# Complexity in Predator Prey Dynamics: Population Increase via Reciprocal Predation

Xuenan Li, University of Michigan

Supervised by Prof Charles Doering and Prof David Goluskin

August 30, 2017

## Abstract

In nature, there are many predator-prey relationships. And we can easily tell which is the predator and which is the prey. However, in some stories, for instance, eagle and snake, we know that eagles catch snakes, while snakes steal eagles' eggs. Since the interaction is more complex, we can't easily tell who eat whom. And we name this kind of interaction Reciprocal Predation. This report is about some interesting properties of this Reciprocal Predation.[1]

## 1 A list of work done

· Development of our model for reciprocal predation
· An interesting phenomenon: Population Increase via Reciprocal Predation
· Investigation of evolutionary stability of reciprocal predation behavior

## 2 Introduction of our 5D system

As discussed in the abstract, reciprocal predation deals with three types of creatures: eagles, snakes and eggs of the eagles. To expand our model, we name eagles as critters and snakes as varmits. So basically, critters are the predators and varmits are the preys. Critters also lay eggs, while varmits hunt for these eggs. Also, we separate critters and varmits into two types: hungry and sated. In this model, we believe there should be some advantages to become sated. So the death rate for the sated are zero, which means that sated will never die, but they will die when they become hungry. The following is our model[3]:

$$\dot{E} = -\delta_E E - vE + BS - \varepsilon khE \tag{1}$$

$$\dot{H} = vE - \delta_H H + MS + BS - \frac{\Phi H}{1 + H/K} - \varepsilon rkhH \tag{2}$$

$$\dot{S} = -BS - MS + \frac{\Phi H}{1 + H/K} + \varepsilon rkhH \tag{3}$$

$$\dot{h} = -\delta_h h + \mu s + 2\beta s - \frac{\phi h}{1 + h/k} - \varepsilon KhE - \varepsilon rKhH \tag{4}$$

$$\dot{s} = -\beta s - \mu s + \frac{\phi h}{1 + h/k} + \varepsilon KhE \tag{5}$$

**Coordinates**   E is the number of eggs;
H is the number of hungry critters;
S is the number of sated critters;
h is the number of hungry varmits;
s is the number of sated varmits.

**Parameters**   $\delta_E, \delta_H, \delta_h$ are death rate of critters' eggs, hungry critters, and hungry varmits. B, $\beta$ are birth rate of critters and varmits. The hungry will eat and become sated at the eating rate. $\Phi, \phi$ are the eating rate of critters and varmits. The sated will also metabolize and become hungry at the metabolism rate. M, $\mu$ are the metabolism rate for critters and varmits. The eggs will be hatched at the rate $v$. K and k are the capacity of environment to sate the critters and varmits simultaneously. So a single critter becomes sated at a rate $\frac{\Phi}{1+H/K}$, $\frac{\phi}{1+h/k}$ for the varmit. r is the risk of hungry varmits caught by critters when they go outside for eggs. $\varepsilon$ is the rate of reciprocal predation.

1

# 3 Population Increase via Reciprocal Predation (PIRP)

The population increase discussed here is under the condition of weak predation, when $\varepsilon$ is super small. By setting time derivatives equal to zero in Equations (1)-(5) and taking derivatives with respect to $\varepsilon$ about zero, we obtain the condition for parameters to have population increase under weak predation:[4]

$$\frac{\frac{\delta_H}{v}(1+\frac{M}{B})[1+2\frac{\delta_H}{B}\frac{\delta_H}{\Phi}(1+\frac{M}{B})(1+\frac{\delta_E}{v})^2]}{1+2\frac{\delta_H}{B}(1+\frac{\delta_E}{v})} < r < \frac{\frac{\delta_H}{v}(1+2\frac{\delta_h}{\beta})}{(1+\frac{\mu}{\beta})[1+2\frac{\delta_h}{\beta}\frac{\delta_h}{\phi}(1+\frac{\mu}{\beta})]}$$

When r falls into this range, the biomass for critters (H + 2S) and varmits (h + 2s) will both increase when $\varepsilon$ is small.

