

EFFECT OF PREDATOR ARMOR EVOLUTION ON
PREDATOR-PREY ECOSYSTEMS

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Abstract

Investigating the evolution of defensive weaponry in animals, such as armor plates, elongated teeth, and horns, alongside its effect on the population dynamics of the predator-prey ecosystem can provide insight into why some animals have or haven't developed such ornaments. Preliminary research has delved into instances in which defensive weaponry have developed in various groups of animals, including mammals, reptiles, archosaurs, and fish, alongside hypothesis testing using computational models of coevolution between predator and prey species. However, whether introducing an evolution of defensive weaponry in an ecosystem would be beneficial or detrimental to the survival of its species is an open problem.

In this dissertation, we tackle the question “in theory, would armor evolution in predators lower the average evolutionary time until extinction in different predator-prey ecosystems?”. Discrete-time discrete-space agent-based models are used to simulate 2 groups of ecosystems, those with and without predator armor evolution. The number of timesteps for the predator species to go extinct is measured and compared between the 2 groups. We found that armor evolution in predators is detrimental to lengthening its time until extinction with the exception of the instance in which the prey also exhibit armor evolution. The results additionally aligned with findings from the preliminary studies regarding the coevolutionary arms-race between predator and prey.

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1. Introduction

Ecological studies, especially those related to the population dynamics in predator-prey ecosystems, can be utilized to aid in conservation efforts. For example, due to the decline in the population of apex predators, the population of mesopredators, or predators in the medium range of the predation hierarchy, have increased, negatively affecting the population of the prey species (Prugh et al., 2009). The effect of artificially reducing the population of such population dynamics via lethal control has been studied with both positive and negative results (Connor and Morris, 2015). As an alternative method, apex predator species may be introduced to ecosystems to regulate the population of invasive species or domestic species that can be harmful to the ecosystem (Carpenter et al., 2021). As such, a multitude of studies are conducted in population dynamics is conducted. A thorough understanding the effect of human intervention on population dynamics is essential for conservation efforts.

Additionally, ecological studies can be combined with paleontological studies to aid conservation efforts. In terms of population dynamics, paleontological data has been utilized to estimate the population and survivorship of extinct species (Kurtén, 1954). For example, Bayesian statistics has been utilized to infer speciation and extinction of species based on fossil occurrence (Silvestro et al., 2014; Silvestro et al., 2019). With ongoing research efforts of utilizing paleontology to inform conservation with temporal data and inferences (Dillon et al., 2022), estimates of the survivorship of species would be useful. It is apparent that understanding the population dynamics of extinct species can be beneficial to conservation efforts.

Some of the important elements in predator-prey ecosystems that influence their population dynamics are offensive and defensive anatomy and behavior in predator and prey (Abrams, 2000). While studies on the evolution of the predator-prey arms-race have been conducted in prior research, the effect of such arms-race on the ecosystem is an ongoing problem. This would be especially important in the context of re-introduction of apex predators in ecosystems, since coevolving species, such as apex predators, can be incentivized to evolve both slowly and rapidly, based on the Red King hypothesis (Bergstrom et al., 2003) and the Red Queen hypothesis (Van Valen, 1977), respectively. To narrow down the focus of our research, we chose to investigate the effect of the evolution of defensive systems in predators against dangerous prey on the population dynamics of their ecosystems, which is relevant to the conservation effort of the aforementioned apex predator re-introduction.

In this thesis, we tackle the following question: in theory, could armor evolution in predators lower the average evolutionary time until extinction (TUE) in different predator-prey ecosystems? Specifically, we investigate if there were 2 sets of n ecosystems, the former of which has predators with armor evolution (AE) and the latter of which has predators with no armor evolution (NAE), whether the distribution of TUE for the former be statistically significantly smaller than that of the latter. Predator TUE is chosen as a metric to evaluate the stability of the predator-prey ecosystems since, aside from predator extinction, predator TUE also accounts for prey extinction: predators will always go extinct if there are no more species to prey on. It should be noted that, while the experiments set armor as the default type of defensive weaponry to be experimented with, the findings can be applied to other types of

defenses, such as toxins and their resistance. Additionally, a parallel experiment where the predator TUE for predator AE and NAE when prey also exhibit AE and NAE is conducted to investigate whether the results align with preliminary research.

2. Prior Research

2.1. Field Studies

Anti-prey defense can be conducted using defensive weaponry. In the case of mammals, defensive weaponry in prey were found to appear in those that are vulnerable from easily being spotted and attacked by predators, while weaponry in predators were either used for defense as secondary functionalities, such as the claws in bears and teeth in Machairodontinae (saber-toothed cats), or defense from predation from larger predators, specifically noxious gas (Stankowich, 2012; Stankowich, 2014). Additionally, fear has been interpreted as prey's anti-predation defense. Humans' voices has been observed to induce fear in predators, causing the said predators to be conservative in their foraging activities and having fear act as a defense from a 3rd party for prey (Suraci et al., 2019). In the case of reptiles, the levels of toxicity of the toxin produced by newts (*Taricha*) and level of resistance to the toxin by their predators', garter snakes (*Thamnophis sirtalis*), were found to match in terms of geographical regions in northwest regions of North America (Hague et al., 1999; Brodie et al., 2002). On the other hand, discrepancies, where the garter snakes were able to develop resistance stronger than the toxicity of the newts residing the area, were detected in other regions (Hanifin et al., 2008). For Hanifin et al.'s study, no instances of the opposite were found. From these results, for our experiment, given prey AE, analogous to evolution of newt toxins, we expect the predator TUE for ecosystems with predator AE, analogous to evolution of toxin resistance in snakes, to be statistically significantly larger than those with predator NAE. Additionally, in an ecosystem with mammals, lizards, and the toxic black widow (*Latrodectus hesperus*), while the mammals struggled to defend against the toxin, the 2 lizard species that prey on

