

## Suppression of ecological competition by an apex predator

Taksu Cheon\*

Laboratory of Physics, Kochi University of Technology, Tosa Yamada, Kochi 782-8502, Japan

Shigemi Ohta†

Institute of Particle and Nuclear Studies, KEK, Tsukuba, Ibaraki 305-0801, Japan

(Received 11 August 2003; published 30 August 2004)

In the framework of Lotka-Volterra dynamics with evolutionary parameter variation, it is shown that a system of two competing species which is evolutionarily unstable, if left to themselves, is stabilized by a common predator preying on both of them. Game-theoretic implications of the results are also discussed.

DOI: 10.1103/PhysRevE.70.021913

PACS number(s): 87.23.-n, 05.45.-a, 89.75.Da

From the dominant plants in forest vegetation to the wild beasts in savanna, an often encountered ecological paradox exists in the form of stabilizing influence of the top predator. While two species in direct competition rarely form a stable ecosystem, they often coexist under the dominance of a common predator [1]. The most illustrative example is found in the *trophic pyramids* [2], where the apex predator, the most savage aggressor of all, seems to act as the key guarantor of the stability of the whole system [3]. For species with intellectual capacity, this fact might be explained as a result of conscious effort of enlightened self-interest. But the peacekeeping function of the apex predator is so prevalent throughout ecosystems that the existence of a simple and universal dynamics should be suspected. Although there have been numerous model proposals to understand the phenomenon [4], no compelling explanation with simplicity and transparency has appeared to this date.

The purpose of this paper is to understand the structure and stability of ecosystems composed of competing species in the framework of evolutionary population dynamics [5,6]. The tool we employ is the Lotka-Volterra equation with adiabatic parameter variation [7]. In this approach, the ecological dynamics is determined by the time variation of the variables representing the population of the species, while the adiabatic parameter variation represents the behavioral evolution of the species. The viability of a species in this framework is judged both by the short-time ecological stability of the orbit and also by the long-term evolutionary stability of the shifting parameters.

However, the description clearly is not a faithful one to what is actually happening in nature. It is hard to imagine that a predator species like a lion or shark feeds solely on a single prey species. So what ever meaning we can assign to the single species and single layer of prey idea behind the Lotka-Volterra equation such as in Ref. [7] works at an abstract level. Thus we are obliged to question how valid this abstraction is. For example, can a prey layer population variable be considered a sum of populations of many prey species which are about equally attractive for the predator a

layer above? And should not this summed population variable be independent of the competition among the prey species? In the present work the authors try to step forward toward answering this question.

We focus specifically on a system that consists of two self-sustaining but directly competing species and an apex predator who preys over both competitors. We show that the system evolves towards an evolutionarily stable configuration in which the warring preys are tamed into peaceful coexistence. This is in contrast to the case of two competitors left to themselves, in which there are no evolutionarily stable solutions for coexistence and an “arms race” drives one of the competitors into eventual extinction. We also show that our results can be interpreted in a game-theoretic language as the apex predator turning the prisoner’s dilemma between two competitors into a collaborative game.

Suppose there are two populations of competing species  $x_1$  and  $x_2$  which are preyed upon by a common predator population  $y$  (Fig. 1). We describe the ecological dynamics of this system by the standard Lotka-Volterra equations

$$\begin{aligned}\dot{x}_1 &= b_1 x_1 - a_1 x_1^2 - \sigma_2 x_1 x_2 - \rho_1 x_1 y, \\ \dot{x}_2 &= b_2 x_2 - a_2 x_2^2 - \sigma_1 x_1 x_2 - \rho_2 x_2 y, \\ \dot{y} &= -d y + f \rho_1 x_1 y + f \rho_2 x_2 y.\end{aligned}\quad (1)$$

Here,  $b_1, b_2$  are the reproduction rates for species  $x_1, x_2$ , and  $a_1, a_2$  are the environmental limitation factor to their growth.

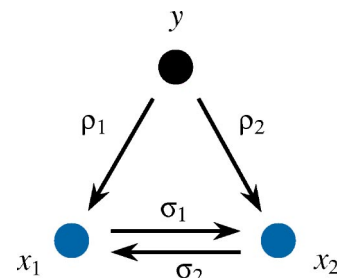


FIG. 1. A symbolic diagram showing the pecking order of the three species system described by Eqs. (1). The arrows represent the aggression and predation with the specified intensities.

