

**A STOCHASTIC SIMULATION MODEL FOR *ANELOSIMUS  
STUDIOSUS* DURING PREY CAPTURE: A CASE STUDY FOR  
DETERMINATION OF OPTIMAL SPACING**

MICHELE L. JOYNER

Department of Mathematics & Statistics  
Institute of Quantitative Biology  
East Tennessee State University  
Johnson City, TN, 37659, USA

CHELSEA R. ROSS<sup>†, ‡</sup>, COLTON WATTS<sup>‡</sup> AND THOMAS C. JONES<sup>‡</sup>

<sup>†</sup>Department of Mathematics & Statistics

<sup>‡</sup>Department of Biological Sciences  
East Tennessee State University  
Johnson City, TN, 37659, USA

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**ABSTRACT.** In this paper, we develop a stochastic differential equation model to simulate the movement of a social/subsocial spider species, *Anelosimus studiosus*, during prey capture using experimental data collected in a structured environment. In a subsocial species, females and their maturing offspring share a web and cooperate in web maintenance and prey capture. Furthermore, observations indicate these colonies change their positioning throughout the day, clustered during certain times of the day while spaced out at other times. One key question was whether or not the spiders spaced out “optimally” to cooperate in prey capture. In this paper, we first show the derivation of the model where experimental data is used to determine key parameters within the model. We then use this model to test the success of prey capture under a variety of different spatial configurations for varying colony sizes to determine the best spatial configuration for prey capture.

**1. Introduction.** It is known that only a few dozen species of spiders show signs of cooperative behavior [1] including cooperative foraging or prey capture, web maintenance, and brood rearing. One such species is *Anelosimus studiosus*. *A. studiosus* is an arboreal social cobweb weaver found in the Southeastern United States exhibiting two distinct behavioral phenotypes: social and subsocial. The subsocial phenotype was first described by Brach in 1977 [4]. In this more common phenotype, an adult female is driven out of the parental web upon maturation and builds a new web of her own. This may occur before or after mating. She lays her eggs in an egg case here and guards the egg case until the juveniles emerge. Juveniles are first regurgitation-fed by their mother. As they mature they are able to eat prey that their mother has caught for them, and eventually actively participate in prey

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capture. The juveniles remain in the parental web, cooperating in prey capture and web maintenance until they reach adulthood, regardless of the survival of the mother.

The social phenotype of *A. studiosus* was not described until 1998 by Furey [7]. The costs and benefits of this system were later analyzed by Jones et al. in 2007 [11]. In this phenotype, social adult females share a web and not only tolerate each other, but purposely aggregate without any evidence of an external motivating factor. They cooperate in prey capture, web maintenance, and brood rearing. The social phenotype is thought to be evolutionarily advantageous in cooler climates where adult mortality is higher. If a female dies before her brood is old enough to survive on their own, they will still be provided for by other adult females in the the social web, giving her a higher average expected fitness than if she had reared her brood alone.

Being from the Family Theridiidae, *A. studiosus* are cobweb weavers. Their arboreal webs display three distinct structures: knockdown threads, a capture sheet, and a retreat. As implied by their name, knockdown threads serve to disrupt the flight path of prey, causing them to fall onto the capture sheet. The capture sheet is densely woven thread that lies predominantly in the horizontal plane. Unlike orb weavers, this thread is not coated with any sticky resin, and prey is often able to freely walk across it. Note, however, that prey do not usually fly out of the web due to the knockdown threads above the capture sheet (unpublished data). The only means of escape is by crawling to the edge or by falling through a damaged section of the capture sheet. Most of the chasing and capturing happens on the capture sheet.

This species cooperatively forages with capture success depending on how quickly, and how many, spiders reach the prey [1]. Thus, we hypothesize that spatial arrangement of mother and spiderlings will affect prey capture success, and, further, that there exists some optimal spatial arrangement for a given colony size. Consider a single spider within the web. There exists some circular area around her such that she can effectively detect, locate, and capture prey that falls into this area with some success rate (see Fig. 1). Note that this area is best thought of as a gradient, with the area closest to the spider as having a success rate of nearly 1.0, and decreasing as the radius of the circle increases. For demonstrative purposes, lets consider a clearly defined circle, delineating the 0.90 success rate area. We will term this circular area as her individual foraging area (IFA). The IFAs of all individuals in the colony as a whole will combine to form a collective foraging area (CFA) in which they have a 0.90 success rate of apprehending prey. Fig. 1 below helps us visualize the advantages and disadvantages of hypothetical spatial arrangements in the web. Spiders are shown in black with their IFAs shown as the gray circles around them.

Observations indicate these colonies change their positioning throughout the day, clustered during certain times of the day while spaced out at other times [21]. It is hypothesized that the colony potentially spaces out more during times in which prey might be more abundant thus maximizing their ability to capture prey. However, it is difficult to determine experimentally the optimal spatial configuration which maximizes prey capture, because we have no control over an individual spider's position or movement within a web. Therefore, to determine the optimal spacing configuration, we develop a model to simulate a spider's trajectory during prey capture. Using this model, we can test the success of prey capture when a prey

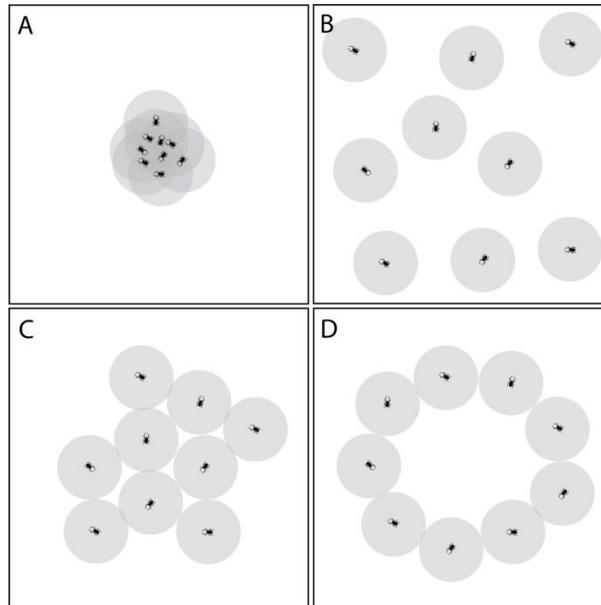


FIGURE 1. Possible spatial positions of juveniles illustrating an individual's foraging area. The combination of all individual foraging areas define the collective foraging area for the colony.

is randomly dropped in the web given different spatial configurations for varying colony sizes.

However, modeling animal movement is a difficult task. Two classic modeling approaches are the use of Lagrangian models or Eulerian models [23]. Lagrangian models are based on random walk behavior and typically applied when modeling trajectories for single animals; whereas Eulerian models describe the expected behavior across an ensemble of individuals. In this paper, we are interested in modeling a single spider trajectory during prey capture, and thus employ Lagrangian modeling strategies. In trying to model a particular animal movement, there are many variables which typically influence an individual's trajectory. Furthermore, even if one could include each of these influences in a model, given the exact same conditions at two different times, it is unlikely the animal will follow the exact same trajectory both times. Given this variability, many of the existing models for single individuals are based on random walks and diffusion processes. Some existing models include modeling movement of female elk [2, 3, 19], elephant-seals [5, 6], deer [3], Pacific coho salmon [17], birds [9, 12], and butterflies [13].

