

# Chapter 12

## A Model for Population Dynamics of the Mimetic Butterfly *Papilio polytes* in Sakishima Islands, Japan (II)

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**Abstract** Based on recent progresses of both experiment and mathematical analysis, we present an extension of the model for population dynamics of the mimetic swallowtail butterfly *Papilio polytes* in Sakishima Islands, Japan (Sekimura et al. J Theor Biol 361:133–140, 2014). The model includes four major variables, that is, population densities of three kinds of butterflies (two female forms *f. cyrus* and *f. polytes* and the unpalatable butterfly *Pachliopta aristolochiae*) and their predator. In this extension, we introduce difference in the predation rate between two forms *f. cyrus* and *f. polytes*. We still assume that both the benefit of mimicry for the mimic *f. polytes* and the cost for the model are dependent on their relative frequencies, i.e., the mortality of the mimic by predation decreases with increase in frequency of the model, while the mortality of the model increases as the frequency of the mimic increases. Taking the density-dependent effect by carrying capacity into account, we set up an extended model system consisting of three ordinary differential equations (ODEs), analyze it mathematically, and provide computer simulations that confirm the analytical results.

**Keywords** *Papilio polytes* • Batesian mimicry • Population dynamics • Mathematical model • Computer simulations • Relative abundance of the mimic • Sakishima Islands

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## 12.1 Introduction

*P. polytes* is a mimetic swallowtail butterfly species widely distributed across India and Southeast Asia, including Southeast of China, the Philippines, Taiwan, and the Ryukyu Islands of Japan (Clarke and Sheppard 1972). *P. polytes* exhibits the female limited polymorphism, that is, the female is polymorphic, whereas the male is monomorphic and exhibits a white bar on the black hindwing. In the Ryukyu Islands located in the southwest of Japan, the female of *P. polytes* has two different forms, the mimetic form *f. polytes* and the nonmimetic form *f. cyrus* resembling the monomorphic male in appearance. The form *f. polytes* mimics the unpalatable butterfly *Pachliopta aristolochiae* as a mimetic model, which has a large white area in the center and a row of submarginal red spots on the black hindwing (Fig. 12.1). Mimicry in the female of *P. polytes* is known to be Batesian mimicry.

Yamauchi (1994) built a population dynamic model of Batesian mimicry, in which two populations of both model and mimic species were considered. The dynamic model has two components, growth at intrinsic growth rate and carrying capacity and reduction by predation. The probability of a predator catching prey on an encounter was assumed to depend on the frequency of the mimic. He applied the dynamic model to field records of butterflies in Ryukyu Islands, and his model has successfully explained some features, e.g., multiple dynamic equilibria between the model and the mimic in the field. However, his model did not account for realistic



**Fig. 12.1** The female limited polymorphism of the mimetic butterfly *Papilio polytes* and the model butterfly *Pachliopta aristolochiae*. *Top left*: *P. polytes* *f. cyrus* (nonmimetic form). *Top right*: *P. polytes* *f. polytes* (mimetic form). *Bottom left*: *P. polytes* male. *Bottom right*: the model *Pachliopta aristolochiae*

model-mimic systems such as polymorphism in *P. polytes* and intraspecific competition between the mimic f. *polytes* and the non-mimic f. *cyrus*.

Sekimura et al. (2014) presented a mathematical model for population dynamics of *P. polytes* observed in the Sakishima Islands (i.e., the Miyako Islands and the Yaeyama Islands), which are the southernmost island group of the Ryukyu Islands, Japan (Fig. 12.2). The model system consists of three ordinary differential equations (ODEs), in which variables are population densities of three butterflies, the unpalatable butterfly *P. aristolochiae* and two female forms of *P. polytes*. The model was constructed on the basis of field data in the islands and also experimental data in the laboratory. Using mathematical analysis and computer simulations of the system equations, they clarified the logical relationship hidden behind field data on the population dynamics of the mimetic butterfly *P. polytes* in Sakishima Islands. In particular, they discussed both temporal change in the relative abundance (RA) since 1975 in Miyako-jima Island and variation in the RA in Sakishima Islands.

Before going into details of our extended model and results, we summarize field data briefly in Sect. 12.2 and describe main features of mimicry of *P. polytes* in Sect. 12.3.

