

Coevolution in Hide and Seek: Camouflage and Vision

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Abstract

Predator-prey interactions are one of the most common co-evolutionary dynamics in Nature. We consider a model of the coevolution of prey appearance and predator vision, where a successful result is visually apparent. While using a neurophysiologically-based model of vision and a rich developmental process for prey patterning, we show that predator-prey coevolution can maintain engagement. Backgrounds with large regional differences generally lead to prey that appear as mixtures of the regions. Finally, we find that engagement between predators and prey is supported by greater background complexity.

One of the most visually-striking phenomena in predator-prey coevolution is prey crypsis, the ability of prey to avoid detection by predators. Chameleons and cuttlefish take this behavior to the extreme and physically alter their pigmentation to match their environment, which can even be realized synthetically in robots (Morin et al., 2012). However, prey crypsis is often manifested as static pigmentations, such as stationary Turing patterns (Turing, 1952), that are selected for being advantageous in particular environments. Inspired by Bond and Kamil (2002), where blue jays are used to interactively evolve moth phenotypes, we study the effect of background complexity on the coevolution of prey appearance and predator vision.

There is an intimate coevolutionary relationship between predator vision and prey appearance. Visual systems are generally adapted for stimuli that exert selective pressure on the organism, such as food, prey, predators, and mates. Even when visual systems have adapted to attenuate visual signals from their relevant stimuli, there is still the challenge of visual attention. Visual attention can be roughly thought of as a way of prioritizing a visual field based on interest. Improper allocation of visual attention can mean the difference between catching dinner or going home hungry.

In this research we study the coevolution of prey appearance and visual attention in predators. Prey appearance is evolved via genetic programming, such as in (Sims, 1991a; Reynolds, 2011). Predator vision is evolved using a neurophysiologically-based model of visual attention (Itti

and Koch, 2001). We focus on the effects of environmental complexity on this coevolutionary interaction.

Merilaita (2003) shows that greater background complexity can increase prey detection times by predators. In even earlier work on background matching in camouflage, it was suggested that visual complexity may favor color polymorphism, because there will often be many polymorphisms that can achieve similar patterns (Endler, 1984). These and other works focus on camouflage via background matching, but there are alternative forms of camouflage, in particular, disruptive colorations. In contrast to background matching, where an entity attempts to blend in with the background, disruptive and distractive colorations are patterns that attempt to draw the observer away from the pattern. Disruptive colorations have been shown to be an effective tool for camouflage when tested against live predators (Schaefer and Stobbe, 2006; Cuthill et al., 2005). A number of visual properties significant to predator-prey interactions have been identified in these contexts, including background complexity, prey contrast, and object density (Dimitrova and Merilaita, 2010, 2012, 2014). In our model, the capacity for complexity in prey is greatly enhanced by utilizing a developmental mechanism to produce color images of moderate dimensions, as compared to previous work which explores the selective favorability of simple patterns (Dimitrova and Merilaita, 2014) or directly-represented greyscale images (Bond and Kamil, 2002).

In previous work, we have explored the coevolution of predators and prey (Ficici and Pollack, 1996), finding that such systems are often subject to pathologies such as convergence to mediocre stable states (Ficici and Pollack, 1998), loss of gradient, incorrect focusing, and relativism (Watson and Pollack, 1996). Within the ecology literature, predator-prey systems are commonly studied, including analytical and computational models as well as empirical studies. However, analytical models of predator-prey systems can quickly become infeasible for study as the number of species increases. Furthermore, analysis of phenomena such as predator preference runs into difficulty when accounting for alternative food sources under ecological dynamics (van