In Section 2, we formulate a stochastic differential equation (SDE) model for the movement of a spider from the species *Anelosimus studiosus* during prey capture using a combination of drift and diffusion terms [2, 3, 19]. We then fit the model to experimental data using an inverse problem methodology in Section 3. We briefly discuss the simulation of prey for use in testing spatial configuration in Section 4. In Section 5, we use the model to test multiple spatial configurations and analyze the success of prey capture for each configuration and various colony sizes. We then make some conclusions and some remarks about future directions in Section 6.

**2. Model derivation.** Following the work by Brillinger et. al. [2, 3] and Preisler et. al. [19], we derive a SDE model for the spider movement of the form

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

where  $\mathbf{r}(t) = [X_s(t), Y_s(t)]'$  denotes the location of the spider at time  $t$ ,  $\mu$  is a drift parameter,  $\Sigma$  is a diffusion parameter, and  $\mathbf{W}$  is assumed to be a Brownian process.

In this model, we assume that the only directional influence in the movement comes from the vibrational cues of the prey, and all other directional influences are negligible. Unlike predators with good vision, spiders can only obtain their directional cues through vibrations in the web. *A. studiosis* behaves similarly to *Hololena curta* [16] in which prey localization usually requires several pauses where the spider stops and feels for the prey. After each pause, the spider reorients itself closer in line with the direction it perceives the prey is located. However, there is generally error in the *perceived* prey direction and the *actual* prey direction, possibly due to the distance from the spider to the prey, debris in the web, the force exerted by the movement (or lack of movement) of the prey, or even the spider's own movement.

Let  $\theta_o(t)$  denote the optimal direction the spider should travel to capture the prey at time  $t$ , i.e., the direction directly from the spider to the prey. Let  $\epsilon = \epsilon(d)$  represent the error in the direction of travel due to noise in directional cues which we assume to depend on  $d$ , the distance between the spider and prey. Then the actual direction the spider will travel in the next time step is given by  $\theta_a(t)$  where  $\theta_a(t) = \theta_o(t) + \epsilon(t, d)$ . See Fig. 2 for an illustration. As mentioned previously, the spider stops to feel for cues and then reorients its direction after these pauses. We let  $\tau$  be the mean time the spider will travel before pausing to reorient and  $\{t_{u_1}, t_{u_2}, \dots, t_{u_n}\}$  be a sequence of times at which the spider will update its direction. Here  $t_{u_{i+1}} = t_{u_i} + \tau_i$  where  $\tau_i$  is taken from an exponential distribution with mean  $\tau$ . Then the directional component  $\mu$  in Equation (1) at time  $t$ ,  $t_{u_i} < t < t_{u_{i+1}}$ , is given by

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

where  $v_s$  represents the average speed of the spider (including time for pauses) and  $d_i$  represents the distance between the prey and spider at update time  $t_{u_i}$ . We use experimental data (see below) to estimate the values  $v_s$ ,  $\tau$  (mean update time), and  $\epsilon(t_{u_i}, d_i)$  (directional error of the spider). The diffusion component in Equation (1) is given by

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

where we take  $\sigma_x = \sigma_y = \sigma$  and determine the value of  $\sigma$  which best fits the model to the experimental data (see below). Substituting the directional and diffusion terms in Equation (1), we have for  $t$ ,  $t_{u_i} < t < t_{u_{i+1}}$ , the model is given by

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

**3. Data collection and parameter estimation.** In order to estimate the parameters for the model, experimental data was collected for four video-taped feedings on a wired web within a laboratory setting; see Fig. 3. The wire structures on which the spiders constructed their webs consisted of a single length of pliable wire manipulated into a circular arena with a semicircular vertical arch. The circular arena

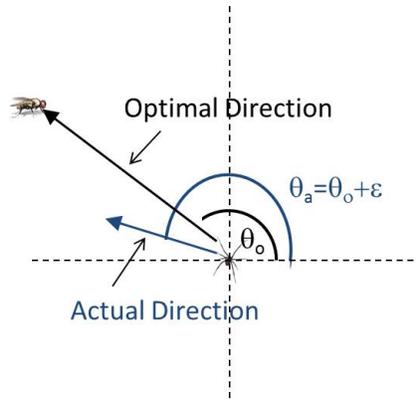


FIGURE 2. Schematic illustrating the optimal direction from the spider's current location to the prey and the actual direction the spider may take given error in directional cues from the prey.

was then covered with a hairnet to provide substrate for capture sheet construction. One adult female *A. studiosus* was maintained on each of these structures for several weeks prior to video-taped feedings to permit web development. We note that although uniformity was maintained for the wire frame upon which the web was developed, there was no mechanism in place to assure uniformity of the actual web construction. Video-taped feedings were recorded from below the capture sheet using a camcorder. During these feedings a flightless *Drosophila hydei* (fly) was blown into the knockdown threads and allowed to fall onto the capture sheet. The spider would then emerge from the retreat, chasing and eventually subduing the fly. The videos were then digitized using Tracker software [18] and imported into Matlab [14]. Any lag time in the spider's initial response to the prey was neglected; the recording of data began only after there was an initial response of the spider.

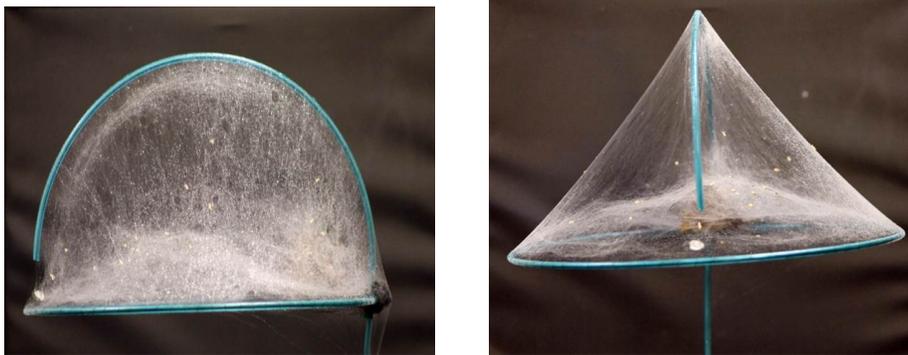


FIGURE 3. Wired webs in the laboratory setting. These webs were used to simulate actual webs. Video recordings were made based on feedings within the web.

In determining the error,  $\epsilon(t, d)$ , for the directional component, we assume that the mean of  $\epsilon(t, d)$  will decrease as the distance  $d$  to the spider decreases. Therefore,

using experimental data, for a given distance  $d$ , we seek  $e(d)$ , a function representing the expected value of  $\epsilon(t, d)$ , i.e.  $E(\epsilon(t, d)) = e(d)$ . Since spiders determine the direction based on vibrations, we assume the prey is a vibrational point source. The amplitude of the vibrations of a point source will decrease as a function of  $\frac{1}{r}$  where  $r$  is the distance from the point source [10]. As the amplitude of the signal from the prey decreases, the error in the direction the spider travels should increase. Therefore, the mean error function for the model should have an inverse relationship to the amplitude function. We define the error function as