## 12.2 Field Records of *Papilio polytes* Observed in Sakishima Islands

### 12.2.1 Observation of Temporal Change in the Population of the Mimetic Female of *P. polytes* in Miyako-jima Island

Uesugi (1992) observed temporal change of the relative abundance of the mimic f. *polytes* in all the females of *P. polytes* for 14 years from 1975 to 1989 after the establishment of the model *P. aristolochiae* in the land. Here, the relative abundance (RA) of the mimic denotes the population ratio of f. *polytes* to all the two forms (f. *cyrus* and f. *polytes*) and is defined as follows:

$$\text{RA} = \frac{\text{population of the mimic f. } \textit{polytes}}{\text{population of the non-mimic f. } \textit{cyrus} + \text{population of the mimic f. } \textit{polytes}} \times 100 (\%)$$

The observational result revealed that the RA increases with the date like the sigmoidal curve, and in 1985 about 10 years after starting observation, the RA reached at a saturated value (or the value of equilibrium) of about 50% (Fig. 12.5a).

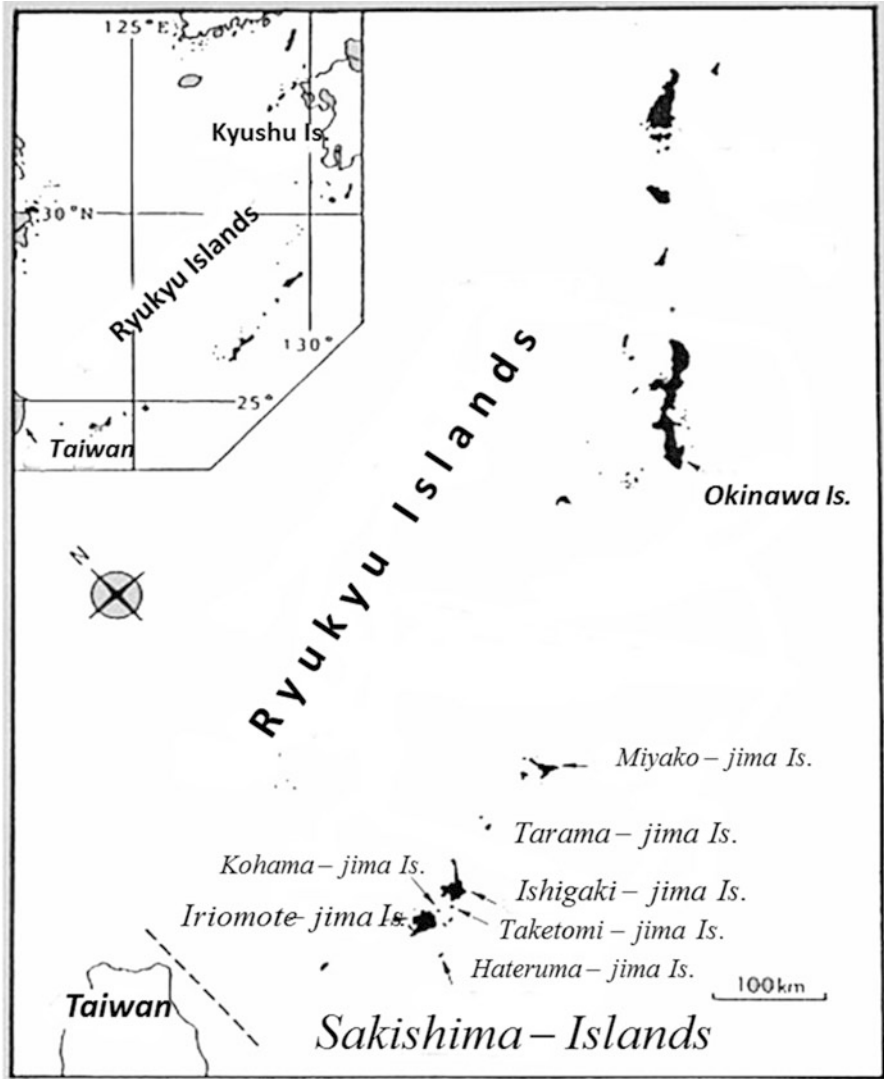


Fig. 12.2 Map of the Sakishima Islands, Japan. The Sakishima Islands are located at the southeast end of Japan and part of the Ryukyu Islands, which include both the Miyako Islands and the Yaeyama Islands. The Miyako Islands include Miyako-jima Is., Tarama-jima Is., etc., and the Yaeyama Islands include Ishigaki-jima Is., Hateruma-jima Is., Iriomote-jima Is., Taketomi-jima Is., Kohama-jima Is., etc.

