

Coevolutionary Dynamics Caused by Asymmetries in Predator-Prey and Morphology-Behavior Relationships

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Abstract

Predator-prey interactions are the key element of ecological systems. We present the results of morphology-behavior predator-prey coevolution in a 3D physically simulated environment. The morphologies and behaviors of virtual creature predators and prey are evolved using a genetic algorithm and random one-on-one encounters in a shared environment. There are two levels of asymmetries in the model: One is between two species, predators and prey, and the other is between two traits in each species, morphology and behavior. We analyze and discuss the complex coevolutionary dynamics caused by the asymmetries on the basis of quantitative characterization of morphology and behavior.

Introduction

Predator-prey interactions are the key element of ecological systems (Legreneur et al., 2012). Predation pressures in food chains shape diversity and functions of organisms (Agrawal, 2001). Many predators employ various strategies capturing their prey, and at the same time, many prey employ various protective mechanisms against their predators (Edmunds, 1974). These strategies arose through the coevolution between predators and prey. Furthermore, in the coevolution, morphology and behavior have been tightly coupled in each species. Therefore, the process can be regarded as double coevolution of morphology-behavior and predator-prey couplings (Fig. 1).

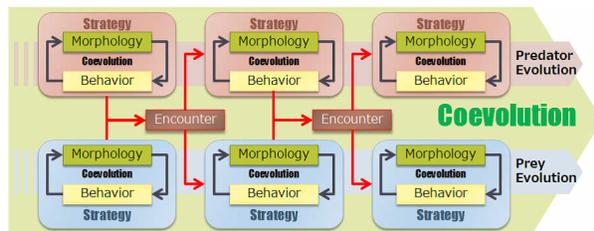


Figure 1: Double coevolution of morphology-behavior and predator-prey.

Predator-prey systems are conventionally studied in mathematical biology (population dynamics) using mathematical

methods (e.g., Lotka-Volterra equations) by analyzing evolutionary changes at the population level (Murray, 2003). However, these studies have not focused or have not been able to focus attention on coevolution of morphology and behavior of individual virtual creatures. On the other hand, virtual creature models in Artificial Life, following the pioneering study (Sims, 1994b), allow us to analyze the morphology and behavior coevolution in 2D and 3D environments (Ventrella, 1998; Taylor and Massey, 2000; Chaumont et al., 2007; Miconi and Channon, 2006; Pilat and Jacob, 2008; Turk, 2010; Azarbadegan et al., 2011). Additionally, due to the physical nature of the simulation, we are able to compare the resulting virtual creatures with biological organisms sharing similar morphological and behavioral traits (Chaumont et al., 2007). Some studies explored competitive coevolution in this framework (Sims, 1994a; Miconi, 2008). However, they have not focused on the morphology-behavior coevolution under the predator-prey coevolution and have not analyzed the strategies based on their morphological and behavioral characteristics.

The purpose of our study is to understand the evolutionary dynamics of the predator and prey strategies emerging in the context of this double coevolution. We perform double coevolution of morphology-behavior and predator-prey couplings by using a simple predator-prey scenario in a 3D physically simulated environment. As a first step of our investigation, we observed the emergence of various morphological and behavioral prey defensive strategies and found a weak tendency for the order of strategy emergence between morphologies and behaviors by using cross-correlation methods in the simulated environment (Ito et al., 2012, 2013). In this paper we give a simple quantitative characterization of morphology and behavior of each virtual creature. We track the evolutionary changes in special indices for both predators and prey species, specifically through the evolutionary process in which prey evolve one of the defense strategies, “Guard Strategies”. We then discuss the coevolutionary dynamics in terms of the asymmetries in the predator-prey and morphology-behavior relationships.

Model

We use the Morphid Academy open-source simulation system (Pilat and Jacob, 2008) to evolve virtual creatures in a 3D physically simulated environment (Fig. 2). Morphid Academy has previously been used to successfully evolve virtual creatures for locomotion (Pilat and Jacob, 2008), light-following (Pilat and Jacob, 2010), and sustained resource foraging (Pilat et al., 2012). The presented coevolution of predators and prey provides an example of simulating several agents in a shared environment of Morphid Academy in a coevolutionary context.



