A Game Theory Based Predation Behavior Model

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1 Abstract

In this paper we first use a simplified non-cooperative zero sum Game Theory model model to investigate how predators and preys of different body sizes use different strategies in predation. Then we extend it with a more realistic general sum model for further analysis. We assume both predator and prey have two strategies in predation: active and passive so the model is a 2×2 matrix. We apply the energy acquisition and loss to define payoff matrix for predator and prey in the models. By calculating the mixed strategy Equilibrium we show smaller predators tend to use passive strategy more than larger predators and preys always prefer active strategy. Our model results could be explained by Kleiber's Law as well. In an evolutionary perspective, natural selection tends to select and preserve these different strategies.

2 Keywords

Predation and Antipredation Behavior,Game Theory Model, Body Size, Energy

3 Introduction

When we observe our little garden, we could see spiders, ambush bugs and pray mantis hide themselves silently for their victims, while other little butchers, such as dragonflies and tiger beetles, actively move around to find their food sources. Correspondingly, on the other side of the survival game, preys also have different strategies to avoid being killed: some of them don't move quite much and have camouflage that makes them hard to tell from the ambient and hence almost invisible to the predator; others have very good locomotive system and if they run faster than the predator, they survive.

Then we are very much interested in these questions: why both predators and preys have these different strategies in predation? Why some animals sacrifice their ability of fast moving? Why a spider as large as a leopard sitting on its web, as we might see in some sci-fi movies like *X Files*, could never survive

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in natural habitat? Why zebras cannot only use their stripe to fool the lions but still need to run fast? How does body size influence predation behavior?

Previous work has concentrated on the behavior for either the predator such as actively pursuing, waiting and ambushing (C.L.Craig 1989, D. Austin et al. 2006)or for the prey such as camouflage and mimic(O.H.Holen and R.A.Johnstone 2004, D. Austin et al. 2006). Other papers are discussing both predators and preys behavior (P.Domenici 2001, A.R.E.Sinclair, S.Mduma and J.S.Brashares 2003, V.Krivan 2007). Besides, researchers have also investigated the role of body size in predation for both predator and prey but most of the work are qualitative(C.W.Osenberg and G.G.Mittelbach 1989, T.Day, P.A. Abrams and J.M. Chase 2002, J.S. Weitz and S.A Levin 2006, M.C. Urban 2008, V.H.Rudolf 2008, N. Owen-Smith et al. 2008, D.R. Macnulty et al. 2009, T.H. Homes and M.I. McCormick 2009).

We think Game Theory model should be appropriate for this kind of problem because predation is indeed a game played between predator and prey. Various work has been done in this area (A.Johansson and G.Englund 1995, J.I.Hammond, B. Luttbeg and A. Sih 2007, V. Krivan, R. Cressman and C. Schneider 2008, J. Garay 2009). While it is critical to define the payoff matrix for a Game Theory model, J.M. McNamara et al.(J.M. McNamara et al. 2005) and U. Brose (U. Brose et. al 2008) have suggested using energy as a measurement of predation benefit or loss. While Game Theory is naturally linked with evolution, we consider it another advantage of using Game Theory Model to explore the evolution path of predation behavior.

However, so far few research has been done for how predation and antipredation behavior evolve for predators and prey with different body sizes. In this paper we develop two types of 2 player non-cooperative Game Theory model, zero sum and general sum, to investigate why and how different predators and preys use different strategies in the survival game.

4 Zero Sum Game

Remember predation is a fatal game, a first and reasonable model is zero sum game, where the payoff gained by the predator is the payoff lost by the prey. Consequently, here we only focus on the payoff of the predator because the payoff of the prey is just the opposite of that of the predator.

