

How What Kills You Makes You Stronger

Senior Honors Thesis-Winter 2012

Michael Norman

This work describes the development and analysis of several nonlinear ecological models combining age structures and mutual predation searching for a phenomenon called Population Increase through Mutual Predation (PIMP). Many examples, motivated by recorded real world biological behavior, showed such behavior. However there is no evidence that such models would be stable to evolutionary effects. Thus it is unlikely that any such systems would be found in nature.

I. INTRODUCTION

The natural world is extremely complex. Even a small ecosystem can contain hundreds of species that interact with each other, through resource competition, predation, mutualism and so on. It seems impossible that in such a huge system every interaction is optimized to produce a healthy system. Yet the persistence of such ecosystems over millions of years suggest that this can not be far from the truth. The question becomes which interactions are most beneficial to the ecosystem. Does nature prefer interactions that have the most immediate benefit to a particular species? Is it possible that a seemingly harmful action like the introduction of a predator can increase the total size of a species in an indirect way? While we leave it to the ecologists to tell us exactly what Mother Nature decides is best, we can show with simple models that it is certainly possible for directly harmful interactions to have an overall positive impact on a species and on an ecosystem as a whole. In particular we focus on a model for Population Increase through Mutual Predation (PIMP). We looked at many different systems: two dimensional predator prey models, four dimensional model with and without carrying capacities, and higher dimensional models with two major types of creatures. In each system we include a predation term and investigate what happens when we go from a system without predation to one which does. In particular we looked at what happened to the fixed points and tried to see if it was possible to increase the total biomass in a given species or in the system as a whole. We then attempted to determine if

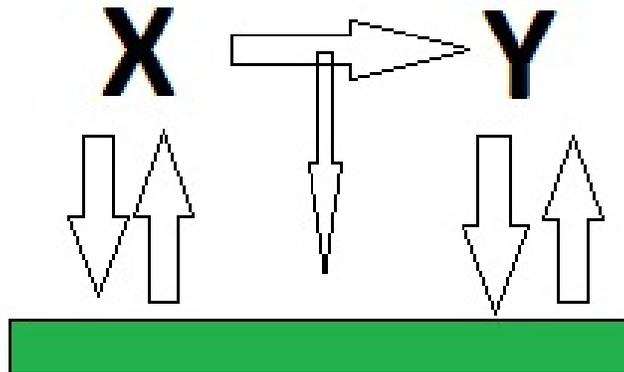


FIG. 1: Representation of 2D System

such models were Evolutionarily Stable Strategies (ESS), i.e. is the systems behavior stable to mutations and invasions by similar species. This is extremely important for ecologists because it is believed only a stable strategy could be found in nature.

II. 2-D MODEL

The simplest case of predator prey is a single prey species that lives off the environment and a predator species that eats the prey and can survive on its own if necessary. We can visualize it the following way (FIG 1). Arrows denote the flow of biomass. Most importantly we see that biomass moves from x to y due to the predation. We also see that a small of the mass of the prey is lost during the predation. This makes sense because not every bit of an animal can be consumed, for example bones and hair.

From this it is very clear that the predation will help the predator species and hurt the prey. But the question becomes how big is the impact on each species relative to other factors. If the prey grows very rapidly it is possible that it will not really notice the loss due the predator. And on the other hand the predator could receive much higher benefits from eating the prey than scavenging from the environment. In this scenario we can imagine that the total biomass in the system could increase even though the prey species must necessarily go down.

Below we given equations for such a model, including a growth rate for each species and a carrying capacity due to the fact the environment can only support so many of a given

species. The predation term has an efficiency $\eta < 1$ corresponding to the fact that not all the biomass of the prey is useful.