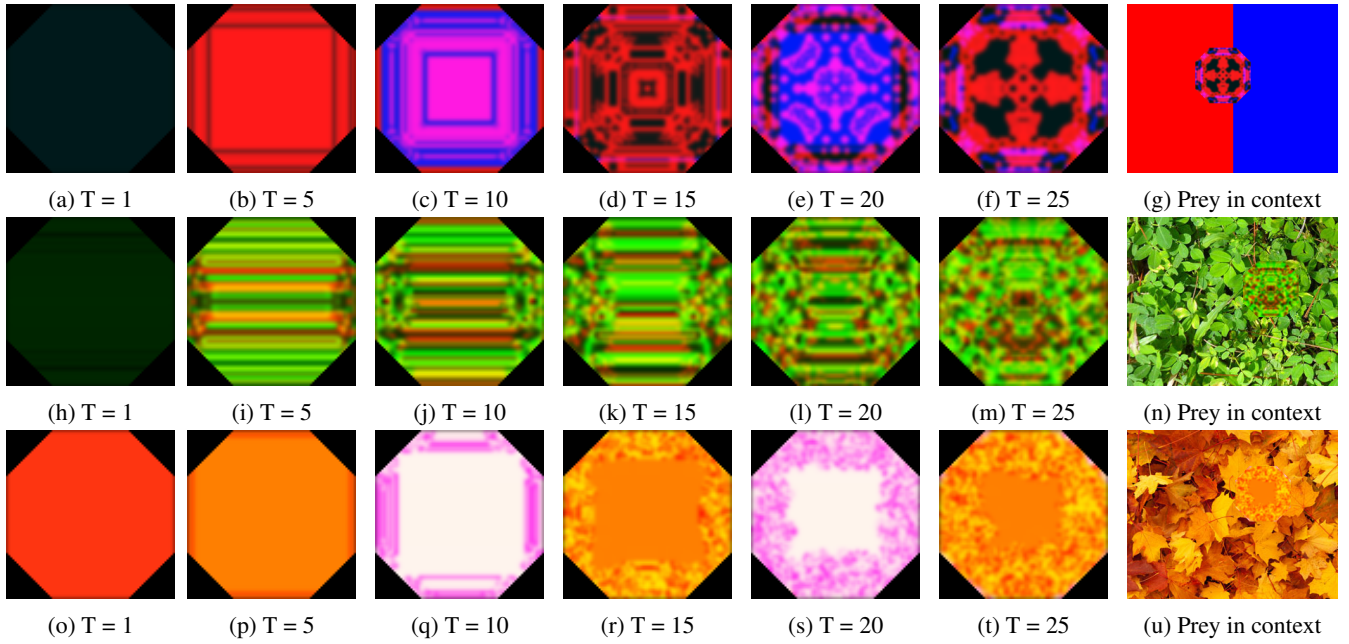


Figure 1: Time-series of prey morphogenesis.

Baalen et al., 2001; Leeuwen and Brännström, 2013).

The pathologies of competitive coevolution can be readily explained in the language of predator-prey systems. Loss of gradient, when one population becomes worse such that it no longer exerts selective pressure on the competing population, or better such that the competing population can no longer maintain engagement. Examples of this would include evolutionary advances in a predator-prey ecosystem where prey can achieve greater escape velocities, leading to diminished returns for predators, and in real ecosystems, probably triggering the predators to seek another food source. Incorrect focusing is when members of one population overspecialize in interactions with specific competitors such that they fail to generalize to other competitive interactions and are prone to extinction. Examples of incorrect focusing are not as common in real ecosystems, where a large number of coevolutionary interactions continually apply selective pressure. In competitive coevolutionary interactions, the quality of an individual is a function of its competitors. This relativism in scoring means that an individual that appears to be more fit to an external observer, may be just as fit as a lower quality individual relative to a given set of competitors. In Nature, this is less of an issue for similar reasons to incorrect focusing, there are continual pressures from many aspects of the ecosystem and environment such that these disambiguations will occur infrequently.

Predator-Prey Coevolution

When simulating predator-prey coevolution, we use a 2-population competitive coevolution model. The prey pop-

ulation consists of a set of genetic programs that encode a generative function for their visual appearance. The predator population consists of a set of numerical weights for a saliency detection algorithm. Prey receive points for not being detected, or causing the predator to incorrectly classify the background as prey. Predators receive points based upon the accuracy of how they perceive the environment.

There are a number of ways to compute the fitness in co-evolving populations. We focus on pairwise competitions. Sims uses best v. best competitive coevolution (Sims, 1994), where each population competes against the best individual of the competing population. However, best v. best can lead to incorrect focusing and disengagement by assigning greater fitness to individuals that overspecialize in defeating the champion competitor. Tournaments can reduce the number of comparisons from $O(N^2)$ to $O(N \log N)$, but still represent approximations of a full pairwise competition (Angeline and Pollack, 1993). All v. all competitive coevolution reduces the tendency for focusing, but comes at great computational cost. Nevertheless, we compute the complete payoff matrix via all v. all pairwise competitions to facilitate coevolutionary engagement between all species.

