Population Dynamics of Some Mutualistic Relationships

J. Yoshimura[a,b,c], H. Amagai[a], T. Suzuki[a], T. Togashi[b] and T. Miyazaki[b]

[a]Department of Systems Engineering, Shizuoka University, Hamamatsu 432-8561, Japan.

[b]Marine Biosystems Research Center, Chiba University, 1 Uchiura, Amatsu-Kominato, 229-5502, Japan.

[c]Department of Environmental and Forest Biology, State University of New York College of Environmental Science and Forestry, Syracuse, New York 13210, USA.

Abstract: Symbiosis or mutualism is one of major ecological interactions between two species, where the both species gain benefits *via* the interactions. We consider the population dynamics of mutualistic interactions with positive density and frequency dependences. We specifically suppose the dynamics of Müllerian mimicry in butterflies for positive density dependence, where the mortality of both species is reduced depending on the relative frequency of the other species. Positive frequency dependence is studied in contrast with positive density dependence, and supposing the general relationships of symbiosis. We assume that the two species are under the Lotka-Volterra density-dependent competition. The equilibria are compared with the cases of competition alone. Unlike the traditional model of positive density dependence, population explosion does not appear in the current dynamics, but the new equilibrium is simply achieved. It is because the effects of positive density or frequency dependence are restricted to parts of mortality. Symbiotic relationships never invoke infinite population growth, because of limited effects on population growth. However, the two models show a distinctive difference for the coexistence. Positive density dependence does not promote coexistence of species. Only when the coexistence is achieved under competition, the equilibrium densities are increased. In contrast, positive frequency dependence always promotes coexistence. This change is also qualitative. Whether Müllerian mimicry is a special case of mutualism, or mutualism does not promote coexistence under competition is an open question.

Keywords: Müllerian mimicry; Positive density dependence; Positive frequency dependence; Symbiosis

1. INTRODUCTION

Mutualism or symbiosis is often considered as one of the major categories of ecological interactions of populations or species. Recently, mutualism is also suggested as an important factor of community stability in general (Golick, Atkins and Losey, 1978, May 1982). However, the population dynamics of mutualistic relations are rarely described, except the case of positive density dependence (May 1982, Bertness and Hacker, 1994, 1997, Stiling, 1999). The population equation with positive density dependence is in contrast with the negative density dependence of the Lotka-Volterra type competition (May, 1976, Ginzberg, 1983, Boucher, 1985, Tainaka et al., 2003). However, the positive density dependence is problematic, since the strong mutualism leads to the infinite population growth or population explosion (May, 1982, Tainaka et al., 2003).

Here we consider the population dynamics of mutualistic interactions. One such example is the dynamics of Müllerian mimicry in butterflies, in which the benefits of mimicry are mutual between the two toxic butterfly species. Müllerian mimicry is one of famous example of symbiotic

relationships (Wicker, 1968). Its evolutionary mechanisms have been studied extensively (Futuyma and Slatkin, 1983). However, the population processes of such mutualistic relationships are not well known.

Recently frequency dependence is discussed as a new type of population interactions in the dynamics of competition (Kuno, 1992, Yoshimura and Clark, 1994) and predation (Hori, 1993, Takahashi and Hori, 1994). The known dynamics of frequency dependence are strikingly different from the traditional population dynamics, in which density dependence is the regulatory factor. Positive frequency dependence is applicable to Batesian mimicry, because the frequency of model is a critical factor of the predatory escape of the mimic. In contrast, Müllerian mimicry is the case, where the positive density dependence is expected.

This paper describes the basic population dynamics of positive density and frequency dependences. We assume that the mortality of both species is reduced depending on the density or relative frequency of the other species. We also assume that the two species are under density-dependent competition. These processes may describe some features of

Müllerian mimicry and other mutualistic relationships.