$$\dot{x} = ax\left(1 - \frac{x}{M}\right) - b\frac{xy}{c+x} \quad (1)$$

$$\dot{y} = dy\left(1 - \frac{y}{N}\right) + b\eta\frac{xy}{c+x} \quad (2)$$

We have chosen to leave dimensional parameters in so that results can easily be compared and terms retain their ecological meaning. It is easy to show that when $b=0$ (meaning the systems are uncoupled) that the only nontrivial fixed point is (M, N) . Finding the fixed points with $b > 0$ involves cubic equations and thus the answers are too complicated to be of use. Instead we look at the derivatives near the fixed point with respect to b evaluated at zero. We find:

$$\left.\frac{dx}{db}\right|_{b=0} = -\frac{MN}{a(c+M)} \quad (3)$$

$$\left.\frac{dy}{db}\right|_{b=0} = \frac{\eta MN}{d(c+M)} \quad (4)$$

Thus if $T = x + y$, then

$$\left.\frac{dT}{db}\right|_{b=0} = \left(\frac{\eta}{d} - \frac{1}{a}\right)\frac{MN}{c+N} \quad (5)$$

Unsurprisingly the prey species will go down and the predator species will increase. But it is clear that there are parameters where $\left.\frac{dT}{db}\right|_{b=0}$ is positive. When $a\eta > d$, T will increase when we turn the predation on. We made a simple plot of T at the fixed point against b with all values =1 except $a=2$ and three values of η . We found numerically that the fixed point was always stable.

Most importantly we see that when the efficiency is high enough, meaning the predator has to eat less prey before they become full, the total biomass increases greatly for small b . This is exactly the scenario described above where the predation hurts the prey much less than it helps the predator. But we see when the predation strength is too high all the prey get eaten and the predator has to go back to living just off the environment, thus the final state of the predator is exactly that of the state without predation. We find that if $b > \frac{ac}{N}$ the prey cannot survive.

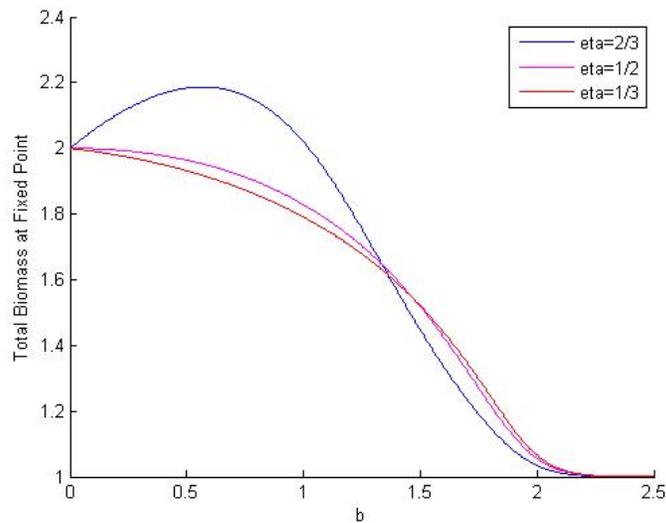


FIG. 2: Total Biomass at Fixed Point

III. 2-D BENEFICIAL CANNIBALISM

One type of recorded interaction is between newts and salamanders. Both species of amphibian will eat the other species' eggs. When parameters are identical for both species this interaction is equivalent to one species where the adults (A) will eat its own eggs (E).

$$\dot{E} = -\mu E + \beta A - \epsilon \frac{\phi ES}{C + E} \quad (6)$$

$$\dot{A} = \eta \mu E - \beta A + \gamma A \left(1 - \frac{A}{K}\right) + \epsilon \kappa \frac{\phi ES}{C + E} \quad (7)$$

Both η and κ are less than one. η is the fraction of the eggs that end up hatching into adults. This turns out to be the most important parameter.

We find that is possible for both the adult and the egg populations to be greater for nonzero predation values. This can only happen when the hatching rate is very low. This allows the adults to use the eggs as a reasonable food source because there is a low risk of eating a viable egg. This result is similar to PIMP (the mutual part is missing - it requires a least three species) and shows us that age structure is a crucial part of the model.

