2022-26

Workshop on Theoretical Ecology and Global Change

2 - 18 March 2009

Mutualism or cooperation among competitors promotes coexistence and competitive ability

HERNANDEZ DE RODRIGUEZ Maria Josefina
(Zhang Z.)*

Universidad Central de Venezuela
Instituto de Zoologia Tropical
Facultad de Ciencias, Apartado 47058, 1041-A
Caracas
VENEZUELA

Available online at www.sciencedirect.com

SCIENCE DIRECT®

Ecological Modelling 164 (2003) 271–282

ECOLOGICAL MODELLING

www.elsevier.com/locate/ecolmodel

Mutualism or cooperation among competitors promotes coexistence and competitive ability

Zhibin Zhang*

Institute of Zoology, Chinese Academy of Sciences, 19 Zhongguancun Lu, Haidian, Beijing 100080, China

Received 6 December 2001; received in revised form 6 January 2003; accepted 17 February 2003

Abstract

In the Lotka-Volterra competition model and similar competition models, species can only coexist if between-species competition is weaker than within species. Prior modeling and field studies have shown that coexistence can be promoted by reducing the competitive ability between species through spatial or temporal niche differentiation. Colonization, disturbance, aggregations in patchy habitats, resource transport and supply rates, predation, sex ratio mediation have been suggested to promote species coexistence. The role of mutualism in promoting species coexistence has never been quantitatively studied. In this study, by starting from the traditional Lotka-Volterra competition model, a new general model with introduction of mutualism between two competitive species is proposed. We hypothesized that the interaction of one species to the other is flexible instead of always negative; the zero growth isoclines of the competing species are parabolic. Three conclusions are drawn from this modeling study. First, mutualism is a new way of promoting coexistences of two species. Second, mutualism often increases the carrying capacities of both species, and then promotes their competitive abilities. Third, the mutualism-competition model is also appropriate to describe the dynamics of cooperation and competition between individuals or groups within species, and mutualism between plants and animals. The behind mechanism lies in mutualism or cooperation reduced the severity of competition at low density. Inferior competitor, if cooperative to superior competitor, is also possible to survive. Since mutualism or cooperation is commonly seen among competitors or between prey and predators, its role in shaping social or community structure is worth to explore.
© 2003 Elsevier Science B.V. All rights reserved.

Keywords: Competition; Mutualism; Cooperation; Coexistence; Stability; Complex system

---

1. Introduction

Competition and mutualism are two important interactions among species. According to definitions by Krebs (1994, p. 230), competition occurs when two species use the same resources or harm each other when seeking resource; mutualism is defined as living of two species in close association with one another with the benefit of both. Competition also occurs among individuals or groups within species, often more furiously because they use the very similar resources. Within species, mutualism is called cooperation (Alocock, 1989, p. 479), which is commonly seen in social animals and in human society.

The famous competition model was proposed independently by Lotka (1925) and Volterra (1926) in Italy. In this model, coexistence occurs only when the crowd-tolerability and competitive capacity of species are well balanced. Otherwise, low crowd-tolerable and low competitive species (inferior competitor) will be removed by the superior competitor. The hypothesis of the Lotka-Volterra model is that the interaction of one species to the other is always negative, and linear

---

* Fax: +861062556418.
E-mail address: zhangzb@panda.ioz.ac.cn (Z. Zhang).

0304-3800/03/$ – see front matter © 2003 Elsevier Science B.V. All rights reserved.
doi:10.1016/S0304-3800(03)00069-3

to the population size of its competitor. Many competitive models or community models were further developed by slightly modifying the Lotka-Voletrra model, often by introducing non-linear isoclines, but without changing the monotonous and negative relationship between the growth rate of the focal species (e.g. Paine, 1966; May, 1973; Renshaw, 1991; Zhang and Hanski, 1998).

Since resources are limited, competition between two species is inevitable. The intensity of competition may increase as disturbance and stress decline (Grime, 1988). But purely competition as described by the Lotka-Volterra model often results in species exclusion or coexistence with reduced carrying capacity of both species. According to the model, both species with the lower carrying capacity would not be favored when competing with other rivals. Therefore, pure competition does not help coexistence of multiple species though it is a driving force for natural selection. Species can only coexist if between-species competition is weaker than within-species as revealed in the Lotka-Volterra model, and this result was further confirmed in many other similar models (e.g. Renshaw, 1991; Droseel et al., 2001). There are many ways of reducing inter-specific competition, mainly through niche differentiation, spatially or temporally. Prior modeling and field studies have shown that food preference, predation, habitat heterogeneity, rate-limiting supply of nutrition, foraging strategies, nutrition transportation and segregation can stabilize the coexistence of competitive species by reducing the competitive ability between species (e.g. Paine, 1966; Harper, 1969; Crawley, 1983; Hustor and De Angelis, 1994; Leibdd, 1997; Hamback, 1998; Rita and Ranta, 1998; Lenas et al., 1998; Vayenas and Pavlon, 1999; Droseel et al., 2001). The difference in colonization ability may also promote coexistence if the dispersal is negatively correlated to the competitive ability (e.g. Hastings, 1980; Hanski and Ranta, 1983; Nee and May, 1992; Hanski and Zhang, 1993; Tilman, 1994). Disturbance is also possible to modify species competition through reducing the dominance of superior competitor. Moderate disturbance has been proved to support maximum coexistence (e.g. Connell, 1978; Huston, 1979; Tilman, 1982a). Although the superior competitor can exclude the inferior one in a continuous and homogeneous environment, simulation by Atkinson and Shorrocks (1981), and Hanski (1981) indicated that independent aggregations in patchy habitats help coexistence of the inferior competitors. Aggregation enhances intra-specific competition and reduces inter-specific competition. Resource transport and supply rates are also possible to promote coexistence (Hustor and De Angelis, 1994). Predation has been demonstrated to promote coexistence of prey through mediating competition among preys (e.g. Paine, 1966; Harper, 1969; Crawley, 1983; Hamback, 1998; Droseel et al., 2001). Zhang and Jiang (1993, 1995), Zhang and Hanski (1998) showed that through sex ratio mediation, instead of through reducing inter-specific competition, coexistence was obtained.

Resources-related niche differentiation alone is hard to explain the coexistence of species, which obviously exploit very similar resources. For example, all plants living together use light, CO_2, nitrogen and water. The phytoplankton species in water also use very similar resources. The competition among individuals or groups within species is also very strong because they exploit very similar resources. Therefore, it is still necessary to explore the alternative mechanism of species or group coexistence.

