Causes vs Benefits in the Evolution of Prey Grouping

Ritwik Biswas\textsuperscript{1,4}, Charles Ofria\textsuperscript{1,2,3}, David M. Bryson\textsuperscript{1} and Aaron P. Wagner\textsuperscript{1}

\textsuperscript{1} BEACON Center for the Study of Evolution in Action, Michigan State University, East Lansing, MI 48824, USA
\textsuperscript{2} Department of Computer Science and Engineering, Michigan State University, East Lansing, MI 48824, USA
\textsuperscript{3} Program in Ecology, Evolutionary Biology, and Behavior, Michigan State University, East Lansing, MI 48824, USA
\textsuperscript{4} College of Engineering, The University of Michigan, Ann Arbor, MI 48109, USA

Abstract

The presence of predators alters the evolutionary pressures acting on prey populations, often driving them to engage in new behaviors in order to avoid being the target of an attack. One common anti-predator behavior is group formation, which can reduce the odds of any individual prey being the target of a given attack, typically scaling inversely with the number of prey in the group. This “dilution effect” is often hypothesized to be the primary driver of prey group formation as an anti-predator strategy. However, groups may help with predator avoidance in other ways as well. For example, prey behaviors or physical characteristics that visually confuse predators may reduce their ability to target an individual and make a kill. Indeed, some have suggested that the “predator confusion” effect alone is sufficient to drive the evolution of grouping in prey. Here we examine coevolving populations of predators and prey using the Avida digital evolution platform. We evaluate the relative importance of these two potential drivers of the evolution of prey grouping and show that the dilution effect, an inherent property of most prey groups, readily creates the pressures necessary for the evolution of prey grouping. In contrast, we found no evidence that predator confusion plays a significant role in prey group formation. Instead, the dilution effect alone is indicated as the primary driver of anti-predator prey grouping strategies.

Introduction

Organism clustering is recurrent in nature, as is demonstrated by diverse species, such as fish, cattle, and bees (Patridge 1982, Omholt 1987). Much literature has dealt with the environmental factors and selective pressures favoring such strategies (Jakobsen et al 1988, Mooring et al 1992). For example, bees huddle in high-density groups in order to conserve heat energy and ultimately increase their lifespan (Nagy et al 1976). However, clustering is also hypothesized to be an evolutionary favored strategy in the context of predation avoidance (Kunz et al 2006), and is sometimes considered the most influential facilitator of the evolution and expression of cooperative and grouping behaviors in prey populations (Krams 2010). From the perspective of an individual prey, spatial grouping reduces the chance of being the target of a predator attack (Turner et al 1986). This simple dilution effect is thought to be one of the primary selective pressures favoring the evolution grouping in prey, a hypothesis supported by empirical models (Foster 1981, Turner et al 1986).

Although dilution is believed to be a dominant force favoring prey grouping, additional factors such as probability of detection, coordinated evasion, or predator confusion could play additional, potentially critical, roles (Reynolds 1987). With respect to the last, clustering by prey is often argued to confuse predators as to the nature of the group and the individuals in it (Kunz et al 2006, Cosner et al 1999, Jeschke and Tollrian 2007). Additionally, prey may exhibit confusing behavioral or morphological traits (Relyea 2001), e.g. rapid and erratic changes in directions or confusing flashes of color. The evolution of these confusion traits may reduce the overall odds of a predator being able to successfully target individuals in the group for an attack. As such, others have suggested that predator confusion creates selective pressure for prey grouping (Millinksi 1979).

While there is ample evidence indicating that confusion traits can benefit individuals already living in groups, it is not clear whether those benefits were necessary for the evolution of grouping strategies. This uncertainty arises for several reasons: (1) The dilution effect is an inherent property of most prey groups (Foster 1981, Delm 1990). It does not require the evolution of additional behavioral or morphological traits in order to come into play. By contrast, the confusion effect relies on the existence of additional prey traits that confuse predators once prey are in groups (Krakauer 1995, Millinksi 1984). Thus it would be a large evolutionary leap for confusion to be the factor initially favoring grouping. (2) Predators evolve sophisticated sensory and behavioral mechanisms for detecting and pursuing prey (Bengtson 2002, Abrams 2000). If predators and prey are locked in perception-confusion arms-races (Dawkins et al 1979), we would expect predators to evolve traits to counter confusion effects, thus weakening their impact over time. The strength of the dilution effect, however, is dependent only on the number of prey in a group and the number of predators attacking. Thus, the strength of its effect should be expected to remain stable over evolutionary time. (3) The confusion effect presupposes that predators can be confused by prey behaviors (Landeau et al 1986, Millinksi 1979, Krakauer 1995). E.g., whales are unlikely to be dependent on the sorts of traits that fish might exhibit to confuse predators closer to their own body size. Equally, blind predators will not be confused by visual deceptions. Dilution, however, is not dependent on any such
close mapping between predator and prey traits, and thus should be a factor more commonly at play. (4) To date, no studies have evaluated the effects of confusion on the evolution of grouping strategies without removing the effects of dilution. E.g., while Kunz et al (2006; similarly also Olson et al. 2013) showed that confusion is sufficient to evolve grouping in prey, they show this only for clonal groups – a rare and specialized circumstance which has the side effect of removing the dilution effect.

