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An individual-based model of the social spider
Anelosimus studiosus

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ABSTRACT

The social spider *Anelosimus studiosus* exhibits a number of social structures: from nests with a single territorial female to colonies containing dozens of adult females cooperating on tasks like web maintenance and brood care. One hypothesis for this diversity of social structures is that cooperation is only favored when there is a higher mortality risk to adult females or when the dispersal of juveniles is delayed. To test this hypothesis I constructed an individual-based model that simulates a population of *A. studiosus* over time. The model is continuous in space and discrete in time and takes into account biological processes like predation, natural mortality, dispersal, and intraspecific conflict over resources. Calibration of the model was informed by data collected from field experiments on populations of *A. studiosus* in southern Florida. Results of the model show that populations with multiple-female colonies suffer proportionately less from increased predation and delayed dispersal, which is in agreement with previous hypotheses. The model also reveals that predation and dispersal influence the proportion of multiple-female nests because the rate of their formation is density-dependent. Although this paper primarily serves to describe the motivation for and design of the individual-based model, several avenues for future implementation of the model exist and appear promising.

Cooperatively social behavior has a number of disadvantages to solitary living, including increased intraspecific competition for resources like nest sites and food (Cahan 2001), increased exposure to contagious diseases and parasites (Hoogland 1979), and decreased foraging time for individuals on guard duty (Bednekoff & Woolfenden 2003). Because of these and other costs associated with cooperative living, social behavior is thought to only evolve under very specific ecological conditions (Alcock 1989). Some of the ecological correlates of spider sociality include an abundant food supply to encourage the delayed dispersal of juveniles, high intraspecific competition to pressure some individuals toward the use of previously unexploited resources like prey items too large to be captured by a single spider, and frequent environmental disturbances that would be less detrimental to large nests maintained by numerous spiders (Riechert 1985; Avilés 1997).

The subsocial spiders, which exhibit extended parental care, provide a unique opportunity to test hypotheses regarding the ecological conditions under which cooperation can emerge in populations comprised of non-cooperative individuals. Jones et al. (ms) advocate a brood-fostering model to account for the existence of cooperation in the subsocial spider *Anelosimus studiosus* along a latitudinal gradient. This brood-fostering model posits that populations that occur in areas with colder temperatures are subject to a longer altricial period, which increases the time that juveniles are vulnerable to mortality. Associated with delayed offspring development is an increased probability that the mother will perish while her offspring still depend on her for survival. Under certain circumstances, this increased period of vulnerability is an adequate incentive for mothers to form multiple-female colonies so that if one mother perishes her young will be cared for by one or more other *A. studiosus* females.

For delayed dispersal to have such a strong influence on the social structure of this spider, there must be strong selection against the survival of *A. studiosus* mothers over time. In an investigation of the interactions that occur between *A. studiosus* and other spider species that frequent its nests, Perkins et al. (ms) showed that at least two groups of spider nest associates are predators on the inhabitants of host nests. The authors of that study also found that juveniles are more likely to survive encounters with predators when their mothers are present. Hence, the fact that predators frequently invade *A. studiosus* nests, along with the increased survival probability of juveniles who live with their mothers, suggests that predation on *A. studiosus* nests could be a selective pressure for cooperative behavior in delayed-dispersal populations.

In this study I explored the population level consequences of delayed-dispersal and increased predation pressure on *A. studiosus* populations comprised of either single- or multiple-female nests. Since experimental manipulations of predation and delayed-dispersal in entire *A. studiosus* populations are not feasible, this type of experiment is best performed on simulated populations. Here I simulate *A. studiosus* populations using a spatially-explicit individual-based model, the parameters of which were informed by empirical data collected in the field. The model, which is continuous in space and discrete in time, tracks the number of individuals in each nest and accounts for predation by nest invaders, natural mortality, maturation of offspring, dispersal of newly-matured females, and conflicts between females with overlapping nests. These conflicts either result in one female killing the other, two females tolerating each other, or two females engaging in a cooperative association with each other. The outcome of these conflicts is dependent on phenotypic aggression scores assigned to each individual. These aggression scores also underlie the dispersal distances exhibited by newly-matured adult females.