\*Electronic address: taksu.cheon@kochi-tech.ac.jp

†Electronic address: shigemi.ohta@kek.jp

The coefficient  $d$  is the decay rate for the predator  $y$ , and  $f$  is the efficiency of its predation. In the last equation, a term proportional to  $y^2$  could be added for consistency with other equations, but this can be shown to introduce simply a technical complication without affecting the main line of our arguments. Also, specifying separate predation efficiencies for  $x_1$  and  $x_2$  makes no essential difference, because the result can be turned into the original form (1) with rescaling of variables. The parameters  $\rho_1$  and  $\rho_2$  are the aggression intensities of the apex predator  $y$  towards  $x_1$  and  $x_2$ , respectively. Similarly,  $\sigma_1$  and  $\sigma_2$  are the aggression intensities of  $x_1$  to  $x_2$  and of  $x_2$  to  $x_1$ , respectively. We assume all parameters to be positive real numbers. At this stage, we treat all of them as fixed numbers, making no distinction between the Roman denominated “environmental” parameters and Greek denominated “behavioral” parameters. A nontrivial fixed point  $x_i(t)=X_i, y(t)=Y$  ( $\dot{X}_i=\dot{Y}=0$ ) with  $i=1, 2$  is given by

$$\begin{aligned} X_1 &= \frac{1}{f} \frac{d(a_2\rho_1 - \sigma_2\rho_2) - f(b_2\rho_1 - b_1\rho_2)\rho_2}{a_2\rho_1^2 + a_1\rho_2^2 - (\sigma_1 + \sigma_2)\rho_1\rho_2}, \\ X_2 &= \frac{1}{f} \frac{d(a_1\rho_2 - \sigma_1\rho_1) + f(b_2\rho_1 - b_1\rho_2)\rho_1}{a_2\rho_1^2 + a_1\rho_2^2 - (\sigma_1 + \sigma_2)\rho_1\rho_2}, \\ Y &= -\frac{d}{f} \frac{a_1a_2 - \sigma_1\sigma_2}{a_2\rho_1^2 + a_1\rho_2^2 - (\sigma_1 + \sigma_2)\rho_1\rho_2} \\ &\quad + \frac{(a_2b_1 - b_2\sigma_2)\rho_1 + (a_1b_2 - b_1\sigma_1)\rho_2}{a_2\rho_1^2 + a_1\rho_2^2 - (\sigma_1 + \sigma_2)\rho_1\rho_2}. \end{aligned} \quad (2)$$

The stability of the fixed point is determined by the behavior of the linearized map

$$M = \begin{pmatrix} -a_1X_1 & -\sigma_2X_1 & -\rho_1X_1 \\ -\sigma_1X_2 & -a_2X_2 & -\rho_2X_2 \\ f\rho_1Y & f\rho_2Y & 0 \end{pmatrix}. \quad (3)$$

Namely, the fixed point is stable when real part of all the eigenvalues  $\lambda$  of  $M$  determined by

$$|\lambda I - M| = 0 \quad (4)$$

is negative.

When the fixed point is of a stable, attracting sort, neighboring orbits form an absorbing spiral in phase space. We now assume that the evolutionary pressure of selection and adaptation are at work. We can then regard the aggression intensities  $\rho_1$ ,  $\rho_2$ ,  $\sigma_1$ , and  $\sigma_2$  as *evolutionarily adjustable parameters* which evolve along the path that simultaneously increase the functions  $X_1[\sigma_1]$ ,  $X_2[\sigma_2]$ , and  $Y[\rho_1, \rho_2]$  until they reach the optimal values. There are several indirect pieces of evidence supporting the existence of this type of adiabatic evolution among real-life ecosystems [8,9]. It is convenient to start with the maximization condition for the apex predator  $\partial Y / \partial \rho_1|_{\rho_1^*} = 0$  and  $\partial Y / \partial \rho_2|_{\rho_2^*} = 0$ . We note that this is just a technical choice, and the results are valid as long as the time scale of the maximization of  $X_1[\sigma_1]$  and  $X_2[\sigma_2]$  is comparable to that of  $Y[\rho_1, \rho_2]$ . We then have the relations

