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The Effect of Temperature on the Development Rate of
Anelosimus studiodus (Araneae: Theridiidae)

Sarah E. Dalrymple
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ABSTRACT

The US has only one social spider species, which ranges from south Florida to New Jersey. The nests of the social spider, *Anelosimus studiosus*, predominantly consist of a mother and her clutch of babies. However, at higher latitudes and at cold-water sites within latitude, multiple female colonies can be found, and the incidence increases with latitude. The presence of a latitudinal gradient in the social behavior of these spiders suggests that temperature may underlie the variation in social structure noted for this species. This study examines the effect that temperature has on the development rate of *A. studiosus* juveniles, under the hypothesis that longer development time leads to a greater probability of a single mom dying before her offspring reach independence. By sharing a nest with other females, each female's offspring may be fostered by the others if she should die. Both field and lab studies were conducted in east Tennessee. In the field study, we correlated air temperature and development rates of offspring at their natural web sites over an eight-week development period. A temperature-controlled lab experiment was also conducted on brooding females collected from sites between southern Florida and Tennessee (26°N - 36°N). Half of the clutches were reared at 22°C (cold water site equivalent) and the other half at 27°C (as at warm water sites). Again growth rate was monitored. The results from both experiments support the hypothesized relationship between temperature and rate of juvenile development.

INTRODUCTION

Most spider species are territorial and can even be cannibalistic. Cooperative behavior in spiders is very uncommon, but has evolved several times, resulting in extended social behavior in several dozen spider species (Avilés 1997, Buskirk 1981). Quasisocial organisms are those that, as adults, share a nest and have cooperative brood care (Wilson 1971). Colonial spiders (e.g. Lubin 1980) live in aggregate webs throughout their entire life cycle, but retain territories within the web and do not have cooperative brood care (Avilés 1997). Subsocial (Wilson 1971, Krafft 1979) spiders display parental care and cooperative behavior between offspring only until a certain point in the life cycle, at which time the members of the nest disperse to form their own webs (Avilés 1997).

Most of these cooperative species live in tropical or sub-tropical areas, but there is one cooperative spider species in the United States, *Anelosimus studiosus*, that inhabits the southeast region of the country (Brach 1977). In the United States there are both single-female webs and communal webs containing many females (Furey 1998). Therefore, this species exhibits both subsocial and quasisocial behavior. Furthermore, a pattern exists in the distribution of their behavior: single-female webs occur most commonly and throughout the range of the species and multiple-female webs occur less commonly, but with greater frequency at higher latitudes (Jones *et al*, in preparation, personal observation). In *A. studiosus* populations in southern Florida, around 26°N, there are no known multiple-female webs and the first observed small multiple-female webs appear around 30°N in the Florida panhandle. In east Tennessee, several large multiple-female colonies have been observed, at least one of which contains an estimate of over 1,000 spiders (Furey 1998, Jones & Parker 2002, personal observation). These large colonies are usually found over cold water sites, while most webs over warm water are single-female. There are both costs and benefits encountered with positive sociality (summarized in Jones & Parker 2002), which determine whether social behavior in a population will evolve.

Thomas Jones and Susan Riechert have proposed a model to explain this spatial-scale pattern of cooperative behavior of *A. studiosus* (Jones *et al*, in preparation). According to the model, single female spiders are not as successful at fostering offspring as females in multiple-female webs at higher latitudes. Juvenile spiders require the care of their mother until they are able to participate in prey capture and web maintenance and construction by themselves. This level of independence is usually reached between the fourth and fifth instars (Brach 1977, Jones & Parker 2002). If the mother dies before this developmental stage is reached, the babies will die. The model predicts that lower temperatures at high latitudes slow the development rate of juveniles. This prolonging of the developmental period results in a greater probability that the mother spider will die before her offspring are mature. Females at higher latitudes may compensate for this by grouping together and cooperating with other females in web construction, web maintenance and prey capture. This cooperation among females, accompanied by the indiscriminate care for young (Brach 1977, Jones (personal communication)), ensures that all offspring will be cared for in the case that a mother dies prematurely