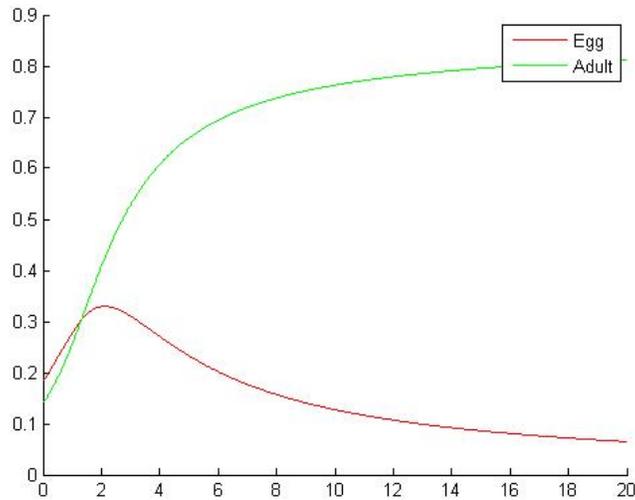


FIG. 3: Total Biomass at Fixed Point

IV. 4-D MODEL WITHOUT CARRYING CAPACITIES

While it is interesting that the total biomass can increase through a simple predator-prey interaction, we are more interested if introducing predators can increase the biomass in both species. For this we need two predator species. In order that these effects don't trivially cancel out we also induce an age structure. We create a system similar to what might one might find in a simple isolated pond, where amphibians and insects fight against each other for survival. We have frogs that lay eggs which hatch into tadpoles which then grow into frogs and dragonflies which give birth to larva. The lives of larva and dragonflies are quite different, with the latter being very short lived and whose sole purpose is to reproduce. In our system the dragonfly larva(L) can eat the tadpoles (T) while the adult frogs (F) can eat the dragonflies (D). (This interaction was observed by Michigan Professor Earl Werner and is the initial inspiration for the project.) Again we have some loss of mass through the predation processes. The system, in pictures and equations, is as follows:

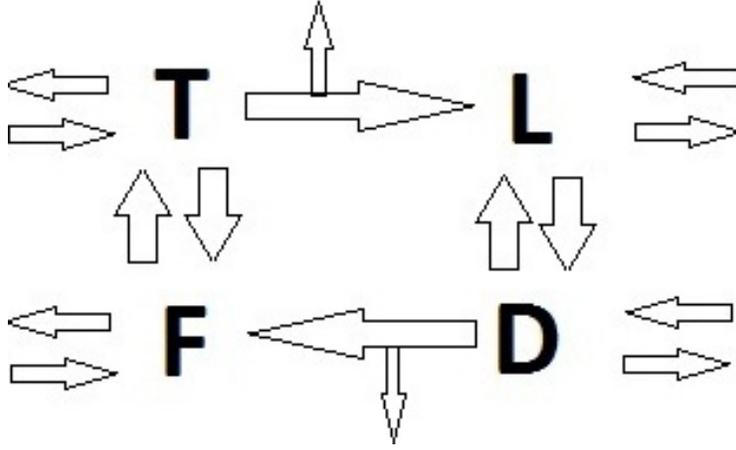


FIG. 4: Representation of full 4D System

$$\dot{T} = -\gamma T + \beta F - \kappa \frac{LT}{1 + \mu T} \quad (8)$$

$$\dot{F} = \alpha T - \zeta F + \eta_F \lambda \frac{FD}{1 + \nu D} \quad (9)$$

$$\dot{L} = -\gamma' L + \beta' D + \eta_I \kappa \frac{LT}{1 + \mu T} \quad (10)$$

$$\dot{D} = \alpha' L - \zeta' D - \lambda \frac{FD}{1 + \nu D} \quad (11)$$

We decided to nondimensionalize this in the following way:

$$\dot{T} = -T + F - d \frac{LT}{1 + T} \quad (12)$$

$$\dot{F} = aT - bF + g \frac{FD}{1 + D} \quad (13)$$

$$\dot{L} = -hL + jD + e \frac{LT}{1 + T} \quad (14)$$

$$\dot{D} = L - kD - f \frac{FD}{1 + D} \quad (15)$$

where the parameters are as follows:

$$a = \frac{\alpha\beta}{\gamma^2} \quad b = \frac{\zeta}{\gamma} \quad d = \frac{\kappa}{\alpha'\nu} \quad e = \frac{\eta_I \kappa}{\gamma\mu} \quad f = \frac{\lambda}{\beta\mu} \quad g = \frac{\eta_F \lambda}{\gamma\nu} \quad h = \frac{\gamma'}{\gamma} \quad j = \frac{\alpha'\beta'}{\gamma^2} \quad k = \frac{\zeta'}{\gamma} \quad (16)$$