$$\begin{aligned} \rho_1^* &= \frac{d2a_1a_2b_1 - b_1\sigma_+\sigma_1 + a_1b_2\sigma_-}{f a_2b_1^2 + a_1b_2^2 - b_1b_2\sigma_+}, \\ \rho_2^* &= \frac{d2a_1a_2b_2 - b_2\sigma_+\sigma_2 - a_2b_1\sigma_-}{f a_2b_1^2 + a_1b_2^2 - b_1b_2\sigma_+}. \end{aligned} \quad (5)$$

These conditions give the expressions

$$\begin{aligned} X_1^* &= \frac{2a_2b_1 - b_2\sigma_+}{4a_1a_2 - \sigma_+^2}, \\ X_2^* &= \frac{2a_1b_2 - b_1\sigma_+}{4a_1a_2 - \sigma_+^2}, \\ Y^* &= \frac{f a_2b_1^2 + a_1b_2^2 - b_1b_2\sigma_+}{d 4a_1a_2 - \sigma_+^2}. \end{aligned} \quad (6)$$

The quantities  $-X_1^*$  and  $-X_2^*$  as functions of  $\sigma_1$  and  $\sigma_2$  act as the “potential surface” for the variation of  $\sigma_1$  and  $\sigma_2$ . In Eqs. (5) and (6), the notation  $\sigma_{\pm} \equiv \sigma_1 \pm \sigma_2$  is used. With the definitions  $\alpha \equiv \sqrt{a_1a_2}$  and  $\beta \equiv (\sqrt{a_2/a_1})(b_1/b_2)$ , the valid parameter range for  $X_i$  and  $Y$  being positive and stable ( $\text{Re } \lambda < 0$ ) is given by

$$\sigma_1 + \sigma_2 < \min\{\alpha\beta, \alpha/\beta\}. \quad (7)$$

That the stability requirement is satisfied can be checked by the fact that all coefficients of the third-order polynomial equation (4) are of same sign within this parameter range.

The evolution of  $\sigma_1$  and  $\sigma_2$  depends on their starting values. With a straightforward calculation, we obtain

$$\begin{aligned} \frac{\partial X_1^*}{\partial \sigma_1} < 0, \quad \frac{\partial X_2^*}{\partial \sigma_2} < 0: \sigma_1 + \sigma_2 < \sigma_{cr}, \\ \frac{\partial X_1^*}{\partial \sigma_1} \frac{\partial X_2^*}{\partial \sigma_2} < 0: \sigma_1 + \sigma_2 > \sigma_{cr}, \end{aligned} \quad (8)$$

within the range of Eq. (7). The critical aggression intensity  $\sigma_{cr}$  is given by

$$\sigma_{cr} \equiv \max\{\alpha\beta/2, \alpha/2\beta\}. \quad (9)$$

If the sum  $\sigma_1 + \sigma_2$  is below  $\sigma_{cr}$ , both  $\sigma_1$  and  $\sigma_2$  will move toward  $\sigma_1 = \sigma_2 = 0$ . Namely, two competing species shall settle for a peaceful coexistence as the common preys of a predator  $y$ . On the other hand, if the sum starts above a critical value,  $\sigma_1$  and  $\sigma_2$  will increase until one of the competing species is extinct at that critical value. The situation becomes immediately clear with a glance at numerical example depicted in Figs. 2 and 3.

A crucial point is that the master  $y$  acts as a punisher, according to Eqs. (5), which inhibits the increase of  $\sigma_1$  and  $\sigma_2$ . Figure 4 serves as a graphical illustration of this effect. Increasing  $\sigma_i$  will induce an increase of  $\rho_i$ , which incurs damage upon  $x_i$ . We stress that no special mechanism is assumed for  $y$  to police the system at the outset, yet the dynamics seems to explain our common sense observation about apex predators.