The soundness of this model rests on the assumption that, within a normal range of temperatures, spider development rate increases with increasing temperature. There have been many studies done that test the effect of temperature on development and body size in ectotherms, and it is well-accepted that growth and development in ectotherms is faster at high temperatures than at low temperatures (see Table 1 for examples). In spiders, instar duration usually decreases with increasing temperature and molting depends on a certain species-specific threshold temperature (Pulz 1987). Although this positive relationship between temperature and development rate is usually present, some ectotherms may display rate isomorphy (Van Rijn *et al* 1995), meaning their developmental rate is independent of temperature. A recent review shows that there have been several studies that confirm the existence of rate isomorphy in some insects (Jarosík *et al* 2002). This study is needed to test the relationship between development rate and temperature in *A. studiosus*. I performed a lab and field experiment using all single-female webs from areas throughout the southeastern United States to answer this question.

METHODS

Lab experiment

Brooding females were collected from 10 sites, with two sites representing each of the following latitudes: 26, 28, 30, 32, and 36° N. I housed each female with her egg case in a 500 mL plastic container that had a perforated lid for ventilation. A 2 to 3 inch section of a 'twist tie', twirled into a spiral shape, was placed into each of these containers to serve as a structure on which the spiders could anchor their webs. Within two weeks, all spiders had constructed webs within the containers; most settled within the twist tie structure.

As each egg case hatched, I placed the container housing that family into one of two growth chambers so that an even number of females from each population was exposed to a temperature of 27°C and 22°C. Both chambers offered, on average, a 12-hour day period, but because we experienced problems with the regulation of day period in each chamber we cannot say that the day length was held constant. As this spider in nature lives in shrubs in the immediate vicinity of water, we kept a tray filled with water on the bottom shelf of each growth chamber to maintain humidity.

I monitored the containers twice a week, at which time all exuvia from molting juveniles were removed from the containers with forceps. This number was recorded and represented the number of molting events that had taken place since the last day the container was checked. I also recorded the number of juvenile spiders in each container once each week. All spiders were misted with water and fed *ad libitum* twice a week. In order to reduce the occurrence of competition among the juveniles for food, I added one fly per three spiders at the lowest juvenile stages at each feeding time. When most of the juveniles were third or fourth instars, I added roughly one fly per juvenile twice each week. If any spiders were above the fourth instar, two flies per spider per week were added. Approximately 3 extra flies were added for the adult female at each feeding time. It should be noted that this was a rough estimate of how we determined how many flies to add to each container. The containers were left in the chambers and data was collected continually until all individuals had reached at least the fifth instar.

Field Experiment

Thomas Jones and I chose four field sites along water sources with varying temperatures in East Tennessee. Field sites with different water temperatures were selected to test for the effect of temperature on spider development rate. The sites at Melton Hill Lake and Chilhowee Lake had cooler average water temperatures than the sites at Ish Creek and I.C. King Park. Dams used for flood control in this region maintain stable temperatures in these bodies of water. At each of these sites, we marked 20 webs in Virginia Pines overhanging the water that contained a female *A. studiosus* with her egg case. A temperature sensor that recorded the daily maximum and minimum air temperatures was also placed near the webs in a shaded area. We monitored each of these webs once a week, accessing sites by motorboat, pirogue, or kayak. At this time the webs were measured, the approximate age of the juveniles recorded, and the temperature of the water taken.

This monitoring continued until eight weeks had elapsed since the hatching of the egg case. At that point, we collected the webs to record the ages of the juvenile spiders. In order to collect all spiders from the web, we clipped the entire end of the branch containing the web. The ages were determined according to the size of the juveniles within a week of the collection of the webs. There were some web losses throughout the experiment at every site due to predation, parasitism, web submersion in the water, and other factors. These webs were not included in the analysis.