For two species competing (or partially competing) for resources, it is generally believed that the presence of one species should affect negatively on the other. In fact, positive interaction also exists among competing species. For example, the leguminous plants compete for light, CO_2, water, minerals with other plants, but they also provide nitrogen to the neighboring plants and then facilitate the growth of other plants (Bertness and Leonard, 1997). Similarly, some mycorrhizal plants provide minerals to the other plants. Plant diversity is promoted by mycorrhizal infection (Bergelson and Crawley, 1988). Recent studies indicated that plant diversity is good for the community production (Diaz and Cabido, 2001; Loreau et al., 2001, Tilman et al., 2001). The production of mixture plants is often higher than the production of the plant with highest production. This phenomenon is called as overyielding (Hector, 1998; Kaiser, 2000; Fridley, 2001). Mutualism is generally believed to be one of the reasons why there is high production or overyielding in community with more plants.

Mutualism also occurs in plant–animal system. Herbivore is not always negative to plants. For inferior competitive plants, herbivores are important to keep coexistence of plants by depressing the superior competitors (e.g. Crawley, 1983; Hamback, 1998). Herbivore is well known to facilitate grassland (McNaughton, 1976). Herbivore is negative to grass by browsing grass, but positive to grass by facilitating nutrition cycle. Moderate grazing is the best. The grassland will be degenerated without herbivore grazing. The mutualism also exists among forest and seed-eaters. Small rodents are recognized to be both seed predators and seed dispersers (e.g. Sork, 1984; Jensen and Nielsen, 1986; Miyaki and Kikuzawa, 1988; Herrera, 1995). If rodents are too abundant, they will eat all seeds, and certainly stop the seeding regeneration of forests; but if rodents are all removed, the seeding regeneration is also stopped without seed dispersal and burying by rodents. These examples implied that mutualism could be a mediating factor in reducing intensity of competition among competitors or intensity of predation to prey. Similarly, prey is not always positively to predator as traditionally believed (e.g. the Lotka-Volterra prey-predator model). In Inner Mongolia grassland of China, the response of the Brandt's vole to the grass vegetation is parabolic because this small herbivore only prefers moderate grass (Zhong et al., 1999). If the grass is too sparse, there is no enough food and shelter; but if the grass is too dense or too high, it is hard for them to communicate among individuals (Zhong et al., 1999). In a two-dimensional Lotka-Volterra type model, Llodze et al. (2000) showed that indirect competition between producer (plant) and grazer (beetle) for phosphorus, which is presumed to affect growth rates of both producer and grazer (Elser et al., 2000), can shift predator-prey from type (+, −) to an usual (−, −) class, indicating that prey is not always positive to predator, but negative when prey is too abundant.

Within species, mutualism among groups or individuals is called as cooperation, which is widely observed in behaviors of social animals and humans (Alocock, 1989). In evolutionary terms, the spread of altruistic without benefit is a paradox. Several models have been proposed to explain the emergence of cooperation at individual level. Lloyd (1995), by using the cellular automata method, modeled the famous Prisoners' dilemma. The proportion of defect prisoner and silent prisoner changes from stable, periodical to chaotic, depending on the gain value of defect prisoners when meeting silent ones. Koella (2000) found if the model parameters such as amount of cooperation, dispersal and group size are allowed to evolve, cooperation can be important for survival. In these models, the strategy of each individual is not fixed, but evolved to maximize the fitness of the individual. The individual can perform good or bad behavior depending on the performance of the partner.

Within species, competition between cooperative individuals or groups is very intense because they need very similar resources, thus, the over-expending the partner will bring threat to the survival its self. But a over-weak partner cannot bring enough benefit. The foraging success of some carnivores often depends on their group size. Moderate group increase the foraging efficiency through information flow among individuals. But if the group size is too large, food would be not enough to feed them all; if too small, the foraging cooperation is not realized for social animals (Rita and Ranta, 1998). Therefore, the trade-off between good behavior and bad behavior is worth to explore. But at present we lack simple models such as differential equations to describe the shift between good and bad behaviors.

The complicated positive (Yang) and negative (Yin) interactions have been elucidated for thousands years in Chinese traditional philosophy, the Moderate Philosophy (Zhong Yong Zhi Dao). This philosophy holds the theory that everything is dual. Its positive or negative nature changes along with the change of its environment, often depending upon the quantity of the thing. Extreme (too many/much or too few/little) performance is not favored, but moderate way is recommended. This philosophy is also feasible in describing the mutualism or cooperation phenomenon appeared in inter- or intra-specific competition system, and in prey-predator system.

The mutualism or cooperation between competitors or between prey and predators pose a great challenge to the traditional models of describing multiple-species interactions (e.g. May, 1973). In these models, the interaction type between species is either positive or neutral, or negative, not evolved according to population change of the partner though the degree of a specific interaction can be changed. The zero growth isoclines of one species to the other species are often monotonously either positive or negative. This is not suitable to describe the mutualism or cooperation among 'enemies'. In this study, by starting from the traditional Lotka-Volterra competition model, a new two-species interaction model considering the mutualism or cooperation between competitors is proposed. In this model, not only the interaction degree, but also the interaction type is allowed to change. We hypothesized that the interaction of one species to the other is not monotonous; but positive at low density, negative at high density. Thus, the zero growth isoclines of the competing species are parabolic. The population size of one species reaches maximum when the population size of its competitor approaches middle, lower when it is smaller or large than the middle value. In this study, the concept 'species' below also applies to intra-specific groups or dominance of individuals within species.