black widows, *Sceloporus occidentalis* and *Elgaria multicarinata*, were found to be resistant to the toxin in varying degrees (Thill et al., 2022). Out of the 2 lizard species, while both species' sprint speeds were unaffected, the former suffered muscle and immune system damage while the latter was unaffected. Thill et al. hypothesize that such discrepancies in toxin resistance between species may be caused by the degree of interaction between the species.

In the case of garter snakes, it has been hypothesized and documented that the anti-prey resistance is utilized to store toxins ingested into their body during predation and reuse as a method for their own anti-predation defenses (Williams et al., 2012; Savitzky et al., 2012). The relationship between anti-predation and anti-prey defense may be hierarchical depending on the structure of the predator-prey ecosystem.

Evolution of defensive weaponry has also been inferred from fossil records. While the true behaviors of animals and functionalities of extinct animals cannot be determined with high confidence (Hone, 2024), there is evidence of anatomical ornaments having been in intraspecific or interspecific combat, especially in herbivorous dinosaurs (Farke, 2014). For example, statistical, histological and chemical analyses were conducted to infer lesions from traumatic origin in basal frills of the ceratopsian, triceratops, hinting at them being used for intraspecific combat (Farke et al, 2009; D'Anastasio et al., 2022). However, as mentioned before, difficulties arise in inferring behavior from fossil evidence as observations of lesions can be of non-traumatic origin; lesions in ceratopsians have been determined to be from bone disease (Tanke et al., 2006).

It should be noted that, while defensive weaponry is observed or inferred in extant and extinct animals, it does not necessarily indicate that such morphology emerged solely as an adaptation for anti-prey or anti-predator defenses. In the case of garter snakes, low levels of resistance to the newts' toxins have been found in earlier stages of their evolutionary lineage, despite the species in such stages not interacting with the newts' toxins (Motychak et al., 1999). While the syncervical in Neoceratopsians are used to support their large basal skulls, their origin are found to not correlate with the development of such functionaity (Vanburen et al., 2015).

Anti-prey defense can also be in the form of ethology, where the predator behaviors are based on the foraging cost, or the risk of injury while hunting prey (Mukherjee et al., 2013). Foraging costs are based on the amount of food needed to make the predator be indifferent to the danger of fetching the food from its location and whether the fitness, defined by the net energy gain and the predation survival rate, is equal across all of such locations (Brown et al., 2004). Extant mammalian and avian predators are observed to disproportionately succeed in capturing substandard prey individuals, such as those that are weak and injured, based on their species' general defensive capabilities (Temple, 1987). As a result, the predators adapt their hunting strategies to reflect the foraging costs. Barn owls (*Tyto alba*) are found to conduct risk management while hunting gerbils (*Gerbillus andersoni allenbyi*) by having a tendency to avoid the risk of injury, unless it is hungry, in which it doubles the said risk (Embar et al., 2014). Eagle owls (*Bubo bubo*) actively prefer to hunt substandard rabbits (*Oryctolagus cuniculus*) by observing the latter's visual cue indicating health (Penteriani et al., 2008).

Apex predators are known to conduct prey switching, where they target prey species with the least foraging cost, based on the defensive capabilities of the prey (Tallian et al., 2017) with evidence extending to extinct species (Zong et al., 2022). While ethology is not the focus of our research, it is evident that foraging cost minimization is an important element of predation attempts.

Additionally, apex predators are observed to conduct self-regulation in their population density, via the tradeoff between reduction of reproduction rate and infanticide and cooperative hunting and parental care, to prevent over-exploitation of prey and driving prey to extinction (Wallach et al., 2015a). This can be expanded to conservation, where apex predators can be introduced to ecosystems to regulate both the other species in the ecosystem and itself (Wallach et al., 2015b).

On a microscopic scale, the evolution of predator-prey dynamics in ecosystems composed of the predatory ciliate (*Tetrahymena thermophila*) and various strains of bacteria has been researched (Cairns et al., 2020). In Cairns et al.'s work, both ciliate and bacterial strains were evolved using serial propagation over several years. By comparing the population dynamics of both the ancestral and evolved strains, the effect of coevolution on the 2 species' traits are observed. Prey evolution is seen to hinder the rate of population increase and equilibrium density in predators. We therefore expect the predator TUE with prey AE to be statistically significantly smaller than that without prey AE.

In addition to predator-prey ecosystems, coevolution of defensive systems in animals can also be applied to host-parasite ecosystems, where the parasite attempts to infect the host and the host attempts to resist the parasite(Betts et al., 2018; Chevallereau et al., 2022) . For simplicity this study focuses on the predator-prey ecosystem; however, implications may arise for the context of host-parasite systems.

