Delayed juvenile dispersal benefits both mother and offspring in the cooperative spider *Anelosimus studiosus* (Araneae: Theridiidae)

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Anelosimus studiosus juveniles usually remain in their natal webs with their mothers until maturity, forming temporary colonies in which individuals cooperate in web maintenance and prey capture. In a semi-natural environment, we experimentally removed juveniles from their natal webs at mid-development. In the control group, the juveniles were immediately replaced in their natal webs; in the experimental removal group, the juveniles were not replaced and a sample of them were allowed to build individual webs. Colonies and solitary juveniles were exposed to natural prey densities and censused regularly for numbers and stages of spiders, and for prey capture. On average, juveniles in colonies survived longer, developed faster, and had more resources per individual than did solitary juveniles. However, some of the solitary juveniles obtained more resources than individual juveniles in colonies. Mothers in the control group survived longer and produced second broods earlier than mothers in the experimental removal group. Within the control group, older and larger colonies captured more and larger prey. Larger colonies had a lower coefficient of variation in prey captured per juvenile. Overall, delayed juvenile dispersal benefits both juveniles and mothers. *Key words: Anelosimus studiosus,* delayed dispersal, parental care, parental investment, risk sensitivity, social spiders. *[Behav Ecol 13:142–148 (2002)]*

Delayed juvenile dispersal is often associated with extended parental care that benefits offspring (Altmann et al., 1977; Clutton-Brock, 1991). Trivers (1972) asserts that the cost of parental care, or to any form of parental investment, is the reduction in the parent's ability to invest in other offspring. When resources are limited, parents must "solve" the problem of how to allocate resources between their current and future broods to maximize fitness. The optimal allocation of resources will balance survival enhancement of the current brood with the cost in the parent's ability to survive and produce future broods (Williams, 1966).

Delayed juvenile dispersal is also associated with cooperative breeding in which offspring forego dispersal and their own reproduction, and directly help with the rearing of non-descendant kin (Brown, 1987; Koenig et al., 1992). Theory predicts that cooperative breeding will be favored when ecological constraints limit the opportunities of juveniles to disperse and breed (Emlen, 1984; Koenig et al., 1992; Stacey, 1979). Another perspective on the evolution of cooperative breeding focuses on the advantages to juveniles from remaining to help. The benefit to being a non-breeding helper is explained by kin selection, and depends on their relatedness to the offspring produced and their ability to enhance the success of the breeder (Hamilton, 1964).

There may, however, be intermediate cases in which juveniles remain with their parents beyond an altricial phase and enhance their parent's ability to produce future offspring, even if they are not directly involved in rearing them. This could occur if the juveniles become active in defense or foraging and thus increase the survivorship of and/or the resources available to their parents. In this way an early cost to a parent's future reproductive success of providing parental care may be recouped later as the juveniles mature. In such intermediate systems, quantifying the effects of delayed dispersal on the juvenile's fitness, and on the parent's future reproductive success, would provide insight into the evolution of cooperative breeding and sociality.

In this study, we explore the costs and benefits of delayed juvenile dispersal in the spider *Anelosimus studiosus,* in which juvenile dispersal is usually delayed until maturity, and mothers provide parental care. While in their natal webs, maturing juveniles participate in web maintenance and prey capture, and adult females have the potential to produce multiple broods. Within this species there is variation in the timing of juvenile dispersal. Sub-adult spiders are able to build new webs and forage on their own (Brach, 1977; Jones and Parker, 2000), and in nature sub-adult females are occasionally found living singly in new webs (personal observation). Also, in a population in Tennessee (which is at the northern edge of their range), colonies with multiple adult females have been observed (Furey, 1998; personal observation). This behavioral plasticity facilitates experimental manipulation of dispersal, and quantification of fitness costs and benefits to both mother and offspring.

Female spiders provide parental care by covering their eggs with silk, and many species construct a cocoon which maintains humidity levels, buffers temperature changes and provides mechanical protection from parasites (Foelix, 1996). In many species females guard their egg cases from predators and parasites, and in a few species the mother may, for a short time, provision her offspring through regurgitation or provide them with paralyzed prey (Foelix, 1996). Though the vast majority of spiders are solitary and aggressive, a few dozen species

exhibit sociality beyond this short period of maternal care (Avilés, 1997; Buskirk, 1981). Social structures range from temporary colonies formed by delayed juvenile dispersal, to large, permanent colonies within which individuals cooperate in foraging, web maintenance, defense, and brood care. It is widely believed that the permanently cooperative spiders evolved by extending the maternal-juvenile interaction period of species in which there is maternal care (for review see: Avilés, 1997). Because of this is has been suggested that non-orb web building spiders are preadapted for communal living in that they need only to extend the period of group cohesiveness and mutual tolerance into adulthood to become permantently social (Krafft, 1982). In this regard, the timing of juvenile dispersal in *A. studiosus* should be under fine selective control by local ecological conditions.