We analyze the equilibria using phase planes. The equilibria are then compared with the cases of the Lotka-Volterra type competition alone. Positive density dependence does not promote the coexistence, but stabilize the coexistence by enlarging the equilibrium densities. In contrast, frequency dependence always promotes coexistence. In either case, the dynamics leads to a new equilibrium without any population explosion. We discuss the population dynamics of various forms of mutualistic interactions. We also discuss the importance of such mutualistic interactions for the coexistence and stability of species in natural communities and ecosystems.

2. MODEL OF POSITIVE DENSITY AND FREQUENCY DEPENDENCES

2.1. Reduction in mortality

In Müllerian mimicry both a mimic and its model are poisonous or unpalatable. Müllerian mimicry in poisonous butterflies is known to reduce mortality of both the mimic and model (Wickler, 1968). Experienced birds learn the wing patterns of poisonous or unpalatable butterflies and avoid catching them. However naïve (inexperienced) birds with almost no learning experience tends to prey on these poisonous butterflies. Therefore, butterflies are eaten by naïve birds until the birds learn their wing patterns.

If there are two poisonous butterflies similar in wing patterns, their predation rates are reduced by enhancing the learning experience of naïve birds. If birds cannot recognize the difference in their wing patterns, birds predate and learn them as a single species. Therefore, the mortality of each butterfly is reduced depending on the total density of both species. Suppose two sympatric species S_i (i =1,2). The reduction rate in predatory mortality, d_i, should depend on the total density:

$$d_i = d_i (N_1 + N_2) = 1/(N_1 + N_2), \ i=1,2. \qquad (1)$$

where N_i is the population size of species i. Here we assume $N_1 + N_2 \geq 1$, so that $d_i \leq 1$. Note that $d_i = 1$ indicates no reduction in mortality, whereas $d_i = 0$ is the 100% reduction in mortality.

In contrast, symbiosis may be more like frequency dependence. The existence of symbionts may enhance the population growth of a species by increasing the survival of the individuals. We would expect the mutualistic benefits in such symbosis, e.g., that between lycaenid butterfly and ants, that between hermit crabs and sea anemones, and lichen (symbiosis between fungi and algae). In symbiosis, the existence of the other species reduces the cost/mortality of the symbionts. Then the relative frequency f_i of a species is an appropriate measure of mortality reduction, such that:

$$f_i = f_i (N_1, N_2) = N_i /(N_1 + N_2), \ i=1,2. \qquad (2)$$

Here f_i indicates that the existence and population size of the mutualistic partner enhances the reduction of mortality. With no partner, $f_i = 1$ (no reduction) and with infinite partners, $f_i = 0$ (the 100 % reduction in mortality).

We should note that the density-dependent reduction in mortality might be applicable to Müllerian mimicry. However, the frequency-dependent reduction cannot be applicable, because both mimics and models gain benefits of other individuals irrespective of species. Thus, the frequency-dependent equation (Eq. 2) should not be applicable to the mutualism appeared in Müllerian mimicry.

The partial mortality of each species may be reduced depending on the total density or the relative frequency of the other species. It is natural that such reduction is limited to a certain kind of mortality, e.g., bird predation in Müllerian mimicry. These functions may be complex, but for simplicity we assume that the reduction rate of a species $h_i = d_i$ or f_i (Equations 1 and 2).

2.2. Population dynamics equation

To evaluate mortality separately from birth rates, the population growth rate r_i is separated into birth and mortality rate. Let $b_i = b_i(N_i, N_j, \alpha_{ij})$ and $\hat{m}_i = \hat{m}_i(N_i, N_j, \alpha_{ij})$ denote the birth rate and mortality rate, respectively (Fig. 1). Note that the term $\hat{m}_i$ includes the reduction of mortality incurred by mutualistic interactions. The population dynamic equations are then expressed as

$$\frac{dN_i}{dt} = (b_i - \hat{m}_i)N_i. \qquad (3)$$

The terms b_i and $\hat{m}_i$ are defined as

$$b_i = b_{ik} + (b_{i0} - b_{ik})\left(1 - \frac{N_i + \alpha_{ij}N_j}{K_i}\right) \qquad (4)$$