2.2. Model-Based Approach

Our method utilizes artificial life, where biological organisms are simulated using computational models, specifically agent-based models, which represents features of the organisms in the form of individual agents often interacting with each other (Sayama, 2015), and evolutionary algorithms, which gradually alter the agents to maximize an objective function over generations, as inspired by evolution (Sean, 2010). In the case of evolutionary algorithms, each individual agent's properties, such as its morphology and behavior are referred to as phenotype, and the representation of the phenotype as a binary, integer or floating-point vector is referred to as genotype. For example, if an agent, representing a simulated organism, is set to move around in a 2D space using an artificial neural network, the behavior of the agent and the neural network itself are phenotypes and the 1D vector storing all of the weight values of the neural network is the genotype. Evolutionary algorithms define an objective or fitness function, which describes a numerical value that the evolving agents attempt to maximize. For example, the fitness of the aforementioned simulated organism may be the time in which it manages to avoid other agents in the 2D space. The genotypes of the agents with the highest fitness per generation are selected,

replicated, and mutated, or modified in terms of values, to make the population of agents for the next generation.

Predator-prey ecosystems have been simulated in preliminary studies. Sutherland and Jacobs' (1994) work utilizes the Wa-Tor model (Dewdney, 1984), a discrete-space discrete-time agent-based model which incorporate predation, reproduction, and predator starvation, to demonstrate that the prey population density is dependent on the predator reproduction and starvation times and the predator population density is dependent on the prey reproduction time, aligning with the Lotka-Volterra (LV) model, differential population dynamics model for predator-prey interactions.

Utilizing such findings, we can simplify our predator-prey ecosystem simulations with the properties found in the LV model, specifically in which the predator reproduction occurs for every successful predation attempt.

Genetic algorithms, a subclass of evolutionary algorithms, have been used to simulate evolution of species in preliminary studies. Werner and Dyer's (1991) work has the blind male agents attempt to move toward stationary female agents to reproduce. Each female agent emits a “sound” signal based on the location of the nearest male agent in its peripheral vision. The male agent “listens” to the signal and attempts to move toward the female agent. While our method does not include communication between agents, the aspect in which agents produce actions based on their peripheral vision is utilized. Luke et al.'s (1996) work simulates predator-prey ecosystems with different intraspecific and interspecific breeding and coordination mechanisms. For

simplicity, we do not utilize diverse breeding methods, instead only utilizing mutation from 1 parent.

Mokhtar's (2012) work is, from our understanding, the sole research that delves into anti-prey mechanisms for predators using artificial life. In addition to the aforementioned defensive weaponry, behaviors found in single-celled organisms, particularly bacteriophage's incorporation of DNA and reproduction and symbiotic relationships, such as flora bacteria and the human gut, are considered as anti-prey and predatory behaviors. A combination of gene regulatory networks and metabolic networks are used to model the 2 behaviors, and evolutionary algorithm is used to find solutions that balance between them. In contrast to such network models, our method utilizes agent-based models and simplifies the mechanisms of predation and anti-prey systems to a stochastic death per predator-prey interaction.

LV models are an alternative method for analyzing the effect of predator and prey evolution on population dynamics using mathematical models. Brown et al. (2016) utilizes the LV model to investigate the arms race between the predators' offense, in the form of fear against their prey, and prey's "vigilance", as their defense against such fear. As the predator and prey coevolve, the predators adapt their fear to increase as their population increases, and the prey's population decreases. As a result the prey increase their defenses, and the predators' population decreases. The population dynamics are observed to converge to a stable equilibrium or oscillation using this feedback loop. Mougi and Yoh's (2010) work utilizes a combination of the LV model and the quantitative trait evolution model, which models the coevolution between 2

competing species, to observe the population dynamics with different adaptation rates for the predators' offense and the prey's defense. It is found that the population dynamics reach a stable equilibrium when the adaptation rate for the prey's defense is greater than the predators' offense; otherwise, the dynamics result in an oscillation. For our experiment, we expect the population dynamics for all experiments except those with prey AE to show oscillations, while prey AE should converge to an equilibrium.

3. Method

3.1. Experiment Setting

We simulated the predator-prey ecosystem using a 2D discrete-space discrete-time agent-based model. The environment is set up as a grid world with predator and prey agents occupying certain cells. Each agent contains a set of floating point numbers as a genotype. When an agent crosses a boundary, it is transported to the cell at opposite side of the grid.

Each predator and prey agent is able to see the surrounding 3x3 square excluding the cell it is occupying, or the Moore neighborhood, and can conduct 1 of 4 actions: left turn, right turn, no movement, and forward movement. Each predator agent is controlled by a feed forward neural network of 8 input neurons, 8 hidden neurons, and 4 output neurons, the weights of which are stored in the genotype. The activation functions for the input and hidden layers are the sigmoid function, and that for the output layer is the softmax function. The action is chosen by the largest value within the 4 output neurons.

Each prey agent is controlled by a random walker, more specifically a uniform distribution that chooses between the aforementioned 4 actions.

For every timestep, each agent attacks the closest opposing agent, in this case predator against prey and vice versa, within the aforementioned 3x3 square including the cell it is occupying. Every agent being attacked is set to perish probabilistically based on a

single floating point value a in the genotype describing the armor, where $0 \leq a \leq 1$.

The probability that the predator agent survives the encounter is

$$s_{\text{default}} + a(1 - s_{\text{default}}),$$

where s_{default} is a hyperparameter indicating the probability that the agent survives the encounter without armor. The prey are not equipped with armor; therefore, they are set to perish after every attack from a predator.