The parameter setting for the following graphs are: $\Phi = \phi = 64$, all death rate are 2, all the other parameters other than $\varepsilon$, r are 1. The PIRP condition for this setting is: $1 < r < 4$.
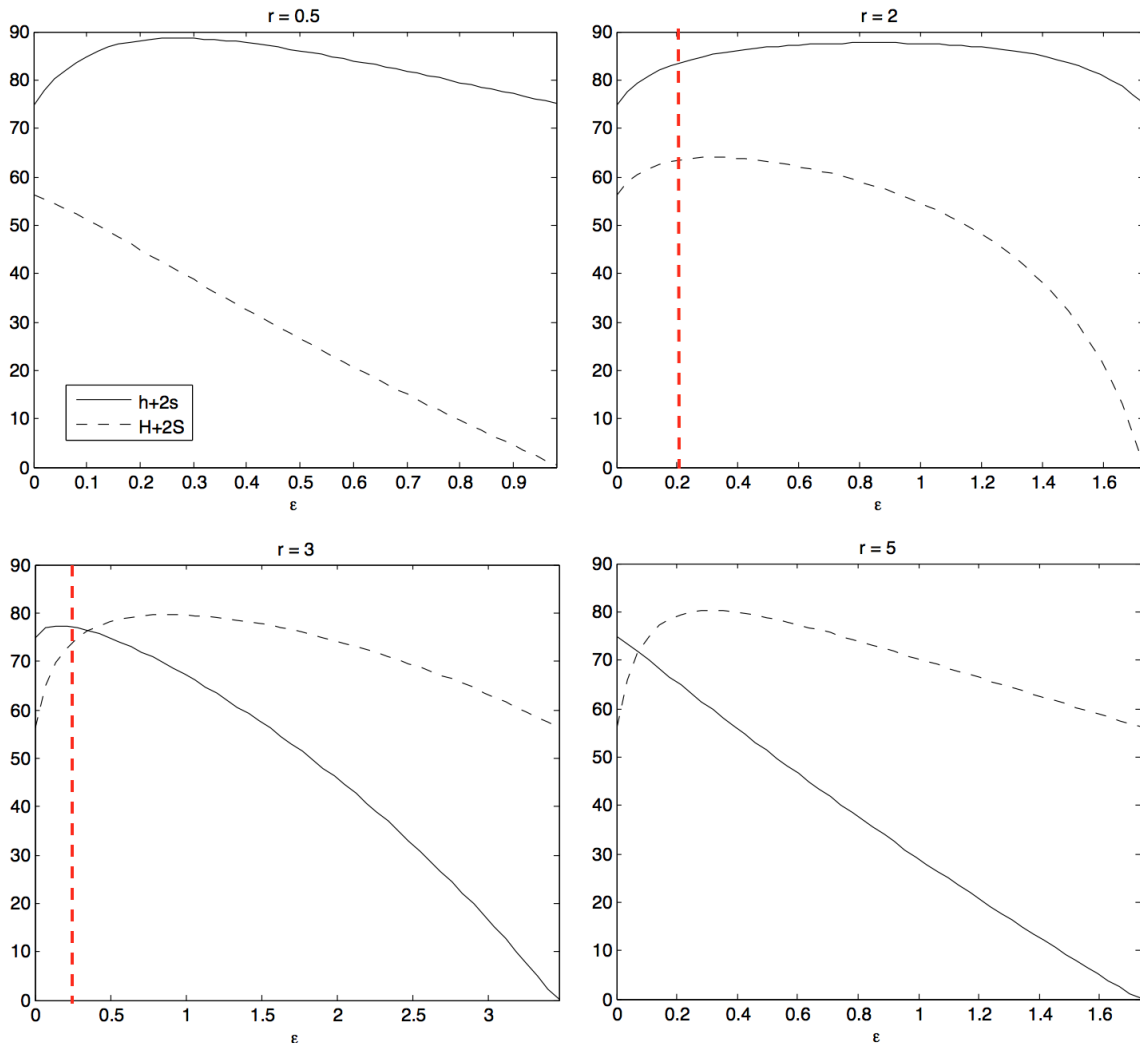