Figure 2: Virtual creatures evolved in Morphid Academy.

Agents

The agents are virtual creatures comprised of several 3D rectangular solid body parts connected with simple hinge joints. Their physical phenotype is developed from a directed graph (Fig. 3). The nodes represent body parts and the links represent joints.

The genotype graph undergoes evolution through a genetic algorithm. We termed the root body part as the *torso*, and all the other parts as *limbs*.

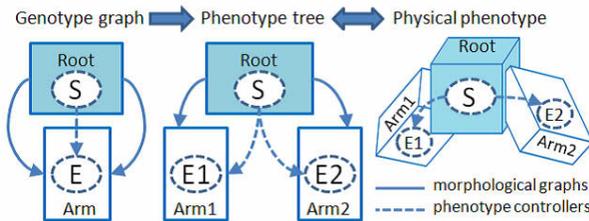


Figure 3: The development from genotype to phenotype.

The controller of a virtual creature is a recurrent neural network embedded in body nodes. There are three types of neurons: input, calculation and output. The input neurons represent sensory information from the environment,

the computational neurons process the input and the results are fed into the output neurons as joint effectors that power the joints, making the creature move. The creature sensor detects other living agents nearest to the virtual creature within a sensing range r . This virtual creature model is a simplification of Sims' Blockies model (Sims, 1994b) and is fully described in (Pilat and Jacob, 2008). The simplification in body and neural structure decreases the evolutionary search space and has been demonstrated to perform well for various evolutionary tasks.

Experimental Environment

To represent a predator-prey encounter, we simulate a single prey creature with a single predator creature in a shared environment. A random prey creature is positioned near the origin of the simulation space. A random predator is then randomly positioned at r_0 distance from the prey as shown in Fig. 4. Both agents are positioned above the simulation plane and allowed to free-fall due to gravity during a stabilization phase. Once they are stable from movement and resting on the ground surface, the evaluation encounter begins and lasts for S simulation time steps. Capturing is defined as the predator touching the torso of the prey with any of the predator's body parts. A captured creature is disabled and cannot be sensed.

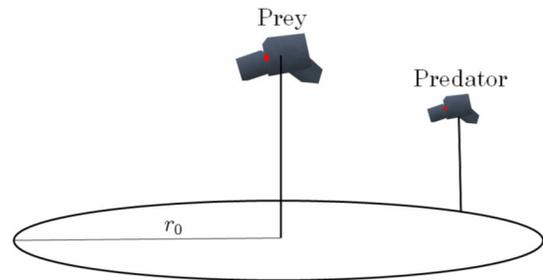


Figure 4: Initial positions of a predator and a prey at the start of the encounter.

Evolution

Two populations are concurrently evolved, representing the predators and the prey. A steady-state genetic algorithm is used with tournament selection of 3 predator-prey pairs.. Fitness of each agent is calculated from the result of an encounter between the randomly selected predator-prey pair. For each tournament, one or two individuals, per population, with the best fitness can produce a child through one of the genetic operators of copy, crossover or grafting. The child replaces the worst performing of the 3 individuals of the corresponding population (prey or predator). Mutation is applied to the resulting child individual and includes: mutation of the morphological nodes or link parameters, addition

of morphological nodes, and the addition or removal of morphological links.

Fitness Functions

The fitness of each agent is calculated after the predator-prey encounter by a fitness function. The fitness of a predator is defined by Eq. 1. Fitness of 5000 is allocated if the predator has captured the prey with an additional maximum of 5000 points proportional to the capture time. If the prey is not caught, the fitness is proportional to the distance gained towards the prey, based on the initial distance r_0 and the final distance r_n .

$$F_{pred} = \begin{cases} 5000 + 5000 \times \frac{t-t_n}{t} & (\text{caught}) \\ 5000 \times \frac{r_0-r_n}{r_0} & (\text{missed}, r_0 \geq r_n) \\ 0 & (\text{missed}, r_0 < r_n) \end{cases} \quad (1)$$