Similarly to the LV model (Lotka, 1920), for every prey agent killed by a predator agent, the predator agent is reproduced and spawned in a random location, with a normalized random floating point vector added to the genotype as the mutation. While the LV model spawns the reproduced predator agent in the location of the deceased prey agent, in our experiment, the reproduced predator agent is set in a random location to avoid the parent and child from immediately competing with each other, such as in the case of the subsequently defined PvP experiment. Every predator agent is automatically killed after $t - 1$ timesteps to incentivize them to kill as many prey and reproduce as much as possible within a given window of time. The prey agents are set to reproduce probabilistically every timestep.

In conclusion, each predator agent genotype contains the weights of the neural network and the armor value a , resulting in a 97-dimensional floating-point vector.

The number of timesteps until extinction of predators, between n ecosystems whose predators have evolving armor and n ecosystems whose predators do not have evolving armor, are compared.

Table 1: Hyperparameters for the Vanilla experiment as decided by maximizing the predator TUE for NAE using CMA-ES

Hyperparameter	Agent Type	Value
Grid Size		22x22
Initial Population	Predator	10
	Prey	14
Reproduction Rate	Prey	0.1
Survival Rate without Armor ($s_{default}$)	Predator	0.63
	Prey	0.02
Timesteps Until Death	Predator	13

The hyperparameters of the experiment are set to have the population of both predator and prey species to oscillate over time. As seen later in the population dynamics for NAE in the Vanilla experiment in Table 1, maximizing the number of timesteps until extinction of predators was found to result in more oscillations in population; therefore the hyperparameters were chosen to maximize such using a Python CMA-ES implementation (Hansen et al., 2019).

In addition to the aforementioned experiment setting, which will be referred to as Vanilla, 4 more experiments each with different modifications from the original were conducted.

- PreyNN - Prey controlled by neural network
- PreyAE - Prey have armor evolution
- Directional - Predator armor is directional
- PvP - Predators can attack each other

