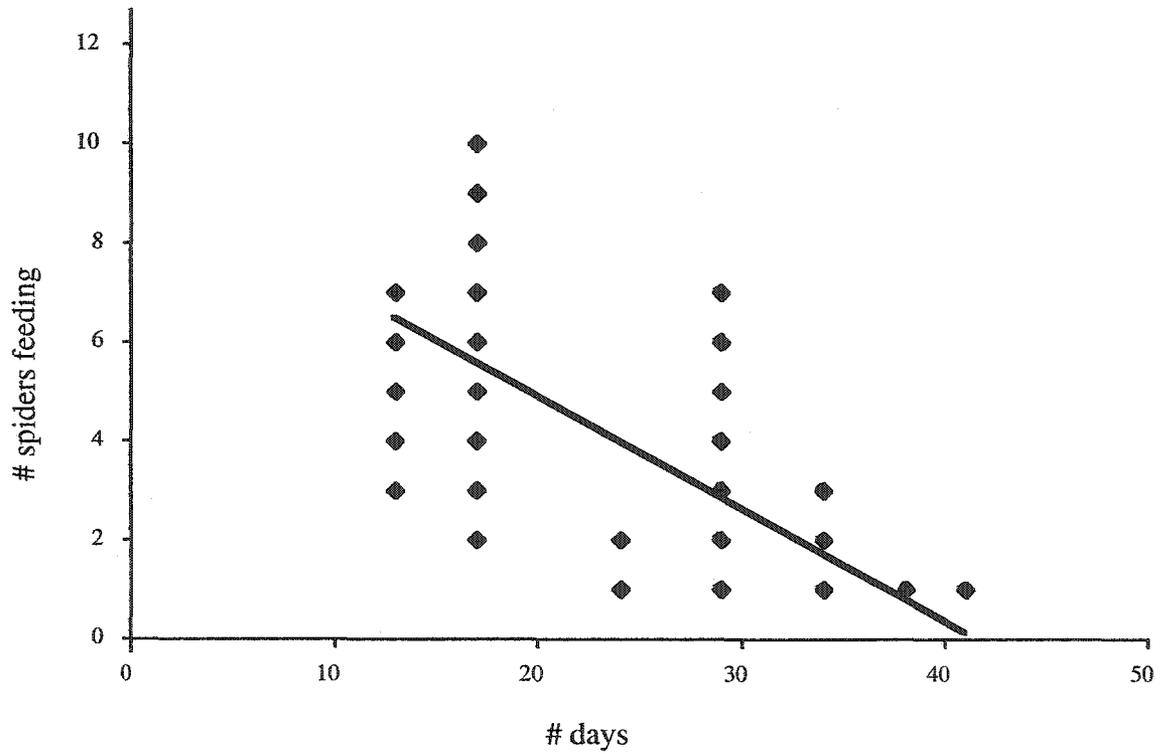


Figure I.1: Decline in the numbers of spiders sharing prey items as a function of the number of days since observations began.

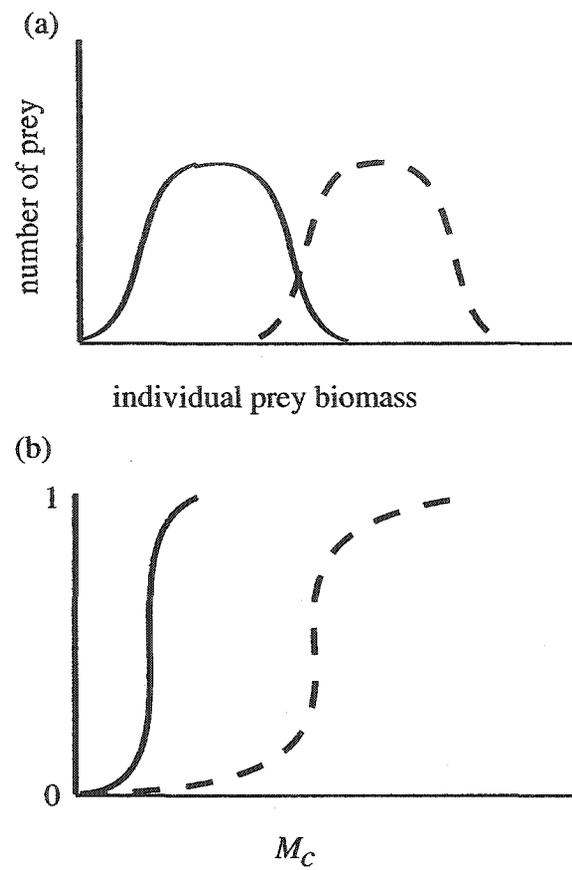


Figure I.2. Change in S_c with respect to increasing M_c in environments providing mainly small vs. mainly large prey. (a) Both environments prey size is normally distributed. (b) In the environment with smaller prey, S_c reaches 1 at low colony mass, while in the environment with larger prey, S_c does not reach 1 until considerably greater colony mass.

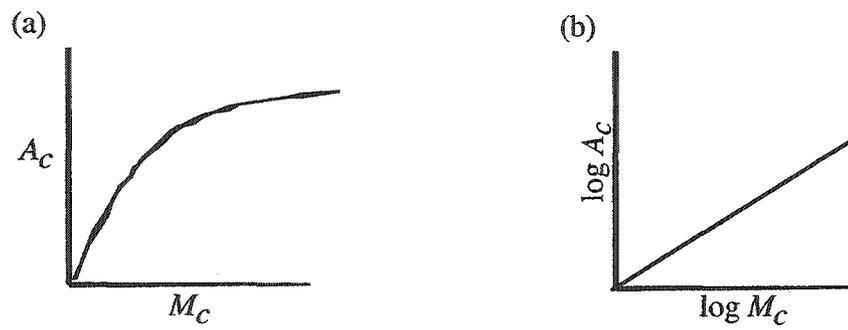


Figure I.3. Predicted relationship between colony mass M_c and web surface area A_c as (a) a power function, and as (b) a linear function with slope $2/3$ on a logarithmic scale.

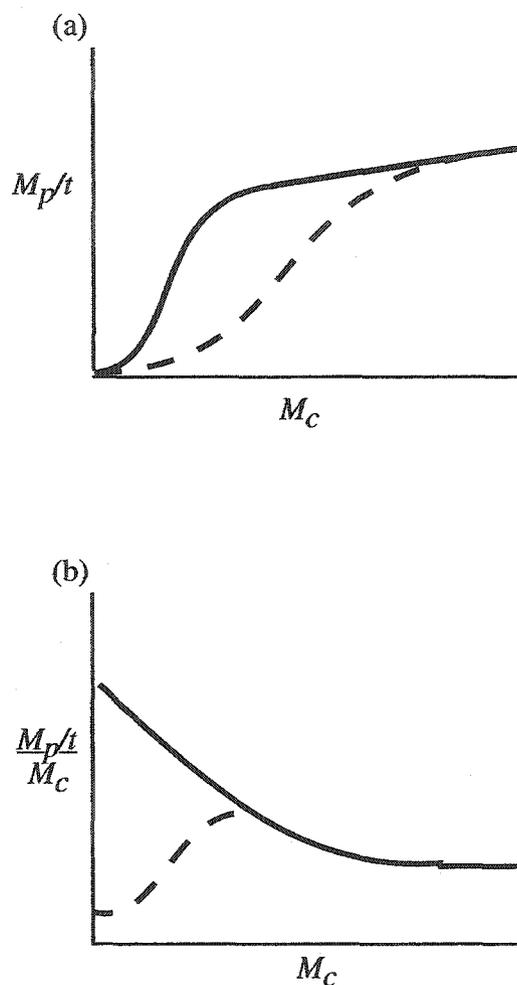


Figure I.4. Changes in prey capture rate M_p/t with colony mass M_c in environments with different prey sizes. (a) In an environment with small prey ($a=0.5, r=10$; solid line), colony prey capture increases quickly before leveling. In an environment with larger prey ($a=0.1, r=2$; dashed line), prey capture increases more slowly. (b) These different prey environments produce different changes in per capita prey capture rate $(M_p/t)/M_c$.

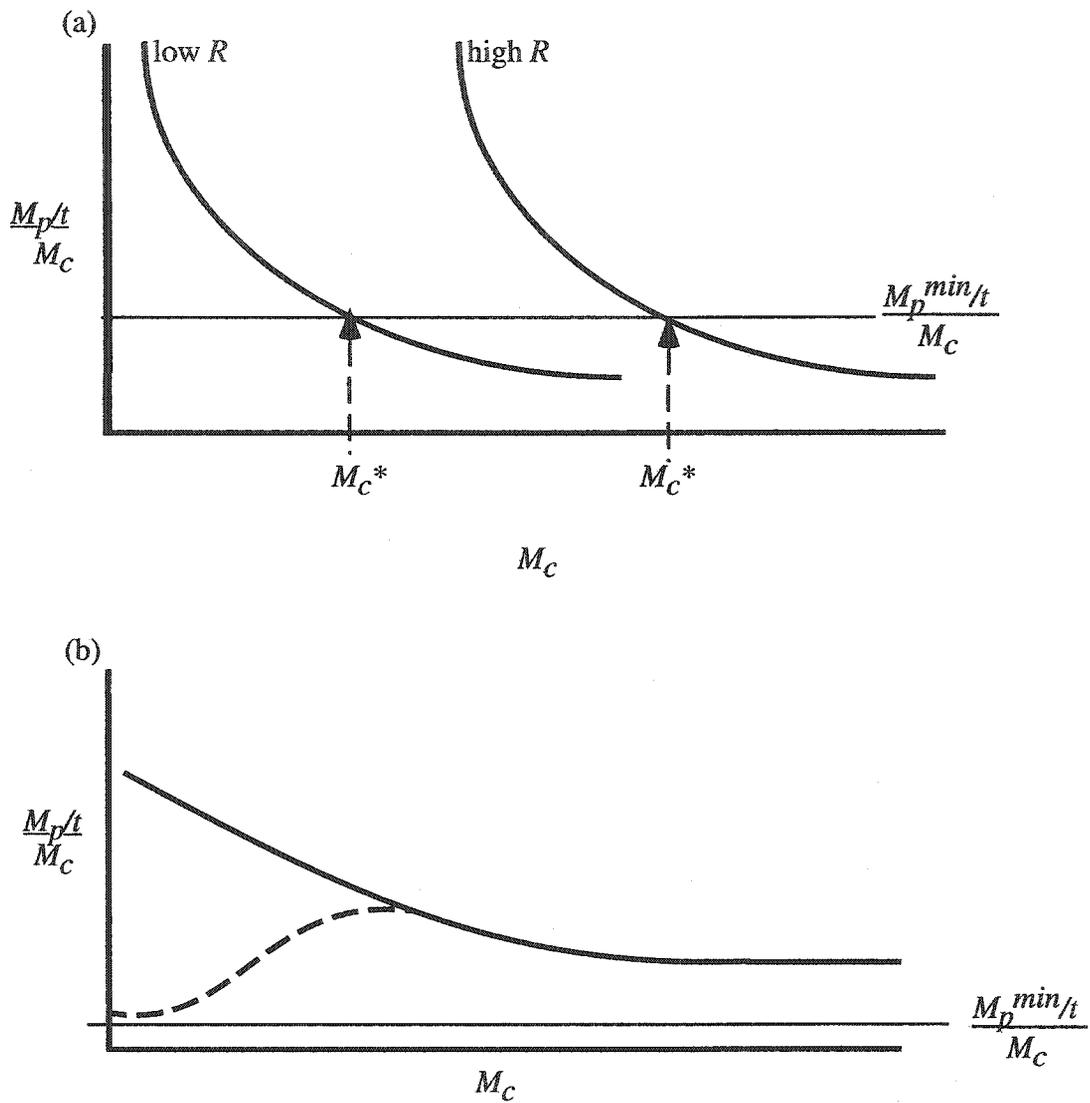


Figure I.5. Changes in per capita prey capture with colony size and the limit hypothesized to be imposed by individuals' minimum prey requirements (a) in two environments with small prey sizes but different prey abundances R , and (b) in two environments with similar prey abundances but different prey sizes. As in previous figures, the solid line represents an environment with mainly small prey, and the dashed line represents an environment with mainly large prey.

Table I.1. Symbols in the energetic model and their meanings.

Symbol	Meaning
M_c	Mass of colony
V_c	Volume of colony web
A_c	Area of colony web
M_i	Mean mass of individuals in colony
N	Number individuals in colony; M_c/M_i
ρ	Density of individuals in colony web; M_c/V_c ; a constant
R	Productivity of environment
M_p/t	Mass of prey captured per unit time
S_c	Proportion of prey that colony can capture due to prey size distribution in environment
r	Rate of increase for S_c in relation to M_c
a	Prey capture success of a solitary spider

CHAPTER II: Relationship between prey abundance and sociality

Introduction

It is likely that sociality arose from subsociality, and subsociality arose from solitary living (Kullman 1972; Krafft 1986). Thus, in addition to exhibiting an intermediate form of sociality, current subsocial species may resemble the ancestral subsocial species from which their social congeners originated. Several lines of evidence suggest that availability of prey (flying insects) may have influenced this evolutionary transition. Increased prey abundance has been shown to delay dispersal (Ruttan 1990) and increase cooperation in subsocial species (Rypstra 1986; Leborgne et al. 1994; Lubin and Henshel 1996; Evans 1998). Powers and Avilés (2003) showed that dispersal patterns in a subsocial spider are consistent with the hypothesis that resource competition within the nest drives natal dispersal in this spider. Also, while social species occur solely in lowland tropical or subtropical regions (Levi 1956, 1963; Avilés 1997; but see Furey 1998), where flying insects tend to be large on average (Schoener & Janzen 1968; Barlow 1994; Hawkins & Lawton 1995), subsocial species occur predominantly in temperate or tropical highland regions where prey are typically smaller. Furthermore, flying insects are likely to be more abundant in lowland tropical rainforests where

temperatures and humidity levels remain relatively high throughout the year (Janzen 1973; MacArthur 1972; Young 1982). Thus, social colonies probably experience an overall greater prey biomass, allowing them to delay dispersal longer and reach much larger colony sizes. These ecological trends among and within species suggest that greater prey availability has allowed the development of social colonies in the tropical lowlands.

To further understand the influence of prey abundance on sociality in spiders, I investigated the hypothesis that greater prey biomass, in the form of greater numbers and/or larger prey sizes, allowed the evolution of permanent sociality in spiders. Social spiders can only occur in high prey biomass environments, such as the tropical lowlands, because the large, highly dense colonies of these species require high prey biomass. Temperate and tropical highland environments cannot support social spider colonies because they provide lower biomasses of prey. Three predictions can be made based on this hypothesis: (1) spiders in subsocial colonies approaching the dispersal phase experience lower biomass and sizes of available prey than non-dispersing spiders of a similar age in social colonies, (2) social colonies capture larger prey compared to subsocial colonies, and (3) within subsocial species, colonies in the early communal stage experience higher prey availability and per capita prey capture rates than colonies

approaching the dispersal phase. I examined these predictions by comparing prey availability and capture across two subsocial species and two social species within the spider genus *Anelosimus* (Theridiidae).

Methods

Study system

The genus *Anelosimus* contains at least three social species and several subsocial species (Levi 1963; Levi 1972). Originally an Old World genus, most *Anelosimus* species occur in the New World. The most recent phylogeny of the genus indicates a basal subsocial condition with sociality arising at least twice (Varas 1998; I. Agnarsson, personal comm.). I studied two social species found in lowland tropical rainforests in Ecuador, *A. eximius* and *A. domingo*, and two subsocial species phylogenetically close to *A. jucundus* – *A. panamericana* found throughout South and Central America and in cloud forest areas in Ecuador, and *A. arizona*, found in riparian areas of Southern Arizona (the latter two species are being described within the recent revision of the genus by I. Agnarsson).

A. eximius and *A. domingo* are typically found in tropical lowland rainforest in Central and South America, with *A. eximius* distributed from Panama to southern Brazil

(Levi 1963). I studied these species at The Estación Biológica Jatun Sacha (450 m; S 01° 04' 13.2", W 77° 36' 41.4") in Ecuador. The average temperature at this site remains near 25°C throughout the year with an average of 200 rainy days per year (Fig. II.1a). The rainy season (mean monthly precipitation 364.41 ± 22.62 mm) lasts from March through June, and the dry season (mean monthly precipitation 231.47 ± 20.23 mm) October through February with January being the driest month (185.07 ± 18.06 mm). July through September is intermediate in precipitation (mean monthly precipitation 285.68 ± 21.48 mm). At this site, both species build nests in the forest understory, but only *A. eximius* builds nests along the forest edge.

Colony cycles of these species are asynchronous, with separate colonies often containing different ages of spiders at the same time of the year and spiders within colonies remaining together for several generations. To account for any differences in flying insect abundances between rainy and dry seasons, I studied these species during the rainy season (June 2002: n=4 *A. eximius* colonies, n=3 *A. domingo* colonies; May-June 2003: n=5 *A. eximius* colonies), during the dry season (January 2002, n=6 *A. eximius* colonies, n=3 *A. domingo* colonies), and during the transition from rainy to dry season (August 2001: n=14 *A. eximius* colonies, n=3 *A. domingo* colonies).

I studied a population of *Anelosimus panamericana* in the cloud forest area at the Yanayacu Biological Station and Center for Creative Studies (2073.17 m, 2073.17 m, S 0° 36' 0", W 77° 52' 0"). At this site, the rainy season lasts from April through September (mean monthly precipitation 327.47 ± 33.07 mm), and the dry season from December through February (146.46 ± 22.69 mm; Fig. II.1b). March, October, November have intermediate levels of precipitation (207.96 ± 23.71 mm). The temperature remains near 17°C throughout the year except in July and August when it drops to approximately 15.5°C. At this site, colonies have only been found in secondary growth and are common along roads.

Anelosimus arizona (studied as *A. jucundus* by Avilés and Gelsey 1998 and as *A. cf. jucundus* by Powers and Avilés 2003) is morphologically similar, but not identical to *Anelosimus jucundus* (O. P. Cambridge 1986), a subsocial species described from montane areas in Costa Rica, Panama, and Ecuador (Levi 1956, 1963; I. Agnarsson pers. comm.). The population of *A. arizona* included in this study was located in Garden Canyon (1524.70 m; N 31.49°, W 110.32°), a temperate riparian area in southern Arizona. At this site, average monthly precipitation is approximately 33.03 ± 16.61 mm, but with large variability across months and between years (Fig. II.1c). Temperature is highest (~24°C) from May through September and drops to approximately 10°C from

November through March. It remains at an intermediate level (~17°C) in April and October. At this site, *A. arizona* colonies are most abundant within approximately 10 m of a perennial creek.

Within *A. panamericana* and *A. arizona*, colonies tend to exhibit seasonally synchronized phenologies. *A. arizona* colonies at Garden Canyon begin in late summer (July-August) as solitary females with single eggsacs. Spiderlings hatch in early fall (September) and remain together until spring, remaining dormant throughout winter. Mothers care for their offspring during part of this period but die before the onset of winter, in some cases being consumed by her offspring. In late spring (April-May), spiders disperse as late juveniles and subadults to form new, solitary webs in which they mate and females begin new colonies (Avilés and Gelsey 1998). At Yanayacu, *A. panamericana* colonies tend to exhibit less age structure synchronicity, contain more spiders, and exhibit more cooperation and nest sharing among older instars (K.S. Powers unpublished data). Females produce new clutches during the dry season (December-February), with multiple females occasionally sharing a single nest. Colonies are less synchronized during the rainy season when older juveniles and subadults can be found in communal nests and also in solitary webs. Communal webs are sometimes even cohabited by adult males, adult females, and spiderlings at this time. Thus, although *A.*

panamericana and *A. arizona* are both subsocial, the Yanayacu population appears more similar to its social relatives compared to the Garden Canyon population. I studied the Yanayacu population at three separate times of the year: once (February 2002, n=83 colonies) when colonies contained adult females with spiderlings, and twice (June 2002, n=66 colonies; and August 2001, n=94 colonies) when colonies contained either late juveniles, subadults, and adults living communally (June) or adults and subadults living solitarily (August). I studied the Garden Canyon population during the early cooperative stage when colonies contained adult females and their offspring (October 2001, n=60 colonies) and during the later communal stage when later instar juveniles and subadults were approaching dispersal (April 2001, n=61 colonies).