Figure 1: Variation of varmit biomass (h + 2s) and adult critter biomass (H + 2S) with predation strength $\varepsilon$, for various rates of egg-stealing success, r. The r = 2 and r = 3 values lie in the PIRP regime, where both biomasses increase for small $\varepsilon$. As predation strength increases, either critters or varmits ultimately vanish.

# 4 7D system with intraspecies competition

As we can see from the above 5D equations, if $\varepsilon = 0$, there is no interaction between critters and varmits. We then have the idea to consider varmits of different types with different willingness to go outside to hunt for critters' eggs. The different willingness will be shown as different $\varepsilon$. To simplify this model, we basically have two phenotypes (observable behavior) of varmits.

The two phenotypes are egg-eaters ($h_1, s_1$) and non-egg-eaters ($h_2, s_2$). The egg-eater will go outside for critters' eggs, while the non-egg-eaters prefer to stay away from the critters and just get the

2

resource from the environment. Both of these two phenotypes will eat from the same environment, so they have the intraspecies competition against each other. The following is our 7D model with intraspecies competition.

$$\dot{E} = -\delta_E E - vE + BS - \varepsilon kh_1 E \tag{6}$$

$$\dot{H} = vE - \delta_H H + MS + BS - \frac{\Phi H}{1 + H/K} - \varepsilon rkh_1 H \tag{7}$$

$$\dot{S} = -BS - MS + \frac{\Phi H}{1 + H/K} + \varepsilon rkh_1 H \tag{8}$$

$$\dot{h}_1 = -\delta_h h_1 + \mu s_1 + 2\beta s_1 - \frac{\phi h_1}{1 + (h_1 + h_2)/k} - \varepsilon Kh_1 E - \varepsilon rKh_1 H \tag{9}$$

$$\dot{s}_1 = -\beta s_1 - \mu s_1 + \frac{\phi h_1}{1 + (h_1 + h_2)/k} + \varepsilon Kh_1 E \tag{10}$$

$$\dot{h}_2 = -\delta_h h_2 + \mu s_2 + 2\beta s_2 - \frac{\phi h_2}{1 + (h_1 + h_2)/k} \tag{11}$$

$$\dot{s}_2 = -\beta s_2 - \mu s_2 + \frac{\phi h_2}{1 + (h_1 + h_2)/k} \tag{12}$$

The only two difference between this 7D system and the original 5D system are: two more equations for non-egg-eaters ($h_2, s_2$); the intraspecies competition inside varmits, which is shown in the eating rate as $\frac{\phi}{1 + (h_1 + h_2)/k}$.

**Questions of interest**   Now we have two varmit phenotypes in the environment, we might ask the question which type will finally take over or these will two types just coexist in the same area? This is the question of evolutionary stability of the varmits' behavior. Once one type has already taken over, if some day in the future, some of this type change their habit and become the other type, will this little change make the winning situation flip over? In the next part, we will run the numerical method to explore this 7D system.

## 4.1   Numerical analysis

### 4.1.1   Numerical simulation

Here we give one parameter setting. In this setting, we fix everything except r (the risk hungry varmits exposed to critters when they hunt for eggs). $\Phi = 256, \phi = 64, M = \mu = 1$, all the death rates are 2 and all the parameters other than $\varepsilon$ and r are 1. $\varepsilon = 0.01$, since $\varepsilon$ should be super small. And r is the free parameter.