### 12.2.2 Variation in the Relative Abundance (RA) in Sakishima Islands

Uesugi (1992) also observed variation in the RA in Sakishima Islands. In order to investigate the relationship between two populations of the model *P. aristolochiae* and the mimic *f. polytes*, he recorded three populations of the model and two female forms of *P. polytes* in seven islands from island to island in the Sakishima Islands in 1982, 14 years after the establishment of the model in the Yaeyama Islands. The horizontal axis in Fig. 12.5b shows the advantage index (AI) of Batesian mimicry, which is defined to be the population ratio of the model to all the related butterflies as follows:

$$\text{AI} = \frac{\text{population of the model}}{\text{population of the model} + \text{populations of } f. \text{ cyrus and } f. \text{ polytes}} \times 100 (\%)$$

The vertical axis in Figs. 12.5a and 12.5b is the relative abundance (RA), which denotes the population rate of the form *f. polytes* to all two forms (*f. cyrus* and *f. polytes*).

Field data, which is shown by solid circles in Fig. 12.5b, clearly shows the positive correlation between the AI and the RA, which means that the higher the population ratio of the model butterfly in an island, the higher the ratio of the mimetic female to all females in the island.

## 12.3 Extended Mathematical Model for Population Dynamics of *P. polytes*

We first summarize fundamental facts on the mimicry, which will allow us to design the content of the mathematical model of three variables, that is, three kinds of populations of the model *P. aristolochiae*, the mimic *f. polytes*, and the non-mimic *f. cyrus*.

### 12.3.1 Fundamental Facts on the Mimicry of *P. polytes*

#### 12.3.1.1 Difference in Predation Risk Between Two Forms *f. polytes* and *f. cyrus*

The butterfly *P. polytes* has two female forms: one is the non-mimic *f. cyrus* that resembles the monomorphic male with a white bar on the black hindwing, while the other is the mimic *f. polytes* that resembles the unpalatable butterfly species *P. aristolochiae* (Fig.12.1). The mimetic form *f. polytes* is considered to have an

advantage over *f. cyrus* with respect to protection from predation, when it lives in sympatry with the model *P. aristolochiae*. In reality, Uesugi (1996) examined the idea positively by learning experiments. Unexperienced birds, brown-eared bulbuls, *Hypsipetes amaurotis oryeri* as predators, were first trained to take food from two feeders in a cavity and then offered *P. aristolochiae* in one of the feeders. After experiencing an uncomfortable encounter with this butterfly, the birds reduced the frequency of taking regular food from the feeder where the butterfly had been placed. On the other hand, Ohsaki (1995) paid attention to the rates of beak marks by predators on wings of both palatable and unpalatable butterflies. By analyzing the number of beak marks on butterfly wings caught in Borneo, he found that by comparing the species *P. polytes* and the model species *P. aristolochiae*, nonmimetic females were selectively attacked, while males, mimetic females, and models were attacked less. Thus, the mimic *f. polytes* is considered to gain benefit of reduced predation risk by living in sympatry with the model *P. aristolochiae*.

However, we should note an experimental result on survival rates of the mimetic form *f. polytes*, the nonmimetic form *f. cyrus*, and male in Taketomi-jima Is., where the model *P. aristolochiae* and the mimetic female *f. polytes* are both absent (Uesugi 1997). Uesugi (1997) used a releasing and re-catching method, that is, he released at first 300 butterflies into the field and then caught again released butterflies day after day for a week in the field. The result was remarkable, that is, the survival rate of the mimetic *f. polytes* was statistically significantly lower than those of the nonmimetic *f. cyrus* and male. This means that the mimetic *f. polytes* has received an apparent disadvantage for survival in Taketomi-jima Is. in comparison with the nonmimetic *f. cyrus* and male.

#### 12.3.1.2 Males Prefer the Non-mimic *f. cyrus* to the Mimic *f. polytes*?

The mimetic female *f. polytes* might be less distinguishable than the nonmimetic female *f. cyrus* by the male, because the form *f. polytes* resembles a different species *P. aristolochiae*, while the form *f. cyrus* resembles the male of the same species. This means that *f. cyrus* could get more chances to mate with the male than *f. polytes*. In reality, Uesugi (1997) counted mating times of young butterflies of both *f. cyrus* and *f. polytes* just after emergence. The result was striking to show that *f. polytes* had no approach from the male and no count, while *f. cyrus* could mate with the male. From the viewpoint of making offspring, the non-mimic *f. cyrus* has an advantage over the mimic *f. polytes*. Thus, viewing from the preference of the male to females in the species, the mimicry is not always beneficial.