We decided to try to make this look as much like a 3-D system as possible. (The behavior of the three dimensional case is easier to observe and was the subject of study in earlier projects.) This means making the total insect population ($L+D$) as constant as possible. We start by just examining the system without predation (which is linear) and studying the parameters h,j,k which tell us about the insects. We want the eigenvalues negative (we need the species to die without predation, especially since the other option is unbounded population growth) and as far from each other possible. In this scenario after a short transient the L and D would lie on the less negative eigenvector, thus the sum would be constant. We found values producing this behavior and then explored phase space looking for limit cycles. We did not find anything of interest in the region suggested by the 3-D results. However under very contrived (ie seemingly very nonbiological) parameters, we discovered stable fixed points and data that suggests an unstable limit cycle. However no data suggesting a Hopf Bifurcation was found.

V. 4-D MODEL WITH CARRYING CAPACITY

Since the idea of PIMP really only makes sense if the species can survive without relying on the predation we decided to move on to a system which includes carrying capacities for both species. We decided to remove direct interaction between prey and the environment. This makes sense because adult dragonflies usually only live long enough to reproduce and rarely eat. In this case the baby frogs are better thought of as eggs. The eggs contain all the necessary resources to feed the offspring inside until it is ready to hatch into a frog. So we analyzed the following system.

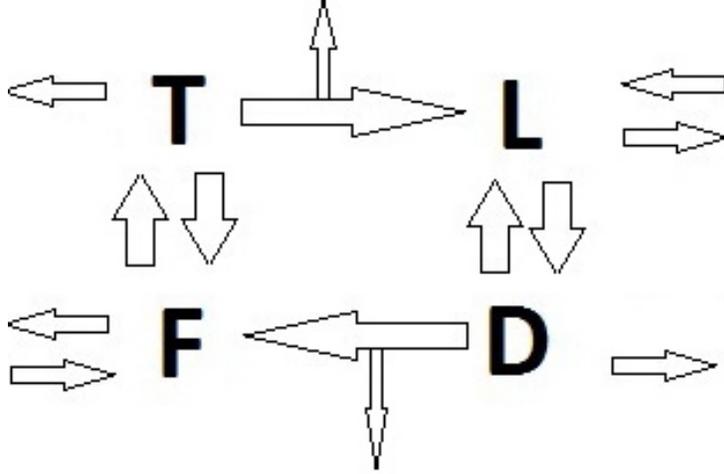


FIG. 5: Representation of full 4D System with Carrying Capacities

$$\dot{T} = -\alpha T + \beta F - \epsilon \frac{LT}{A+T} \quad (17)$$

$$\dot{F} = \eta_1 \alpha T - \beta F + \gamma F \left(1 - \frac{F}{N}\right) + \eta_4 \epsilon \rho \frac{FD}{B+D} \quad (18)$$

$$\dot{L} = -\tilde{\alpha} L + \tilde{\beta} D + \tilde{\gamma} L \left(1 - \frac{L}{M}\right) + \eta_3 \epsilon \frac{LT}{A+T} \quad (19)$$

$$\dot{D} = \eta_2 \tilde{\alpha} L - \tilde{\beta} D - \epsilon \rho \frac{FD}{B+D} \quad (20)$$

The major difference from before is the amount of resources the species can take from the environment and whether or not that can be enough to let one species live without the other.