The effects of maternal care on juvenile spiders are well documented. In the spider *Theridion pictum* (Theridiidae), egg cases which were left unguarded suffered drastically reduced hatching success (Ruttan, 1991). Mothers in the spider, *Coelotes terrestris* (Agelinidae), provision and protect their offspring after hatching until they disperse as juveniles after about a month, after which the mother can produce another brood (Horel and Gundermann, 1992). The mother's parental investment has a significant positive effect on brood survivorship, and only a relatively small negative effect on her ability to produce a second brood (Gundermann et al., 1997). Benefits of permanent sociality in spider species include: increased individual survivorship (Avilés and Tufiño, 1998; Christenson, 1984; Riechert, 1985), reduced individual silk costs (Riechert et al., 1986; Tietjen 1986), capturing larger prey (Nentwig, 1985; Pasquet and Krafft, 1992; Rypstra, 1990; Rypstra and Tyrey, 1989) and reduced predation (Henschel, 1998). However, in social spiders, females are less fecund than in solitary females (Riechert, 1985; Vollrath, 1986; Wickler and Siebt, 1993). Costs of sociality also include competition within the group (Rypstra, 1993), increased incidence of parasitism (Avilés and Tufiño, 1998), and susceptibility to diseases (Henschel, 1998). Sociality in spiders is also a risk-averse strategy in which individuals in groups have a reduced variance in prey capture compared to solitary individuals (Rypstra, 1989; Smith, 1983; Uetz, 1988a, 1996).

Under controlled laboratory conditions, *A. studiosus* juveniles in colonies capture more individual resources than single juveniles, and prey capture per individual increases with the age of juveniles in the colony, but decreases with number of juveniles in colony (although the total amount of prey capture increases; Jones and Parker, 2000). The same study found that variation in prey capture decreases with the number of juveniles present. Such results suggest that delayed dispersal benefits juveniles in that they have a greater and steadier intake of resources, but that there may be an upper limit to colony size. In this article, we explore similar questions in a semi-natural field situation. As in the laboratory study, we removed juveniles to examine the effect of delayed dispersal on juvenile development and survivorship, and on the mother's survivorship and future reproductive success. We also examined the effects of juveniles on prey capture dynamics. We expected that the laboratory-observed enhancement of individual resources associated with delayed dispersal would be confirmed in this semi-natural study, and delayed dispersal may also reduce the predation risk of juveniles. We hypothesized that delayed dispersal is beneficial to juveniles, and predicted that juveniles in colonies would have better survivorship and develop faster than isolated juveniles. Based on a laboratory experiment in which the presence of juveniles in webs created a lasting increase in prey capture (Jones and Parker, 2000), we also predicted that a mother's future reproductive success will be enhanced by delayed juvenile dispersal.

METHODS

Study species

Anelosimus studiosus is a New World Theridiid spider that ranges from Argentina to New England. They construct webs in the branches of shrubs and low trees in open habitat near water (Brach, 1977). Adult spiders are relatively small (about 8 mm long), and their webs consist of a hammock-like sheet with loosely organized capture threads above. Unlike an orb-web, this type of web can easily be expanded and foraged upon by multiple individuals. This species is described as subsocial (Wilson, 1971) in that juveniles and adult males are tolerated in an adult female's web, but other adult females usually are not (Brach, 1977; personal observation; but see Furey, 1998). Recently dispersed adult females build their own webs and are fertilized either before or after leaving their natal webs. Occasionally, females disperse at their penultimate instar and undergo their final molt in their new webs (personal observation). Adult females guard their egg cases tenaciously and feed newly emerged juveniles by regurgitation. First and second (post-emergent) instar juveniles are altricial and remain deep in the web where the mother presents them with captured prey items. As the juveniles develop beyond this phase, they participate to an increasing extent in prey capture and web maintenance. If the mother is still alive as her daughters mature, she becomes aggressive toward them and will drive them from the web. If the mother has died, one of the maturing females will dominate and retain the web during her 6th or 7th instar. Males are mature after six instars and disperse from their natal webs without aggression from other webmates (Brach, 1977). Voucher specimens have been placed in The Museum of Biological Diversity at The Ohio State University.