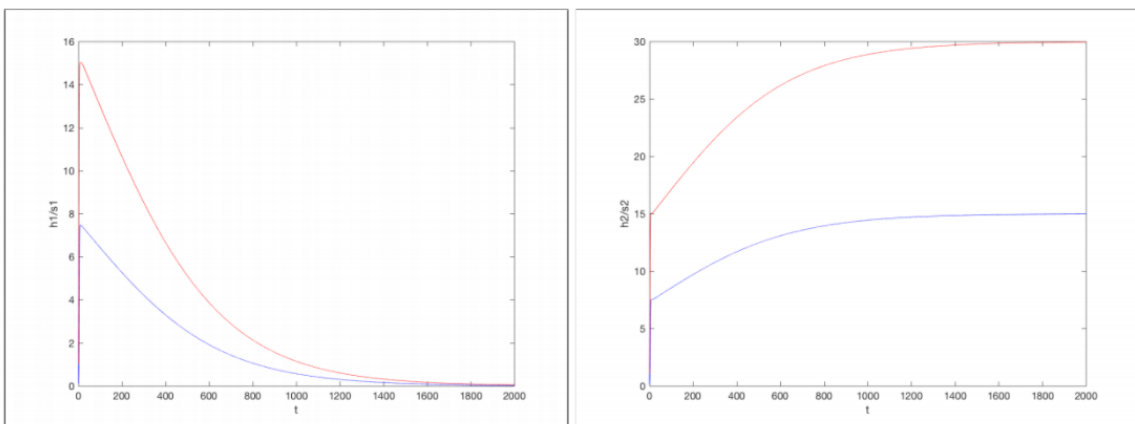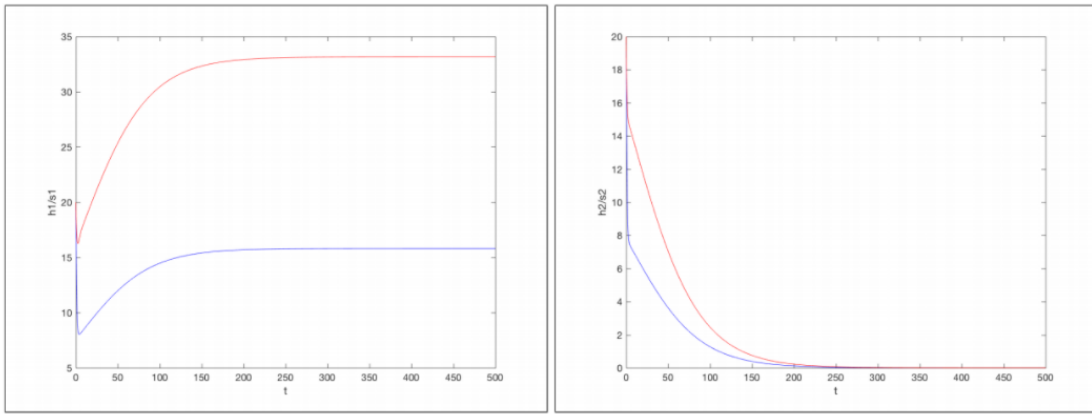**Case 1: r = 1.1**   This r gives the result of winning of non-egg-eater.



Figure 2: The left one is a figure of the total number of egg-eaters (blue for $h_1$, red for $s_1$) and the right one is a figure of the total number of non-egg-eaters (blue for $h_2$, red for $s_2$). Here we can see that finally non-egg-eaters survive, while all egg-eaters die out.

3

**Case 2: r = 0.5**   This r results the winning of egg-eater.



Figure 3: The left one is a figure of the total number of egg-eaters (blue for $h_1$, red for $s_1$) and the right one is a figure of the total number of non-egg-eaters (blue for $h_2$, red for $s_2$). Here we can see that finally egg-eaters survive, while all non-egg-eaters die out.