### 12.3.1.3 Physiological Life Span of Two Forms *f. cyrus* and *f. polytes*

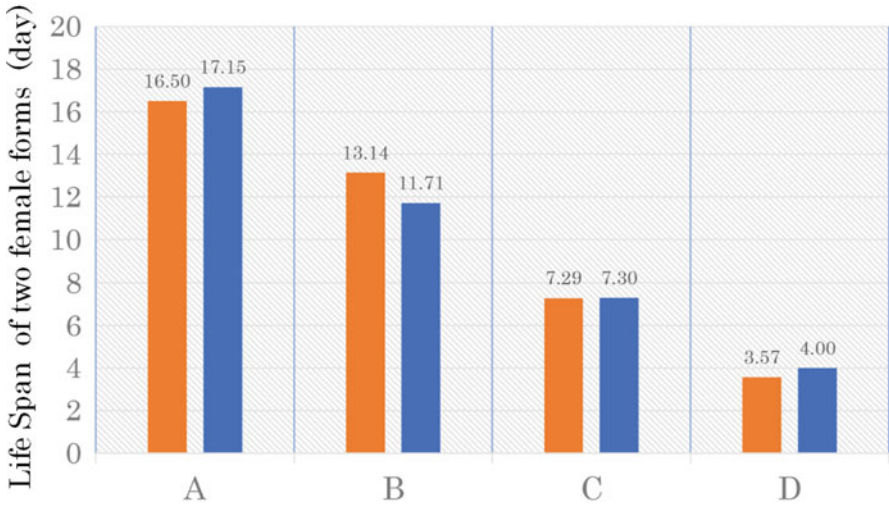
Ohsaki (2005) measured physiological life spans of flying three types (the male, the non-mimic *f. cyrus*, and the mimic *f. polytes*) in Itami City Museum of Insects, Japan, and found that the order of the life span length is as follows: *f. cyrus* > the male > *f. polytes*. The problem is why the life span of the mimic *f. polytes* is the shortest. To explain the reason, Ohsaki proposed a hypothesis that the mimic *f. polytes* pays an additional cost for producing red colored pigments (carotenoid) by activating biochemical reaction networks in cells. The hypothesis coincides with the result that the bigger the red colored area on the wing that the butterfly has, the shorter the physiological life span that the butterfly has.

On the other hand, by using *P. polytes* caught in Okinawa Island, Kinjyo (2000) showed that the physiological life span of *f. cyrus* and *f. polytes* is dependent on the feeding condition. For example, there is no statistically significant difference in the life span when both *f. cyrus* and *f. polytes* are fed in a good condition, under which honey is given every day (i.e., the mean life span, 23.5 days for *f. cyrus* and 22 days for *f. polytes*, respectively). When butterflies are fed in other conditions, under which plain water or no honey is given, mean life spans of the non-mimic *f. cyrus* become 8.8 days (with plain water) and 5.3 days (with no food), and those of the mimic *f. polytes* become 7.8 days (with plain water) and 4.6 days (with no food), respectively. This result shows that in nature, when environmental condition or food conditions (e.g., long rainy weather, dry weather) become worse, the life span of both *f. cyrus* and *f. polytes* becomes shorter rapidly. In any case, the result shows that the life span of *f. cyrus* is somewhat longer than that of *f. polytes*.

For the last several years, Sekimura measured the life span of both *f. cyrus* and *f. polytes* in the laboratory and found that in a regular condition at 25 °C room temperature, there was no statistically significant difference in the life span of both *f. cyrus* and *f. polytes* under different feeding conditions (Fig. 12.3).

### 12.3.2 Mathematical Model of Three ODEs for Population Dynamics of *P. polytes* with Intraspecific Competition

In order to analyze field data summarized in Sect. 12.2, we present here a mathematical model for population dynamics of *P. polytes*. The model system consists of three ordinary differential equations (ODEs), in which variables are population densities of three butterflies, the unpalatable butterfly *P. aristolochiae* and two female forms of *P. polytes*. The male of *P. polytes* is not included directly in the system but included indirectly through parameter values such as intraspecific competition coefficients.