$$e(d) = \frac{\alpha d}{d + \beta} \quad (3)$$

where  $\alpha$  and  $\beta$  are constants. (Note:  $(e(d))^{-1} = f(1/d)$  which is the correct relationship.) The constants  $\alpha$  and  $\beta$  are determined by measuring the error in each step from the digitized data for each of the four videos. The errors are then ordered as a function of the distance between the prey and spider and grouped in 0.5 cm bins. The median error in each bin for an individual spider is calculated and plotted against its associated distance. For example, consider a single spider, spider  $k$ ,  $k = 1, 2, 3, 4$ , and the bin consisting of distances between the spider and prey,  $d$ , such that  $2 \leq d < 2.5$ . Assume there are  $m$  time steps such that  $2 \leq d < 2.5$ , and let  $e_1^{(k)}, e_2^{(k)}, \dots, e_m^{(k)}$  be all the directional errors associated with these time steps. Then the error in direction for spider  $k$  and this bin is given by the median of  $\{e_1^{(k)}, e_2^{(k)}, \dots, e_m^{(k)}\}$ . Figure 4 displays the collection of all the median errors for all spiders plotted against its associated distance within the bin. A curve of the form in Equation (3) is then fitted to the error data using Minitab [15]. The fitted curve is shown in Fig. 4. In instances where the spider is initially greater than 10cm from the prey, the error function given by Equation (3) with  $\alpha = 0.83$  and  $\beta = 0.51$  did not result in a good fit of the model realizations to the experimental data. We assume that for larger distances, the spider may have knowledge of the prey in the web but cannot determine with much accuracy the location of the prey. More experiments must be done to confirm this assumption. Nonetheless, multiplying the mean error function  $e(d)$  by a factor of 2.5 for only those values of  $d$  such that  $d > 10\text{cm}$  resulted in a reduction of over 25% error in the model realizations versus experimental data. We note that a statistical comparison test shows there is no significant difference between the error function modeled by Equation (3) and a constant error function  $e(d) = e_0$ . However, there is a difference biologically as we expect the spider to be able to localize the direction of the prey better when it is closer to the prey. Moreover, to accomplish the goal of the model in this paper (to simulate the movement of a spider towards a prey), initial derivations of the model (not presented in this paper) suggest we should not expect successful localization of the simulated spider to the prey if a constant error function is implemented.

The directional vector in our model (see Equation (2)) for any time  $t$  is given by the term  $[\cos(\theta_a), \sin(\theta_a)]$  where  $\theta_a = \theta_o(t_{u_i}) + \epsilon(t_{u_i}, d_i)$ . Therefore, to simulate the direction the spider will travel from time  $t$  to time  $t + dt$  where  $dt$  is some incremental unit of time, we first determine  $\vec{u}_{sp} = [x_p(t_{u_i}) - x_s(t_{u_i}), y_p(t_{u_i}) - y_s(t_{u_i})]$  which is the directional vector from the spider to the prey at the time of the last pause, i.e., at time  $t = t_{u_i}$ , where  $(x_p(t_{u_i}), y_p(t_{u_i}))$  is the location of the prey and  $(x_s(t_{u_i}), y_s(t_{u_i}))$  is the location of the spider at the pause time  $t = t_{u_i}$ . The angle  $\theta_o$  is simply the angle  $\vec{u}_{sp}$  makes with the positive  $x$ -axis and the distance  $d_i = \|\vec{u}_{sp}\|$  is the distance from the spider to the prey at the start of the pause. The error is

assumed to be normally distributed with mean  $e(d_i)$  as determined by Equation (3) and is calculated using the *normrnd* command in Matlab.

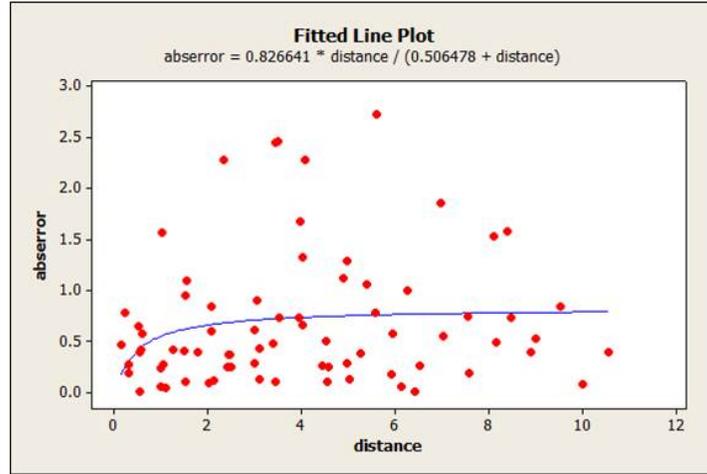


FIGURE 4. Directional errors from experimental data and a fitted function of the form given in Equation (3).

The remaining parameters in Equation (2) are estimated using a least squares inverse problem formulation. Since the goal is to use the model to predict the success or failure of prey capture depending on spatial configurations, the time required for the spider to reach the prey and the total distance traveled by the spider are the most important elements for analysis. Moreover, we already mentioned that the spider is likely to take a slightly different route each time even if all other conditions remain constant. Therefore, we seek parameters  $\tau$  and  $\sigma$  which minimize the error in total time and total distance traveled between the simulated spider using the model and actual spiders using experimental data. We note here that data was only collected for the trajectory of a spider in a successful prey capture. No data was not collected on unsuccessful attempts as we are not concerned about optimal starting locations for a single spider. For a single spider, the optimal position of a circular web will always be the center of the web if there are enough trials taken. Therefore, the data collected was intended to capture the trajectory taken and more generally the total distance traveled by the spider to the prey and the time required to travel this distance. If the spider reaches the prey fast enough, the prey will not be able to escape.

For each of the four videos,  $k = 1 \dots 4$ , we compute the total time  $T_k$  which it takes for the spider to reach the prey once in motion and the total distance  $D_k$  the spider travels during that time. The data was collected used the Tracker software as mentioned previously which collects the location of the spider at fixed time increments  $\Delta t$ . Therefore, if  $n$  is the number of total data points,  $T_k = (n - 1)\Delta t$ . The calculation of  $D_k$  requires calculating each incremental distance traveled and then adding these incremental distances, i.e.

$$D_k = \sum_{l=1}^{n-1} \|[x_s(t_{l+1}) - x_s(t_l), y_s(t_{l+1}) - y_s(t_l)]\|,$$

where  $(x_s(t_l), y_s(t_l))$  is the position of the spider at time  $t_l$ ,  $l = 1, 2, \dots, n$ . Since Brownian motion is included in the model, each realization of the model is unique, i.e., each realization will result in a slightly different path taken by the simulated spider. Therefore, we compare the variables  $T_k$  and  $D_k$  with the average of these variables across one thousand realizations of the model. Let  $\mathbf{q} = [\sigma, \tau]$ . For an individual spider, we let the initial position of the simulated spider equal the initial position of the actual spider. The model given by Equation (2) is then used to estimate the location of the simulated spider at each subsequent time  $t = t_i + \Delta t$  given the specified parameter  $\mathbf{q}$  until the distance between the simulated spider and actual prey is less than the distance between the actual spider and actual prey. Then  $T_j(\mathbf{q})$  and  $D_j(\mathbf{q})$ , the total time and total distance traveled by the simulated spider for realization  $j$ , are calculated for each simulation  $j = 1, 2, \dots, 1000$ , in the same manner as  $T_k$  and  $D_k$  for the actual spider above. We then use an optimization algorithm *fminsearch* in Matlab [14] to estimate the parameters which minimize the cost function

$$J(\mathbf{q}) = \sum_{k=1}^4 \left[ \left( \frac{\sum_{j=1}^{1000} (T_j(\mathbf{q}))}{1000} - T_k \right)^2 + \left( \frac{\sum_{j=1}^{1000} (D_j(\mathbf{q}))}{1000} - D_k \right)^2 \right]. \quad (4)$$

In order to determine the best parameters describing our data, for each video, we use the exact data for the trajectory of the prey including any pauses in prey movement. Doing this allows us to fix any possible additional error which might be incurred by modeling the prey. For certain parameter values  $\mathbf{q}$ , the simulated spider may take more time steps than given in the original data for the prey. Therefore, to alleviate this problem, we repeat the same prey movement as the original data by only varying the starting location which is defined as the ending location given by the original data. Moreover, the average velocity for each spider in each video is different. Each spider has a unique variable ‘running’ speed and different number and duration of pauses. We do not incorporate pauses or varying running speed in this formulation of the model for the spider, but instead we consider total average speed which accounts for both varying running speeds and pauses. In other words, we assign  $v_s = (v_s)_k$  to the average velocity of the specific spider in video  $k$  which is calculated by

$$(v_s)_k = \frac{D_k}{T_k}$$

where  $D_k$  and  $T_k$  are as described above. Note that  $T_k$  is the total time it takes for spider  $k$  to reach the prey including the time in which the spider was paused.

