**Testing the *confusion effect* hypothesis with swarming digital organisms**

Swarming behavior is one of the most striking examples of collective animal behavior. Consequently, biologists have spent decades studying swarming behavior due to its implications for social intelligence, collective cognition in animals, and its potential applications in automated control of distributed systems1. These decades of research have produced numerous hypotheses about the selective benefits of swarming behavior, such as increased mating success or improved defense against predators (reviewed in [2]). However, due to the long generation times in swarming animals, studying the *evolution* of swarming behavior has often proven difficult3. 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 swarming4. Digital systems have previously been used to provide key insights into core evolutionary processes5, and several well-known studies have adopted digital systems as a method to study swarm behavior (e.g., [6]). 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 noted that predators appeared to become confused by swarming prey in 16 of the 25 systems reviewed3. However, it remains unclear what aspects of swarming behavior confuse the predator. To ameliorate this challenge, Ioannou et al. 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 fish7, offering animal behavior researchers unparalleled control over the interactions between predators and swarming prey.

I propose an extension of Ioannou et al.’s system in which the simulated prey behaviors *evolve* in response to selective pressures applied by the biological predator. This new system will enable behavior researchers to address hypotheses about swarm behaviors in response to biological predators on an *evolutionary* scale, as opposed to studying a fixed swarming behavior as in the current system. I will use my proposed model to examine the predator-prey dynamics between swarming water fleas8 (*Daphnia magna*) and predatory three-spined sticklebacks (*Gasterosteus aculeatus L.*) in Dr. Jenny Boughman’s laboratory at Michigan State University, and address the following hypotheses:

**Hypothesis I:** *Swarming behavior decreases predator attack efficiency*. Previous work has suggested that water flea swarming behavior decreases the attack efficiency of predatory three-spined sticklebacks8. As a first step, I will seek to confirm this hypothesis by projecting a group of 50 simulated prey with evolving behaviors onto the side of a fish tank containing a single stickleback. As a null experiment, the simulated prey will move around the fish tank randomly in an uncoordinated manner. For the alternative experiments, the simulated prey will exhibit pre-evolved swarming behavior: one experiment with loosely grouping prey, and another experiment with cohesive swarming behavior. This hypothesis predicts that the prey that move around randomly instead of grouping will experience significantly more successful attack attempts and shorter attack latencies due to the predator’s preference to attack lone prey.

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 this 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 does not produce a significant difference in the measured responses from the predator, then this would suggest that predators that feed on swarming prey are not 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 [3]: 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.

**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 system4. The benthic-limnetic three-spined stickleback species pair 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 floor9. 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.4

**Broader Impacts:** The benefits of increasing our understanding of collective animal behavior are not limited to the field of behavioral science. Indeed, knowledge about 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 phenomena1. Additionally, this work will provide a model platform for directly interfacing biological research with computational research, which is a rising trend in biology7. 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**

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

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

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

[4] Olson RS, Hintze A, Dyer FC, Knoester DB, Adami C (2012) Predator confusion is sufficient to evolve swarming. *In review, Proc. Nat. Acad. Sci*.

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

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

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

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

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

**QUESTIONS FOR REVIEWERS**

* Are you convinced that this research is worthwhile from the first 2-3 paragraphs?
* I know I need to cut something out, but what should I cut out?
* Do I need to expand my Broader Impacts?