$$\hat{m}_i = (1-p_{i1})m_{i0} + (1-p_{i2})(m_{ik}-m_{i0})\left(\frac{N_i+\alpha_{ij}N_j}{K_i}\right)$$

$$+ h_i\left\{p_{i1}m_{i0} + p_{i2}(m_{ik}-m_{i0})\left(\frac{N_i+\alpha_{ij}N_j}{K_i}\right)\right\} \quad (5)$$

where p_{i1} and p_{i2} are the density-independent and density-dependent fractions of reduced mortality, respectively. The other parameters are as follows. The terms b_{i0} and m_{i0} denote the intrinsic birth and death rates, respectively and $b_{ik} = m_{ik}$ denote the birth and death rates at the carrying capacity $N_i = K_i$. α_{ij}, is the Lotka-Volterra competition coefficient of species j on i. Note that $b_{i0} \geq b_{ik} = m_{ik} \geq m_{i0}$ (Fig. 1). If $h_i = 1$ and/or $p_{i1} = p_{i2} = 0$, Equation 2 collapses to the Lotka-Volterra competition equation with $r_i = b_i - m_i$, where $m_i = \hat{m}_i$ when $p_{i1} = p_{i2} = 0$.
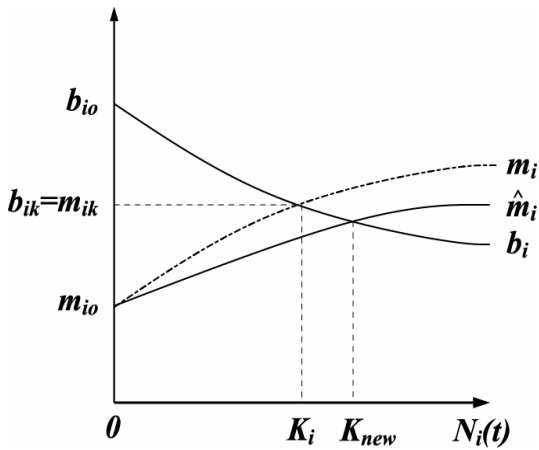

Figure 1. The schematic relationships among the birth rate b_i and mortality rate $\hat{m}_i$. Both b_i and $\hat{m}_i$ are the functions of the current population size $N_i(t)$ (Equations 4 and 5). The actual mortality $\hat{m}_i$ (dotted line) is lower than the mortality without mutualism m_i. Density dependent balance between mortality and birth rates at $N_i = K_i$ moves to the intersection between the solid mortality line $\hat{m}_i$ and the solid birth line b_i ($N_i = K_{new}$).

## 3. RESULTS

Setting $dN_i / dt = 0$, we obtain the zero-growth isoclines for S_i, viz. $b_i - \hat{m}_i = 0$ (Fig. 2). The isocline of positive density dependence is the straight line parallel to that of the Lotka-Volterra competition model (Fig. 2 A), because it is simply enlarged by the total density $N_1 + N_2$. Therefore, $z_d = K_d / \alpha_{12}$. In contrast, the isocline of frequency dependence is a concave curve originated from $N_1 = K_1$ (Fig. 2 B).