2. The Lotka-Volterra competition model

The Lotka-Volterra competition model is often written as follows:

$$\frac{\mathrm{d}N_1}{\mathrm{d}t} = r_1 N_1 \left(\frac{K_1 - N_1 - \alpha N_2}{K_1} \right) \tag{1}$$

$$\frac{\mathrm{d}N_2}{\mathrm{d}t} = r_2 N_2 \left(\frac{K_2 - N_2 - \beta N_1}{K_2} \right) \tag{2}$$

where, N_1, N_2 are population numbers of species 1 and 2, K_1, K_2 are the carrying capacity of species 1 and 2, r_1, r_2 are the instantaneous increase rate of species 1 and 2, α is the competition coefficient of species 2 to species 1, β is the competition coefficient of species 1 to species 2. $K_1, K_2 > 0$; $\alpha, \beta > 0$; $r_1, r_2 > 0$. The zero growth isoclines of Eqs. (1) and (2) are as follows:

$$N_1 = K_1 - \alpha N_2 \tag{3}$$

$$N_2 = K_2 - \beta N_1 \tag{4}$$

As illustrated in Fig. 1, the two competitive species can coexist only when zero growth isoclines intersect shown in Fig. 1b, i.e. when $K_1/\alpha > K_2$ and $K_2/\beta > K_1$. This coexistence condition also equals to that the two isoclines intersect, and the absolute value of slope ($|\mathrm{d}N_2/\mathrm{d}N_1|$) of isoclines of species 1 is larger than the slope ($|\mathrm{d}N_2/\mathrm{d}N_1|$) of species 2. There are no stable equilibriums for the other situations, and one of the species will be excluded under each of the situations (Fig. 1a, c, and d).

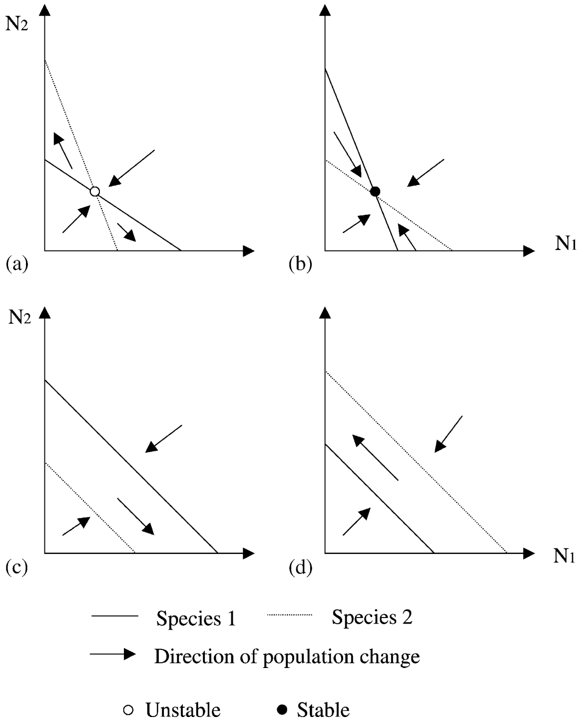

Fig. 1. Phase portrait of zero growth isoclines of the Lotka-Volterra competition model. Coexistence is only possible in case of (b) and impossible in case of (a), (c) and (d).

α, β indicate the degree of inter-specific competition, while K_1, K_2 indicate the tolerance of species to the crowding population. The ecological implication of the competition model is that smaller inter-specific competition facilitates stability of the model; species with smaller carrying capacity (low crowd-tolerability) needs to keep higher competitive ability for survival. The superior species with higher carrying capacity (high crowd-tolerability) and high competitive ability will finally exclude the inferior species with low crowd-tolerability and low competitive ability. At equilibrium, $N_1^* < K_1$, and $N_2^* < K_2$, that is to say, pure competition lowers the carrying capacity of both species.

3. The mutualism model

The mutualism model is often written as follows:

$$\frac{\mathrm{d}N_1}{\mathrm{d}t} = r_1 N_1 \left(\frac{K_1 - N_1 + \alpha N_2}{K_1} \right) \tag{5}$$

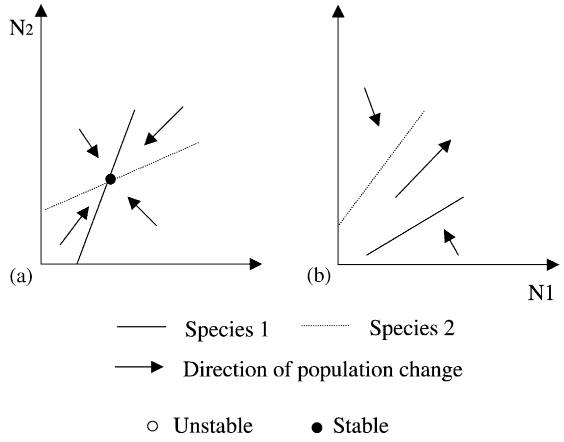

Fig. 2. Phase portrait of zero growth isoclines of the mutualism model. Coexistence is only possible in case (a), impossible in case (b).

$$\frac{dN_2}{dt} = r_2N_2\left(\frac{K_2 - N_2 + \beta N_1}{K_2}\right) \tag{6}$$

where, N_1, N_2 are population numbers of species 1 and 2, K_1, K_2 are the carrying capacity of species 1 and 2, r_1, r_2 are the instantaneous increase rate of species 1 and 2, α is the mutual coefficient of species 2 to species 1, β is the mutual coefficient of species 1 to species 2. K_1, $K_2 > 0$; $\alpha > 0$, $\beta > 0$, r_1, $r_2 > 0$. The zero growth isoclines of Eqs. (5) and (6) are as follows:

$$N_1 = K_1 + \alpha N_2 \tag{7}$$

$$N_2 = K_2 + \beta N_1 \tag{8}$$

There is a stable equilibrium if the two isoclines intersect (Fig. 2a), and $N_1^* > K_1$, and $N_2^* > K_2$. The carrying capacities of both species are increased. In the other situation, no equilibrium point is produced (Fig. 2b). The ecological implication of the mutualism model is that pure mutualism promotes carrying capacities of both species, and has high possibility of forming a stable equilibrium (one of the two possible situations, see Fig. 2) than the pure competition (one of four situations, see Fig. 1).