An intriguing fact is that the critical value  $\sigma_{cr}$  is inversely

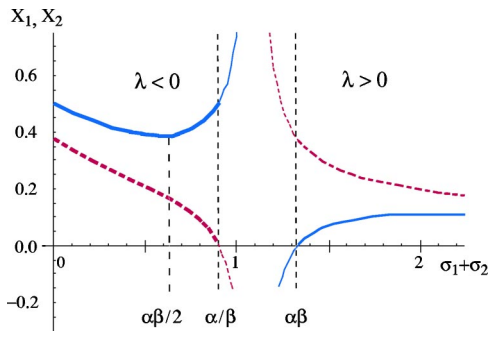


FIG. 2. Fixed-point coordinates  $X_1^*$  and  $X_2^*$  as functions of  $\sigma_1 + \sigma_2$ . The parameters are  $a_1=1, b_1=1, a_2=1.2, b_2=0.9$ , and  $d=2$ . The solid line represents  $X_1^*$  and the dashed line  $X_2^*$ . The fixed point is stable in the region below  $\alpha/\beta$  but unstable above  $\alpha\beta$ . The region in between is unphysical.

proportional to the natural population of one of the prey species,  $b_1/a_1$  or  $b_2/a_2$ . This means that coexistence of competing species under common predator becomes a less likelier outcome for a system with richer resources. This seems to give a partial explanation to the experimentally observed decrease of species at the base levels of trophic pyramids [8].

We next consider the case where the predator leaves the scene—namely,  $y=0$  (Fig. 5). By setting  $\rho_1=\rho_2=0$ , we obtain, in place of Eq. (6),

$$X_1^* = \frac{a_2 b_1 - \sigma_2 b_2}{a_1 a_2 - \sigma_1 \sigma_2},$$

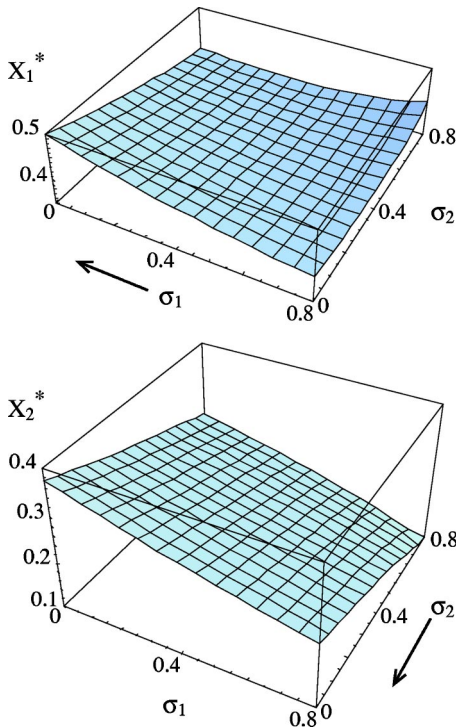


FIG. 3. Fixed-point coordinates  $X_1^*$  and  $X_2^*$  as functions of  $\sigma_1$  and  $\sigma_2$ . The parameters are  $a_1=1, b_1=1, a_2=1.2, b_2=0.9, d=2$ , and  $f=0.7$ . In the region  $\sigma_1 + \sigma_2 < \sigma_{cr} = \alpha\beta/2 = a_2 b_1 / b_2$ , both  $\sigma_1$  and  $\sigma_2$  have to be decreased to make  $X_1$  and  $X_2$  larger.

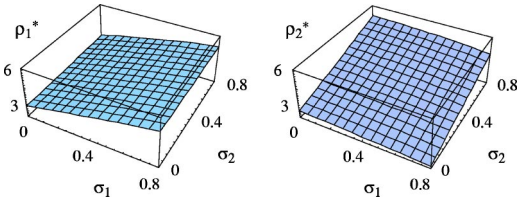


FIG. 4. Aggression intensities  $\rho_1^*$  and  $\rho_2^*$  as functions of  $\sigma_1$  and  $\sigma_2$ . The parameters are the same as in Fig. 3.

