**Integrating computational science with biology to study collective animal behavior**

Biologists have spent decades studying collective animal behavior due to its important implications for social intelligence, collective cognition, and its potential applications in automated control of distributed systems(Couzin 2009). Of the numerous forms of collective animal behavior, swarming behavior is one of the most striking examples observed in nature. After decades of research on swarming behavior, researchers have produced numerous hypotheses about the selective benefits of swarming behavior, such as increased mating success or improved defense against predators (reviewed in Krause & Ruxton 2002). However, due to the long generation times in swarming animals, studying the *evolution* of swarming behavior has often proven difficult(Jeschke & Tollrian 2007). To overcome this difficulty, I developed a computational model that simulates digital organisms with evolving behaviors to examine which of the proposed selective benefits favor the evolution of swarming(Olson et al. 2012; also described in Previous Research statement). Digital systems have previously been used to provide key insights into core evolutionary processes(Lenski et al. 2002), and several well-known studies have adopted digital systems as a method to study swarm behavior (e.g., Couzin et al. 2005). With the computational model I developed, I determined that the *confusion* *effect*, where swarming prey confuse and thereby reduce the attack efficiency of their predators, provides a sufficient (but not necessary) selective advantage to evolve and maintain swarming behavior in prey.

In a recent review of predator-prey systems with swarming prey, Jeschke and Tollrian (2007) noted that predators appeared to become confused by swarming prey in 16 of the 25 systems reviewed. However, it remains unclear what aspects of swarming behavior confuse the predator. To ameliorate this challenge, Ioannou et al. (2012) designed an innovative model system where simulated prey with hard-coded swarming behaviors are projected onto the side of a fish tank containing a single predatory fish, and demonstrated that the predatory fish respond to the simulated prey as if they were real prey. This system offers animal behavior researchers unparalleled control over the interactions between predators and swarming prey.

Here I propose an extension of Ioannou et al. (2012)’s system in which the simulated prey behaviors *evolve* in response to selective pressures applied by the biological predator, to test mechanistic hypotheses regarding how swarming evolves. This new system will enable me to address hypotheses about swarm behaviors in response to biological predators on an *evolutionary* scale, as opposed to studying swarming behavior at a fixed time point in evolutionary history. I will use my proposed model to examine the predator-prey dynamics between swarming water fleas (*Daphnia magna*) and predatory three-spined sticklebacks (*Gasterosteus aculeatus L.*), as in Milinski & Heller (1978), and address the following hypotheses:

**Hypothesis I:** *Swarming behavior decreases predator attack efficiency*. Previous work has suggested that Daphnia swarming behavior decreases the attack efficiency of predatory three-spined sticklebacks(Milinski & Heller 1978). Here I will first seek to confirm this hypothesis in my system by projecting a group of 50 simulated prey with evolving behaviors onto the side of a fish tank containing a single stickleback.

All experiments will be repeated in replicate 30 times. During each experiment, I will measure the number of attacks (measured as the number of capture attempts on the simulated prey) and the latency to the first attack by the stickleback on the simulated prey. With these data, I will compare the mean attack efficiency (# successful attacks / total # attacks) and time to first attack attempt on the simulated prey between experiments to detect if there are significant differences in the predator’s response to the experimental prey behaviors. If swarming behavior produces a significant difference in the measured responses from the predator, this would support the notion that predators that feed on swarming prey are affected by the confusion effect.

**Hypothesis II**: *Larger swarms reduce predator attack efficiency moreso than smaller swarms*. Next, I will repeat the experiment with the pre-evolved cohesive swarms from the first set of experiments and vary the number of simulated prey in the swarm (swarm sizes from Jeschke and Tollrian (2007): 5, 15, 25, 50, 100). This hypothesis predicts that the sticklebacks will perform fewer successful attacks and take longer to attack larger swarms (e.g., of size 20, 40, and 80) than smaller swarms (e.g., of size 5 and 10). If this prediction holds, this is an indication that larger swarms increase the difficulty of predator attacks on individual prey, which is likely the result of the confusion effect. Alternatively, if there is no significant difference in predator response between experiments, then this would provide further evidence that predators that feed on swarming prey are not affected by the confusion effect. Lastly, if predators instead prefer to attack larger swarms than smaller swarms, then this would indicate that the confusion effect is not magnified by swarm size, and attacking larger swarms is advantageous because there are more prey to potentially be captured per attack.