Experimental design

The specimens were collected and experiments conducted in Big Cypress National Preserve in the Florida Everglades, from 5 July to 16 September 1998. Adult females guarding egg cases were collected from shrubs along a 40 km section of a drainage canal by excising the branch of the shrub containing the web. An attempt was made to use females guarding their first broods, by collecting only those in apparently new webs (as judged by the small amount of dead plant material, small number of dead prey, pale color of the female, and shallow position of the web relative to new shrub growth). For purposes of standardization, the brooding females were forced to build new webs on a uniform substrate constructed from roughly circular silk foliage (2–6 cm diameter) arranged along three orthogonal axes (Figure 1). The collected webs were carefully cut away, leaving only the spider with her egg case in her retreat (3–5 cm³ of web). The natural retreat was then used to "seed" a new web by fixing it at the center of the artificial foliage which was individually labeled and then wired into the natural foliage at the study site. Substrates in which the spiders abandoned their webs, as well as those on which the spiders started new webs away from the center of the substrate, were removed from the shrubs, cleaned, and restarted with newly collected specimens. The substrates were arranged in a line of shrubs about one half meter apart and between 1 and 2 m high. They were wired to be flush with, but not touching, the surface of the shrub. Within the first 2 weeks of beginning the experiment, webs in which the female had died or disappeared were cleared and restarted. In all, 99 webs were initiated and maintained in this fashion. Using standardized substrates minimized differences in microhabitat which could affect prey capture success and predation on the spiders, and also facilitated accurate censusing. The day
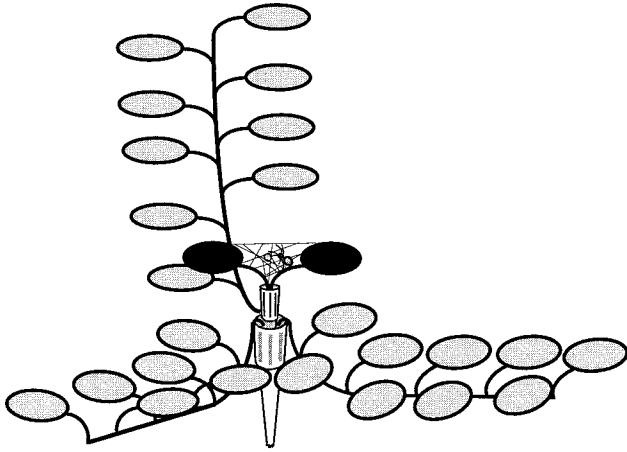
Figure 1
Diagram of artificial web substrate. Three sprigs of silk foliage (light colored leaves) were arranged orthogonally. The web of a brooding female was cut from natural foliage and trimmed down to the the retreat containing the female with her egg case (dark colored leaves). The retreat was then afixed at the center of the artificial foliage from which the female rebuilt her web. An average full-sized web would cover one third to half of the artificial foliage, and none of the webs appeared limited in size by the substrate.

length at the beginning of the study was about 14.3 h, and dropped to 12.7 h by the end. The weather patterns were consistently dry and sunny in the morning with steadily building clouds and heavy rainstorms in the late afternoon. The only changes in this pattern occurred as two hurricanes passed well to the east and west of the study site. None of the local storms were strong enough to dislodge the artificial foliage.

The colonies were left in the shrubs continuously except when they were removed for brief periods of censusing. Censusing was done three times per week (with 2 or 3 days between census days) between 0900 and 1500 h. At each census, the condition of the mother, and the numbers and age classes (instars) of spiders present were recorded. The standardized substrate allowed for systematic censusing, with two counts being regularly made, and three in the case of discrepancy. The identification of juvenile instar was based mainly on the length of their legs. Accuracy in assessment of stage of development was facilitated by frequent censusing, knowledge of the colony's history, and comparisons within webs made possible by overlapping instars. Any captured prey were removed with long forceps, measured, and classified. The webs sustained very little damage in this process. The webs were misted with distilled water at each census to prevent dessication. When the majority of the juveniles reached the fourth instar in colonies in which the mother was alive and present, the colonies were assigned to either the control or removal treatment group. On the first day of assignment, the unassigned colonies with fourth instar juveniles were ranked in order of number of juveniles present. A coin flip decided the treatment of the largest colony, and assignment alternated in descending order of size for the remaining colonies. On subsequent days, the treatment of the unassigned colonies was determined in a similar fashion, except that the assignment of the largest was opposite of the previous assignment.

In the case of the removal treatment, all of the juveniles were removed from the web (after censusing) when the majority of them had reached the fourth instar. Removal was accomplished by using a sharp probe and an aspirator. This process created more web damage than the regular prey removal, but left the webs largely intact. The mother was re-

turned with her web to the shrub, and three of the removed juveniles were allowed to build their own individual webs. This was accomplished by placing the juvenile in a plastic container (500 ml) with a small piece of silk foliage for 24 h. The juvenile would construct a small web on the foliage and this was used to ''seed'' one of the standard substrates which was wired into the natural line of shrubs as described above. In the control group, juveniles were removed, as described above, but were then immediately put back in their natal web and the web returned.