RESULTS

Lab Experiment

For each week of the experiment, a development rate was calculated by dividing the number of exoskeletons collected by the number of juveniles present in the web that week. A similar measurement of development rate was taken at the time when half of the juvenile spiders had reached the fourth instar. We did this by averaging all weekly development rates for that web until that point. The point in time when half of the individuals had reached the fourth instar was determined as the time when the added

weekly development rates, or total development rate, totaled at least 2.5. At this point, the juvenile spiders had molted, on average, 2.5 times, making half of the individuals 3rd instars and half 4th instars. Both measurements of development rate were measured as a number of molting events per week.

The average development rate at the point when half of the spiders were 4th instars was significantly different between the two temperatures (Figure 1; $F = 4.1077$, $p = 0.0492$). There was also a significant decrease in development rate with time in both temperatures (Figure 2; $F = 35.6525$, $p < 0.0001$). There was, however, no significant difference between temperatures in the overall development rates of the webs after six weeks (Figure 2; $F = 1.3797$, $p = 0.2221$), or in the time it took for half of the juveniles to reach the fourth instar (One-Way ANOVA; $F = 2.7$, $p = 0.1050$).

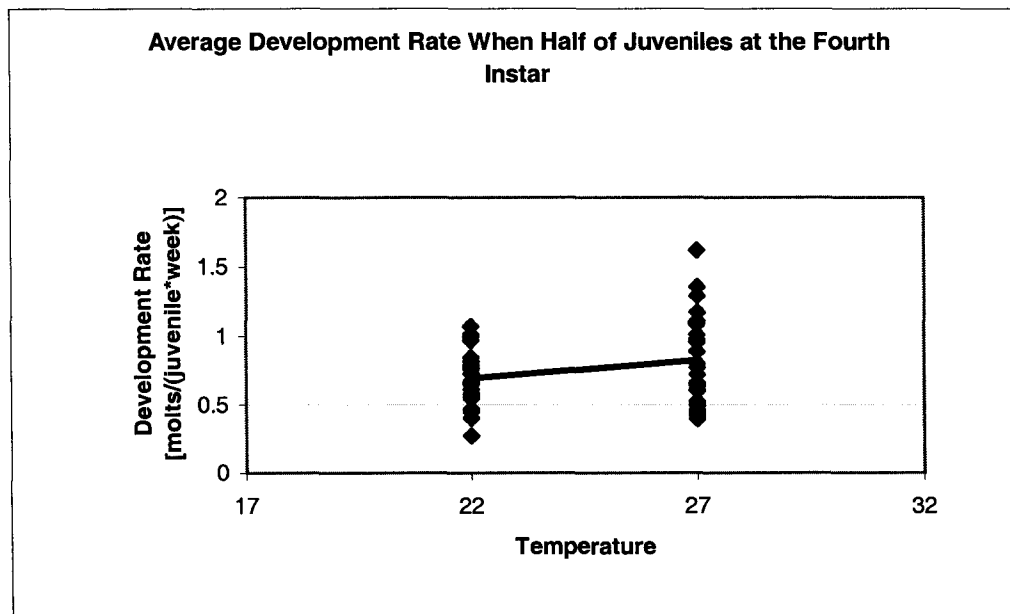


Figure 1. Shows the average weekly development rates for spiders as a function of temperature in the growth chambers. A One-Way ANOVA was used for the statistical analysis.

