

## A MUTUALISM-PARASITISM SYSTEM MODELING HOST AND PARASITE WITH MUTUALISM AT LOW DENSITY

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**ABSTRACT.** A mutualism-parasitism system of two species is considered, where mutualism is the dominant interaction when the predators (parasites) are at low density while parasitism is dominant when the predators are at high density. Our aim is to show that mutualism at low density promotes coexistence of the species and leads to high production of the prey (host). The mutualism-parasitism system presented here is a combination of the Lotka-Volterra cooperative model and Lotka-Volterra predator-prey model. By comparing dynamics of this system with those of the Lotka-Volterra predator-prey model, we present the mechanisms by which the mutualism improves the coexistence of the species and production of the prey. Then the parameter space is divided into six regions, which correspond to the four outcomes of mutualism, commensalism, predation/parasitism and neutralism, respectively. When the parameters are varied continuously among the six regions, it is shown that the interaction outcomes of the system transition smoothly among the four outcomes. By comparing the dynamics of the specific system with those of the Lotka-Volterra cooperative model, we show that the parasitism at high density promotes stability of the system. A novel aspect of this paper is the simplicity of the model, which allows rigorous and thorough analysis and transparency of the results.

**1. Introduction.** Since the Lotka-Volterra predator-prey model was established by Lotka (1925) and Volterra (1926), it has been a powerful tool for explaining and predicting ecological phenomena (Murray 1998). In the model, the predators have a negative effect on the prey through consumption of the prey, while the prey have a positive effect on the predators by providing them with resources. Thus the feedback from the other species is either purely positive or purely negative, without variation in sign. Interactions in nature are not always so invariant. Therefore, these models with fixed interaction types need to be expanded in order to describe the situations in which the type of interaction (having a positive or negative effect) that is displayed at a given time is density-dependent; for example, an interaction that is

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a mutualism when a species that consumes another is at low population density and is a parasitism when it is at high density. In fact, the so-called mutualism-parasitism interactions have been demonstrated in real situations for years.

In plant-animal systems, there exist many examples of mutualism-parasitism interactions. As shown by Miyaki and Kikuzawa (1988), mice that hoard acorns (e.g. *Apodemus speciosus* and *A. argentus*) function as both acorn consumers and acorn dispersers. The mice transport the acorns, scatterhoard them and bury some of them. Although the mice later utilize some of the buried acorns, some survive. Because the mice tend to disperse the buried acorns away from the parent tree, sometimes to more favorable locations, these acorns may have a better chance to germinate and grow up into oaks. When the population density of the mice is small, they eat only a small fraction of the acorns, and there may be a net increase in the recruitment rate of oaks associated with the mice over those that are not. Hence mutualism is the dominant interaction between the mice and oaks when the mice are at low density. However, when the population density of the mice is large, most of the acorns are likely to be directly eaten, and only a small fraction buried. In that case the negative effect of the mice on the oaks exceeds their positive effect. Hence seed parasitism is the dominant interaction between the mice and oaks when the mice are at high density. Therefore, the two species form a density-dependent mutualism-parasitism system.

Another example of mutualism-parasitism is the interaction between the senita cactus and the senita moth, which is classified as an obligate mutualism, meaning that the senita moth is the only pollinator of the senita cactus and the senita cactus the only food source of the senita moth. As described by Holland and DeAngelis (2010), and references in those papers, senita moths work as both pollinators and seed eaters of senita cacti. Adult senita moths oviposit on senita cactus flowers and the larvae eat the seed and fruit of the senita cacti. When the population density of the moths is small, the positive effect of the moths through pollinating is larger than its negative effect by consuming the seed and fruits. Thus the net balance from the moths to the senita cacti is positive and, hence, the senita cacti and senita moths are in mutualism when the senita moths are at low density. However, when the population density of the moths is large, the larvae are so abundant that the negative effect from the moths exceeds their positive effect. Thus the net balance from the moths to the senita cacti is negative. Hence, the senita cacti and senita moths are in parasitism when the moths are at high density. Therefore, the interactions between the two species are an example of mutualism-parasitism.

The interactions between herbivores and both grasses and woody plants may also display a form of mutualism-parasitism. A number of studies of herbivore grazing on grasslands have indicated that net primary production was maximized under intermediate levels of herbivory, compared with both zero or very low levels and high levels of herbivory (McNaughton 1976, 1979, Hilbert *et al.* 1981, Dyer *et al.* 1993). This has come to be known as the herbivore-optimization hypothesis. Although questions have been raised concerning the validity of the hypothesis under many circumstances (e.g. Belsky 1986), studies have shown that the population densities of the herbivores can often determine whether processes such as nutrient cycling are increased, leading to increases in primary production (Molvar *et al.* 1994, Kielland *et al.* 1997). A recent study on North American elk, browsing on woody vegetation, supports the herbivore-optimization hypothesis. Experiments showed that low population densities of elk (and hence low levels of browsing) resulted in

higher levels of net primary production than either zero population or high densities of elk (Stewart et al. 2006).

In order to describe the density-dependent interactions between species, Holland and DeAngelis (2009) established a general uni-directional consumer-resource (C-R) model, which is a part of their C-R theory. In the model, one species has both positive and negative effects on the other, which is represented by positive and negative terms in the equation for the population growth of the second species, each containing the population density of the first species. The second species has either a positive or negative feedback on the first, but not both. Numerical simulations on a specific system showed that varying parameters and/or initial population densities of the species lead to transitions of interaction outcomes among mutualism (+ +), commensalism (+ 0), predation/parasitism (+ -), and neutralism (0 0). Here, the interaction types are defined by the outcomes. For example, predation/parasitism (+ -) represents the situation in which species 2, through interaction with species 1, approaches a population density larger than its carrying capacity (i.e., high production), while species 1 approaches a density less than its carrying capacity when in isolation from species 2. In another study, Neuhauser and Fargione (2004) presented a mutualism-parasitism continuum model to describe the phenomenon that plant-mycorrhizae interactions shift from mutualism to parasitism when the soil fertility varies. Analysis of the model demonstrated that the interaction outcomes transition among mutualism, commensalism and predation/parasitism as the host carrying capacity varies. Here, the host carrying capacity increases with the soil fertility. For more discussion about transition of interaction outcomes, we refer to Wang and Wu (2011), and Wang and DeAngelis (2011). While the results of Holland and DeAngelis (2009) and Neuhauser and Fargione (2004) are novel in showing the transitions of interaction outcomes, the mechanisms by which coexistence and high production are promoted by the mutualism at low density need to be shown in a more rigorous way.