Prey abundance censuses

Web-building spiders are known for hunting and feeding upon flying insects (Foelix 1996). Therefore, to estimate prey availability for the subsocial and social spiders in this study, I positioned no-kill Malaise traps (trapping area=6,244 cm²), a standard tool for sampling flying insects (Malaise 1937 and Marston 1965, cited in Buskirk and Buskirk 1976; used by Buskirk 1975 for similar purposes as defined here), within 2-3 m of and at a similar height as colonies. Every 3h, I recorded the order and

length of each insect found in traps for 3-5 days throughout the day during the sample periods mentioned above. For the three Ecuadorian species in May 2003 and for *A. arizona* in September 2003, I conducted additional hourly censuses in which I did not remove insects between censuses to determine how long they remained in traps. I found that different taxonomic orders of insects remained in the traps for different lengths of time, sometimes less than the 3h census interval ($F_{9,177}=3.28$, $p=0.0007$; Appendix A). To account for this variation and any insects that were missed between censuses, I applied the inverse of the amount of time that each order remained in traps to the observed frequency for each insect order to estimate the actual frequency of insects in traps. I multiplied the frequency at which each insect order was observed in traps by the inverse of the mean amount of time that each order remained in traps to obtain an estimate of the actual frequency of insects in traps. I estimated prey biomass from taxonomic order and body length using Sage (1982): $\ln \text{mass (g)} = a + (b * \text{prey length (mm)}) + (bl * \text{prey length (mm)}^2)$, where a , b , and bl vary with prey order.

Prey capture censuses

In conjunction with prey availability censuses, I assessed colony prey capture. For each species, sample size was determined by the number of colonies that could be

reached within a 3h census interval and by colony prey capture frequency. In subsocial species, colonies occur at high densities and capture prey rarely, so many colonies were monitored. In contrast, colonies of social species occur at low densities and capture prey frequently, so fewer colonies could be monitored. Colonies were further selected to encompass the full habitat range of the species being studied. For example, I studied similar numbers of *A. panamericana* colonies along the cloud forest edge and as far into the forest as colonies occurred.

As in prey abundance censuses, I recorded the order and body length of captured prey every 3h, with prey capture being characterized by freshly dead insects on which at least one spider was feeding. To account for prey items that did not remain visible in the web long enough to be seen during censuses, total prey capture rate was estimated from the frequency and sizes of observed prey in webs and the relationship between prey size and feeding duration (Appendix B). Differences between night and day were also taken into account (Appendix C).

Colony size estimations

I estimated the numbers and ages of spiders in all colonies censused. *A. eximius* and *A. domingo* colonies were too large for counting spiders *in situ* or collecting the nest

and counting spiders in the lab. However, number and age structure of spiders in colonies are related to their nest cross sectional area , so the numbers of spiders in colonies could be estimated by measuring nests of censused colonies using previously estimated relationships provided by L. Avilés and P. Salazar (unpublished data). These relationships are shown in Appendix D. Together estimates of the total numbers of spiders and numbers of subadults and adults could be used to estimate colony age structure. For *A. arizona* and *A. panamericana*, spiders could be counted and identified by observing them directly in the field when nests were small with few large spiders or by collecting nests and sorting spiders from their nest materials in the lab when nests were large. For *A. panamericana* colonies in later stages, the numbers of spiders and age structure in colonies was also sometimes estimated using the relationship between web size and numbers of spiders (Appendix D). I estimated *A. arizona* and *A. panamericana* colony sizes during all census periods except September and June 2003, respectively. For all species, I estimated colony biomasses by measuring the mass of each age class (spiderlings, young juveniles, older juveniles, subadults, and adults) in each species and then multiplying the appropriate mass by the numbers of spiders in each age class.

Prey abundance and prey capture estimates

Overall, I estimated three aspects of available and captured prey: number of prey items per hour, mean prey mass, and total prey biomass per hour. For environmental availability, total number prey items per hour and total biomass per hour were analyzed per unit trap area (prey #/h/cm² and prey mg/h/cm²). For prey capture, the total number of prey items captured per hour by a colony was analyzed per capita (prey #/h/spider). To account for spider body size differences across species, the total prey biomass captured by colonies per hour was analyzed per unit colony biomass (prey mg/h/colony mg). Also, the mean prey sizes captured by a colony were analyzed in relation to the mean spider body sizes within that colony (mean prey mass (mg)/ mean spider mass (mg)).

At Jatun Sacha, *A. eximius* colonies occasionally captured prey that were larger than those found in the Malaise traps (Table II.1). To account for any potential bias in the insect sizes sampled by the Malaise traps, I included these larger prey items among the available prey in analyses on mean prey mass and total prey biomass available to colonies. I included for each insect order all captured prey with a greater mass than was found in the traps for that order (10 Coleoptera, 13 Heteroptera, 14 Hymenoptera, and 2 Orthoptera). Many of these insects may have not become caught in the Malaise traps

because they were mainly ground or plant dwelling, rather than flying, species. To estimate the densities of these insects, the area of the web in which the prey was found replaced trap area, and the frequency of these prey (for total biomass estimations) was calculated based on feeding times for those colonies. I estimated web areas (which are cylindrical or conical for *A. eximius*) by measuring the circumference of the web base with a flexible ruler and then measuring the web height.

Statistical analyses

Analyses use colony and trap means weighted by their number of censuses to account for the different numbers of censuses conducted across species and across seasons within species. The numbers of prey, mean prey mass, and total prey masses of available and captured prey were natural-log transformed to normalize their distributions. All means are reported \pm standard error. Because prey capture occurs infrequently in subsocial colonies, prey capture was not observed for many subsocial colonies even after several days of being monitored. This led to zero values for the mean numbers of prey and mean total prey biomass captured for many colonies. In these cases, distributions could not be normalized, so nonparametric tests were performed.

Results

Subsocial colonies approaching dispersal vs. social colonies

When comparing the habitats of subsocial species as their colonies approached their dispersal phase with the habitats of social species, the cloud forest edge habitat of *A. panamericana* was found to have the highest prey density (#/h/area) of any habitat (Tukey-Kramer: cloud forest edge vs. rain forest edge $q=0.89$, $p<0.05$; cloud forest vs. rain forest interior $q=0.78$, $p<0.05$ and cloud forest vs. Arizona riparian $q=0.64$, in ANOVA comparing all four habitat types $F_{3,48}=15.11$, $p<0.0001$; Fig. II.2a). The other three areas studied – the rain forest edge, the rain forest interior, and the temperate riparian area – did not differ in this respect ($F_{2,27}=1.19$, $p=0.3205$). The rain forest edge habitat, on the other hand, had the largest prey of any other habitat, particularly the cloud forest habitat (Tukey-Kramer: rain forest edge vs. cloud forest $q=0.33$, $p<0.05$ and rain forest edge vs. Arizona riparian $q=1.05$, $p<0.05$ in ANOVA comparing all four habitat types: $F_{3,87}=9.19$, $p<0.0001$; Fig. II.2b). Consequently, the forest edge habitats of the rain forest and the cloud forest had similar overall prey biomasses (Tukey-Kramer: $q=-0.17$, $p>0.05$ in ANOVA comparing all four habitat types: $F_{3,670}=10.85$, $p<0.0001$; Fig. II.2c). The lowland forest interior occupied by both *A. eximius* and *A. domingo* had varying prey sizes that did not differ significantly from those found along the lowland forest edge or in

the cloud forest edge (Tukey-Kramer: $q=-0.30$, $p>0.05$ and $q=-0.10$, $p>0.05$, respectively in same ANOVA above). The overall prey biomass found in this environment was lower than that found in the cloud forest edge (Tukey-Kramer: $q=0.10$, $p<0.05$ in same ANOVA above). The temperate riparian habitat of *A. arizona* had the smallest prey sizes (Tukey-Kramer: riparian vs. rain forest edge $q=1.05$, $p<0.05$, and riparian vs. rain forest interior $q=0.55$, $p<0.05$ in same ANOVA above), and thus the lowest overall prey biomass available of any habitat type (Tukey-Kramer: riparian vs. rain forest edge $q=0.14$, $p<0.05$, riparian vs. rain forest interior $q=0.44$, $p<0.05$, and riparian vs. cloud forest $q=1.36$, $p<0.05$ in same ANOVA above).

Per spider body mass, colonies of the social species captured larger prey than colonies of the subsocial species (Tukey Kramer: *A. eximius* vs. *A. panamericana* $q=1.16$, $p<0.05$; *A. eximius* vs. *A. arizona* $q=1.88$, $p<0.05$; *A. domingo* vs. *A. panamericana* $q=0.42$, $p<0.05$; *A. domingo* vs. *A. arizona* $q=1.27$, $p<0.05$ in ANOVA comparing all four species $F_{3,73}=29.32$, $p<0.0001$; Fig. II.3a). This was due to combined differences across species in mean spider body mass and mean prey mass captured by colonies. *A. eximius* had the largest body sizes and captured the largest prey items ($F_{3,205}=212.92$, $p<0.0001$, and $F_{3,143}=97.93$, $p<0.0001$, respectively; Fig. II.3). In contrast, *A. domingo* had the smallest body sizes and captured medium sized prey. *A. arizona* and *A.*

panamericana captured small prey and had medium and small body sizes, respectively.

A. eximius colonies captured the highest numbers of prey per capita (vs. *A. domingo*: $\chi^2=9.94$, 37 df, $p=0.0016$; vs. *A. panamericana* : $\chi^2=8.27$, 152 df, $p=0.0040$; vs. *A. arizona*: $\chi^2=10.37$, 72 df, $p=0.0013$; Wilcoxon/Kruskal-Wallis pair tests with Chi-square approximation) and acquired the greatest prey biomass per unit spider biomass (vs. *A. domingo*: $\chi^2=10.38$, 37 df, $p=0.0013$; vs. *A. panamericana*: $\chi^2=19.04$, 152 df, $p<0.0001$; vs. *A. arizona*: $\chi^2=10.69$, 72 df, $p=0.0011$). These aspects of prey capture were similar among *A. domingo*, *A. panamericana* , and *A. arizona* (#/h/spider: $\chi^2=0.08$, 175 df, $p=0.9630$; prey mass/h/spider mass: $\chi^2=0.22$, 175 df, $p=0.8944$).

Early vs. late colony stages in subsocial species

In the cloud forest, the density, size, and overall biomass of prey available to *A. panamericana* colonies did not differ between the early stage colonies (February) containing adult females with young juveniles (3.10 ± 0.05 mg and 1.65 ± 0.08 mg) and the later stage colonies (May-August) containing older juveniles and subadults (2.34 ± 0.01 mg and 2.64 ± 0.01 mg) approaching the dispersal phase ($t=0.48$, 26 df, $p=0.4776$; $t=0.20$, 26 df, $p=0.8425$; and $t=0.34$, 26 df, $p=0.7367$; respectively). However, early stage colonies were found to capture more prey items per capita and greater prey biomass per

colony biomass compared to later stage colonies ($\chi^2=7.07$, 184 df, $p=0.0078$; and $\chi^2=10.64$, 184 df, $p=0.0011$; respectively). Furthermore, although absolute prey sizes captured did not differ between these two stages ($t=-1.85$, 86 df, $p=0.0678$), prey captured during the earlier stage were larger relative to spider body sizes compared to prey captured during later stages ($F_{1,64}=-4.35$, $p<0.0001$; Fig. II.4).

In *A. arizona* habitat, higher numbers of prey occurred during the earlier colony stage (September-October) when spiders were in their second and third instars (0.70 ± 0.32 mg and 1.46 ± 0.14 mg) compared to the stage just prior to dispersal (April) when spiders were in their fifth and sixth instars (3.56 ± 0.19 mg and 6.33 ± 0.17 mg; $t=-2.95$, 12 df, $p=0.0122$; Fig. II.5). Otherwise, prey availability did not differ between the two stages (mean prey mass $t=-0.87$, 12 df, $p=0.4033$; prey mass/h/area: $t=-1.66$, 12 df, $p=0.1225$). Larger prey were captured by colonies during the early, communal stage in general ($t=-3.71$, 26 df, $p=0.0010$) and per unit mean spider body mass ($t=-3.38$, 25 df, $p=0.0024$; Fig. II.5). During the early, communal stage spiders also captured more prey items per capita ($\chi^2=4.96$, 72 df, $p=0.0260$) and higher prey mass per spider mass ($\chi^2=7.47$, 72 df, $p=0.0063$).

Discussion

Prey availability and sociality

In this study, environments offering a high prey biomass in the form of large prey items appeared to favor sociality, while environments offering small prey items, in high or low total biomass, seemed to favor subsociality. The environments of the social species had larger prey and generally high total prey biomass. Also, prey were larger, on average, in the rain forest edge habitat compared to the forest understory. Although *A. eximius* colonies also occur in the forest understory, they tend to experience higher success in establishing nests and grow to larger sizes along the forest edge (Leborgne et al 1996). In contrast to the expectation that subsocial species would be found inhabiting environments with lower prey biomass, the habitat of a subsocial species, *A. panamericana*, had the highest numbers of prey and a total prey biomass comparable to the rain forest edge habitat. Environmental prey abundance was lowest in Garden Canyon, the habitat of *A. arizona*, as spiders there approached dispersal. This was due to small prey sizes and moderate to low prey density. These findings suggest that a preponderance of large prey may serve as a critical factor favoring the large, stable colonies of the social species. Concordantly, cooperative foraging groups are often predicted to occur and found in environments with large, abundant resources that require

coordinated group efforts in capture (Packer and Ruttan 1988). Competition is reduced in such systems by prey being too large for a single individual to consume solitarily and/or ephemeral in some way (Clark and Mangel 1986). Thus, while high environmental prey biomass may be essential for supporting large, social colonies, it is unlikely to be the force selecting for them. Based on the findings of this study, environments with smaller prey items appear more likely to favor the smaller, less stable colonies characteristic of subsocial species during the pre-dispersal phase. The size of these colonies is likely to depend on prey biomass, with higher prey biomass supporting larger, more cooperative colonies (e.g. *A. panamericana*), and lower prey biomass supporting smaller, more competitive colonies (e.g. *A. arizona*).

Sociality and prey capture

The idea that environments with large prey items favor sociality in spiders is further supported by the prey availability patterns observed within the subsocial species. Although prey availability showed little change between the early, communal stage and the pre-dispersal stage in the subsocial species, the way in which spiders experienced prey availability was likely to differ between these times. Because spiders were younger and smaller during the earlier stage, prey in the environment probably seemed larger to

them. As spiders grew larger and finally reached the later, pre-dispersal phase, these same prey sizes would seem smaller. Thus, spiders were effectively foraging in different environments in these two stages. The fact that prey density (#/h/cm²) did not differ between stages for *A. panamericana* and that, for *A. arizona*, it was higher during the early, communal stage indicates that the total prey biomass available in these environments was actually higher relative to spider mass during the earlier phases when colonies were stable. Interestingly, in *A. arizona* prey density was found to be even higher during the dispersal phase than during the early communal phase (unpublished data). Thus, spiders were solitary when prey density was highest and prey were smallest relative to their body sizes, but spiders were communal when prey density declined and relative prey sizes increased.

Seasonal fluctuations in temperature may also influence how spiders perceive prey abundance. *A. arizona* colonies remain stable during the winter when temperatures are low (Figure II.1c) and spiders are relatively dormant, not building webs or moving much within the nest (*sensu* Schaefer 1987). Even though prey are available in the environment at this time and occasionally contact nests, spiders do not attack them (personal observation). Colonies become less stable in the spring when temperatures increase and spiders become more active. At this time, spiders begin competing over

captured prey items and dispersing. Increasing ambient temperatures have also been suggested to increase competition and hasten dispersal in the subsocial spider *Badumna candida* (Downes 1993).

Within environments with a high prey biomass concentrated into moderate numbers of very large prey, sociality confers a considerable advantage by enabling the exploitation of large prey items. The ability to access larger prey is a well-known benefit of cooperative foraging in spiders (Nentwig 1985; Rypstra and Tirey 1991; Uetz 1992). In this study, the social species captured the largest prey relative to their body sizes. Furthermore, subsocial species captured larger prey relative to their body sizes during their early communal stage compared to their pre-dispersal phase. Even without taking spider body size differences into account, the prey captured by earlier stage *A. arizona* colonies were larger than those captured by pre-dispersal colonies. It is likely that the mother may have facilitated the capture of large prey items during this stage in the subsocial species (Ruttan 1991).

Sociality may also increase prey capture efficiency in general (Rypstra 1990; Pasquet and Krafft 1992). Despite the highest numbers of prey (#/h/cm²) being found in the habitat of *A. panamericana*, *A. eximius* captured higher numbers of prey per capita. Furthermore, although environmental prey density was similar between colony stages in

A. panamericana, colonies in the early, communal phase captured higher numbers of prey per capita. Together, the ability to capture larger prey items and higher numbers of prey seemed to increase the biomass of prey received per spider mass in some colonies (prey biomass/spider biomass). Despite similar prey biomasses available in the environments of *A. eximius* and *A. panamericana*, *A. eximius* individuals received more prey biomass on average. Furthermore, although absolute prey biomass available in the environments of subsocial spiders did not differ between stages, earlier stage colonies captured more prey biomass per spider biomass. This difference is due, at least in part, to the smaller body sizes of spiders in earlier stage colonies.

Implications for the energetic model and the evolution of sociality

These results change expectations for the energetic model presented in Chapter I. Subsocial species do not necessarily occupy environments with lower prey biomass available, but their environments do present smaller prey (relative to spider body sizes) compared to environments of social spiders. Consequently, we might expect per capita prey capture rates in *A. panamericana* colonies to change according to the solid line in Figure I.3, and *A. eximius* and *A. domingo* colonies to change according to the dashed line. The subsocial species would likely take the form of the curves in Figure I.5a, with

A. panamericana on the right and *A. arizona* on the left. From these illustrations, it is easy to see why *A. arizona* may disperse at smaller colony sizes than *A. panamericana*. However, *A. panamericana* could apparently reach colony sizes as large as those of the social species. This species is only found in colonies ranging from 1-150 spiders, thus indicating that other selective pressures must be limiting colony size. This may be due to the ability of this species to capture higher prey masses per capita at smaller colony sizes. In contrast, the social species are predicted to capture much lower prey masses per capita at smaller colony sizes, and their per capita prey capture rate peaks at intermediate colony sizes, at which fitness has also been found to peak (Avilés and Tufino 1999). Even after decreasing beyond this peak, per capita prey capture may remain higher than that of a solitary forager for a very long time.

The results of this study support the idea that if subsocial species radiated into an environment with low numbers of mainly large prey, they would benefit most by remaining together and feeding on large prey rather than periodically living solitarily and relying on small prey. Such a strategy would provide sufficient food to developing spiders throughout their lives, whereas periods of solitary foraging would lead to severely high mortality rates. Furthermore, as increasingly large colonies developed, the high density of spiders in colonies would likely become more dependent on the highly

concentrated biomass of large prey to sustain colony members, creating a feedback cycle encouraging sociality.