When $\epsilon=0$ we can find fixed points

$$T^* = \frac{\beta}{\alpha} F^* \quad (21)$$

$$F^* = N \left(1 - \frac{\beta(1-\eta_1)}{\gamma}\right) \quad (22)$$

$$L^* = M \left(1 - \frac{\tilde{\alpha}(1-\eta_2)}{\tilde{\gamma}}\right) \quad (23)$$

$$D^* = \eta_2 \frac{\tilde{\alpha}}{\tilde{\beta}} L^* \quad (24)$$

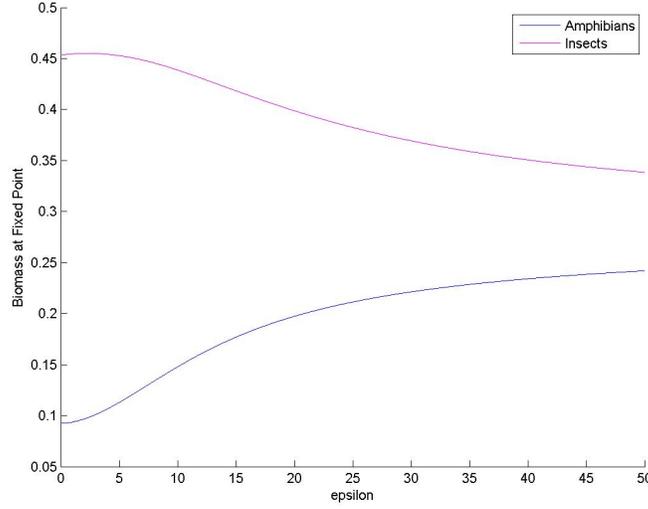


FIG. 6: Total Biomass of Each Species at the Fixed Point

Then examining what happens when we turn on the predation, we see get the following:

$$\frac{dA}{d\epsilon}\Big|_{\epsilon=0} = \frac{(\alpha + \beta)\eta_4\rho\frac{DF}{B+D} - (\alpha + \beta)\eta_1\frac{LT}{A+T}}{\alpha\gamma - \alpha\beta(1 - \eta_1)} - \frac{TL}{\alpha(A + T)} \quad (25)$$

$$\frac{dI}{d\epsilon}\Big|_{\epsilon=0} = \frac{(\tilde{\alpha}\eta_2\eta_3 + \tilde{\beta}\eta_3)\frac{LT}{A+T} - (\tilde{\alpha}\eta_2\rho + \tilde{\beta}\rho)\frac{DF}{B+D}}{\tilde{\beta}\tilde{\gamma} - \tilde{\alpha}\tilde{\beta}(1 - \eta_2)} - \frac{\rho}{\tilde{\beta}}\frac{FD}{B + D} \quad (26)$$

We were able to numerically find parameters that made both of these values greater than zero, thus proving at least the possibility that mutual predation can be helpful to both species involved and the ecosystem as a whole. In FIG 6 we show a plot similar to the one for fixed points in the 2-D system. Unfortunately we found that in order for both species to increase they can only increase a very small (and in every case we found almost unnoticeable) amount. The following graphs have parameters as follows:

$$\alpha = 10 \quad \beta = 2 \quad \gamma = 1.3 \quad \tilde{\alpha} = 2 \quad \tilde{\beta} = 10.5 \quad \tilde{\gamma} = 1 \quad A = B = M = N = 1 \quad \rho = .92 \quad \eta_1 = .4 \quad \eta_2 = \eta_3 = \eta_4 = .7$$

The long term behavior differs greatly from the lower dimensional models. As the predation increased the total amphibian biomass increased and neither species ever goes to zero regardless of how strong the predation is. This makes sense because higher predation helps both species, though it seems to help the amphibians more. FIG 7 shows the total biomass present in the ecosystem.

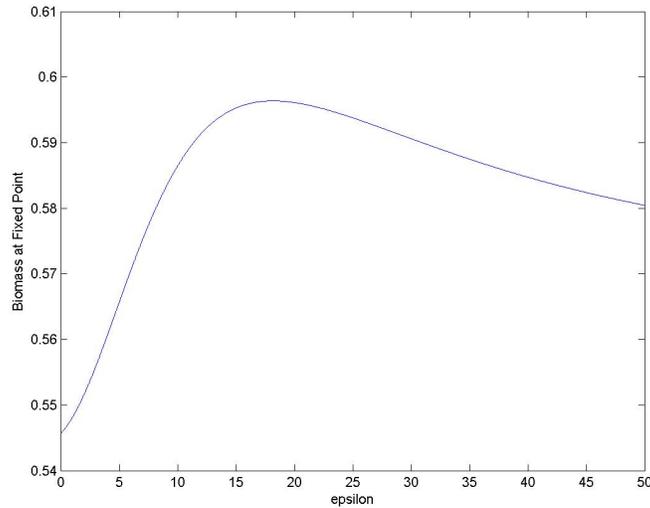


FIG. 7: Total Biomass in the System at the Fixed Point

This shows that no predation appears to be the worst value for the total biomass. Since the model is derived from a real world example, it makes sense that there should be a maximum benefit of the interaction away from the simple uncoupled case. This could be viewed as a necessary but by no means sufficient condition for the possibility of real world observation of the results suggested by other simple models like this.