In this paper, we analyze dynamics of a specific mutualism-parasitism system of two species. A novel aspect of this paper is that a simple pair of linear terms is used to represent the shift between a Lotka-Volterra cooperative (mutualism) model, when the predators are at low density, and a Lotka-Volterra predator-prey model, when they are at high density. This extremely simplified model allows a rigorous analysis and transparency of results that could not be achieved in a more complex model. By comparing the dynamics of the specific system with those of the Lotka-Volterra predator-prey model, we demonstrate the mechanism by which the mutualism promotes the coexistence of the species. We also show the situations in which the prey approaches high rates of productivity, and show the mechanism by which the interaction outcomes vary with the parameters and/or initial population densities of the species. By comparing the dynamics of the specific system with those of the traditional Lotka-Volterra mutualism model, we show that the parasitism at high density enhances stability of the system.

**2. Model.** In this section, we consider a predator-prey model in which the species are in mutualism when the predators are at low density, while they are in parasitism when the predators are at high density. The model is

$$\begin{aligned} dx/dt &= x(r_1 + b_1 y_0 - b_1 |y - y_0|^* - d_1 x), \\ dy/dt &= y(-r_2 + b_2 x - d_2 y), \end{aligned} \tag{1}$$

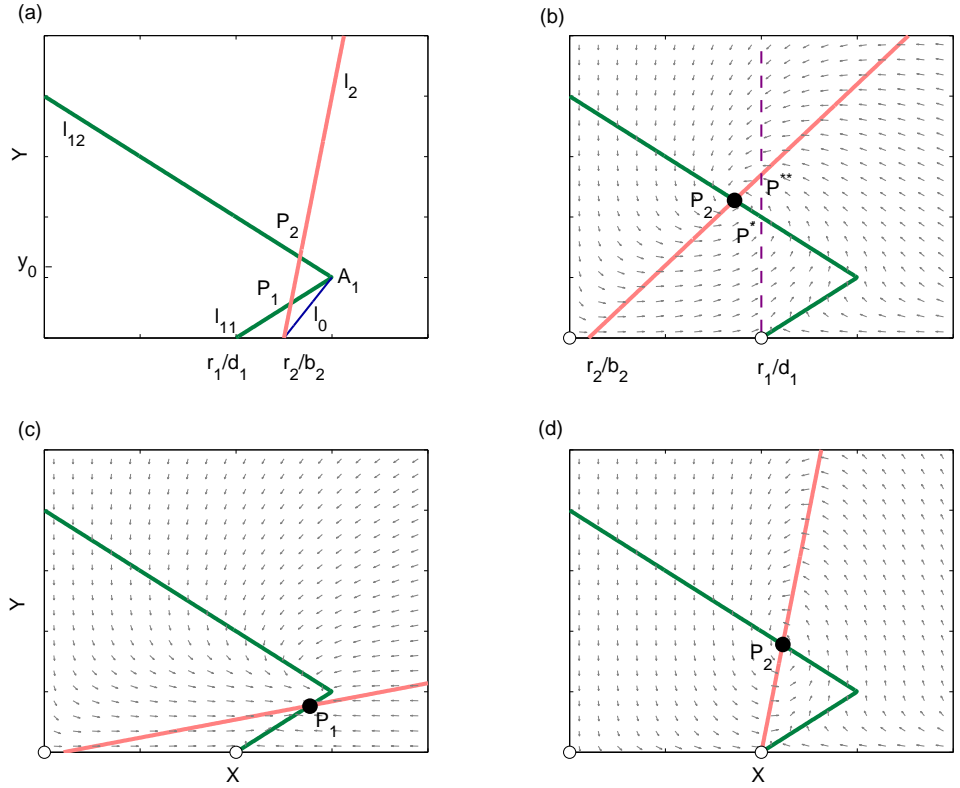


FIGURE 1. Phase portrait diagrams for population dynamics of the mutualism-parasitism system. The green and red lines are zero-growth isoclines for  $x$  and  $y$ , respectively. Vector fields in the phase plane are shown with grey arrows, which display the direction and speed of population trajectories at particular points. Stable and unstable equilibria are represented by filled and open circles, respectively. In Fig. 1a,  $A_1$  denotes the top of  $l_1$  ( $l_{11}$  and  $l_{12}$ ), and  $l_0$  is the line segment connecting  $A_1$  and  $A_2(r_2/b_2, 0)$ . In the following numerical simulations, fix  $r_1 = 0.2, d_1 = b_1 = 0.01, y_0 = 10$ . In Fig. 1b, let  $r_2 = 0.03, b_2 = 0.015, d_2 = 0.01$ . Then  $r_1/d_1 > r_2/b_2$  and  $k_2 > k_0$ . All orbits in  $\text{int}R_+^2$  converge to  $P_2$  with  $p_{21} < r_1/d_1$ . In Fig. 1c, let  $r_2 = 0.006, b_2 = 0.003, d_2 = 0.01$ . Then  $r_1/d_1 > r_2/b_2$  and  $k_2 \leq k_0$ . All orbits in  $\text{int}R_+^2$  converge to  $P_1$  with  $p_{11} > r_1/d_1$ . In Fig. 1d, let  $r_2 = 0.016, b_2 = 0.08, d_2 = 0.01$ . Then  $r_1/d_1 = r_2/b_2$  and  $k_2 > k_0$ . All orbits in  $\text{int}R_+^2$  converge to  $P_2$  with  $p_{21} > r_1/d_1$ .

where  $x$  denotes the population density of the prey and  $y$  denotes that of the predators. All parameters in the system are positive.

In the first equation of (1), let  $y_0 = 0$ , we have  $dx/dt = x(r_1 - b_1y - d_1x)$ . Hence the parameter  $r_1$  denotes the intrinsic growth rate of the prey, and  $r_1/d_1$  represents its carrying capacity when in isolation from the predators. The parameter  $b_1$  denotes the negative effect of the predators on the prey.