**Fig. 12.3** Phylogenetic life span of two female forms *f. cyrus* and *f. polytes* under the feeding condition. The horizontal axis indicates the feeding condition. “A” is the condition under which Calpis (or Calpico) water (i.e., Japanese milk-based soft drink) is given twice a day; “B” is the condition under which the Calpis water with doubling dilution is given twice a day; “C” is the condition under which only water is given twice a day; “D” is the condition under which nothing is given after hatching. The left side (orange-colored) column of each condition corresponds to the average life span of *f. cyrus*, and the right side (blue colored column) is that of *f. polytes*. The number upon each column indicates the average life span. For example, the number 16.50 upon the left column of the condition “A” is the average life span (days) of 10 (*f. cyrus*) individuals. Numbers of individuals used in the experiment are as follows: numbers of (*f. cyrus*) individuals, 10 for the feeding condition “A,” 7 for “B,” 14 for “C,” and 14 for “D,” respectively, and numbers of (*f. polytes*) individuals: 13 for the feeding condition “A,” 7 for “B,” 10 for “C,” and 10 for “D,” respectively. According to our statistical analysis of the data, there is no statistically significant difference in the physiological life span between two forms *f. cyrus* and *f. polytes* for all feeding conditions A–D. In contrast, the data analysis has made it clear that there exists statistically significant effect of the feeding condition (A–D) on difference in the life span

We denote four population densities of the model *P. aristolochiae*, the mimic *f. polytes*, the non-mimic *f. cyrus*, and predator as  $n_1$ ,  $n_2$ ,  $n_3$ , and  $p$ , respectively. Changes of the densities in time become the following three ODEs:

$$\frac{dn_1}{dt} = n_1 \left\{ r_1 \left( 1 - \frac{n_1}{K_1} \right) - \alpha \left( \frac{n_2}{n_1 + n_2} \right) p \right\} \tag{12.1}$$

$$\frac{dn_2}{dt} = n_2 \left\{ r_2 \left( 1 - \frac{n_2 + a_{23}n_3}{K_2} \right) - \beta_2 \left( \frac{n_2}{n_1 + n_2} \right) p \right\} \tag{12.2}$$

$$\frac{dn_3}{dt} = n_3 \left\{ r_3 \left( 1 - \frac{n_3 + a_{32}n_2}{K_3} \right) - \beta_3 p \right\} \tag{12.3}$$



where the population density of predator  $p$  is given as a fixed parameter value. In the system Eqs. (12.1), (12.2), and (12.3), we evaluated the density effect or saturation effect by using carrying capacities  $K_1, K_2, K_3$  ( $=K_2$ ) for *P. aristolochiae*, f. *polytes*, and f. *cyrus*, respectively. We assume that  $K_2, K_3$  have the same value since both f. *polytes* and f. *cyrus* are females in the same species. Growth rates of three butterflies are denoted by  $r_1, r_2, r_3$ , respectively. In Eqs. (12.2) and (12.3), we introduced an intraspecific competition between f. *polytes* and f. *cyrus* through competition coefficients ( $a_{23}, a_{32}$ ). The intraspecific competition effect includes competitions for resources such as nectar and indirectly the male as noted in Sect. 12.3.1.2. The term  $(n_2/(n_1 + n_2))$  multiplied by  $p$  in Eqs. (12.1) and (12.2) represents the effect of mimicry, that is, the negative density effect implying that the increase in the density of f. *polytes*  $n_2$  causes the decrease in both densities of *P. aristolochiae* and f. *polytes*,  $n_1$  and  $n_2$ . Parameters  $\alpha, \beta_2, \beta_3$  represent difference in the predation rate among *P. aristolochiae*, *P. polytes* f. *polytes*, and f. *cyrus*, respectively, and it would be reasonable to assume the inequality  $\alpha < \beta_2, \beta_3$ , because *P. aristolochiae* is an unpalatable butterfly species. In Sect. 12.3.1.1, we noted the result on beak marks by predators showing that nonmimetic females were selectively attacked, while males, mimetic females, and model butterflies were attacked less. This fact is evaluated mathematically in the second term of Eqs. (12.2) and (12.3) by multiplying  $p$  by  $(n_2/(n_1 + n_2))$  ( $<1$ ) for the mimic f. *polytes*, while by 1 for the non-mimic f. *cyrus*.

## 12.4 Mathematical Analysis of the System Equations and Computer Simulations

### 12.4.1 Mathematical Analysis

Based on discussions in Sect. 12.3.1, we consider and analyze mathematically the following three cases of the system Eqs. (12.1), (12.2), and (12.3) classified by growth rate and predation rate of two forms f. *polytes* and f. *cyrus*: (a) case 1,  $r_2 < r_3$  and  $\beta_2 = \beta_3 (= \beta)$ ; (b) case 2,  $r_2 = r_3$  and  $\beta_2 > \beta_3$ ; and (c) case 3,  $r_2 = r_3$  and  $\beta_2 = \beta_3 (= \beta)$ .