The assumption that individuals express a phenotype for aggression that influences multiple behaviors is referred to as a behavioral syndrome (Sih et al. 2004). Although there are currently no empirical verifications that a behavioral syndrome exists in *A. studiosus*, behavioral syndromes have proven to be a viable explanation for the existence of non-adaptive behaviors in other spiders, such as superfluous killing in the desert spider *Agelenopsis aperta* (Maupin & Riechert 2001) and sexual cannibalism in the fishing spider *Dolomedes triton* (Johnson & Sih 2005). Although these examples of behavioral syndromes in spiders feature hyper-aggression as an evolutionarily anomalous behavior, it may be that in *A. studiosus* the seemingly non-adaptive syndrome of non-aggression is a mechanism by which cooperation can arise given the proper ecological conditions. Therefore, the assumption that *A. studiosus* individuals vary with respect to an all-encompassing behavioral syndrome is a plausible explanation for how cooperative behavior could emerge and become fixed in a population of non-cooperative individuals.

MODEL DESCRIPTION

In this study I modeled *A. studiosus* populations using an individual-based model that I implemented in Matlab 6.5 (The MathWorks, Inc. 2002) (see Appendix for code). At the onset of the simulation, nests were randomly placed on a horizontal landscape analogous to a row of vegetation along a waterway (Fig. 1). The vertical position of nests was simulated by a normal random variable with mean and standard deviation equal to those of nests censused in the field, as was the density of nests within each meter-interval (ten nests per meter horizontally) (Riechert & Jones unpublished data). Initially, each nest contained one adult female and juveniles of one instar, where the composition of nests was assigned in a way that resulted in the population being comprised of the same proportion of each instar as natural populations censused in the field.

Variation in aggression

The assumptions of the model with regard to genetic variation and heritability in *A. studiosus* are 1) that all individuals are female and 2) that the phenotype of a juvenile is identical to that of its mother. It is clear that these assumptions are unrealistic, but I believe they are sufficient for the following reasons, respectively: 1) males are abundant, drift among nests, and contribute virtually nothing to their progeny or mates besides sperm, and 2) because the phenotypic significance of males is not well-understood, any attempt to incorporate their genetic contribution to offspring into the model would be nothing more than a guess (reviewed in Riechert & Roeloffs 1993).

Because the initial conditions of the model call for a population of single-female nests, I assume that the majority of females are aggressive and maintain a solitary nest. However, there must be some non-aggressive individuals for the possibility of cooperation to exist. To achieve a phenotypic distribution with mostly aggressive but some non-aggressive individuals, I modeled the initial phenotypic distribution as a normal distribution with a range of values from 0 to 1 (non-aggressive to aggressive). The parameters μ and σ of the normal distribution cannot be informed by existing data, so I chose values that gave the desired distribution of many aggressive and a few non-aggressive individuals.

Maturation and dispersal

Individuals advance to the next instar after a pre-determined number of days. At maturity, these newly-matured females disperse from the parental nest. The direction in which they disperse is random, but the dispersal distance is proportional to each individual's phenotypic aggression score. This feature of the model is a reflection of the empirical result that newly-matured females in populations with a high frequency of multiple-female nests disperse shorter

distances from their parental nests than do individuals from populations in which single-female nests predominate (Riechert & Jones unpublished data). Once a female disperses away from her parental nest, she starts a new nest and achieves a brooding state (egg clutch production).

Interfemale conflict

In each time step the results are checked to see if any two nests overlap, and if so a territorial dispute is simulated between females from the two nests to determine how the matter would be resolved. Each female is placed into one of three categories based on its phenotypic aggression score. A female whose score is less than a threshold parameter for cooperation is considered cooperative, one whose score is greater than a threshold parameter for fighting is considered confrontational, and one whose score fell in between those is considered tolerant. When a confrontational female is involved, the individual with the lower phenotypic aggression score perishes. In the event that one female is tolerant and the other female is either tolerant or cooperative, each ignores the presence of the other. Finally, when both females are cooperative, their nests coalesce and a multiple-female colony emerges.

Predation

Predation on nests is modeled as a two-step process. First, a predator visits a nest on a given night with a probability equal to the proportion of censused nests that were found to contain nocturnal hunting spiders: one of two spider groups that have a significant predation effect on the host (Perkins et al. ms). If no predator visits a nest on a given night, then no mortalities occur in that time step. If a predator does visit a nest, the number of individuals of instar i that are preyed upon is represented by the discrete random variable X_i , where X_i is independent for $i \in \{1, \dots, 5\}$.

Nest predation experiments (Perkins et al. ms) revealed that when nest predators are introduced to a nest, they most often take no prey and very rarely prey on more than a few individuals. The probability distribution that best fits data from nest predation experiments is a Poisson distribution. Consequently, the random variable X_i was simulated by the Matlab function `RANDOM('Poisson')` with the constraint that the number of individuals taken during any predator visit could not exceed the number of spiders in the nest. The parameter λ_i , which is also equal to the expected number of individuals from the i^{th} instar that are preyed upon, is modeled as a proportion of the total number of individuals from that instar in the nest. However, to account for increased nest defense from multiple-female associations, λ_i is inversely proportional to the number of adult females in the nest. It is also inversely proportional to the number of individuals of like instar in the nest, as a greater number of individuals is assumed to afford the nest greater defense against predators. The probability that adult females are preyed upon in the simulation is equal to the frequency that females were preyed upon in nest predation trials (Perkins et al. ms) and varies with context: whether the female is alone, with juveniles, brooding, or in cooperation with other females.