Colonies and individuals were censused for the duration of the experiment, unless all individuals were dead or missing. The experiment lasted until mid-September, at which point all of the original females were missing, had died, or had produced second egg cases.

Plant material that had fallen in the webs was removed to facilitate censusing and removal of captured prey. The total body length of captured prey was measured to the nearest mm, and, if identifiable, the prey were classified to Order. Estimates of the extractable resources in captured prey were made by subtracting the dry weights from the wet weights of prey, based on their length (Sage, 1982).

Data analysis

In analyses examining how colony size affects aspects of prey capture, mean prey captures and coefficients of variation (CV) per census were plotted for the colonies. The effects were tested using regression analyses on one point (mean or CV) per colony, yielding appropriate degrees of freedom. In analyses of effects of colony age on aspects of foraging, data from each colony were used at each instar, resulting in non-independence of the data. To account for this, repeated measures analyses of covariance were performed (Statistica 5.0, 1995), with colony instar as the covariate and individual colony as a random factor. All other analyses and all plots were produced in Excel 5.0a, except Kaplan-Meier tests which were done in SPSS 9.0 (1998).

RESULTS

Within the first 2 weeks of the experiment, 157 brooding females were placed onto artificial foliage. Of these, 44 were not present at the next census and were replaced. An additional 14 abandoned their egg cases; 13 of these were replaced within the first 2 weeks. Of the 99 webs in which the mothers expanded the seed web and egg cases hatched, 55 still had the mother present when the majority of the juveniles present reached the fourth instar. Of these 55 colonies, 27 were assigned to the control group, and 28 were assigned to the removal group. In three of the 44 colonies which were not assigned to treatment groups, both the mother and previously present juveniles were all missing on the same census day, and in the remaining 41 colonies the mother was missing while some juveniles were still present. Of these 41 cases, only two juveniles in one of the colonies molted to the 4th instar and neither of these molted to the 5th instar. A post hoc analysis of the period prior to experimental manipulation found no significant difference in average daily prey capture between the control colonies (mean = 0.259 mg/d) and the removal colonies (mean = 0.246 mg/d, $T = 0.589$, $p = .59$).

Juvenile development

Of the 84 isolated fourth instar juveniles from the removal colonies, 12 died before they could be placed in the experiment. Of the 72 surviving singletons, 29% remained and molted to the 5th instar and 7% of the total remained and molted
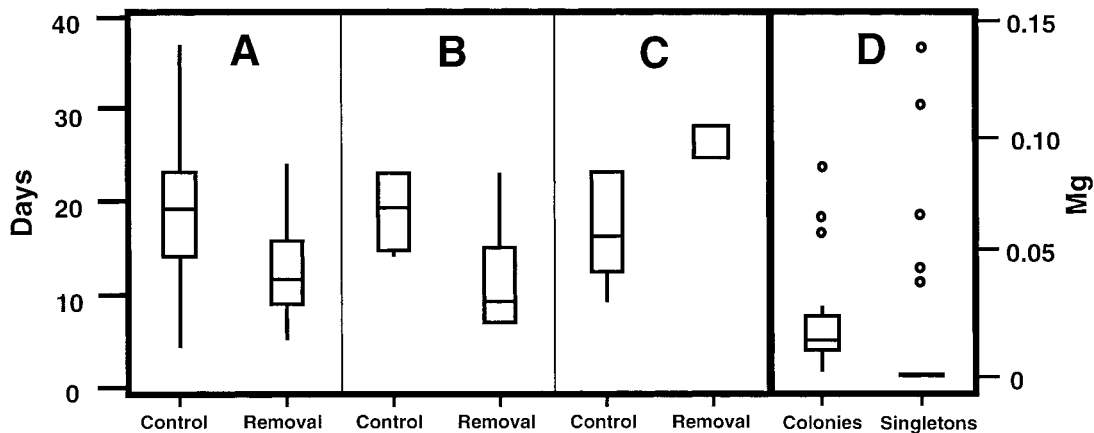
Figure 2
Boxplots comparing aspects of control and removal colonies. The box contains the inner quartile range of the sample (the centerline is the median), the whiskers extend to 90th percentile, and outliers are represented with circles. Plot A compares the number of days mothers were found alive in their webs after experimental manipulation, while plot B compares those which were actually found dead in their webs (not just missing). Plot C compares the number of days after manipulation taken by the mothers to produce second egg cases (of those that did produce them). Plot D compares the prey capture success per individual of juveniles in colonies and those as singletons.

to the 6th instar. Of the 4th instar colonial juveniles, 85% remained and molted to the 5th instar and 25% of the total remained and molted to the 6th instar. These proportions were significantly higher for the colonial juveniles than for the singletons (to the 5th instar $\chi^2 = 103$, $p < .001$; to the 6th instar $\chi^2 = 311$, $p < .001$).

