Spatio-Temporal Analysis of Foraging Behaviors of *Anelosimus studiosus* Utilizing Mathematical Modeling of Multiple Spider Interaction on a Cooperative Web

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Abstract

In this paper, we develop a model for predation movements of a subsocial spider species, *Anelosimus studiosus*. We expand on a previous model to include multiple spider interaction on the web as well as a latency period during predation. We then use the model to test different spatial configurations to determine the optimal spacing of spiders within a colony for successful capture during predation. The model simulations indicate that spiders uniformly spacing out along the edge of the web results in the most successful predation strategy. This is similar to the behavior observed by Ross [25] in which it was determined to be statistically significant that during certain times of the day, spiders were positioned along the edge more than expected under complete spatial randomness.

Keywords: Mathematical Modeling, Stochastic Differential Equation, Multiple Species Interaction, *Anelosimus studiosus*, Foraging Behavior

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Preprint submitted to Journal of Theoretical Biology

August 9, 2016

1. Introduction

Hunting cooperatively can benefit predators both by increasing search efficiency (local enhancement) and in the collective ability to subdue prey [6]. Improving search efficiency is particularly important when resources are scarce and patchily distributed, but only promotes cooperative hunting when resources, once found, are sufficient to feed the group [28, 29]. Some examples include subterranean mole rats searching for large but scarce tubers [10], and vultures searching for carcasses on the savanah [27]. Once prey is located, cooperative hunting allows groups to more effectively chase down and subdue larger prey [17], well known in social animals such as lions [26] and wolves [15]. The examples above are from neurologically complex vertebrate animals which have evolved sophisticated communication and social organization allowing for coordination among group members in searching and subduing prey. In this study we explore how neurologically simpler animals without well-developed communication and coordination mechanisms might also take advantage of cooperative hunting.

Sociality in spiders occurs in only a few dozen of over 45,000 spider species [8], but it has evolved multiple times in mostly tropical habitats, including multiple times within the genus *Anelosimus* [1]. Social spiders build communal webs in which they hunt cooperatively and communally care for broods [14]. Similar to cooperatively hunting mammals, social spiders are able to attack in groups, subduing larger prey for their size than can solitary spiders [30]. Social spiders also maintain larger webs potentially intercepting more prey [23]. In this study we specifically test how different spatial distributions of spiders in a communal web affect the likelihood of the spiders being able to subdue intercepted prey before they escape.

A. studiosus is a spider that varies in its level of sociality among populations across its range. Most populations are subsocial with colonies consisting of a single mother and her offspring' however toward the northern edge of their range, there are social colonies of multiple adult females cooperating in prey capture, web maintenance, and brood care [11]. These spiders are cob-web weavers in which the web consist of knockdown threads, a capture sheet and a retreat. The knockdown threads cause the flight path of the prey to be disrupted, causing them to fall onto the capture sheet. Unlike orb weavers, the capture sheet is not sticky; therefore, if the prey can reach the edge of

1 the web, they can escape. In a paper by Ross [25] (which is summarized in
 2 Section 7), experimental data indicated that spiders within these types of
 3 colonies changed their positioning throughout the day; they were clustered
 4 at certain times while they were spread out and closer to the edges of the web
 5 at other times of the day. The hypothesis, first investigated by Joyner et. al.
 6 [2], was that spiders must stay close to the retreat when the threat of predat-
 7 ors is high; however, they spread out to optimize prey capture during other
 8 parts of the day. The model in [2] was a more simplistic model for predation
 9 in which it was assumed that spiders acted immediately upon detection of
 10 a prey in the web and moved in a similar manner to each other with no
 11 interaction between the spiders of the web. Under these assumptions, they
 12 concluded that the “model predictions generally support the hypothesis that
 13 these spiders can improve their communal prey capture success employing
 14 regular or random distributions, thus increasing their collective foraging area.
 15 The model also predicted that if the spiders position themselves around the
 16 perimeter of the web they are more successful at capturing prey” [2].

17 The original model was modified in the paper by Quijano et. al. [22] to
 18 more accurately include the differences seen in spiders during prey capture.
 19 They developed an aggregate model which incorporated variation in spider
 20 movement. With the modified model, one can now simulate the differences
 21 seen among spiders experimentally. However, since *A. studiosus* is a subsocial
 22 spider species, the spiders work together in foraging and web maintenance.
 23 In this case, we hypothesize that the movements of a single spider should be
 24 influenced by the other spiders in the web as well as the prey. Moreover, ex-
 25 perimental data indicates that not all spiders immediately act when a prey
 26 lands in the web; a latency period is observed. This latency period could
 27 affect the success of prey capture. This paper focuses on the development
 28 and implementation of an extended aggregate stochastic model which takes
 29 into account the interaction of multiple spiders during prey capture and the
 30 incorporation of a latency period. We then use the model under different
 31 initial spatial configurations and under different levels of influence from the
 32 other spiders in the web to determine their effect on the probability of suc-
 33 cessful foraging. In Sections 2 and 3, we summarize the mathematical model
 34 of a single spider and prey during predation. In Section 4, we develop the
 35 methods used to incorporate the influence of other spiders in the web during
 36 prey capture. Section 5 outlines the various spatial configurations used for
 37 simulation purposes. The results of the simulation studies for each of the
 38 configurations for a differing number of spider colonies is given in Section

6. In Section 7, we summarize the experimental results from [25] describing the spatial positioning of *Anelosimus studiosus* across the day and age of development. We given some concluding remarks in Section 8.

2. Mathematical Model of Single Foraging Spider

The predation behaviors of the subsocial spider *Anelosimus studiosus* has been modeled by Joyner et. al. [2] and Quijano et. al. [22] using stochastic differential equations and computational algorithms. In [2], the trajectory of the spider is determined by

$$d\mathbf{r}(t) = \mu\{\mathbf{r}(t), t\} dt + \Sigma\{\mathbf{r}(t), t\} d\mathbf{W}(t) \quad (1)$$

where $\mathbf{r}(t) = [X_s(t), Y_s(t)]'$ represents the location of the spider at time t , dt is an incremental change in time, μ is the directional component, Σ is a diffusion parameter, and $\mathbf{W}$ is assumed to be a brownian process [2]. The diffusion parameter is given by

$$\Sigma\{\mathbf{r}(t), t\} = \begin{bmatrix} \sigma_x & 0 \\ 0 & \sigma_y \end{bmatrix}$$

where it is assumed $\sigma_x = \sigma_y = \sigma$. Furthermore, the drift parameter is specified by

$$\mu\{\mathbf{r}(t), t\} = v_s \begin{bmatrix} \cos(\theta_o(t_i) + \epsilon(t, d_i)) \\ \sin(\theta_o(t_i) + \epsilon(t, d_i)) \end{bmatrix}$$

where v_s is the spider's velocity, $\theta_o(t_i)$ is the optimal direction, i.e., the direction the spider would go if the spider went directly to the prey, and $\epsilon(t, d_i)$ gives the error in direction. By substituting the above terms into Equation (1), the stochastic differential equation is given by

$$\begin{bmatrix} dX_s(t) \\ dY_s(t) \end{bmatrix} = v_s \begin{bmatrix} \cos(\theta_o(t_i) + \epsilon(t, d_i)) \\ \sin(\theta_o(t_i) + \epsilon(t, d_i)) \end{bmatrix} dt + \begin{bmatrix} \sigma & 0 \\ 0 & \sigma \end{bmatrix} d\mathbf{W}(t). \quad (2)$$

The error in direction ϵ is drawn from a normal distribution [22] with mean

$$e(d) = \beta_3 d^3 + \beta_2 d^2 + \beta_1 d + \beta_0 \quad (3)$$

and standard deviation q_1 for distances $8 \text{ cm} \leq d \leq 11 \text{ cm}$ and q_2 for $d < 8 \text{ cm}$. We note that in the formula for $e(d)$, β_0 , β_1 , β_2 , and β_3 are constants estimated in [22] using experimental data and d is the distance between the

1 spider and prey. At distances greater than 12 cm, the error function is set
2 equal to one radian to prevent the error from increasing indefinitely for large
3 distances which could cause the simulated spider to never capture the prey.