Let  $L_1(x, y) = r_1 + b_1y_0 - b_1|y - y_0|^* - d_1x$ . Here, the function  $|y - y_0|^*$  is defined as the smoothed version of the absolute function  $|y - y_0|$ , where the function  $x = |y - y_0|$  is smoothed in a very small neighborhood of its vertex  $(0, y_0)$ . Hence, the isocline  $l_1 : L_1(x, y) = 0$  is smooth. Then the function  $f_1(x, y) = xL_1(x, y)$  is smooth and satisfies

$$\begin{aligned} \partial f_1 / \partial y &= b_1x > 0 \text{ as } y < y_0, \\ \partial f_1 / \partial y &= -b_1x < 0 \text{ as } y > y_0. \end{aligned}$$

Hence the predators have a positive effect on the prey when they are at low density ( $y < y_0$ ), while they have a negative effect on the prey when they are at high density ( $y > y_0$ ). Here, the parameter  $b_1$  also represents the strength of mutualism of the predators when they are at low density. The parameter  $y_0$  denotes the critical threshold of the predators near which the effect of the predators on the prey transitions between positive and negative values. The region of low density,  $0 < y < y_0$ , represents the mutualism range between the predators and prey. In the example of mice and acorns in section 1,  $y_0$  represents the threshold that when the density of the mice is less than it, the net balance of their dispersing and eating acorns is positive; when the density of the mice is larger than it, the net balance becomes negative.

In the second equation of (1), we have  $dy/dt = y(-r_2 + b_2x - d_2y)$ , where it is assumed that there are no costs to the predator in conferring a positive effect on the prey. The constant  $r_2$  corresponds to the mortality of the predators in the absence of the prey. The parameter  $d_2$  denotes the strength of intraspecific competition among the predators, while  $b_2$  represents the positive effect of the prey on the predators. The isocline  $l_2 : -r_2 + b_2x - d_2y = 0$  is as shown in Fig. 1a. We denote  $f_2(x, y) = y(-r_2 + b_2x - d_2y)$ .

The system (1) is a combination of the Lotka-Volterra cooperative model and predator-prey model. Indeed, when the predators are at low density, i.e.,  $y < y_0$ , the system (1) becomes the Lotka-Volterra cooperative model

$$\begin{aligned} dx/dt &= x(r_1 - d_1x + b_1y), \\ dy/dt &= y(-r_2 + b_2x - d_2y). \end{aligned} \tag{2}$$

However, when the predators are at high density, i.e.,  $y > y_0$ , the system (1) becomes the Lotka-Volterra predator-prey model

$$\begin{aligned} dx/dt &= x(r_1 + 2b_1y_0 - d_1x - b_1y), \\ dy/dt &= y(-r_2 + b_2x - d_2y). \end{aligned} \tag{3}$$

**3. Dynamics.** In this section, we show nonexistence of periodic orbits and all possible dynamic behavior of (1).

**Theorem 3.1.** *There is no periodic orbit in (1).*

*Proof.* Let

$$H(x, y) = \frac{1}{xy},$$

then we have

$$\frac{\partial(Hf_1)}{\partial x} + \frac{\partial(Hf_2)}{\partial y} = -\frac{d_1}{y} - \frac{d_2}{x} < 0.$$

It follows from Bendixson-Dulac Theorem (Hofbauer and Sigmund 1998) that there is no periodic orbit in (1). □

As shown in Fig. 1a, there are two equilibria of (1) on the axes, namely  $O(0, 0)$  and  $O_1(r_1/d_1, 0)$ . The Jacobian matrix of (1) at  $O$  is

$$J(O) = \begin{pmatrix} r_1 & 0 \\ 0 & -r_2 \end{pmatrix}.$$

Thus the equilibrium  $O$  is a saddle. In order to consider the interior equilibria of (1), we divide the isocline  $l_1$  into  $l_{11}$  and  $l_{12}$  as follows

$$l_{11} : r_1 - d_1x + b_1y = 0, \quad 0 < y < y_0,$$

$$l_{12} : r_1 + 2b_1y_0 - d_1x - b_1y = 0, \quad y > y_0,$$

where  $l_1$  is smoothed in a small neighborhood of its vertex  $A_1((r_1 + b_1y_0)/d_1, y_0)$ . Thus there are at most two isolated interior equilibria. As shown in Fig. 1a, let  $P_1(p_{11}, p_{12})$  denote the intersection of  $l_{11}$  and  $l_2$ ; let  $P_2(p_{21}, p_{22})$  denote the intersection of  $l_{12}$  and  $l_2$ . Then we have

$$\begin{aligned} p_{11} &= \frac{r_1d_2 - r_2b_1}{d_1d_2 - b_1b_2}, \quad p_{12} = \frac{r_1b_2 - r_2d_1}{d_1d_2 - b_1b_2}, \\ p_{21} &= \frac{r_1d_2 + r_2b_1 + 2d_2b_1y_0}{d_1d_2 + b_1b_2}, \quad p_{22} = \frac{-r_2d_1 + r_1b_2 + 2b_1b_2y_0}{d_1d_2 + b_1b_2}. \end{aligned}$$

Let  $k_{11}$  (respectively,  $k_2$ ) denote the slope of  $l_{11}$  (respectively,  $l_2$ ), and let  $k_0$  denote the slope of  $l_0$ , which is the line segment between points  $A_1$  and  $A_2(r_2/b_2, 0)$ . Here, the point  $A_2$  is intersection of  $l_2$  and the  $x$ -axis. Then we have

$$k_{11} = \frac{d_1}{b_1}, \quad k_2 = \frac{b_2}{d_2}, \quad k_0 = \frac{y_0d_1b_2}{-r_2d_1 + r_1b_2 + b_1b_2y_0}. \quad (4)$$

The dynamic behavior of (1) is shown in three cases.