In case 1, r is 1.1 and results the winning of non-egg-eater. In case 2, r is 0.5 and results the winning of egg-eater. By intuition, we might believe larger risk will be harmful for the egg-eaters, while beneficial to the non-egg-eaters. So we can guess there is a critical $r_c$ where the winning situation will change. In the next part, we will run Matcont (a package in Matlab for numerical bifurcation analysis) to draw the bifurcation diagram.

### 4.1.2   One parameter bifurcation diagram

We still have the same setting as the above: $\Phi = 256, \phi = 64, M = \mu = 1$, all the death rates are 2 and all the parameters other than $\varepsilon$ and r are 1. $\varepsilon = 0.01$, since $\varepsilon$ should be super small. And r is the free parameter.
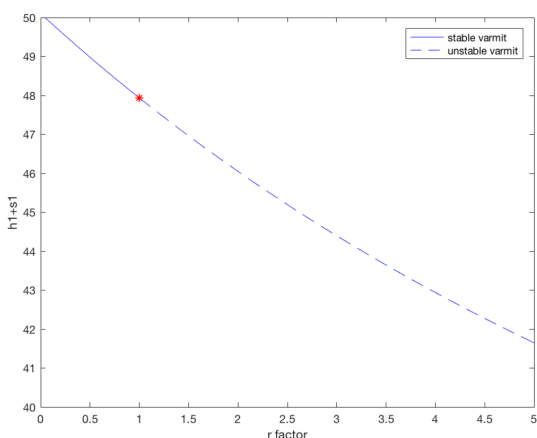


Figure 4: This is the equilibrium continuation for the egg-eater winning equilibrium. The dashed part is unstable, while the solid part is stable.
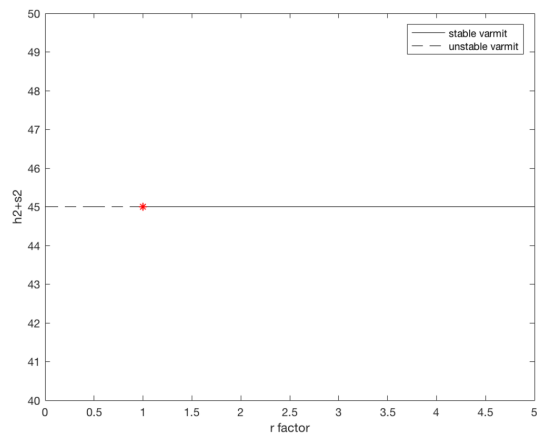
Figure 5: This is the equilibrium continuation for the non-egg-eater winning equilibrium. The dashed part is unstable, while the solid part is stable.

In the above two figures, the free parameter, r factor, is the risk r. The dependent coordinates are the number of related varmits. The bifurcation point in both two figures are at $r = 1$. When $r < 1$, egg-eaters finally take over. When $r > 1$, non-egg-eater finally take over. When $r = 1$, the system gives some chaotic result: you stay wherever you start.

## 4.2   Analytical solution

Obviously, there are several kinds of equilibrium, like equilibrium without egg-eaters, equilibrium without non-egg-eaters or even equilibrium without critters. However, since we focused most our attention on the intraspecies competition, we do not care the equilibrium without critters. The following are the three cases to induce different equilibrium.

4

**Case 1:** $r = \frac{\delta_H \beta}{v(\beta+\mu)}$ **(Deduced system)** This is quite a special case. The system is deduced to some lower dimension, but is all solved. The vertical line in the bifurcation diagram now makes sense since in this case and $h_1$ can be anything.

Notice that the right hand side of this relation only contains 4 parameters: $\delta_H, \mu, v$ and $\beta$. This is also the condition where the bifurcation occurs.