The fitness of the prey is defined by Eq. 2. If the prey escaped from the predator (not caught within the specified simulation time), it receives a fitness value of 5000 with an additional value of up to 5000 points proportional to the distance it moved l_n . Otherwise, the fitness is calculated according to the ratio of the time the prey escaped during t_n over the time limit t .

$$F_{prey} = \begin{cases} 5000 + 5000 \times \frac{l}{l_n} & (\text{escaped}, l_n \leq l) \\ 10000 & (\text{escaped}, 0 \leq l < l_n) \\ 5000 \times \frac{t-t_n}{t} & (\text{caught}) \end{cases} \quad (2)$$

Morphological and Behavioral Indices

Two simple indices are used to characterize morphologies and behaviors of virtual creatures quantitatively and to track their evolution. We use the ratio of the volume of the torso to the total volume as a morphology index (hereafter referred to as MOR). The reason for this is that Guard Strategies are characterized to have big or many limbs protecting a small torso from being captured (Ito et al., 2012). It is more difficult to quantitatively characterize the behavior of virtual creatures to represent the progress of evolution since, in general, the behavior heavily depends on the morphology, which itself is difficult to quantitatively characterize. After conducting preliminary experiments using many candidate indices, we decided on a simple index: the average output of effector neurons (hereafter referred to as BEH), which is intended to approximately represent the mobility of virtual creatures approximately, and does not depend directly on the agent morphology.

Result

Parameters

We evolved predator and prey populations, each of size $i = 30$ and initially random individuals, for $g = 10000$ tournaments. Each evaluation of an encounter was performed for $S = 100000$ simulation time steps with an initial distance $r_0 = 700$ between the agents. For each tournament,

a child was created by asexual copy (probability of 40%), crossover (30%), or grafting (30%). Mutation of the child was performed with prob. of 80% with each mutation able to apply small changes to the whole genome (prob. of 5% per gene). The vision radius of predators was 5000 while the prey were only able to see within 500 distance units. Therefore, the predator is able to sense the prey much earlier than the prey.

In previous studies, we classified the evolved prey's defensive strategies into two types, each with an assortment of evolved morphologies and behaviors: Runaway Strategy which involves fleeing from the predator and Guard Strategies (*Turtle*, *Clam* and *Tower* types) which rely on their morphologies and typically stationary behaviors to provide protection from predation (Ito et al., 2012). It is easy to detect the emergence of the Guard Strategies as they tend to evolve with a sharp increase in the fitness. Therefore, we investigate the relationship between morphology and behavior evolution by focusing on the course of the evolution of Guard Strategies. To control the movement of prey and to promote the emergence of Guard Strategies, we used the modified fitness function of the prey (Eq. 2) and the environmental parameter $l = 100$.

Coevolutionary Dynamics

We performed 30 trials, among which we observed that prey evolved some Guard Strategy (Fig. 5) to prevent predator capture in 17 trials. The prey did not seem to have evolved any defensive strategies in the other trials. We further observed 12 trials with a clear increase in fitness out of the 17 trials. Each of the 12 trials evolved a specific prey strategy: Tower (6), Clam (4), and Turtle (2).

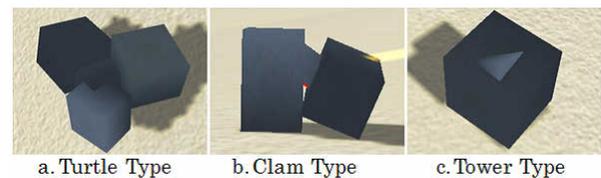


Figure 5: Sample morphologies of the Guard Strategies.