**Case 1.**  $r_2/b_2 < r_1/d_1$ .

In this case, the point  $O_1(r_1/d_1, 0)$  is at the right side of  $A_2(r_2/b_2, 0)$ , as shown in Figs. 1b and 1c. When  $k_2 > k_0$ , there is a unique interior equilibrium  $P_2$ . It follows from Theorem 3.1 and phase portrait analysis that all orbits in  $\text{int}R_+^2$  converge to  $P_2$ , where  $\text{int}R_+^2 = \{(x, y) : x > 0, y > 0\}$ . In order to show the transition of interaction outcomes, we need to give an obvious condition for  $p_{21} > r_1/d_1$ . As shown in Fig. 1b, let  $P^*(r_1/d_1, y^*)$  (respectively,  $P^{**}(r_1/d_1, y^{**})$ ) denote the intersection of  $l_{12}$  (respectively,  $l_2$ ) with the vertical line  $x = r_1/d_1$ . Then we have

$$y^* = 2y_0, \quad y^{**} = \frac{r_1b_2 - r_2d_1}{d_1d_2}.$$

The condition  $p_{21} > r_1/d_1$  is equivalent to the situation that the point  $P^*$  is above  $P^{**}$ , i.e.,  $y^* > y^{**}$ , which can be described as

$$y_0 > y_0^*, \quad y_0^* = \frac{r_1b_2 - r_2d_1}{2d_1d_2}. \quad (5)$$

Hence  $y_0^*$  is a threshold for the transition of interaction outcomes of species 1.

When  $k_2 \leq k_0$ , there is a unique interior equilibrium  $P_1(p_{11}, p_{12})$ . By the monotonicity of  $l_{11}$ , we have  $p_{11} > r_1/d_1$ . It follows from Theorem 3.1 and phase portrait analysis that all orbits in  $\text{int}R_+^2$  converge to  $P_1$  with  $p_{11} > r_1/d_1$ , as shown in Fig. 1c. Hence we have the following results.

**Proposition 1.** *Let  $r_2/b_2 < r_1/d_1$ .*

- (i) *When  $k_2 > k_0$ , all orbits in  $\text{int}R_+^2$  converge to  $P_2(p_{21}, p_{22})$ ;  $p_{21} > r_1/d_1$  if and only if  $y_0 > y_0^*$ .*

(ii) When  $k_2 \leq k_0$ , all orbits in  $\text{int}R_+^2$  converge to  $P_1(p_{11}, p_{12})$  with  $p_{11} > r_1/d_1$ .

**Case 2.**  $r_2/b_2 = r_1/d_1$ .

In this case, the points  $O_1(r_1/d_1, 0)$  and  $A_2(r_2/b_2, 0)$  coincide, as shown in Figs. 1d, 2a and 2b. When  $k_2 > k_0$ , there is a unique interior equilibrium  $P_2$  with  $p_{21} > r_1/d_1$ . Similar to the discussion in case 1, all orbits in  $\text{int}R_+^2$  converge to  $P_2$ . When  $k_2 = k_0$ , the line segment  $\overline{A_1A_2}$  consists of stable equilibria and the system (1) is degenerate, while (1) is a so-called constant motion in the mutualism region  $\{(x, y) : x > 0, 0 < y < y_0\}$  (Hofbauer and Sigmund 1998). It follows from phase portrait analysis that all orbits in  $\text{int}R_+^2$  converge to the continuum line segment  $\overline{A_1A_2}$ , as shown in Fig. 2a. When  $k_2 < k_0$ , there is no interior equilibrium. All orbits in  $\text{int}R_+^2$  converge to  $O_1$ , as shown in Fig. 2b. Hence we have the following results.

**Proposition 2.** Let  $r_2/b_2 = r_1/d_1$ .

- (i) When  $k_2 > k_0$ , all orbits in  $\text{int}R_+^2$  converge to  $P_2(p_{21}, p_{22})$  with  $p_{21} > r_1/d_1$ .
- (ii) When  $k_2 = k_0$ , all orbits in  $\text{int}R_+^2$  converge to the equilibrium segment  $\overline{A_1A_2}$ .
- (iii) When  $k_2 < k_0$ , all orbits in  $\text{int}R_+^2$  converge to  $O_1(r_1/d_1, 0)$ .

**Case 3.**  $r_2/b_2 > r_1/d_1$ .

In this case, the point  $O_1(r_1/d_1, 0)$  is at the left side of  $A_2(r_2/b_2, 0)$  as shown in Figs. 2c and 2d. When  $k_2 > k_0 > 0$ , we have  $k_2 > k_0 > k_{11}$ . By (4),  $k_0 > 0$  can be described as

$$y_0 > \frac{r_2d_1 - r_1b_2}{b_1b_2}. \tag{6}$$

There are two interior equilibria  $P_1$  and  $P_2$  as shown in Fig. 2c. By  $k_2 > k_{11}$ , we have  $b_2/d_2 > d_1/b_1$ , i.e.,  $d_1d_2 - b_1b_2 < 0$ . The Jacobian matrices of (1) at  $P_1$  and  $P_2$  are

$$J(P_1) = \begin{pmatrix} -d_1p_{11} & b_1p_{11} \\ b_2p_{12} & -d_2p_{12} \end{pmatrix},$$

$$J(P_2) = \begin{pmatrix} -d_1p_{21} & -b_1p_{21} \\ b_2p_{22} & -d_2p_{22} \end{pmatrix}.$$

Since  $\det J(P_1) = (d_1d_2 - b_1b_2)p_{11}p_{12} < 0$ , the equilibrium  $P_1$  is a saddle. Since  $\det J(P_2) = (d_1d_2 + b_1b_2)p_{21}p_{22} > 0$  and  $\text{tr}J(P_2) = -d_1p_{21} - d_2p_{22} < 0$ , the equilibrium  $P_2$  is asymptotically stable. By Theorem 3.1, all orbits in  $\text{int}R_+^2$  above the separatrix of  $P_1$  converge to  $P_2$ , while those below the separatrix of  $P_1$  converge to  $O_1$ , as shown in Fig. 2c.

When  $k_2 = k_0$ , the equilibria  $P_1$  and  $P_2$  coincide and  $P_1$  becomes a saddle-node point (Hofbauer and Sigmund 1998). All orbits in  $\text{int}R_+^2$  above the separatrix of  $P_1$  converge to  $P_1$ , while those below the separatrix of  $P_1$  converge to  $O_1$  as shown in Fig. 2d.