#### 12.4.1.1 Case 1: $r_2 < r_3$ and $\beta_2 = \beta_3 (= \beta)$

This is just the case that was analyzed in our previous paper (Sekimura et al. 2014), where following inequalities were assumed,  $r_2 < r_3$ , i.e., (growth rate of f. *polytes*)  $<$  (growth rate of f. *cyrus*), and  $\alpha < \beta$ , i.e., (predation rate of *P. aristolochiae*)  $<$  (predation rate of f. *polytes*).

We put one more assumption on the survival of *f. cyrus*,  $r_3 > \beta p$ , i.e., the growth rate of *f. cyrus* is larger than the predation rate. Note that the population  $n_3$  tends to zero when  $r_3 \leq \beta p$ , since  $dn_3/dt \leq 0$ .

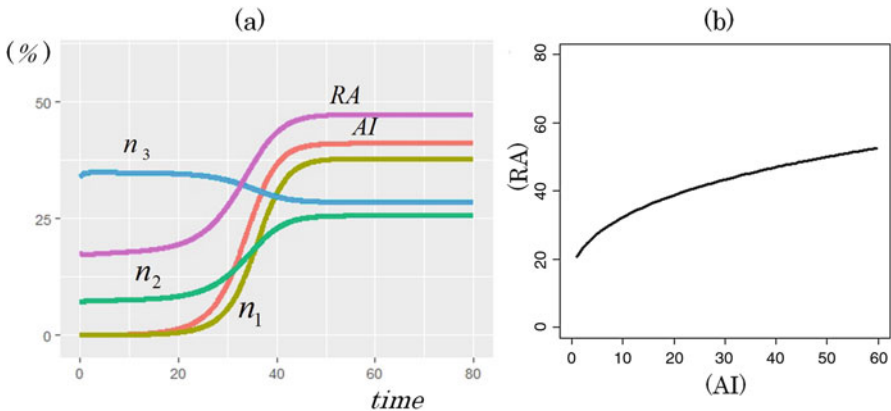
We summarize here main analytical results and computer simulations by solving the system Eqs. (12.1), (12.2), and (12.3).

**[Result C1-1]** The change of relative abundance (RA) of the mimic in the female of *P. polytes* with respect to the carrying capacity  $K_1$  of the model is positive, that is,

$$\frac{d}{dK_1} \left( \frac{n_2}{n_2 + n_3} \right) = \frac{d(RA)}{dK_1} > 0 \tag{12.4}$$

**[Result C1-2]** The change of the advantage index (AI) with respect to the carrying capacity  $K_1$  of the model is positive:

$$\frac{d}{dK_1} \left( \frac{n_1}{n_1 + n_2 + n_3} \right) = \frac{d(AI)}{dK_1} > 0 \tag{12.5}$$



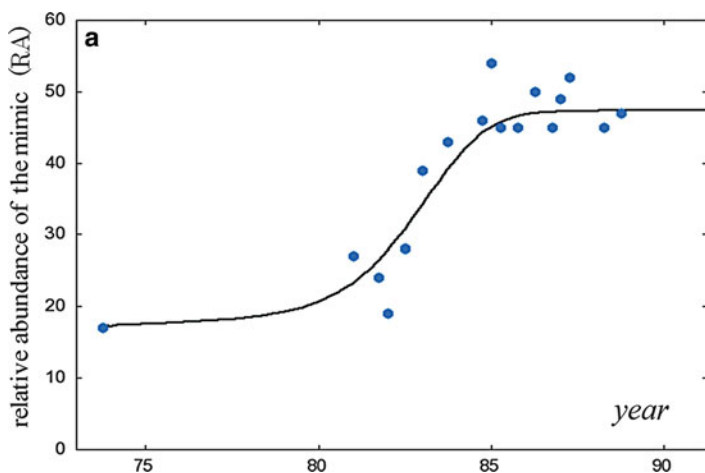
**Fig. 12.4** Simulation results on temporal changes of all related quantities  
**(a)** The blue line denotes the population density  $n_3$  of the non-mimic *f. cyrus*, the green line is the density  $n_2$  of the mimic *f. polytes*, the purple line is the RA, the orange line is the AI, and the ocher line denotes the density  $n_1$  of the model *P. aristolochiae*, respectively. Parameter values used in numerical simulations are as follows, and the stability condition for the positive equilibrium is satisfied with these parameter values:  
 $r_1 = 0.5, r_2 = 1.0, r_3 = 2.0; K_1 = 50, K_2 = 50; a_{23} = 23 \cdot 0.5, a_{32} = 0.35; p = 0.5; \alpha = 0.6, \beta_2 = \beta_3 = 1.0; n_{10} = 0.01, n_{20} = 7.2, n_{30} = 34$  (initial values)  
**(b)** Numerical simulation results of the positive dependence of the RA on the AI. Parameter values used in the numerical simulation are all the same as in Fig. 12.4a