The optimal parameters found were  $\tau = 0.30$  and  $\sigma = 1.06$ . Using these optimal parameter values in Equation (2), we have the average errors in  $T$  and  $D$  given in Table 1 for one thousands realizations of the model. For three of the four videos, the percent relative error is close to or less than 5% which indicates a very good fit between the model and experimental data. The distributions across the thousand simulations for total time and total distance traveled for each realization are plotted in Fig. 5 where the red line indicates the total time and total distance traveled for the actual spider. For videos 1-3, the distributions also indicate a good fit for the model; however, for video 4, the actual data appears to be an outlier of the model and hence the model does not incorporate all aspects of the spider movement necessary to accurately mimic the spider in video 4. We will hypothesize on the

reasons for this below when we compare realizations of the model to the actual spider trajectories.

TABLE 1. Goodness of Fit of the Model to Experimental Data using Optimal Parameters

Video $k$	$T_k$ (s)	$E(T_j)$ (s)	Rel Error	$D_k$ (cm)	$E(D_j)$ (cm)	Rel Error
1	5.2720	5.1817	0.0171	8.1806	7.9779	0.0248
2	18.9190	19.1397	0.0117	20.0717	20.0261	0.0023
3	2.4690	2.6060	0.0555	5.8780	6.1435	0.0452
4	7.6740	3.9121	0.4902	17.4791	8.8003	0.4965

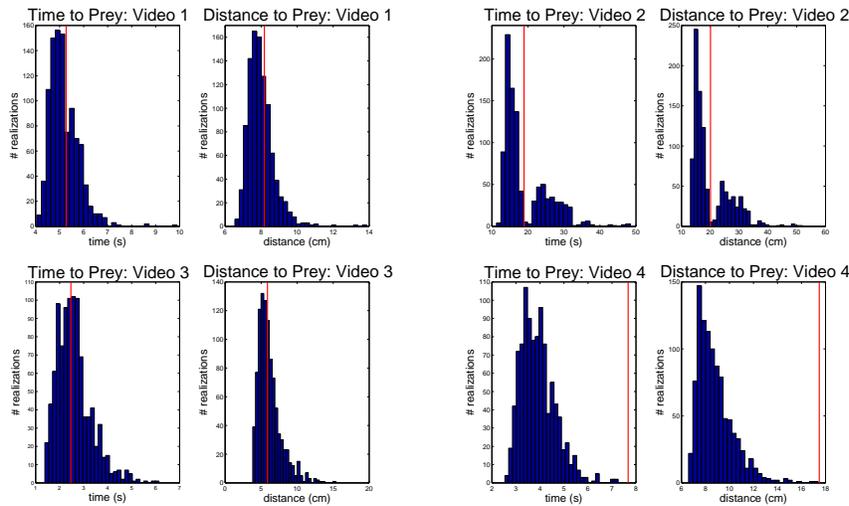


FIGURE 5. Videos 1, 2, 3, and 4: Distribution for the total time and total distance traveled by the simulated spider using Equation (2) with optimal parameter values  $\tau = 0.03$  and  $\sigma = 1.06$ . The red line indicates the value for same value for the actual spider from the data.

Fig. 6 illustrates realizations of the model given by Equation (2) using optimal parameter values. As expected, each realization has a different trajectory; however, the path of the simulated spiders and actual spiders are quite similar. For Video 4, we note that in each of the simulations shown in Fig. 6, the simulated spider reaches the prey faster than the actual spider. Upon examining Video 4, after the spider has traveled approximately halfway between its starting location and the prey, it reorients itself in the wrong direction, travels until it pauses again and then reorients itself back in the appropriate direction. In the derivation of the model, we assume the spider will always reorient itself in a more precise direction assuming the distance between the prey and spider is decreasing. It may be the case that there is a slight probability that the spider will veer off in the wrong direction even if the spider is close to the prey. More data must be taken to test this assumption and quantify the associated probability if it happens in multiple cases. Therefore,

we do not incorporate this in the model at this time. We also note that Video 4 is the only video in which the prey makes a significant attempt at escape as noted by the longer blue line in Figure 6. This may also play a role in the parameter estimation. Again, more data must be taken to test this assumption.

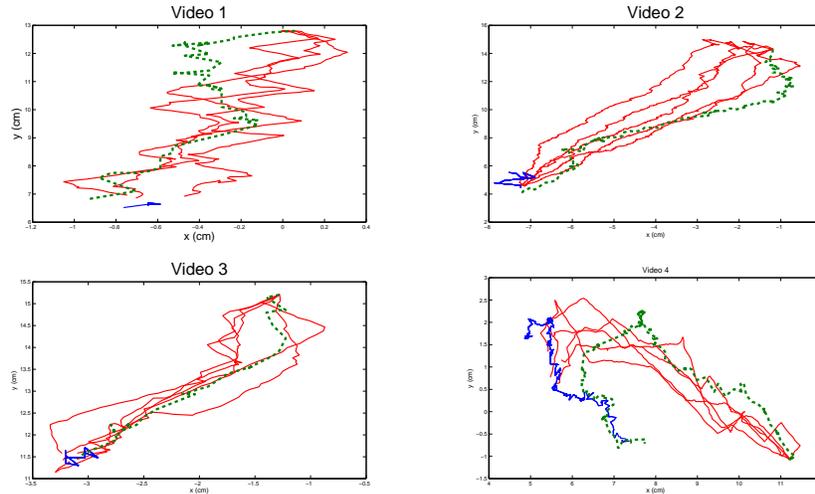


FIGURE 6. Videos 1, 2, 3 and 4: The figure shows the trajectory for the prey (short solid blue line), the actual spider trajectory (green dashed line) and realizations for the simulated spider trajectory (long solid red lines) using Equation (2) with optimal parameters  $\tau = 0.03$  and  $\sigma = 1.06$ .

**4. Prey simulation.** In the previous section, we used the actual prey data to determine optimal parameters for the model in Equation (2) of spider movement during prey capture. We need to be able to simulate prey movement as well in order to test possible spatial configurations for successful prey capture. Unlike we did in the previous section, we do not use quantitative prey data to fit a model for prey movement. However, we make certain assumptions on prey movement based on observations. We note that for simulating prey movement, our assumptions are based on observations of *Drosophila hydei* (flightless flies) during feeding times; the assumptions may be different for other types of prey.