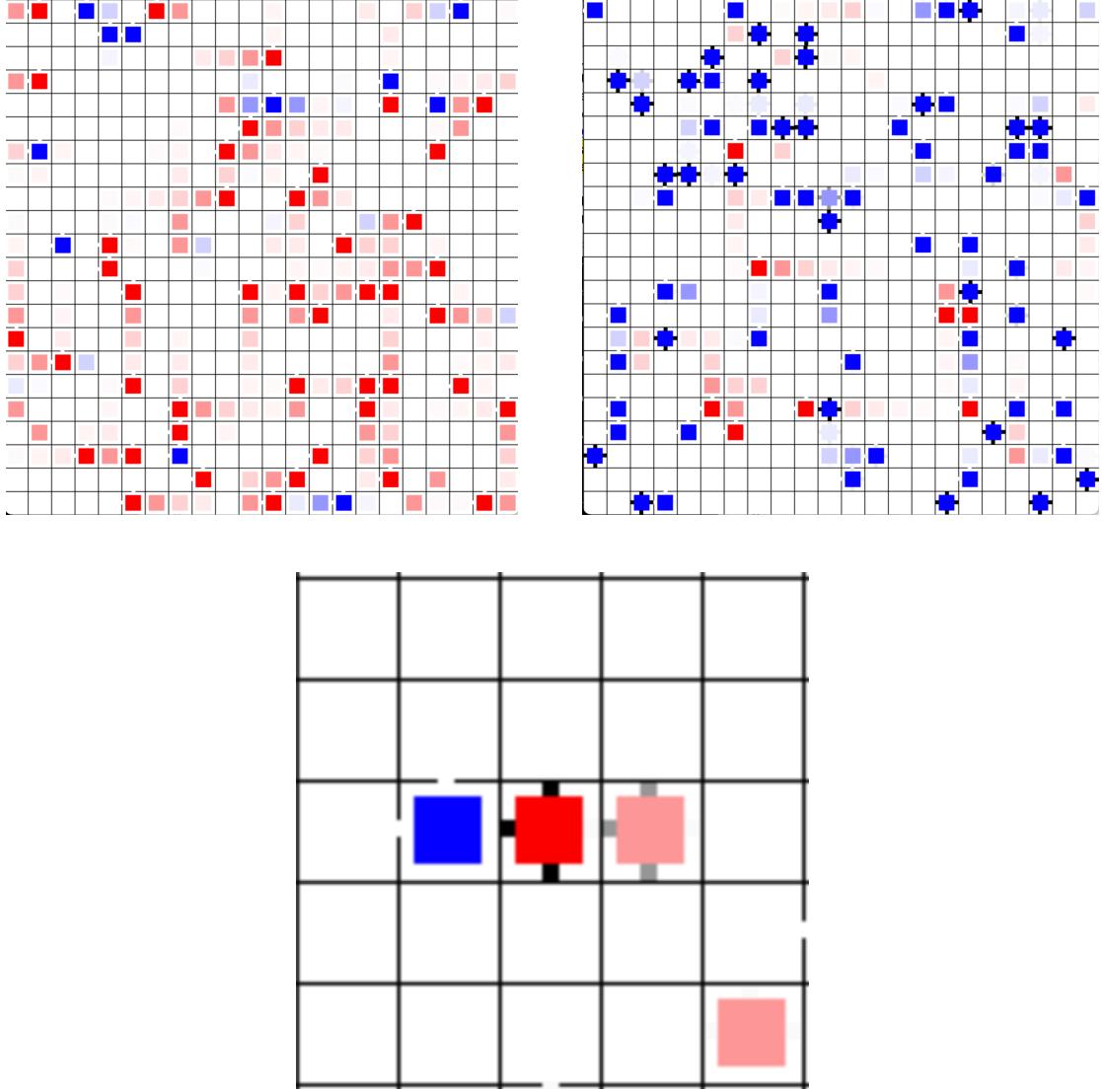


Figure 1: Visualized examples of the predator-prey ecosystems. The red cells indicate the predator agents, the blue cells indicate the prey agents, and the black squares on the perimeter of the cells indicate armor. The opacity of the black squares indicates the value of the armor a . For every agent, their previous 3 positions are indicated using gradually faded colors. Top left: A snapshot of Vanilla, where the majority of the agents are predators. Neither predators or prey have evolved armor. Top right: A snapshot of PreyAE, where the majority of the agents are prey. The prey are evolving armor. Bottom: A segment of a snapshot of Directional, showing that the predator only has armor on the top, left, and bottom.

For the PreyNN experiment, each prey agent is equipped with a 96-dimensional floating point genotype containing a neural network with the same architecture as that

for the predators. Mutation, in which a normalized random floating-point vector is added, is applied for every prey reproduced by its parent. The PreyAE experiment equips each prey agent with a 1-dimensional floating-point genotype containing an armor value in the same manner as the predator agents. The Directional experiment defines the predator armor a as a 4-dimensional floating-point vector describing the armor value associated with top, bottom, left, and right directions of the agent. Its probability of being killed by another agent depends on the relative direction of the attacker. PvP enables the predators to be attacked by other predators in addition to the prey.

Visualized examples of these experiments are as Figure 1.

Each experiment was conducted 100 times. The maximum number of timesteps was set as 1000.

3.2. Comparison

For each experiment, a comparison of the sample distributions of the predators' TUE between AE and NAE ecosystems is conducted.

First, the normalcies of the 2 distributions are tested using the Shapiro-Wilk (SW) test, which sets a sample dataset fitting a predetermined distribution as the null hypothesis, and the Kolmogorov-Smirnov (KS) test, which sets 2 sample distributions belonging to the same population distribution as the null hypothesis. For the KS test, each sample

dataset is compared with a normal distribution, whose mean and standard deviation are those of the sample dataset.

Using the results of the normalcy tests, the sample distributions between AE and NAE ecosystems are compared. If both distributions are found to be normal, the Welch's T-test is used. Otherwise, the KS test and the Mann-Whitney-Wilcoxon U-test is used. All 3 tests sets 2 sample distributions belonging to the same population distribution as the null hypothesis. The U-test can additionally test the null hypothesis in which one distribution is greater than the other. The null hypothesis in which NAE is greater than AE is used for this analysis. A Bonferroni correction is applied for the 3 tests, since there are 5 pairwise comparisons, turning the p-value threshold from 0.05 to 0.01.

It should be noted that the T-test was not used since all pairwise combinations of AE and NAE sample distributions included at least 1 non-normal distribution.

4. Results

The hyperparameters selected are as Table 1. The comparison results are as Table 2 and 3. The mean, standard deviation, maximum, and minimum predator TUE for every experiment are as Table 4. The resulting population dynamics for the maximum and minimum predator TUE are displayed in Figure 2 and 3.

Looking at Figure 2 and 3, it is evident that longer predator TUE results in oscillatory behavior in the population dynamics, with the exception of PreyAE.

All distributions except the NAE sample distribution in PreyAE were non-normal. While the KS test for the NAE sample distribution in PvP resulted in the acceptance of the null hypothesis, the subsequent comparison analysis was not affected since the AE sample distribution was non-normal. As a result, the T-test was not used for the distribution comparisons.

All experiment except the U-test for Directional are concluded to have the NAE sample distribution and the AE sample distribution come from different parent distributions. Additionally, all experiments except for PreyAE resulted with the distribution for NAE being greater than that for AE.

While the U-test on the Directional experiment accepted the null hypothesis in which NAE and AE sample distributions have the same parent distribution, since the p-value was merely 0.002 above the 0.01 threshold and the null hypothesis in which NAE

Table 2: P-values of SW and KS tests where the null hypothesis is that a distribution is normal. The bold values indicate p-values above 0.05, where the null hypothesis is accepted.

		Distribution is normal	
		SW	KS
Vanilla	NAE	$2.43 \cdot 10^{-9}$	0.06
	AE	$6.15 \cdot 10^{-6}$	0.03
PreyNN	NAE	$2.64 \cdot 10^{-6}$	0.002
	AE	$8.46 \cdot 10^{-12}$	0.002
PreyAE	NAE	0.33	0.48
	AE	$1.29 \cdot 10^{-6}$	0.002
Directional	NAE	$1.79 \cdot 10^{-10}$	0.003
	AE	$8.48 \cdot 10^{-8}$	0.04
PvP	NAE	$1.61 \cdot 10^{-7}$	0.16
	AE	$1.58 \cdot 10^{-8}$	$3.22 \cdot 10^{-4}$

Table 3: P-values of KS and U-tests where the null hypothesis is that the 2 sample distributions are from the same parent distribution. The bold values indicate p-values above 0.01, where the null hypothesis is accepted.

	NAE equal to AE		NAE greater than AE
	KS	U-test	U-test
Vanilla	$9.88 \cdot 10^{-3}$	0.002	1.00
PreyNN	$9.88 \cdot 10^{-3}$	0.004	1.00
PreyAE	$2.68 \cdot 10^{-25}$	$1.43 \cdot 10^{-24}$	$7.14 \cdot 10^{-25}$
Directional	0.004	0.012	0.99
PvP	$3.04 \cdot 10^{-14}$	$3.59 \cdot 10^{-12}$	1.00

sample distribution is greater than AE sample distribution was accepted, we treat the 2 distributions as having come from 2 different parent distributions.