From inequalities (12.4) and (12.5), we see that the ratio of change of the relative abundance (RA) to change of the advantage index (AI) with respect to the carrying capacity  $K_1$  of the model is also positive:

$$\frac{d(RA)}{dK_1} / \frac{d(AI)}{dK_1} > 0 \tag{12.6}$$

The inequality (12.6) provides the analytical evidence for the field record on the positive dependence of the RA on the AI in Sakishima Islands in Fig.12.5b (Uesugi 1992) noted in Sect. 12.2.2.

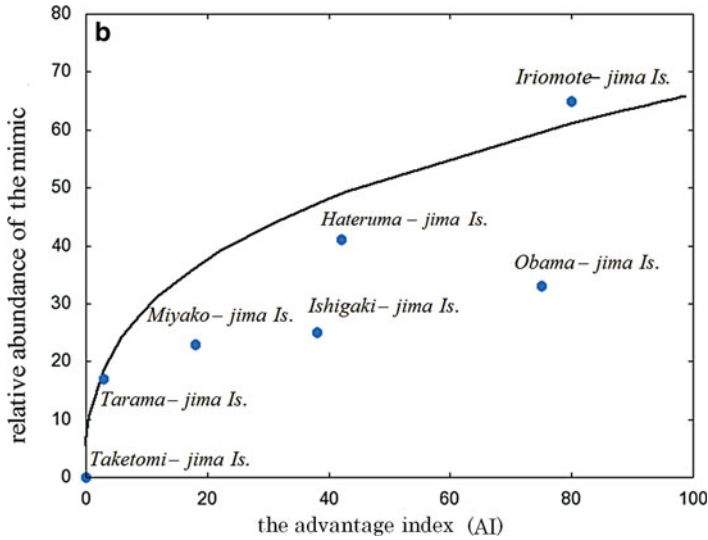
Parameter values used in numerical simulations of Figs. 12.4, 12.5a and 12.5b are chosen as follows, so as to satisfy the existence and stability condition for the equilibrium of all the three population densities  $E_{123} = (n_1, n_2, n_3)$ ,  $r_1 = 0.5$ ,  $r_2 = 1.0$ ,  $r_3 = 2.0$ ,  $K_1 = 50$ ,  $K_2 = 50$ ,  $a_{23} = 0.5$ ,  $a_{32} = 0.35$ ,  $p = 0.5$ ,  $\alpha = 0.6$ ,  $\beta = 1.0$ ,  $n_{10} = 0.01$ ,  $n_{20} = 7.2$ , and  $n_{30} = 34$ , where  $n_{i0}$  denotes the initial value of  $n_i$ .



**Fig. 12.5a** Temporal change in the population of the mimetic female of *P. polytes* on Miyako-jima Island and its numerical simulation results

Solid circles (●) show temporal change in the relative abundance (RA) of the mimetic form *f. polytes* to all the females of *P. polytes* for 14 years after the establishment of the model *P. aristolochiae* on Miyako-jima Is. in 1975. The solid line shows numerical simulation results of temporal change in the RA by use of the Eqs. (12.1), (12.2), and (12.3). Parameter values used in numerical simulations are all the same as in Fig. 12.4a, and the stability condition for the positive equilibrium is satisfied with these parameter values:

$$r_1 = 0.5, r_2 = 1.0, r_3 = 2.0; K_1 = 50, K_2 = 50; a_{23} = 0.5, a_{32} = 0.35; p = 0.5; \alpha = 0.6, \beta_2 = \beta_3 = 1.0; n_{10} = 0.01, n_{20} = 7.2, n_{30} = 34 \quad (\text{initial values})$$



**Fig. 12.5b** Variation in the relative abundance (RA) in Sakishima Islands and its numerical simulation results

The horizontal axis shows the advantage index (AI), which is defined as the number ratio of the model to all the related butterflies (the model and two female forms of *P. polytes*). The vertical axis is the relative abundance (RA). *Solid circle* (●) represents the RA corresponding to the AI on each Island of 7 Islands (i.e., Taketomi-jima Is., Tarama-jima Is., Miyako-jima Is., Ishigaki-jima Is., Hateruma-jima Is., Obama-jima Is., and Iriomote-jima Is.) in Sakishima Islands (From Uesugi 1992). The *solid line* (i.e., Fig. 12.4b) represents numerical simulation results by use of the Eqs. (12.1), (12.2), and (12.3), which clearly show the positive dependence of the RA on the AI with a convexity. The inequality (6), which is an analytical result of the system equations, provides the theoretical basis on the positive dependence. Parameter values used in the numerical simulation are all the same as in Fig. 12.5a.