When  $k_2 < k_0$  or  $k_0 < 0$ , there is no interior equilibrium. All orbits in  $\text{int}R_+^2$  converge to  $O_1$  as shown in Fig. 2b. Hence we have the following results.

**Proposition 3.** Let  $r_2/b_2 > r_1/d_1$ .

- (i) When  $k_2 > k_0 > 0$ , all orbits in  $\text{int}R_+^2$  above the separatrix of  $P_1$  converge to  $P_2$  with  $p_{21} > r_1/d_1$  and those below the separatrix of  $P_1$  converge to  $O_1(r_1/d_1, 0)$ .

- (ii) When  $k_2 = k_0$ , all orbits in  $\text{int}R_+^2$  above the separatrix of  $P_1$  converge to  $P_1$  with  $p_{11} > r_1/d_1$ , while those below the separatrix of  $P_1$  converge to  $O_1(r_1/d_1, 0)$ .
- (iii) When  $k_2 < k_0$  or  $k_0 < 0$ , all orbits in  $\text{int}R_+^2$  converge to  $O_1(r_1/d_1, 0)$ .

In order to show the situations in which the prey approaches a high production, we have the following corollary from Propositions 1, 2 and 3.

**Corollary 1.** *The prey in the system (1) approaches a high production if and only if one of the following conditions is satisfied: (i)  $r_2/b_2 < r_1/d_1, k_2 > k_0$  and  $y_0 > y_0^*$ ; (ii)  $r_2/b_2 < r_1/d_1, k_2 \leq k_0$ ; (iii)  $r_2/b_2 = r_1/d_1$  and  $k_2 \geq k_0$ ; (iv)  $r_2/b_2 > r_1/d_1, k_2 \geq k_0 > 0$  and the initial density point is not below the separatrix of  $P_1$ .*

**4. Coexistence.** In this section, we demonstrate features of the system (1) by comparing dynamics of (1) with those of the Lotka-Volterra models.

We show that the mutualism at low density promotes coexistence of the species by comparing the dynamics of (1) with those of the Lotka-Volterra predator-prey model. Indeed, when there is no mutualism in (1), i.e.,  $y_0 = 0$ , the system (1) becomes the Lotka-Volterra predator-prey model

$$\begin{aligned} dx/dt &= x(r_1 - d_1x - b_1y), \\ dy/dt &= y(-r_2 + b_2x - d_2y). \end{aligned} \quad (7)$$

It is known that when  $r_1/d_1 \leq r_2/b_2$ , all orbits of (7) in  $\text{int}R_+^2$  converge to the equilibrium  $(r_1/d_1, 0)$ , which corresponds to extinction of the predators (Hofbauer and Sigmund 1998). However, under the same condition, the species can coexist in (1) when there is mutualism at low density (i.e.,  $y_0 > 0$ ). This can be described in the following situations A and B.

*Situation A.* When  $r_1/d_1 = r_2/b_2$ , i.e.,  $b_2 = r_2d_1/r_1$ , it follows from Proposition 2 that the two species can coexist if  $k_2 \geq k_0$ . By (5),  $k_2 \geq k_0$  can be expressed as

$$b_1 \geq \frac{d_2r_1}{r_2}. \quad (8)$$

That is, when the positive effect  $b_2$  of the prey on the predators is intermediate ( $b_2 = r_2d_1/r_1$ ), the predators can persist in (1) if the positive effect  $b_1$  of the predators on the prey is not small ( $b_1 \geq \frac{d_2r_1}{r_2}$ ). Here,  $b_1$  can not be regarded as the negative effect of the predators on the prey since by Proposition 2, the interior equilibrium is on the line segment  $l_{11}$ , which is in the mutualism region.

*Situation B.* When  $r_1/d_1 < r_2/b_2$ , i.e.,  $b_2 < r_2d_1/r_1$ , it follows from Proposition 3 that the two species can coexist if  $k_2 \geq k_0$  and the initial density point is not below the separatrix of  $P_1$  (see Fig. 2c). By (5),  $k_2 \geq k_0$  can be expressed as

$$y_0 \geq y_0^{**}, \quad y_0^{**} = \frac{r_2d_1 - r_1b_2}{b_1b_2 - d_1d_2}. \quad (9)$$

Here, we have  $r_2d_1 - r_1b_2 \geq 0$  by  $r_1/d_1 \leq r_2/b_2$ , while we have  $b_1b_2 - d_1d_2 > 0$  by  $k_{11} < k_2$  as shown in Fig. 2c. Thus  $y_0^{**} > 0$ , while  $y_0^{**}$  is a threshold for the species coexistence. That is, when the positive effect  $b_2$  of the prey on the predators is small ( $b_2 < r_2d_1/r_1$ ), the predators can persist in the system (1) if the mutualism region is not small ( $y_0 \geq y_0^{**}$ ) and the initial density of the predators is relatively large (the initial density point is not below the separatrix of  $P_1$ ).