According to Lucas (W.F.Lucas 1983), We divide the predators into two major groups, representing two different strategies: active predator who actively searches and pursues their preys and passive predator who waits and ambushes their preys. Typical active predators include large carnivore mammals, some birds and small insect predators including tiger beetles, ladybugs, etc. Typical passive predators include some reptiles and some arthropods such as spiders, ambush bugs and praying mantis. Similarly, preys have two strategies, either active and passive as well. Herbivore mammals, grasshoppers and some other insects are active preys while scale insect is the representative of passive preys. So the game is essentially a 2×2 matrix.

4.1 Payoff Matrix of Predators

Consider the following payoff matrix for predators:

	Active Prey	Passive Prey
Active Predator	E_1	E_2
Passive Predator	E_3	E_4

The mixed strategy Nash Equilibrium could be explained as the percentage of the predator choosing different strategies from individual perspective. It could also be interpreted as proportion of different type of predators in the population since in the two population evolution model, dynamic equilibrium is similar to Nash Equilibrium. In our research, we adopt the latter definition of mixed strategy equilibrium. To calculate this equilibrium point, let $X = (x, 1 - x)$ represents the mixture strategy, thus

$$xE_1 + (1 - x)E_3 = xE_2 + (1 - x)E_4$$

$$x = \frac{E_3 - E_4}{E_2 + E_3 - E_1 - E_4} \tag{1}$$

4.2 Model Description

The mixed strategy is determined by formula (1). Then he key work now is to specify E_k. Lucas (W.F.Lucas 1983) has suggested using energy as an indicator of predation payoff and I agree with this definition. Lucas has considered two basic forms of energy consumption for predators: basal energy consumption based on basal metabolism rate (E_{BM}), energy consumption during searching for prey (E_S) and one form of energy acquisition: energy from food(E_F).

E_{BM} is proportional to 1.5 power of predator's body size (B) multiply daytime (defined as 1 here);

E_S is proportional to 1.5 power of B multiply searching distance (r) .

E_F is proportional to power of 2 of prey's body size i multiply possible prey quantity(Q). We suggest Q is proportional to r multiply probability of finding the prey (n) then multiply probability of killing that prey (k).

$$\begin{cases} E_{BM} = k_1 B^{1.5} \\ E_S = k_3 B^{1.5} r \\ E_F = rknk_2 i^2 \end{cases}$$

For the active-active strategy combination (which would gain E_1 for the predator), the total energy acquisition is $E_F - E_{BM} - E_S$; for the active-passive combination (which would gain E_2 for the predator),preys choose to hide themselves. It would help them reduce the probability of being found by predator; however, if they are spotted, their probability of being killed becomes larger. We use coefficient α and β to modify these new probabilities as αk and βn ($\alpha > 1$, $\beta < 1$).

While for the passive-active combination, the predator does not have energy consumption in searching for preys; instead, the preys who accidentally encountered the predator would probably be killed. We assume predators and preys are almost the same size and the active prey will go as far as the active

predator; thus we assume here the possible prey quantity Q' for a passive predator equals previous Q. For the last combination, we simply assume $E_4=0$ because neither the prey nor the predator is active; the predator would then get nothing. Notice that according to the previous definition, E_4 would be negative ($E_4=-E_{BM}$). That's mathematically reasonable for modeling but not ecologically feasible. A negative payoff means prey would gain energy from predator, which is ironic.

Consequently, all the four payoffs can be written as follows:

$$E_1 = E_F - E_{BM} - E_S = rknk_2i^2 - k_1B^{1.5} - k_3B^{1.5}r \tag{2}$$

$$E_2 = E_F - E_{BM} - E_S = \alpha\beta rknk_2i^2 - k_1B^{1.5} - k_3B^{1.5}r \tag{3}$$

$$E_3 = E_F - E_{BM} - E_S = rknk_2i^2 - k_1B^{1.5} \tag{4}$$

$$E_4 = 0 \tag{5}$$

Now put them back into equation (1) and

$$x = \frac{rknk_2i^2 - k_1B^{1.5}}{\alpha\beta rknk_2i^2 - k_1B^{1.5} - k_3B^{1.5}r + rknk_2i^2 - k_1B^{1.5} - rknk_2i^2 + k_1B^{1.5} + k_3B^{1.5}r} \tag{6}$$