Some phase plains for positive density dependence are shown in Fig. 3. The relationships between species are identical to those of the Lotka-Volterra competition model, while the four intercepts are proportionally enlarged. Thus the equilibria is qualitatively identical to those of the competition model. For the case of coexistence, the equilibrium densities of both species are increased proportionally (Fig. 3 A). Therefore, coexistence is said to be quantitatively promoted. However, in the other three cases, the relationship is also enlarged. Therefore, exclusion is said to be actually strengthened (one case is shown in Fig. 3 B).
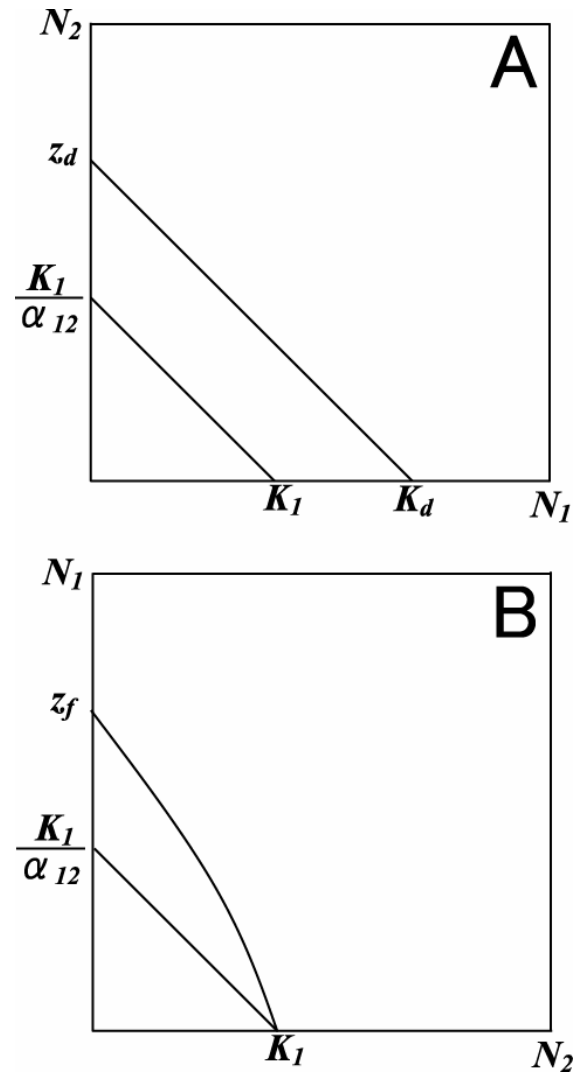
Figure 2. Isoclines for the population dynamics of positive density and frequency dependences. The isoclines of Lotka-Volterra competition model are also shown for comparison. (A) positive density dependence: the N_1- and N_2-intercepts are K_d and z_d, respectively. (B) positive frequency dependence: the N_1- and N_2-intercepts are K_1 and z_f, respectively. Both z_d and z_f are larger than K_1/α_{12}, the N_2-intercept of the competition model.
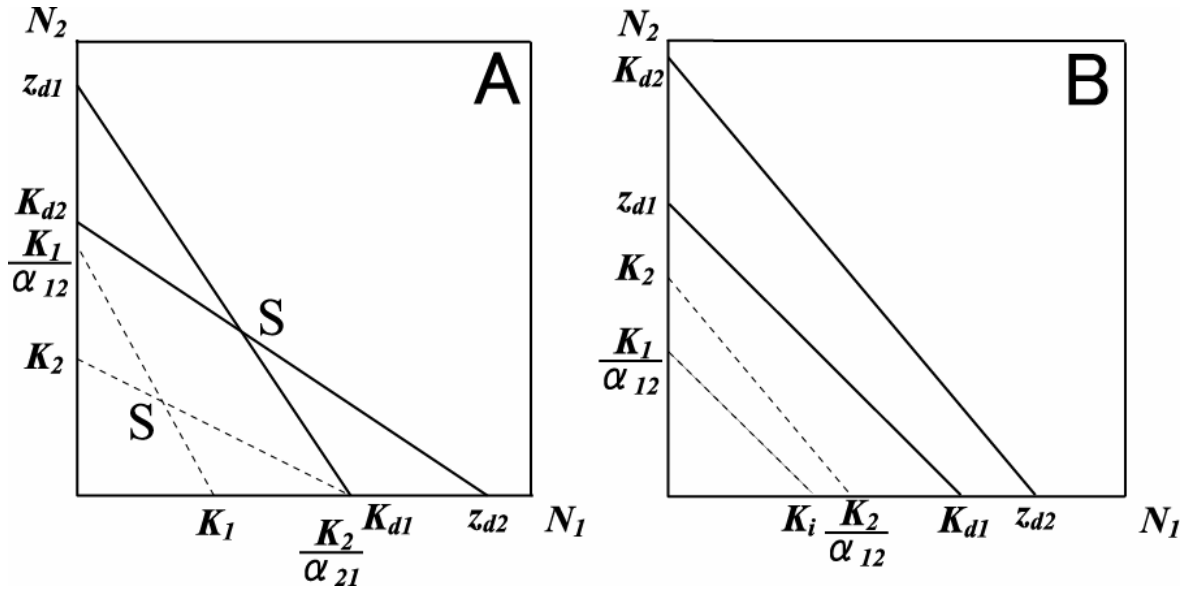