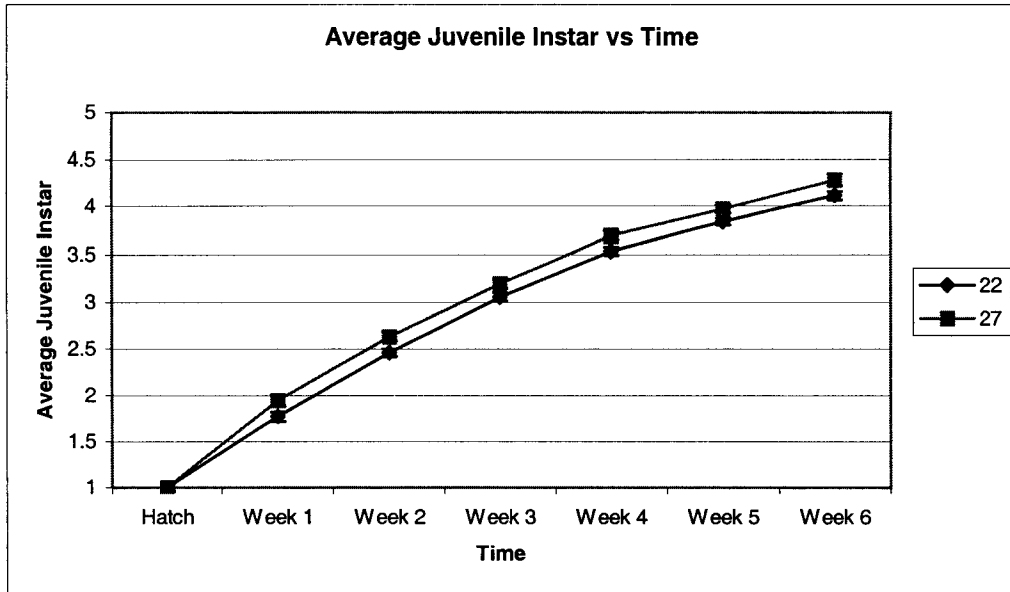


Figure 2. Shows the development of the juvenile spiders at the two different temperatures as a function of time. The overall trend in development rate with time was tested using a Repeated Measures ANOVA. The average development rate as a function of temperature was also tested with a Repeated Measures ANOVA.

Field Experiment

Melton Hill Lake (MH) and Chilhowee Lake (CL) were cool water sites, with average water temperatures of 24.4°C and 24.0°C respectively during a five-week period from July 15 to August 19. I.C. King Park (ICK) and Ish Creek (IC) were warm water sites, with average water temperatures of 28.4°C and 30.5°C respectively during the same time period. The average instar of juvenile spiders over the second instar in the webs was 3.5431 at CL; 3.45 at MH; 3.8421 at ICK; and 3.9435 at IC. There was a highly significant positive correlation between the average age of juveniles in the webs and the water temperatures at the sites from which they were collected (Figure 3; $F = 8.8$, $p = 0.0048$, $n = 45$).

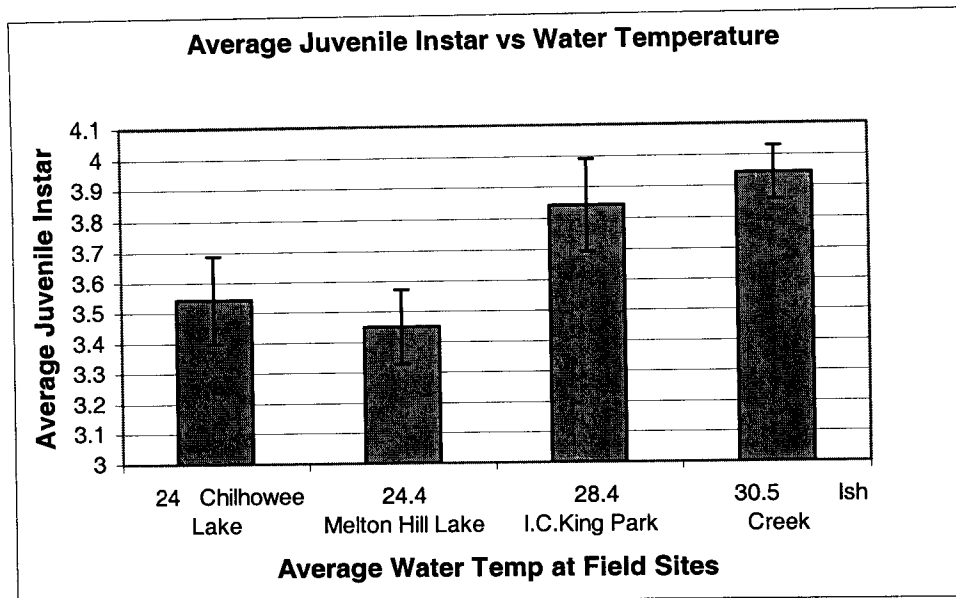


Figure 3. The average age of juveniles in webs collected at the four different field sites plotted against the average water temperatures at those sites. One-Way ANOVA test used for statistical analysis.

