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Linking body size and energetics with predation strategies: A game theoretic modeling framework

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In memory of John F. Nash (1928–2015).

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ABSTRACT

Predation is the ultimate survival game between the predator and prey. In this study, we use game theory as a modeling framework to demonstrate why and how different strategies in predation for both predator and prey are chosen based on body size and energetics. Two distinct and mutually exclusive strategies, active and passive, are considered for both players; hence the corresponding predation can be formulated as a 2×2 game. The payoffs are defined using energetics (energy gain and loss), with functional response to predator/prey body size. The game is formulated as a realistic general sum model and the numerical results of Nash equilibrium for different body sized predators and preys are calculated: in general, smaller sized predators and preys tend to use active strategy more often (mixed strategy equilibrium), and larger sized tend to choose active strategy exclusively (pure strategy equilibrium). The long-term evolutionary stability of the predator–prey system is also investigated, and the Nash equilibrium derived from these games are shown evolutionarily unstable. In summary, this study provides a unified modeling framework to study how animal body size and energetics determine predation strategies, and can easily extend to more complicated conditions, such as across multiple trophic levels.

1. Introduction

Predation and antipredation are the most ruthless survival game in nature. In order to survive and thrive, both the predator and prey have evolved different strategies to fight against each other. Predators can either move very fast and nimbly (e.g. dragonfly, tiger beetle, hawk, etc.), or wait patiently to capture the victim (e.g. web-weaving spiders, ambush bugs, etc.). Similarly preys also have different strategies to choose from: either moving even faster than predator (e.g. gazelle against cheetah), or staying still and use camouflage to avoid the predators (e.g. spittle bugs). While certain predators (or preys) choose a specific strategy in the predation game (either purely active or passive, Sih, 1985; Ives and Dobson, 1987; Packer and Caro, 1997; Jennions et al., 2003; Hugie, 2004), some can choose and switch between different strategies and maximize its payoff from the survival game (Craig, 1989; Sandoval, 1994; Sinclair et al., 2003). Of the diverse predator–prey interactions, several studies have emphasized the role of body size and its influence on how predators choose their predation strategy (Osenberg and Mittelbach, 1989; Owen-Smith and Mills, 2008; Petchey et al., 2008).

To quantitatively investigate how animals use different strategies in the predation and antipredation, game theory provides a natural modeling framework, since predation can be regarded as a survival game for both players. Game theory was originally proposed by Von Neumann and Worgenstern (1944) and Nash (1950) to study conflicts between different players. The key concept in game theory is Nash equilibrium, where neither player can increase their payoff when choosing strategy at Nash equilibrium (Nash, 1950, 1951; Osborn, 2004). Then the original idea of Nash equilibrium was extended to the concept of Evolutionary Stable Strategy (ESS), from an evolutionary perspective to study whether Nash equilibrium is stable under long terms (Smith and Price, 1973; Smith, 1982; Bulmer, 1994). Game theory has been applied in many areas in biology such as resource allocation (Chen, 2010), epidemics (Reluga, 2010), and animal conflict (Johansson and Englund, 1995; DeDeo et al., 2010). In short, game theory provides reasonable and comprehensive explanations for many important ecological and evolutionary processes, as summarized by McNickle and Dybzinski (2013).

As for the game theory models, the critical issue is to determine the Nash equilibrium (and also ESS if investigating evolutionary dynamics). Nevertheless it is impossible to derive the Nash equilibrium without proper formulation of the payoff matrix. A

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commonly used term to define the payoff is fitness (Skonhoft, 2006), and sometimes more specifically, energy gain/loss (Lucas et al., 1983). Thus, energetics can be used to describe the energy gain and loss for both the predator and the prey in the predation game (Brown et al., 1993; Brown and Kotler, 2004). Furthermore, animal body size is shown to relate to energetics (Kleiber, 1932), and the corresponding scaling law (also known as power law) in physiology (e.g. metabolism rate) and ecology is widely studied (West et al., 1997; Mand, 2004; Marquest et al., 2005; Kolkotrones et al., 2010; Schuster, 2010; Hechinger et al., 2011). Consequently, animal body size explicitly correlates to the potential energy gain and loss during the predation, and is a critical factor to determine the payoff matrix.

So far, there is no comprehensive study of using game theory and energetics to study predation behavior. Whether there is pure or mixed Nash equilibrium in these games and whether they are evolutionarily stable are still unclear. Other study has utilized different system to define payoff matrix and investigated the long-term stability (Dieckmann et al., 1995). The objective of this study is to provide a unified game theory framework for modeling animal predation and antipredation using energetics to define payoff matrix, and investigate how animal body size influences the predation strategies. We develop a two-player non-cooperative game, and investigate the long-term stability of equilibrium in evolutionary dynamics.