Prey

Prey patterns are produced through a process of algorithmic morphogenesis. The process is much like the standard notions of chemical morphogenesis (Turing, 1952), where a system of reactions determines chemical kinetics while a diffusion system transports chemical species, contributing to pattern formation. However, instead of a standard system of reactions, we employ genetic programming to serve as an

algorithmic chemistry.

The use of genetic programming to evolve images and dynamical systems has been a part of the ALife community since the early years (Sims, 1991b, 1992). These ideas were extended to the evolution of self-constructing and self-repairing patterns (Miller, 2004). However, much of the work on evolved computer graphics has focused on interactive evolution, perhaps in part because of the complexity of developing a computer vision system capable of scoring images in a meaningful way. The interactive evolution of generative images has recently achieved widespread popularity with the Picbreeder website (Secretan et al., 2011). Of particular relevance to this study is the recent work on the interactive evolution of camouflage (Reynolds, 2011), where a sophisticated texture rendering system is employed to generate patterns for human-guided selection. Finally, alternative biologically-inspired generative representations may be of interest for achieving patterns that may be closer to those of natural systems (Cussat-Blanc and Pollack, 2012).

Genetic programming is an evolutionary method for discovering computer programs (Koza, 1992), where the programs may represent robot controllers, machine learning classifiers, developmental processes, or many other things. The algorithms used to evolve genetic programs are often very similar to those employed by genetic algorithms, with particular exception to how variation is performed. We use the array method of program representation (Koza, 1994) which is most conveniently bounded by program size limits in units of number of nodes (200 nodes for the prey).

Prey programs are functions of 3 inputs (x , color, and current value) that return a floating point, which are iterated over all color channels at each (x,y) coordinate of the prey, in this case an octagon of radius 41 and (x,y) coordinates are scaled to $[-1,1]$. This function output is then squished with a hyperbolic tangent. Prey programs can be composed of the following terminal and function set:

$x, \text{color}, \text{value}, +, -, *, /, \text{iflte}, \text{sin}, \text{cos}, \text{tanh}, \text{min}, \text{max}, \text{abs}, \text{hypot}, \text{sec}, \text{csc}, \text{cot}, \text{tan}, \text{gamma}.$

Prey are iterated function systems. During each iteration, first the GP program is evaluated once per location and color channel, then a Gaussian filter is convolved with the image as a heuristic pseudo-diffusion. This pseudo-diffusion can introduce artifacts at the boundaries, which we partially alleviate by cropping the prey by a single pixel along the boundary. An example figure can be seen in Figure 1.

Predators

Predator vision is modeled based upon a neurophysiological model of visual attention (Itti and Koch, 2001). Images are broken down into a set of feature maps of intensity, color difference, and orientation, then combined into 42 features taken as differences across multiple scales. Predator genotypes encode weights for each feature map, which are lin-