4. The competition and cooperation model

In the competition and mutualism model, we hypothesize that the zero growth isoclines is not a negative liner function to the population size of the competitor. Instead, it is a parabolic function to the population size of the competitor (Fig. 3). That is to say, mutualism happens at low density, but competition happens at high density. Then, the competition and mutualism model is constructed as follows:

$$\frac{dN_1}{dt} = R_1N_1(c_1 - N_1 - a_1(N_2 - b_1)^2) \tag{9}$$

$$\frac{dN_2}{dt} = R_2N_2(c_2 - N_2 - a_2(N_1 - b_2)^2) \tag{10}$$

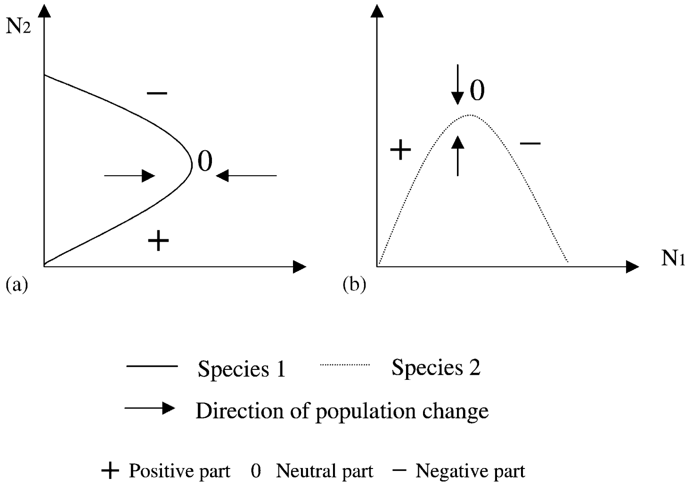

Fig. 3. The parabolic zero growth isoclines of species 1 (a) and species 2 (b). +, 0, − indicate the positive part, neutral part and negative part of the isoclines, respectively.

where, R_1, R_2, a_1, a_2, b_1, b_2, c_1, c_2 are constants, and R_1, $R_2 > 0$, c_1, $c_2 > 0$, a_1, $a_2 > 0$. The zero growth isoclines of Eqs. (9) and (10) are as follows:

$$N_1 = -a_1(N_2 - b_1)^2 + c_1 \tag{11}$$

$$N_2 = -a_2(N_1 - b_2)^2 + c_2 \tag{12}$$

The parameter a_1, a_2 determine the degree of curve of the parabolic isoclines, and b_1, b_2, c_1, c_2 determine the shift of isoclines along axis N_1, N_2.

From Eqs. (11) and (12), it is obvious that if $N_1 = b_2$, then $N_2 = c_2$; and if when $N_2 = b_1$, then $N_1 = c_1$. Therefore, c_1, c_2 is the maximum equilibrium population size of species 1 and 2 when the population size of the opposite species is b_2, b_1, respectively. When $N_1 = 0$, $N_2 = -a_2{b_2}^2 + c_2$, and when $N_2 = 0$, $N_1 = -a_1{b_1}^2 + c_1$. This means that the carrying capacity of species in the competition and mutualism model is highest not when the population size of the opposite species is zero as described in the Lotka-Volterra competition model, instead when it is b_1 or b_2. This is caused by mutualism at low population level of the competitors.

Generally, the parabolic isoclines include three parts: positive part (+), neutral part (0) and negative part (−). The positive part, neutral part or negative part is the part of isoclines when the slope (for species 1, the slope is dN_1/dN_2; for species 2 the slope is dN_2/dN_1) is positive (+), neutral (0) or negative (−) (Fig. 3).

The phase portraits of Eqs. (11) and (12) are quite complex, determined by parameters a_1, a_2, b_1, b_2, c_1, c_2. Many phase portraits of the two isoclines can be produced by adjusting these parameters, with the number of intersects from zero to four. If both $b_1 \leq 0$ and $b_2 \leq 0$, the phase portrait is a particular case, which is very similar to the Lotka-Volterra model. Thus, the competition and mutualism model can be converted into a purely competition model.

It is difficult to present all figures in this paper due to the limited space. However, the intersection types of the two zero growth isoclines, which determine whether it is a stable equilibrium or an unstable one, are not too many. There are three cases for intersection of three parts of the two isoclines. First, isoclines do not intersect, and of course no stable equilibrium is produced. Second, the two isoclines intersect but do not cross through each other (only contact without crossing). It is also impossible to produce any stable equilibrium points. Third, the two isoclines intersect and cross though each other at intersection point. Theoretically, if three parts (+, 0, −) of isoclines of species 1 and 2 intersect, there are nine possible combinations of intersections. The intersection points between two isoclines of species 1 and 2 are represented as '+ +', '− −', '+ −' or '− +', '0 +' or '+ 0', '− 0' or '0 −', '0 0'. Considering the absolute values ($|dN_2/dN_1|$) of slope of two isoclines at intersection points, there one more extra case for both '+ +' and '− −' interactions. Thus, there are total 11 kinds of intersection points of the two isoclines (Fig. 4). $C_k (k = 1, 2, 3, \ldots 11)$ is the code number of the intersection type. The stabilities of the 11 intersections are also presented in the

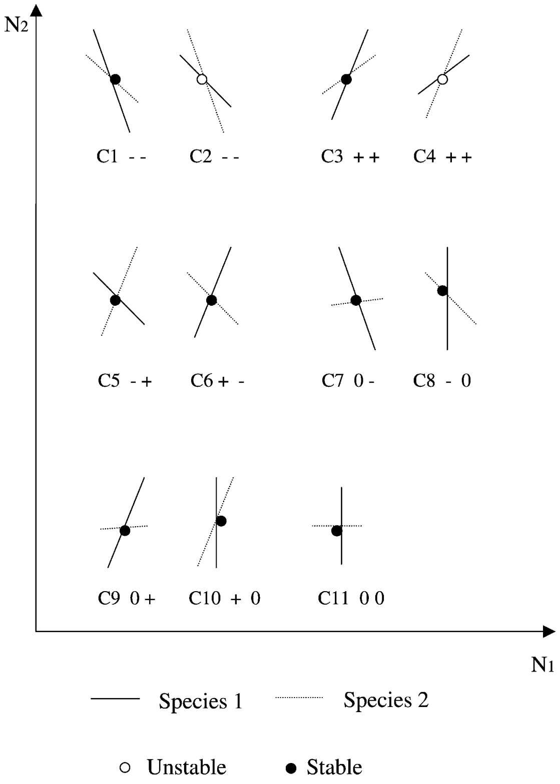

Fig. 4. Eleven possible intersections of two parabolic zero growth isoclines of two competing species, and there stabilities. $C_k (k = 1, 2, 3, \ldots 11)$ indicates the code of intersection type. '+ +', '− −', '+ −/− +', '0 +/+ 0' and '0 0' indicate the intersections of positive part '+', or negative part '−' or neutral part '0' of the two isoclines. Only intersections C_2 and C_4 are unstable equilibrium points.