Currently there is no data to verify in natural settings whether the prey lands in one location more frequently than any other. Therefore, the starting location for the prey is chosen by generating a uniformly random point on a circle of radius  $R$  where  $R$  is the radius of the web. Observations indicate the prey typically does not pick an ideal direction to move (such as to the nearest edge of the web); instead, the prey is observed to pick a random direction. Furthermore, the prey is observed to ‘walk’ in the given direction for a period of time and then change to another random direction. Although there is no observed correlation in the previous direction and new direction, we assume that the prey will not make a  $180^\circ$  change in direction and, therefore, restrict the mean amount of change in prey direction. We assume the new direction,  $\theta_{p_{i+1}}$  is chosen so that  $\theta_{p_{i+1}} = \theta_{p_i} + \Theta$  where  $\Theta$  is a random variable with mean  $\pi/4$ .

A ‘death chase’ was typically observed once the spider was ‘close enough’ to the prey. During the death chase, the prey changed direction (normally in the opposite direction of the spider) and increased its velocity. We account for this in the prey model by assuming that if  $d < 3\text{cm}$ , where  $d$  is the distance between spider and prey, the velocity of the prey,  $v_p$ , doubles and  $\theta_p$  is chosen so the prey moves in the opposite direction of the spider. Similar to the model of spider movement in the previous section, we let  $\tau_p$  be the mean time the prey will travel before changing directions and  $\{t_{pu_1}, t_{pu_2}, \dots, t_{pu_n}\}$  be a sequence of times at which the prey will change its direction. In this case, we assume the prey does not change directions as often as the spider, and therefore, we set  $\tau_p = 1.5 * \tau$  where  $\tau$  is the mean update time for the spider movement model in the previous section. Therefore, in the prey model, the directional component,  $\mu$ , in Equation (1) for time  $t$ ,  $t_i \leq t < t_{i+1}$ , is given as

$$\mu\{\mathbf{r}(t), t\} = v_p \begin{bmatrix} \cos(\theta_{p_i}) \\ \sin(\theta_{p_i}) \end{bmatrix}$$

where  $\theta_{p_i}$  is the direction of prey movement at time  $t$  as discussed above. The diffusion component for the prey model is assumed the same as in the spider model. Thus, the model for the prey based on observations is given for time  $t$ ,  $t_i \leq t < t_{i+1}$ , by

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

In the next section, we also consider an informed prey where  $\theta_p$  is chosen so the prey is always heading in the direction of the nearest edge of the web at all times until the death chase. When the death chase begins (at  $d < 3\text{ cm}$ ), the prey behaves as above and moves in the opposite direction from the spider.

**5. Testing of Spatial Configurations for optimal prey capture.** In this section, we use the models developed in Sections 2 - 4 to test the success of prey capture given various initial spatial configurations for the spider colony. We analyze the effects of spatial configurations for both a social colony (adult spider colony which cooperates in prey capture) and a subsocial colony (a mother and juvenile colony which cooperate in prey capture). In the case of a social colony, we make the assumption that all adult spiders behave the same and according to the model in Equation (2). It is well-known for certain species of animals, directional cues are also given by neighbors within their flock or herd [9]. In these simulations, we assume any additional cues given by other spiders within the colony are negligible but should be included in future updates to the model. Grinstead et. al. [8] also gave evidence that spiders exhibiting behavioral characteristics for boldness are more likely to actively participate in prey capture than other adult spiders in the colony. This differentiation of behavior is not included in the current model but should be explored in the future. Furthermore, in the case in which the prey is a fly, we assume only one adult female is needed to capture the prey. We do not make assumptions about larger prey in this paper since we do not have data on which to base a prey model for larger species.

In the subsocial colony, we assume the juvenile behaves according to Equation (2) during prey capture with only a difference in speed and ability to capture the prey individually. Observations indicate juveniles move at a slower speed than their mother, and more juveniles are required to effectively capture the prey. For the simulations in this section, the juveniles are assumed to travel at half the speed

of the mother, i.e.  $v_j = v_s/2$  where  $v_s$  is chosen to be the average of all spider velocities,  $(v_s)_k$ , from the experimental data,  $k = 1, \dots, 4$ . We further assume that one juvenile cannot capture a prey by itself; however, it will slow down the prey. Therefore, if one juvenile reaches the prey, the prey's speed is reduced by  $1/4$ . If two juveniles reach the prey, the speed of the prey is reduced by  $3/4$  of the original speed. If three or more juveniles or the mother reach the prey, the prey is assumed to be captured, i.e., a success for the spider. On the other hand, if the prey reaches the edge of the web before being captured, the prey is considered to have escaped, i.e. a failure for the spider colony.

In determining possible spatial configurations the spiders might form in the web, we consider two distinct factors that might influence an individual's position: *preference* of proximity with respect to certain structures within the web, and *distribution* with respect to other members in the colony. For preference, we consider that individuals might prefer the interior of the web, the edges of the web, or have no preference. In subsocial colonies, we also consider that spiderlings might prefer to be close to or far from their mother. Fig. 7 below shows the five different preferences under a random distribution with  $n = 25$ . In this case, spiders were placed directly on the edge, or within half the radius of the center of the web for the edge and interior preferences. A 4.0 cm radius around mom was used for the close to and far from mom preferences, and mom was given the position of  $(2.665, 0)$  based on data taken in a related project [21]. There are biological advantages to the different preferences considered.

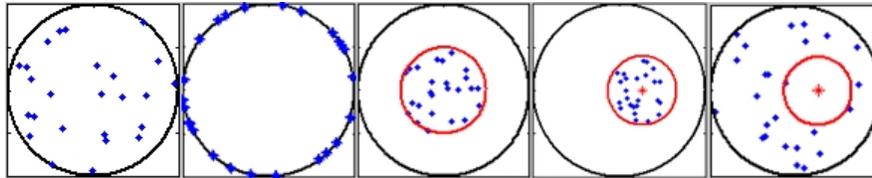


FIGURE 7. The five different preferences from left to right: none, edge, interior, close to mom, far from mom. Mom is indicated by a red star, and the 4.0cm circle around her is shown in red. The 5cm circle is shown to indicate the interior in the middle image. All shown with a random distribution and  $n = 25$ .

The interior of the web could provide more protection from predators and parasites. It would allow the spider to feel the vibrations from crawling predators, and be surrounded by knockdown threads which might offer some protection against flying predators and parasitic wasps. It may also be beneficial for individuals to be in the center of the web, which is equidistant from all the edges where prey might escape. Being in the center would minimize the maximum possible initial distance prey could land from the spider. If the spider was on the edge, the spider may have a maximum possible initial distance to the prey equal to the diameter of the web; whereas, if the spider was located in the center of the web, the maximum possible initial distance to any prey would be cut in half, i.e., the radius of the web.

Being on the edge, however, might also be beneficial since most prey items will have to crawl to the edge to escape. If members of a colony cooperated, they could increase the collective foraging area (CFA) by lining the edges of the web so that their individual foraging areas (IFAs) are adjacent, such as in Fig. 1D. Since prey

must crawl to the edge, the interior of this ring would also be part of the CFA. In a natural environment, many edges of the web are anchored to leaves or other solid structures that could provide protection from weather and predators/parasites.

In terms of the juveniles' positioning with respect to mom, being close to mom might provide some protection, especially at younger ages. Mom also is the sole food source for spiderlings when they are young, and remains the predominant hunter while she survives. On the other hand, since mom is the most efficient hunter, it might be best if the spiderlings are further from mom to aid in slowing down or apprehending prey that lands outside of mom's IFA. When spiderlings are close to mom, they are nearly useless in aiding in prey capture since they have a much slower velocity.