Natural mortality

Because *A. studiosus* populations are regulated by more than predation by other spiders, I also incorporated the effects of natural mortality into the model. This includes mortality caused by non-spider predators, diseases and parasites, harsh climatic conditions, and other potential risks. Because the dynamics of these factors are assumed to be irrelevant to the question at hand, I chose not to model them explicitly. Instead, the number of individuals lost to natural mortality at each time step is simulated as a Poisson random variable. Similar to predation, I chose to model natural mortality as a Poisson random variable because at any given time step one would

assume that few or no individuals are lost in this way. The parameter λ_i is again modeled as a proportion of the number of individuals of instar i in the nest.

The specific values that should be assigned to λ_i are unclear however, as no data concerning rates of natural mortality are currently available. To address this shortcoming, I first considered the fact that all other processes and parameters in the model are informed by empirical data and should therefore already be naturally calibrated to this system. I then assumed that the natural population from which these data were collected was unlikely to be in the midst of any drastic change in its size or attributes. To find the final piece of this parameterization puzzle, I tested a number of possible parameter values for the rate of natural mortality and chose the value that resulted in the least change in population size from the initial conditions after 100 time steps. With natural mortality as somewhat of a background effect, I was then free to manipulate other parameters for the purposes of hypothesis testing.

HYPOTHESIS TESTING

Although the primary goal of this paper is to articulate the motivation for and development of an individual-based model for *A. studiosus* populations, I also wish to demonstrate the hypothesis-testing potential of this approach. This model is a powerful tool that can be used to ask a number of questions, but I chose to first address the influence that predation intensity and altricial period have on populations of *A. studiosus*. That is, what type of social structure (i.e., single- or multiple-female nests) best enables *A. studiosus* populations to persist when 1) predation occurs more frequently and 2) dispersal is delayed by a lengthened altricial period? To achieve populations with these two different social structures, I manipulated the mean phenotypic aggression scores at the onset of each simulation such that predominantly solitary

populations had a mean phenotypic aggression score of around 0.92 (where the threshold score for interfemale conflicts is 0.75) and predominantly cooperative populations had a mean phenotypic aggression score of around 0.08 (where the threshold score for nest coalescence is 0.25).

Each type of population was subjected to increased predation, which was simulated by increasing the probability that a predator visits a nest in a given time step. To increase mortality via predation I could have manipulated either the probability that a predator visits a nest or the expected number of individuals taken from the nest once the predator visits. Because I am interested in the consequences of a potentially larger predator population on *A. studiosus*, I chose not to manipulate the latter variable because the number of individuals taken from the nest is a reflection of the social composition of the nest and the behavioral interactions that occur between predator and prey, which are unchanged by the frequency of predator visits. In this study I doubled the predator visitation frequency observed in natural populations, although any amount of increase could have been chosen. Juvenile dispersal was delayed by increasing the number of time steps required before a juvenile could progress from one instar to the next. Specifically, I lengthened the altricial period of each juvenile instar by 50% and also lengthened the gestation and brooding periods of females by 12.5% each.

Because there were two manipulations with respect to each of the three variables of interest (i.e., social structure, predation, and altricial period), experimentation on these simulated populations consisted of eight (2^3) different treatments. Each treatment was replicated twenty times on populations occurring in a 4-by-10 m landscape over a period of 200 time steps. The level of replication, population size, and simulation duration were chosen in this manner because of computational limitations. Extensions of this study may feature higher replication (although as

few as five replicates have been used in other IBMs (see Railsback and Harvey 2002)), a larger landscape (possibly 4-by-500 m: the size of transects in field studies of *A. studiosus* (Jones et al. ms)), and a greater number of time steps so that the effects of selective forces like predation and delayed dispersal may be fully realized.

RESULTS

The negative impact of predation on the number of adult females was significant for phenotypically aggressive populations (ANOVA, $F = 70.85$, $P < 0.0001$) (Table 1). Lengthening the altricial period also had a significantly negative impact on the number of adult females in phenotypically aggressive populations (ANOVA, $F = 122.10$, $P < 0.0001$). The interaction of predation and altricial period length also had a significantly negative impact on adult females in these populations (ANOVA, $F = 96.47$, $P < 0.0001$). Similar effects of predation and altricial period length were observed for the number of juveniles of each instar (Table 1).