In order to understand what conditions push prey to evolve and exhibit grouping behaviors, we tested for the effects of both dilution and predator confusion in a coevolving predator-prey system. We show that while the dilution effect readily promotes the evolution of prey grouping, no mechanism of confusion had any impact on clustering behavior. Note that we discuss these traits in the context of prey ‘grouping’, ‘clustering’, or ‘herding’. We consider such life strategies to be distinct from ‘swarming’, which is a more specialized behavior that is explicitly responsive to behavioral stimuli such as the presence of predators (Okubo 1986) or expectations of finding food (Salge & Polani 2011). That is, hyenas live in groups (Karanth et al 2000), but clearly don’t swarm. Wildbeest live in groups, not swarms, but may swarm when attacked (Silk 2007, Gueron et al 1993). Bees live in groups and swarm to change nests (Beekman & Ratnieks 2000, Boreham & David 1987). Some fruit flies swarm to find mates, but live life alone (Sivinski et al. 1997).

Because other studies evaluating the confusion effect have demonstrated grouping as a life-history strategy (Kunz 2006, Olson et al. 2013), not as a behavioral response to stimuli, we focus on factors favoring the evolution of grouping.

**Methods**

We used the digital evolution software platform Avida (Oftria et al. 2009; Bryson & Oftria 2013) to evaluate the effects of dilution and confusion on the evolution of grouping as an anti-predator behavior. Avida is valuable for this kind of work in carrying the main benefits of simulations, for example, rapid generation times and full control over configuration options. However, unlike in population genetic simulators and genetic algorithms, evolution in Avida is unrestricted and unguided, not requiring the use of explicit selection functions to impose fitness values on individuals. Instead, Avida is utilizes natural selection, with an organism’s fitness being determined entirely by its ability to survive, interact with other organisms (Fortuna et al. 2013) collect needed resources (Walker & Oftria 2012), and reproduce. Avida is an instance of real evolution occurring in a virtual world (Pennock 2007).

Avida has been successfully used in many experiments involving antagonistic coevolution (e.g., Zaman et al. 2011; Fortuna et al. 2013) as well as altruism (e.g., Goings et al. 2004; Clune et al. 2011) and cooperation (e.g., Knoester et al. 2008; Goldsby et al. 2012, 2014)

Avida organisms consist of a sequence of genetic instructions. An organism must execute genomic instructions to take individual actions, with the dynamic series of actions collectively describing the organism’s traits and behaviors (i.e. its phenotype). Potential actions include those governing the sensing and processing of information (e.g., sensory information about other organisms or objects), movement, and reproduction, as well as instructions controlling internal logic and the order in which genetic instructions are executed. During reproduction, a parent’s genome is copied into its offspring, with experimenter-defined mutation probabilities for substitutions, deletions, and insertions. If a substitution or insertion mutation does occur, a new instruction, randomly selected from the full set of all available instructions, is placed into the offspring genome. As a consequence of mutational changes, organisms frequently have new genotypes and express novel phenotypes, yielding associated intra-population variation in fitness. Taken together, these conditions allow Avida to satisfy the necessary conditions for adaptive evolution via natural selection: replication, inheritance, variation, and differential fitness.

**Environment**

Avida environments are built on a grid-cell base, with organisms having an effective physical size of one cell. Thus, all organisms have potential neighbors on eight sides. Here, unlike in most prior Avida experiments, multiple organisms can simultaneously occupy any given cell so collisions between organisms do not need to be considered. (Wagner et al. 2013). All experiments were conducted in a 101 by 101 grid-cell toroidal environment. The toroid design allows for ‘borderless’ environments, eliminating any artifacts due to boundary or related effects. An additional difference from previous predator-prey Avida experiments (Lehmam et al. 2013, Wagner et al. 2013, Fish et al. 2014) is that resources in the environments used here were unlimited and ubiquitous.