Figure 3. Phase planes for positive density-dependence with the Lotka-Volterra competition (Equations 1,3-5). The zero-growth isoclines are a straight line parallel to that of competition only, anchored at $(K_{d1}, 0)$ and $(0, z_{d1})$ for $i = 1$, or at $(0, K_{d2})$ and $(z_{d2}, 0)$ for $i = 2$. (A) Coexistence is possible under competition only (**S**: stable equilibrium). (B) Coexistence is impossible under competition only. The isoclines are not only parallel to, but also proportional to the original competition-only isoclines, that is $z_{di} = K_{di} / \alpha_{ij}$ ($i,j=1, 2$).
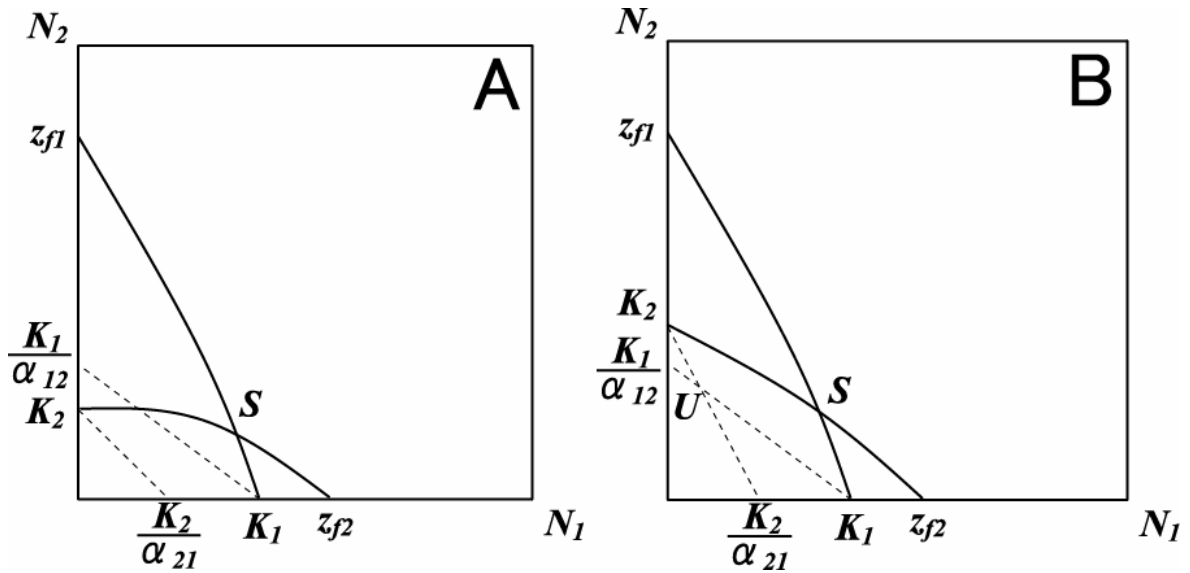
Figure 4. Phase planes for positive frequency-dependence with the Lotka-Volterra competition (Equations 2-5). The zero-growth isoclines are a concave curve anchored at $(K_1, 0)$ and $(0, z_{f1})$ for $i = 1$, or at $(0, K_2)$ and $(z_{f2}, 0)$ for $i = 2$. The letters **S** and **U** indicates stable and unstable coexistent equilibria, respectively. (A) Coexistence is achieved ($z_{f2} > K_1$) when species S_1 only survives under competition only. (B) Coexistence is achieved ($z_{f2} > K_1$ and $z_{f1} > K_2$) when either S_1 or S_2 survives under competition only.