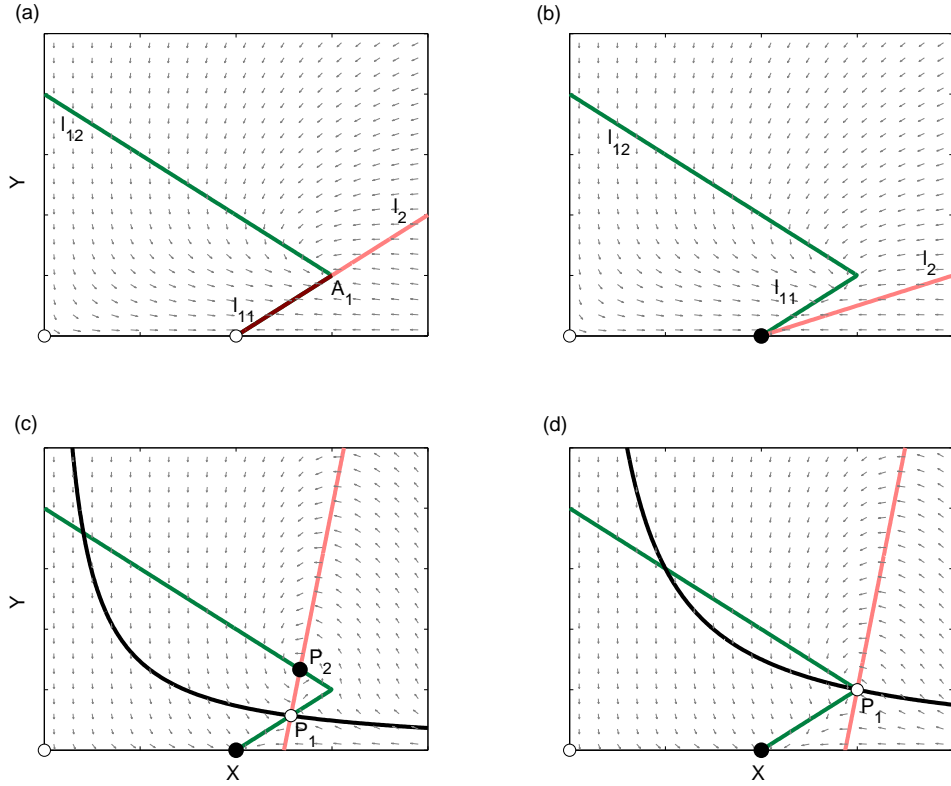


FIGURE 2. Phase portrait diagrams for dynamical behavior of the mutualism-parasitism system. Zero-growth isoclines for  $x$  and  $y$  are represented by green and red lines, respectively. Grey arrows in the phase plane display the direction and speed of vector fields. Filled and open circles denote stable and unstable equilibria, respectively. Saddle points have a black line (separatrix), which subdivides the plane into two basins of attraction that correspond to particular equilibria. In the following numerical simulations, fix  $r_1 = 0.2, d_1 = b_1 = 0.01, y_0 = 10$ . In Fig. 2a, let  $r_2 = 0.2, b_2 = d_2 = 0.01$ . Then  $r_1/d_1 = r_2/b_2$  and  $k_2 = k_0$ . All orbits in  $\text{int}R_+^2$  converge to the equilibrium set  $l_{11}$ . In Fig. 2b, let  $r_2 = 0.1, b_2 = 0.005, d_2 = 0.01$ . Then  $r_1/d_1 = r_2/b_2$  and  $k_2 < k_0$ . All orbits in  $\text{int}R_+^2$  converge to  $O_1(r_1/d_1, 0)$ . In Fig. 2c, let  $r_2 = 2, b_2 = 0.08, d_2 = 0.01$ . Then  $r_1/d_1 < r_2/b_2$  and  $k_2 > k_0$ . All orbits above the separatrix (the black line) of  $P_1$  converge to  $P_2$  with  $p_{21} > r_1/d_1$ , while those below the separatrix tend to  $O_1(r_1/d_1, 0)$ . In Fig. 2d, let  $r_2 = 2.3, b_2 = 0.08, d_2 = 0.01$ . Then  $r_1/d_1 < r_2/b_2$  and  $k_2 = k_0$ . All orbits above the separatrix (the black line) of  $P_1$  converge to  $P_1$  with  $p_{11} > r_1/d_1$ , while those below the separatrix tend to  $O_1(r_1/d_1, 0)$ .

We show that the parasitism at high density in (1) enhances stability of the system by comparing dynamics of (1) with those of the Lotka-Volterra cooperative

model (2). As shown by Hofbauer and Sigmund (1998), all orbits of (2) in  $\text{int}R_+^2$  converge to infinity when  $b_1 \geq d_1d_2/b_2$  and  $b_2 > r_2d_1/r_1$ . That is, population densities of the species tend to infinity if the positive effects  $b_1$  and  $b_2$  are not well balanced. The tendency to infinity corresponds to an unstable situation since a limited environment can not support infinite individuals. This tendency will not happen in (1). Indeed, when  $y > y_0$ , the system (1) becomes (3) where we have

$$dx/dt = x(r_1 + 2b_1y_0 - d_1x - b_1y) < x(r_1 + 2b_1y_0 - d_1x).$$

Since solutions of the logistic equation  $dx/dt = x(r_1 + 2b_1y_0 - d_1x)$  are bounded, then the solutions  $x(t)$  of (3) are bounded. Hence, it follows from  $dy/dt = y(-r_2 + b_2x - d_2y)$  that the solutions  $y(t)$  in (3) are bounded. Thus the orbits  $(x(t), y(t))$  of (1) are bounded. Similarly, when  $y < y_0$ , the first equation of (1) is  $dx/dt = x(r_1 - d_1x + b_1y) < x(r_1 + b_1y_0 - d_1x)$ , and hence the orbits of (1) are bounded. Therefore, the tendency of the orbits to infinity in (2) is prohibited in (1) by the parasitism at high density ( $y > y_0$ ).

**5. Transition of outcomes.** In this section, according to the results in section 3, we divide the parameter space into six regions and demonstrate how and in which order the interaction outcomes transition when the parameters and/or initial population densities of the species vary. Meanwhile, the mechanism by which the mutualism improves the production of the prey is shown. In order to show the roles of all parameters in the transition of interaction outcomes, we consider the seven-dimensional parameter space  $(b_1, b_2, d_1, d_2, r_1, r_2$  and  $y_0)$  in (1).