**Hypothesis III**: *The structure of the predator’s visual system plays a significant role in the efficacy of the confusion effect*. Lastly, I will test the hypothesis proposed in my previous work that the efficacy of the confusion effect as a defensive mechanism can be reduced if the predator evolves a more focused visual system(Olson et al. 2012). Benthic-limnetic stickleback species pairs exhibit significantly different foraging behavior: the *limnetics* typically feed on plankton in clear water near the surface of lakes, whereas the *benthics* feed on small invertebrates in the cloudy water on the lake floor(Ostlund-Nilsson et al. 2006). As in the previous experiments, I will project 50 simulated prey onto the side of separate fish tanks for each species. This hypothesis predicts that the limnetics will exhibit significantly higher attack efficiency and shorter attack latencies than the benthics due to the limnetic’s specialized, focused visual system for hunting agile prey in clear water. Thus if this prediction holds, the confusion effect could also provide a selective advantage for predators that feed on swarming prey to evolve a narrow, focused retina to reduce the efficacy of the confusion effect.

**Intellectual Merit**: The interdisciplinary research proposed herein significantly advances the field of behavioral science by merging a biological system with an *evolving* computational system. This new model offers behavior researchers unprecedented experimental control over the predator-prey dynamics of the system and the ability to test hypotheses about the *evolution* of behavior in response to predation. Michigan State University is a prime location to perform this research because it offers a lab focused on stickleback research to host my project (Dr. Jenny Boughman’s lab); a computational lab with a strong track record of studying evolutionary processes and evolving animal behavior *in silico* (my advisor, Dr. Chris Adami’s lab); and a heavy concentration on interdisciplinary research between biologists and computer scientists (NSF BEACON Center, and collaboration with Dr. Fred Dyer). My previous work on research directly related to my proposed research has prepared me to design and complete these experiments, and I am already in the process of presenting and publishing the results of my previous research in venues such as the ALife XIII conference, the SwarmFest 2012 conference, and journals such as the Proc. Nat’l Acad. Sci.

**Broader Impacts:** Increasing our understanding of collective cognition and decision-making in animals has applications in Artificial Intelligence, Artificial Life, Robotics, distributed control systems, and many other fields that seek to understand how individual behaviors can result in emergent phenomena(Couzin 2009). Additionally, this work will provide a model platform for directly interfacing biological research with computational research, which is a growing trend in biology(Ioannou et al. 2012). In addition to distributing my research through conventional academic means, I will continue to actively share my research and passion for science with college undergraduates and K-12 audiences through my involvement in the NSF BEACON Center’s outreach program, as well as science fairs and volunteering at the local museum.

**References**

Couzin ID, Krause J, Franks NR, Levin SA (2005) Effective leadership and decision-making in animal groups on the move. *Nature* 433:513-516.

Couzin, ID (2009) Collective cognition in animal groups. *Trends in Cognitive Sciences* 13:35-43.

Ioannou CC, Guttal V, Couzin ID (2012) Predatory fish select for coordinated collective motion in virtual prey. *Science*337(6099), 1212-1215.

Jeschke JM, Tollrian R (2007) Prey swarming: which predators become confused and why? *Animal Behaviour* 74:387-393.

Krause J, Ruxton GD (2002) Living in Groups. *Oxford University Press*, USA.

Lenski RE, Ofria C, Pennock RT, Adami C (2003) The evolutionary origin of complex features. *Nature* 423:139-144.

Milinski M, Heller R (1978) Influence of a predator on the optimal foraging behaviour of sticklebacks (*Gasterosteus aculeatus* L.). *Nature*275, 642-644.

Olson RS, Hintze A, Dyer FC, Knoester DB, Adami C (2012) Predator confusion is sufficient to evolve swarming. *In review.* Preprint: http://arxiv.org/abs/1209.3330

Ostlund-Nilsson S, Mayer I, Huntingford FA (2006) Biology of the Three-Spined Stickleback. *Taylor & Francis*.