4 Pauses and varying velocities are included in the model using an algorithm
5 developed by Quijano et. al. [22] shown in Figure 1. The algorithm has two
6 main loops, the pause loop (when $v_s = 0$) and the run loop (when $v_s > 0$).
7 In the algorithm, D_p and D_r denote the durations of the pause and run
8 respectively, and T_p and T_r are the timers for the pause and run. We assume
9 the duration of the pause is drawn from an exponential distribution with
10 mean q_3 , the velocity varies according to a uniform distribution with mean
11 q_4 , and the duration of the run follows a truncated normal distribution with
12 mean q_5 and degree of variance q_6 . Justifications for the chosen distributions
13 can be found in [22] where a linear relationship was also established between
14 q_1 and q_2 ,

$$q_2 = \alpha_0 + \alpha_1 q_1, \quad (4)$$

16 and an exponential relationship was established between q_5 and q_6 ,

$$q_6 = \gamma e^{\lambda q_5}. \quad (5)$$

18 A summary of parameter definitions can be found in Table 1.

Table 1: Summary of parameters.

Definition	Symbol
Mean error for long distances	q_1
Mean error for short distances	q_2
Mean duration of pause	q_3
Mean velocity	q_4
Mean duration of run	q_5
Degree of variance	q_6

19 Since a subsocial spider colony is typically composed of a mother and
20 her juveniles, it is necessary to consider the juvenile as well. We make a
21 few minor adjustments to the model in the case of a juvenile spider. Our
22 first assumption is that juveniles cannot run as fast as the adult mother;
23 therefore, if the spider is a juvenile, the mean velocity of the juvenile is
24 reduced to a quarter of the mother's mean velocity, i.e. $\frac{1}{4}q_4$. Furthermore,

Figure 1: The Stochastic Model Algorithm.

for an adult spider, it is assumed that if a spider is within a certain capture distance from the prey, it is not possible for the prey to escape and is therefore considered captured. We extend the capture criteria for multiple spiders depending on who falls within the capture distance. If the mother is within the capture distance, then the prey is considered captured regardless of how many juvenile are within the capture distance. If the mother is not within the capture distance, there must be at least three juveniles within the capture distance in order for the prey to be considered captured. Basically, it takes three or more juvenile spiders to take down a prey while an adult spider can take down a prey by itself [2]. In the next section, we consider the movement of the prey.

3. Mathematical Model of Prey

It is important to model the prey since it is the main trajectory point which the spiders need to locate. The movement of the prey has never been studied closely when being hunted by *A. studiosus*. Theoretically, the prey moves in different directions depending upon whether they are aware they are being hunted or not. Therefore, we consider two types of prey for the purpose

1 of simulating the predation movements of *A. studiosus*, namely perceptive
 2 and careless prey as done in [2]. Assuming, the movement of the prey is
 3 modeled similar to the spider, the stochastic differential equation for the
 4 prey movement is given by

$$5 \quad \begin{bmatrix} dX_p(t) \\ dY_p(t) \end{bmatrix} = v_p \begin{bmatrix} \cos(\theta_p(t_i)) \\ \sin(\theta_p(t_i)) \end{bmatrix} dt + \begin{bmatrix} \sigma & 0 \\ 0 & \sigma \end{bmatrix} d\mathbf{W}(t) \quad (6)$$

6 where v_p is the velocity of the prey, $\theta_p(t_i)$ is the angle of incidence at an update
 7 time t_i , and $\mathbf{W}$ is the assumed brownian process. The velocity of the prey
 8 is given by a fixed value, $v_p = 0.2557$ cm/s, and the diffusion component
 9 is given by $\sigma = 0.25$ [2]. The duration of time until the prey changes its
 10 direction is taken from an exponential distribution with mean of 5 seconds
 11 [2].

12 The perceptive prey is a type of prey that is aware that it is being hunted
 13 as soon as it lands on the web. It locates the nearest edge and walks accord-
 14 ingly to escape. Let $P(t) = [X_p(t) \ Y_p(t)]$ indicate the x and y coordinates of
 15 the prey at time t . Assume the web is square with length $\diamond$ and the bottom
 16 left corner is located at the point $(0,0)$. In assuming the prey walks to the
 17 closest edge, the prey will immediately walk either left to the point $(0, Y_p(t))$,
 18 straight to the point $(X_p(t), \diamond)$, right to the point $(\diamond, Y_p(t))$ or back to the
 19 point $(X_p(t), 0)$ (see Figure 2). Let $E(t)$ be a matrix whose rows $E_i(t)$ consist
 20 of the location of these adjacent points on the edge at time t , i.e.,

$$21 \quad E(t) = \begin{bmatrix} 0 & Y_p(t) \\ X_p(t) & \diamond \\ \diamond & Y_p(t) \\ X_p(t) & 0 \end{bmatrix}.$$

22 We want to calculate the distances from the prey to the four edges and take
 23 the minimum distance. Let l be a vector of distances from the adjacent edge
 24 points to the prey at time t with components given by

$$25 \quad l_i(t) = \| E_i(t) - P(t) \|$$

26 for rows $(i) = \{1, 2, 3, 4\}$. Let $e_m(t)$ be the row index such that $\min(l(t)) =$
 27 $l_{e_m}(t)$. Thus, $E_{e_m}(t)$ indicates the point towards which the prey will travel.
 28 We assume the mean direction is towards this point with error in the direction
 29 of variance 1. Therefore the angle of incidence of a perceptive prey at time

1 t is given by

$$2 \quad \theta_p(t_i) \sim \tan^{-1} \left(\frac{N(E_{em}(t), 1) - P(t)}{\| N(E_{em}(t), 1) - P(t) \|} \right) \quad (7)$$

3 where $N(a, b)$ represents the normal distribution with mean a and variance
4 b .

Figure 2: Perceptive Prey

5 The careless prey is a type of prey that is unaware that it is being hunted.
6 Assuming the careless prey can move everywhere with all of the direction are
7 equally likely, the angle of incidence of a careless prey is given by

$$8 \quad \theta_p(t_i) \sim U(0, 2\pi) \quad (8)$$

9 where $U(0, 2\pi)$ is a uniform distribution with upper and lower bounds of 0
10 and 2π .

11 4. Mathematical Modeling of Multiple Spiders' Interaction

12 Since a colony of subsocial spiders share the same web, the influence of
13 the surrounding objects could affect the direction of the spiders. In order to
14 model the interaction of the spiders on the web, we incorporate aspects of the
15 model developed in the paper by Heppner et. al. [9] which investigated the
16 movement of coordinated bird flocks flying towards their home nest. Using
17 similar terminology for the behavior of *A. studiosus* during predation as that
18 used for the coordinated bird flocks [9], for multiple spiders in the web, we
19 add two important aspects to the model:

- 1 • **Homing:** The spiders will travel towards the *perceived* location of the
2 prey (recall there is error in the spider's perceived location of the prey
3 and the prey's actual location). The perceived location of the prey will
4 be determined based on both the influence from the vibrations thought
5 to be that of the prey as well as the directional cues given from other
6 spiders in the web.
- 7 • **Interaction:** For a particular spider, the level of influence from the
8 other spiders in the web is based on the distances to the other spiders.