$$X_2^* = \frac{a_1 b_2 - \sigma_1 b_1}{a_1 a_2 - \sigma_1 \sigma_2}. \tag{10}$$

The linearized map now takes a two-by-two matrix form

$$M = \begin{pmatrix} -a_1 X_1 & -\sigma_2 X_1 \\ -\sigma_1 X_2 & -a_2 X_2 \end{pmatrix}, \tag{11}$$

in place of Eq. (3). A straightforward calculation gives the condition for  $X_1^*$  and  $X_2^*$  to be a viable fixed point—namely,  $X_1^*, X_2^* > 0, \text{Re } \lambda < 0$ —in terms of the allowed region for the aggression intensity as

$$\sigma_1 < \alpha/\beta, \sigma_2 < \alpha\beta. \tag{12}$$

However, in this region, it is easy to check the relation

$$\frac{\partial X_1^*}{\partial \sigma_1} > 0, \frac{\partial X_2^*}{\partial \sigma_2} > 0. \tag{13}$$

Therefore, in this case, both  $\sigma_1$  or  $\sigma_2$  shall eventually be increased beyond the range (12), and there is no evolutionarily stable coexisting solutions for two competing species. Namely, in the absence of a common master, depending on their initial populations, one of the competing species is always driven to extinction by the arms race of increasing  $\sigma_1$  and  $\sigma_2$  (Fig. 6).

In order to fully understand the generic shape of the ecosystem, we would have to generalize our arguments to more trophic levels than two and also more species than two within a single trophic level. For example, two species might be in indirect competition through predation on a common prey. More involved and sophisticated approaches may have to be called for [8,10,11]. In the current work, no precise specification for the evolutionary dynamics of behavioral parameters has been required. While we stress that this is an advantage, construction and analysis of more detailed models with such specifications are attractive possibilities.

Finally, some remarks in the broader context of game theory [12] are in order. There is an obvious game-theoretic interpretation of the results (6) and (10). For the sake of simplicity, let us set  $a_1=a_2=a$  and  $b_1=b_2=b$ . We now regard

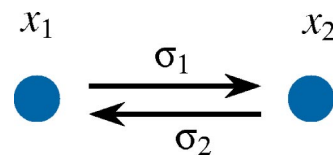


FIG. 5. A symbolic diagram showing the two competing species described by Eqs. (1) with  $\rho_1=\rho_2=0$ .

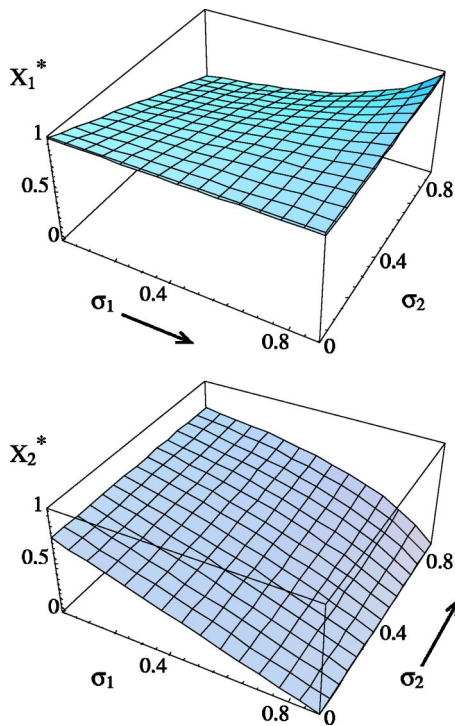


FIG. 6. Fixed-point coordinates  $X_1^*$  and  $X_2^*$  for the case without the apex predator as functions of  $\sigma_1$  and  $\sigma_2$ .  $X_1^*$  will increase  $\sigma_1$  and  $X_2^*$  will increase  $\sigma_2$  to achieve local advantage, which will eventually doom  $X_2^*$  to extinction. The parameters are  $a_1=1$ ,  $b_1=1$ ,  $a_2=1.2$ , and  $b_2=0.9$ .