**Reproduction**

In these experiments, organisms were required to eat at least one unit of resource before they were allowed to replicate. Unlike in most other Avida experiments where organisms must individually copy each genomic instruction, we allowed them to execute a single genomic “repro” instruction. Meeting these requirements for reproduction could be trivial, and thus we also set a minimum age for reproduction of 5,000 instructions executed, or approximately 167 updates. Updates are the primary measure of time in Avida, with each organism, on average, executing 30 instructions per update. Organisms can evolve to use up to four execution threads (Oftria et al. 1999), allowing them to process multiple portions of their genome at once. In simple terms, evolving to use multiple threads allows for near-simultaneous execution of multiple actions (akin to walking while chewing gum).

In effect the primary consequence of having a minimum age, with no other major requirements for reproduction, is to ensure that the evolutionary pressure to which prey populations are reacting is simply survival in the face of predation threats. Upon reproduction, there was a 25% chance of a single genomic instruction substitution occurring in the offspring, with 5% chances each for single insertion and deletion mutations. Organisms were born into the cell faced by their parent. Organisms were removed if they did not reproduce before reaching the maximum age limit of 6,000 cycles (~200 updates).
Predation
The basic mechanics of the predator-prey system in Avida have been described in (Fortuna et al. 2013, Lehmann et al. 2013, Wagner et al. 2013, Fish et al. 2014). In brief, all organisms are born as ‘juveniles’ that have not expressed any of the behaviors that facilitate resource consumption or predation. In order to consume resources, and be classified as prey, juveniles must execute a ‘set-forage-target’ instruction. Likewise, any organism that attacks a prey organism (or a juvenile) are automatically classified as a predator. As an alternative to these mechanisms, juveniles can choose to adopt the same predator/prey status as their parent if the parent had executed a ‘teach-offspring’ instruction and the juvenile executed a ‘learn-parent’ instruction. In order to promote the early adoption of a prey or predator classification, juveniles in these environments were killed if they attempted to move.

Each organism has a position on the world grid and can face any of the 8 cardinal or diagonal directions. Predation occurs when an organism executes an ‘attack’ instruction while there is a prey or juvenile organisms in the cell they are facing. If there are multiple non-predator organisms in the faced cell, a random organism is targeted. If a valid target organism does occupy the faced cell and a kill is made, the predator gains all of the resources accumulated by that prey, including those in the form of stored resources (typically in the form of ‘bonus’), completed tasks, and merit (see below). Via that intake of completed prey tasks, predators satisfied the ‘eat once’ prerequisite for reproduction if prey they consumed had fed from the environment. Classified predators were prevented from resetting their forage targets to become prey.

Movement
Because the resources in these experimental environments were always available, prey were under no pressure to move in the absence of predators. However, since predators must evolve out of the ancestral prey population, either prey need to be mobile in order for predators to evolve into the system, or predators must move immediately from the point where they first evolve. Accordingly, we rewarded prey for up to 10 executions of the move instruction by applying small increases in how quickly they could execute their genomic program. In Avida, an organism’s merit determines the rate it can execute instructions. That is, an organism with a merit of two will execute twice as many instructions per update as an organism with a merit of one (all organisms are born with a merit of one). Thus prey could increase their metabolic rate simply by moving up to 10 steps, adding one to their merit with each step. This simple mechanism introduced pressures for prey to realize the minimum initial movement rates to facilitate the evolution of predators from the populations.

Populations
Because resources did not limit the number of prey in an experiment, we set a cap of 1000 organisms for each evolving population in every treatment (see below). When the birth of a new organism would have caused the population size to exceed this level, a random organism was removed from the existing population. Additionally, we set a minimum prey population size of 500, below which predation was prevented. In effect, hitting this minimum level serves only to force predators to retry an attack as reproduction in the system is continuous and so another prey was likely born elsewhere in the system almost immediately following a prevented attack. To standardize levels of predation pressure across trials, predator populations were limited to 50 or 100 individuals (as indicated in the results). If classification of a new predator would push the predator population above the set limit, a randomly selected predator was removed from the population.