Fig. 6 shows a typical evolution trial in which *Clam* type Guard Strategy emerged. The blue and red lines in the middle graph represent the average fitness of the prey and predators, respectively. Each of the top and bottom graphs (top: prey, bottom: predators) represents a distribution of virtual creatures in the space defined by the two indices (X-axis: MOR, Y-axis: BEH, both in a logarithmic scale after normalization). In these graphs, a circle represents an individual, with its radius proportional to its fitness. We can estimate that the individuals close to each other have similar phenotypes. Specifically, two individuals sharing the same X-coordinate have the similar morphological characteristics,

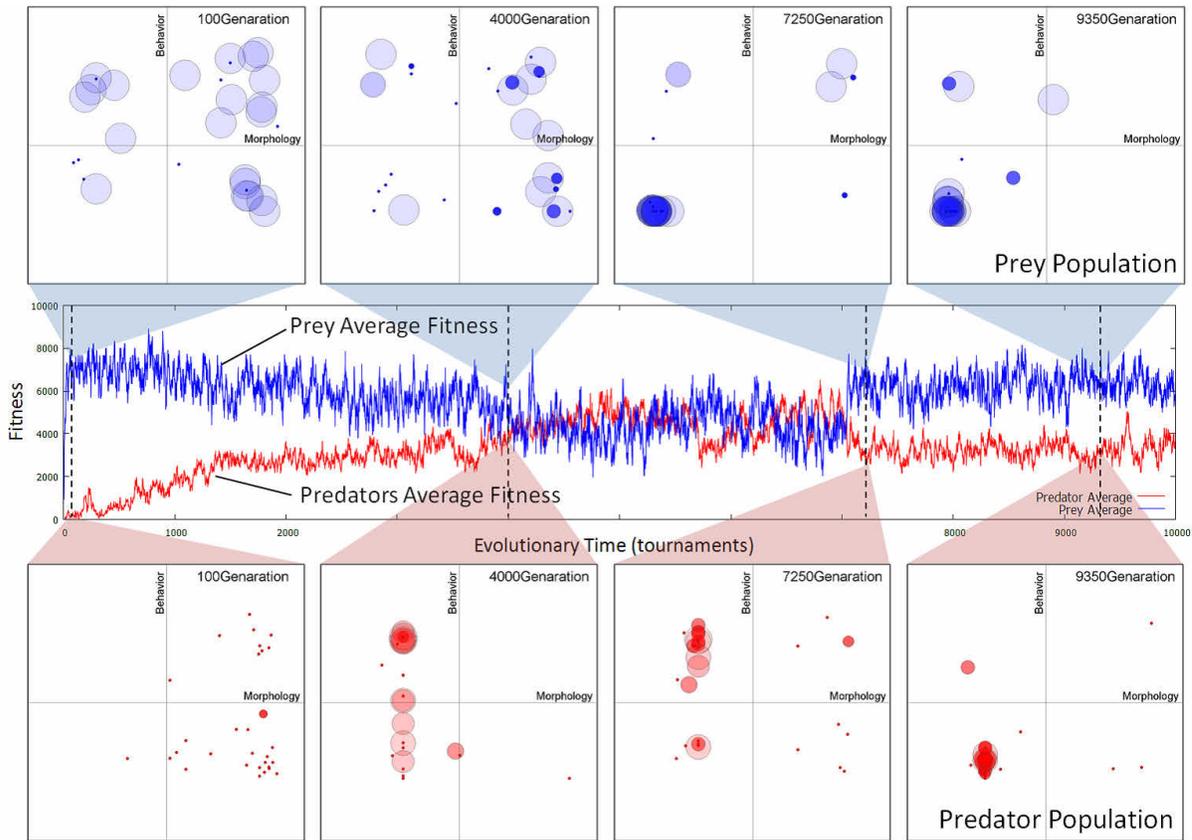


Figure 6: The evolution of the average fitness and the distributions of individuals on the trait space.

and sharing the same Y-coordinate corresponds to the similarity of their behaviors.

In early generations, the average fitness of the predator (prey) population was very low (high), which is also shown by the small (large) radius of the circles on the corresponding trait space. It corresponds to the situation in which the predators could not catch the prey at all. A wide distribution of the circles on the trait space of predators or prey reflects a wide variety of morphologies and behaviors of randomly generated individuals.