9 Recall that the directional component of Equation (2) has an angle of
10 incidence for spider $u \in \{1, 2, \dots, n\}$ is given by

$$11 \quad \quad \quad \iota_u = \theta_o(t_i)_u + \epsilon(t_i, d)_u \quad (9)$$

12 where ι_u is the angle of incidence influenced by the prey, $\theta_o(t_i)_u$ is the optimal
13 angle to the prey, and $\epsilon(t_i, d)_u$ is the error function (Eq. (3)). This angle
14 of incidence directs the spider to its perceived location of the prey. This is
15 where they sense the vibration from the prey. The spider does not know
16 exactly where the prey is initially, but the angle of incidence is where they
17 need to look for the prey. This is under the assumption that the prey has a
18 full level of influence without any influence from other spiders.

19 4.1. Perceived Location of Prey

20 Consider multiple spiders on the web and the spiders are moving. Since
21 the spiders detects the prey through vibrations, the success of finding the
22 prey depends on how much the prey produce vibrations along with the other
23 spiders vibrations. We assume that the angle of incidence is dependent on
24 the prey's level of influence. We define the prey's level of influence to be
25 $0 \leq \omega_p \leq 1$ where 0 is no influence and 1 is where there is full influence from
26 the prey. Note that if $\omega_p = 1$, then the spider will know exactly where to
27 search for the prey. If $\omega_p < 1$, then the range of search increases since the
28 level of influence is weaker. Suppose $\omega_p < 1$, then the spider has to search
29 for the prey at a range depending upon the prey's level of influence. This is
30 called the range of vibration localization. This is the range of where a spider
31 should look for the prey after they felt a vibration in an area. The range of
32 the angle of incidence is given by

$$33 \quad \quad \quad \iota_u \pm \pi(1 - \omega_p). \quad (10)$$

Figure 3: Range of localization.

Figure 3 shows an illustration of the range of localization where ι_u is the angle of incidence and the interval $(\iota_u - (1 - \omega_p), \iota_u + (1 - \omega_p))$ is the range. The spider will search for the prey in all directions within the range of localization. Assuming all directions within the range are equally likely and $\omega_p < 1$, the angle of incidence for spider $u \in \{1, 2, \dots, n\}$ is taken from a uniform distribution from $\iota_u - (1 - \omega_p)$ to $\iota_u + (1 - \omega_p)$ which is given by

$$\phi_u \sim U(\iota_u - (1 - \omega_p), \iota_u + (1 - \omega_p)). \quad (11)$$

If $\omega_p = 1$, then the range is $(\iota_u - 0, \iota_u + 0)$. If $\omega_p = 0$, then the range is $(\iota_u - \pi, \iota_u + \pi)$ which is the full unit circle from 0 to 2π . Let S be an $n \times 2$ vector containing the location of spider $u \in \{1, 2, \dots, n\}$. The matrix S is given by

$$S = \begin{bmatrix} X_1 & Y_1 \\ X_2 & Y_2 \\ \vdots & \vdots \\ X_n & Y_n \end{bmatrix}.$$

Then the location perceived for the prey by spider u is given by

$$\rho_u = S_u + d_u[\sin(\phi_u) \cos(\phi_u)] \quad (12)$$

1 where d_u is the distance from spider u to prey and $S_u = [X_u(t) \ Y_u(t)]_u$ is the
2 current location of spider u at time t .

3 Now we consider the effect of other spiders on the web as well. Each
4 object on the web contributes to the final direction of a spider. Assuming
5 the prey and the spiders are the only objects on the web, each object has a
6 level of influence based upon the amount of movement detected. We assume
7 the spiders know, at some level, the difference between the movement of
8 the prey versus the movement of the other spiders on the web; therefore
9 we consider these levels of influence differently. Above, we discussed the
10 effect of the influence of the prey. For multiple spiders, we assume the level
11 of influence of other spiders on the web is directly related to the distance
12 between the spiders.

13 Let n be the number of spiders on a web. Let $S_u = [X_s \ Y_s]_u$ be the
14 position of the spider at time t for spider $u \in \{1, 2, \dots, n\}$. We leave out the
15 term t since it is implied in the equation. Let δ be an $n \times n$ distance matrix
16 at time (t) given by

$$17 \quad \delta = \begin{bmatrix} \delta_{11} & \delta_{12} & \cdots & \delta_{1n} \\ \delta_{21} & \delta_{22} & \cdots & \delta_{2n} \\ \vdots & & \ddots & \vdots \\ \delta_{n1} & \delta_{n2} & \cdots & \delta_{nn} \end{bmatrix} \quad (13)$$

18 where

$$19 \quad \delta_{uv} = \| S_u - S_v \| \quad (14)$$

20 is the distances from spider $u \in \{1, 2, \dots, n\}$ to spider $v \in \{1, 2, \dots, n\}$. If $u = v$,
21 then the diagonals should be equal to zero since a spider is zero distance to
22 itself.

23 Now suppose there are 2 spiders S_1 and S_2 with a prey P , see Figure 4.,
24 The angle of incidence ϕ_1 and ϕ_2 points towards the perceived locations, ρ_1
25 and ρ_2 , of the prey. We define ϕ_{12} as the angle of incidence from spider S_1
26 to the perceived location of the prey according to spider S_2 . Similarly, ϕ_{21}
27 is the angle of incidence from spider S_2 to the perceived location of the prey
28 according to spider S_1 . Recall the perceived location of each spider is given
29 by Eq. (12). Then the angle of incidence of a spider based on the perceived
30 locations of the other spiders, is calculated by

$$31 \quad \phi_{uv} = \tan^{-1} \left(\frac{\rho_v - S_u}{\| \rho_v - S_u \|} \right). \quad (15)$$

1 We let Φ be an $n \times n$ matrix containing the angles of incidence based on the
 2 perceived locations of the other spiders,

$$3 \quad \Phi = \begin{bmatrix} \phi_{11} & \phi_{12} & \cdots & \phi_{1n} \\ \phi_{21} & \phi_{22} & \cdots & \phi_{2n} \\ \vdots & \vdots & \ddots & \vdots \\ \phi_{n1} & \phi_{n2} & \cdots & \phi_{nn} \end{bmatrix}.$$

4 The diagonal of Φ is equal to ϕ_u given in Equation (11) since this is the angle
 5 of incidence of spider u to the prey. The other entries of ϕ indicate the angle
 6 of incidence from spider u to the perceived location of the prey according to
 7 spider v .

Figure 4: Location Perception Illustration.

8 4.2. Latency Period

9 Before we implement the extended model for multiple spiders into the
 10 SDE, we must include the latency period of each spider. The latency period
 11 is the amount of time the spider waits until it decides to pursue the prey
 12 after the prey lands on the web. Once a spider is moving, the other spiders
 13 will start to realize that it is time to move. Thus, the latency period is
 14 influenced by how many spiders are moving. The latency period of each

1 spider is different. Using data given in [22], it was determined that the
 2 latency period across multiple spiders satisfies an exponential distribution
 3 with mean 16.81s. Initially, there are no moving spiders. The extended
 4 model for multiple spiders is used only if more than one spider is moving.