$\sigma_i$  ( $i=1,2$ ) as the control parameter of the strategy of population  $x_i$  for the game played between  $x_1$  and  $x_2$  whose payoff tables are given by  $X_1^*[\sigma_1, \sigma_2]$  and  $X_2^*[\sigma_1, \sigma_2]$ . To facilitate the understanding, the game tables for two discretized points for  $\sigma_1$  and  $\sigma_2$  are tabulated in Table I. For the case without the common predator, Eqs. (10), the game is a continuous strategy version of prisoner’s dilemma [13,14], whose outcome is  $\sigma_1 \rightarrow a$ ,  $\sigma_2 \rightarrow a$ , which leads to the extinction of either  $x_1$  or  $x_2$ . With the introduction of the apex predator, the

TABLE I. The game table  $X_1^*[\sigma_1, \sigma_2]$  for  $x_1$  discretized at  $\sigma_1$ ,  $\sigma_2=a/3$  (“dove”), and  $2a/3$  (“hawk”). The left-hand side is the table for the case with apex predator (6) and the right-hand side, without apex predator (10). The game table  $X_2^*[\sigma_1, \sigma_2]$  for  $x_2$  is obtained by transposition of row and column. The Nash equilibrium is indicated with boldface.

		With Apex predator		No Apex predator	
$\sigma_1 \backslash \sigma_2$		$a/3$ dove	$2a/3$ hawk	$\sigma_1 \backslash \sigma_2$	
$a/3$ dove		$3b/8a$	$3b/9a$	$a/3$ dove	$6b/8a$
$2a/3$ hawk		$3b/9a$	$3b/10a$	$2a/3$ hawk	$6b/7a$
					$6b/14a$
					$6b/10a$

game table is turned into one of collaborative game, whose outcome is the coexistence  $\sigma_1 \rightarrow 0$  and  $\sigma_2 \rightarrow 0$ . Note that the game table is symmetrized under the presence of the apex predator:  $X_2^*[\sigma_1, \sigma_2]=X_1^*[\sigma_2, \sigma_1]$ . This could be interpreted as the sign of altruistic behavior [15]. The advantage of having the apex predator as a “law enforcer” is evident, and the loss of half of the populations to the predator would be an acceptable tradeoff.

Application of Lotka-Volterra equations (1) is not limited to the ecological population dynamics. Indeed, with the help of replicator dynamics [6], a game-theoretic interpretation Eqs. (1) itself is possible in terms of mixed strategy in a generalized prisoner’s dilemma [15]. As such, the current analysis of the stabilizing effect of the apex predator should have direct pertinence to the problem in social and economic settings.

In summary, we have established, for Lotka-Volterra systems with evolutionary parameter variation, that two competing species are evolutionarily unstable, but can be stabilized by the introduction of an apex predator. We hope this to be a start for a systematic understanding of stable ecosystems.

[1] *Model Systems in Behavioral Ecology: Integrating conceptual, theoretical, and empirical approaches*, edited by L.A. Dugatkin (Princeton University Press, Princeton, 2001).  
 [2] C. Elton, *Animal Ecology* (Sidgewick and Jackson, London, 1927).  
 [3] R.T. Paine, *Am. Nat.* **100**, 65 (1966).  
 [4] J. M. Chase *et al.*, *Ecol. Lett.* **5**, 302 (2002), and references therein.  
 [5] R.M. May, *Stability and Complexity in Model Ecosystems* (Princeton University Press, Princeton, 1974).  
 [6] J. Hofbauer and K. Sigmund, *The Theory of Evolution and Dynamical Systems* (Cambridge University Press, Cambridge, England, 1988).  
 [7] T. Cheon, *Phys. Rev. Lett.* **90**, 258105 (2003).  
 [8] M. Lässig, U. Bastolla, S.C. Manrubia, and A. Valleriani,

*Phys. Rev. Lett.* **86**, 4418 (2001).  
 [9] S. Foitzik, C.J. DeHeer, D.N. Hunjan, and J.M. Herbers, *Proc. R. Soc. London, Ser. B* **268**, 1139 (2001).  
 [10] V.M. de Oliveira and J.F. Fontanari, *Phys. Rev. Lett.* **89**, 148101 (2002).  
 [11] D. Chowdhury, D. Stauffer, and A. Kunwar, *Phys. Rev. Lett.* **90**, 068101 (2003).  
 [12] J. Maynard Smith, *Evolution and the Theory of Games* (Cambridge University Press, Cambridge, England, 1982).  
 [13] R. Axelrod, *The Evolution of Cooperation* (Basic Books, New York, 1984).  
 [14] H. Gintis, *Game Theory Evolving* (Princeton University Press, Princeton, 2000).  
 [15] T. Cheon, *Phys. Lett. A* **318**, 327 (2003).