VI. CRITTERS, VARMINTS, AND EVOLUTION

Once we had established the existence of PIMP we need to test whether or not it is a stable phenomenon. This is done by introducing several varieties of each species, assigning each a different predation parameter while keeping all other terms fixed and then allowing the varieties to compete with each other. Ideally the varieties with predation values at the peak of the PIMP curve would become the dominant species and drive the others to extinction. However we did not find the desired species. The winner was determined only by the risk involved in the interaction. For example, if insects could eat tadpoles without much risk of getting eaten themselves then whichever species with the highest predation term won. If the risk was too high, the lowest variety won. (The behavior at the crossover point cannot be found using numerical methods nor would it be interesting because it is a structurally unstable point.) We are not sure exactly what causes this behavior.

We decided to remove some of the typical ecological assumptions that gave rise to the terms used before in an attempt to get a better understanding of the possible evolutionary stability of PIMP. We decided to separate the species into hungry animals and sated animals. One species called critters (capital letters) lays eggs that can be eaten by varmints (lower case letters) which lay no eggs. The critters can defend their nests and eat varmints attempting to steal eggs. We used a model where sated creatures have exactly twice the mass of hungry animals and eggs. The following model keeps track of both numbers and biomass in the system.

$$\dot{E} = -\delta_E - \nu E + BS - \epsilon h E \quad (27)$$

$$\dot{H} = -\delta_H + \nu E + BS + MS - \frac{\Phi H}{1 + H/K} - \epsilon r h H \quad (28)$$

$$\dot{S} = -\delta_S - BS - MS + \frac{\Phi H}{1 + H/K} + \epsilon r h H \quad (29)$$

$$\dot{h} = -\delta_h + 2\beta s + \mu s - \frac{\phi h}{1 + h/k} - \epsilon h E - \epsilon r h H \quad (30)$$

$$\dot{s} = -\delta_s - \beta s - \mu s + \frac{\phi h}{1 + h/k} + \epsilon h E \quad (31)$$

These equations make sense for individuals because

$$\dot{E} + \dot{H} + \dot{S} + \dot{h} + \dot{s} = -\delta_E - \delta_H - \delta_S - \delta_s - \delta_h - \epsilon h E - \epsilon r h H + BS + \beta s$$

so the numbers of animals only changes when something is born, dies, or gets eaten.

We also see a sensible measure of biomass because

$$\dot{E} + \dot{H} + 2\dot{S} + \dot{h} + 2\dot{s} = -\delta_E - \delta_H - 2\delta_S - \delta_s - 2\delta_h - MS - \mu s + \frac{\Phi H}{1 + H/K} + \frac{\phi h}{1 + h/k}$$

so mass only changes when sated animals metabolize food, hungry animals eat from the environment, or creatures die.

We first attempted to find an area where PIMP is evolutionarily stable by varying just the varmints. Since they are the active hunters it makes sense that their variability would determine the stability of the system. However we found the same results as before. If the risk term r was too high the lowest predation term always wins because less individuals get eaten, otherwise the highest one wins because they have a larger supply of food. We then decided to allow both species to evolve by including many types of critters each with a different risk factor associated to it. The full system is as follows.