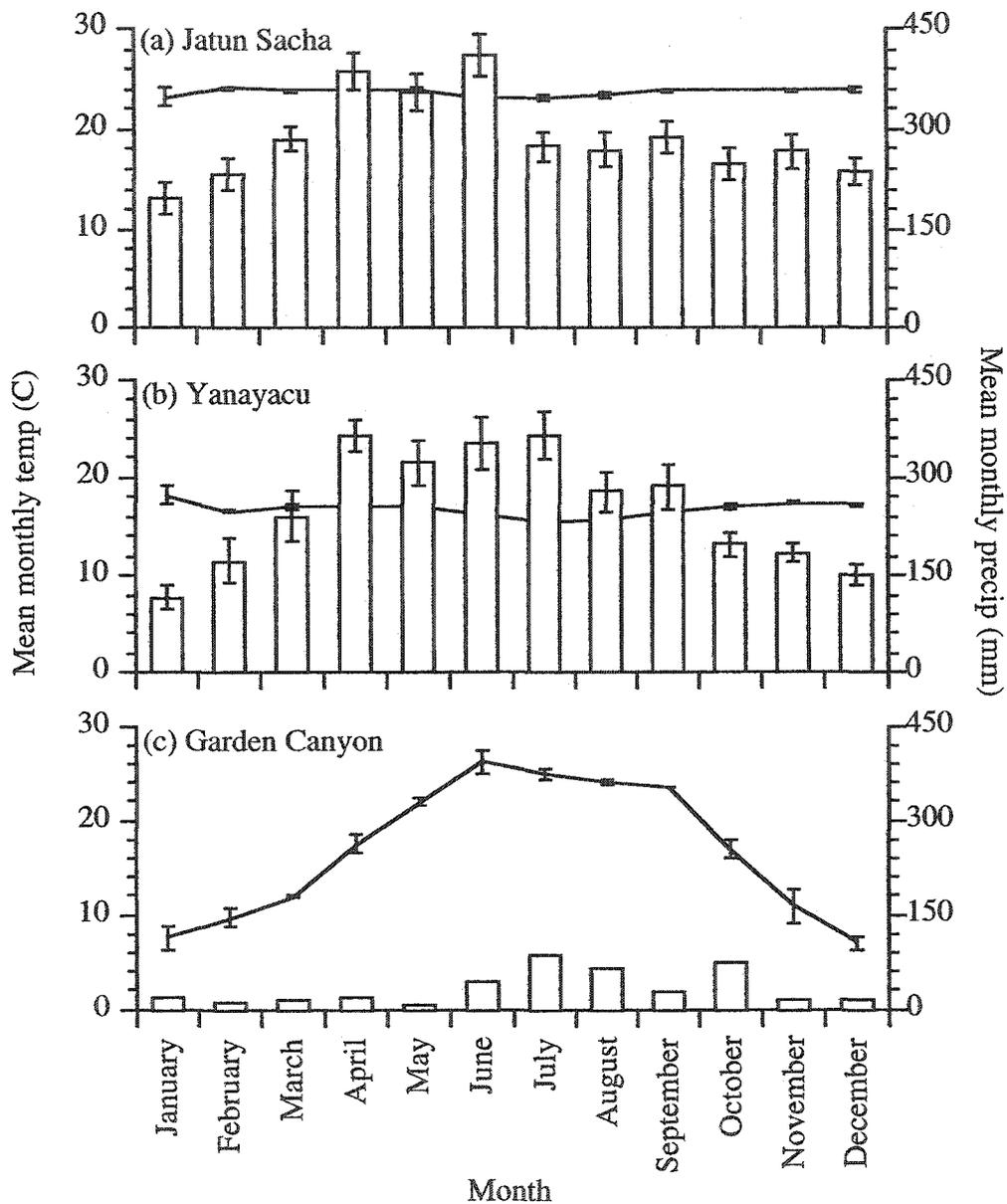


Figure II.1: Seasonal weather patterns at (a) Jatun Sacha, (b) Yanayacu, and (c) Garden Canyon. Columns represent total monthly precipitation (mm) and lines represent mean monthly temperature (C). In both cases, standard error bars refer to variation among years: $n=24$ years for Jatun Sacha, $n=14$ years for Yanayacu, $n=3$ years for Garden Canyon. SE bars are not provided for precipitation means from Garden Canyon due to extreme variation among years. Climate data for the Ecuadorian sites were provided by R. Sierra; those for Garden Canyon were provided by the Meteorological Lab at Fort Huachuca Military Base.

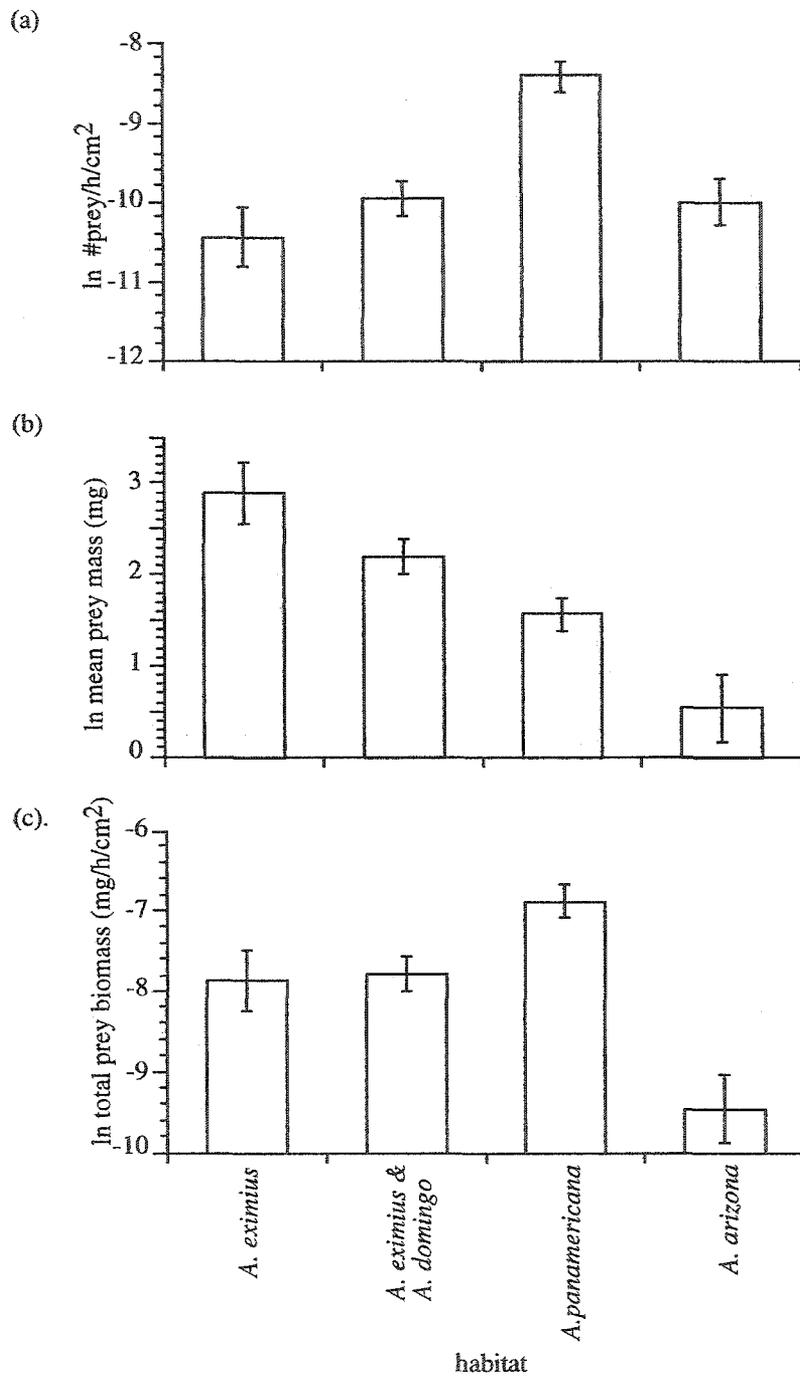


Figure II.2: Prey availability across the lowland rain forest edge (*A. eximius*), the rain forest understory (*A. eximius* & *A. domingo* shared habitat), the cloud forest edge (*A. panamericana*), and the temperate riparian area (*A. arizona*). Prey availability is expressed as (a) prey density (the number of prey flying through an area per hour), (b) the mean mass of these prey, and (c) the total prey biomass (mass of prey flying through an area per hour).

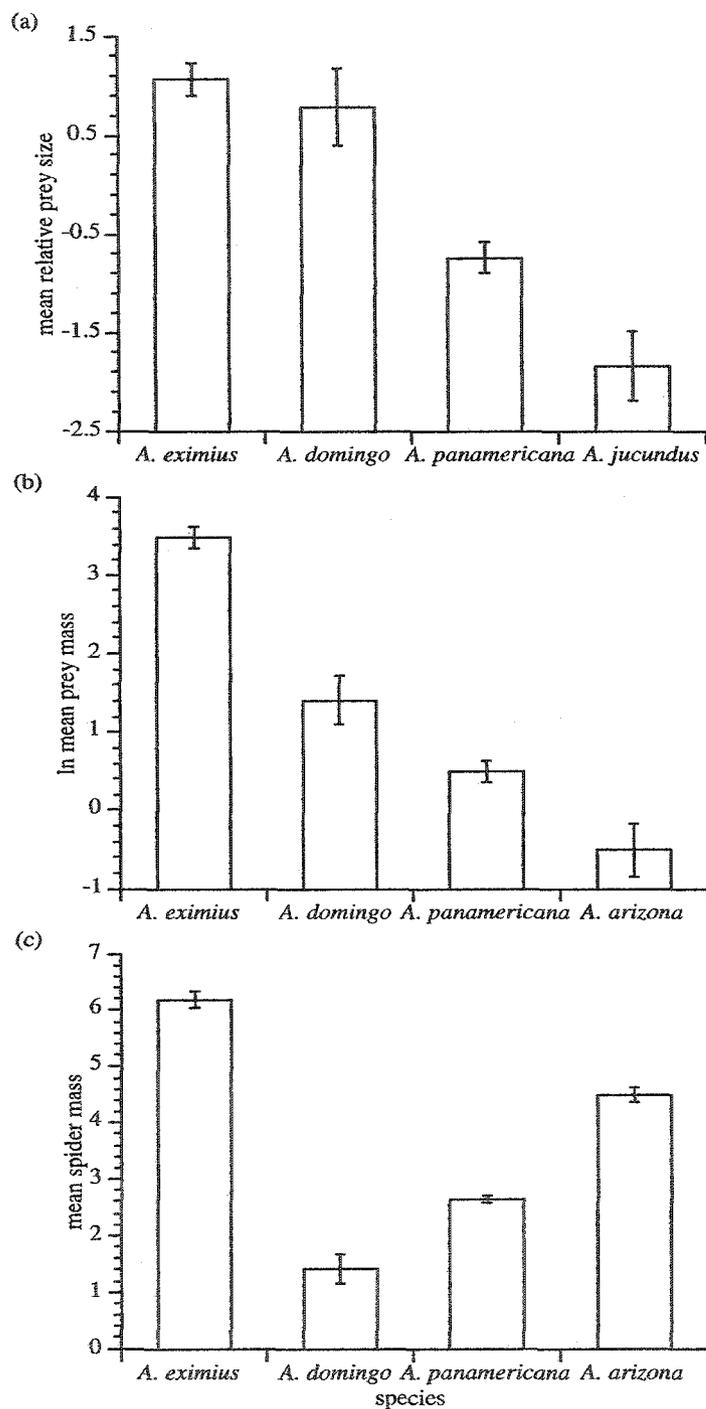


Figure II.3: Sizes of prey captured by colonies in relation to spider body mass during colony census periods. Overall, this is expressed as (a) mean relative prey mass (mean prey mass (mg) / mean spider mass (mg)), which is broken down into (b) mean prey mass, and (c) mean spider mass. Error bars represent standard error.

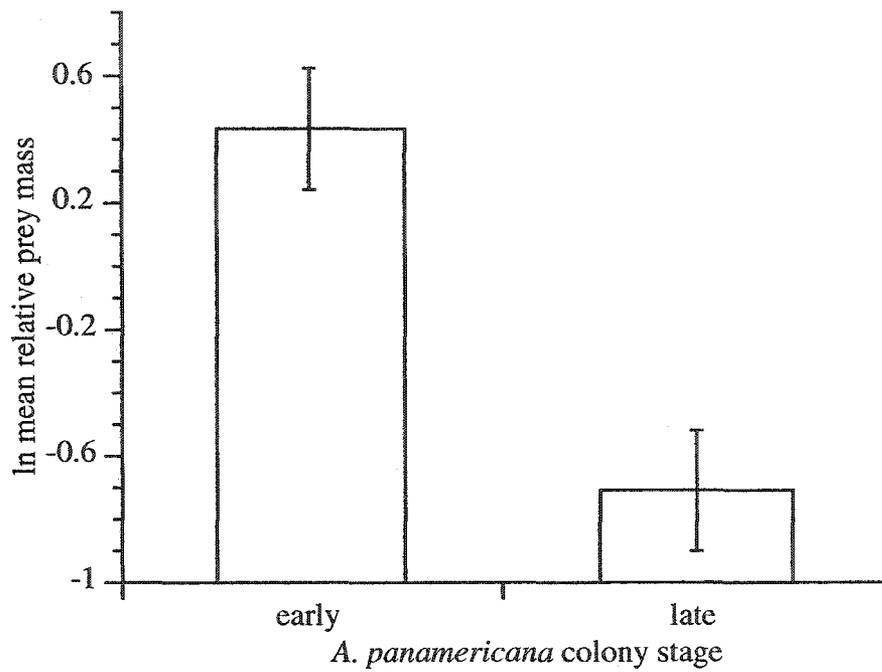


Figure II.4: The mean relative prey mass (mean prey mass (mg) / mean spider mass(mg)) captured by *A. panamericana* colonies during their early communal phase vs. their later stage when spiders were approaching the dispersal phase.

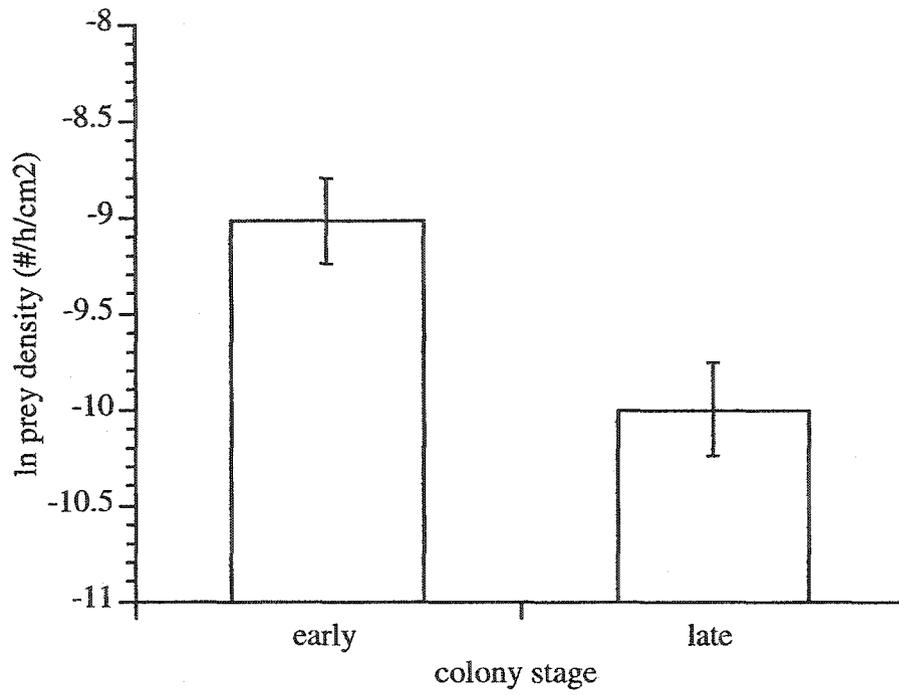


Figure II.5: The environmental prey density (prey #/h/cm²) estimated for *A. arizona* during their early, communal stage vs. the later colony stage when spiders were approaching the dispersal phase.

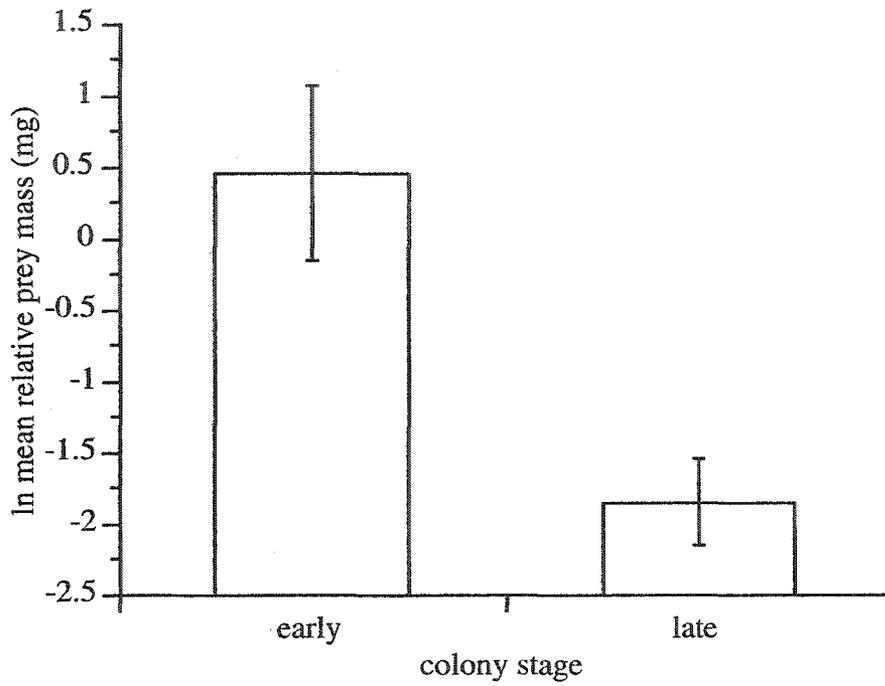


Figure II.6: The mean relative prey mass (mean prey mass (mg) / mean spider mass (mg)) captured by *A. arizona* colonies during the early, communal stage vs. the later colony stage when spiders were approaching the dispersal phase.

Table II.1: For *A. eximius*, the size ranges of prey found in Malaise traps vs. colonies for each major insect order.

Insect order	Traps:	Colonies:	Traps:	Colonies:
	min mass (mg)	min mass (mg)	max mass (mg)	max mass (mg)
Coleoptera	1.2	1.2	40.7	230.0
Heteroptera	0.9	0.6	11.6	280.0
Hymenoptera	0.6	0.6	18.0	70.7
Diptera	0.2	0.2	60.3	18.0
Lepidoptera	0.9	0.9	183.4	183.4
Orthoptera	3.3	5.3	72.5	200.0

Chapter III: Relationship between colony size and prey capture in different environments

Introduction

A major difference between social and subsocial species is in the magnitude of their colony sizes (D'Andrea 1987; Avilés 1997). Subsocial spider colonies begin with a single adult female whose offspring leave the natal nest before reaching reproductive maturity. So, colony size is limited to a single clutch and a single generation. In contrast, in social spiders colonies may be initiated with several adult females whose descendants remain together for several generations. Consequently, social spider colonies reach much larger sizes. The ability to form larger, longer-lived colonies has likely provided the opportunity for further social behaviors to arise such as cooperative brood care.