After that, until around the 4500th generation, predator fitness gradually increased while prey fitness slightly decreased. Large circles on the predator trait space, which represent the evolved predators, can be seen to create an elongated cluster, with data points having similar X-coordinates and a large variety of Y-coordinates. This indicates that the effective strategies that emerged in this predator population have similar morphological characteristics but diverse behavioral characteristics. In the trait space of the prey, the number of individuals with high fitness decreased while individuals with low fitness increased, as a consequence of the predator population's evolution. The tendency for some in-

dividuals of the prey population to maintain high fitness in this generation may be simply due to them encountering incompetent predators.

At some point near the 7000th generation, a switch in fitness performance occurred. This was due to the emergence of individuals with a strong defensive Guard Strategy, as shown in Fig. 8, which suddenly took over the population, represented as the reduction of the circle distribution on the trait space. Notice that when comparing the distribution of predators of the 7250th generation with that of the 4000th generation, there are many circles whose size decreased while their positions were the same. This means that although the major strategy of the predators (depending on a specific morphology) did not change between these two generations, they failed to catch the prey adopting the emerging Guard Strategy.

Finally, the cluster of the predators on the trait space shifted downward in 9350th generation. It means that the predators changed their strategy by adjusting their behaviors to adapt to the prey strategy. However, the prey population kept high fitness with their Guard Strategy unchanged.

What Happened when a New Strategy Emerged?

Here we present a method to investigate the dynamics of morphology-behavior coevolution. We track the evolving populations especially when Guard Strategy emerged, by sequentially plotting the average position of the population of predators or prey on the trait space. The fitness-weighted center is used when calculating an average position. Note that we ascribed the fitness to the weight when we calculated the center of the mass. What we see from the coevolutionary trajectory and the fitness transitions includes the evolutionary order of the emergences of new or improved morphology and behavior.

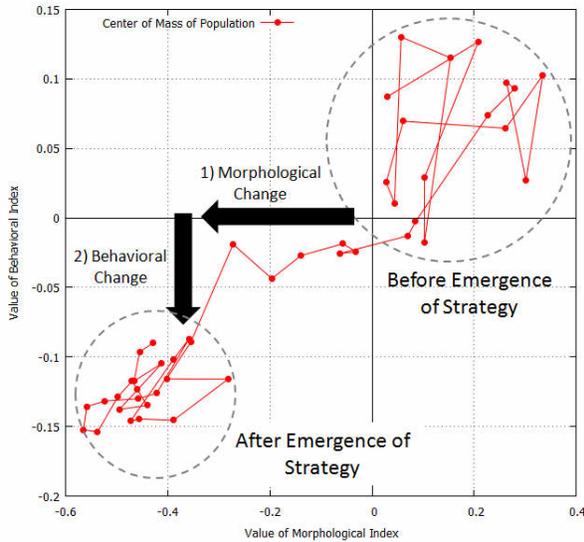


Figure 7: A typical evolutionary trajectory on the trait space when Guard Strategies (*Clam* and *Turtle* types) evolved in the prey population.

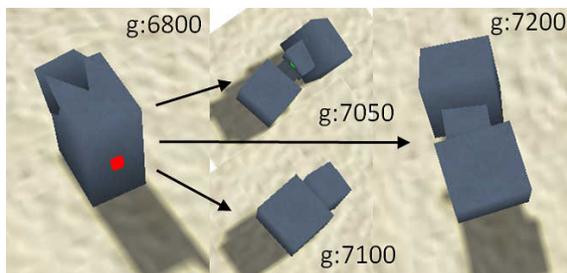


Figure 8: The virtual creatures with the best fitness in each generation appearing in the evolution trial shown in Fig. 7. The right three individuals have obtained the guard strategy and are the offspring of the left one.

Fig. 7 and 9 show the two typical evolutionary trajectories

when Guard Strategies emerged. The horizontal and vertical movements correspond to the morphological and behavioral changes of the prey population, respectively. Therefore, we can estimate that Fig. 7 show that the morphological changes preceded the behavioral changes when the defense strategy was acquired, in other words, the morphological characteristics of the strategy spread in the population before behavioral characteristics spread. Fig. 8 shows an ancestor and its three offspring prey with Guard Strategy in this evolution trial, all of which obtained the best fitness in each generation.