Sensors
Evolved strategies can make use of visual sensors capable of providing information about the external environment (i.e. they can evolve sight). The sensory apparatus in Avida is designed to be highly configurable, permitting the evolution of complex sensory strategies. Overall, the sensory system includes four controlling inputs and eight information outputs. Outputs place descriptive integers into particular registers and organisms can determine which registers receive which types of information. Mechanisms allowing the organisms to process and react to that information must also be evolved. Inputs allow organisms to choose to collect information about particular types of objects (e.g., predators vs. prey) over a specified distance. Additionally, organisms can use their sensors to collect more information about a specific object (e.g., the closest of the specified type or one at a specified distance), or a count of all objects of that type in their visual field. Sensory outputs include seen object counts, object values (e.g., value of an environmental resource, or ‘fitness’ of a prey in terms of their collected resource level), the identity of the closest object of the type searched for in the visual field, the type of object being described (e.g., predator vs. prey), and any group identifiers for the first organism seen (see ‘Opinion Confusion’, below). Sensors return data from a 45-degree visual field. In these experiments, maximum sight distance was set to 10 cells. A complete list of sensor default behaviors is available in the Avida documentation. Note that ancestral organisms have no sensors. It is entirely up to evolution to discover pathways for vision, a discovery that will not be realized unless vision is a useful adaptation.

Treatments
In order to evaluate the effects of predation pressures on the evolution of prey grouping behaviors, we evolved prey under eight different sets of conditions for one million updates, realizing ~5,800 prey generations of evolution in each. We initialized all 30 replicates of each treatment by introducing a single, simple prey organism that repeatedly fed, turned randomly, moved, and attempted to reproduce. Treatment names indicated with italics below correspond with their labels in Figure plots.

No Predators (control): In the primary control, prey evolved in environments in which we prevented predators from evolving into the system by preventing the ‘attack’ instruction from functioning.

Predators: In our baseline predator treatment, predators and prey coevolved without any induced experimenter interference. This treatment offers the primary test of whether predators cause prey to evolve grouping strategies.
**No Vision:** In this treatment, the visual sensors for all organisms were prevented from functioning. Thus, this treatment, when compared with the Predators treatment, offered an indication of the importance of visual information in predator decision-making. That is, if prey form groups even when predators cannot see them, prey are clearly not grouping in order to visually confuse them. Instead, prey grouping here would indicate the dilution effect alone was responsible for prey grouping.

**Artificial Confusion:** In two treatments we established artificially enforced ‘confusion’ effects in order to allow direct comparison with previous studies (e.g., Olson et al. 2013). We do not contend that either of these treatments actually induces confusion (in contrast with Olson et al. 2013). Rather, they attempt to mimic the hypothesized outcomes of an attack if predators are confused. Specifically, in the Artificial Confusion treatment, the odds of a predator successfully making a kill, given an attack, is set to 1.0 – (0.10 * r), where r is the number of prey neighboring the targeted prey. Thus a prey would be completely protected if there were 10 other prey in its cell or in neighboring cells. Similarly, in the Artificial Confusion Inverse treatment, the odds of a predator making a successful kill were set to 1 / r. These odds operate independent of a predator’s true understanding of visual cue information. Thus, it enforces a hypothesized outcome of confusion, even in the absence of actual predator confusion.

Visual confusion: In the three remaining treatments, we created conditions that would allow prey to evolve behaviors that would, explicitly, confuse predators by reducing the accuracy of sensory information. Specifically, each of these three treatments introduces a probability that the predator will receive random data from visual sensors when looking at prey, with the probability being dependent on the behavior of the prey seen. If triggered, the visual outputs for determining the distance to the first prey in sight, the counts of prey in the visual field, the value (‘fatness’) of the first prey, and the group id (‘opinion’, see below) of the first prey would all be random numbers. In effect, these treatments offer opportunities for prey to evolve behaviors that ‘blur’ the vision of their attackers.

In the Density Confusion treatment, the odds of predators receiving random visual inputs was, as in the Artificial Confusion treatment, set to 1.0 – (0.10 * r). Unlike the Artificial Confusion treatment, however, this equation did not directly define the odds of an attack succeeding or failing.

Similarly, in the Opinion Confusion treatment, the odds of predator receiving confused visual information was set to 1.0 – (e / o), where e is the number of opinions being expressed by the nearest prey and its neighbors and o is the total number of opinions possible. Opinions effectively allow prey to form group identities, outside of the predator-prey classification system. Here, there were four possible opinions (0,1,2,3). Accordingly, a predator will always receive confused visual information whenever four opinions are being simultaneously expressed in the group of prey around the prey nearest the predator. Opinions are set whenever an organism executes a ‘join-group’ instruction, with the modulus of the value in the associated register determining the opinion used.