Prey availability is a likely factor limiting colony size in subsocial species, as subsocial and social species tend to occupy different types of environments. While subsocial spiders occur in temperate and tropical highland regions, social spiders are found exclusively in lowland tropical environments (Avilés 1997; but see Furey 1998) where prey are likely to be larger and possibly more abundant (see Chapter II). Furthermore, subsocial species have been shown to delay dispersal when provided a

surplus of prey (Ruttan 1990; Rypstra 1986; Leborgne et al. 1994; Lubin and Henshel 1996; Evans 1998). Because social spiders have evolved from subsocial-like ancestral species (Kullman 1972; Krafft 1986), understanding the foraging-related costs and benefits of increasing colony size in these different prey environments may shed light on the environmental conditions that have allowed permanent sociality and larger colony sizes to evolve.

For spider colonies, prey capture rate depends on the amount of web area exposed to the environment, the local density of flying insects, and the ability of spiders to capture prey items contacting their webs (Buskirk 1975; Riechert et al. 1986; Ward 1986; Uetz 1988; Uetz and Hodge 1990). One potential cost of group foraging in spiders involves the possibility of diminishing prey per capita with increasing colony size as presented in the energetic model in Chapter I. Social spiders tend to build three-dimensional, asymmetrical webs (Avilés 1997). As with most three-dimensional objects, web surface area is likely to increase at a decreasing rate with web volume, so that changes in web volume at larger web sizes lead to smaller changes in web area. If spiders continue to contribute a constant web volume as colony size increases, then available web area per spider will decrease, leading to fewer prey items contacting the web per spider. Lowered per capita prey contact rates may still satisfy colony prey requirements if environmental

prey density is high. Also, by having larger webs, prey may be less likely to escape, and by having more spiders in the web, colonies may become more successful at capturing the prey that contact the web, offsetting the costs of reduced prey contact (e.g. Uetz 1989). For example, an often-noted benefit of spider sociality is the ability to capture larger prey items (Chapter II; Nentwig 1985; Rypstra 1990; Pasquet & Krafft 1992). For these reasons, large colony sizes may only be a viable option in environments with high prey density, and large colony sizes may actually be favored in environments where larger prey items comprise a considerable portion of available prey.

To further understand how prey environments have shaped colony size distributions across social and subsocial species, I investigated the potential costs and benefits of increasing colony size for three communal *Anelosimus* species in different environments – a social species, *A. eximius*, in a lowland tropical rain forest with a high prey biomass of mainly large insects; a subsocial species, *A. panamericana*, in a tropical cloud forest with a high prey biomass of mostly small insects; and another subsocial species, *A. arizona*, in an arid, temperate riparian area with a low prey biomass of generally small insects. In each of these populations, I addressed the following questions: (1) How does the number of spiders in a colony relate to its web area?, (2) Do larger colonies have less web area available per spider?, (3) Do larger colonies capture

less prey per capita? If prey availability has influenced the evolution of colony size, then these questions should produce qualitatively different results for social and subsocial species. In particular, social spiders should experience fewer costs and more benefits at larger colony sizes, while subsocial spiders should experience the converse. In terms of the model presented above, this hypothesis makes four predictions: (1) across environments, M_c should be directly proportional to R , and high R should correlate with larger M_c^* , (2) V_c/N is constant, $A_c \propto V_c^{2/3}$, and $A_c/N \propto N^{-1/3}$ (Fig. I.3); (3) in environments with large prey, larger colonies capture larger prey, and (4) $(M_p/t)/N$ is related to colony mass differently across prey environments such that in environments with mainly small prey, $(M_p/t)/N$ is related to colony mass by a negative function with slope close to $-1/3$, while in environments with larger prey, $(M_p/t)/N$ increases with colony mass before decreasing (Fig. I.4b).

Methods

Study species

A. eximius is typically found in the tropical lowland rain forests of Central and South America (Levi 1963). I studied this species at The Estación Biológica Jatun Sacha (450 m; S 01° 04' 13.2", W 77° 36' 41.4") in northeastern Ecuador. The two subsocial

species included in this study, *A. panamericana* and *A. arizona*, have not yet been formally described. *A. panamericana* has been found throughout South and Central America and in cloud forest areas in Ecuador (I. Agnarsson pers. comm.). I studied this species at Yanayacu Biological Station and Center for Creative Studies (2073.17 m, S 0° 36' 0", W 77° 52' 0"). I studied the other subsocial species, *A. arizona*, in Garden Canyon (1524.70 m; N 31.49°, W 110.32°), a temperate riparian area in southern Arizona. This species is morphologically similar to *Anelosimus jucundus* O. P. Cambridge 1986, a subsocial species described from montane areas in Costa Rica, Panama, and Ecuador (Levi 1956, 1963; I. Agnarsson pers. comm.).

Colony size and prey capture

The colony sizes and prey capture rates used in this study are a subset of those presented in the previous chapter (Chapter I). For the purposes of this study, I have only considered the numbers of spiders in colonies, not colony biomass, as a measure of colony size. For the subsocial species *A. panamericana* and *A. arizona*, only colonies approaching, and in some cases beginning, the dispersal phase have been included; however, no dispersed spiders have been included. For *A. eximius*, only colonies containing later stage juveniles, subadults, and adults have been included here to maintain

relatively similar colony age structures among species and among colonies within species.

Web measurements

Anelosimus webs are characterized by a basal web-basket filled with nest materials and capture webbing extending upward and sometimes outward to surrounding vegetation (for drawing see Avilés 1997 or Simon 1891). The capture web interior is scaffolded with lines of silk that catch or entangle prey falling through the web. The capture webbing tends to take a cone or cylinder shape depending on the amount of silk extending the full height. Using a flexible/bendable ruler, I measured two circumferences of each web – one just above the nest and another at the very top where it attached to vegetation. I also measured the height of the web. I then calculated the web area by multiplying the average of the two circumferences by the height. Web volume was also calculated with these measurements. More complex sets of measurements were required for webs not conforming to a single cylinder or cone, a more common problem in the subsocial species. In these cases, I divided the web into its component three-dimensional geometric shapes with quantifiable areas and volumes and combined the areas (and

volumes) after they were calculated for each part to approximate the entire web area and volume.

Statistical analyses

All continuous variables included in analyses – colony size, web area, web area per spider, web volume per spider, number prey captured per hour per capita, mean prey mass, and prey mass captured per hour per capita – were natural log transformed to normalize their distributions. For *A. panamericana*, analyses relating the number of spiders in a colony and colony web size variables (i.e. web area, web area per spider, and web volume per spider) include only colonies for which the number of spiders was counted directly, rather than estimated via web area. All *A. panamericana* colonies have been included in analyses involving prey capture. Central tendencies are presented as medians or means \pm standard error.

Results

Colony size and web area

Colony sizes varied widely across species, ranging from 54 – 4,888 spiders in *A. eximius* colonies, 1 – 131 spiders in *A. panamericana* colonies, and 1 – 7 spiders in *A.*

arizona colonies ($F_{2,89}=204.66$, $p<0.0001$; Table III.1; Fig. III.1). As predicted, the species in environments with higher prey biomass (*A. panamericana* and *A. eximius*) reached larger colony sizes than the species inhabiting an environment with much lower prey biomass available (*A. arizona*). Also as predicted, capture web area correlated positively with colony size in all three species (Table III.1; Table III.2; Fig. III.2). On a log-log scale, web area increased with a slope of 0.44 in *A. panamericana* and 0.97 in *A. arizona*, compared to the predicted slope of 0.66 in the energetic model. *A. eximius* colonies had larger web areas than the subsocial species (Tukey-Kramer: *A. eximius* vs. *A. panamericana* $q=2.77$, $p<0.05$, and *A. eximius* vs. *A. arizona* $q=3.75$, $p<0.05$ in ANOVA $F_{2,89}=109.84$, $p<0.0001$), and web areas of *A. eximius* colonies increased according to a quadratic function, reaching a limit at larger colony sizes (Table III.1; Fig. III.2a).

In *A. eximius* and *A. panamericana*, the species with larger colony sizes, the amount of web area available per spider decreased as colony size increased (Table III.1; Fig. III.3) with slopes of -0.32 and -0.55, respectively, the former closely resembling that predicted by the energetic model, - 0.33. Also as in the energetic model, web volume per spider (an indicator of web contribution per spider) remained constant as colony size increased in *A. eximius* and *A. arizona* (Table III.1; Table III.2; Fig. III.4). *A.*

panamericana did not follow this prediction, however, as its per capita web volume decreased with increasing colony size.

Prey capture

While prey capture occurred at some time during census periods for nearly all *A. eximius* colonies (12 of 15 total colonies monitored), it occurred rarely in colonies of the subsocial species (37 of 123 *A. panamericana* colonies, and 9 of 44 *A. arizona* colonies; in Wilcoxon comparisons, *A. eximius* vs. *A. panamericana*: 142 df, $\chi^2=18.20$, $p<0.0001$; *A. eximius* vs. *A. arizona*: 58 df, $\chi^2=18.90$, $p<0.0001$). The number of times a colony was censused did not appear to determine whether or not prey were captured (184 df, $\chi^2=0.01$, $p=0.9131$ in nominal logistic model including species). Colonies with larger web areas were more likely to capture prey in *A. panamericana* and *A. arizona* (122 df, $\chi^2=36.97$, $p<0.0001$, and 42 df, $\chi^2=30.23$, $p<0.0001$, respectively; Fig. III.4). Surprisingly, prey capture was not related to the numbers of spiders in *A. panamericana* colonies (122 df, $\chi^2=0.39$, $p=0.5303$) or in *A. arizona* colonies after taking into account web area (42 df, $\chi^2=0.32$, $p=0.5708$ for colony size in ANCOVA with web area).

The numbers of prey captured per capita decreased with increasing colony size similarly across all three species (Table III.1; Table III.2; Fig. III.5). Such negative

slopes were predicted throughout colony size ranges in environments with mainly small prey and for intermediate to larger colony sizes in environments with large prey. While the mean masses of prey captured did not change with colony size in the subsocial species, larger *A. eximius* colonies captured larger prey as predicted for species inhabiting environments with large prey. Consequently, spiders in *A. eximius* colonies received consistent amounts of prey mass, while those in *A. panamericana* colonies that captured prey received less prey mass as colony size increased. Spiders in *A. arizona* colonies that captured prey also received consistent amounts of prey mass (Table III.1). Overall, *A. eximius* and *A. arizona* did not exhibit their predicted patterns in per capita prey mass captured— a peak at intermediate colony sizes and a decrease with increasing colony size, respectively – and *A. panamericana* followed the predicted relationship, decreasing at a greater rate than expected (Table III.2).

Discussion

The relationships quantified in this study often resembled those predicted by the energetic model presented in Chapter I. In particular, the changes in web size and the numbers of prey captured per capita were similar to initial expectations. Also, the directions of relationships generally followed those predicted in the model. The lack of a peak in the relationship between prey capture and colony size in *A. eximius* may be due to

the range of colony sizes sampled. The smallest colony that was included contained 54 spiders, which may be enough to capture the largest insects contacting the web.

Consequently, the increase predicted by the energetic model may actually occur among smaller colony sizes. A decrease in the numbers of prey captured per capita was observed in this species and may correspond with the decreasing part of the peak predicted. Prey mass captured per capita, however, did not decrease. It is also possible that the predicted pattern would have been observed if more colonies were included.

The distribution of colony sizes for each species support the idea of selection for colony sizes that maximize prey intake. Colonies of the subsocial species tended to be small, the colony size at which per capita prey capture was found to be highest. However, this trend is complicated by many colonies not capturing prey at all during census periods. Most colonies of the social species were also at the smaller end of their range. Concordantly, Avilés and Tufino (1999) estimated maximum fitness around colony sizes of approximately 60 spiders in this species, and the numbers of prey captured per capita were highest at this size, although prey mass captured per capita did not change with colony size.

Colony sizes differed across species by at least an order of magnitude. Web area increased with colony size (and therefore web volume) for all species. As predicted by a

geometric relationship between volume and surface area of standard three-dimensional objects, web area appeared to reach a limit among the largest colony sizes, which occurred in *A. eximius*. Consequently, increases in colony size and web volume for large colonies (with $\geq 1,000$ spiders) correlated with smaller changes in web area. For this species, the amount of web area available per spider decreased overall despite spiders contributing a constant web volume. This represents the point at which spiders could be expected to benefit the least from their web-building contributions. In the species with much smaller colony sizes, *A. panamericana* and *A. arizona*, web area increased linearly with colony size throughout their colony size ranges. Also, at these colony sizes, changes in web area per spider did not differ qualitatively from changes in web volume per spider.

Despite web area per spider decreasing with colony size in *A. eximius* and a corresponding decrease in the numbers of prey items captured per capita, spiders received constant prey mass across colonies of different sizes. This was due to larger colonies capturing larger prey on average, a capability probably enabled by more spiders being present in the web (e.g. Nentwig 1985; Ward 1986; Rypstra and Tirey 1991; Uetz 1992). Thus, within the size range studied (~50—5,000 spiders), colonies experienced no negative effects of increasing colony size. However, *A. eximius* colonies containing

~20,000 spiders have also been found at this site (unpublished data). It is likely that, at some point, the environment imposes a limit on the prey sizes available to colonies, and then the average size of prey captured no longer increases with colony size. At this colony size, the amount of prey mass received per capita would likely decrease.

Colony size conflicts in subsocial species

According to the findings of this study, subsocial spiders face a conflict in increasing colony size. Although larger colonies produce webs with larger areas, which are more likely to capture prey, the amount of prey received per spider in colonies that capture prey tends to decrease with increasing colony size. As colony size increased in *A. panamericana*, spiders experienced the benefits of lower web volume contributions and greater prey capture probability (via larger communal webs), but they also experienced the cost of decreasing per capita prey capture. Spiders in *A. arizona* colonies experienced the same benefits, but on average, they did not experience losses in per capita prey mass captured. It is important to note, however, that *A. arizona* spiders approaching the dispersal phase do not cooperate in prey capture or tolerate communal feeding (Fig. I.3, Chapter I). Prey captured by colonies at this stage are typically fed upon by single spiders, so prey are not distributed evenly among colony members. It

may be that if prey were distributed evenly among colony members, no spider would receive enough to survive and reach maturity because environmental abundance is too low (Chapter II). This may explain why spiders in *A. arizona* colonies stop cooperating as they approach the dispersal phase, but those in *A. panamericana* colonies of a similar stage continue cooperating.

One way to resolve this conflict for physically robust, competitive spiders is to remain in the natal nest until all other colony members have dispersed, thereby benefiting from a larger web area without the costs of competition or sharing prey with others. Several costs associated with dispersal could also be avoided by this strategy. The probability of successful nest foundation is low for social spiders (Vollrath 1982; Christenson 1984; Leborgne et al. 1994). Moreover, dispersal imposes high mortality rates in *A. arizona* (79% estimated by Avilés and Gelsey 1998), and in the theridiid widow spider (Lubin et al. 1993). Dispersers can also miss foraging opportunities and possibly lose body mass (Kim 2000; Jakob, et al. 2001). Nest reoccupation has been proposed for *A. arizona* (Avilés and Gelsey 1998). Given the advantages listed above, in prey rich environments adequate prey capture over time could lead to multiple females remaining in the parent nest to reproduce and found new colonies, thereby setting the stage for larger colony sizes and, subsequently, increased cooperation to evolve. Nest

sharing by multiple females has actually been reported for *A. studiosus*, a typically subsocial species (Furey 1998). Newly founded *A. panamericana* nests also sometimes contain multiple females with egg sacs and/or their young (unpublished data). These benefits could be even greater for spiders living in colonies with highly related individuals, because they would be ensuring frequent prey capture for relatives in addition to themselves. This does not appear to be the case in *A. panamericana*, as spiders from obviously different clutches and mothers frequently cohabit the nest as the dispersal phase begins. However, the subsocial spider *Stegodyphus lineatus*, benefits when feeding in groups of siblings, as opposed to non-siblings, because their efficiency is higher (Schneider 1996).

Determinants of foraging group size

Generally, group foraging benefits animals by allowing them to find and exploit otherwise unattainable resources. At the same time though, animals in foraging groups face the potential disadvantage of sharing or competing over resources with other group members. The group size that maximizes resource acquisition for individuals in foraging groups is likely to depend on local resource distribution and abundance as well as taxon specific foraging strategies and requirements (Pulliam and Caraco 1984; Clark and

Mangel 1986; Packer and Ruttan 1988). Sociality and subsociality represent two distinct foraging group sizes in spiders. Because they have similar foraging strategies, environmental resource distribution and abundance are likely to be the more important factors determining their most profitable group size. Examining the benefits and costs of increasing group size for the species presented here and in other studies should provide some explanation for the vastly different colony sizes seen between subsocial and social spiders.

Large group size confers web-building benefits that could be particularly advantageous in environments where sources of web damage are common and predation is potentially high. Increasing colony size allows spiders to build larger, denser and complex communal webs but expend less effort while doing so (Tietgen 1986; Evans 1998; Jakob 1991). For example, *A. panamericana* individuals appeared to contribute less web volume as colonies grew larger. In particular environments where web damage occurs frequently due to heavy rain, wind, struggling prey, and falling debris (Craig 1988), reduced silk investment may save spiders considerable amounts of resources that they could otherwise invest in growth (Higgins 1995). Furthermore, while saving on silk costs, spiders can still experience the prey capture benefits that larger webs and colonies confer, such as higher prey capture success of large prey and higher prey capture

efficiency (Ward and Enders 1986; Uetz and Hodge 1990; Caraco et al. 1995; Jones and Parker 2000). Also, larger, complex webs often provide extensive protective retreats that serve an important function in predator protection (Henschel 1998; Evans 1998).

Another potential benefit of increasing foraging group size for spiders is a reduction in prey capture variability. In *A. arizona*'s subsocial congener, *A. studiosus*, colony prey capture rates are less variable for individuals in larger colonies (Jones and Parker 2002). Group living has been found to also reduce spatial and temporal variability in prey capture and increase prey capture efficiency for colonial, orb-weaving spiders (Uetz and Hodge 1990; Caraco et al. 1995).

In some cases (Jones and Parker 2002), total per capita prey capture rate increases with colony size, but more often, it actually decreases. This has been found for colonial, subsocial, and social species (Ward 1986; Jakob 1991; Jones and Parker 2000), including the subsocial species examined in this study. At best, per capita prey capture may remain constant, as shown for a social species, *A. eximius*, in this study and for a subsocial species, *A. studiosus* (Jones and Parker 2002). Exactly how per capita prey capture rates change with colony size probably depends on environmental prey abundance, as group-living in spiders is frequently associated with high prey abundance (Uetz 1988; Rypstra 1989; Uetz 1992; Chapter II). Prey size may be particularly important, as the number of

prey captured per capita decreased with colony size in all three species including *A. eximius*. Only an ability to capture increasingly larger prey allowed *A. eximius* colonies to provide a constant prey biomass to colony members.

These costs and benefits provide insight into where social vs. subsocial species may occur. Assuming that colony sizes are determined solely by the costs and benefits discussed above (the colony size that maximizes energy intake), species with the largest colonies may be expected to occur where web destruction happens frequently, a high threat of predation exists, and high prey mass is available but varies spatially and/or temporally, often ephemerally (Clark and Mangel 1986). These conditions reflect those typical of *A. eximius* occupying lowland rain forests where rains are torrential and a high prey biomass is clumped into somewhat low numbers of large insects that spiders are unable to preserve in the web for long periods of time (Pulliam and Caraco 1984; Rypstra and Tirey 1991). In contrast, smaller colonies may be expected to occur where similar benefits exist, but prey abundance is limited and so the cost of sharing or competing can not be overcome. A smaller colony size may offer a balance between experiencing some of the benefits of group living (reduced silk costs, predator protection) and minimizing the costs of reduced prey intake.