5 Let M be a 'moving vector' of length n . The moving vector is a binary
 6 indicator for each spider indicating whether the spider is moving "1" or it is
 7 still at rest "0". The initial moving vector where all spiders are initially at
 8 rest is given by

$$9 \quad M_o = \begin{bmatrix} 0 \\ 0 \\ \vdots \\ 0 \end{bmatrix}.$$

10 The final moving vector where all of the spiders are moving is

$$11 \quad M_f = \begin{bmatrix} 1 \\ 1 \\ \vdots \\ 1 \end{bmatrix}.$$

12 We order the spiders so spider 1 is the first to start moving, spider 2 is the
 13 second, etc. We assume the first spider will wait the entire latency period
 14 before moving; however, we assume that after the first spider has started
 15 moving, the wait time for the second spider to initially move will be reduced
 16 by a factor of $\frac{1}{n}$ where n is the number of spiders in the web. Therefore, if the
 17 latency period for spiders 1 and 2 (as initially drawn from the exponential
 18 distribution) are initially given by $\tau_1^{(0)}$ and $\tau_2^{(0)}$ respectively, then the latency
 19 period remaining before spider 2 moves is given by

$$20 \quad \tau_2^{(1)} = \left(1 - \frac{1}{n}\right) \left(\tau_2^{(0)} - \tau_1^{(0)}\right)$$

21 (the time remaining in second spider's latency period is reduced by $\frac{1}{n}$). Simi-
 22 larly, the latency period for all the remaining spiders $u \in \{2, \dots, n\}$ is reduced
 23 according to

$$24 \quad \tau_u^{(1)} = \left(1 - \frac{1}{n}\right) \left(\tau_u^{(0)} - \tau_1^{(0)}\right).$$

25 However, once spider 2 moves, we assume there is a further reduction in the
 26 remaining latency time for all the spiders (since more spiders are moving).

1 The latency period is now reduced by a factor of $\frac{2}{n}$. Therefore, we have for
 2 $u \in \{3, \dots, n\}$,

$$3 \quad \tau_u^{(2)} = \left(1 - \frac{2}{n}\right) (\tau_u^{(1)} - \tau_2^{(1)})$$

4 where $\tau_u^{(1)} - \tau_2^{(1)}$ is the amount of the latency period already passed. In
 5 general, if r spiders are moving, the updated latency period remaining for
 6 spiders $\{r+1, \dots, n\}$ is given by

$$7 \quad \tau_u^{(r)} = \left(1 - \frac{r}{n}\right) (\tau_u^{(r-1)} - \tau_r^{(r-1)}).$$

8 4.3. Level of Influence

9 Finally, we need to incorporate the level of influence each moving spider in
 10 the web has on the other moving spiders in the web. The level of influence is
 11 a measure of how much an object influences the movement and the direction
 12 of the spider. We again emphasize that *when* a spider moves (latency period)
 13 and the *direction* in which it moves (perceived location) are *both* influenced
 14 by other spiders in the web according to the level of influence neighbors have
 15 on its movement. Assuming the level of influence of the spiders depends on
 16 the distances between them, if two spiders are close to each other then those
 17 spiders would have more influence on each other's movement than the spiders
 18 located at longer distances. Let Ω be an $n \times n$ matrix at time (t) ,

$$19 \quad \Omega = \begin{bmatrix} \omega_{11} & \omega_{12} & \cdots & \omega_{1n} \\ \omega_{21} & \omega_{22} & \cdots & \omega_{2n} \\ \vdots & \vdots & \ddots & \vdots \\ \omega_{n1} & \omega_{n2} & \cdots & \omega_{nn} \end{bmatrix}, \quad (16)$$

20 where the entry ω_{uv} indicates the level of influence from spider $u \in \{1, 2, \dots, n\}$
 21 to spider $v \in \{1, 2, \dots, n\}$ and is given by

$$22 \quad \omega_{uv} = \begin{cases} \frac{1 - \omega_p}{\sum_{k=1, k \neq v}^n \left(\frac{\delta_{uv}}{\delta_{kv}}\right)^2} & u \neq v \\ \omega_p & u = v \end{cases} \quad (17)$$

23 where ω_p indicates the level of influence of the prey. We note that if $u = v$,
 24 the only influence is from the prey. When $u \neq v$, the term for ω_{uv} adds more

1 influence to spiders that are closer and less influence when other spiders are
2 further away; i.e. the weight of influence is inversely proportional to the
3 distance from the spider (the smaller the distance, the greater the influence).
4 To make sure the influence matrix is calculated correctly, the matrix ω should
5 have the property of

$$6 \quad \sum_{k=1}^n \omega_{kc} = 1$$

7 for columns $c \in \{1, 2, \dots, n\}$. The initial level of influence is

$$8 \quad \Omega(0) = \begin{bmatrix} 1 & 0 & \cdots & 0 \\ 0 & 1 & \cdots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \cdots & 1 \end{bmatrix},$$

9 the identity matrix. This is under the assumption no spiders are moving
10 initially. We make a note that in the simulations of our model, we assume
11 that all individual spiders have the same motivation to pursue detected prey.
12 There is much empirical evidence to suggest that this is not the case in *A.*
13 *studiosus* colonies, and that, in fact, individuals have distinct and consistent
14 ‘personalities’ of aggressiveness across contexts [21]. Furthermore, the com-
15 position of personalities in the foraging group are known to affect the overall
16 foraging success of the colonies [18, 19, 20]. Future modifications of our
17 model could incorporate a ‘personality parameter’ which effects the level of
18 influence to explore the interplay between personality, spacing, and foraging
19 success.

20 4.4. Implementation

21 Now that we have the perceived location, moving variable, and level of in-
22 fluence, we implement the extended model for multiple spiders into Equation
23 (2). Recall that Ω and Φ are the levels of influence and the angles of incidence
24 respectively. Let Φ^ω be the angles of incidence based on the corresponding
25 levels of influence. Thus,

$$26 \quad \Phi^\omega = \Omega \cdot \Phi$$

$$\begin{aligned}
\Phi^\omega &= \begin{bmatrix} * & \omega_{12} & \cdots & \omega_{1n} \\ \omega_{21} & * & \cdots & \omega_{2n} \\ \vdots & \vdots & \ddots & \vdots \\ \omega_{n1} & \omega_{n2} & \cdots & * \end{bmatrix} \cdot \begin{bmatrix} \phi_1 & \phi_{12} & \cdots & \phi_{1n} \\ \phi_{21} & \phi_2 & \cdots & \phi_{2n} \\ \vdots & \vdots & \ddots & \vdots \\ \phi_{n1} & \phi_{n2} & \cdots & \phi_n \end{bmatrix} \\
&= \begin{bmatrix} \phi_1 & \omega_{12}\phi_{12} & \cdots & \omega_{1n}\phi_{1n} \\ \omega_{21}\phi_{21} & \phi_2 & \cdots & \omega_{2n}\phi_{2n} \\ \vdots & \vdots & \ddots & \vdots \\ \omega_{n1}\phi_{n1} & \omega_{n2}\phi_{n2} & \cdots & \phi_n \end{bmatrix}
\end{aligned}$$

The diagonal entries of Φ^ω is forced to equal ϕ_u (Eq. (11)), since this angle of incidence is already accounted for in the range of localization based on the prey's level of influence.

Let's denote Θ_u as the final direction of travel for spider u . Assuming the angle of incidence ϕ_u is independent from the angles of incidence influenced by the other spiders, we take ϕ_u and add it to the sum of the angles of incidence influenced by the other spiders and divide this by the number of moving spiders. Thus,

$$\Theta_u = \phi_u + \frac{1}{r} \sum_{k=1, k \neq u}^n \Phi_{uk}^\omega \quad (18)$$

for columns $k \in \{1, 2, \dots, n\}$. Figure 5 shows the final direction in the case of the two spiders given in Figure 4. The thick black arrow and Θ_1 and Θ_2 indicates the direction and magnitude of the velocity for spider 1 and 2 respectively.