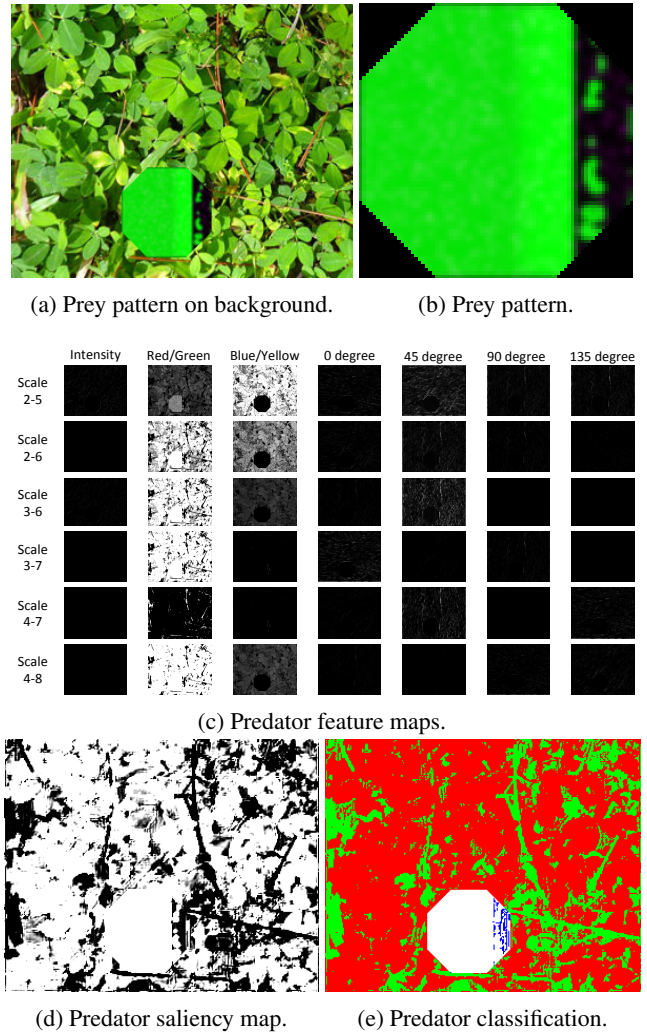


Figure 2: Diagram of predator's visual system. 2a shows the prey pattern situated on the grassy background. 2b shows a zoom-in of the prey pattern. 2c shows the weighted feature maps used by an example predator. 2d shows the corresponding saliency map for the feature maps in 2c. 2e shows the same example predator's classification of 2a, where red indicates incorrectly classified background, green indicates correctly classified background, white indicates correctly classified prey, and blue indicates incorrectly classified prey.

early combined into a saliency map. The saliency map encodes the priority of attention at each location in the visual field. We allow the saliency map to take on both positive and negative values, where positive values indicate a prediction of the prey's position. For a more detailed description of the components of the vision model, see (Itti and Koch, 2001).

Saliency-based models of visual attention have a long history in studies of the neuroscience of vision (Niebur et al., 1993; Itti and Koch, 2001; Borji and Itti, 2013). There are now many algorithms for visual attention, some based on

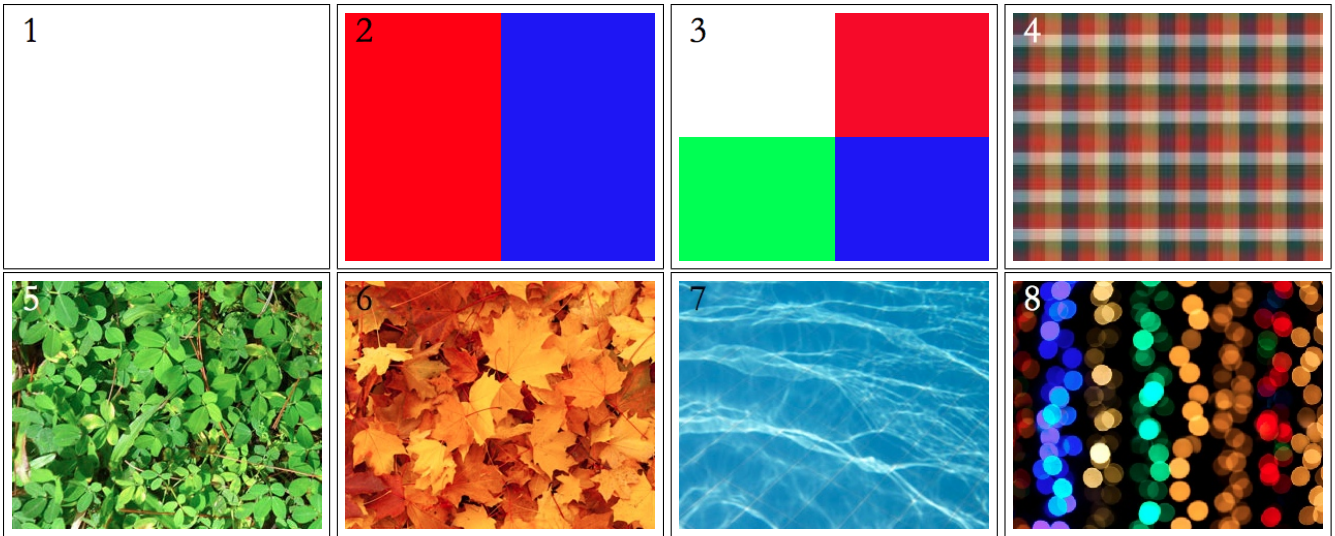


Figure 3: Prey environments used in experiments.

neurophysiology and some engineered for optimality. A comprehensive review of current visual attention algorithms can be found in (Borji and Itti, 2013). We use a bottom-up model based upon (Itti and Koch, 2001), which has been shown to correlate with human eye movements (Parkhurst et al., 2002; Itti, 2005). In the traditional model of Itti, where feature maps are aggregated hierarchically into the saliency map, first by grouping features by type into conspicuity maps, then combining conspicuity maps to compute the saliency map. Our model uses the simplification of combining all feature maps to immediately compute the saliency map.