In *A. panamericana* colonies, prey capture events were rare, but when they occurred, spiders were likely to receive more prey mass if in a small colony or living solitarily. In larger *A. panamericana* colonies with larger web areas, prey capture was likely to occur more often, possibly outweighing the disadvantage of decreased prey mass availability per capita in large colonies.

Deviations from these predictions may arise due to other constraints on group size such as nest site availability, intense predation, or intrinsic population dynamics. Furthermore, groups rarely reflect the sizes that seem optimal. Rather, they tend to exhibit equilibria that are larger than the predicted optima and involve competition and asymmetries in body size and behavior (Packer and Ruttan 1988). This may explain why *A. eximius* colonies tend to grow beyond the size at which all females will reproduce (Avilés and Tufiño 1998), something suggested to result from insufficient prey within the nest (Vollrath and Rohde-Arndt 1982). Avilés and Tufiño (1998) have shown that, for *A. eximius* colonies occupying the forest interior, lifetime reproductive fitness for females is highest in colonies containing 60 females, but the colonies included in this study contained a median of 144 females and as many as 2,131 females. During their study, juvenile survival increased with colony size, but the number of females reproducing decreased. Given that per capita prey capture remained constant with increasing colony

size in the data presented here and female reproduction requires higher prey intake (Venticinque et al. 1993), this result may be due to an asymmetrical allocation of prey in favor of developing juveniles. In such situations where increasing colony size decreases prey capture per capita or other components of fitness, groups may remain together simply because the alternative – dispersal – is costly, and even at very large colony sizes, individuals may receive more prey than they would foraging solitarily (Jones and Parker 2000). Moreover, even as prey capture decreases, the net benefit may remain relatively high due to predator protection and decreased silk production costs.

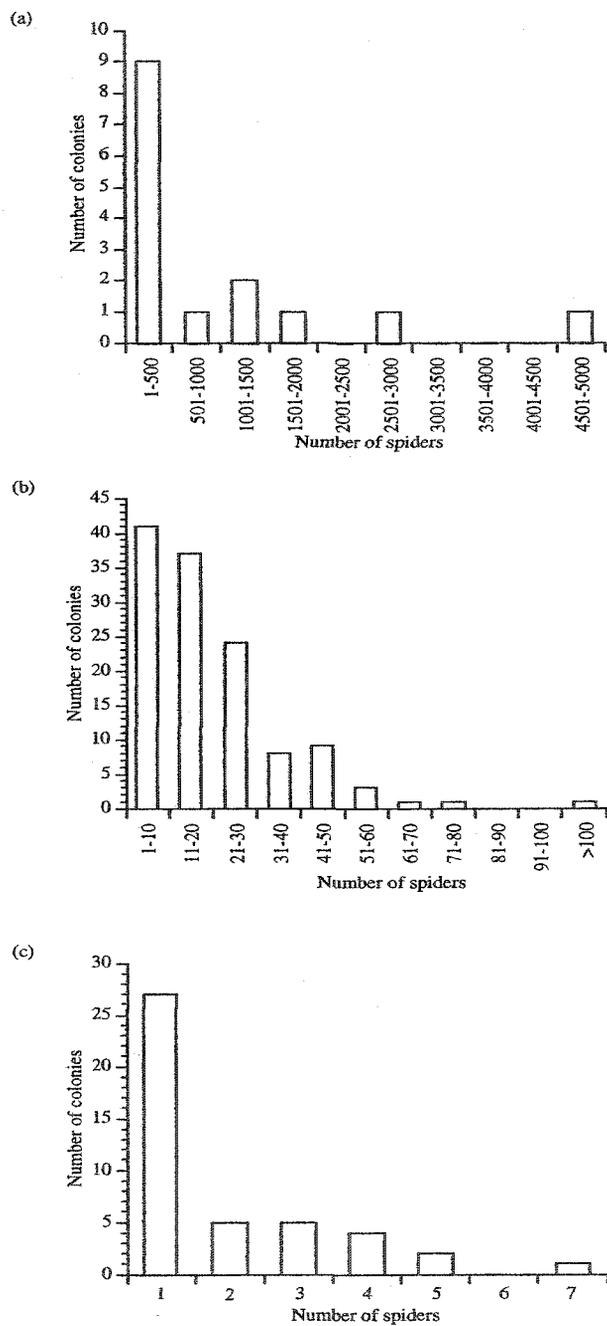


Figure III.1: Colony size distributions for (a) *A. eximius*, (b) *A. panamericana*, and (c) *A. arizona*.

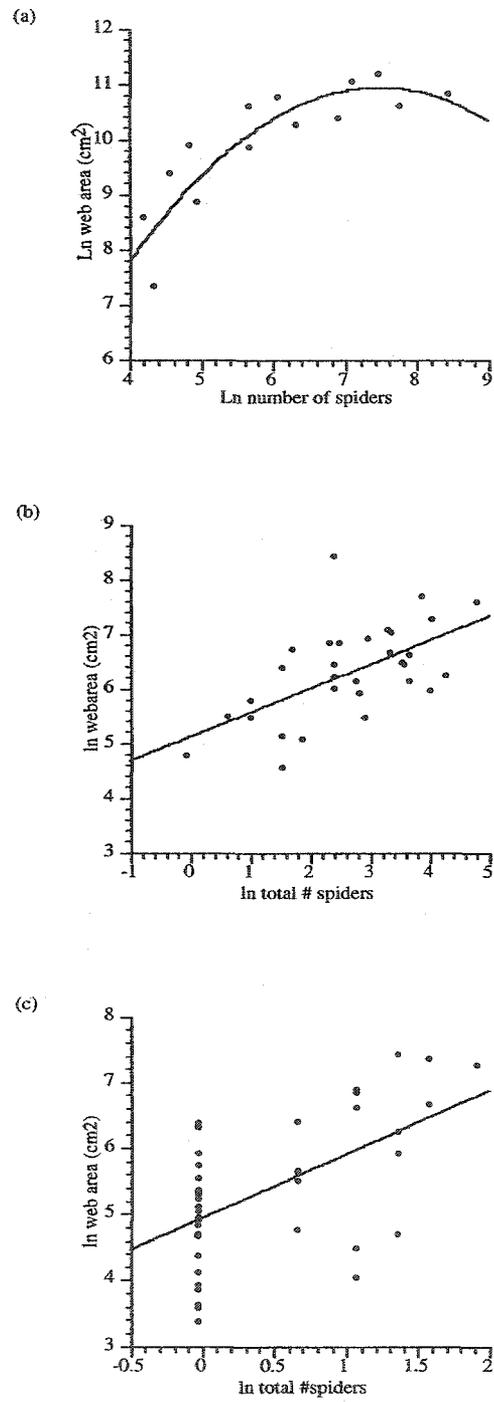


Figure III.2: Relationship between colony size and web area in (a) *A. eximius*, (b) *A. panamericana*, and (c) *A. arizona*.

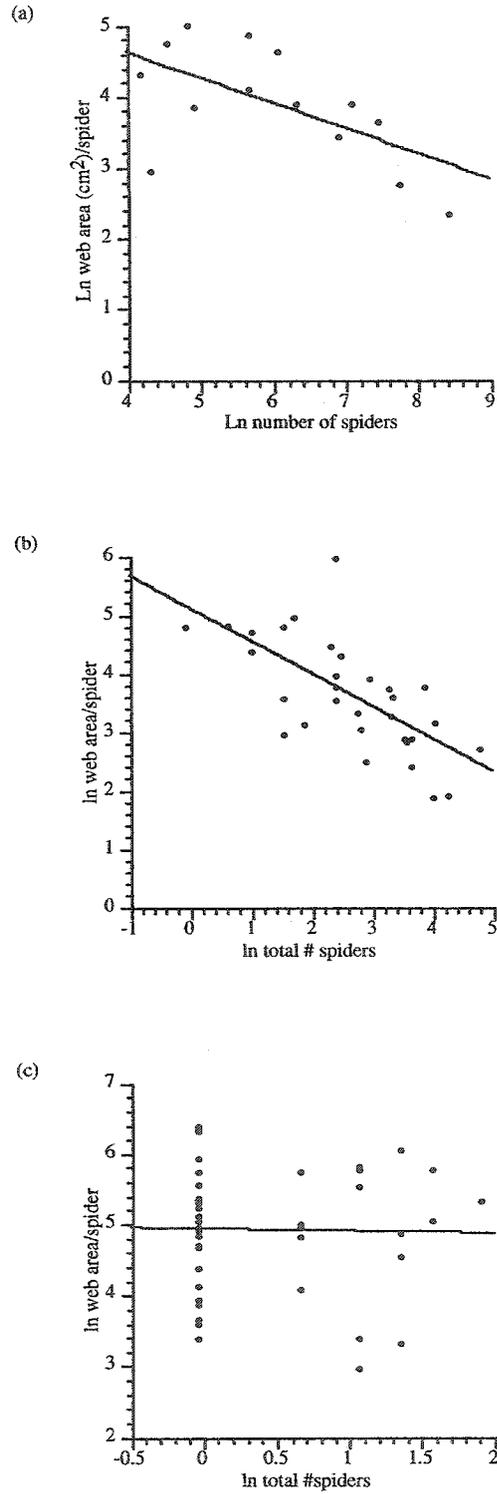


Figure III.3: Relationship between colony size and the amount of web area available per spider in (a) *A. eximius*, (b) *A. panamericana*, and (c) *A. arizona*.

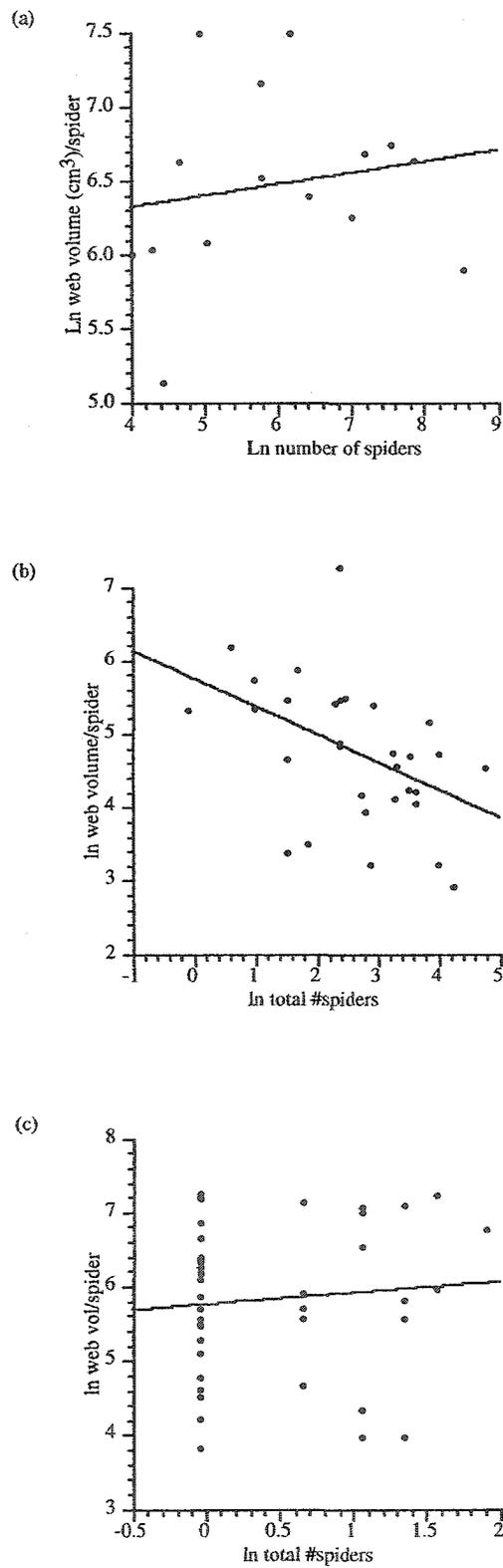


Figure III.4: Relationship between colony size and average amount of web volume produced per spider in (a) *A. eximius*, (b) *A. panamericana*, and (c) *A. arizona*.

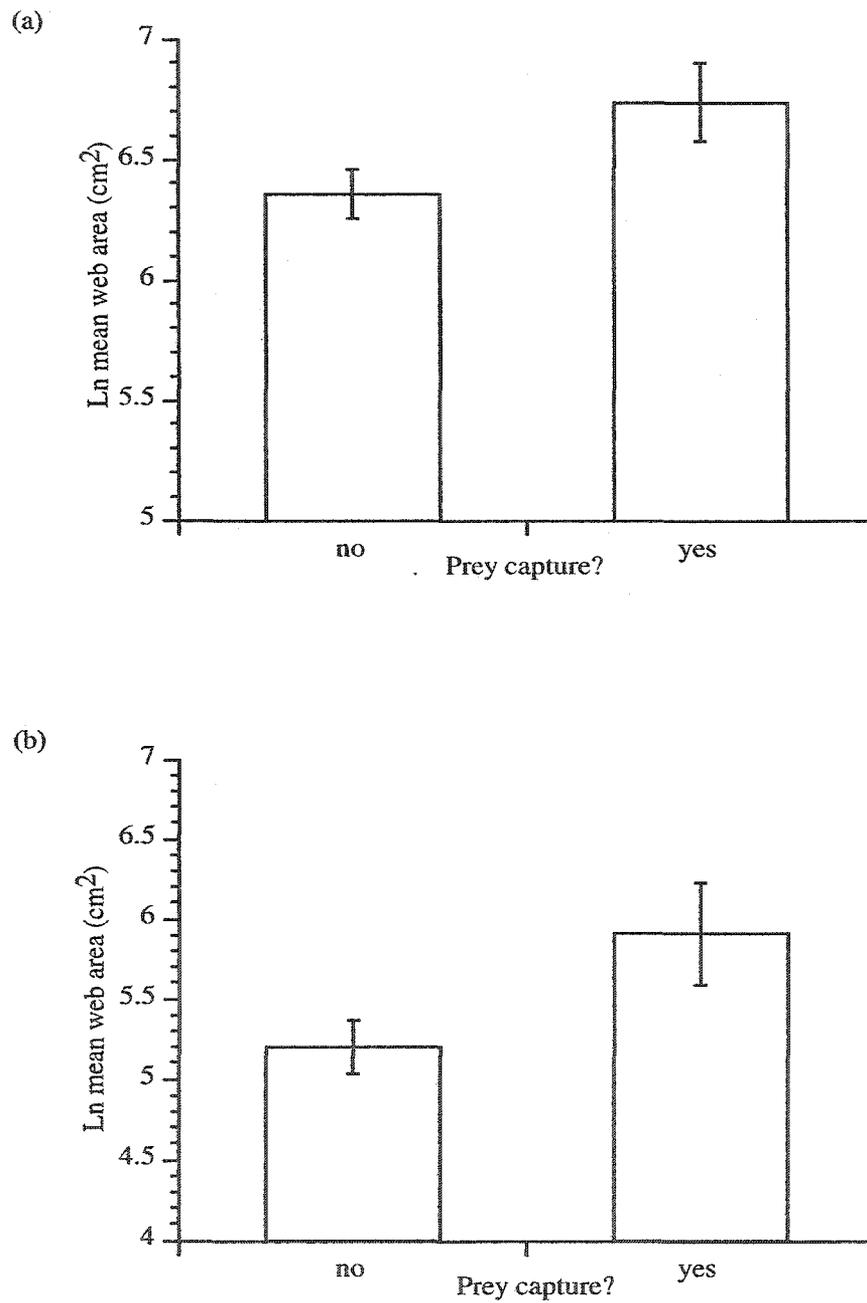


Figure III.5: Difference in web area between colonies that did vs. did not capture prey in (a) *A. panamericana*, and (b) *A. arizona*.

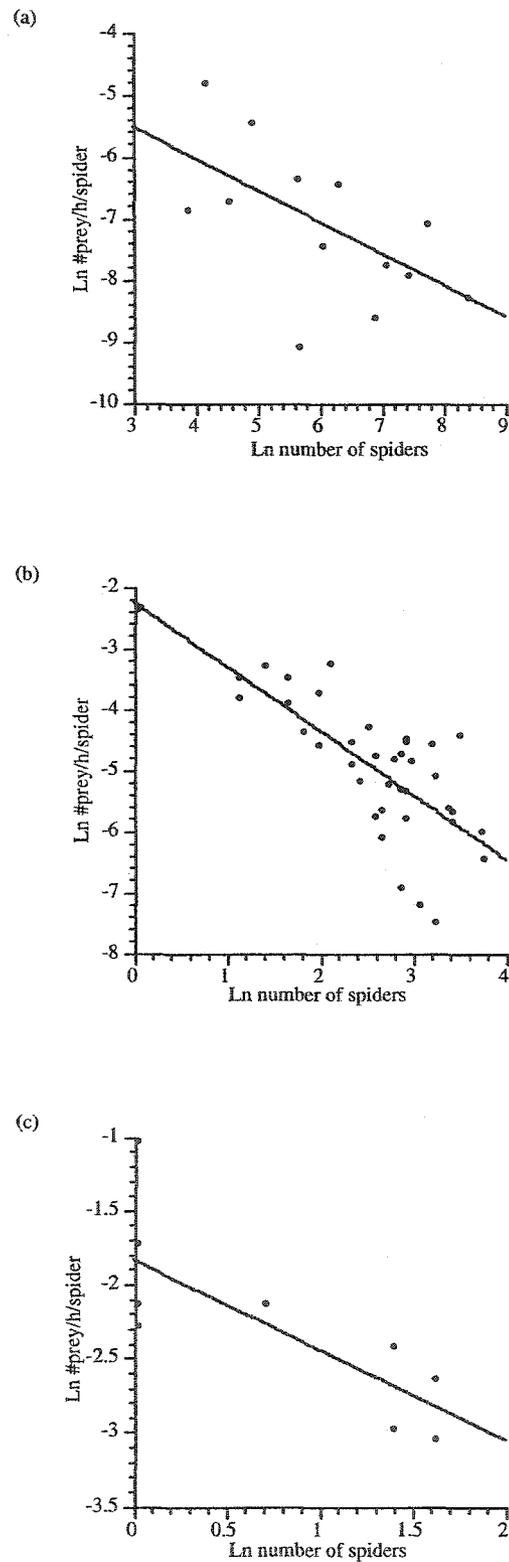


Figure III.6: In (a) *A. eximius*, (b) *A. panamericana*, and (c) *A. arizona* colonies that captured prey, the relationship between colony size and the average number of prey captured per hour per capita.