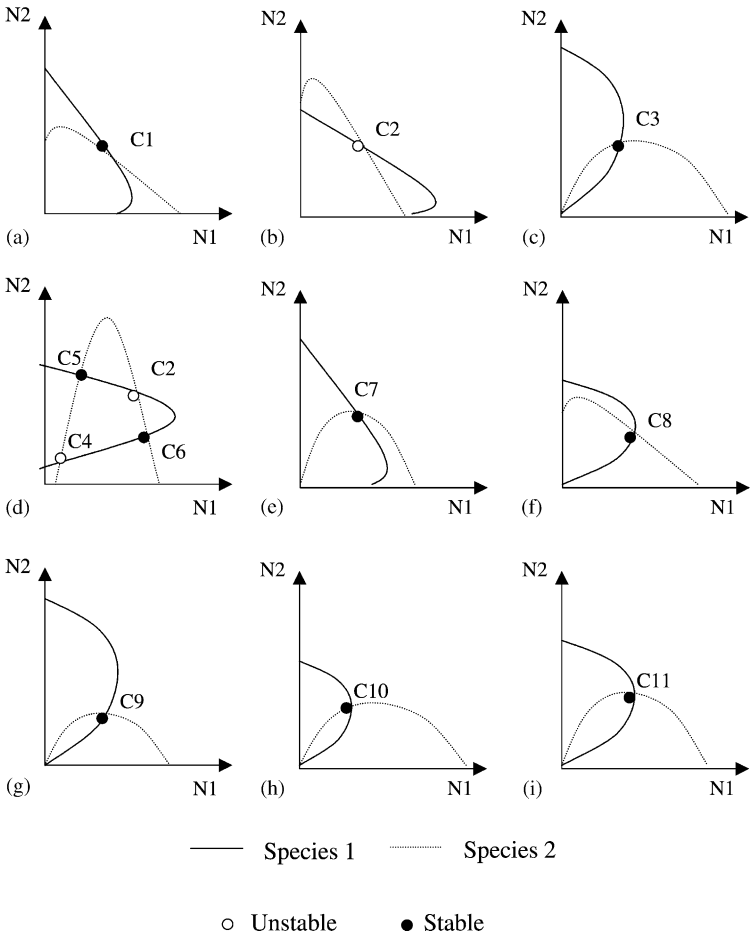

Fig. 5. (a–i) Examples of intersections of two parabolic zero growth isoclines in the competition and mutualism model, showing the 11 kinds of intersections of two isoclines. $C_k (k = 1, 2, 3, \dots 11)$ indicates the code of intersection type in Fig. 4. Stable equilibriums are produced in most situations.

figure. Examples of these 11 intersection types in the competition and mutualism model by simulation are illustrated in Fig. 5a–i. The stabilities of all intersections are determined by using phase analysis, and by simulation.

As shown in Figs. 4 and 5, most intersections result in stable equilibrium points at crossings of two parabolic isoclines (9 stable equilibrium points of 11 situations). There are only two cases (C_2, C_4) (Fig. 5d and i), which result in unstable equilibrium. The cases C_4 cannot produce independently without producing other stable intersects (Fig. 5d). In fact, unstable coexistence is produced only when two negative parts of the isoclines intersect (− −), and the absolute value of slope ($|dN_2/dN_1|$) of isoclines of species 2 at intersection point is larger than that ($|dN_2/dN_1|$) of species 1 Figs. 4 and 5b, d). Thus, 10 of the 11 situations can produce stable equilibrium points, much higher than the pure competition model (1/4), and the mutualism model (1/2). Therefore, mutualism obviously promotes species coexistence in the competition model, and at the same time, competition can also promotes species coexistence in the mutualism model (see Section 5). The case C_1 and C_2 are produced similarly to the Lotka-Volterra competition model (cf. Fig. 1a and b with Figs. 4 and 5a, b, d); while the C_3 is produced similarly in the mutualism model (cf. Fig. 2a with Figs. 4 and 5c).

In the competition and mutualism model, if interactions are moderate, and sympatric along $N_2 = N_1$, both species can reach the maximum carry capacity (e.g. Fig. 5i), much higher than the carrying capacity (K_1, K_2) without the presence of the other competitor. Therefore, mutualism can also promote the competitive ability through increasing the carrying capacity of species. If interactions are approaching sympatric and intense, four intersects are produced, with two stable equilibriums (e.g. Fig. 5d).

Interestingly, the six kinds of interactions between, two species in community or ecosystem level are all observed in the competition and mutualism model (Fig. 4). The symbol ‘+ +’ represents mutualism, ‘− −’ represents competition, ‘+ −’ or ‘− +’ represents predation or parasitism, ‘+ 0’ or ‘0 +’ represents commensalism, ‘− 0’ or ‘0 −’ represents amensalism and ‘0 0’ represents neutralism. Except for one intersection point of ‘+ +’ and one intersection point of ‘− −’, all stable equilibriums are achieved in the competition and mutualism model.

5. Discussions

We draw three conclusions from this modeling study. First, mutualism or cooperation is an alternative way of promoting coexistences of two competitors. Second, mutualism increases the carrying capacity of both competitors, and then promotes their competitive ability. Third, the mutualism-competition model is also appropriate to describe the dynamics of cooperation and competition between individuals or groups within species, and mutualism between plants and animals.

From this modeling study, we demonstrated that mutualism or cooperation could result in coexistence among competitors. This is a very different mechanism for species coexistence from that proposed by previous studies mentioned before. The mechanism of mutualism or cooperation in stabilizing the competition system may be that it adjusts the competition ability and crowd-tolerance differently. Normally, for the three unstable equilibrium cases in the competition model in Fig. 1a, c, and d, stable equilibriums are realized in Fig. 1b through spinning the isoclines of species 1 or 2, the purpose of spinning of isoclines is to make more competitive species less crowd-tolerable.