Juvenile prey capture

The prey mass captured per juvenile per day was significantly higher for colonial juveniles than for singletons (Figure 2D; Mann-Whitney $U = 2122$, $p < .001$), though the variances in prey capture among colonials and among singletons were not significantly different ($F = 0.65$, $p = .92$). The majority (64 out of 72) of the singletons never captured prey; of the eight juveniles which did capture prey, all of them molted to the 5th instar, and five of those remained and molted to the 6th instar. Thirteen of the singletons which did not capture prey molted to the 5th instar, but none to the 6th instar. However, of 4th instar singletons that did capture prey, the average daily prey capture was 0.67 mg/d, significantly higher ($T = 3.2$, $p = .006$) than the daily prey capture of individual fourth-instar colonial juveniles.

Effects of delayed dispersal on the mother's survival

After the experimental manipulation (removal of fourth instar juveniles, or removal with replacement), the mothers were found living in their webs longer in the control colonies (Figure 2A; Kaplan-Meier test, mean = 20.31 d, 95% CI 16.7–23.9 d) than those in the removal colonies (Figure 2A; Kaplan-Meier test, mean = 12.6 d, 95% CI 10.3–14.9 d). Since it was impossible to know the fate of missing mothers, a similar analysis of those actually found dead in their webs revealed that mothers whose offspring had been removed were found dead significantly sooner (Figure 2B; Kaplan-Meier test, mean = 11.4 d, 95% CI 8.8–14.0 d) than mothers in the control webs (Figure 2B; Kaplan-Meier test, mean = 18.6 d, 95% CI 16.1–21.1 d). There were no significant differences in variance found for either measure between the treatment groups.

Effects of delayed dispersal on the mother's future reproduction

Only ten of the 55 mothers who remained in their webs to be assigned to treatment groups produced second egg cases.

Though seven of these were in the control group, they were not significantly more likely to produce second egg cases than the removal females ($\chi^2 = 2.15$, $0.1 < p < .15$). However, the control group mothers produced their egg cases significantly sooner than the removal group (Figure 2C; $U = 28$, $p = .024$). No difference in variance in time until production of a second egg case was found between the two groups ($F = 9.0$, $p = 0.1$).

Effects of colony dynamics on prey capture

The prey capture dynamics of the control colonies were affected by both the age and number of juveniles present. The mean colony prey capture per census was positively correlated with the instar of the juveniles (Figure 3A; $F = 13.86$, $p < .001$), and was driven by significantly positive relationships between juvenile instar and both mean length of prey captured (Figure 3B; $F = 7.91$, $p < .001$), and mean number of prey captured (Figure 3C; $F = 57.2$, $p < .001$). Comparisons of prey capture dynamics with the number of juveniles present used data collected after the colonies had reached the third instar, as this is when the juveniles begin to participate in web maintenance and prey capture. There was a significant positive relationship between the mean colony prey capture per census and the average number of juveniles in the colony (Figure 4A; $R^2 = 0.58$, $p < .001$), and this was also driven by significantly positive relationships between the average number of juveniles and both the mean length of prey captured (Figure 4B; $R^2 = 0.21$, $p < .015$) and mean number of prey captured (Figure 4C, $R^2 = 0.63$, $p < .001$).

The total prey captured per census was divided by the number of juveniles in the colony during the trial to estimate how much prey was available to individuals. The prey capture per juvenile per census increased significantly with instar of juveniles ($F = 2.62$, $p = .029$), but did not change with the average number of juveniles present (Figure 5; $R^2 = 0.03$, $p = .35$).