2. Material and methods

2.1. The energetics

We assume two distinct and mutually exclusive predation strategies for the predator: pure active (searching and chasing the prey) and pure passive strategies (waiting and ambushing the prey). Similarly the prey also has these two different strategies to choose from: actively fleeing, or passively hiding. Consequently, there are a total of four different strategy combinations (and four corresponding payoffs associated with these four strategy combinations). While the zero sum game is a reasonable starting point to study the predation game, it does not reflect the asymmetric relationship between predator and prey in the community. Failure in predation usually only wastes some energy and time for the predator, but failure in antipredation will cost the prey's precious life, which is a much higher cost (i.e. the life-dinner principle). To reflect such asymmetry in the predation, we introduce general sum game as the extension for the original zero sum game. In the general sum game, the payoff of the predator for a certain strategy combination is not necessarily the negative value of the payoff of the prey. Hence we will formulate the payoff matrix for both the predator and the prey.

Energetics is a commonly used measurement to define the payoff matrix. There are two types of energy outflow in predation, basic metabolism (E_M), which maintains vital physiological processes, and energy cost during searching/chasing in predation (E_S) are considered. There is one energy income from prey as food source (E_F, assuming successful predation). In this study, E_M is proportional to the 1.5th power of predator's body size (measured in body length, B), E_S proportional to product of B to the 1.5th power and searching/chasing distance of predation (r), and E_F proportional to product of square of prey's body size (b), searching distance (r), probability of finding prey (η), and probability of killing prey (γ) (Lucas et al., 1983). The mathematical expressions of these types of energy are shown below.

$$\begin{cases} E_M = \kappa_1 B^{1.5} \\ E_S = \kappa_2 B^{1.5} r \\ E_F = \eta\gamma\kappa_3 b^2 \end{cases}$$

2.2. The payoff matrices

We start with the payoffs for the predator first. The payoff in the first strategy combination (when the predator and prey both choose active strategy) is the net energy gain in the predation. That is, energy income from prey (E_F) minus two forms of energy costs (E_M and E_S): $E_F - E_M - E_S$. The formulation of the payoff in the first strategy combination is shown in equation 1. Next we adopt similar idea to define the active predator/passive prey strategy combination. The basic metabolism (E_M) remains the same for the predator and we assume the active predator searches the same distance for the passive prey as against an active prey (in the first strategy combination), hence energy cost in predation (E_S) is also the same. The only difference comes from the quantity and energy of prey (E_F) and we use two new coefficients, α and β, to adjust probability of finding the prey (η), and probability of killing the prey (γ), respectively. Active predator spends less energy against passive prey than against active prey. Consequently the energy cost in predation is modified as: $Es = \phi\kappa_2 B^{1.5} r$ where ϕ ($\phi < 1$) is the modification coefficient to reflect such difference. The final formula is shown in Eq. (2).

For the passive predator/active prey strategy combination, we assume the number of prey is sufficient and the passive predator can get as much energy from food as choosing active strategy. So the only energy cost comes from basic metabolism (E_M). There is no energy cost in predation, thus $E_S = 0$. Moreover, we assume passive predator should harvest less prey (hence less energy) than its active counterpart. The energy income from food is modified as: $E_F = \omega\eta\gamma\kappa_3 b^2$, where ω ($\omega < 1$) is the coefficient reflecting such modification. The expression is shown in Eq. (3). Finally for the passive-predator/passive-prey combination, we assume the predator cannot get any food in this condition (because the prey does not come to predator), so the net energy is flowing out. Passive predator actually loses net energy (basic metabolism only) if facing against passive prey hence the payoff is negative of $E_M = \kappa_1 B^{1.5}$. The mathematical formulations of predator's payoffs in all four combinations are shown below (Eqs (1)–(4)), and the Nash equilibrium will be derived numerically for different predators with various body sizes.

$$E_1 = E_F - E_M - E_S = \eta\gamma\kappa_3 b^2 - \kappa_1 B^{1.5} - \kappa_2 B^{1.5} r \quad (1)$$

$$E2 = E_F - E_M - E_S = \alpha\beta\eta\gamma\kappa_3 b^2 - \kappa_1 B^{1.5} - \phi\kappa_2 B^{1.5} r \quad (2)$$

$$E_3 = E_F - E_M = \omega\eta\gamma\kappa_3 b^2 - \kappa_1 B^{1.5} \quad (3)$$

$$E_4 = -E_M = -\kappa_1 B^{1.5} \quad (4)$$

Similarly, we still use energetics to define the payoffs for the prey. Furthermore, to accurately reflect the asymmetric interaction between predator and prey in the predation, we suggest the payoff should include a penalty for death, and the payoff has three components: basic metabolism energy cost, death penalty (if killed) and energy consumption during escape (if survived). We model this death penalty proportional to basic metabolism energy consumption and up to a coefficient δ ($\delta > 1$), also up to the total death probability, $\eta\gamma$ (probability of being found multiplied by probability of being killed, assuming being found and killed as independent events). For the passive prey against active predator, there is no energy cost for escaping from the predator, and the only cost is the potential death penalty. For passive prey against passive predator, we normalize the payoff as the basic metabolism cost, because there is no potential predation in this strategy combination. The mathematical expression of the four payoffs for preys are given in Eqs. (5)–(8):

$$E'_1 = -\kappa_1 b^{1.5} - \delta\gamma\eta\kappa_1 b^{1.5} - (1 - \gamma\eta)\kappa_1 b^{1.5} \quad (5)$$

$$E'_2 = -\kappa_1 b^{1.5} - \delta\alpha\beta\gamma\eta\kappa_1 b^{1.5} \quad (6)$$