For distributions, we consider the traditional spatial distributions of regular, random, and clustered, with the addition of a grouped distribution. Examples of these distributions are shown below in Fig. 8 with no preference and  $n = 25$ . Clustering can happen in many different ways. While a clustered distribution in this instance contains all points randomly distributed in a 1 cm radius circle, a grouped distribution consists of several small clusters, the center of which are randomly distributed within the preference. Thus, the grouped distribution is between a clustered and random distribution. The size of clusters was set to be four since laboratory observations led us to believe that it would take at least three spiderlings to subdue and kill a prey item, and when there were leftover individuals they were placed into clusters to make groups of five until the colony size was achieved.

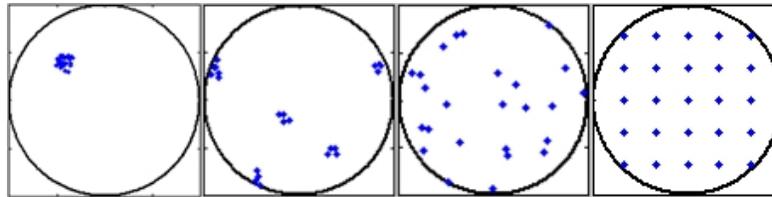


FIGURE 8. The four different distributions from left to right: clustered, grouped, random, and regular. All shown with no preference and  $n = 25$ .

Different distributions provide different advantages. A clustered distribution might offer the most information sharing as well as food sharing. A regular distribution would cover the most area, while a grouped distribution would allow spiders to attack in bands, more effectively subduing the prey while covering more area than a clustered distribution. We note that although these advantages are justifications for why these distributions might exist within a social or subsocial colony, we do not incorporate any of these advantages within the model itself. For example, although a clustered distribution might offer the most information sharing, we do not specifically include any information sharing within the model, etc..

Since the prey is considered to be randomly placed in the web at various starting locations and the paths of the spiders will be different for every run, we want to quantify the variation expected in the number of successful captures. Therefore, we run 100 simulations ten times for each combination of preference and distribution to determine the average percentage the spider successfully captures the prey as well as the standard deviation about the mean for each configuration. Let  $n_s^{(k)}$

indicate the number of successful spider captures during the 100 simulations for trial  $k$ ,  $k = 1, \dots, 10$  (note that this number is also the percent of successful captures for trial  $k$ ). We assume  $n_s$  is normally distributed and use the *mean* and *std* commands in Matlab to calculate the mean and standard deviation respectively for each spatial configuration. We perform simulations for both social colonies and subsocial colonies with both uninformed and informed prey for five different colony sizes,  $n = 5, 10, 15, 20, 25$ , where  $n$  is the number of adults in a social colony or the number of juveniles in a subsocial colony. The uninformed prey is as described in Section 4 in which the prey randomly changes directions as observed in experimental settings. The informed prey is assumed to move in the direction of the nearest edge. Table 2 gives the results for social colonies, and Table 3 gives the results for subsocial colonies for the varying colony sizes.

TABLE 2. **Social Colony** with Uninformed and Informed Prey: Percent of Successful Prey Captures for Various Spatial Configurations with Standard Deviations given in Parenthesis

Uninformed Prey						
Pref.*	Distr.*	n = 5	n = 10	n = 15	n = 20	n = 25
Edge	Regular	94.9 (2.18)	98.0 (1.63)	99.3 (0.82)	99.4 (0.70)	99.3 (0.95)
Edge	Random	93.9 (2.60)	95.6 (1.84)	97.8 (1.22)	97.8 (1.81)	98.6 (1.35)
Edge	Grouped	85.9 (1.60)	88.8 (3.61)	91.2 (2.90)	92.3 (2.00)	94.2 (2.44)
Edge	Clustered	83.6 (3.57)	83.6 (3.78)	85.1 (3.84)	87.0 (2.31)	86.5 (3.98)
Center	Regular	81.1 (2.92)	80.6 (2.07)	80.9 (3.00)	80.3 (3.23)	80.8 (5.05)
Center	Random	81.4 (4.45)	80.2 (4.24)	80.9 (3.87)	81.8 (3.39)	81.9 (3.84)
Center	Grouped	81.8 (4.29)	81.4 (3.81)	81.5 (2.76)	80.3 (5.70)	82.7 (3.86)
Center	Clustered	82.2 (3.29)	81.0 (4.06)	79.3 (3.97)	81.8 (6.27)	81.9 (2.69)
None	Regular	84.6 (3.92)	81.7 (3.74)	88.1 (3.07)	93.5 (3.63)	90.1 (2.64)
None	Random	86.5 (2.76)	88.8 (3.64)	89.1 (2.51)	91.7 (1.57)	92.3 (1.83)
None	Grouped	85.6 (4.09)	83.2 (4.05)	86.8 (3.05)	87.8 (3.89)	88.4 (2.12)
None	Clustered	84.9 (2.69)	84.9 (2.13)	83.7 (3.23)	83.5 (3.84)	85.2 (2.62)
Informed Prey						
Pref.*	Distr.*	n = 5	n = 10	n = 15	n = 20	n = 25
Edge	Regular	93.9 (1.79)	97.7 (1.25)	99.2 (0.92)	99.2 (0.63)	99.1 (0.74)
Edge	Random	87.2 (2.25)	93.9 (2.60)	97.5 (1.27)	98.6 (0.97)	98.1 (1.20)
Edge	Grouped	57.4 (5.58)	72.8 (5.35)	79.2 (4.73)	81.9 (2.08)	85.0 (3.50)
Edge	Clustered	56.8 (4.61)	58.9 (5.90)	61.4 (3.98)	61.4 (4.35)	63.3 (5.35)
Center	Regular	75.5 (3.06)	72.0 (4.14)	77.4 (4.40)	77.0 (4.24)	76.0 (4.45)
Center	Random	73.3 (2.50)	75.0 (3.27)	74.3 (4.19)	77.8 (4.16)	77.1 (4.63)
Center	Grouped	67.1 (3.73)	72.8 (4.16)	74.8 (3.82)	77.4 (2.80)	76.2 (3.88)
Center	Clustered	67.6 (5.95)	70.5 (3.81)	71.8 (3.33)	68.8 (2.62)	70.2 (3.65)
None	Regular	81.3 (4.37)	85.3 (3.40)	89.6 (2.32)	93.2 (2.62)	90.0 (3.27)
None	Random	81.2 (3.05)	84.4 (2.84)	87.7 (4.81)	89.9 (2.92)	89.9 (3.35)
None	Grouped	63.8 (3.58)	73.3 (5.03)	79.6 (4.03)	83.8 (2.57)	83.5 (5.19)
None	Clustered	62.7 (5.27)	62.4 (5.82)	68.0 (5.27)	64.7 (4.57)	65.6 (5.87)

\*Pref. stands for spatial preference within the web. Distr. stands for distribution

The results indicate that prey capture success is affected by the colony demographics and spacing behavior, as well as the flies behavior (Tables 2 and 3). We note that although the average number of successful prey captures is different for subsocial spiders than social spiders, the trends across the varying distributions are the same when comparing Tables 2 and 3. Therefore, to avoid redundancy, we only discuss the general trends for the social spider in this paper and indicate that trends for subsocial spiders are similar. Some general trends associated with the spiders?preference for position and spacing in the web are mostly clearly illustrated under the social spider/informed fly?scenario. Comparing different spacing distributions for specific position preferences, the predominant trend was that regular and random spacing tended to perform similarly higher than grouped and clustered distributions (Fig. 9A-C). An exception in the case of edge preference was that regular spacing performed better than random at smaller colony sizes (Fig. 9A).