The negative impact of predation on the number of adult females was significant for phenotypically non-aggressive populations (ANOVA, $F = 31.24$, $P < 0.0001$) (Table 2). Lengthening the altricial period also had a significantly negative impact on the number of adult females in phenotypically non-aggressive populations (ANOVA, $F = 5.32$, $P < 0.025$). The interaction of predation and altricial period length did not have a significant impact on adult females in these populations (ANOVA, $F = 0.59$, $P < 0.45$). Similar effects of predation and altricial period length were observed for the number of juveniles of each instar (Table 2).

Regardless of predation intensity, the number of adult females in phenotypically non-aggressive populations was significantly smaller than that in phenotypically aggressive populations when the length of the altricial period was normal (t -test, $t > 4.9$, $P < 0.0001$).

However, when the altricial period was lengthened, the numbers of adult females in phenotypically aggressive and non-aggressive populations were statistically indistinguishable (t -test, $t < 0.75$, $P > 0.48$).

For populations in which multiple-female nests were observed, increased predation had a negative impact on the proportion of nests that contained multiple females (ANOVA, $F = 30.23$, $P < 0.0001$) (Table 2). Similarly, populations with longer altricial periods also had a significantly smaller proportion of nests that contained multiple females (ANOVA, $F = 4.59$, $P < 0.04$). The interaction of these factors had no effect on the proportion of nests containing multiple females (ANOVA, $F = 0.118$, $P < 0.75$) (Table 2).

DISCUSSION

As one might expect, increasing predator visitation frequency decreased *A. studiosus* population sizes over time. This effect was observed on both aggressive and non-aggressive populations and on populations subject to both normal and lengthened altricial periods. Although both types of populations suffered significant losses to increased predation, phenotypically non-aggressive populations suffered proportionally fewer losses than did phenotypically aggressive populations (44% versus 58%, respectively). This subtle disparity is likely a consequence of the increased defense that multiple-female colonies were assumed to have over single-female nests. This result is not enough to conclude that non-aggressive populations have a clear advantage over their aggressive counterparts, but it does agree with the hypothesis that non-aggressive populations suffer proportionally fewer losses from predators and therefore might be selected for under certain levels of predation.

Delayed dispersal also had a negative impact on all types of simulated populations. However, the relationship between the numbers of adult females in phenotypically aggressive and non-aggressive populations differed with altricial period length. When the length of the altricial period was normal, populations comprised of single-female nests were larger than those comprised of multiple-female nests. When these populations were subjected to a lengthened altricial period, the number of females in each type of population was about the same. Much like increased predation, a longer altricial period may not give multiple-female nests an advantage, but it does appear to level the playing field for these two different social strategies. With an even longer altricial period, non-aggressive populations may actually have an advantage over aggressive populations (or at least enough of an advantage for multiple-female nests to persist and be selected for over time).

An unexpected result of these simulations was that the proportion of multiple-female nests in non-aggressive populations was influenced by predation and altricial period. In particular, increased predation and a longer altricial period resulted in proportionately fewer multiple-female nests. It is interesting to note that a negative influence of these factors is also observed on the total number of nests and the number of adult females in the population. If these patterns are related, it may be that a smaller population size results in fewer opportunities for nests to coalesce and therefore a smaller proportion of multiple-female nests. This may explain why single-female nests are still observed in abundance even when ecological conditions favor cooperation (e.g., only 17% of females in east Tennessee populations occur in multiple-female nests).

The results presented in this paper serve a number of purposes. First, the differential responses of aggressive and non-aggressive populations to changes in predation and altricial

period generally agree with hypotheses from previous work. In addition, they show the potential to provide further insight into those hypotheses, subject to improved calibration and testing of a greater expanse of parameter space. Second, the fact that these results generally agree with biologically-informed predictions serves to validate the model as a realistic tool for simulating experimental manipulations on *A. studiosus* populations. Finally, the model also produced the unexpected result that predation and altricial period influence the proportion of multiple-female nests in a colony. This finding is particularly exciting, as it underscores the motivation for individual-based modeling and simulations in general: to uncover patterns and processes that might otherwise not be revealed in field or laboratory studies.

Future uses of this model include exploring the conditions under which cooperation is favorable by tracking the reproductive success of individuals exhibiting different social strategies. If initiated with a phenotypic aggression distribution that covers a broad range of values, the model could also be used to explore how selection for cooperative behavior might occur in a population of predominantly single-female nests. Such an investigation could provide valuable insight into the evolution of cooperative behavior in *A. studiosus* and other species.