To complete our model incorporating multiple spider interaction, we replace the angle of incidence of Equation (2) by Equation (18). Thus, the extended stochastic differential equation for multiple spiders is given by

$$\begin{bmatrix} dX_u(t) \\ dY_u(t) \end{bmatrix} = v_u \begin{bmatrix} \cos(\phi_u + \frac{1}{r} \sum_{k=1, k \neq u}^n \Phi_{uk}^\omega) \\ \sin(\phi_u + \frac{1}{r} \sum_{k=1, k \neq u}^n \Phi_{uk}^\omega) \end{bmatrix} dt + \begin{bmatrix} \sigma_u & 0 \\ 0 & \sigma_u \end{bmatrix} d\mathbf{W}(t) \quad (19)$$

for spider $u \in \{1, 2, \dots, n\}$ and n is the number of spiders. To simplify,

$$\begin{bmatrix} dX_u(t) \\ dY_u(t) \end{bmatrix} = v_u \begin{bmatrix} \cos(\Theta_u) \\ \sin(\Theta_u) \end{bmatrix} dt + \begin{bmatrix} \sigma_u & 0 \\ 0 & \sigma_u \end{bmatrix} d\mathbf{W}(t).$$

If $r = 1$, then Equation (19) reduces to Equation (2). If $r > 1$, then the SDE that governs the predation movement for multiple spiders is Equation (19).

Figure 5: Final Direction Illustration. (see Figure 4)

1 Recall that the algorithm in Figure 1 is the algorithm for one spider. Since
2 we have a model that includes multiple spiders on the web, the algorithm is
3 extended. Figure 6 shows the extended algorithm where $\tau_u^{(r)}$ is added after
4 the starting position and Θ_u is added after the second updates.

5. Spatial Distributions of Spider Colony

6 The main purpose of modeling the predation movement of the *A. studio-*
7 *sus* is to determine if the spiders position themselves accordingly such that
8 they can catch the most prey and avoid potential predators. To determine
9 the optimal spatial distribution of the spiders in the web for prey capture,
10 we model and test different spatial distributions. We define the size of the
11 web to be a square with length $\diamond$ (as discussed in Section 3). We also need
12 a defining threshold of when the spider is considered near the edge. This is
13 denoted by $\hat{\diamond}$.

Figure 7: Random Spatial distribution ($n = 16$); Red dot (mother), Black dots (juveniles), and Blue dot (prey).

- 1 For a web size of $\diamond$, the initial location of spider $u \in \{1, 2, \dots, n\}$ for a edge
- 2 random spatial distribution is given by

$$S_u(0) = [X_u(0) \ Y_u(0)] \sim \bar{E}_{(U(1,4))} \quad (21)$$

- 4 where the subscript of $\bar{E}$ is the row of the matrix $\bar{E}$ taken from a uniform
- 5 distribution from 1 to 4. Figure 8 is an example.

Figure 8: Edge Random Spatial distribution ($n = 16$); Red dot (mother), Black dots (juveniles), and Blue dot (prey).

6 5.3. Clustered

- 7 In a clustered distribution, spiders are randomly placed close to each
- 8 other at a random reference point. Let R_c be the reference point taken from

1 a uniform distribution given by

$$2 \quad R_c = [R_x \ R_y]_c \sim [U(\hat{\diamond}, \diamond - \hat{\diamond}) \ U(\hat{\diamond}, \diamond - \hat{\diamond})].$$

3 For a web size of $\diamond$, the initial location of spider $u \in \{1, 2, \dots, n\}$ for a clustered
4 spatial distribution is given by

$$5 \quad S_u(0) = [X_u(0) \ Y_u(0)] \sim [N(R_x, \hat{\diamond}) \ N(R_y, \hat{\diamond})]_c \quad (22)$$

6 where N is the normal distribution with mean R_x and R_y for the xy location
7 with a standard deviation of $\hat{\diamond}$. If R_c is really close to the edge, this will cause
8 the normal distribution to pick a random point outside of the web. Thus, we
9 truncate the normal distribution if R_c is really close to the edge (i.e. 0 and
10 $\diamond$). Figure 9 is an example.

Figure 9: Clustered Spatial distribution ($n = 16$); Red dot (mother), Black dots (juveniles), and Blue dot (prey).

11 5.4. Edge Clustered

12 We define ‘Edge Clustered’ to be the clustered distribution in which the
13 reference point is on the edge of the web. First we randomly pick a point
14 from the edges similar to the *Edge Random*, and we pick a random point
15 from those 4 random points. This is given by

$$16 \quad R_{ec} = [R_x \ R_y]_{ec} \sim \bar{E}_{(U(1,4))}.$$

17 where the subscript of $\bar{E}$ is the row of the matrix $\bar{E}$ taken from a uniform
18 distribution from 1 to 4. For a web size of $\diamond$, the initial location of spider
19 $u \in \{1, 2, \dots, n\}$ for a edge clustered spatial distribution is given by

$$20 \quad S_u(0) = [X_u(0) \ Y_u(0)] \sim [N(R_x, \hat{\diamond}) \ N(R_y, \hat{\diamond})]_{ec} \quad (23)$$

1 where N is the normal distribution with mean R_x and R_y for the xy location
 2 with a standard deviation of $\hat{\diamond}$. Since the R_{ec} is at the edge, this will induce
 3 the normal distribution to pick a random point outside of the web. Thus, we
 4 truncate the normal distribution if R_{ec} is really close to the edge (i.e. 0 and
 5 $\diamond$). Figure 10 is an example.

Figure 10: Edge Clustered Spatial distribution ($n = 16$); Red dot (mother), Black dots (juveniles), and Blue dot (prey).

6 5.5. Uniform

7 In a uniform distribution, the spiders are located on the web in a grid-
 8 like pattern. Let $\aleph$ be the number of rows and columns of the grid given by
 9 $\aleph = \left\lceil \frac{n}{\sqrt{n}} \right\rceil$ for $n \in \{4, 9, 16, 25, \dots\}$. Let A and B be vectors of possible x and
 10 y values of each spider given by

$$11 \quad A_i = B_i = \frac{\diamond i}{\aleph + 1}, i \in \{1, \dots, \aleph\}.$$

12 The location of spider $u \in \{1, 2, \dots, n\}$ is given by

$$13 \quad S_u(0) = [X_u(0) \ Y_u(0)] = [A_i \ B_j] \quad (24)$$

14 for $i, j \in \{1, \dots, \aleph\}$. Figure 11 is an example.

15 5.6. Edge Uniform

16 ‘Edge Uniform’ spatial distribution is where the spiders are placed uni-
 17 formly along the edge. To place the n spiders on a $\diamond \times \diamond$ web, we take $d = P/n$

Figure 11: Uniform Spatial distribution ($n = 16$); Red dot (mother), Black dots (juveniles), and Blue dot (prey).

1 where P is the perimeter of the square, d is the distance between successive
2 spiders, $\diamond$ is the length of the sides, $\hat{\diamond}$ is the edge threshold, and n is the
3 number of spiders. Note that we want the spider in between the threshold.
4 So, the perimeter should have $P = \diamond - 2(\hat{\diamond}/2)$. Therefore, $d = \frac{\diamond - \hat{\diamond}}{n}$.