4.3   Model Results

The expression form of x can be simplified to

$$x = \frac{rknk_2i^2 - k_1B^{1.5}}{\alpha\beta rknk_2i^2 - k_1B^{1.5}} \tag{7}$$

Generally, the larger the predator is, the longer distance it could cover; the larger the prey is, the more probable it would be found by predator but less probable to be killed. Therefore we assume r is proportional to B, n is proportional to i and k is inversely proportional to i. That is,

$$r = k_4B; \quad n = k_5i; \quad k = \frac{i}{k_7}$$

Apply these to equation (7):

$$x = \frac{\dfrac{k_2k_4k_5Bi^2}{k_7} - k_1B^{1.5}}{\dfrac{\alpha\beta k_2k_4k_5Bi^2}{k_7} - k_1B^{1.5}} \tag{8}$$

Combine the coefficients, let new k_2 equals previous $\dfrac{k_2k_4k_5}{k_7}$, γ equals previous $\alpha\beta$, then:

$$x = \frac{k_2i^2 - k_1B^{0.5}}{\gamma k_2i^2 - k_1B^{0.5}} \tag{9}$$

Since k_2 is the coefficient of energy acquisition from food, it should be much larger than k_1 and k_3; otherwise the animal would soon starve to death because of unbalance of energy flow. For predators and preys who have identical sizes where $i = B$ and $k_2 >> k_1$, $x \approx \dfrac{1}{\gamma}$ and γ is the parameter describing predation success enhancement of active predator against passive prey than active prey. Let $\gamma = 1.6$ for small predators and preys where $i = B = 1$ then we get approximate proportion of active predator to

be 62.5% in the population.

When the predator and prey body sizes become larger, it is more difficult for predator to kill the prey so we suggest γ decreasing to 1.25 then $x = 80\%$ correspondingly. When their sizes are very large, γ drops to approximately 1, yielding almost 100% large predators to be active. These results could explain our initial questions why only small predators tend to use passive strategies.

5 Model Extension: General Sum Game

In the previous section, we assume the game between the predator and the prey is zero-sum. However, the ecological hierarchy of predator and prey are distinct and hence we might consider a more realistic model than zero sum model. The payoff of prey should be much larger than the predator: the failure of predation means loss of some energy for a predator; but on the other hand, failure to escape from predation means loss of entire life, which is a much severe penalty for the prey. Hence we introduce general sum game into the model with some more realistic assumptions discussed as follows.

5.1 Payoff matrix

The pay offs of predator are similar to the zero sum game condition except a few modifications:

1. Active predator uses less energy against passive prey, where $E_S = \phi k_3 B^{1.5} r$

2. Passive predator gets less prey than its active counterpart, where $E_F = \omega r k n k_2 i^2$

3. Passive predator would gain $E_{BM} = -k_1 B^{1.5}$ instead of zero against passive prey.

From the prey perspective, the pay off of active prey comprises two parts: penalty of death and penalty of energy cost against predation. The death penalty is defined as δ times of base metabolism energy consumption. The penalty of escape is defined as $(k_3 i^{1.5}$. Since active prey is more likely to escape from passive predator, the probability of being killed is modified from kn to ωkn.

According to these assumptions we could construct the payoff matrix for both players, predator and prey.