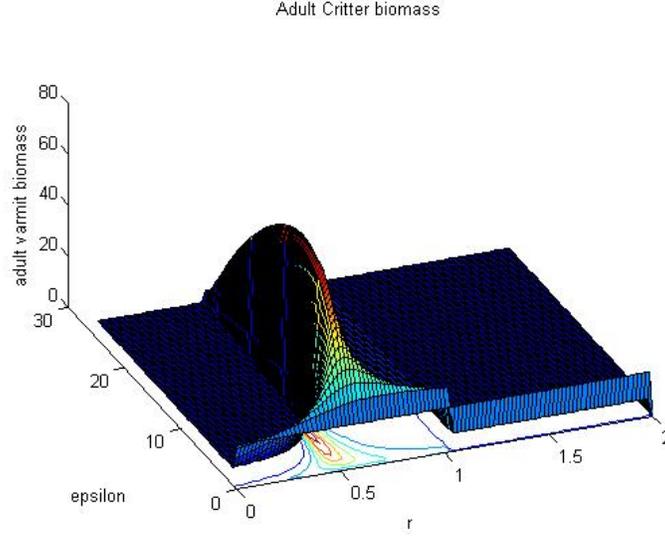


FIG. 8: Adult Critter Biomass

$$\dot{E}_I = -\delta_E E_I - \nu E_I + BS_I - \sum_j \epsilon_j h_j E_I \quad (32)$$

$$\dot{H}_I = -\delta_H H_I + MS_I + BS_I - \Phi \frac{H_I}{1 + \frac{1}{K} \sum_J H_J} - \sum_j r_I \epsilon_j h_j H_I \quad (33)$$

$$\dot{S}_I = -\delta_S S_I - MS_I - BS_I + \Phi \frac{H_I}{1 + \frac{1}{K} \sum_J H_J} + \sum_j r_I \epsilon_j h_j H_I \quad (34)$$

$$\dot{h}_i = -\delta_h h_i + \mu s_i + \beta s_i - \phi \frac{h_i}{1 + \frac{1}{k} \sum_j h_j} - \sum_J \epsilon_i h_i E_J - \sum_J r_J \epsilon_i h_i H_J \quad (35)$$

$$\dot{s}_i = -\delta_s s_i - \mu s_i - \beta s_i + \phi \frac{h_i}{1 + \frac{1}{k} \sum_j h_j} + \sum_J \epsilon_i h_i E_J \quad (36)$$

We calculate and plot the final biomass at the fixed point after varying by r and ϵ . Two such plots (FIG 8 and FIG 9) show the total adult biomass for critters and varmints respectively.

We are currently investigating both analytical and numerical data of this system. We are also attempting to find a reasonable way of measuring the fitness of a species that allows us to make predictions of which species is likely to survive and outcompete the others. However there is no agreement even among professional ecologists as to a good measure of evolutionary fitness. Since being sated is preferable to being hungry ideas included the ratio of sated to total $\frac{s}{s+h}$ and the ratio of birth to death $\frac{\beta s}{\delta_h + \delta_s + \epsilon r h H}$. However neither method

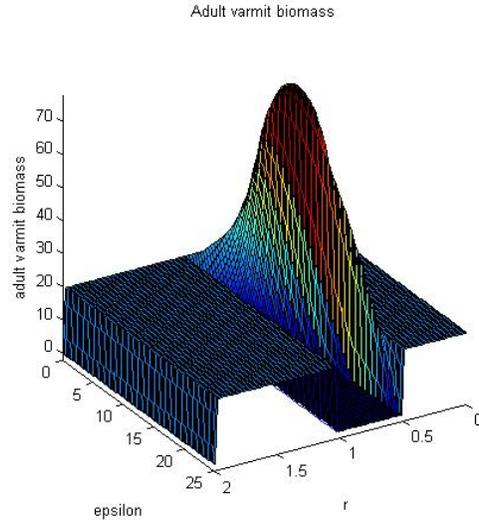


FIG. 9: Adult Varmint Biomass

produced good clear results. The second method would predict whether a species would grow or shrink but would always be one at fixed points which tells us nothing about which species might be more fit to compete. Work on this project will continue this fall.

Acknowledgments

This project was supervised by Professor Charlie Doering. Majority of work was done in tandem with Nathan Golovich. This is an expansion of work done by Charlie Doering and Columbia graduate student David Goluskin. We thank Michigan Professor Earl Werner for the original observations of frogs and dragonflies and Professors Aaron King and Pej Rohani for suggesting ways to make our models ecologically interesting.