Table 4: Mean, standard deviation (std), maximum (max), and minimum (min) predator TUE. For NAE in PvP experiment, the minimum predator TUE excluding 0 is listed in a parenthesis. The maximum capacity of timesteps is set as 1000.

		Mean	Std.	Max.	Min.
Vanilla	NAE	110.28	60.33	419	22
	AE	87.48	40.09	225	24
PreyNN	NAE	106.31	61.25	327	18
	AE	84.94	46.42	347	27
PreyAE	NAE	28.23	7.02	49	12
	AE	52.44	15.42	74	15
Directional	NAE	113.82	67.29	377	23
	AE	93.86	46.76	250	30
PvP	NAE	219.17	168.09	1000	0 (22)
	AE	80.69	35.35	212	20

Comparing the distribution from each experiment modification to that of the Vanilla experiment, as seen in Table 5, both NAE and AE distributions from PreyAE are less than those from Vanilla. It can also be noted from Table 5 that the NAE and AE distributions from PvP are statistically significantly greater than those of Vanilla. This coincides with the result seen in Table 4, in which the maximum predator TUE for NAE in PvP exceeded 1000 timesteps.

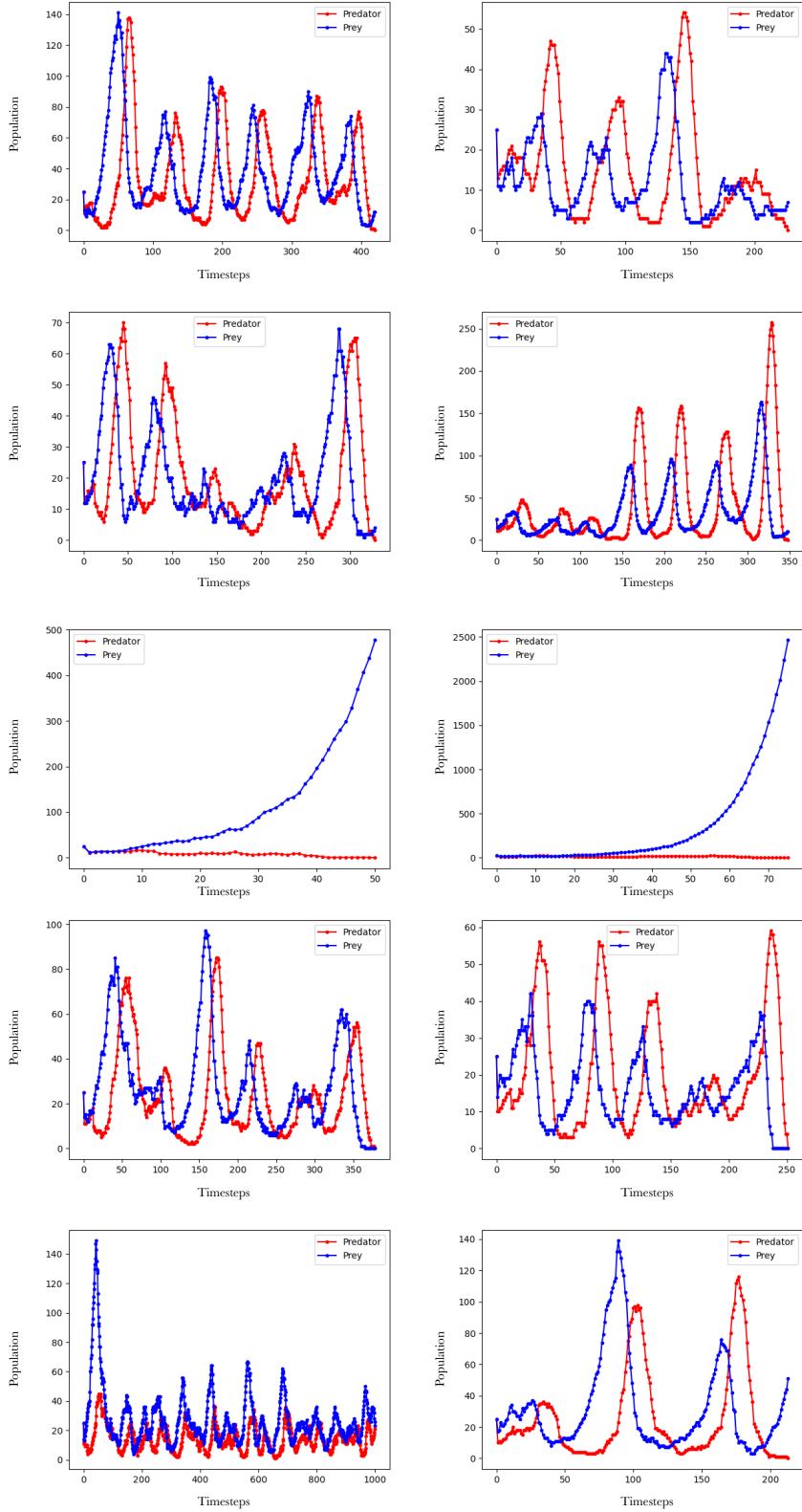


Figure 2: Population dynamics of ecosystems with the maximum predator TUE for every experiment setting. The rows are in the order of Vanilla, PreyNN, PreyAE, Directional, and Pvp. The columns are in the order of NAE and AE. The x-axis is the timesteps and the y-axis is the population.