5 If we label the edges as s_1 (bottom edge), s_2 (right edge), s_3 (top edge),
6 and s_4 (left edge), then we place the first spider at the center of side 1. We
7 force the first spider to be at the center instead of placing it randomly on
8 side 1 to induce symmetric displacement of the spiders about a vertical line
9 at the center of the square. After the first spider is placed, we place the next
10 spider to the right at a distance of d . If the next spider has a distance $\hat{d} < d$
11 where $\hat{d}$ is the distance from the previous spider to the corner, then the next
12 spider goes on to the next side with a distance $d - \hat{d}$ from the corner. Thus,
13 the location of spider $u \in \{1, 2, \dots, n\}$ is given by

$$14 \quad X_u(0) = (X_u(0), Y_u(0)) = \begin{cases} (\diamond/2, \hat{\diamond}/2), & u = 1 \\ (\hat{\diamond}/2 + (d - \hat{d}), \hat{\diamond}/2), & \hat{d} < d, s_4 \rightarrow s_1 \\ (X_{u-1} + d, \hat{\diamond}/2), & s_1 \\ (\diamond - \hat{\diamond}/2, \hat{\diamond}/2 + (d - \hat{d})), & \hat{d} < d, s_1 \rightarrow s_2 \\ (\diamond - \hat{\diamond}/2, X_{u-1} + d), & s_2 \\ (\diamond - \hat{\diamond}/2 - (\diamond - \hat{\diamond}), \diamond - \hat{\diamond}/2), & \hat{d} < d, s_2 \rightarrow s_3 \\ (X_{u-1} - d, \diamond - \hat{\diamond}/2), & s_3 \\ (\hat{\diamond}/2, \diamond - \hat{\diamond}/2 - (\diamond - \hat{\diamond})), & \hat{d} < d, s_4 \rightarrow s_1 \\ (\hat{\diamond}/2, X_{u-1} - d), & s_4 \end{cases}$$

15 Since we started at the center of side 1, then the n th spider should be at a

1 distance of d to the left of the first spider.

Figure 12: Edge Uniform Spatial Distribution ($n = 16$)

2 5.7. Grouped

3 ‘Grouped’ is defined by the spiders being distributed in groups, where
 4 a group is defined as a certain number spiders who are close together. If a
 5 spider is by itself but separate to a group of spiders, then it is also considered
 6 a group of one spider. Let G be the number of groups given by

$$7 \quad G \sim U(\{2, 4\})$$

8 where $U(\{2, 4\})$ is a uniform distribution with sample space $\{2, 4\}$. We want
 9 to find G number of reference points for G groups. Let R_g be a matrix
 10 containing G reference points which is given by

$$11 \quad R_g = [R_x(0) \ R_y(0)]_g = [U(\hat{\diamond}, \diamond - \hat{\diamond}) \ U(\hat{\diamond}, \diamond - \hat{\diamond})]$$

12 for $g \in \{2, \dots, G\}$. Each group should be far enough from each other to be
 13 considered separate groups. Suppose we have G groups, then the sum of the
 14 number of spider is

$$15 \quad \sum_{g=1}^G \hat{s}_g = \hat{s}_1 + \hat{s}_2 + \dots + \hat{s}_g = n$$

16 where $\hat{s}_g$ is the number of spiders of group g . The total number of spiders is
 17 randomly distributed among G groups. This is given by

$$18 \quad \hat{s}_g = U\left(1, \left\lceil \frac{n}{g} \right\rceil\right).$$

1 Given R_g and $\hat{s}_g$, then the location of the spiders for each group is given by

$$2 \quad S_k(0) = [X_k(0) \ Y_k(0)] \sim [N(R_g, \hat{\diamond}) \ N(R_g, \hat{\diamond})] \quad (25)$$

3 where $k \in \{1, \dots, \hat{s}_g\}$. If R_g is really close to the edge, this will cause the
 4 normal distribution to pick a random point outside of the web. Thus, we
 5 truncate the normal distribution if R_g is really close to the edge (i.e. 0 and
 6 $\diamond$). Figure 13 is an example.

Figure 13: Grouped Spatial distribution ($n = 16$); Red dot (mother), Black dots (juveniles), and Blue dot (prey).

7 5.8. Edge Grouped

8 ‘Edge Grouped’ is where the spiders are distributed in groups along the
 9 edge. The method to randomly place the spider on the web in this kind of
 10 distribution is the same method as grouped, but we randomly pick reference
 11 points from the edges. First we randomly pick a point from the edges similar
 12 to the *Edge Random* and we pick a random point from those 4 random points.
 13 This is given by

$$14 \quad R_{eg} = [R_x \ R_y]_{eg} \sim \bar{E}_{(U(1,4))}.$$

15 where the subscript of $\bar{E}$ is the row of the matrix $\bar{E}$ taken from a uniform
 16 distribution from 1 to 4. Given R_g and $\hat{s}_g$ (see *Grouped* section), then the
 17 location of the spiders for each group is given by

$$18 \quad S_k(0) = [X_k(0) \ Y_k(0)] \sim [N(R_{eg}, \hat{\diamond}) \ N(R_{eg}, \hat{\diamond})] \quad (26)$$

19 where $k \in \{1, \dots, \hat{s}_g\}$. If R_{eg} is really close to the edge, this will cause the
 20 normal distribution to pick a random point outside of the web. Thus, we
 21 truncate the normal distribution if R_{eg} is really close to the edge (i.e. 0 and
 22 $\diamond$). Figure 14 is an example.

Figure 14: Edge Grouped Spatial distribution ($n = 16$); Red dot (mother), Black dots (juveniles), and Blue dot (prey).

6. Simulation Results

Using the spacial distributions from the previous section and the new model for multiple spiders, we want to determine the success rate for prey capture given a particular spatial distribution. For simulation purposes, we assume a square web with dimension $\diamond = 28$ and initial location of the prey chosen from a uniform distribution, i.e.

$$S_p(0) = [X_p(0) \ Y_p(0)] \sim [U(\hat{\diamond}, \diamond) \ U(\hat{\diamond}, \diamond)] \quad (27)$$

where U is the uniform distribution. We consider four different spider colonies consisting of 4, 9, 16, and 25 spiders. (These size colonies allow a complete grid for the uniform spatial distribution.) We consider both the perceptive and careless prey with varying levels of influence, $0 < \omega_p < 1$ incremented in steps of 0.1.

Given 4 different colony sizes, 7 spatial distributions, 2 prey phenotype, and 11 levels of influences, there are 616 combinations of these parameters. We perform 1000 simulations for each combination and record the proportion of wins (the spider captures the prey), losses (the prey reaches the edge of the web and escapes), and neither (the spiders cannot find the prey or have no motivation to pursue the prey after 2 minutes). As a note, the case in which the spider doesn't pursue the prey is also evidenced in the experimental lab; therefore, this result is consistent with experimental trials. In total, there are 616,000 simulations to perform. We only summarize the results in this section.

1 In Figures 15 - 22, there are two plots, one for the proportion of spider
 2 wins and one for the mean time required to capture the prey both as a
 3 function of the level of influence of the prey ω_p . In each plot, there are
 4 eight curves which denote four different colony sizes for each type of prey
 5 (perceptive versus careless). As one would expect, the proportion of spider
 6 wins increase as the level of influence of the prey gets closer to 1. Recall
 7 the level of influence ω_p determines how strongly the spiders sense the prey.
 8 The stronger the influence of prey, the more likely the spiders will find the
 9 prey and catch it regardless of prey type. Moreover, as ω_p approaches 1, the
 10 situation in which the prey doesn't locate the edge and the spider doesn't
 11 pursue the prey decreases to zero. When $\omega_p = 0$, spiders who won basically
 12 found and caught the prey by random chance. Similarly, in almost all cases,
 13 the chances of winning increases as the colony size increases, regardless of
 14 prey type.