DISCUSSION

Lab Experiment

The significant difference between the development rates of the webs at the time when half of the juveniles were fourth instars supports the hypothesized increase in development rate with increasing temperature. There were several reasons for choosing this point in development as the critical point for this experiment. First, we could not discount the possibility that we may have missed some exoskeletons during the course of the experiment, especially those of the first instars molting to the second instar. Using the time when there had been, on average, 2.5 molts per individual, therefore, was a good measurement of the time when at least half of the spiders had reached the fourth instar.

There were also some individuals in the webs that tended to mature at a slower rate than the others. In many cases, by the time that all of the juveniles had reached the fourth instar, some were already at the sixth instar. We wanted to get an accurate picture of the amount of time it would take for most of the juveniles to be able to survive without

the aid of their mother. We eliminated the effect of these slower maturing individuals by using the development rate calculated at that point in time.

There was no significant difference between the two temperatures in the total development of the spiders over a six-week period, nor in the time it took for half of the juveniles at each temperature to reach the fourth instar. One possible reason that the time was not significant is because the webs were only checked twice a week. Therefore, we could only tell when molting events had occurred to within three or four days.

Considering the development rate was a better measure of the progress in development because we could take into account how far along in development the spiders were and the time it took them to get there. Almost none of the webs had a total average development of exactly 2.5 molts per individual on the day they were checked. Most were past this point, to varying degrees. Some had already had three molts per individual on average by the time they were checked, while others were just over 2.5 molts per individual. It was more accurate to consider the average development rate of the webs because two webs that had the same recorded time to the point when at least half of the juveniles were at the fourth instar could still be at different stages of development.

There were also several problems experienced with the growth chambers. Several times near the end of the experiment, the power went out in the building and the chambers did not maintain a steady temperature. In these cases, the spider families still in the chambers were not considered for data analysis. The chambers also did not have a working light meter. In each chamber the light period was not constant throughout the experiment. One final consideration is the diet of the spiders. The all-*Drosophila* diet may not have provided the best nutrition for the spiders and could have affected the growth rate of the juveniles.

To correct for these problems and to double-check the results, another smaller-scale experiment is currently being run. Currently, only females from southern Florida have been tested because they are the only spiders that have produced egg cases. The lights have been repaired in the growth chambers and the *Drosophila* diet is replaced with crickets. This change in diet could also have some effect on the experimental results.

Field Experiment

The results of the field experiment provide considerable support for the increased development rate of juvenile spiders with increasing temperature. The juveniles in the webs above warmer water were significantly older than the juveniles in the webs above colder water. When the average age of juvenile spiders was computed, only the juveniles above the second instar were counted. In several webs it was noted throughout the experiment that the female had a second egg case. We assumed that any juveniles under the third instar after eight weeks were from a second brood.

One interesting result from this experiment was the fact that there was no significant difference between the maximum and minimum air temperature at the four sites. This could imply that there is also no difference in the average air temperatures at the sites. This would suggest that something about the temperature of the water itself, and not the surrounding air, is affecting the spiders' development rate. There are several ways this could be occurring. One possible explanation is that different water temperatures could be associated with different insects or other prey items of the spiders. It could be that warmer water temperatures favor insects that are better prey for the spiders or that more prey items occur over warm water. Another explanation is that the humidity resulting from the different water temperatures influences the growth rate in some way. Air over warmer water is expected to be more humid. This could have various indirect impacts on the spiders, but none have been investigated in this study.

Another possible explanation for the air temperature anomaly is that the maximum and minimum temperatures at a site are not good predictors of the average daily temperature. The temperature sensors that we used only recorded current temperatures and the daily minimum and maximum temperatures for up to one week. Therefore, we do not have data on the average daily temperature, which would be a more accurate estimate of the temperatures to which the spiders were exposed longest. Although the temperature sensors were placed in the shade, very warm or cool gusts of wind could have produced the maximum or minimum temperature recorded by the sensor, thereby creating an inaccurate depiction of the air temperature that day.