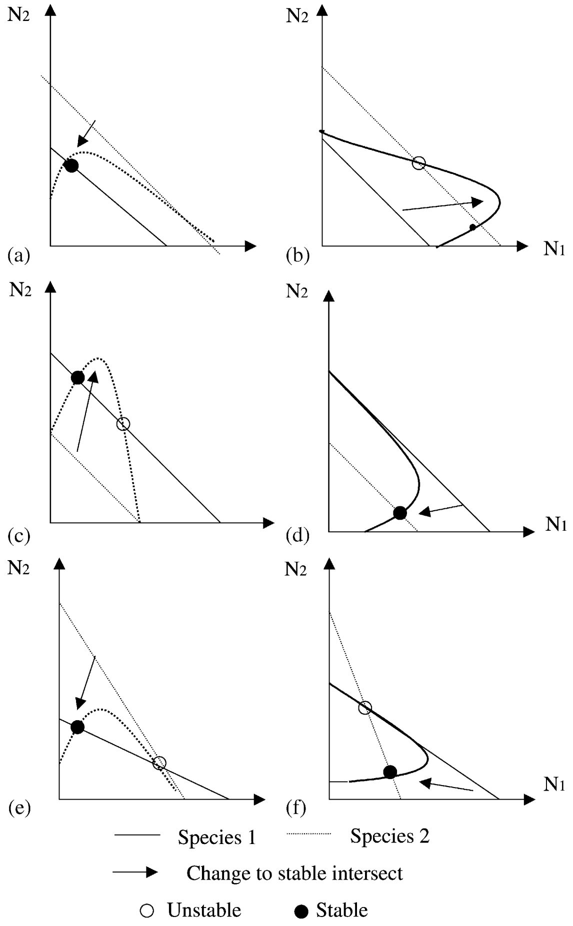

Fig. 6. Illustration how positive interactions promote stability of competition system. Stable equilibrium points (a–f) are realized through bending the liner isoclines in Fig. 1a, c, and d.

Now the balance is completed differently in the competition and mutualism model, through bending the isoclines (Fig. 6), instead of spinning the isoclines. For the unstable equilibrium case in Fig. 1d, stable equilibrium can also be produced by bending down the left side of isoclines 2 in the competition and mutualism model (Fig. 6a) or by bending up the right side of isoclines 1 (Fig. 6b). Similarly, for case of Fig. 1c, stable equilibrium can be produced by bending up the up side of isoclines 2 (Fig. 6c) or bending down the low side of isoclines 1 (Fig. 6d). For the case of Fig. 1a, stable equilibrium can also be produced by bending down the upside of isoclines 2 (Fig 6e) or by bending down the low side of isoclines 1 (Fig. 6f). This

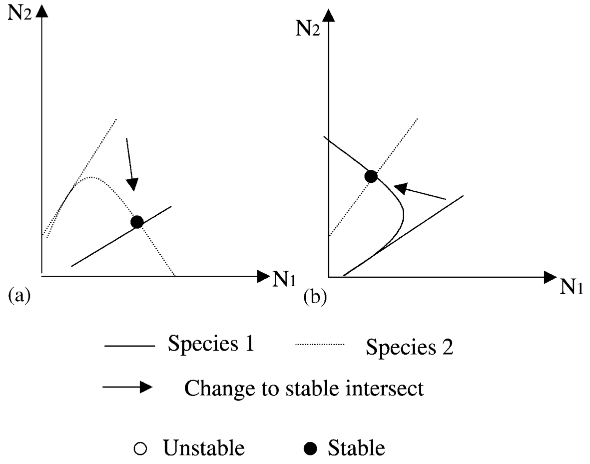

Fig. 7. Illustration how negative interactions promote stability of mutualism system. Stable equilibrium points (a and b) are realized through bending the liner isoclines in Fig. 2b.

indicates that positive interaction promotes stability of competition model. For unstable equilibrium case in mutualism model (Fig. 2b), stable equilibrium can be produced by making the isoclines of the two species as shown in Fig. 7a and b. This indicates that competition can also promote stability of mutualism model. Such role of competition has long been neglected.

The ecological implication drawn from the Lotka-Volterra is that crowd-tolerability and the competitive ability must be balanced. Otherwise, equilibrium is impossible to obtain. Species, if less competitive and less crowd-tolerable, will be excluded. In our competition and mutualism model, the significance of crowd-tolerability and ability of competition are somehow reduced due to the effect of cooperation. The fate of a competitive species is determined by the crowd-tolerability, competitive ability and cooperative ability. Less competitive and less crowd-tolerable species, though impossible to coexist in the Lotka-Volterra model, if more cooperative to the superior competitor, is able to coexist with its competitor in the new model. Thus, cooperative inferior is also possible to survive in a competitive and mutualism system. This result implies that, mutualism is good for stabilizing a competitive system, and then may be an important mechanism for species coexistence in community or ecosystem level.

If the two species are ecologically same in the Lotka-Volterra model, i.e. $K_1 = K_2$, and $\alpha = \beta$, the two isoclines overlap. This is also an unstable case for the Lotka-Volterra model (May, 1976; Hubbell, 1979; Hubbell and Forster, 1986; Zhang and Lin, 1997). In the competition and mutualism model, if the two species are ecologically same, i.e. $R_1 = R_2 = R$, $a_1 = a_2 = a$, $b_1 = b_2 = b$, $c_1 = c_2 = c$, then the isoclines of the two species are as follows:

$$N_1 = -a(N_2 - b)^2 + c \qquad (13)$$

$$N_2 = -a(N_1 - b)^2 + c \qquad (14)$$

It is obvious that the two isoclines never overlap. They are symmetrical along $N_2 = N_1$.

Gause (1934) claimed that two ecologically same or identical species (using same or similar resources) are impossible to coexist based on the result of the Lotka-Volterra model. This is also known as the Gause's competition and exclusion rule (Hardin, 1960). According to Gause's rule, the coexistence of species must be the result of niche differentiation among species, spatially or temporally; otherwise, they do not coexist (Begon et al., 1990). Prior modeling or field studies have shown that coexistence can be promoted by reducing the competitive ability between species through various ways, including colonization (e.g. Hastings, 1980; Hanski and Ranta, 1983; Nee and May, 1992; Hanski and Zhang, 1993; Tilman, 1994), disturbance (e.g. Connell, 1978; Huston, 1979, Tilman, 1982b), aggregations in patchy habitats (Atkinson and Shorrocks, 1981; Hanski, 1981), resource transport and supply rates (Hustor and De Angelis, 1994), predation (e.g. Paine, 1966; Harper, 1969; Crawley, 1983; Hamback, 1998; Droseel et al., 2001), sex ratio mediation (Zhang and Jiang, 1993, 1995; Zhang and Hanski, 1998).

Several studies doubted the Gause's rule (e.g. Cole, 1960; Hubbell, 1979; Hubbell and Forster, 1986; Fragerstrom, 1988; Keddy, 1989). They argued that the extinction process is very slow through competition for guilds, the rate of speciation is higher than the extinction rate; the numbers of species produced is larger than the extinct ones by competition. Therefore, two identical species can coexist. Chesson (1991) has given critiques to such kind of views. Zhang and Lin (1997) proved that the time of coexistence for asymmetric competition drop rapidly even when the difference of the competitive ability between species is very minor. Zhang and Jiang (1993, 1995), Zhang and Hanski (1998) found the sex ratio mediation is possible to promote species coexistence theoretically, and then speculated that two identical species can coexist, and one single ecological niche can support more than one species. This is inconsistent with the Gause' competition and exclusion hypothesis. At present, there is no field observation to support the mechanism of the sex ration mediated coexistence.