Finally, we included a treatment in which the physical orientation of prey determined the odds of a predator’s vision being confused. Specifically, in the Facing Confusion treatment, the odds of a predator confused visual information was set to 1.0 – (f / 8), where f is the number of different directions the prey (those surrounding the prey nearest the predator) are facing.

**Measuring Grouping**

In order to quantify the realized levels of prey clumping, we used a density-based measure that considered the position of all organisms in the two-dimensional grid environment. Since multiple organisms could occupy any cell, we calculated prey clumping as \( 1 – (n / p) \), where n is the number of unique cells occupied and p is the total number of prey organisms in the system. Thus, a clumping value approaching 1.0 indicates that all prey were in the same single cell (a maximum grouping scenario), a value of 0.5 would indicate that prey were clumped with an average of two individuals per cell, and a value of zero would indicate little to no clumping (each organism in their own cell).

![Figure 1: The dilution effect alone drives the evolution of prey grouping strategies. Prey (blue points) evolved in the absence of predators (A) show no tendencies toward spatial grouping. However, when coevolving with predators (red; B-D), the dilution effect quickly drives prey to form large and tight groups for protection, even in the absence of any confusion effects. Fewer ‘visible’ prey indicates that they are sharing cells (overall population sizes are consistent across images).](image-url)
Software
We used Avida version 2.13 for all experiments, using the EX virtual hardware as in Wagner et al 2013 and Lehmann et al. 2013. Among other modifications to the base Avida system, the EX virtual hardware sets the definitions and capacities for organisms to evolve predation and visual sensors. Data were post-processed using Python 2.7.1. Statistical analyses and plotting were conducted in R version 2.15.2 using the ggplot2 library.

Results
After 1 million updates of evolution, even in the absence of any confusion effects, the presence of predators pushes prey to evolve aggregation strategies (Figure 1, online video at http://youtu.be/18dQyroyA8S), with the measured level of prey clumping increasing from a mean of 0.068 (min = 0.05, max = 0.093, sd = 0.009) with No Predators to 0.485 (min = 0.017, max = 0.948, sd = 0.273) with Predators (Figure 2).

When predators’ odds of making a kill are artificially reduced based on local prey densities (i.e. Artificial Confusion and Artificial Confusion Inverse), relatively to the default Predators treatment, clumping levels cover a narrower breadth of values (mean = 0.402, min = 0.103, max = 0.934, sd = 0.193 for Artificial Confusion, mean = 0.309, min = 0.0704, max = 0.844, sd = 0.172 for Artificial Confusion Inverse). However, even these imposed reductions in attack success rates do not significantly increase grouping; prey clumping values remain in the range of the majority of the simpler, and far more natural, Predators treatments. Similarly, Density, Opinion (prey type), and Facing confusion mechanisms did not substantially impact the extent of clumping (Density: mean = 0.500, min = 0.030, max = 0.951, sd = 0.254; Opinion mean = 0.549, min = 0.042, max = 0.956, sd = 0.273; Facing mean = 0.550, min = 0.034, max = 0.956, sd = 0.281). Additionally, extending the maximum sight distance to 100 also had no appreciable effect over that introduced simply by the introduction of predation pressures (Figure 4). At the same time, increasing the maximum predator population size to 100 greatly extended the spread of the data, with fewer prey populations evolving to form tight groups (Figure 4). We speculate that the latter effect is related to reductions in the protection provided by the dilution effect when predator attack rates are very high (Figure 5).

The lack of difference between the Predators and No Predator Vision treatments further highlights the strength of...
Specifically, we explored differences in evolved tendencies of grouping in prey. We evaluated the factors contributing to the natural evolution of swarming. After all, if predators cannot see prey, a proportion of their total lifetime instruction executions. Values for individual populations are shown with small grey points. When attack success is artificially reduced (Artificial Confusion treatments), median rates of sensor use by predators sits near zero. Otherwise, predators evolve to use sight even though it is not a requirement for successful predation. Values above zero for No Predator Vision treatments indicate predators that used their sensors while still in a juvenile state, presumable due to drift.

Additionally, it is useful to realize that the root evolutionary cause of prey aggregations is not a cooperative strategy. Instead, as it is ultimately a consequence of the dilution effect, the initial selective pressures for grouping arise from selfish movement strategies for minimizing one’s own probability of being subject to an attack. While this self-interest will drive prey to aggregate, the resulting ‘swarms’ simply represent groups of organisms exhibiting correlated, selfish strategies, not cooperative behaviors.