The equilibrium cases for positive frequency dependence are shown in Fig. 4. Here coexistence is always promoted by the existence of the other species. Equilibrium states are qualitatively changed from exclusion to coexistence. Coexistence becomes possible if the effects are larger than a certain threshold (Fig. 4 A and B). If coexistence is maintained under competition, positive frequency dependence simply enlarges the equilibrium density, as in the case of coexistence with positive density dependence (Fig. 3 A). However, the stability is also increased by increasing the curvatures of the isoclines, unlike that of positive density dependence.

4. DISCUSSIONS

The current results show that mutualistic interactions do not invoke population explosion. The new equilibria are simply achieved in all cases. Mutualistic interactions usually affect some limited aspects of life history. In the current model, only partial mortality is reduced by mutualistic interactions. It is possible that reproduction or birth rate may be increased to a certain limit. However, the effects of such interactions are always limited or restricted in some form or another. Lattice model is another type of such limitations (Tainaka et. al., 2003). Symbiotic relationships never invoke infinite population growth, because of limited effects on population growth.

Our results also show that positive density dependence does not promote coexistence unless coexistence is already achieved (Fig. 3). For example, Müllerian mimicry does not promote coexistence of butterflies. It only increases the equilibrium density of butterflies if coexistence is originally attained before the evolution of mimicry. This is rather paradoxical, since symbiotic relations are thought to be evolved, because of the benefit incured by the existence of symbionts. Symbiosis is thought to promote coexistence of the symbionts, because of mutual benefits.

There are at least several plausible hypotheses or interpretations explaining this result:

(1) Müllerian mimicry does not promote the coexistence of butterflies, but only increases the equilibrium densities. It is a special case of symbiosis that does not involve positive frequency dependence.

(2) The current state of coexistence in butterflies is the evolutionary outcome of Müllerian mimicry. The evolution process is different from positive density dependence.

(3) Müllerian mimicry is an evolutionary outcome of Batesian mimicry in poisonous butterflies. The low-density (rare) butterflies evolve their mimicry to the high-density (common) model via Batesian mimicry. The population dynamics of Batesian mimicry is positive frequency dependence.

(4)Müllerian mimicry involves some unknown kind of positive frequency dependence.

Thus the population dynamics of positive density dependence that is developed for Müllerian mimicry does not promote the coexistence of butterflies.

In contrast with positive frequency dependence, positive frequency dependence promotes coexistence by changing the equilibrium states qualitatively (Fig. 4). Recently negative frequency dependence is proposed in competition (Kuno, 1992, Yoshimura and Clark 1994) and predation (Stiling, 1999, e.g., Hori, 1993, Takahashi and Hori 1994). In principle, positive frequency dependence seems valid to symbiotic relationships. However, the functional relationships of Müllerian mimicry indicate that positive frequency dependence is not applicable. It is an open question whether Müllerian mimicry is a special case of mutualism or not. In our original model, the Lotka-Volterra competition is assumed. For example, in lichens, algae and fungi could be under competition for space because of the limited space for growth of cells. However, symbiosis may be evolved only under no competition between symbionts.

Positive frequency dependence can be applicable to Batesian mimicry (Wickler 1968), where the mimic only gains the benefits of predatory avoidance, while the model may incur the costs of mimic when numerous. In this case, the model butterflies may suffer the cost of mimic if the mimic becomes frequent. Here both the mimic involves positive density dependence and the model may suffer negative frequency dependence.

Because the community stability is enhanced by mutualistic interactions (Golick, Atkins and Losey, 1978, May, 1982), many of the present natural communities may be evolved and sustained by such mutualistic interactions. There are many different types of mutualistic interactions within a complicated food web. Some may depend on the density of the other species; some on the frequency; and others may be the combination of both. We have to evaluate the functional response of individuals in natural community to determine the population-level effects of such interactions. As Tainaka et al. (2003) suggested, mutualistic interactions may only be effective when the environmental conditions are good (in a certain range), but competition arises under severe environmental conditions. Both mimicry and

mutualistic interactions are unsolved topics in the population study of ecological interactions.

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