In the absence of the average daily temperature data, the weekly water temperatures are probably a better indicator of this than the maximum and minimum air

temperatures. Water's high specific heat results in more constant temperatures with less fluctuation. The water should more closely reflect the average air temperature and would be less influenced by occasional extreme temperatures. For all of these reasons, we chose to use the average water temperature for the analysis of juvenile development at these sites.

The more convincing evidence for the increased development rate with temperature comes from the field study. This is encouraging because the support comes from spiders in their natural setting, with minimal disturbance and most likely represents differences that could be occurring on a larger latitudinal scale. The results obtained from the cold and warm water sites in East Tennessee can be extrapolated to represent differences in temperature between latitudes. There is most likely a large difference between the average water temperature at 26°N, where all webs are single-female, that around 30°N, where the multiple-female colonies begin to appear, and that at 36°N, where very large multiple-female colonies can be found. It now seems probable that the model for the pattern of sociality in *A. studiosus* is, in fact, due to this difference in temperature and the increased development rate accompanying it.

General Conclusions

Many previous studies have explored the relationship between development rate and temperature in diverse ectotherm taxa. In Table 1, I have listed such studies on arthropods and their findings. According to this data, in almost all of these species there is an increase in development rate with increasing temperature. Most of the organisms are insects, but in all studies of spiders reported, there has been a positive correlation between temperature and development rate. This study concludes the same relationship between development and temperature in *A. studiosus*.

CLASS						
(Order)	<i>Species</i>	Temperature Effect	Reared	Temps tested (C)	Developmental stages tested	Reference
ARACHNIDAE						
(Acari)						
	<i>Ixodes scapularis</i>	+	lab/ field	0 - 32	preoviposition, preeclusion, premolt	Ogden et al 2004
	<i>Eutetranychus banksi</i>	+	lab	15 - 32	egg - adult	Childers et al 1991
(Araneae)						
	<i>Bathyphantes gracilis</i>	+	lab	9 - 21	egg sac	Thorbek et al 2003
	<i>Erigone atra</i>	+	lab	9 - 21	egg sac	Thorbek et al 2003
	<i>Erigone dentipalpis</i>	+	lab	9 - 21	egg sac	Thorbek et al 2003
	<i>Erigone promiscua</i>	+	lab	9 - 21	egg sac	Thorbek et al 2003
	<i>Ergonidium graminicolum</i>	+	lab	15 - 35	egg - adult	Li 1995
	<i>Meioneta rurestruis</i>	+	lab	9 - 21	egg sac	Thorbek et al 2003
	<i>Oedothorax apicatus</i>	+	lab	9 - 21	egg sac	Thorbek et al 2003
	<i>Oedothorax fuscus</i>	+	lab	9 - 21	egg sac	Thorbek et al 2003
	<i>Oedothroax retusus</i>	+	lab	9 - 21	egg sac	Thorbek et al 2003
	<i>Tenuiphantes tenuis</i>	+	lab	9 - 21	egg sac	Thorbek et al 2003
CRUSTACEA						
(Amphipoda)						
	<i>Gammarus lawrencianus</i>	+	lab/ field	5 - 23.8	embryonic & interbrood	Sinervo & Doyle 1990
(Brachyura)						
	<i>Liocarcinus holsatus</i>	+	lab	5 - 24	embryonic & larval	Choy 1991
	<i>Necora puber</i>	+	lab	5 - 24	embryonic & larval	Choy 1991
(Decapoda)						
	<i>Cancer magister</i>	+	lab/ field data	N/A	larval	Moloney et al 1994
(Harpacticoida)						
	<i>Bryocamptus zschokkei</i>	+	lab	3.5 - 20	egg & naupliar	O'Doherty 1985
INSECTA						
(Coleoptera)						
	<i>Leptinotarsa decemlineata</i>	+	lab	17 - 34	prepupal - pupal	Lopez et al 1997
(Diptera)						
	<i>Rhagoletis completa</i>	+	lab	8 - 32	preoviposition, egg, larval, pupal	Kasana & Aliniazee 1994
	<i>Haematobia thirouxi potans</i>	+	lab	15 - 30	egg, larval, prepupal, pupal	Fay 1985
	<i>Myiopharus doryphorae</i>	+	lab	20 - 32	1st instar - adult	Lopez et al 1997
	<i>Rhagoletis mendax</i>	M (N,-)	lab/ field	20, 25	postdiapause pupal	Teixeira & Polavarapu 2002
(Ephemeroptera)						
	<i>Ephemerella ignita</i>	+	lab	4.5 - 18	larval	Rosillon 1988
(Hemiptera)						
	<i>Nabis americanoferus</i>	+	lab	18 - 31	egg - adult	Guppy 1986
	<i>Lipaphis erysimi</i>	+	lab	6.2 - 37	birth - adult	Liu & Meng 2000