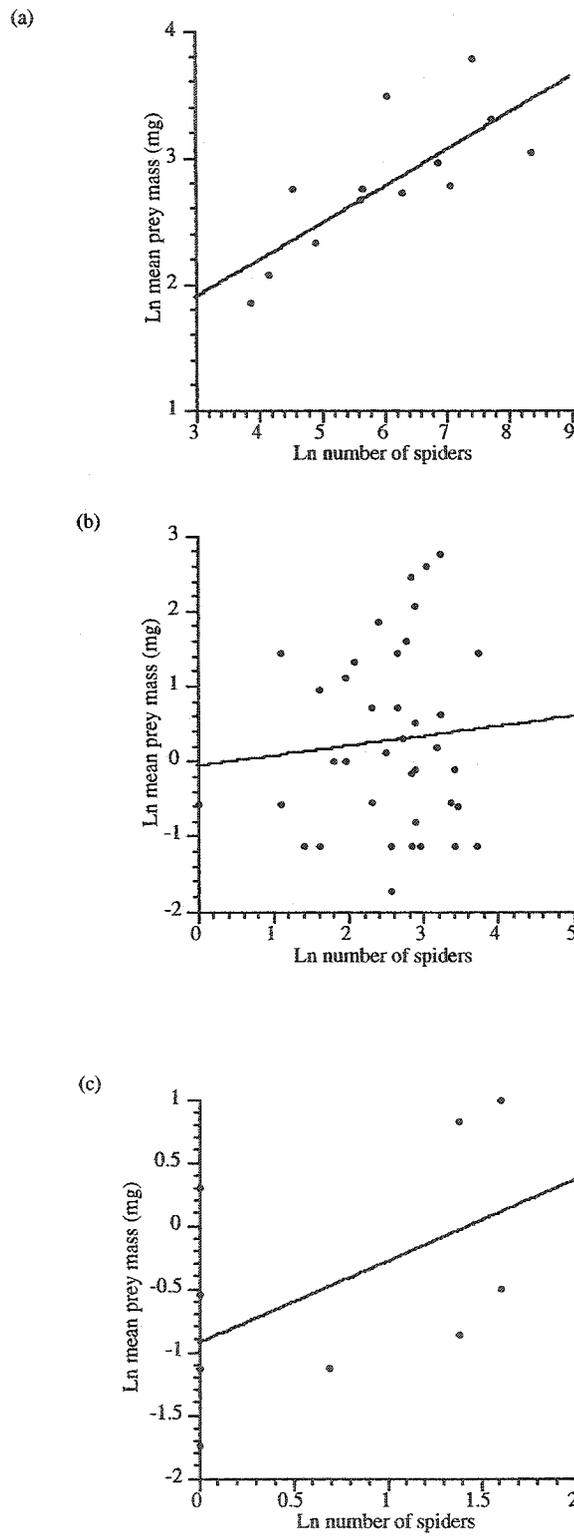


Figure III.7: The relationship between colony size and the mean mass of captured prey in (a) *A. eximius*, (b) *A. panamericana*, and (c) *A. arizona* colonies that captured prey.

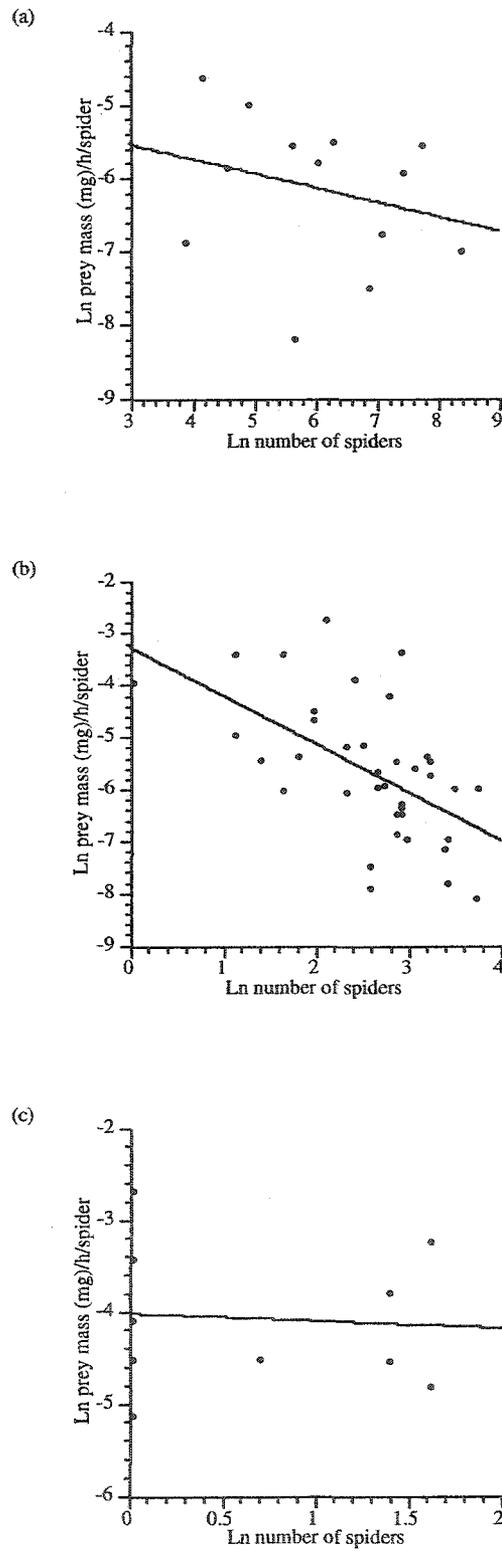


Figure III.8: In (a) *A. eximius*, (b) *A. panamericana*, and (c) *A. arizona* colonies that captured prey, the average amount of prey mass captured per hour per capita.

Table III.1: Relationships of web size and prey capture with colony size. For each species, the direction in which each variable changed with colony size is indicated by either “0” = no change with colony size (i.e. $p > 0.05$), “+” = a direct correlation, or “-” = an inverse correlation. All statistics refer to linear regressions except those provided for *A. eximius* web area, which refer to a quadratic regression. One symbol denotes significance at the 0.05 level; two symbols denote significance at the 0.001 level; and three symbols denote significance at the 0.0001 level. Only colonies that captured prey have been included in prey capture analyses.

	<i>A. eximius</i>	<i>A. panamericana</i>	<i>A. arizona</i>
Colony size median	316 spiders	17 spiders	1 spider
Web area	++ $r^2=0.78, F_{2,13}=20.05$	++ $r^2=0.35, F_{1,30}=15.55$	+++ $r^2=0.32, F_{1,43}=19.77$
Web area/spider	- $r^2=0.33, F_{1,14}=6.44$	— $r^2=0.46, F_{1,30}=24.95^{**}$	0 $r^2=0.001, F_{1,43}=0.02$
Web volume/spider	0 $r^2=0.03, F_{1,14}=0.41$	- $r^2=0.21, F_{1,30}=7.54$	0 $r^2=0.01, F_{1,43}=0.38$
Prey #/h/spider	- $r^2=0.50, F_{1,12}=10.91$	— $r^2=0.58, F_{1,36}=48.82$	- $r^2=0.58, F_{1,8}=10.91$
Mean prey mass	+ $r^2=0.55, F_{1,12}=13.21$	0 $r^2=0.003, F_{1,36}=0.12$	0 $r^2=0.34, F_{1,8}=4.21$
Prey mass/h/spider	0 $r^2=0.18, F_{1,12}=2.41$	— $r^2=0.31, F_{1,36}=15.89$	0 $r^2=0.00, F_{1,8}=0.00$

Table III.2. Predicted vs. measured relationships between the numbers of spiders in colonies and the variables listed for the three species studied. "None" refers to cases in which no relationship was predicted/ found for the variable indicated. Numbers represent the slopes of relationships plotted linearly on log-log scales. "+" indicates the direction of such a relationship with no specified slope. Functions with other shapes are represented otherwise.

	<i>A. eximius</i>		<i>A. panamericana</i>		<i>A. arizona</i>	
	model	data	model	data	model	data
Web area	0.66	quadratic	0.66	0.44	0.66	0.97
Web area/spider	-0.33	-0.32	-0.33	-0.55	-0.33	none
Web volume/spider	none	none	none	none	none	none
Prey #/h/spider	Fig. I.4b	-0.60	-0.33	-1.01	-0.33	-0.61
Mean prey mass	+	0.30	none	none	none	none
Prey mass/h/spider	Fig. I.4b	none	-0.33	-0.94	-0.33	none

CHAPTER IV: Effect of prey capture on dispersal timing in a subsocial spider

Introduction

Sociality has arisen at least 10 times in spiders and is currently expressed in at least 17 spider species (Avilés 1997). Unlike solitary spiders, which disperse soon after egg sac emergence and maintain distinct, independent territories, social spiders typically remain in their parental colony for their entire lives. Within colonies, nestmates cooperate in web building, prey capture, feeding, and brood care (Buskirk 1981; Christenson 1984; D'Andrea 1987; Avilés 1997). Social colonies can last for several generations, and only at very large colony sizes, inseminated adult females may disperse to form new colonies. Consequently, social colonies develop into reproductively isolated lineages with low genetic variability and female-biased sex ratios (Avilés 1997; Avilés et al. 2000).

It is widely believed that social spider species evolved from ancestors resembling extant subsocial species (Kullman 1972; Krafft 1986). Subsocial spiders express an intermediate form of sociality, living communally and cooperating as juveniles but dispersing and living solitarily as subadults and adults. If social spiders evolved from subsocial ancestors, then the subsocial dispersal phase would have been suppressed at

some point during the transition to sociality. For this reason, we can gain insight into the factors that have led to the evolution of sociality by studying the causes of dispersal in current subsocial species.

Prey availability is a likely factor influencing dispersal in subsocial spiders. The resource competition hypothesis states that siblings disperse from their natal colonies to avoid competing in resource-limited habitats (Hamilton and May 1977). In subsocial spiders, competitions over prey ensue just prior to dispersal, suggesting prey limitation within colonies and implicating dispersal as a mechanism for avoiding competition and gaining access to resources outside the colony. Supporting this idea is the frequent finding that increased prey abundance strongly reduces competition and delays the onset of dispersal in subsocial colonies (Ruttan 1990; Rypstra 1986; Leborgne et al. 1994; Lubin and Henshel 1996; Evans 1998). Conversely, subsocial spiders can become cannibalistic when starved (Bilde and Lubin 2001). Powers and Avilés (2003) have provided evidence supporting the resource competition hypothesis for a subsocial spider, *Anelosimus arizona*, in southern Arizona by showing that, overall, spiders disperse relatively short distances and that males and females disperse similar distances. Within this same population, I have examined spiders' responses to varying levels of prey to further understand how resource competition influences dispersal in subsocial spiders.

I explored the idea that subsocial spiders disperse in response to insufficient prey availability within the natal nest. I did this by first examining how different prey amounts affect spider survival, growth, and metabolic rates within colonies. I then estimated the effect of these same prey levels on spiders' dispersal timing. If spiders disperse to access prey outside the colony, as proposed by the resource competition hypothesis, then levels of prey that reduce spider survival, growth and metabolic rates should also lead to earlier dispersal. Furthermore, within colonies, spiders receiving less prey (due to competition for example) should disperse sooner than those receiving more prey should.

Methods

Study system

I studied a population of *A. arizona* in Garden Canyon (1524.70 m; N 31.49°, W 110.32°), a riparian area on Fort Huachuca of southern Arizona. At this site, colonies are distributed in patches of one to approximately fifty along a perennial creek. *A. arizona* in this region (Avilés and Gelsey 1998) is morphologically and behaviorally similar to *Anelosimus jucundus* (O. P. Cambridge 1986), a subsocial species described from montane areas in Costa Rica, Panama, and Ecuador (Levi 1956, 1963; I. Agnarsson pers.

comm.), but it has not yet been formally described. The dispersal season for this population lasts approximately 3 months, from mid-May to mid-August (Avilés and Gelsey 1998). During this time, spiders in their juvenile and subadult instars (4 through 7) gradually leave the natal nest and establish new, solitary webs typically within 5 m of their natal nests (Powers and Avilés 2003).

Prey level treatments

For ten weeks (23 March to 22 May 2001), I maintained 59 colonies at three prey levels and measured their responses in spider survival, growth, and metabolic rate in an environmentally controlled lab at the University of Arizona with light and temperature conditions resembling those in Garden Canyon (12-hr light cycle, at 21°C ambient temperature). I formed artificial colonies by collecting 31 colonies in Garden Canyon, sorting spiders from their nest materials, and then dividing colonies into groups of six. When dividing original colonies, I distributed spider ages and sizes evenly among new colonies to make them as similar as possible in total mass ($F_{2,58}=1.06$, $p=0.3543$), mean body mass ($F_{2,58}=1.06$, $p=0.3543$), and instar ($F_{2,58}=2.29$, $p=0.1107$); no spiders from different colonies were combined into new colonies. I placed each new colony in a container of a standard volume (2 L) with sticks for web support and randomly assigned

it to one of three prey level treatments – low (n = 20 colonies), medium (n = 19 colonies), and high (n = 20 colonies). The medium prey level consisted of ten *Drosophila melanogaster* (~13 mg) provided twice per week, a lab diet that typically allows growth rates resembling those of spiders in the field (personal observation). The low prey level consisted of five *D. melanogaster* (~6 mg), and the high prey level consisted of fifteen *D. melanogaster* (~20 mg). With each feeding, I liberally provided colonies with water.

Survival and growth within colonies

I measured two aspects of spider growth – mass and length of the tibia and patella segments on the most anterior pair of legs (abbreviated TP1). In spiders, TP1 length is considered the best indication of instar/age (Foelix 1996). I measured the TP1 lengths and masses of all spiders at the start of the ten week period (23 March). Then, for each week during weeks four (17 April) through nine (22 May), I randomly selected three colonies from each prey level to measure; throughout this six week sampling period, I selected each colony only once. Mass was measured to the nearest 0.1 mg, and TP1 was measured to the nearest 0.1 mm using an ocular ruler on a dissecting scope.

I also measured metabolic rate for three randomly chosen spiders (or less if more than three spiders had died in the colony) from sampled colonies. Metabolic

measurements resembled the protocol from Watson & Lighton (1994) and were performed with a Sable Systems TR2 flow-through respirometry system (Sable Systems, Salt Lake City, Utah) in a room with controlled temperature (21 °C) and humidity conditions. Spiders were allowed to acclimate to their chambers for at least 1 h. Then, over a period of ~7 h, the respirometer measured resting rates of carbon dioxide emission (VCO_2 , in l/h) by periodic sampling of CO_2 built up by spiders remaining inactive in their chambers (5 ml syringes). Flow rates of 100 ml/min through the respiratory chambers were maintained with a mass flow controller. A total of 32 chambers were monitored in each run, with six chambers remaining empty to control for drifts in recordings and to establish a reliable baseline. Respiratory data were compiled using DAN (Data Analysis Program for Metabolic Measurements).

Differences in spider survival among prey levels in 2001 were unclear (see Results). To further clarify the effect of prey level on survival, I maintained an additional 34 artificially formed colonies, again containing six spiders each, at varying prey levels from 24 March to 1 June in 2002. As in 2001, the total mass, mean spider mass, and mean spider age (TP1) were similar across prey levels at the onset of this experiment ($F_{2,34}=0.09$, $p=0.9142$; $F_{2,34}=0.03$, $p=0.9743$, and $F_{2,34}=0.63$, $p=0.5376$, respectively). This time, I increased variation among prey levels by providing one (~12mg), two (~24mg),

and three (~36mg) *Musca domestica* twice per week to colonies in the low (n = 12 colonies), medium (n = 11 colonies), and high (n = 11 colonies) prey level groups, respectively. I supplemented *M. domestica* food with Pedigree brand dogfood, a technique shown to provide spiders with higher levels of survival and growth compared with the typical feeding regime of sugar and powdered milk alone (D. Mayntz personal communication). Also, I increased the sample size of colonies measured each week by measuring the spiders in every colony rather than selecting only three colonies from each prey level. I counted spiders and measured spider mass and TP1 as in 2001, but I conducted fewer measurement periods (four compared to seven), allowing greater intervals of time to pass between sets of measurements – 46 days, 12 days, and 11 days, respectively, compared to 25 and 7 days. I did not measure spider metabolic rates in 2002.

Dispersal timing estimations

After monitoring the effects of prey level in the lab, I placed colonies in the field to estimate spiders' dispersal times. In 2001, colonies that had already been measured in the lab were placed in the field during week seven (10 May). The remaining colonies were placed in the field during week ten (29 May). Placement time is taken into account

in all analyses on dispersal timing to control for any potentially confounding effects on dispersal time. I estimated dispersal times for all colonies containing at least three spiders upon field placement (in group 1: 2 low prey level colonies, 4 medium prey level colonies, 6 high prey level colonies; in group 2: 5 low prey level colonies, 6 medium prey level colonies, 9 high prey level colonies). The numbers of spiders in colonies when placed in the field varied between three and six but did not differ consistently across prey level groups ($F_{2,30}=0.02$, $p=0.9847$, $\text{mean}=4.06\pm 0.17$ SE spiders per colony). I positioned colonies on branches resembling those with natural nests in vegetation, position, and height from the ground. Spatially, I arranged colonies in sets of three, one colony per prey level, and I randomly assigned colonies to possible nest sites within trees. To encourage nest building and to monitor movements out of the nest, I enclosed colonies in nets containing nest materials. Once per week (17 May to 27 June for group 1 and 6 June to 27 June for group 2, or until a nest contained only one or no spider), I removed the nets in the evening (at approximately 1900 h) and recorded the instars and sexes of spiders in nests. In the morning (at approximately 0800 h), I recorded the spiders in nests again, covered nests with nets, and fed colonies according to their prey level. By comparing the ages and sexes of spiders in nests between the time of net removal and the next morning, I was able to infer the ages and sexes of spiders that dispersed. Occasionally, spiders

disappeared while colonies were covered by the nets. It is possible that these spiders dispersed through minor tears resulting from wind or rain. Although the nets protected spiders from predatory intruders, they did not protect them from other conspecifics; cannibalism is common in spiders, especially under conditions of starvation (refs, pers. obs.). Even when spiders are killed by other means, they can be consumed by their colony mates. Because it was impossible to distinguish between spiders that may have escaped enclosures and those that were killed within enclosures, these spiders as well as dead spiders found in the nest were not included among dispersers or philopatric individuals in analyses.

From 1 June to 15 July 2002, I again estimated dispersal times for 21 (7 low prey level colonies, 6 medium prey level colonies, 8 high prey level colonies) of the 34 lab colonies exposed to varied prey levels. In contrast to the previous year however, I measured the masses and TP1 lengths of, and then individually marked, all spiders before placing colonies in the field. This allowed me to identify individuals (and therefore their original masses and TP1 lengths) in the field. Using mass as a proxy for access to prey, I was then able to compare dispersal times between spiders receiving more vs. less prey. As in 2001, the number of spiders per colony did not vary across prey levels at the onset ($F_{2,20}=2.98$, $p=0.0760$; mean= 5.1 ± 0.21 SE spiders per colony). I maintained colonies in

net enclosures and censused spiders before and after removing nets one night per week for six weeks. During each census, I recorded the presence or absence of each individual in each colony to determine which spiders had dispersed and which spiders remained. Again, spiders that disappeared while nets were covered or were found dead were considered separately from dispersers and philopatric individuals.

Staged competitions

To determine the effect of spider size on the outcome of competitions over prey, pairs of spiders differing in size were presented prey items during May 2001. Spiders (penultimate instar males and females) were weighed and then marked with colored powder. Combinations of sex and relative size (i.e. smaller vs. larger) were alternated in a factorial design to control for any potentially confounding effects of sex. To stage competitions between spiders, two spiders were introduced simultaneously to a vial containing one *Drosophila melanogaster* (~1.0 mg), a prey type resembling the average size of prey available to spiders in the field just prior to and during the dispersal phase (0.9 ± 0.24 SE mg; Chapter II). For the 3 h that followed, all aggressive behaviors were recorded as well as which spider eventually captured and fed on the prey item. Introductions that did not result in a spider feeding were classified as a “draw”. Spiders

that did not feed during the observation period were fed afterward to maintain constant feeding levels among individuals to be used again.

Statistical analyses

Multiple factor ANOVA models were used to test for effects of prey level on spider growth, metabolic rate, and dispersal timing. In these models, colony ID was included as a random effect nested within prey level and week was included as a covariate. Distributions of spider mass, TP1 lengths, and metabolic rates were nonnormal, so they are natural log transformed in analyses. Mean values are reported with \pm standard error.

Results

Prey requirements for metabolism, growth, and survival

Measurements of spiders maintained in the lab showed that prey level affected spider survival and growth directly and metabolic rate indirectly. In 2002, the proportions of colonies surviving varied over time with prey level (Table IV.1; Fig. IV.1), with higher proportions of colonies surviving in the higher prey level group compared to the low and medium prey level groups ($t=2.92$, 130 df, $p=0.0044$, for the

contrast between the high prey level group vs. the low and medium groups). In 2001 however, the numbers of survivors in colonies did not vary with prey level (Table IV.1).