Evolutionary Algorithm

We use a genetic algorithm for both the predator and prey populations. Individuals are selected with tournament selection using tournament sizes of 3. Selected individuals are mutated (45%), crossed over (45%), or replicated (10%) in the successive generation. Prey are crossed over using standard subtree mutation and crossover (Koza, 1992), while predators are mutated by adding a vector of small Gaussian mutations to the genome and recombined via uniform crossover. The evolutionary algorithm is run for 500 generations in all experiments in this study.

Experiments

We consider a number of environmental backgrounds of varying complexity. We obtained 5 naturally patterned images¹ and created 3 simple images, shown in Figure 3. Images were prepared by cropping regions to a size of 300x240. While a number of methods have been developed

within the computer vision community to characterize image complexity, we report on the JPEG file size. The concept of complexity resides at the heart of the field of data compression, hence our choice to use it as a metric of image complexity. Image sizes in the same order as Figure 3: 446B, 1.3kB, 1.7kB, 14k, 47k, 123k, 93k, and 126k. During simulations prey position and rotation is randomly determined. Prey position is randomly chosen such that the prey resides entirely within the background environment, and rotation is uniformly chosen from all 4 possible 90 degree rotations. 25 independent trials are conducted for each background environment². Due to the computational costs of simulating prey morphogenesis, predator vision, and computing complete pairwise payoff matrices, we use population sizes of 100 for both the predators and prey. The same random seeds are used for each background, such that the initial populations have the same constituents for each random seed, but then quickly diverge as selection and mutation vary the populations. In Figures 4, 5, 6, and 7 we use two colors, red and blue, to indicate data reported for the population average and best individual, respectively.

When measuring the degree of background matching that is present in a given population over evolutionary time, we use the same 42-D feature vector that is used by predator vision. Merilaita and Lind (2005) previously suggested that quantification of background matching in prey can be misleading if it isn't computed with respect to the predator's perception. When measuring the distance between a prey and the background we take the Euclidean distance between the average feature vector of the background image and the

¹Images are public-domain, and are retrieved from <http://www.publicdomainpictures.net/>.

²Due to computational difficulties, a few runs were incomplete. Complete runs per background (ordered as in Figure 3): 24, 21, 25, 23, 25, 24, 22, 23

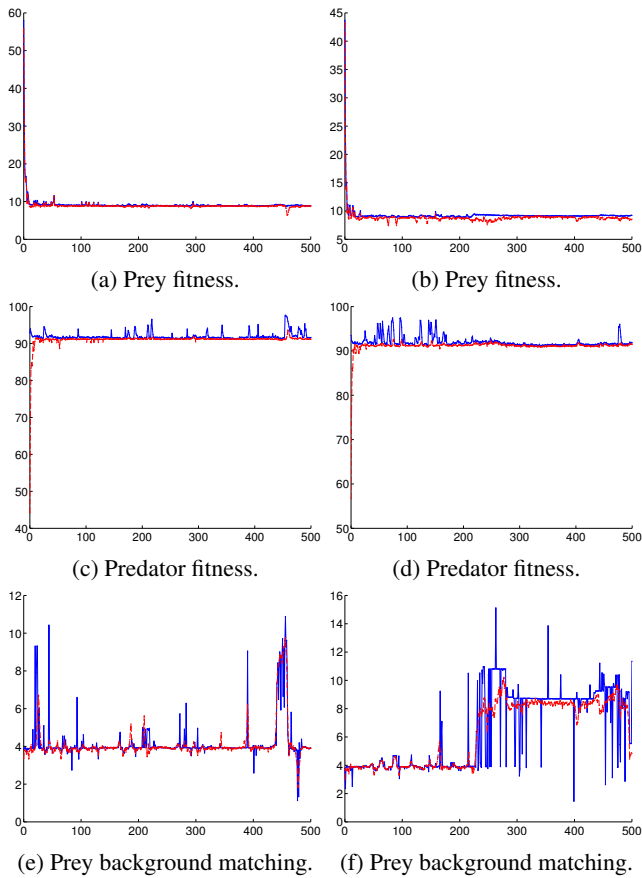


Figure 4: Example evolutionary trajectories of fitness and background similarity. X-axis is time. Subcaption indicates respective Y-axis.

average feature vector of the prey. For evolving populations we measure the average of the average feature vector of all prey in the population.