The limited effects of blinding predators and of increasing potential sight distance highlights additional reasons why confusion behaviors are of only marginal importance in the evolution of swarming. After all, if predators cannot see prey, prey cannot visually confuse them. Moreover, because predators and prey coevolve, arms race dynamics dictate that predators will evolve behavioral counter-measures to prey anti-predator behaviors. Accordingly, attack rates are expected to remain consistent across treatments, as they do here (Figure 3). More broadly, in order for there to be a confusion effect, predators need to evolve visual perception. The dilution effect however, is simply achieved whenever prey aggregate, whether intentionally or by chance, thereby “diluting” any one prey’s odds of being targeted, without diminishing the overall chances of a predator making a kill. The dilution effect requires fewer conditions and is, on the whole, a simpler and more fundamental effect (Foster 1981, Delm 1990).

Discussion

We evaluated the factors contributing to the natural evolution of grouping in prey species coevolving with predators. Specifically, we explored differences in evolved tendencies of prey to form groups in order to gain protection from predators as a consequence of simple dilution, naturally evolved confusion behaviors, and artificially induced confusion effects. Our results clearly show that grouping tendencies increase with the introduction of predators, regardless of any confusion effect or behavioral treatments (Figure 2). This increased tendency to aggregate appears to be due entirely to the inherent dilution effect.

Figure 5. Maximum attack rates scale with predator densities, but not sight distance. Shown are the mean (large points) and median (small boxes) attack rates under treatments that extended the maximum sight distance of organisms out to 100 cells (the width and height of the world) and, separately, treatments that raised the predator population cap from 50 to 100. Values for individual populations are shown with small grey points. No Predators, Predators, and Density Confusion data are repeated here (from Fig. 3) for comparison. In general, very high attack rates may dissolve any benefits accrued via the dilution effect, thereby reducing the tendency of prey to aggregate.

Overall, these results indicate that the presence of predators alone induces prey clumping, primarily due to the dilution effect. Furthermore because they are already clumped, any confusion processes have no impact on the tendency to form aggregations.

Effects of the treatments on attack rates experienced by prey (Figure 3) tell a story similar to that of clumping behavior: dilution effects dominate confusion effects and once clumped, prey populations do not further substantially reduce attack rates via the evolution of any confusion behaviors. Mean (min-max; sd) attack rates for each treatment were Predators = 0.115 (0.003 - 0.294; 0.089), No Vision = 0.0942 (0.006 - 0.259; 0.0673), No Predator Vision = 0.0812 (0.003 - 0.372), Artificial Confusion = 0.0474 (0.0 - 0.152; 0.038), Artificial Confusion Inverse = 0.0395 (0.0 - 0.101; 0.030), Density Confusion = 0.0866 (0.0 - 0.319; 0.880), Opposition Confusion = 0.101 (0.005 - 0.262; 0.0787), and Facing Confusion = 0.0948 (0.002 - 0.339; 0.0819).

Figure 6. When permitted, predators evolve vision for hunting in most populations. Shown are the evolved mean (large points) usage of visual sensors by predators as a proportion of their total lifetime instruction executions. Values for individual populations are shown with small grey points. When attack success is artificially reduced (Artificial Confusion treatments), median rates of sensor use by predators sits near zero. Otherwise, predators evolve to use sight even though it is not a requirement for successful predation. Values above zero for No Predator Vision treatments indicate predators that used their sensors while still in a juvenile state, presumable due to drift.
Although they do not promote the evolution of grouping behaviors, various forms of confusion may still have subtle effects on prey behaviors. Specifically, while dilution directly controls the probability of being selected and attacked by a predator, confusion behaviors can reduce the probability of being killed given an attack. Thus, it is the dilution effect that drives the evolution of anti-predator prey grouping strategies. Once prey are grouping, however, the further evolution of confusion behaviors can continue to benefit prey, even if they are not responsible for the evolutionary origin of grouping per se. In other words, dilution causes prey to evolve swarming, while confusion behaviors can provide additional benefits once grouped.

Acknowledgments

We thank G. Wright for his assistance in developing components of the experimental system and members of the MSU Digital Evolution Laboratory for fruitful discussion. This work was supported by the BEACON Center for the Study of Evolution in Action (NSF Cooperative Agreement DBI-0939454) and the Michigan State University Institute for Cyber Enabled Research.

References