Predator/Prey	Active	Passive
Active	$rnkk_2 i^2 - k_1 B^{1.5} - rk_3 B^{1.5}$	$\alpha\beta rnkk_2 i^2 - k_1 B^{1.5} - \phi rk_3 B^{1.5}$
Passive	$\omega rnkk_2 i^2 - k_1 B^{1.5}$	$-k_1 B^{1.5}$

Table. Payoff Matrix of Predator

Predator/Prey	Active	Passive
Active	$-\delta knk_1 i^{1.5} - (1-kn)k_3 i^{1.5}$	$-\delta\alpha\beta knk_1 i^{1.5}$
Passive	$-\delta\omega knk_1 i^{1.5} - (1-kn)k_3 i^{1.5}$	0

Table. Payoff Matrix of Prey

5.2   Model Results

For small predators and prey, again we define $B = i = 1$. Other coefficients are set to:

$$r = 1, n = k = 0.5, \alpha\beta = 1.6, \delta = 20, \omega = 0.8, \phi = 0.5, k_1 = 1, k_2 = 20, k_3 = 2$$

The corresponding payoff matrix is:

Predator/Prey	Active	Passive
Active	(2, -6.5)	(6, -8)
Passive	(3, -5.6)	(-1, 0)

While we do not consider single pure strategy equilibrium here, let $X = (x, 1 - x)$ and $Y = (y, 1 - y)$ represent mixture of strategies. By solving this game we get the mixed equilibrium as $x = 78.9\%$ and $y = 87.5\%$ respectively.

For larger predators and prey like large insects or small mammals, let $B = i = 5$. They have longer searching distance, say, $r = 10$. Because larger predators tend to endure hunger better than smaller predators, the energy acquisition coefficient is reduced to $k_2 = 15$ in this condition. Other coefficients remain the same. The corresponding payoff matrix is:

Predator/Prey	Active	Passive
Active	(0.70, -72.67)	(1.38, -89.44)
Passive	(0.74 -62.60, -5.6)	(-0.01, 0)

Here the mixture equilibrium is $x = 78.9\%$ and $y = 97.5\%$ respectively. The larger predator tends to use similar mixture strategies as smaller predator and larger prey prefers active running-away strategy.

For larger predators such as large mammals, let $B = i = 25, r = 100$ and $k_2 = 12.5$, the corresponding payoff matrix is:

Predator/Prey	Active	Passive
Active	(1.70, -0.81)	(3.00, -1.00)
Passive	(1.56, -0.70)	(0, 0)

Notice for predator, active strategy strictly dominate passive strategy, then active-active strategy combination is the equilibrium, which means both large predators and preys will use pure active strategy without computation.

6   Discussion

From the model we could draw the conclusion that predators and preys of different sizes tend to have different strategies in the survival game: passive strategy is better for smaller predators but not good choice for prey. Passive strategy is like high stake gamble, it would gain either large payoff for

predator, or simply nothing. On the other hand, active strategy has less risk.

Kleiber (M. Kleiber 1932) had shown the basal metabolism rate (BMR) scales to the 3/4 power of the animal's mass in his famous Kleiber's Law. This is also the basis of our payoff matrix where Lucas (W.F.Lucas 1983) has proved BMR is 1.5 power of animal's body size, which is equivalent to Kleiber's law. For smaller predators, their BMR is relatively higher than larger predators. So if they choose active strategy and fail to catch their prey for a few times, they would soon starve to death. Consequently, passive strategy is an insurance against running out of energy for smaller predators. However, larger predators don't have this problem as we could see leopard don't need to hunt again for another several days or a few weeks.

For the preys, as we discussed before, because of the asymmetric hierarchy in the ecosystem, their pressure is much larger than the predator. No matter what size they are, active strategy is always a better choice. Hence Kleiber's law coincides and qualitatively explains our model results.

Our model is the first attempt to link physiology, behavior and evolution together using a Game Theory Model and the results are reasonable. Nevertheless, several questions still remain in our model. While we assume the active searching distance is proportional to body size, the predator could extend their foraging range if they realize the food source is scarce. This problem could be solved by introducing a distribution for foraging range but the computational effort is intensive so we don't suggest doing so.

Furthermore, the food web is so complex that few animals are pure predators. In other words, except a few large apex predators, smaller predators are often preys of other predators. It would be very interesting to incorporate a middle level predator and an apex predator into the model and investigate this three components system dynamics.