Background Matching

Background matching is generally successful for all backgrounds in this study (see Figures 1n and 1u for particularly compelling examples), with a notable exception and some unexpected insights. First, let us reiterate the argument initially proposed by Endler (1984). The regions of the background on which the prey are selected lead to correlations between the prey patterns and those regions of the background, because better matches generally win. In our study the random repositioning and rotation of the prey means that prey effectively have a uniform probability of being tested at each location in the image. Therefore, prey that match the average background region in the image are predicted to generally be a better fit. However, *a priori* it is unclear what prey patterns will appear in environments with stark differences, or natural complexity. In Figure 1g, we show one example of such a situation, where on a background of

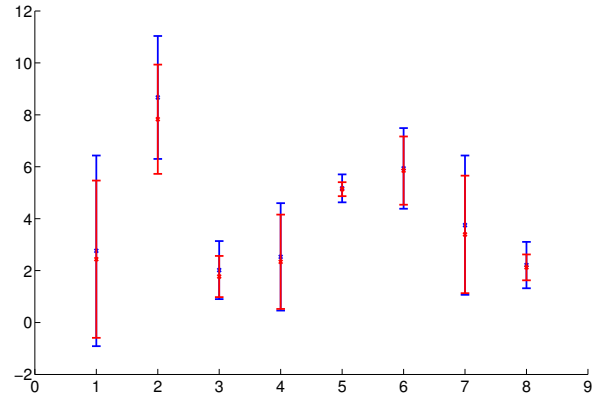


Figure 5: Background matching in prey. Y-axis indicates distance from the background, see Experiments for description of distance from background. Smaller means a better match. X-axis is the ordering of backgrounds in Figure 3.

half blue and half red the prey adopts a strategy that contains both red and blue which can be easily mutated to favor one color over the other. This is a common trend in our results; prey evolved on backgrounds with large differences at the scale of the prey favor polymorphic populations.

Interestingly, there is not a clear relationship between prey fitness and prey background matching. While this is not surprising in some senses, because fitness under competitive coevolution is a function of the competing population, where an improvement in one population masks an improvement in the competing population. It does suggest that the presence of a third-party in competitive coevolution, the environment, can non-trivially alter the coevolutionary dynamics. We discuss this in greater detail when reflecting on the representation of predator vision and prey appearance. Nevertheless, because we randomly position and orient prey, we suggest that it may be worthwhile to pursue non-random prey movement to reduce the background-averaging tendency of prey.

Coevolutionary Dynamics

On first glance, the coevolutionary dynamics in this study are fraught with the Red Queen effect. Originally presented as a dynamic describing the constant probability of extinction (van Valen, 1973), the Red Queen effect is often described as the requirement that “takes all the running you can do, to keep in the same place” (Carroll, 1871). Figure 4 shows 2 example evolutionary trajectories from the white background. In one (Figures 4a, 4c, and 4e), the prey population evolves to a near perfect solid white pattern (see the 8th image in Figure 8), and in the other (Figures 4b, 4d, and 4f), the prey population evolves first to a light grey then fixates on a yellow cross pattern for an extended period (see the 17th image in Figure 8) and ends at generation 500 with a black prey pattern as the champion. Nevertheless, by simply

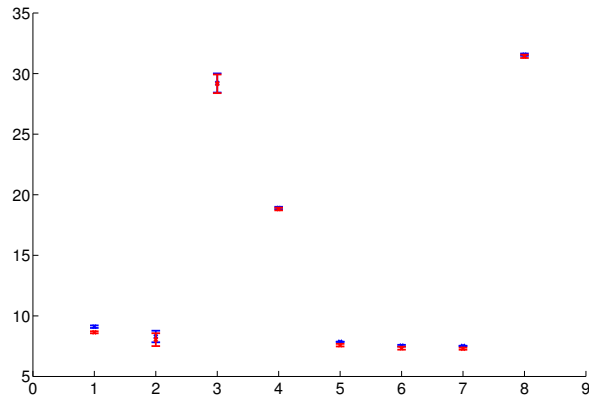


Figure 6: Prey fitness. X-axis is time. Y-axis is prey fitness. Bigger is better.