**Case 2:** $r \neq \frac{\delta_H \beta}{v(\beta+\mu)}$ and $h_2 \neq 0$ **(Winning of non-egg-eater)** In this case, $h_1 = 0$. So we only get the equilibrium without egg-eaters. This is easy to calculate and David has already solved it. I just borrowed it from his report of September, 2011. It is on the top of page 4.

$$H_0 = K[\frac{\Phi}{\delta_H} \cdot \frac{1}{1+M/B} \cdot \frac{1}{1+\delta_E/v} - 1] \tag{13}$$

$$E_0 = \frac{\delta_H}{v}H_0 \tag{14}$$

$$S_0 = \frac{\delta_H}{B}(1+\frac{\delta_E}{v})H_0 \tag{15}$$

$$h_2 = k[\frac{\phi}{\delta_h} \cdot \frac{1}{1+\mu/\beta} - 1] \tag{16}$$

$$s_2 = \frac{\delta_h}{\beta}h_2 \tag{17}$$

**Case 3:** $r \neq \frac{\delta_H \beta}{v(\beta+\mu)}$ and $h_2 = 0$ **(Winning of egg-eater)** This is just the case when the non-egg-eater vanishes. It is exactly the same as the above original 5D system.

$C_1 = \frac{(\beta+\mu)}{\beta}\varepsilon r K^2 - \varepsilon \frac{\delta_H}{v}K^2$

$C_2 = \frac{\beta+\mu}{\beta}\delta_h$

$C_3 = \frac{(B+M)\delta_H}{Bv}\varepsilon k^2 - \varepsilon r k^2$

$C_4 = \frac{(B+M)\delta_H(\delta_E+v)}{Bv}$

$\alpha_h = (C_2 - C_1)C_3$

$\zeta_h = C_1\Phi + (C_2-C_1)C_4 - \phi C_3 + (C_2-C_1)C_3$

$\gamma_h = C_1\Phi - C_4\phi + (C_2-C_1)C_4$

$\alpha_H = (C_4-C_3)C_1$

$\zeta_H = C_3\phi + (C_4-C_3)C_2 - \Phi C_1 + (C_4-C_3)C_1$

$\gamma_H = C_3\phi - C_2\Phi + (C_4-C_3)C_2$

$$h_{1\pm} = k[\frac{-\zeta_h \pm \sqrt{\zeta_h^2 - 4\alpha_h\gamma_h}}{2\alpha_h}] \tag{18}$$

$$H_\pm = K[\frac{-\zeta_H \pm \sqrt{\zeta_H^2 - 4\alpha_H\gamma_H}}{2\alpha_H}] \tag{19}$$

## 4.3 Stability

Since we have already solved the whole system, we can move on to the stability of different equilibrium. This part is solving the determinant of a 7x7 matrix. The calculation is annoying but the result is simple. The determinant for both equilibrium is linearly to the factor $r \cdot \frac{v(\beta+\mu)}{\delta_H\beta} - 1$. So the stability is exactly the same shown in the above bifurcation diagram. In our model, the stability of equilibrium is the evolutionary stability of the winning situation. So we will use evolutionary

stability in the conclusion of this section.

$r \cdot \frac{v(\beta+\mu)}{\delta_H \beta} - 1 < 0$: winning of egg-eater is evolutionary stable; winning of non-egg-eater is evolutionary unstable.

$r \cdot \frac{v(\beta+\mu)}{\delta_H \beta} - 1 > 0$: winning of non-egg-eater is evolutionary stable; winning of egg-eater is evolutionary unstable.