To explore the effects of colony dynamics on variability of prey capture, we used coefficients of variation to account for differences in means. The CV in overall per-census prey capture did not change with either the instar of juveniles in colony ($F = 1.12$, $p = .23$), nor with the average number of juveniles present (from the third to sixth instar; $R^2 = 0.07$, $p = .18$). The CV in the more biologically relevant prey capture per juvenile per census did not change with juvenile instar (F
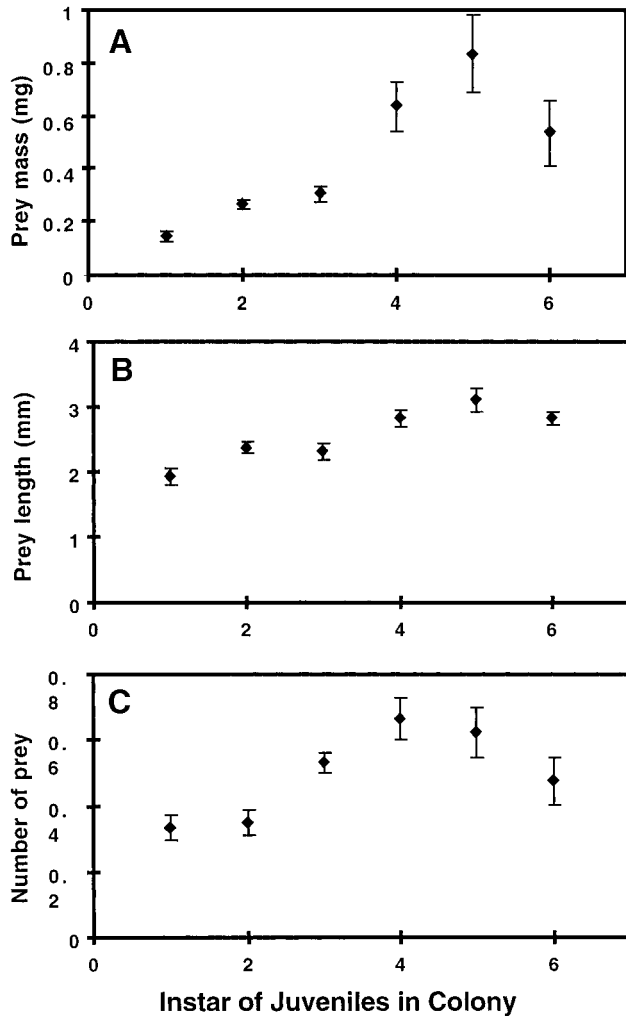
Figure 3
Aspects of prey capture in control colonies as a function of juvenile development, and tested statistically with repeated measures ANOVA. Total mass of daily prey capture (A), prey length (B) and number of prey (C) are plotted as a function of the instar of the majority of the juveniles in the colony. The points represent the mean of means of colonies, with standard error bars, over the specified period.

Figure 4
Aspects of prey capture in control colonies plotted as a function of colony size, and statistically tested with linear regression. Mean total mass of daily prey capture (A), mean prey length (B) and mean number of prey captured per day (C) are plotted as a function of the average number of juveniles in the colony during the period they were in the third through sixth instar.

$= 1.43$, $p = .22$), but declined significantly with average number of juveniles present (from the third to sixth instar; Figure 6; $R^2 = 0.17$, $p = .03$).

DISCUSSION

We examined the effects of delayed juvenile dispersal on a mother's future reproductive success after the point at which juveniles begin to assist in web maintenance and prey capture. The cost to the mother's future reproductive success of provisioning her early instar juveniles has not been measured, but this study does suggest that the presence of later instar juveniles enhances the mother's future reproductive success. Mothers were found living in their webs longer with juveniles present, and the mothers were known to have died, did so earlier when juveniles were absent. Overall, this study suggests that production of second broods is relatively uncommon, and the control group mothers were not found to be more likely to produce them than removal group mothers (though the trend was in that direction and the sample was very small).
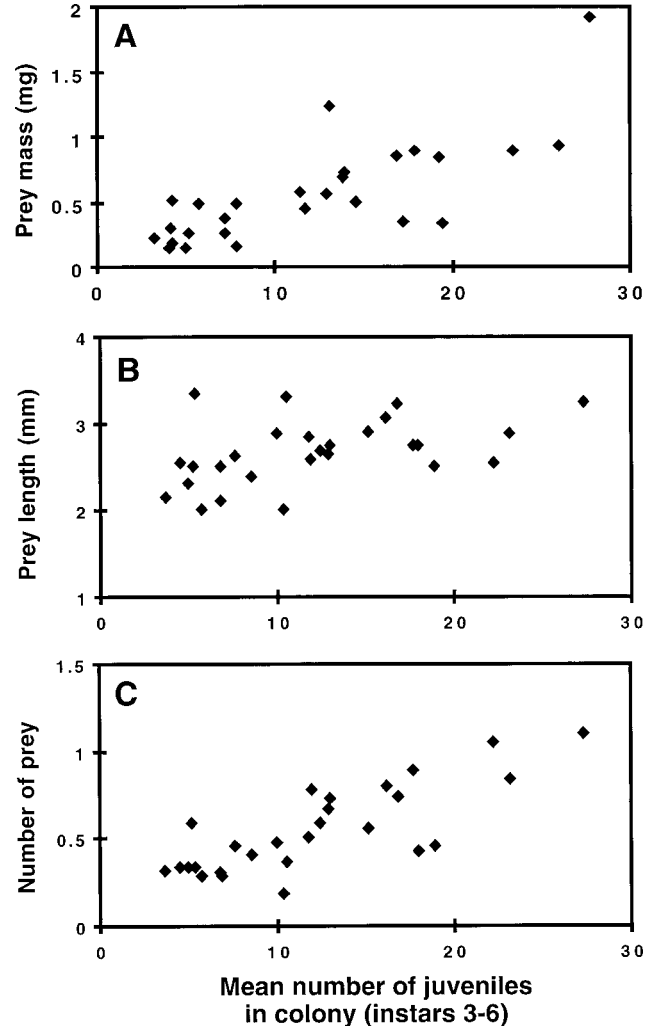
Despite the small sample of second egg cases, mothers with juveniles present produced them significantly sooner than those without. This finding is intriguing because the behavior of the juveniles in their natal web enhances the production of non-descendant kin, even though they are not directly involved in rearing them.