15 We take a closer look at the edge random spatial distribution in Figure
 16 16. One question which is interesting to consider is how lucky the spiders
 17 can be in capturing the prey if they simply position themselves randomly at
 18 the edge but have no sense for where the prey is located ($\omega_p = 0$). Figure
 19 16(a) shows that there is a 30% chance of winning at maximum colony size
 20 of $n = 25$ even though $\omega_p = 0$ and the prey is perceptive. This is higher than
 21 any other spatial distribution where the maximum chance of capturing the
 22 prey by simple luck is typically less than 10% with the exception being when
 23 the spiders are grouped on the edge (see Figure 22). Also, in the case of
 24 random edge distribution (Figure 16), it takes only 30 – 50 seconds to catch
 25 the prey by 'luck'. This range is lower than the other spatial distributions
 26 indicating they are able to capture the prey faster even when they have
 27 no influence from the prey itself. We can also discern from Figure 16 that
 28 both the mean time elapsed and proportion of wins appear to approach an
 29 equilibrium as ω_p approaches 1. When $\omega_p > 0.6$, the benefit of being able
 30 to *better* sense the prey, i.e. increase ω_p , has less increase in impact on the
 31 overall success in capture. One other pattern which is distinguishable is that
 32 the mean time elapsed has a discernible pattern where the time elapsed is
 33 increasing beginning at $\omega_p = 0$ and decreasing around $\omega_p = 0.2$. One would
 34 expect simply a decrease in time as ω_p gets larger; therefore, we are uncertain
 35 of the meaning for this discernable pattern.

36 Our ultimate goal was to determine which spatial distribution works best
 37 for the spiders during predation. Figure 23 shows the proportion of wins
 38 for each distribution, level of prey influence and colony size. Red indicates

Figure 15: Results with random spatial distribution with four colony sizes. The blue and green lines indicates careless and perceptive prey respectively. (ex. $n_c = 4$ means colony of size 4 with careless prey.)

Figure 16: Results with edge random spatial distribution with four colony sizes. The blue and green lines indicates careless and perceptive prey respectively. (ex. $n_c = 4$ means colony of size 4 with careless prey.)

- 1 a higher success rate. There is an obvious difference between the careless
- 2 and perceptive prey groups. Naturally, the proportion of spider wins with
- 3 perceptive prey is lower than the proportions with careless prey, because the

Figure 17: Results with clustered spatial distribution with four colony sizes. The blue and green lines indicates careless and perceptive prey respectively. (ex. $n_c = 4$ means colony of size 4 with careless prey.)

Figure 18: Results with edge clustered spatial distribution with four colony sizes. The blue and green lines indicates careless and perceptive prey respectively. (ex. $n_c = 4$ means colony of size 4 with careless prey.)

- 1 perceptive prey immediately tries to escape to the nearest edge. This is where
- 2 the comparison between two prey type is very important in determining
- 3 which spatial distribution works best for the spiders, because regardless of

Figure 19: Results with uniform spatial distribution with four colony sizes. The blue and green lines indicates careless and perceptive prey respectively. (ex. $n_c = 4$ means colony of size 4 with careless prey.)

Figure 20: Results with edge uniform spatial distribution with four colony sizes. The blue and green lines indicates careless and perceptive prey respectively. (ex. $n_c = 4$ means colony of size 4 with careless prey.)

- 1 prey type the spiders need to catch as many prey as possible. If one focuses
- 2 on a single level of influence, say $\omega_p = 0.6$, the best success rate happens
- 3 when the spiders are positioned uniformly on the edge followed closely by the

Figure 21: Results with edge grouped spatial distribution with four colony sizes. The blue and green lines indicates careless and perceptive prey respectively. (ex. $n_c = 4$ means colony of size 4 with careless prey.)

Figure 22: Results with edge grouped spatial distribution with four colony sizes. The blue and green lines indicates careless and perceptive prey respectively. (ex. $n_c = 4$ means colony of size 4 with careless prey.)

- 1 spiders positioned randomly on the edge. This makes sense since typically
- 2 prey cannot fly out of the web and must move to an edge to escape.

Figure 23: Proportion of Wins

1 7. Experimental Results

2 In the thesis by Ross [25], data is presented on the variation of the position
3 of *A. studiosus* in the web throughout the daily cycle. Considering the fact
4 that this species cooperatively forages, they hypothesized that there existed
5 some optimal spatial arrangement of mother and spiderlings in the web that
6 maximizes the amount of prey captured. It was found that the mother and
7 spiderlings do position themselves differently throughout the web both as a
8 function of the age of the juvenile as well as a function of the time of day. At
9 certain times during the day, the spiderlings were spaced closer to the edge
10 than what would be expected under complete spatial randomness. During
11 this same time of day, they were farther from their neighbor than at other
12 times of the day. This observation, together with the model simulations in
13 this paper, appear to support the hypothesis that the spiders are positioning
14 themselves for optimal prey capture during certain intervals of the day. In
15 this section, we summarize the experimental results; for a detailed analysis,
16 we refer the reader to [25].

17 7.1. Methods

18 For this study, *A. studiosus* females with egg cases were collected at the
19 end of May 2012 at Fort Patrick Henry Lake in northeast Tennessee (36° 30 N;
20 82° 28 W). These spiders with their egg cases were placed in 16x16 cm square,
21 transparent, closed containers of 3 cm depth. Hair nets were stretched across
22 the openings of these containers to provide a substrate on which the spiders
23 could build their webs. The shape of these containers caused to spiders to
24 build compressed, nearly two dimensional webs, essentially simplifying the
25 webs to only capture sheets as no debris was provided for the spiders to use
26 as a retreat. Spiders were maintained in the lab on a 12:12 light/dark cycle
27 with lights on at 08:00 and lights off at 20:00. They were fed a mixture of
28 live termites, crickets, and drosophila twice a week. Water was provided by
29 misting the webs three times a week.

30 Once the juveniles emerged and reached the third instar (known to be
31 when they become active in the colony [5, 12]), their positions in the webs
32 were manually plotted by placing the containers over a grid and plotting
33 one point for the abdomen of each spiderling on a copy of the grid. The
34 position of the mother was specifically noted. Ten colonies were used and
35 the positions of all the spiders in the web were plotted every four hours
36 starting at 03:00 for 24 hours. Dark observations were made under deep

1 red light (invisible to spiders [8]) so as not to disrupt any diel or circadian
2 rhythms the spiders might have. A total of four observation days were used:
3 one when the spiderlings reached the 3rd instar, one at the end of the growing
4 season, and two in between as dictated by development. Points were digitized
5 using WebPlot Digitizer software [24]; see the left plot in Figure 24 (the red
6 point indicates the position of the mother). This provided x - y coordinates
7 of a high degree of accuracy that could be imported into Excel, MATLAB,
8 MINITAB, and R.