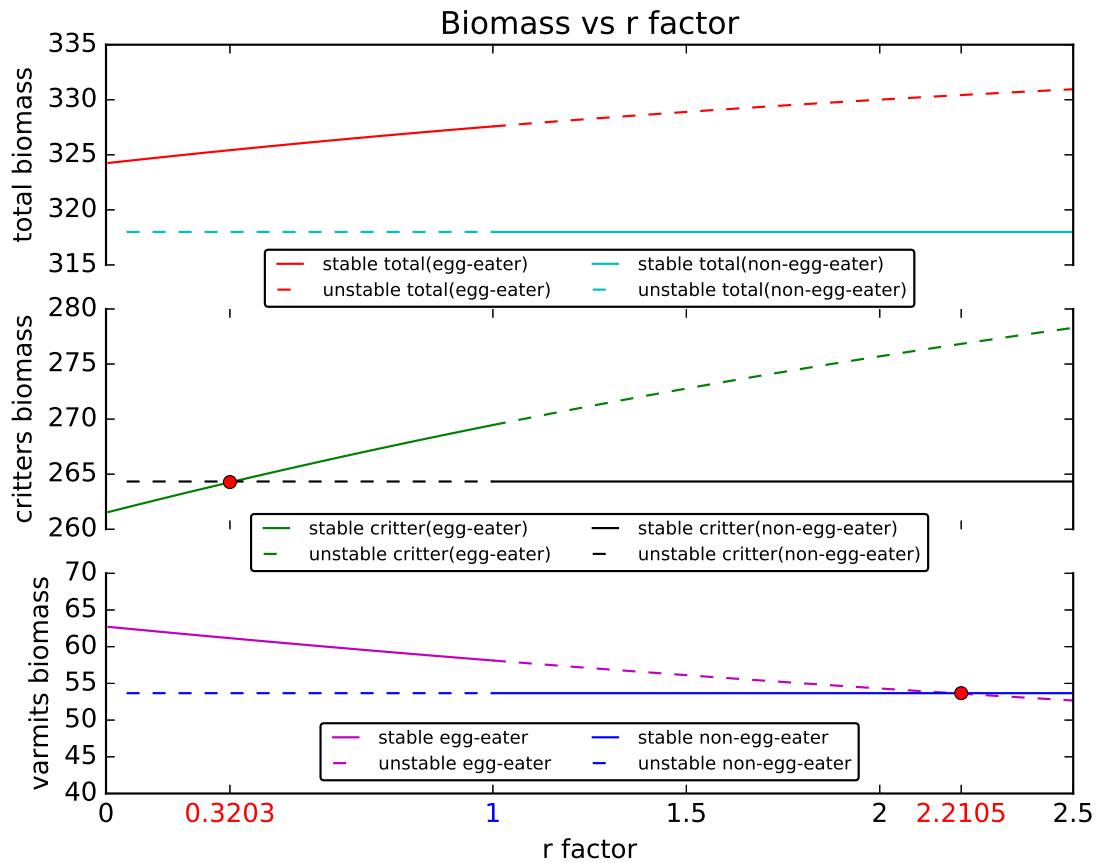# 5 A graph that contains everything



Figure 6: This is a graph of r-factor against biomass of different creatures. Here r-factor is $r \cdot \frac{v(\beta+\mu)}{\delta_H \beta}$. Obviously, we can see that when r-factor is 1, there is the change of stability (solid to dashed or dashed to solid). The two red numbers on the x-axis are the condition for PIRP. When the r-factor falls into this range, biomass of critters and varmits will increase at the same time if the reciprocal predation is weak.

# 6 Conclusion

As we can see from the above graph, when r factor falls into the PIRP range, the evolutionary stability of either winning situation is unsure. By intuition, we always believed that the beneficial behavior is evolutionary stable (unable to be invaded by other changes). However, here in this model, we see that even we have the population increase for both critters and varmits (PIRP), which is beneficial to both species, the winning situation can be either evolutionary stable or not. This is new to the evolutionary theory.

# References

[1]  E. E. Werner and J. F. Gilliam (1984)  The ontogenetic niche and species interactions in size-structured populations

[2]  J. P. Whitehead and C. R. Doering (2007) Notes on some age structure trophic dynamics

[3]  David Goluskin (15 October 2010) Who ate whom: Population dynamics with age-structured predation

[4]  David Goluskin (September 8 2011) Critters and varmits