Higher prey level led to greater body mass and larger TP1 lengths in 2001 and to larger TP1 lengths in 2002 (Table IV.2). Spider mass and TP1 length were correlated measures of spider size (2001: $r^2=0.79$, $F_{1,110}=415.19$, $p<0.0001$; 2002: $r^2=0.81$, $F_{1,178}=769.59$, $p<0.0001$). Furthermore, spider mass strongly influenced metabolic rate (Table IV.3; linear regression, $\ln MR=-2.2005+1.1307(\ln \text{mass})$: $r^2=0.59$, $F_{1,132}=191.85$, $p<0.0001$; Fig. IV.2), although metabolic rate was not directly related to prey level ($F_{2,132}=2.06$, $p=0.1364$; Table 3).

Effect of prey level on dispersal

In 2001, the proportions of spiders dispersing from colonies did not vary with prey level (Table IV.4). When variation among prey levels was increased in 2002, spiders dispersed more slowly from colonies in the higher prey level group compared to colonies in the low group, and the proportion of dispersers was high in colonies of the medium prey level group (Table IV.4; Fig. IV.3).

During both dispersal seasons, mortality had little impact on the numbers of spiders remaining in colonies. In 2001, death occurred in seven colonies (of 31 total) during the dispersal phase. In six of these seven colonies, only one spider died, and in the

other colony, two spiders died. The proportions of spiders that died within colonies after being placed in the field was lower than in the lab (0.32 ± 0.15 in the lab vs. 0.06 ± 0.03 in the field; paired t-test: $t=7.25$, 30 df, $p < 0.0001$). In 2002, mortality occurred in seven of the 21 colonies monitored – five colonies with one death and two colonies with two deaths. The proportions of colonies that died in the field was not significantly higher than in the proportions that died in the lab (0.15 ± 0.03 in the lab vs. 0.08 ± 0.03 in the field; paired t-test: $t=1.49$, 20 df, $p=0.1512$).

When individuals were tracked during the 2002 dispersal season, spiders with greater initial masses stayed in colonies for longer periods of time (effect of \ln spider mass on # days until dispersal in ANOVA model with prey level and colony, $R^2=0.44$, $F_{1,97}=5.25$, $p=0.0247$; Fig. IV.4). Within colonies, the mean initial mass of dispersers (as measured before spiders were placed in the field) was significantly lower than that of nondispersers on 7 June (paired t-test: $t=3.39$, 12 df, $p=0.0054$), 13 June ($t=2.45$, 15 df, $p=0.0271$), 23 June ($t=2.30$, 13 df, $p=0.0384$), and 2 July ($t=2.89$, 10 df, $p=0.0160$). By 15 July however, dispersers and nondispersers had similar initial masses ($t=1.09$, 10 df, $p=0.3020$); at this point, most colonies contained only one or two spiders (6 colonies with 1 spider, 4 colonies with 2 spiders, and 1 colony with 3 spiders; Table IV.5).

Due to variation in dispersal timing across prey levels, the numbers of spiders remaining in colonies decreased differently across prey level groups over time – from approximately 4 to 0 for the low prey level group, from 4 to 1 for the medium prey level group, and from 5 to 1 for the high prey level group (prey level*#days interaction in ANOVA model with prey level, # days, and colony nested within prey level, $R^2=0.87$, $F_{10,125}=2.30$, $p=0.0188$). In 2001, reoccupation occurred in only high prey level nests (12 of 15 total). In 2002, most high (six of eight) and medium (five of six) prey level nests were reoccupied, while most low prey level nests were not (two of seven nests with two spiders remaining in one nest; Table IV.5).

Staged competitions

Of the 20 competitions staged, 12 resulted in a spider winning, evidenced by its feeding on the prey item provided. In these competitions, the larger spider was more likely to win than the smaller spider (paired t-test: $t=2.50$, 11 df, $p=0.0296$; Fig. IV.5). In the eight remaining introductions, no spider fed. Whether introductions resulted in a spider feeding did not depend on the mass difference between competitors ($\chi^2=1.48$, 19 df, $p=0.2238$). In competitions in which there was a winner and the smaller spider won access to the prey item, its mass difference (0.7 ± 0.2 mg) tended to be smaller than the

mass difference present when the larger spider prevailed (3.3 ± 0.8 mg; $\chi^2=7.41$, 11 df, $p=0.0065$).

Discussion

The findings of this study provide further support for a resource competition based explanation for dispersal in this population. Prey levels varied in a way that affected spider growth and survival when dispersal was prevented. Although prey level did not directly affect metabolic rate, metabolic rate increased with spider size, which varied with prey level. Higher prey levels delayed dispersal among and within colonies, as spiders receiving more prey (evidenced by their greater body masses) remained in their parent colonies for longer periods of time. This effect often led to nests maintained at the higher prey levels being reoccupied by relatively large spiders. Furthermore, larger spiders were more likely to win competitions over prey with smaller spiders. This result suggests that spiders that lose competitions over prey initially will become less capable of accessing prey within their natal colonies over time.

Spiders gain a clear advantage by maximizing their prey intake rate as late juveniles and subadults. Those with larger body sizes often mature earlier and have larger adult body sizes, two factors which can influence their mating success (Vollrath

1980; Uetz 1992; Ward and Lubin 1993; Henschel, et. al. 1995; Schneider 1997). Adult females may require higher prey intake rates for egg production (Vollrath and Rohde-Arndt 1982), and larger body sizes tend to correspond generally with greater fecundity in arthropods such as spiders (Higgins 1992; Ward and Lubin 1993; Marshall and Gittleman 1994; Simpson 1995).

Colonial foraging is one strategy by which spiders can maximize their prey intake rate. In *A. arizona*'s subsocial congener, *Anelosimus studiosus*, delayed dispersal confers higher, less variable prey capture rates for spiders remaining in their parent colonies compared to spiders living solitarily (Jones and Parker 2000), which can increase their survival and growth rates (Jones and Parker 2002). Group living has been found to also reduce spatial and temporal variability in prey capture and increase prey capture efficiency for colonial, orb-weaving spiders (Uetz and Hodge 1990; Caraco et al. 1995). However, balancing resource distribution in this manner does not appear to be favored in environments with low prey availability (Uetz 1988), perhaps because not enough prey can be captured to sustain all colony members (Uetz 1992). For *A. arizona*, available prey biomass is constant between the early communal stage and the time of year when spiders begin to disperse. However, increasing metabolic rates with spider size indicate that spider requirements increase as individuals develop. Resource requirements are also

likely to increase as spiders grow larger because, generally, larger spiders tend to build larger webs (Eberhard 1988; Leborgne et al. 1994) with thicker strands of silk (Craig 1987). Although prey capture typically increases with spider age and colony size, per capita prey capture can concurrently decrease (Jones and Parker 2002; Chapter III).

Whether colonies remain together or disintegrate may depend on the likelihood of prey capture rates keeping pace with increasing requirements or at least remaining higher than those of solitary spiders (Ward 1986).

When prey availability becomes limited for subsocial colonies, smaller spiders are likely to experience the most difficulty accessing resources. Within colonies, cooperation deteriorates as the dispersal phase approaches (Fig. I.3, from Chapter I), and larger spiders have a greater chance of winning competitions over prey, as shown here and in other studies (Ward 1986; Uetz 1992; Whitehouse and Lubin 1999). This can lead to increasing body size variation within colonies (Whitehouse and Lubin 1999; Gonzaga and Vasconcellos 2002), due to resources not being distributed evenly among colony members. In social spider colonies, this asymmetry may be maintained without dispersal of some colony members (Ebert 1998). In this study, the smaller spiders within colonies dispersed before the larger spiders. The only chance that competitively disadvantaged individuals may have of acquiring prey would be to feed from “leftovers” or capture prey

without alerting other spiders. Given the web vibrations produced during prey capture, the latter would be difficult except perhaps while other spiders are already feeding on previously captured prey; in fact, increased detection of prey contacting a web and the ability to quickly alert other colony members has even been proposed as a benefit of web-sharing (Uetz 1992). Moreover, when a smaller spider accesses a prey it may be less able to deter intruders (Ward 1986). When a spider decides to disperse is likely to depend on the prey capture rate it would experience foraging solitarily (Packer and Ruttan 1988) and the costs associated with dispersal such as missed foraging opportunities, potential weight loss and possibly death (Lubin et al. 1993; Kim 2000; Jakob, et al. 2001). Despite the benefits of group living and the costs of dispersal, solitary living may provide a more viable option for spiders not receiving prey in the natal nest, in the same way that foraging patch choice has been shown to greatly affect spider size and reproductive success in crab spiders (Morse 1988, reviewed in Uetz 1992). Although prey capture appears rare for solitary *A. arizona*, some have been seen capturing as much as 0.36 mg/h in prey mass in this population, whereas spiders living in colonies containing up to eight spiders are likely to receive less than 0.10 mg/h in prey mass per spider (Chapter II). A similar pattern has been found for *A. studiosus*, in which prey capture is rare but occasionally highly profitable (Jones and Parker 2002).

In addition to competing for prey, nestmates may compete for the parental nest as a resource. In 2001, reoccupation occurred in only high prey level nests (12 of 15 total). In 2002, most high (six of eight) and medium (five of six) prey level nests were reoccupied, while most low prey level nests were not (only two were reoccupied out of seven). There may be an advantage to occupying a nest that has already withstood the test of a previous generation, especially when it provides frequent prey capture (via a larger web area for example, *sensu* Chapter III and Jones and Parker 2000) and retreats from predators (Tietgen 1986; Evans 1998). Avilés and Gelsey (1998) found that nearly half of the parental nests within their study area were reoccupied by females and used for another generation. Furthermore, these reoccupied nests had a lower chance than newly established nests of going extinct (50% compared to 19%, respectively), although their sample size was too low for statistical significance. Even while other nestmates occupy the parental nest, it may reduce costs associated with web-building for its inhabitants (Reichert, et al. 1986). It has been shown that, to some extent, spiders who receive less prey spend more time and resources building webs compared to larger, satisfied spiders (Higgins 1995; Ebert 1998; Pasquet et al. 1999). The larger, more competitive spiders that win competitions over prey would clearly profit from this cost to benefit ratio. *A. arizona* dispersers also occasionally compete for newly established nests. In such

competitions between resident and intruder, the larger spider typically remains (unpublished data).

The resource competition hypothesis states that individuals disperse to avoid competing with relatives for resources (Hamilton and May 1977; Dieckmann, et al. 1999). In addition to the individual fitness component that I examined in this study, there is an inclusive fitness component that would predict that spiders receiving more prey disperse sooner to avoid depriving their siblings of prey. This may be the case for *Stegodyphus mimosaurum* in which spiders of intermediate sizes, relative to their nestmates, are first to disperse (Ward 1986), perhaps because they have enough resources to endure dispersal and are losing competitions with larger spiders within the natal nest; but even this example involves a competitive component. An inclusive benefit may also drive dispersal in colonies of the social spider *Anelosimus jabaquara*, however, in which dispersing females tend to be larger on average than philopatric females (Gonzaga and Vasconcellos 2001). These dispersing females appear to practice a somewhat different reproductive strategy than females remaining in colonies by producing larger clutches of smaller offspring.

Implications for the evolution of sociality

In concordance with the resource competition hypothesis, any dispersal driven by competition over prey should be delayed in areas with higher prey abundance compared to those with lower prey abundance. Exposure to relatively high prey levels over evolutionary time could then allow the development of lineages with delayed dispersal and eventually complete philopatry, thereby setting the stage for greater colony sizes and increased cooperation to evolve. The geographic distribution of sociality in spiders supports this idea. While social species occur solely in tropical or subtropical regions (Levi 1956, 1963; Avilés 1997; but see Furey 1998) where prey tend to be larger on average (Schoener and Janzen 1968; Barlow 1994; Hawkins and Lawton 1995), subsocial species occur predominantly in temperate regions or the highlands where prey are expected to be smaller. A frequently purported advantage of communal living in spiders is the ability to capture larger prey (Rypstra 1990; Pasquet and Krafft 1992). This additional prey source afforded by colonies cooperating in prey capture may provide an overall greater prey biomass to colonies in the tropics, allowing them to delay dispersal longer and reach much larger colony sizes.

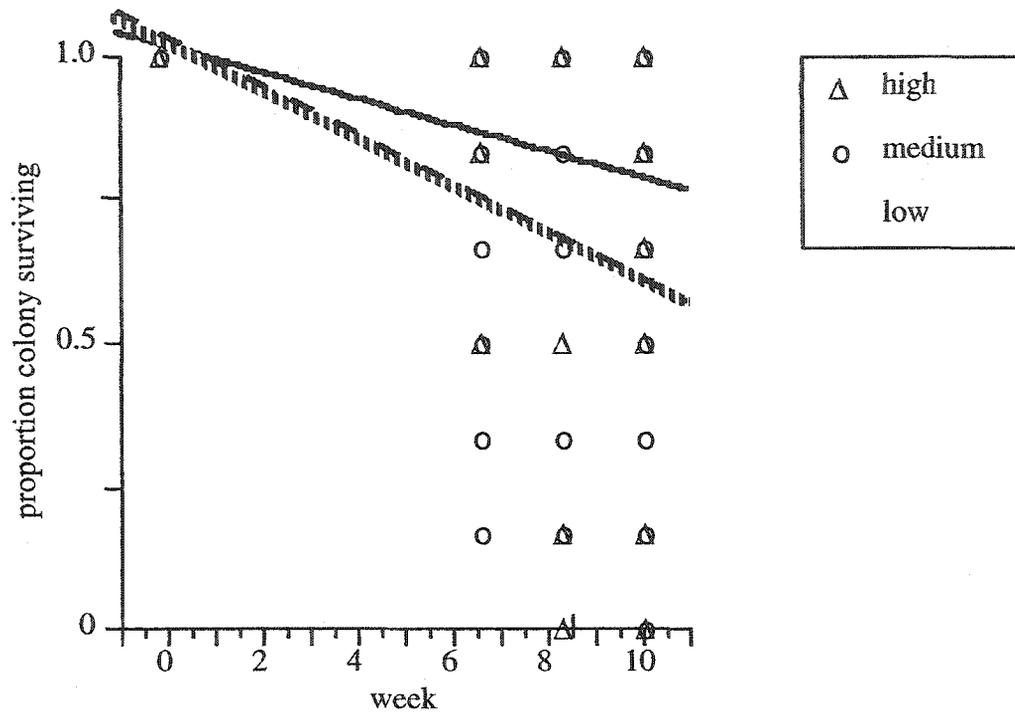


Figure IV.1: Effect of prey level on the proportions of spiders surviving in colonies in 2002. Solid line = high prey level group; dashed line = medium prey level group; dotted line = low prey level group.

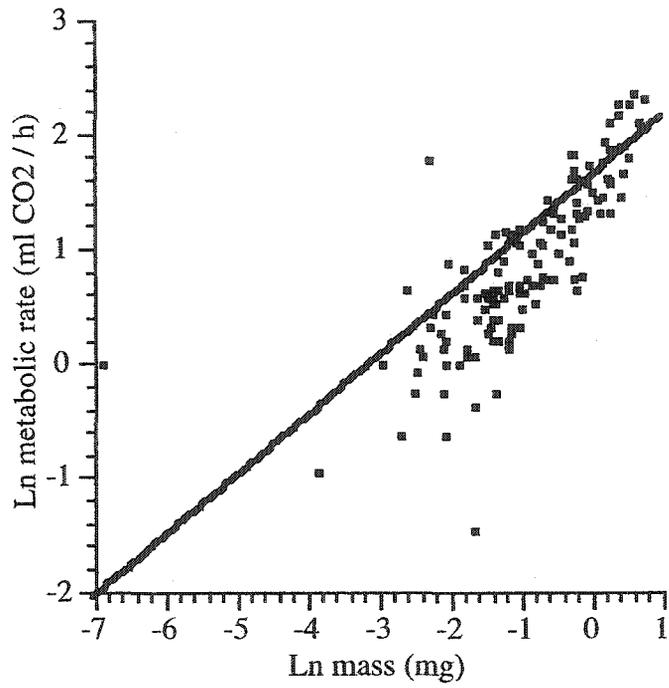


Figure IV.2: Relationship between spider body mass and metabolic rate.

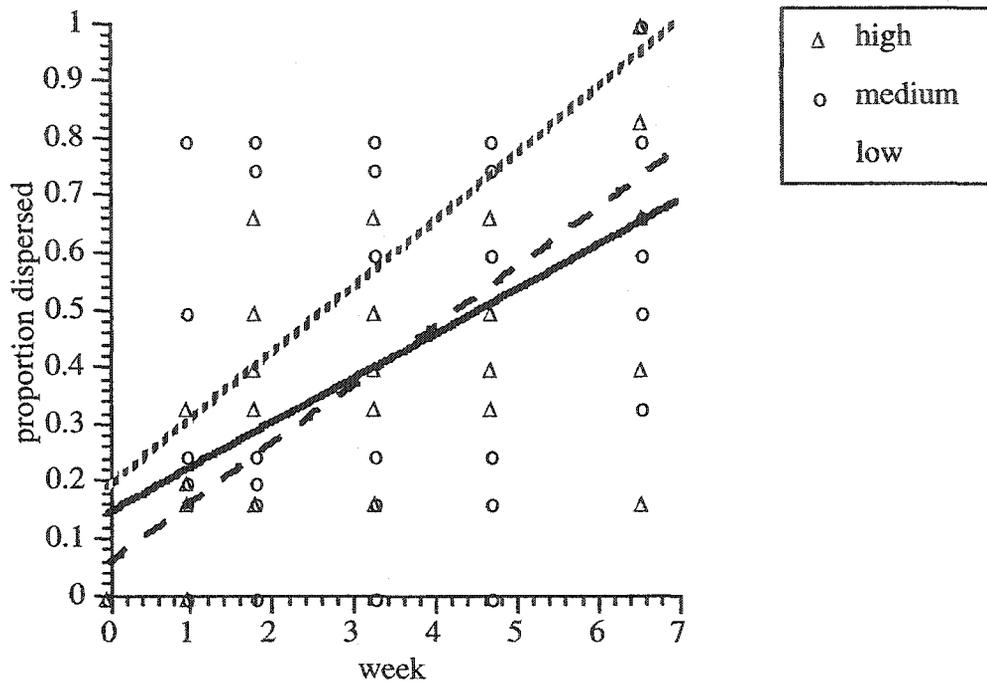


Figure IV.3: Effect of prey level on the proportions of spiders dispersing over time in 2002. Solid line = high prey level group; dashed line = medium prey level group; dotted line = low prey level group.