On the contrary, Fig. 9 shows roughly that the behavioral changes preceded the morphological changes. Fig. 10 shows an ancestor and its three offspring prey with Guard Strategy in this evolution trial, all of which obtained the best fitness in each generation. They are characterized as its immovability as compared with the creatures shown in Fig. 7.

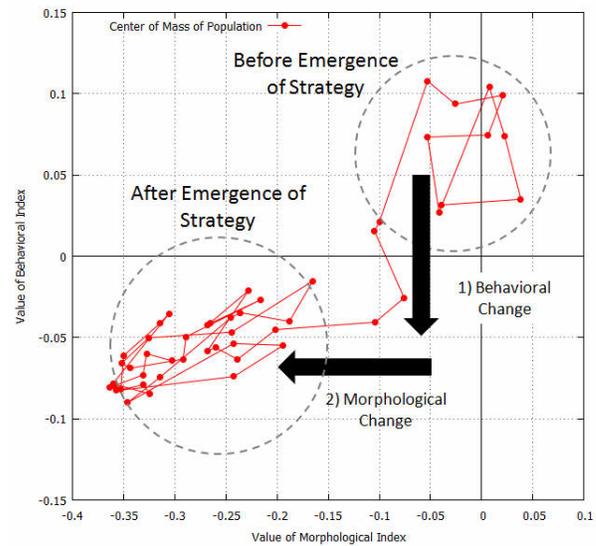


Figure 9: A typical evolutionary trajectory on the trait space when Guard Strategies (*Tower* type) evolved in the prey population.

It should be noticed that, as a general tendency of the step-wise evolutionary process, the fitness did not increase necessarily in accordance with the evolution of morphology or behavior. Instead, it clearly increased when either morphology or behavior was improved, which followed the evolution of the other. This observation tells us about close coupling between morphological and behavioral evolutions in the emergence of new strategies.

The difference in the evolutionary order of new trait emergence at least partly depends on the characteristics of evolved strategies. Guard strategies can be classified into the mobile and immobile ones. The former and the latter

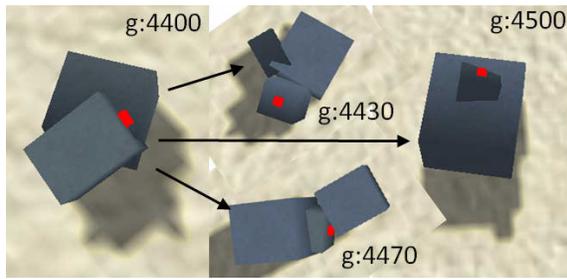


Figure 10: The virtual creatures with the best fitness in each generation appearing in the evolution trial shown in Fig. 9. The right three individuals have obtained the guard strategy and are the offspring of the left one.

correspond to the creatures in Fig. 8 (*Clam* and *Turtle* types) and Fig. 10 (*Tower* type), respectively. In general, immobility tends to need a specific sort of behavior while keeping some degree of freedom of their morphology. This might be the cause of the particularity of the emergence of the *Tower* type strategy in the context of the evolutionary order of the trait evolution. We will discuss the relationships between asymmetric properties and evolutionary dynamics in more general sense in the next section.

Discussion

This paper demonstrates that we can observe the complex coevolutionary dynamics that takes place concurrently at predator-prey and morphology-behavior levels in a 3D physically simulated world. We discuss here that its complexity arises at least partly from the asymmetric properties in these relationships.

Dynamics Caused by Population-Level Asymmetry

The predators were required to perform the following sequence of behaviors in the experiments: detecting a prey, approaching it, and then touching its torso part. Especially, successful methods for approaching need better morphology and behavior realizing faster movement and quick direction change, despite the fact that the bodies of both predators and prey are constructed and controlled by the same rules described in the Model section. In contrast, a prey adopting a simple strategy, such as moving forward in some direction, could be rather strong. Therefore, in general the selection pressure is considered stronger in the predator population than in the prey population. This asymmetry is not specific to our model but universal in natural ecosystems.