Firstly, it follows from Proposition 1 that when  $b_2 > r_2d_1/r_1$  and  $y_0 < y_0^*$ , all orbits in  $\text{int}R_+^2$  converge to  $P_2$  with  $p_{21} < r_1/d_1$  (see Fig. 1b); when  $b_2 > r_2d_1/r_1$  and  $y_0 = y_0^*$ , all orbits in  $\text{int}R_+^2$  converge to  $P_2$  with  $p_{21} = r_1/d_1$ ; when  $b_2 > r_2d_1/r_1$  and  $y_0 > y_0^*$ , all orbits in  $\text{int}R_+^2$  converge to  $P_2$  with  $p_{21} > r_1/d_1$ , or converge to  $P_1$  with  $p_{11} > r_1/d_1$  as shown in Fig. 1c. Hence when  $b_2 > r_2d_1/r_1$ , the parameter space can be divided into three regions: I =  $\{b_2 > r_2d_1/r_1, y_0 < y_0^*\}$ , II =  $\{b_2 > r_2d_1/r_1, y_0 = y_0^*\}$  and III =  $\{b_2 > r_2d_1/r_1, y_0 > y_0^*\}$ , which correspond to the interaction outcomes (+ -), (+ 0) and (+ +), respectively. When we fix all but  $b_2$  and  $y_0$ , the regions can be shown as the regions of I, II and III in the  $b_2y_0$  parameter plane in Fig. 3. That is, when the parameter point  $(b_2, y_0)$  varies from regions I, to II, and to III, the interaction outcomes transition in the order of (+ -)  $\rightarrow$  (+ 0)  $\rightarrow$  (+ +). The ecological meaning is that when the positive effect of the prey on the predators is large ( $b_2 > r_2d_1/r_1$ ), the interaction outcomes transition from parasitism, commensalism to mutualism as the mutualism region between the predators and prey increases from small ( $y_0 < y_0^*$ ), intermediate ( $y_0 = y_0^*$ ), to large regions ( $y_0 > y_0^*$ ).

Secondly, it follows from Proposition 2 and (8) that when  $b_2 = r_2d_1/r_1$  and  $b_1 \geq r_1d_2/r_2$ , all orbits in  $\text{int}R_+^2$  converge to  $P_2$  with  $p_{21} > r_1/d_1$  (see Fig. 1d) or to the equilibrium set  $l_{11}$  (see Fig. 2a); when  $b_2 = r_2d_1/r_1$  and  $b_1 < r_1d_2/r_2$ , all orbits in  $\text{int}R_+^2$  converge to  $O_1$  (see Fig. 2b). Here, we define the parameter region IV =  $\{b_2 = r_2d_1/r_1\}$ . When we fix all but  $b_2$  and  $y_0$ , the region can be shown as that of IV in Fig. 3. In this region, the interaction outcomes transition from (0 0) to (+ +) as the positive effect of the predators increases from small ( $b_1 < r_1d_2/r_2$ ) to large values ( $b_1 \geq r_1d_2/r_2$ ). The ecological meaning is that when the positive effect of the prey is intermediate ( $b_2 = r_2d_1/r_1$ ), the interaction outcomes transition from neutralism to mutualism as the the positive effect of the predators increases from small to large values.

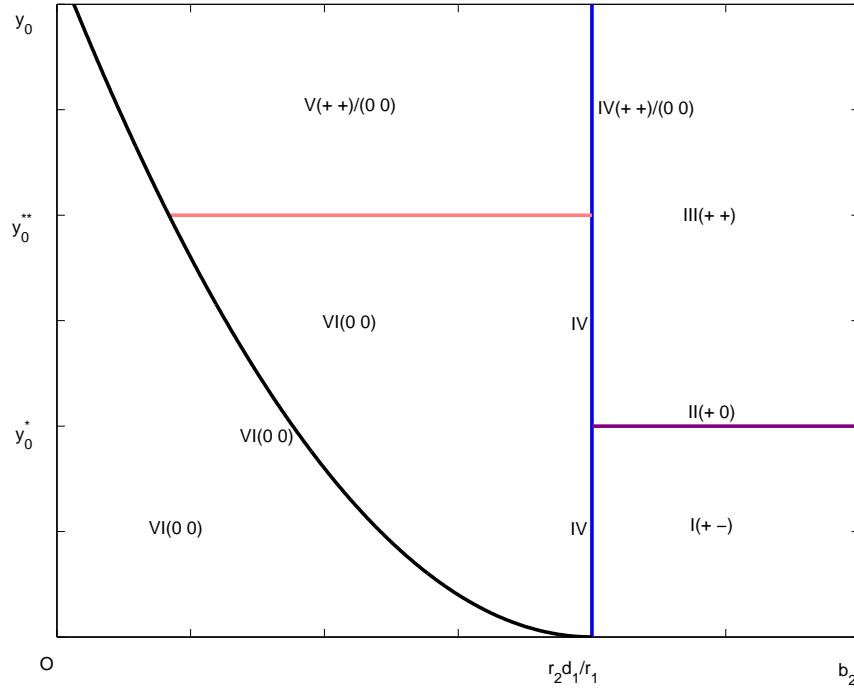


FIGURE 3. The mechanism by which the interaction outcomes vary with the factors and/or initial population densities is shown: (a) when  $b_2 > r_2d_1/r_1$ , the outcomes transition in the order of  $(+ -) \rightarrow (+ 0) \rightarrow (+ +)$  as the mutualism interval  $y_0$  changes from small, intermediate to large values, which is shown in regions I, II and III; (b) when  $b_2 = r_2d_1/r_1$ , the outcome transitions in the order of  $(0 0) \rightarrow (+ +)$  as the positive effect  $b_1$  of the predators on the prey changes from small to large values, which is shown in region IV; (c) when  $b_2 < r_2d_1/r_1$ ,  $y_0 > (r_2d_1 - r_1b_2)/(b_1b_2)$  and  $y_0 \geq y_0^{**}$ , the outcomes transition in the order of  $(0 0) \rightarrow (+ +)$  as the initial population density of the predators varies from small to large values, which is shown in region V; (d) when  $b_2 < r_2d_1/r_1$ ,  $y_0 \leq (r_2d_1 - r_1b_2)/(b_1b_2)$  and  $y_0 < y_0^{**}$ , the outcomes become  $(0 0)$  as shown in region VI.

Thirdly, it follows from Proposition 3(i)(ii), (6) and (9) that when  $b_2 < r_2d_1/r_1$ ,  $y_0 > (r_2d_1 - r_1b_2)/(b_1b_2)$  and  $y_0 \geq y_0^{**}$ , all orbits which are above the separatrix of  $P_1$  converge to  $P_2$  with  $p_{21} > r_1/d_1$ , while those below the separatrix of  $P_1$  converge to  $O_1$  (see Fig. 2). Here, we define the parameter region  $V = \{b_2 < r_2d_1/r_1, y_0 > (r_2d_1 - r_1b_2)/(b_1b_2), y_0 \geq y_0^{**}\}$ . When we fix all but  $b_2$  and  $y_0$ , the region can be shown as that of V in Fig. 3. In this region, the interaction outcomes transition from  $(0 0)$  to  $(+ +)$  as the initial density point varies from the area below the separatrix of  $P_1$  to that above the separatrix. The ecological meaning is that when the positive effect of the prey is small ( $b_2 < r_2d_1/r_1$ ) but the mutualism region is large, the interaction outcomes transition from neutralism to mutualism as the initial density of the predators increases from small to large values.