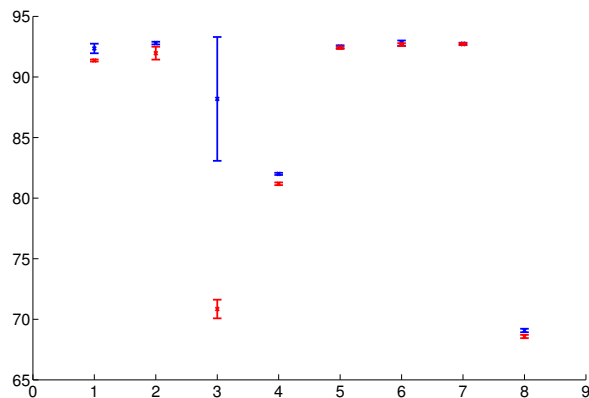


Figure 7: Predator fitness. X-axis is time. Y-axis is predator fitness. Bigger is better.

inspecting the fitness of the predators and prey it is not obvious that there has been any major change in the predator-prey interactions, certainly not to the degree that has previously been described as loss of gradient, suggesting that this dynamic is akin to relativism (Watson and Pollack, 2001).

From the set of backgrounds we used in these experiments, simple backgrounds led to the greatest degree of relativism. In particular, multiple trials with the white background resulted in evolutionary trajectories that first converged to near-white prey patterns, followed by a divergence from background similarity leading to colored patterns. We suspect that one of the reasons for this relativism was related to background discrimination ability in predators. In particular, predators make absolute decisions regarding the location of prey, where a slight change in prey hue can lead to predator misclassification. Probabilistic decisions may facilitate environmental engagement by allowing predators some degree of uncertainty in detecting prey.

Representation

Representation often has a significant impact on evolutionary dynamics by, amongst other effects, affecting the genetic distances between phenotypes and constraining the space of possible phenotypes. We utilize a genetic programming representation for prey which, by incorporating a heuristic pseudo-diffusion, is capable of producing a wide array of prey patterns. Yet these patterns are likely to have limitations that arise from both the function set used as the basis for prey programs and the instabilities that arise under diffusion (although in some systems diffusive instabilities can provide macroscopic stability, such as Turing patterns (Turing, 1952)). Furthermore, there is no interaction between prey patterns and the environment. Not only do some species exhibit active camouflage, but there are links between visible pigmentation and diet (Whitehead et al., 2012).

We suspect that the representation of predator vision is one of the more significant variables worthy of future investigation. Figure 7 suggests that predators have difficulty with multi-colored images. Prey also perform better on backgrounds with homogeneous color schemes, both in terms of fitness and background similarity, Figures 6 and 5 respectively. Due to the competitive nature of the model, it is unclear whether the bias towards homogeneous color schemes is due to the predators or the prey, but we suspect that it is due to the representation of predator vision. By considering alternative visual attention algorithms, such as those reviewed in (Borji and Itti, 2013), we expect to observe prey patterns that reflect the properties of the visual attention algorithm.

Conclusions

We have presented a model of the coevolution of predator vision and prey camouflage, where prey utilize a developmental process to form complex multicolored patterns and predators use a neurophysiologically-based model of visual attention. Prey successfully evolve to match their background, with some exceptions that are predicted to stem from randomized prey movement, and predators successfully evolve the ability to discriminate between prey and background. We observe a type of coevolutionary relativism, where competing populations remain engaged while drifting away from their environment. This type of divergence from background matching generally happens in simpler backgrounds, leading to the hypothesis that background complexity can facilitate coevolutionary engagement on background matching problems.

While other coevolutionary studies have found that pursuer-evader tasks can lead to mediocre stable states (Ficci and Pollack, 1998), we find that coevolution in our model is generally engaged and leads to effective background matching. We suggest that it is the richness of the model that facilitates engagement. However, background