In the experiments, we frequently observed a typical coevolutionary dynamics “arms race” in which two evolving populations reciprocally drive one another to increasing levels of complexity. It was clearly shown that the asymmetry in the difficulty of required strategies caused the preceding evolution of the predators. The coevolutionary dy-

namics always started with the acquisition of the capturing strategies by predators as described in the previous section. This is due to the fact that the selection pressure acted more strongly on the predators in the initial stage in which both populations were occupied with randomly generated strategies. The prey started devising strategies in response to the increase in the selection pressure caused by the emergence of the effective strategies of the predators. A typical evolutionary scenario following the initial stage was regarded as a step-by-step evolution composed of several repetitions of alternate strategy improvement corresponding to the previous improvement of the other population. We also found in the experiments that the required time for predators to find or improve their strategies tended to be longer than in the case of prey. This is also due to the asymmetry between the predator-prey relationships.

Dynamics Caused by Individual-Level Asymmetry

When comparing the changes in morphology and those in behavior, our impression, based on the experience with the coevolutionary experiments, is that a morphological change (e.g. the loss/growth of the limbs) tends to bring about a drastic change in the strategy. If this hypothesis is correct, a change in morphology and that in behavior in evolution correspond to an operator for global search and that for local search in the context of optimization problems. In other words, the morphology evolution has a potential to be a driving force to break away from the stalemate and in contrast, the behavioral evolution has a role to adjust the performance of the current strategy.

This hypothesis agrees well with the experimental results as follows. As for prey strategy evolution, we usually observed an emergence of an effective defense strategy characterized by a unique morphology, accompanied with a sharp increase in fitness. As for predator strategy evolution, we observed an emergence of a novel morphology that was followed by a gradual behavior evolution with the diversity in behavior, producing a gentle increase in fitness. However, only in the case of responding to the emergence of a novel prey strategy, behavior evolution played a great role compared with morphology evolution. These results can be further generalized as a hypothesis for morphology-behavior coevolution. Morphology evolution tends to precede behavior evolution in the case the evolution is rather independent of the other species evolution, while behavior evolution tends to precede or work dominantly in the case the evolution is responsive to a novel strategy evolved in another species. This hypothesis is also supported by previous results (Ito et al., 2013).

Conclusion

We presented the results of evolutionary experiments investigating morphological and behavioral dynamics of a coevolutionary predator-prey scenario in a 3D physically simu-

lated environment. We defined a number of indices to quantify aspects of the morphologies and behaviors of our creatures, and used these to analyze the coevolutionary dynamics. The evolutionary dynamics of the strategies showed an “arms race” between the predators and prey, a typical feature of natural coevolutionary scenarios. We also temporally analyzed the coevolutionary dynamics of the morphology and behavior, focusing on the order in which new traits emerge. Our results illustrate how double coevolution, between predator and prey on the one hand and morphology and behavior on the other, can lead to asymmetrical development of morphology and behavior at both the intra-species level and the inter-species level. These two asymmetries led to complex coevolutionary dynamics in our 3D physical simulated framework, and likely do so in predator-prey interaction scenarios in general, both in artificial frameworks and in nature.

Our model could be extended in various directions. One obvious direction would be to use a scenario with many-to-many encounters. Such evolutionary experiments may shed light on the origin of group hunting and prey herding behaviors that are prevalent in the biological world (Sumpter, 2011). Furthermore, this direction might add a new direction to understanding the effect of the phenotypic change on the population dynamics (Pimentel, 1961; Rosenzweig and MacArthur, 1963). Another direction would be to investigate how the dynamics of double coevolution concentrated on in this paper can be applied in the field of engineering, including evolutionary robotics.