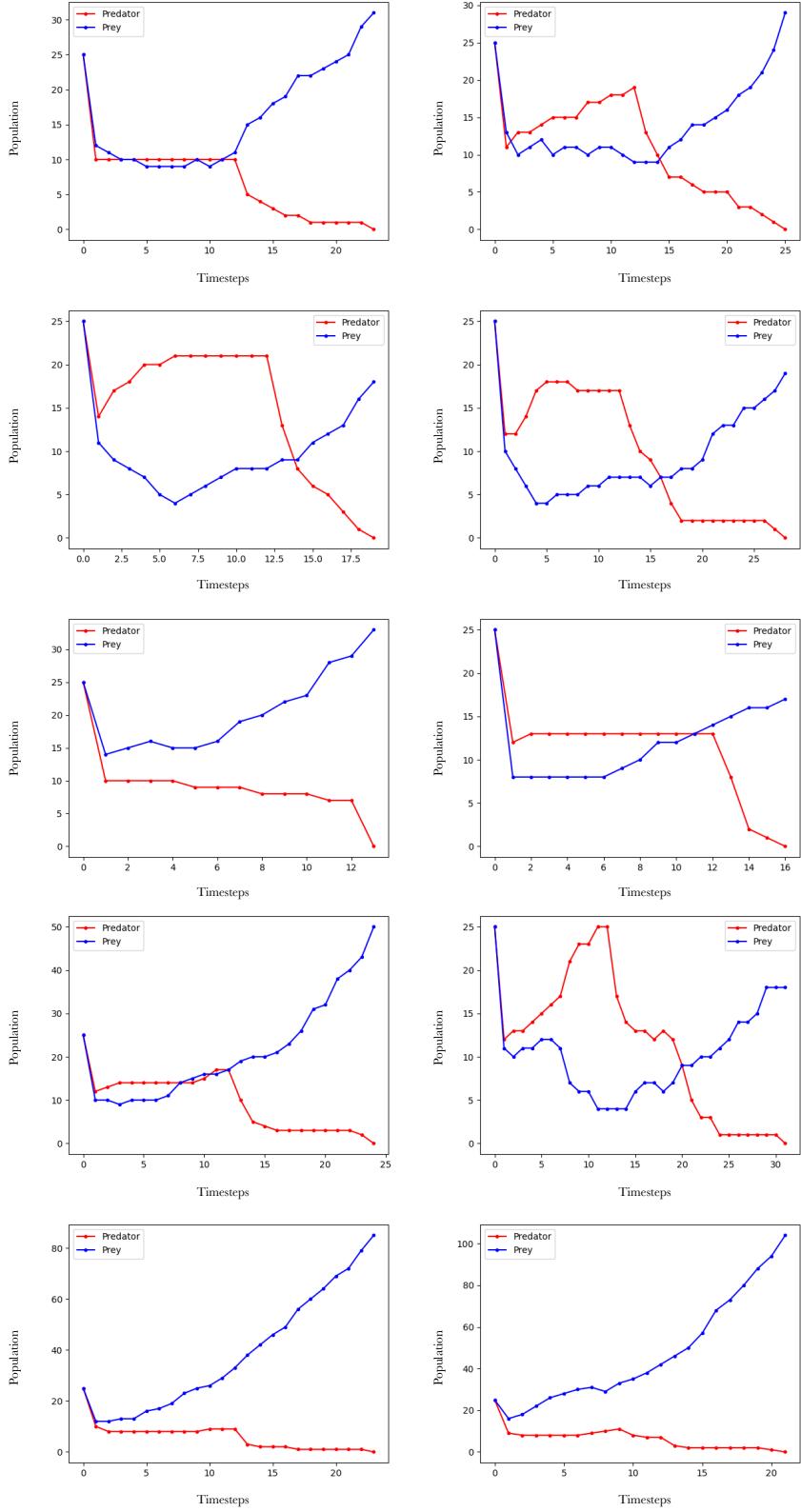


Figure 3: Population dynamics of ecosystems with the minimum predator TUE for every experiment setting excluding 0. The rows are in the order of Vanilla, PreyNN, PreyAE, Directional, and PvP. The columns are in the order of NAE and AE. The x-axis is the timesteps and the y-axis is the population.

Table 5: P-values of KS and U-tests indicating whether the distributions for Vanilla are greater than or equal to PreyNN, PreyAE, Directional, and PvP. The top and bottom tables indicate NAE and AE. The bold values indicate p-values above 0.01, where the null hypothesis is accepted.