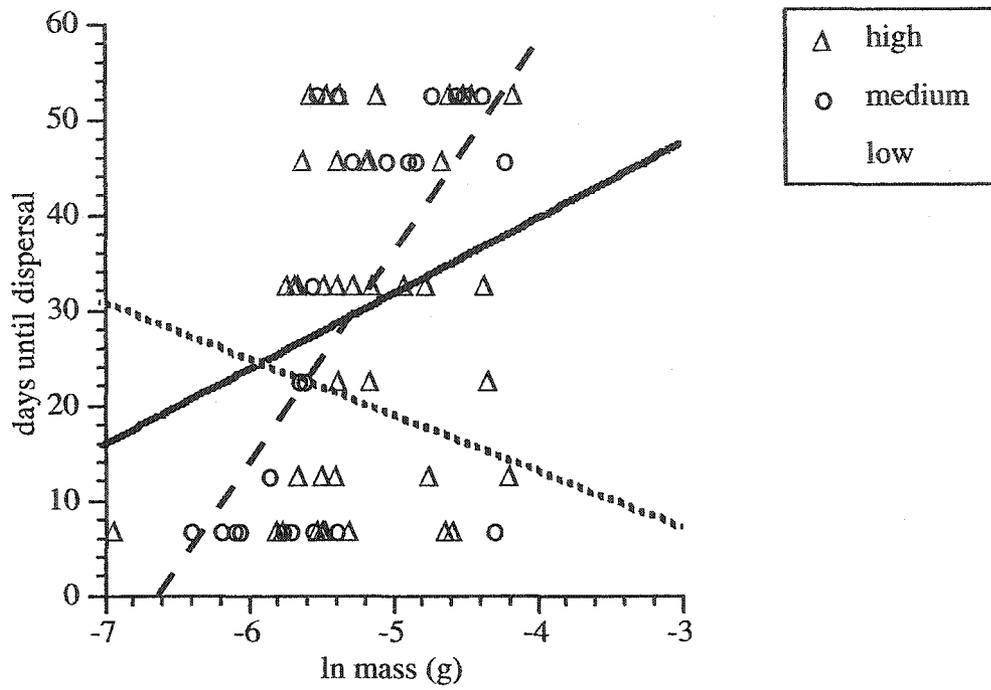


Figure IV.4: Relationship between spider body mass before being allowed to disperse and dispersal timing combined in 2002. Solid line = high prey level group; dashed line = medium prey level group; dotted line = low prey level group.

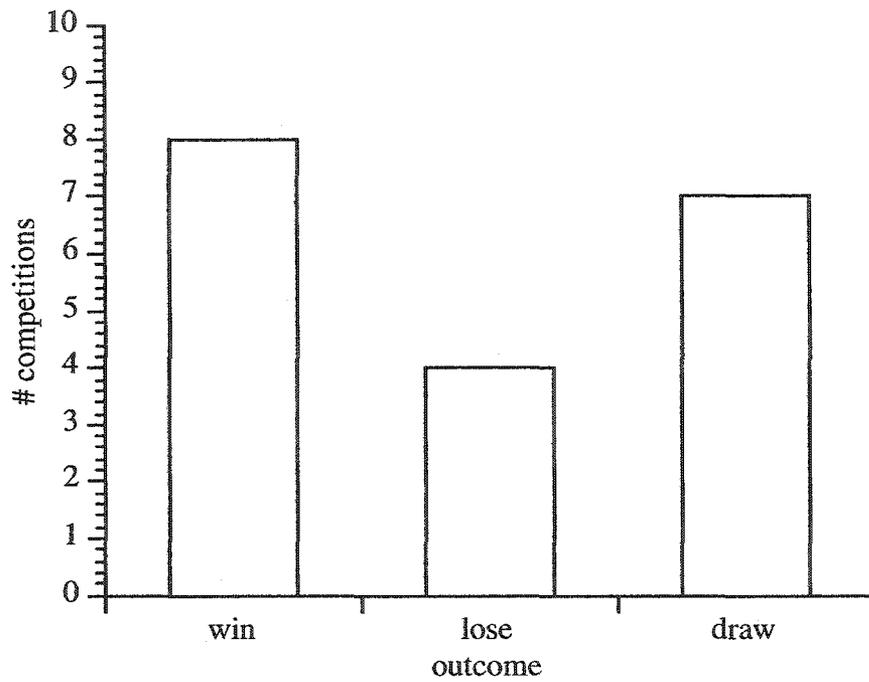


Figure IV.5. The number of times that the larger spider in a staged competition won vs. lost vs. there was no winner.

Table IV.1: ANCOVA results for the effect of prey level on proportions of spiders surviving in the lab colonies during 2001 and 2002 with time (week) as a covariate and proportions weighted by number survivors.

	df	F	P
2001: Whole model, $R^2=0.72$	117	2.42	0.0005
Colony ID	56	0.50	0.5123
Week	1	125.71	< 0.0001
Prey level	2	0.0001	0.9999
Prey level \times Week	2	1.30	0.2811
2002: Whole model, $R^2=0.51$	131	2.64	< 0.0001
Colony ID	32	1.97	0.0063
Week	1	40.16	< 0.0001
Prey level	2	0.02	0.9772
Prey level \times Week	2	3.70	0.0283

Table IV.2: ANCOVA results for the effect of prey level on mean body masses (g) and TP1 lengths (mm) of spiders surviving in the lab during 2001 and 2002. Interaction terms show that, in both years, prey level determined how spider body sizes changed over time.

	df	F	P
2001: mass, $R^2=0.63$	567	14.38	< 0.0001
Colony ID	56	9.12	< 0.0001
Week	1	226.08	< 0.0001
Prey level	2	0.62	0.5401
Prey level \times Week	2	16.25	< 0.0001
2001: TP1, $R^2=0.74$	558	23.30	< 0.0001
Colony ID	56	10.21	< 0.0001
Week	1	629.59	< 0.0001
Prey level	2	2.49	0.0912
Prey level \times Week	2	6.60	0.0015
2002: mass, $R^2=0.68$	664	36.12	< 0.0001
Colony ID	32	26.43	< 0.0001
Week	1	87.83	< 0.0001
Prey level	2	0.51	0.6051
Prey level \times Week	2	2.51	0.0825
2002: TP1, $R^2=0.55$	667	20.93	< 0.0001
Colony ID	32	13.35	< 0.0001
Week	1	46.61	< 0.0001
Prey level	2	0.45	0.6381
Prey level \times Week	2	3.38	0.0384

Table IV.3: ANOVA results for the effect of prey level and mean body mass on spider metabolic rate (VCO_2 in ml/h) in 2001.

	df	F	P
Whole Model, $R^2=0.80$	132	6.77	< 0.0001
Colony ID	47	1.79	0.0103
Prey level	2	2.06	0.1364
Ln mass (g)	1	28.26	< 0.0001

Table IV.4. ANOVA results for the effect of prey level on the proportions of colonies dispersed over time. Proportions for colonies are weighted by the numbers of dispersed.

	df	F	P
2001, $R^2=0.82$	156	5.70	< 0.0001
Colony ID	29	5.68	< 0.0001
Week	1	9.74	0.0035
Prey level	2	0.60	0.5558
Prey level \times Week	2	0.47	0.6287
2002: all 3 levels, $R^2=0.81$	261	13.16	< 0.0001
Colony ID	18	3.79	< 0.0001
Week	1	22.00	< 0.0001
Prey level	2	4.66	0.0151
Prey level \times Week	2	3.79	0.0273
2002: low vs. high, $R^2=0.81$	200	14.05	< 0.0001
Colony ID	13	9.10	< 0.0001
Week	1	20.10	< 0.0001
Prey level	1	8.59	0.0065
Prey level \times Week	1	5.33	0.0248
2002: med. vs. high, $R^2=0.80$	154	6.19	0.0164
Colony ID	12	8.19	< 0.0001
Week	1	13.48	0.0006
Prey level	1	1.74	0.1959
Prey level \times Week	1	6.19	0.0164

Table IV.5. The frequencies of nest reoccupation across prey levels in 2001 and 2002 and body masses of spiders that remained in the parent colony vs. dispersed in 2002.

Prey level	# colonies Total	# colonies Reoccupied	Mean mass Dispersed (mg)	Mean mass Remaining (mg)
2001				
Low	6	0	—	—
Medium	11	0	—	—
High	15	12	—	—
2002				
Low	7	2	6.21 ± 0.73	4.10 ± 0.60
Medium	6	5	5.22 ± 0.90	8.78 ± 1.47
High	8	6	5.95 ± 0.57	8.62 ± 1.57

APPENDIX A: Insect order and time in Malaise traps

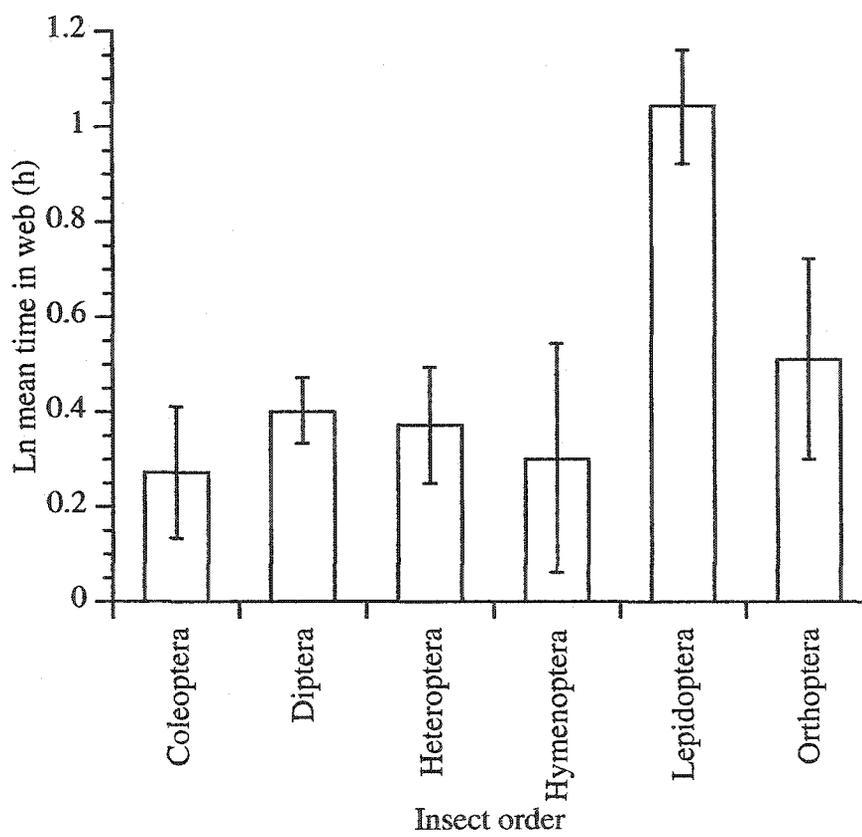


Figure A.1 Amount of time that insects of each order could be seen in Malaise traps.

APPENDIX B: Estimation of total prey capture rates

Hourly censuses conducted for *A. eximius* (May 2003), the early and late colony stages of *A. panamericana* (January 2004 and August 2001/May 2003), and the early colony stages *A. arizona* (September 2003) showed that feeding duration correlated with prey size in these populations (Table B.1). Therefore, to account for this variability and for any insects that may have been missed during the 3h censuses, total prey capture rate was estimated from the frequency and sizes of observed prey in webs and the relationship between prey size and feeding duration. For example, when a small prey item was seen captured in a nest during a census, this prey item was considered to represent a higher number of prey items of its size to compensate for its lower likelihood of being seen in the web. For subsocial species, feeding times were measured separately for different colony stages to take into account differences in spider body sizes. When possible, the feeding times corresponding to the same season and/or year were applied as a correction factor. Otherwise, seasons were combined and used as a correction factor.

For *A. arizona* colonies approaching the dispersal phase and *A. domingo* colonies, prey capture occurred too infrequently to detect a relationship between prey size and feeding duration. However, feeding duration was still taken into account for these

colonies according to processes described below. For *A. arizona*, feeding times of subadults and adults were measured in the lab for prey items (*Drosophila melanogaster*, ~1.0 mg) resembling the average size of prey available to colonies in Garden Canyon (0.9 ± 0.24 mg). Spiders fed on these prey items for an average of 0.7 h. Because spiders in *A. arizona* colonies approaching the dispersal phase do not cooperate in capture and feeding (K.S. Powers, unpublished data) and these spiders capture prey within a narrow size range (0.17 mg – 2.66 mg), this feeding time could be applied as a correction factor in estimating actual prey capture frequencies for *A. arizona* colonies approaching the dispersal phase.

In *A. domingo*, feeding times were estimated according to prey length, colony size, the number of censuses in which spiders were observed feeding on the prey item, and the amount of time that passed between censuses. When moths of varying lengths were introduced to a single colony (containing approximately 500 adults and subadults, 1750 spiders total) in a random order, feeding time increased with prey length, but this relationship was not significant probably due to a low sample size ($r^2=0.60$, $F_{1,4}=4.54$, $p=0.1231$). When feeding time was observed for an *A. domingo* colony, it was assumed that spiders fed on prey of similar sizes for the same amount of time. This concept was also applied to colonies of similar sizes. It is likely that colony size influenced feeding

time, as spiders fed for longer on same-sized prey in smaller colonies (e.g. 392 minutes for a 4 mg moth in a colony with 473 spiders compared to 150 min for same prey in a colony with 1750 spiders).

Table B.1: For each species, the relationship between a prey item's size and the amount of time that spiders could be observed feeding on it in the web. The measure of prey size (length vs. mass) used depended on which was a stronger predictor of feeding time as indicated by r-square values.

Species	Sampling period	Ln hours in web =	Statistics
<i>A. eximius</i>	January 2002 and May 2003	$-0.56+(0.51* \ln \text{ length (mm)})$	$r^2=0.21, F_{1,98}=26.23, p<0.0001$
<i>A. panamericana</i>	January 2004	$5.26+(0.80* \ln \text{ dry prey mass (g)})$	$r^2=0.35, F_{1,11}=5.36, p=0.0427$
<i>A. panamericana</i>	May 2003	$1.32+(0.17* \ln \text{ dry prey mass (g)})$	$r^2=0.29, F_{1,49}=19.23, p<0.0001$
<i>A. panamericana</i>	August 2001	$4.86+(0.61* \ln \text{ dry prey mass (g)})$	$r^2=0.71, F_{1,11}=24.27, p=0.0006$
<i>A. jucundus</i>	September 2003	$6.75+(1.24* \ln \text{ dry prey mass (g)})$	$r^2=0.32, F_{1,17}=7.44, p=0.0149$

APPENDIX C: Differences in prey between day and night

Often, the numbers and sizes of prey available to and captured by colonies differed between day and night. Thus, to account for the fact that more censuses were conducted during the day than during the night, while time is split evenly between these two periods in tropical latitudes, a weighting factor was applied to equalize the contribution of data collected during these two periods to the relevant analyses. Within species, for those census periods in which no nighttime censuses were conducted and differences between night and day were found for other census periods, expected nighttime prey sizes and prey densities were estimated from the known differences. For example, prey caught in Malaise traps near *A. eximius* and *A. domingo* colonies during May 2003 showed that fewer but larger prey were available at night than during the day (prey density: $F_{1,137}=15.97$, $p<0.0001$; mean prey mass: $F_{1,81}=7.09$, $p=0.0095$). The same was true for prey captured by *A. eximius* colonies (# prey captured/h: $F_{1,147}=4.60$, $p=0.0337$; $F_{1,85}=4.50$, $p=0.0369$; mean prey mass at night = mean prey mass in day + 10 mg). To estimate the numbers and masses of prey that would have been caught in traps at night, the difference was simply applied to the numbers and masses of prey found in traps during the days corresponding to that time period (prey density at night = prey density in

day - 0.41 prey/h/trap; mean prey mass at night = mean prey mass in day + 2 mg), and likewise for prey captured in colonies (# prey captured/h at night = # prey captured/h during day - 0.27 prey/h; mean prey mass; mean prey mass at night = mean prey mass in day + 10 mg).

For *A. panamericana*, more prey items were available during the day than at night, but prey size and prey capture were similar between night and day. Therefore, the frequencies of prey found in traps in *A. panamericana* habitat were adjusted based on censuses conducted during June 2003 (prey density: $F_{1,758}=29.58$, $p<0.0001$; prey density at night = prey density in day - 0.49 prey/h/trap). Mean masses of available prey did not differ between day and night in *A. panamericana* habitat ($F_{1,676}=2.65$, $p=0.1039$), nor did the frequency and sizes of prey captured by *A. panamericana* differ between day and night (#/h/colony: $F_{1,1827}=0.21$, $p=0.6405$; mean prey mass: $F_{1,66}=3.00$, $p=0.0943$).

In *A. arizona* prey availability and prey capture did not differ either between day and night during censuses conducted during April-May 2001 and September 2003 (available prey #/h/trap $F_{1,301}=0.16$, $p=0.6941$ and available mean prey size $F_{1,203}=0.48$, $p=0.4879$; captured prey #/h/colony $F_{1,1418}=1.33$, $p=0.2498$ and captured mean prey size $F_{1,24}=1.54$, $p=0.2281$, with all analyses taking into account seasonal differences). Prey capture was too infrequent to make these comparisons in *A. domingo*, so nighttime

censuses, when available, were weighted equally with daytime censuses. Otherwise, only daytime censuses were considered for this species.

APPENDIX D: Colony size estimations

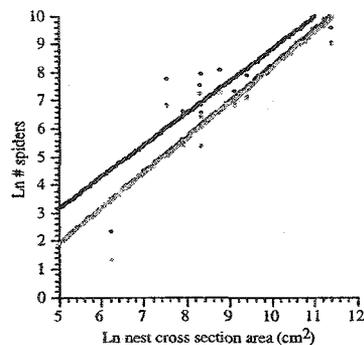
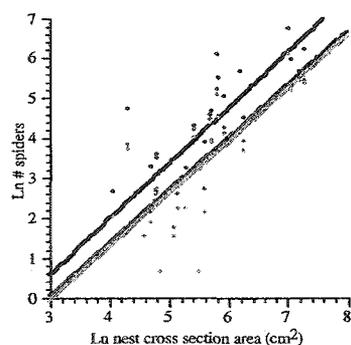
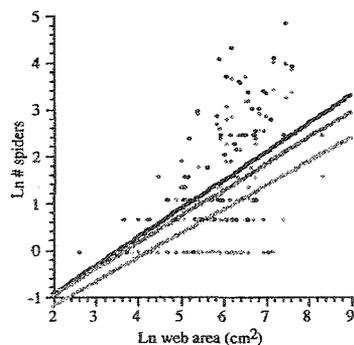
(a) *A. eximius*ln total # spiders = $-6.0413 + 1.51828$ (ln nest cross sectional area); $r^2=0.79$, $F_{1,11}=37.29$; $p<0.0001$ ln #subadults and adults = $-6.6094 + 1.49914$ (ln nest cross sectional area); $r^2=0.82$, $F_{1,11}=45.33$, $p<0.0001$ ln #females = $-6.5505 + 1.48477$ (ln nest cross sectional area); $r^2=0.82$, $F_{1,11}=45.45$, $p<0.0001$ (b) *A. domingo*ln total # spiders = $-3.5432 + 1.35606$ (ln nest cross sectional area); $r^2=0.49$, $F_{1,23}=21.03$; $p<0.0001$ ln #subadults and adults = $-3.9771 + 1.32714$ (ln nest cross sectional area); $r^2=0.59$, $F_{1,23}=30.16$, $p<0.0001$ ln #females = $-4.0558 + 1.32068$ (ln nest cross sectional area); $r^2=0.57$, $F_{1,23}=29.37$, $p<0.0001$ (c) *Anelosinus panamericana*:ln total # spiders = $-2.9058 + 0.87504$ (ln web area); $r^2=0.50$, $F_{1,36}=34.95$; $p<0.0001$ ln #subadults and adults = $-2.5201 + 0.76975$ (ln web area); $r^2=0.54$, $F_{1,36}=40.42$, $p<0.0001$ ln #females = $-2.6829 + 0.68556$ (ln web area); $r^2=0.45$, $F_{1,36}=24.22$, $p<0.0001$

Figure D.1: Relationships between nest area or web area and the numbers of spiders in colonies used to predict colony sizes for (a) *A. eximius*, (b) *A. domingo*, and (c) *A. panamericana*. Black dots and regression lines represent the total numbers of spiders in colonies; medium gray dots and regression lines represent the numbers of subadult and adults in colonies; light gray dots and lines represents the numbers of subadult and adult females in colonies. Data for estimating the numbers of spiders in colonies of the social species *A. eximius* and *A. panamericana* used with permission of L. Avilés and P. Salazar.

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