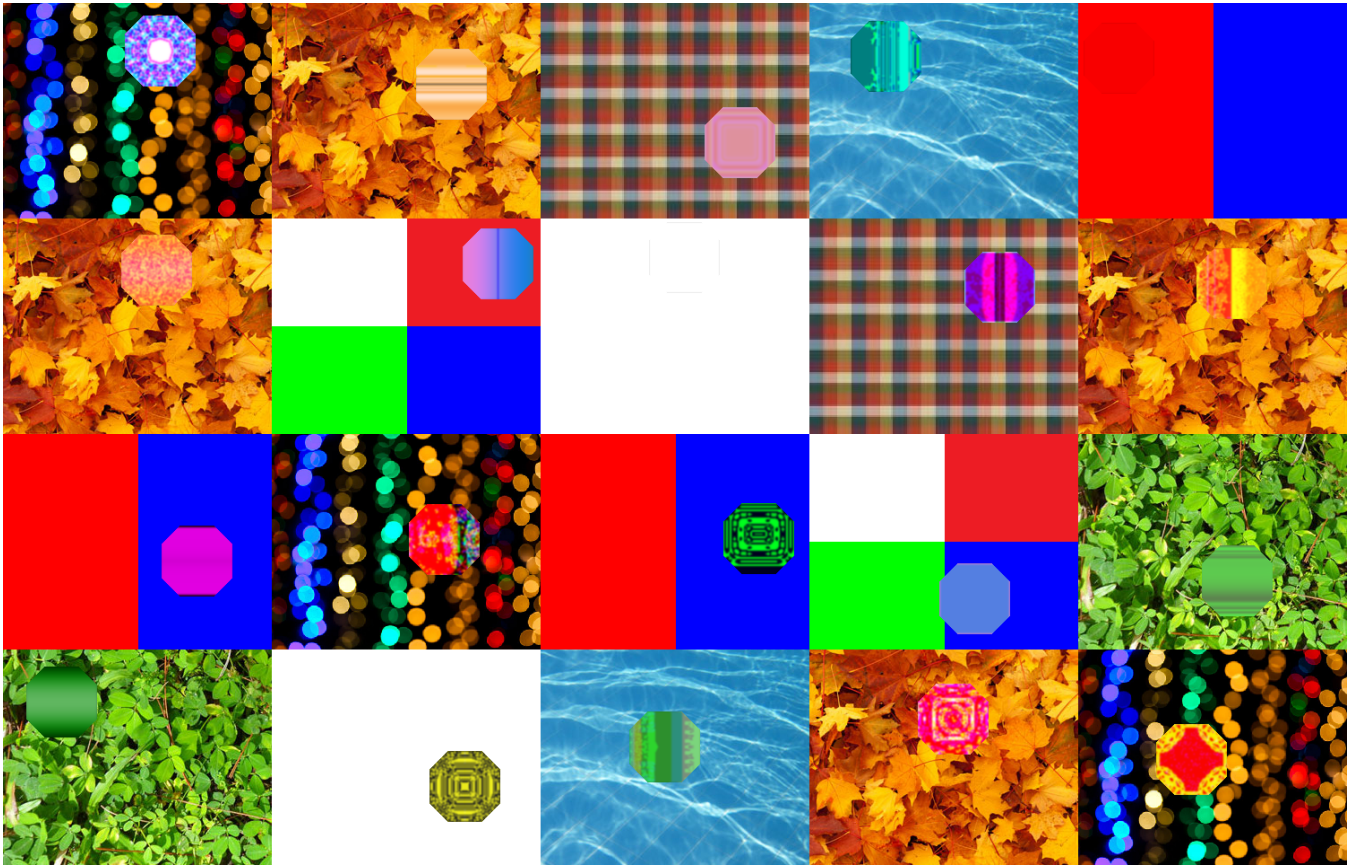


Figure 8: Collage of some of the best matching, and most interesting prey patterns

matching is not always achieved. In particular, simple environments with stark differences where only partial background matching is possible tend to favor prey that can readily mutate to match regions of the environment. This suggests that polymorphic populations may be an effective response to a highly variable background. In the case of complex backgrounds we find that predators and prey are generally more engaged, and background complexity appears to support the advance of the coevolutionary ratchet, leading to effectively camouflaged prey.

Future Work

There are many avenues for future research stemming from this work. We suggest only two examples. First, many natural predators learn over time, whereby they may become better at identifying prey during their lifetime, see (Troschianko et al., 2013). Second, in Nature, prey patterns act as signals, both to prey and to mates. It may prove interesting to consider the dynamics of mate signaling which has led to such brilliant patterns as peacocks' plumage. Along this line, we have previously discovered models and corresponding parameters capable of leading to the emergence of such costly signaling (Harrington et al., 2012).

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