The Lotka-Volterra competition model is hard to explain the coexistence of species exploiting very similar resources, and also hard to explain why individuals or groups within species can coexist together. The ecological niche of individuals or groups within species must be very similar, and competition among them must be so furious that it is impossible for them to coexist in the Lotka-Volterra model. In our model, this kind of coexistence is possible through cooperation or mutualism.

Furthermore, our model also demonstrated that cooperation or mutualism can promote the competitive ability of competitors through increasing their carrying capacities. This is impossible in Lotka-Volterra model as well as in the other similar competitive models. The reason lies in that the zero growth isoclines in the competitive and mutualism model are often protuberant, while the isoclines in the Lotka-Volterra competition model is linear, and in many other non-linear models, the isoclines are often cupped. When two linear or cupped curves intersect, they often produce a stable equilibrium at which the population sizes are much smaller than the carrying capacity (K_1 or K_2) without the presence of the competitor. In our model, stable equilibrium with population size much larger than the original carrying capacity of both competitors can be achieved.

The emergence and evolution of cooperation among competing individuals has been addressed by many previous studies, but mostly by using massive simulation models, e.g. the cellular automata model by Lloyd (1995) and the artificial life model system with digital organisms by Langton (1989) and Holland (1975). All these models showed that cooperation among competitors is favored by selection. At present, there no differential models dealing with both mutualism or cooperation and competition except for the simulation models. The advantage of our model is that it is simple and easy to understand why cooperation can help survival and coexistence.

The unique feature of our model is that the interaction type among species or interaction type among individuals or groups within species is no longer constant or density-independent as the Lotka-Volterra model or other modified models, e.g. the multiple species model by May (1973). Instead, in the new model, the interaction type among species or individuals is density-dependent; too more or too less competitors (or prey or predator) is not good for the other competitor (or predator or prey). This model would be extended to a new general community model of multiple species. In contrast with the prediction by May (1972) that model ecosystem with more species are more unstable, our model would predict that with mutualism or cooperation, more complex and more efficient ecosystem is possible to achieve. This is because mutualism could reduce the intensity of intra-specific competition. The mutualism in prey-predator system may work similarly as in the competition system. Intense predation does not good to coexistence of prey and predator. Mutualism between prey and predator will certainly reduce the intensity of predation, and then promotes stability of prey-predator system.

The benefit of mutualism or cooperation is obvious in real world though it has not been described quantitatively before. It is widely accepted that cooperation among people or groups in human society can increase working efficient. Cooperation among lions also increases hunting efficiency. Group alerting among some animals could increase the survival of the whole community. Thus, mutualism or cooperation should be favored by natural selection. Mutualism or cooperation among inferior competitors helps to narrow the difference of competitive ability with the superiors, and then contributes to coexistence. Competitor benefited from cooperation would be more competitive, and have more chance of winning battle over its rivals. So mutualism or cooperation must be a very important driving force in shaping society and community structures.

Acknowledgements

This work is co-supported by Chinese Academy of Sciences Innovation Program KSCX2-1-03, KSCX2-SW-103 and National Basic Research Program (G2000046802), NSFC 39893360.

References

Alocock, J., 1989. Animal Behavior, 4th ed. Sinauer Associates INC, Sunderland, Massachusetts, p. 596.

Atkinson, W.D., Shorrocks, B., 1981. Competition on a divided and ephemeral resources: a simulation model. J. Anim. Ecol. 50, 461–471.

Bergelson, J.M., Crawley, M.J., 1988. Mycorrhizal infection and plant species diversity. Nature 334, 202–203.

Begon, M., Harper, J.L., Townsend, C.R., 1990. Ecology, 2nd ed. Blackwell Scientific Publications, Oxford.

Bertness, M.D., Leonard, G.H., 1997. The role of positive interactions in communities: lessons from intertidal habitats. Ecology 78, 1976–1989.

Chesson, P.L., 1991. A need for niches? Trends in Ecology and Evolution 6, 26–28.

Cole, L.C., 1960. Competitive exclusion. Science 132, 348–349.

Connell, J.H., 1978. Diversity in tropical forests and coral reefs. Science 199, 1302–1310.

Crawley, M.J., 1983. Herbivory: The Dynamics of Animal–Plant Interactions. Blackwell Scientific, Oxford.

Diaz, S., Cabido, M., 2001. Vive difference: plant functional diversity matters to ecosystem processes. Trends in Ecology and Evolution 16, 646–655.

Droseel, B., Higgs, P.G., McKane, A.J., 2001. The influence of predator-prey population dynamics on the long-term evolution of food web structure. J. Theor. Biol. 208, 91–107.

Elser, J.J., Fagan, F.F., Denno, R.F., Dobberfuhl, D.R., Folarin, A., Huberty, A., Interlandi, S., Kilham, S.S., McCauley, E., Schulz, K.L., Siemann, E.V., Sterner, R.W., 2000. Nutritional constrains in terrestrial and freshwater food webs. Nature 408, 578–580.

Gause, G.F., 1934. The Struggle for Existence. Williams and Wilkins, Baltimore.

Grime, J.P., 1988. The C-S-R model of primary plant strategies—origins, implications and tests. Plant Evolutionary Biology. In: Gottieb, L.D., Jain, S.K. (Eds.), Chapman and Hall, London, pp. 371–393.

Fragerstrom, T., 1988. Lotteries in communities of sessile organism. Trends in Ecology and Evolution 3, 303–306.

Fridley, J.D., 2001. The influence of species diversity on ecosystem productivity: how, where, and why? Oikos 93, 514–526.

Hamback, P.A., 1998. Seasonality, optimal foraging and prey coexistence. Am. Naturalist 152 (6), 881–895.

Hardin, G., 1960. The competitive exclusion principle. Science 131, 1292–1297.

Hanski, I., 1981. Coexistence of competitions in patchy environments with and without perdition. Oikos 37, 306–312.

Hanski, I., Ranta, E., 1983. Coexistence in a patchy environment: three species of Daphnia in rock pools. J. Anim. Ecol. 52, 263–279.