TABLE 3. **Subsocial Colony** with Uninformed and Informed Prey: Percent of Successful Prey Captures for Various Spatial Configurations with Standard Deviations given in Parenthesis

Uninformed Prey						
Pref.*	Distr.*	n = 5	n = 10	n = 15	n = 20	n = 25
Edge	Regular	94.1 (2.38)	98.5 (1.08)	99.9 (0.32)	100 (0.00)	100 (0.00)
Edge	Random	92.3 (2.95)	96.0 (2.16)	97.3 (0.67)	97.2 (1.62)	98.7 (1.42)
Edge	Grouped	87.4 (4.40)	87.8 (3.08)	89.5 (2.92)	92.1 (2.42)	92.6 (2.07)
Edge	Clustered	88.5 (2.64)	87.5 (2.22)	87.7 (2.41)	88.8 (3.16)	88.5 (3.75)
Center	Regular	84.6 (4.86)	83.3 (3.20)	73.7 (4.62)	72.4 (4.97)	74.1 (3.73)
Center	Random	83.2 (4.49)	79.5 (4.03)	77.0 (2.62)	77.0 (6.13)	77.0 (4.37)
Center	Grouped	83.8 (5.16)	83.2 (3.91)	81.9 (2.60)	81.5 (3.81)	77.7 (5.42)
Center	Clustered	86.0 (3.40)	87.2 (4.59)	85.4 (3.72)	83.7 (2.67)	83.6 (3.17)
None	Regular	74.8 (3.94)	70.9 (5.22)	76.9 (4.77)	85.4 (2.88)	73.5 (6.75)
None	Random	81.4 (3.06)	79.1 (2.13)	75.9 (3.63)	79.4 (3.03)	77.6 (4.22)
None	Grouped	84.0 (3.23)	82.6 (3.86)	80.6 (4.62)	78.0 (5.79)	78.7 (4.85)
None	Clustered	83.8 (2.44)	83.2 (3.19)	83.5 (1.96)	84.8 (3.58)	86.8 (4.18)
CM**	Regular	86.4 (4.33)	82.4 (2.01)	83.2 (4.32)	81.1 (4.07)	81.8 (3.26)
CM**	Random	85.6 (3.17)	84.0 (2.98)	80.4 (3.47)	82.4 (3.31)	80.0 (4.35)
CM**	Grouped	84.6 (4.79)	86.2 (3.29)	84.5 (3.98)	84.2 (1.62)	83.7 (4.37)
CM**	Clustered	87.1 (3.14)	85.9 (2.69)	87.0 (3.02)	86.9 (3.21)	84.6 (3.92)
FM**	Regular	71.0 (2.62)	72.8 (4.83)	72.8 (4.66)	75.2 (5.12)	73.9 (5.67)
FM**	Random	77.5 (5.60)	78.0 (2.00)	80.0 (4.59)	79.6 (4.62)	80.4 (3.78)
FM**	Grouped	83.0 (3.50)	82.6 (3.37)	79.8 (3.08)	80.4 (3.92)	77.1 (5.53)
FM**	Clustered	85.2 (3.43)	85.5 (3.78)	84.2 (5.61)	83.5 (3.78)	83.3 (3.77)

Informed Prey						
Pref.*	Distr.*	n = 5	n = 10	n = 15	n = 20	n = 25
Edge	Regular	89.5 (2.17)	97.5 (1.78)	99.2 (0.92)	98.8 (1.14)	99.3 (1.06)
Edge	Random	83.8 (3.55)	92.1 (2.13)	92.9 (3.41)	96.2 (1.99)	97.6 (1.08)
Edge	Grouped	70.0 (5.16)	73.8 (4.10)	78.2 (4.21)	83.2 (4.64)	80.9 (5.22)
Edge	Clustered	69.3 (5.14)	68.0 (6.43)	69.7 (4.60)	68.1 (5.70)	69.0 (5.27)
Center	Regular	63.5 (4.28)	61.2 (5.07)	58.0 (2.98)	58.2 (3.55)	59.2 (4.61)
Center	Random	61.8 (5.94)	61.6 (7.14)	57.7 (5.54)	60.3 (4.30)	55.8 (4.10)
Center	Grouped	64.3 (5.81)	64.1 (4.04)	60.7 (5.38)	58.4 (4.43)	60.2 (5.22)
Center	Clustered	67.3 (3.40)	67.4 (4.27)	65.5 (3.92)	66.8 (5.41)	67.3 (3.27)
None	Regular	67.5 (5.06)	70.5 (3.87)	80.0 (5.70)	87.7 (1.83)	80.1 (3.84)
None	Random	71.3 (6.30)	75.4 (4.40)	78.5 (2.99)	81.1 (3.28)	84.6 (3.86)
None	Grouped	67.3 (4.11)	66.3 (4.24)	70.4 (3.34)	71.3 (4.03)	73.8 (2.94)
None	Clustered	64.8 (3.68)	66.0 (4.24)	67.9 (5.28)	68.8 (6.78)	66.4 (6.19)
CM**	Regular	65.8 (2.53)	61.4 (4.25)	60.5 (5.44)	61.1 (3.57)	65.3 (3.71)
CM**	Random	62.6 (4.48)	64.0 (2.58)	64.1 (4.89)	62.5 (3.60)	64.5 (4.97)
CM**	Grouped	64.3 (5.64)	66.9 (5.49)	63.6 (4.79)	62.1 (5.22)	64.4 (6.74)
CM**	Clustered	64.7 (4.30)	66.9 (4.68)	67.1 (6.08)	69.7 (5.17)	64.7 (3.06)
FM**	Regular	69.2 (3.82)	74.7 (6.24)	82.3 (3.83)	80.8 (3.12)	84.3 (2.71)
FM**	Random	72.9 (3.18)	79.4 (3.90)	83.6 (3.92)	84.4 (3.37)	86.0 (3.77)
FM**	Grouped	68.3 (4.57)	71.7 (4.14)	71.5 (3.66)	71.4 (4.45)	75.6 (3.13)
FM**	Clustered	67.1 (3.48)	68.6 (3.66)	69.2 (3.88)	65.8 (4.80)	68.6 (5.08)

\*Pref. stands for spatial preference within the web. Distr. stands for distribution.

\*\* CM stands for close to mom. FM stands for far from mom.

Clustered spacing performed consistently lowest across preferences, and the level to which grouped spacing outperformed clustered increased with colony size (Fig. 9A-C). Comparing different preferences for position in the web across distributions, in the cases of regular and random distributions, preference for the edge outperformed the other preferences at all colony sizes, followed by no preference, with preference for the center consistently performing the worst (Fig. 10A & B). In the grouped distribution, preference for the center shows the highest performance at the smallest colony size, but is similarly outperformed by preference for the edge and no preference above colony sizes of 10 (Fig. 10C). In the clustered distribution, preference for the center showed the highest performance across colony sizes, followed by no preference and then preference for the edge (Fig. 10D).