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TABLES

Table 1. Mean values of summary variables after the simulation was run on a population of phenotypically aggressive *A. studiosus* for 200 time steps ($n = 20$).

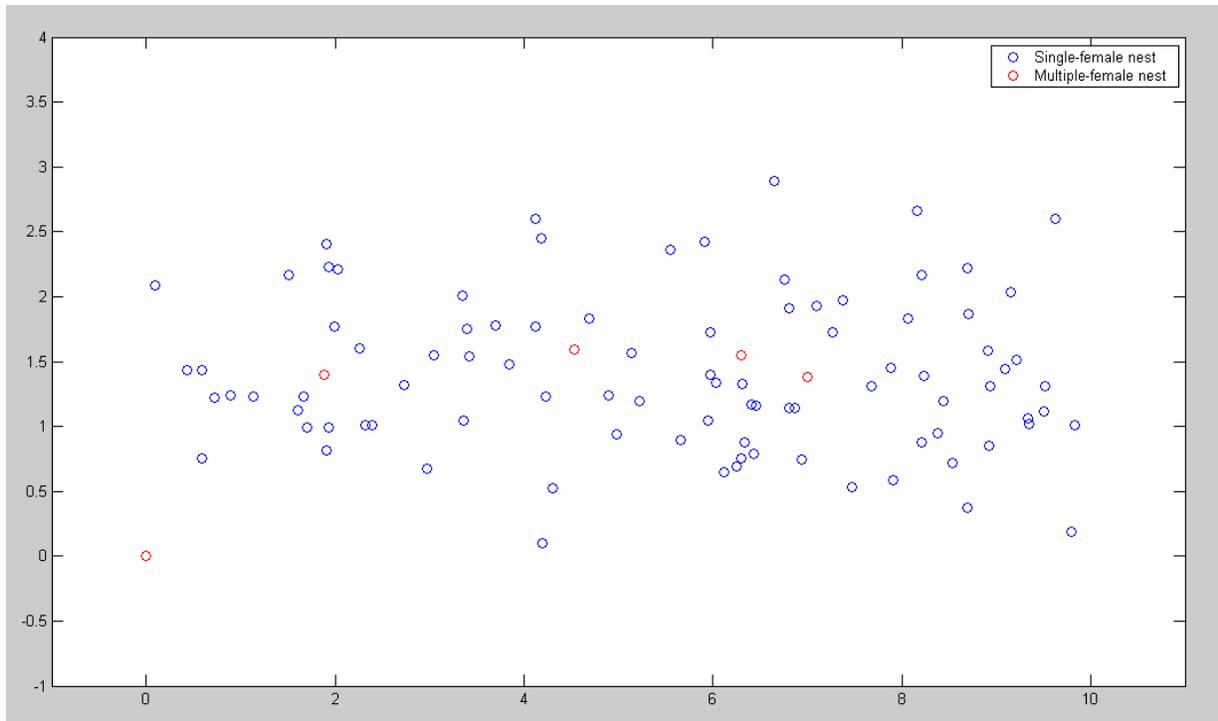
Predation	Normal		High	
	Normal	Long	Normal	Long
Altricial period				
Single-female nests	57.9	18.6	25.0	6.3
Multiple-female nests	0	0	0	0
Proportion females in multiple-female nests	0	0	0	0
Females	51.4	15.4	21.7	4.5
1 st instar	107.4	18.5	44.1	7.1
2 nd instar	69.3	16.6	30.1	6.3
3 rd instar	29.6	8.4	11.0	8.4
4 th instar	20.8	2.8	7.0	1.5
5 th instar	13.5	3.0	5.6	0.7
Eggcases	10.3	4.1	5.5	1.2

Table 2. Mean values of summary variables after the simulation was run on a population of phenotypically non-aggressive *A. studiosus* for 200 time steps ($n = 20$).

Predation	Normal		High	
	Normal	Long	Normal	Long
Altricial period				
Single-female nests	9.7	9.1	8.8	4.6
Multiple-female nests	4.0	3.7	1.5	0.8
Proportion females in multiple-female nests	0.70	0.56	0.36	0.27
Females	18.5	15.9	10.4	5.2
1 st instar	24.8	4.6	25.4	1.8
2 nd instar	18.6	7.6	17.4	2.7
3 rd instar	1.4	7.0	9.7	3.0
4 th instar	7.3	3.3	10.4	1.3
5 th instar	5.3	1.8	3.4	0.7
Eggcases	5.4	3.0	4.3	1.6

FIGURES

Figure 1. Visualization of the spatial distribution of nests during a simulation.



APPENDIX

The code I used to run simulations in Matlab is presented on the following pages.