The 72 juveniles removed during the 4th instar that were placed into the experimental regime all built webs typical of small Theridiid spiders, confirming the finding that juveniles can adopt a solitary lifestyle (Brach, 1977; Jones and Parker, 2000). However, single juveniles in this study were less likely to survive and develop than were colonial juveniles. The mean prey capture per juvenile was higher for colonial juveniles than for singletons. The finding that mean prey capture per juvenile is increased by delayed dispersal is corroborated by the facts that, within the control group, prey capture was positively affected by both the age and the number of juveniles present in colonies. Control colonies captured prey at a higher rate, and were able to capture larger prey as the juveniles matured, and if there were more juveniles present. The amount of prey captured per juvenile increased within colo-
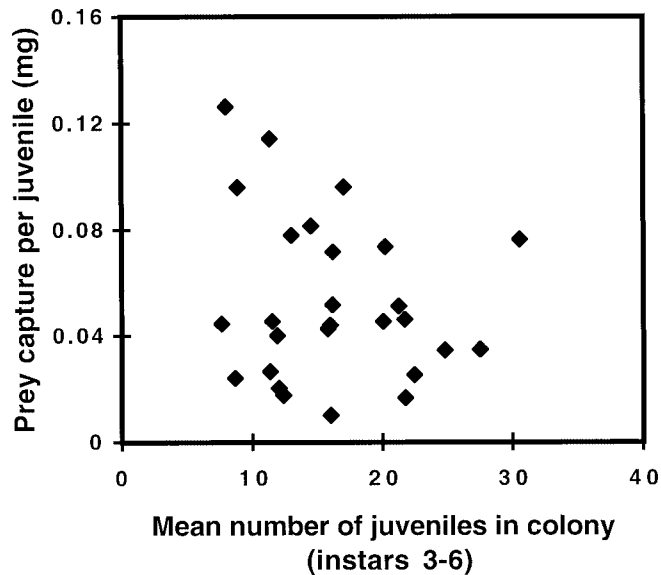
Figure 5
Prey capture per juvenile plotted as a function of colony size. Prey capture per juvenile was calculated as the estimated total mass of prey captured during a census period divided by the number of juveniles present during the period, divided by the number of days in the period. Colony size is defined as the average number of juveniles in the colony during the period they were in the third through the sixth instar.

Figure 6
Coefficient of variation in prey capture per juvenile as a function of colony size. Plotted are CVs in prey capture per juvenile over the period the juveniles were in the third to the sixth instar.

nies as they developed, but neither increased nor decreased as an effect of colony size. This suggests that, from a juvenile's perspective, there may be no difference in mean resources obtained from being in a larger or smaller colony. This contrasts with a laboratory study which found a decline in resources per juvenile as a function of colony size (Jones and Parker, 2000).