As discussed in Section 1, prey typically must crawl to the edge of the capture sheet to escape, which is generally supported by laboratory observations. However, it has been occasionally observed that prey can fall through the capture sheet or

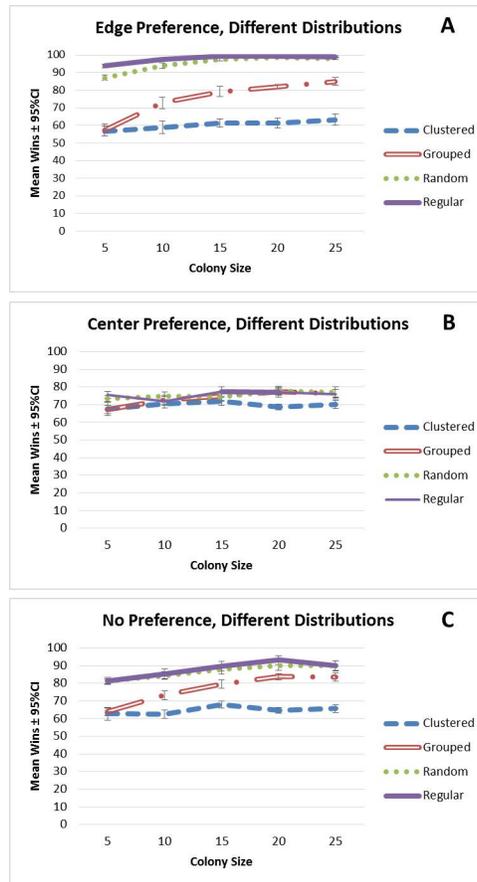


FIGURE 9. Figures A-C illustrate the effect of different distributions on success of prey capture when assuming a fixed preference for either the edge, center or no preference respectively. The figures were generated using the information given in Table 2 when considering social colonies and an informed prey.

escape vertically. Thus, the time to prey capture may also play a role in natural foraging success. Therefore, we considered a social colony of average size 10 and examined the time taken for a simulated spider to capture the prey when arranged in each of the configurations. The results are given in Fig. 11. When considering the time taken for the simulated spiders to capture prey, the preferences for the web center and no preference took less time than the preference for the edge consistently among the different distributions (Fig. 11A). Regular and randomly distributed spiders captured prey consistently fastest, followed by the group distribution, with the clustered distribution taking the longest to capture prey (Fig. 11B). Whereas preference for the edge resulted in the largest proportion of successful prey captures (Table 2), preference for the edge also resulted in the longest time to the prey (Fig. 11A). This indicates a tradeoff especially if larger prey might be more likely to break through the capture sheet. A faster time may result in fewer successful prey captures, but if the capture is a large prey, the nutritional benefit may be the

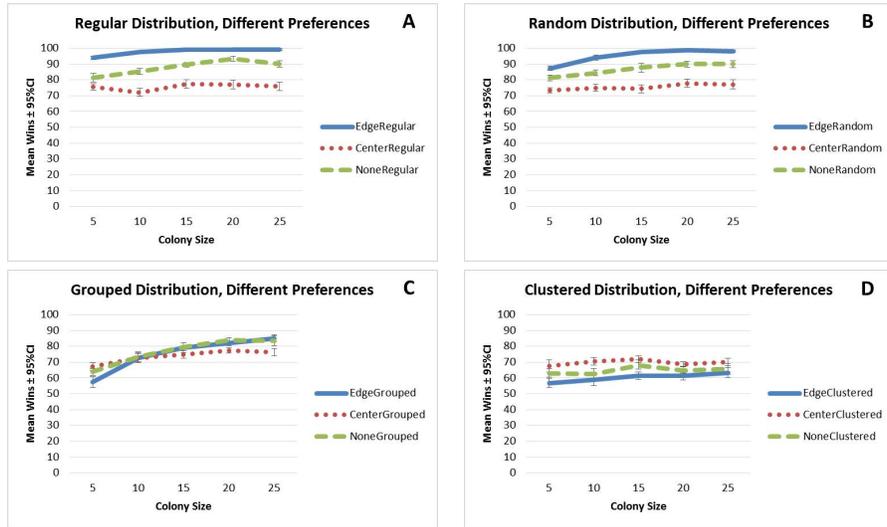


FIGURE 10. Figures A-D illustrate the effect of different preferences on success of prey capture when assuming a fixed distribution of regular, random, grouped, or clustered respectively. The figures were generated using the information given in Table 2 when considering social colonies and an informed prey.

same. Therefore, in order to determine which spatial configuration is indeed more beneficial, more studies may need to be conducted to determine the likelihood of prey of various sizes to fall through the capture sheet.

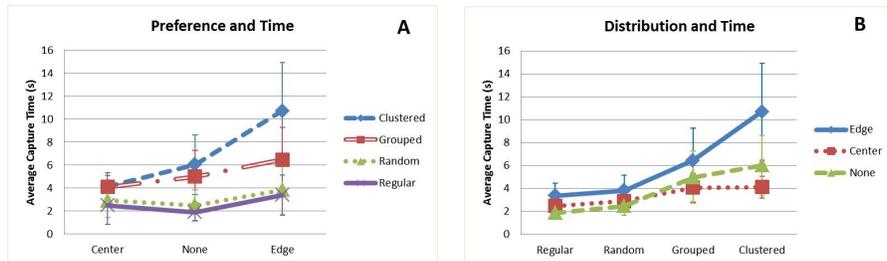


FIGURE 11. Figures A and B illustrate the average time required to reach the prey for a social colony of average size 10 under different preferences (Figure A) and different distributions (Figure B). An uninformed prey was assumed in these simulations.

**6. Conclusions.** This study suggests how spatial positioning in communal webs can affect foraging success. Social spiders are particularly interesting in that the web serves to facilitate cooperative prey capture [1] and also information sharing [24]. In this paper, we developed a model to simulate the movement of *Anelosimus studiosus* during prey capture. The model was fitted to quantitative experimental data taken from four digitized video recordings during feedings in a laboratory

setting. In three of the four videos, the average error between the model and actual data for the variables total time for prey capture and total distance traveled during that time was 5% or less. In the fourth video, the spider reoriented in an opposite direction from that assumed in the model. More data must be taken to determine if this behavior occurs frequently, and if so, this behavior would need to be included in future models. Future models should also investigate the inclusion of actual pauses in the movement of the spider. In the current model, average velocity was used instead of using a ‘running’ velocity and pause times. However, this is an important feature of prey localization for spiders and therefore warrants further investigation.

A model for prey movement was also derived according to observations from spider feedings of flies. A model for an average fly was derived as well as an ‘informed fly’ in which we assumed the fly behaved most efficiently in its escape. Both models in conjunction with the spider model were then used to test a variety of initial spatial configurations for colonies of varying sizes to determine the best spatial orientation for prey capture. The model predictions generally support our hypothesis that these spiders can improve their communal prey capture success employing regular or random distributions, thus increasing their collective foraging area. The model also predicted that if the spiders position themselves around the perimeter of the web they are more successful at capturing prey.

Nonetheless, we found potentially conflicting results when considering the time required to capture the prey under different spatial configurations. While the model often predicted that positioning around the edge of the web led to the highest likelihood of success, that position had the longest time to capture. Further study of how different types of prey behave in these webs, and how spiders handle them, is warranted.

It is important to note, however, that this model only considers foraging success. Optimal positioning would also reflect the relative risk of the spiders being preyed upon [20]. Evidence suggests that exterior positions in spider groups are more exposed to predation [22], again, further study is needed to interpret predictions here with natural observations.

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*E-mail address:* [joynerm@etsu.edu](mailto:joynerm@etsu.edu)

*E-mail address:* [zcrr23@goldmail.etsu.edu](mailto:zcrr23@goldmail.etsu.edu)

*E-mail address:* [wattsj@goldmail.etsu.edu](mailto:wattsj@goldmail.etsu.edu)

*E-mail address:* [jonestc@etsu.edu](mailto:jonestc@etsu.edu)