References

- Agrawal, A. (2001). Phenotypic plasticity in the interactions and evolution of species. *Science*, 294(5541), page 321.
- Azarbadegan, A., Broz, F., and Nehaniv, C. L. (2011). Evolving sims’s creatures for bipedal gait. In *Proceedings of 2011 IEEE Symposium on Artificial Life (IEEE ALIFE 2011)*, pages 218–224.
- Chaumont, N., Egli, R., and Adami, C. (2007). Evolving virtual creatures and catapults. *Artificial Life 13*, pages 139–157.
- Edmunds, M. (1974). *Defence in Animals: A survey of anti-predator defences*. Longman Group Limited.
- Ito, T., Pilat, M. L., Suzuki, R., and Arita, T. (2012). Emergence of defensive strategies based on predator-prey coevolution in 3d physical simulation. In *Proceedings of the 6th International Conference on Soft Computing and Intelligent Systems, and the 13th International Symposium on Advanced Intelligent Systems 2012 (SCIS-ISIS2012)*, pages 890–895.
- Ito, T., Pilat, M. L., Suzuki, R., and Arita, T. (2013). Alife approach for body-behavior predator-prey coevolution: Body first or behavior first? In *Proceedings of the 18th International Symposium on Artificial Life and Robotics (AROB18th)*, pages 551–554.
- Legreneur, P., Laurin, M., and Bels, V. (2012). Predator-prey interactions paradigm: a new tool for artificial intelligence. *Adaptive Behavior 20(1)*, pages 3–9.
- Miconi, T. (2008). In silicon no one can hear you scream: evolving fighting creatures. In *Proceedings of the 11th European conference on Genetic programming (EuroGP’08)*, pages 25–36.
- Miconi, T. and Channon, A. (2006). Analysing co-evolution among artificial 3d creatures. *Artificial Evolution*, 3871, pages 167–178.
- Murray, J. (2003). *Mathematical Biology I: An Introduction*. Springer-Verlag.
- Pilat, M. L., Ito, T., Suzuki, R., and Arita, T. (2012). Evolution of virtual creature foraging in a physical environment. In *Proceedings of the 13th International Conference on the Simulation and Synthesis of Living Systems (ALIFE13)*. MIT Press.
- Pilat, M. L. and Jacob, C. (2008). Creature academy: A system for virtual creature evolution. In *Proceedings of the IEEE Congress on Evolutionary Computation (CEC 2008)*, pages 3289–3297.
- Pilat, M. L. and Jacob, C. (2010). Evolution of vision capabilities in embodied virtual creatures. In *Proceedings of the 12th annual Conference on Genetic and Evolutionary Computation Conference (GECCO 2010)*, pages 95–102.
- Pimentel, D. (1961). Animal population regulation by the genetic feed-back mechanism. *The American Naturalist*, 95, pages 65–79.
- Rosenzweig, M. L. and MacArthur, R. H. (1963). Graphical representation and stability conditions of predator-prey interactions. *The American Naturalist*, 97, pages 209–223.
- Sims, K. (1994a). Evolving 3d morphology and behavior by competition. In *Proceedings of the 4th International Works on Synthesis and Simulation of Living Systems (ALIFE IV)*, pages 28–39.
- Sims, K. (1994b). Evolving virtual creatures. In *21st Annual Conference on Computer Graphics and Interactive Techniques (SIGGRAPH 94)*, pages 15–22.
- Sumpter, J. T. D. (2011). *Collective Animal Behavior*. Princeton University Press.
- Taylor, T. and Massey, C. (2000). Recent developments in the evolution of morphologies and controllers for physically simulated creatures. *Artificial Life*, 7 (1), pages 77–87.
- Turk, G. (2010). Sticky feet: evolution in a multi-creature physical simulation. In *Proceedings of the 12th International Conference on the Simulation and Synthesis of Living Systems (ALIFE12)*, pages 496–503.
- Ventrella, J. (1998). Attractiveness vs. efficiency: How mate preference affects locomotion in the evolution of artificial swimming organisms. In *Proceedings of the Sixth International Conference on the Simulation and Synthesis of Living Systems (ALIFE6)*, pages 178–186.