	Distribution Equal to Vanilla		Vanilla Greater Than Distribution
	KS	U-test	U-test
PreyNN	0.37	0.40	N/A
PreyAE	$5.60 \cdot 10^{-50}$	$9.03 \cdot 10^{-51}$	1.00
Directional	0.70	0.99	N/A
PvP	$1.70 \cdot 10^{-9}$	$7.14 \cdot 10^{-7}$	$3.57 \cdot 10^{-7}$

	Distribution Equal to Vanilla		Vanilla Greater Than Distribution
	KS	U-test	U-test
PreyNN	0.21	0.29	N/A
PreyAE	$1.00 \cdot 10^{-11}$	$2.36 \cdot 10^{-13}$	1.00
Directional	0.97	0.61	N/A
PvP	$3.36 \cdot 10^{-13}$	$4.77 \cdot 10^{-11}$	$2.38 \cdot 10^{-11}$

5. Discussion

The results indicate that having predator AE decreases the average predator TUE in different predator-prey ecosystems with the exception of those with prey AE, in which predator AE increases the TUE. Predator AE being beneficial to predator TUE when prey AE is present aligns with Hanifin et al.'s (2008) work, where the all predatory garter snakes outside of northwest region of North America had developed better resistance, or defense, against the preyed newt's toxins, or offense. Additionally the lizard species *E. multicarinata* preying on the black widow has been found to have the toxin resistance be more effective than the black widows' toxin's offense (Thill et al., 2022). This is also analogous to human intervention having negative effects on the ecosystem by inducing fear in carnivores and hindering their foraging activities (Suraci et al., 2019). Additionally, predator AE being detrimental to predator TUE aligns with how apex predators exhibit behaviors which self-regulate its reproduction rate and predation rate to prevent over-exploitation of prey (Wallach et al., 2015a; Wallach et al., 2015b).

The distribution for predator TUE in PreyAE was statistically significantly smaller than that for other experiments for both predator AE and NAE. This aligns with Cairns et al.'s (2020) work, where the evolution in the preyed bacteria's defense hindered the population growth in predatory ciliates. This is also apparent in Figure 2, where the predator population is significantly less than that of the prey for the majority of the timesteps. It can be interpreted that the predators went extinct quicker than the other experiments, since the their population growth was hindered by the prey AE.

Having predators attack each other as in PvP resulted in statistically significantly longer predator TUE than that in other experiments. This aligns with Wallach et al.'s (2015a) work in which apex predators exhibited behavior that would reduce the reproduction rate, such as infanticide. Our observation indicates that having the predators attack each other contributed in preventing over-exploitation of prey, and having a mechanism to enable the tradeoff resulted in better management of the population dynamics of the ecosystem as a whole.

Additionally, examining Figure 2, the population dynamics of highest-performing ecosystems for all experiments, with the exception of PreyAE, resulted in oscillation, as expected from Mougi and Yoh's (2010) work. However, unexpectedly, while the predator population for PreyAE converged to an equilibrium, albeit as 0, the prey population seems to be steadily increasing. This may be due to the possibility that the predator TUE for PreyAE is significantly less than optimal, as inferred from Table 5, in which the distributions for the predator TUE are statistically significantly less than those in other experiments. In a future work, the population dynamics for PreyAE when the hyperparameters are set by CMA-ES to have a near-optimal predator TUE may be investigated. Regardless of its potential results, it is evident from other results that the introduction of PreyAE reduces the predator TUE.

As indicated in 2. Preliminary Studies, armor, or more generally defensive weaponry, can be applied to various concepts, including morphological features, such as horns, teeth, claws, toxins, resistance against toxins, ethological features, such as fear and

vigilance, and ecosystem types, such as predator-prey, symbiotic, and host-parasite systems. The results for our experiments may bring about implications in such contexts.

From the results of our experiment and the observations made in biology in preliminary studies (Hanifin et al., 2008; Thill et al., 2022; Suraci et al., 2019), it may be possible that, since evolution in anti-prey defense in predators can be beneficial to lengthening predator TUE whenever there is evolution in anti-predator systems, biological ecosystems may have more instances of predators winning the arms-race against the prey as opposed to the latter. This hypothesis can be applied to extinct animals, whose ecosystems can be difficult to discern merely from fossil evidence. In the case of the aforementioned triceratops, evidence that the species was preyed on by tyrannosaurus has been presented (Erickson et al., 1996). With the possibility of large basal frills in triceratops having been used for combat (Farke et al., 2009; D'Anastasio et al., 2022), it may be possible that the anti-prey defense in tyrannosaurus, such as teeth, claws, and large body size, may have been more effective than the offense from the former.

It should be noted that our study may not be reflective of real biological counterparts depending on the ecosystem. As indicated by the documented cases of anti-prey defenses in predators being utilized for their own anti-predator defenses (Williams et al., 2012; Savitzky et al., 2012), predator-prey ecosystems can be hierarchical. In the case of fear being utilized as anti-predator and anti-prey defenses, "spatiotemporal variations", in which spatial properties, such as the geographic region, open spaces,

and vegetation, and temporal properties, such as lighting, time of day, and hibernation periods, can affect the animals' response to fear (Palmer et al., 2017; Palmer et al., 2022). Having multiple predator species against 1 prey species can result in different levels of anti-prey defense between the species (Thill et al., 2022). Additionally, preliminary studies have been conducted using simulations that incorporate prey refuge, predation fear, and population perturbation (Rao et al., 2023). Addition of such features may generate different insights into more complex predator-prey ecosystems.

Future works can be expanded to analyzing the diversity of the evolved predator and prey species throughout the lifetime of the ecosystem, as the diversity of such species have been observed to affect the population dynamics (Kasada et al., 2014). There may be correlations between diversity and the predator TUE. Additionally, the offenses and defenses of both predator and prey species have been observed to have association with the frequencies of the oscillations in LV models (Mougi and Yoh, 2010). Analyzing the oscillations obtained from running ecosystems in agent-based models may bring insight on how well they match with the results obtained from using LV models, although performing regression and estimation of phases in noisy data as seen in Figure 2 may bring about difficulties.

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