Finally, it follows from Proposition 3 (iii) that as  $b_2 < r_2 d_1 / r_1$ , all orbits in  $\text{int}R_+^2$  converge to  $O_1$  when  $y_0 \leq (r_2 d_1 - r_1 b_2) / (b_1 b_2)$  or  $y_0 < y_0^{**}$ . Here, we define region  $\text{VI} = \{b_2 < r_2 d_1 / r_1, y_0 < y_0^{**}\} \cup \{b_2 < r_2 d_1 / r_1, y_0 \leq (r_2 d_1 - r_1 b_2) / (b_1 b_2)\}$ . Indeed,  $\text{VI} = \text{int}R_+^2 - \text{I} - \text{II} - \text{III} - \text{IV} - \text{V}$ . When we fix all but  $b_2$  and  $y_0$ , the region can be shown as that of VI in Fig. 3. In this region, the interaction outcomes are (0 0). The ecological meaning is that when the positive effect of the prey is small and the mutualism region is also small, the interaction outcomes are neutralism.

Therefore, the parameter space of (1) can be divided into six regions. When the parameters in (1) vary continuously among the regions, the interaction outcomes transition among (+ +), (+ 0), (+ -) and (0 0) in a smooth fashion. In addition, in the region V, varying initial population densities of the species may lead to the transition of outcomes between (0 0) and (+ +).

**6. Discussion.** In this paper, we introduced mutualism to the Lotka-Volterra predator-prey model through a very simple device that did not increase the complexity of the model. Based on the analysis of the mutualism-parasitism system, we demonstrated the mechanisms by which mutualism promotes coexistence of the species and leads to the high production of the prey. We also divided the parameter space into six regions and showed that the interaction outcomes transition continuously when the parameters vary among the regions and/or the initial population densities of the species change. Our work provides a complement to the results by Holland and DeAngelis (2009) and Neuhauser and Fargione (2004).

Based on the Lotka-Volterra predator-prey model, it is known that the prey approaches a population density less than its carrying capacity when in coexistence with the predators. The Lotka-Volterra model is based on the assumption that the predators consume the prey without providing any form of positive feedback to the prey in the process, which is not always consistent with real situations. It follows from the analysis of our mutualism-parasitism system that the prey can approach a high production when the effect of the predators changes from negative to positive as predator population numbers decrease (Corollary 1). Thus our work has potential applications for the growth of some specific species, which can be stated as follows. Firstly, when the positive effect of the prey on the predators is large, as shown in regions I, II and III of Fig. 3, large regions of mutualism between predators and prey can lead to the high production of the prey. Secondly, when the positive effect of the prey on the predators is intermediate, as shown in region IV of Fig. 3, the predators, which have a large positive effect on the prey, will promote the high production of the prey. Finally, when the positive effect of the prey on the predators is small, but the region of mutualism between the predators and prey is large as shown in region V of Fig. 3, large initial densities of the predators will help the prey to approach the high production. For example, the problem of how to enhance the production of oaks in forests has been a challenge in ecology (Miyaki and Kikuzawa 1988; Herrera 1995; Cantrell et al. 2004; Li et al. 2006; Pérez-Ramos and Maran 2008; Wang, Wu and Ruan 2011; Wang, DeAngelis and Holland 2011)). The results in this paper have applications to the problem. Indeed, (a) when each acorn provides high energy for the mice and the mutualism region between the mice and oaks is large (see explanations in section 2), the oaks will approach the high production; (b) when each acorn provides intermediate energy for the mice and the mice are efficient in dispersing and burying the acorns, the oaks will also approach the high production; (c) when each acorn provides low energy for the mice but the

mutualism between the mice and oaks is very large, a high initial density of the mice will lead to the high production of the oaks.

Based on the Lotka-Volterra model for mutualism, it is shown that ‘mutualism between species tends to have a destabilizing effect on the community dynamics’ (May 1974). The destabilizing situation will not occur in the mutualism-parasitism system in this paper. The reason is that in the mutualism-parasitism system, parasitism dominates when the predators are at high density. Then the explosive growth of the prey is not possible. As a result, the explosive growth of the predators is prohibited. Hence, the parasitism at high density promotes stability of the system. Detailed discussions were given by Holland and DeAngelis (2010).

The consumer-resource theory established by Holland and DeAngelis (2009) well described the general mutualism-parasitism interactions, in which the consumer has a positive effect on its resource. In their paper, numerical simulations on a specific system, which is an extension of the Rosenzweig-MacArthur model, show that the positive effect may promote the species coexistence and production of the resource, and result in the transition of interaction outcomes. While the system considered in this work is simpler than their model, rigorous analysis is possible here, which exhibits a quantitative description in how and when the positive effect (including the mutualism region and the strength of mutualism) leads to the promotion and transition.

Numerical simulations in Figs. 1 and 2 display transition of interaction outcomes between the prey and predators. Figs. 1b and 1c exhibit that when the parameter value  $b_2/d_2$  decreases, the prey will approach a density larger than its carrying capacity. Fig. 1d demonstrates a situation in which the two species can coexist if both  $r_2$  and  $b_2$  are large. Figs. 2a and 2b show that the predators will go to extinction when  $b_2/d_2$  decreases. Figs. 2c and 2d demonstrate a situation in which the interaction outcomes are density-dependant: when the initial densities of the species are sufficiently large, the two species coexist and the prey approaches a density larger than its carrying capacity; when the densities are small, the predators will go to extinction while the prey approaches its carrying capacity.

In the specific mutualism-parasitism system, we use the parameter  $b_1$  to represent both the positive and negative effects of the predators on the prey. When we use different parameter values to represent these effects, similar results can be shown in the same way. While the specific mutualism-parasitism model in this paper is simple, our work provides an insightful explanation of the mechanisms involved in the mutualism-parasitism systems.

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