<i>Myzus persicae</i>	+	lab	2.9 - 33	birth - adult	Liu & Meng 1999
<i>Arma custos</i>	+	lab	13.5 - 33	egg, nymphal	Saulich & Volkovich 1994
(Homoptera)					
<i>Acyrtosiphon pisum</i>	+	lab	10 - 28	1st instar - adult	Lamb & MacKay 1988
<i>Aphis gossypii</i> Glover	+	lab	10 - 30	pre-imaginal	Kocourek et al 1994
<i>Aphis gossypii</i> Glover	+	lab	15 - 35	1st instar - adult	Kersting et al 1999
<i>Spissistilus festinus</i>	+	lab	12.8 - 35	nymphal	Spurgeon & Mack 1990
(Hymenoptera)					
<i>Encarsia perniciosi</i>	+	lab	15 - 31	egg - adult	McClain et al 1990
<i>Psyllaephagus yaseeni</i>	+	lab	21.5 - 30	generation times	Patil et al 1993
<i>Tamarixia leucaenae</i>	+	lab	21.5 - 30	generation times	Patil et al 1993
<i>Gonatocerus cicadellae</i>	+	lab	15 - 30	egg - adult	Miura & Yano 1988
(Lepidoptera)					
<i>Lymantria dispar</i>	+	lab	4 - 38	egg, pre-diapause	Gray et al 1991
<i>Mythimna convecta</i>	+	lab	4.3 - 34.8	egg, larval, pupal	McDonald 1990
<i>Plutella xylostella</i>	+	lab	4 - 40	egg - adult	Liu et al 2002
<i>Ancylis comptana</i>	+	lab	14 - 34	preimaginal	Cabriel & Obrycki 1990
<i>Choristoneura fumiferana</i>	+	lab	9.3 - 33	larval	Weber et al 1999
<i>Crociosema plebejana</i>	+	lab	10 - 34	egg - adult	Hamilton & Zalucki 1991
(Plecoptera)					
<i>Pteronarcys californica</i>	+	lab/ field	5 - 20	egg	Townsend & Pritchard 2000
(Thysanoptera)					
<i>Thrips obscuratus</i>	+	lab	10 - 27	egg - adult	Teulon & Kpenman 1991

Table 1. Results from studies showing the effect of temperature on the development rate of arthropods. In the Temperature Effect column, a + sign indicates a positive relationship between temperature and development rate, while a – sign indicates a negative relationship. M indicates a mixed effect and N indicates no effect of temperature on development rate. Each experiment tested constant or fluctuating temperatures included in the temperature ranges listed. In some cases, the temperatures listed are the averages of fluctuating temperature treatments, rather than constant temperature treatments.

This study, as a whole, supports the basic assumption of the model (Jones *et al*, in progress) for the social behavior of *A. studiosus*. Additional studies must be carried out before the model can be confirmed. This study, however, provides basic and necessary support for the model. The results from the experiment currently being carried out will later be analyzed to see if they confirm the results from this study. The more tightly controlled lab conditions in that experiment should provide information in which we can have more confidence.

In the future, a study is needed that can differentiate between the effect of water and air temperature on the spiders. A repeated field experiment with temperature sensors

measuring average daily temperatures could reveal the possible effect of air temperature on the development rate of the spiders that we were not able to confidently conclude with this study.

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