This study suggests that delayed juvenile dispersal in *A. studiosus* is risk-sensitive, as an individual's fitness is affected by the variance around the mean success of different foraging strategies (Real and Caraco, 1986). Several studies have found that spiders foraging in groups have a high mean capture rate and a lower coefficient of variation in prey capture (Rypstra, 1989; Smith, 1983; Uetz 1988a, 1996). Here we find an increase in the mean capture rate in groups, but no decrease in variation in prey capture (although, within control colonies, CV in prey captured per juvenile decreased with colony size). In this case, the fact that most singletons captured no prey caused reduction in both the mean and CV of prey capture relative to those of juveniles in colonies. However, the few singletons that did capture prey obtained an order of magnitude more individual resources than colonial juveniles. It would be predicted that *A. studiosus* juveniles should disperse earlier if in their natal web they are obtaining insufficient individual resources. By foraging alone they will trade the increased probability of not capturing prey for the chance that if they are successful, they will not have to share with webmates. The fact that subadult females are occasionally observed on their own in new webs is consistent with this prediction. This is similar to the risk-sensitive tendency to aggregate observed in a facultatively colonial orb-weaving spider, in which spiders tend to forage in groups under high prey densities, but singly under low prey densities (Uetz, 1988a,b). Risk sensitivity has been previously demonstrated in orb-weaving spiders affecting frequency of web relocation (Caraco and Gillespie, 1986; Caraco et al., 1995), and the tendency to aggregate (Uetz, 1988a,b).
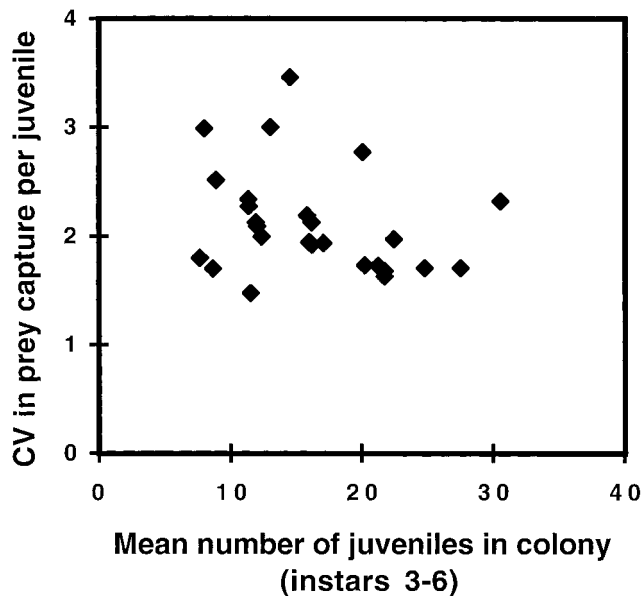
There was considerable loss of both mothers and juveniles from colonies. There was no way to tell the fate of missing spiders, but it is highly unlikely that juveniles were dispersing before the 5th instar, as no juveniles before that stage were ever observed in their own webs while collecting (personal observation). It is possible that the mothers had dispersed when they were missing, but this was not observed in colonies under controlled conditions, and dead females were often found out of their webs (Jones and Parker, 2000). The rate of loss of juveniles was apparently higher between instars one and three, and lower between three and five. Though no interactions with other species were observed, this pattern is consistent with the colonies becoming more resistant to predation as they develop. The drastic loss of juveniles between the 5th and 6th instar most likely represents the onset of juvenile dispersal. The importance of maternal presence to early juvenile survivorship is clearly demonstrated by the fact that none of the juveniles in colonies in which the mother disappeared prior to their reaching the 4th instar survived to the 5th instar (and only two molted to the 4th).

This study suggests that delayed dispersal in *A. studiosus* benefits juveniles throughout their time in their natal webs, and that their presence at later instars is also beneficial to their mother's future reproductive success. Because this species is intermediate in its level of sociality, these results provide evidence of some of the selective forces involved in the evolution of sociality. Whether the delayed dispersal provides an overall enhancement to the mother's future success depends on the cost of her initial investment in the brood, which has yet to be examined. Even if there is not a net enhancement of the mother's future reproductive success, or even if there is a net reduction, delayed juvenile dispersal could still maximize her fitness through the success of the current brood. This system differs from simple parental investment, and is similar to cooperative breeding, because late instar juveniles enhance the production of non-descendant kin (Hamilton, 1964; Koenig et al., 1992). This system differs from cooperative breeding in that, while juvenile *A. studiosus* delay dispersal relative to typical spiders, they do not necessarily delay reproduction nor suffer any cost to their direct fitness. Juve-

nile *A. studiosus* may incur a cost to their direct fitness if the process of dispersing and building a new web takes longer, and/or becomes more risky, as the spiders mature. However, given the significant advantage to colonial juveniles over singletons in terms of survivorship and prey capture, it seems likely that there is an overall enhancement in juveniles' direct reproductive success through delayed dispersal. Juveniles would also gain indirect fitness benefits through their enhancement of future broods, the magnitude of which depends on their relatedness to future broods. Whether or not there is multiple paternity within, or among, broods produced by the same female in this species is not yet known.

In this and other social spider species, cooperative behavior is rudimentary in that social spiders do not exhibit coordinated behaviors. Rather, they behave similarly to solitary spiders, but without aggression toward conspecifics (Avilés, 1997; Krafft, 1982). Prey capture is enhanced in cooperative spider colonies by increased capture area (Riechert et al., 1986; Tietjen, 1986; Jones and Parker, 2000) and a higher probability of prey being subdued once it has entered the web (Nentwig, 1985; Rypstra, 1990). There is no evidence that the juveniles in *A. studiosus* are directing any behaviors toward helping their mother reproduce. It is possible, however, that while the mother is brooding a second egg case the juveniles take over the bulk of the risky behaviors of prey capture and web maintenence, which is similar to behavioral asymmetries seen in their permanently social congener *A. eximius* (Ebert, 1998). Overall, the results presented here on the effects of delayed dispersal on juvenile survivorship and on the mother's future reproductive success suggest an easy evolutionary transition to permanently social colonies.

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