9 7.2. Results

10 To analyze the spiders' spatial point patterns, three main measures were
11 considered: distance to the nearest neighbor [4], distance to the nearest edge
12 [13], and the percent area of the container the convex hull occupied [4] (a
13 fourth measure, distance to mom, can be found in [25]). Readers who have
14 worked with spatial point patterns will be familiar with distance to the near-
15 est neighbor, in which for each point, the distance to all other points is found,
16 and the smallest of these distances is taken to be the distance to the nearest
17 neighbor. The empirical function of cumulative relative frequencies of dis-
18 tances to the nearest neighbor can be compared to the G function [4] which
19 represents what the cumulative relative frequency curve for distance to the
20 nearest neighbor should look like under complete spatial randomness (CSR).
21 An example is given in the middle plot of Figure 24. As the juveniles aged,
22 it was observed that they transitioned from clustering around mom near the
23 center of the web to showing a preference for the edges of the container. The
24 B function [13] is similar to the G function which is used to analyze the
25 distance to the nearest edge. It is the expected cumulative relative frequency
26 curve of the distance of each point to the nearest edge under CSR. Thus,
27 an empirical B function can be compared to the theoretical B function to
28 help detect any deviations in spatial point patterns from CSR. An example is
29 given in the right plot of Figure 24 which indicates in this example that the
30 spiders are closer to the edge than what would be expected under CSR. The
31 convex hull is a commonly used algorithm that chooses the points which form
32 a polygon that is an effective perimeter of the points such that all points lie
33 within or on the convex hull ([4]). The convex hull is commonly thought of
34 by taking an elastic band and stretching it around a set of fixed points, then
35 releasing the band. When the band comes to rest stretched taught around
36 the points, this is the convex hull of the set. An example is shown in the left

Figure 24: An example of the spatial point pattern at one observation time for one colony (at instar 5) along with the G and B function utilized in a portion of this point pattern analysis

1 plot of Figure 24. The area of the convex hull was taken as a percentage of
2 the total area available to the spiders (256 cm^2).
3 To calculate these measurements for each colony at each time and day,
4 an R program written by the authors using the packages *spatstat* and *plotrix*
5 was used on the raw, digitized data. This was done for each observation,
6 of which there were 240 total (10 colonies, 6 times per day, 4 days). These
7 numbers were then imported into MINITAB [16] for basic statistical analysis.
8 The means and medians of each of these measures over time of day and day
9 of development were examined; the trends are shown in Figure 25. The solid
10 lines represent the colonies without mom while the dashed line indicates those
11 colonies where mom is still present. We note there is a change in all three
12 measurements across the course of the day. Colonies without mom always
13 cover a larger percentage of the entire web (indicated by the percent coverage
14 of the convex hull) than those colonies with mom. This coincides with the
15 graph given in the second row, Figure 25, in which the colonies with mom
16 are always closer to the edge. Furthermore, when analyzing the colonies
17 with mom, as the median distance to the edge decreases (get closer to the
18 edge), the median distance to the nearest neighbor appears to increase (more
19 spread out). This potentially could be the spiders spreading out along the
20 edge at certain times of the day. When analyzing changes as a function of
21 the day of development, we see that for colonies without mom, there is very
22 little change in any of the measurements; however, in colonies with mom,
23 spiders tend to be farther from their neighbor, closer to the edge and cover
24 a larger portion of the total area on day 48 than day 6. Further analysis
25 indicated that on day 48, there was a statistically significant preference for
26 the spiderlings to be within 1 cm of the edge as opposed to the interior in a

Figure 25: Medians of convex hull percent area, distance to nearest neighbor and distance to nearest edge shown over time of day and development. Colonies with mom are shown in red while colonies without mom are shown in black

1 majority of the observations.

2 8. Conclusions

3 In conclusion, we adapted a model by Joyner et. al. [2] and Quijano
4 et.al. [22] for the movement of the subsocial spider *Anelosimus studiosus*
5 during predation to include the effects of interaction among spiders in the
6 web while foraging. The interaction took into account the level of influence
7 from the prey as well as the influence from other spiders within the web.
8 Moreover, the model was further adapted to include a latency period exhib-
9 ited by *Anelosimus studiosus* experimentally. The model was then used to
10 test multiple spatial configurations to determine which spatial configuration

1 was the most effective for the colony for foraging. Based on the simulations,
2 the best spatial distribution was an edge uniform distribution in which the
3 spiders spaced out uniformly along the edges of the web. However, spiders
4 spacing out randomly along the edge was a close second in terms of the best
5 spatial configuration. This is similar to the behavior observed by Ross [25]
6 and summarized in Section 7 in which it was determined to be statistically
7 significant that during certain times of the day, spiders were positioned along
8 the edge more than expected under complete spatial randomness. Therefore,
9 one might hypothesize that during this time of the day, the spiders might be
10 positioning themselves to be most successful for foraging.

11 Cooperative hunting can be enhanced if individuals which detect prey
12 signal others to join in the hunt [29]. In most studies, the signal is a display
13 or call specifically communicating to other members of the group to alert
14 them to the presence of prey [10, 27, 28]. However, the signal may not be
15 a specific communication behavior, rather a consequence of the individuals
16 hunting behavior drawing the attention of others in the group. Such could be
17 the case during the final death chase observed in *A. studiosus* [2, 22] in which
18 the prey elevates its escape behavior in proximity to the approaching spider.
19 This increased activity of both spider and prey would likely alert other spiders
20 across a greater expanse of the web. Such recruitment of social spiders to
21 prey has been observed in a social congener *Anelosimus eximius*, where larger
22 prey grasped by a spider recruit spiders from farther away in the web [17].
23 However, an interesting caution to the limits of increasing effectiveness with
24 group size may be demonstrated by groups of foraging bats [7]. In this case
25 the ability of bats to find and track prey was enhanced by foraging in medium-
26 sized groups, and bats could aggregate by eavesdropping on other foraging
27 bats (rather than detecting the prey itself). At high bat densities, however,
28 foraging efficiency was reduced by the echolocation calls masking the prey
29 reflections, and by bats having to track and avoid other bats. Our spider
30 system may follow a similar pattern where the increased vibrations of the
31 ‘death chase’ could draw other spiders to the general location of prey in the
32 web, but make differentiating prey from other spiders more difficult. In the
33 future, the tractable nature of social spider colonies would facilitate empirical
34 studies of detection and coordination in cooperatively foraging animals.

35 Not surprisingly, our simulations found that larger numbers of spiders
36 are more efficient at capturing prey over the same area. However, in *A.*
37 *studiosus* the size of the web correlates very tightly with the number of
38 spiders in the colony [26], and in other social spiders reduction in energetic

1 costs of web maintenance are identified as one the advantages of sociality
2 [15]. Presumably larger webs intercept more prey, but, as shown here, lower
3 densities of spiders are less likely to capture intercepted prey. In future
4 work we will build on this current model exploring how the optimal web size
5 changes with the number of hunting spiders.

6 Cooperative hunting can be enhanced if individuals can coordinate their
7 efforts such as is observed in African wild dogs [8]. Other models suggest
8 that collective foraging can be enhanced without complex or specific com-
9 munication among foragers [28] particularly by increasing the collection prey
10 perception by the group [3]. Our model changes in prey capture efficiency
11 associated with different spatial distributions of spiders in a communal web.
12 This leads to questions and speculation as to if, and how, the spiders could
13 coordinate such distributions. Presumably individual spiders can detect the
14 edge of the web and wait there for prey. However, *A. studiosus*, and other
15 web-building spiders, have relatively poor vision [1] and could not likely see
16 other webmates well enough to coordinate their spacing. Likely they would
17 have to rely on sensing the vibrations of other spiders moving in the web
18 nearby to judge their proximity and move appropriately. In the future we
19 will analyze individuals movements in the web to detect if they are using
20 their limited information to optimize spacing in the web.

21 Acknowledgements

22 This research was partially supported by the NSF grant DMS-1128954.
23 We would also like to acknowledge Nathaniel Hancock and Michael Largent
24 for their efforts in the collection of the data used for this project.

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