Hanski, I., Zhang, D.Y., 1993. Migration, metapopulation dynamics and fugitive coexistence. J. Theor. Biol. 163, 491–504.

Harper, J.L., 1969. The role of predation in vegetation diversity. Brookhavea Symp. Biol. 22, 48–62.

Hastings, A., 1980. Disturbance, coexistence, history and competition for space. Theoretical Population Biology 18, 363–373.

Hector, A., 1998. The effect of diversity on productivity: detecting the role of species complementary. Oikos 82, 597–599.

Herrera, J., 1995. Acorn predation and seedling production in a low-density population of cork oak (*Quercus suber* L.). Forest Ecol. Manage. 76, 197–201.

Holland, J.H., 1975. Adaptation in Natural and Artificial System. University of Michigan Press, Ann Arbor.

Hubbell, S.P., 1979. Tree dispersion, abundance and diversity in a tropical dry forest. Science 203, 1299–1309.

Hubbell, S.P., Forster, R.B., 1986. Biology, chance and history and the structure of tropical rain forest tree communities. In: Diamond, J., Case, T.J. (Eds.), Community Ecology. Harper and Row, New York, pp. 314–329.

Huston, M., 1979. A general hypothesis of species diversity. Am. Naturalist 113, 81–101.

Hustor, M.A., De Angelis, D.L., 1994. Competition and coexistence: the effect of resource transportation and supply rates. Am. Naturalist 144 (6), 954–977.

Jensen, T.S., Nielsen, O.F., 1986. Rodents as seed dispersers in a heath-oak wood succession. Oecologia 70, 214–221.

Kaiser, J., 2000. Rift over biodiversity divides ecologists. Sciences 289, 1282–1283.

Keddy, P., 1989. Competition. Chapman & Hall, London.

Koella, J.C., 2000. The spatial spread of altruism versus the evolutionary response of egoists. The R. Soc. London B 267, 1979–1985.

Krebs, C.J., 1994. Ecology—The Experimental Analysis of Distribution and Abundance, 4th ed. Harper Collins College Publishers, New York, p. 801.

Langton, C.G., 1989. Artificial Life, vol. 6. Santa Fe Institute Studies in the Science of Complexity, Addison-Wesley, Redwood City, CA.

Leibdd, M.A., 1997. Do nutrient-competition models predict nutrient availability in limnetic ecosystems? Oecologia 110, 132–142.

Lenas, P., Thomopoulos, N.A., Vayenas, D.V., Pavloa, S., 1998. Oscillations of two competing microbial populations in configurations of two interconnected chemostats. Math. Biosci. 148, 43–63.

Llodze, I., Kuang, Y., Elser, J., 2000. Stoichiometry in producer-grazer systems: linking energy flow with element cycling. Bull. Math. Biol. 62, 1137–1162.

Lloyd, A.L., 1995. Computing Bouts of the Prisoner’s Dilemma. Scientific American, pp. 111–115.

Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J.P., Hector, A., Hooper, D.U., Huston, M.A., Raffaelli, D., Schmid, B., Tilman, D., Wardle, D.A., 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. Sciences 294, 804–808.

Lotka, A.J., 1925. Elements of Physiological Biology. Dover Publications, New York, 1956.

May, R.M., 1972. Will a larger complex system be stable? Nature 238, 413–417.

May, R.M., 1973. Stability and Complexity in Model Ecosystem. Princeton University Press, Princeton, NJ.

May, R.M., 1976. Estimating r: a pedagogical note. Am. Naturalist 110, 496–499.

McNaughton, S.J., 1976. Serengeti migratory wildebeest: facilitation of energy flow by grazing. Science 191, 92–94.

Miyaki, M., Kikuzawa, K., 1988. Dispersal of *Quercus mongolica* acorns in a broad-leaved deciduous forest. 2. Scatterhoarding by mice. Forest Ecol. Manage. 25, 9–16.

Nee, S., May, R.M., 1992. Dynamics of metapopulations: habitat destruction and competitive coexistence. J. Anim. Ecol. 61, 37–40.

Paine, R.T., 1966. Food web complexity and species diversity. Am. Naturalist 100, 65–75.

Renshaw, E., 1991. Modeling Biological Populations in Space and Time. Cambridge University Press, Cambridge. pp. 137–139.

Rita, H., Ranta, E., 1998. Competition in a group of equal forages. Am. Naturalist 152 (1), 71–81.

Sork, V.L., 1984. Examination of seed dispersal and survival in red oak *Quercus rubra* (Fagaceae), using metal-tagged acorns. Ecology 65 (3), 1020–1023.

Tilman, D., 1982a. Resource Competition and Community Structure. Princeton University Press, Princeton, NJ.

Tilman, D., 1982b. Resources, competition and the dynamics of plant communities. In: Crawley, M.J. (Ed.), Plant Ecology, Blackwell, Oxford, UK, pp. 51–75.

Tilman, D., 1994. Competition and biodiversity in spatially structured habitats. Ecology 75, 2–16.

Tilman, D., Reich, P., Knops, J., Wedin, D., Mielke, T., Lehman, C., 2001. Diversity and productivity in a long-term grassland experiment. Science 294, 843–845.

Vayenas, D.V., Pavlon, S., 1999. Coexistence of three microbial populations competing for three complementary nutrients in a chemostat. Math. Biosci. 161, 1–13.

Volterra, V., 1926. Fluctuation in the abundance of a species considered mathematically. Nature 118, 558–560.

Zhang, D.Y., Lin, K., 1997. The effects of competitive asymmetry on the rate of competitive displacement: how robust is Hubbell's community drift model? J. Theor. Biol. 188, 361–367.

Zhang, D.Y., Hanski, I., 1998. Sexual reproduction and stable and stable coexistence of identical competitors. J. Theor. Biol. 193, 465–473.

Zhang, D.Y., Jiang, X.H., 1993. Differential selection in sexes, genetic drift and stable coexistence of identical species. Oikos 68, 177–182.

Zhang, D.Y., Jiang, X.H., 1995. Local mate competition promotes coexistence of similar competitors. J. Theor. Biol. 177, 167–170.

Zhong, W., Wang, M., Wan, X., 1999. Ecological management of Brandt's vole (*Microtus brandti*) in Inner Mongolia, China. In: Singleton, G., Hinds, L., Leirs, H., Zhang, Z. (Eds.), Ecologically-based Management of Rodent Pests. Australian Centre for International Agricultural Research, Canberra, pp. 199–214.