#### 12.4.1.2 Case 2: $r_2 = r_3$ and $\beta_2 > \beta_3$

This is the case corresponding to experimental results noted in the last paragraphs of Sects. 12.3.1.3 and 12.3.1.1, that is, (a) there is no statistically significant difference in the life span of both *f. cyrus* and *f. polytes* (i.e.,  $r_2 = r_3$ ), and (b) the survival rate of mimetic *f. polytes* is statistically significantly lower than that of nonmimetic *f. cyrus* (i.e.,  $\beta_2 > \beta_3$ ) (this result was obtained by an experiment in Taketomi-jima Is. (Uesugi 1997), where the model *P. aristolochiae* and the mimetic female *f. polytes* are both absent) (Uesugi 1991, 1992).

**[Result C2-1]** First consider the system Eqs. (12.1), (12.2), and (12.3) under the condition  $n_{10} = 0, n_{20} > 0$  and  $n_{30} > 0$ . The setting of initial parameter values corresponds to the situation of Taketomi-jima Is. The uniqueness of the solution of the system implies that  $n_1(t) = 0, n_2(t) > 0$  and  $n_3(t) > 0$  for any  $t > 0$ . Then the solution  $n_2(t)$  and  $n_3(t)$  satisfies

$$\frac{dn_2}{dt} = n_2 \left\{ r_2 - \beta_2 p - r_2 \left( \frac{n_2 + a_{23} n_3}{K_2} \right) \right\} \quad (12.7)$$

$$\frac{dn_3}{dt} = n_3 \left\{ r_3 - \beta_3 p - r_3 \left( \frac{n_3 + a_{32} n_2}{K_3} \right) \right\}, \quad (12.8)$$

which is a traditional Lotka-Volterra competition model. Suppose that  $r_i > \beta_i p$  for  $i = 2, 3$  (otherwise species  $i$  always tends to zero). It is easy to show that:

1.  $n_2(t) \rightarrow 0$  for any  $n_{20} > 0$  and  $n_{30} > 0$ , when

$$a_{23} > \frac{1 - \beta_2 p / r_2}{1 - \beta_3 p / r_3} \quad \text{and} \quad a_{32} < \frac{1 - \beta_3 p / r_3}{1 - \beta_2 p / r_2} \quad (12.9)$$

2.  $n_2(t) \rightarrow 0$  for some  $n_{20} > 0$  and  $n_{30} > 0$ , when

$$a_{23} > \frac{1 - \beta_2 p / r_2}{1 - \beta_3 p / r_3} \quad \text{and} \quad a_{32} > \frac{1 - \beta_3 p / r_3}{1 - \beta_2 p / r_2}. \quad (12.10)$$

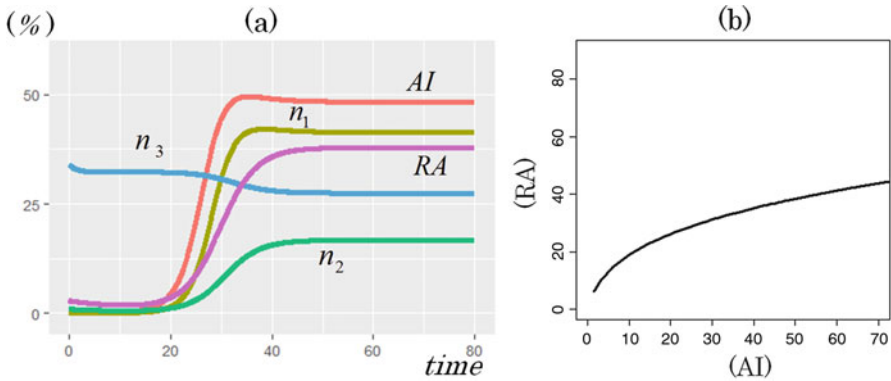
Mathematically we can prove that the equilibrium point  $E_3 = \left( 0, \frac{K_3}{r_3}(r_3 - \beta_3 p) \right)$  is globally stable for system (12.7) and (12.8) under the condition (12.9). Also  $E_3$  and  $E_2 = \left( \frac{K_2}{r_2}(r_2 - \beta_3 p), 0 \right)$  are locally stable under (12.10). Note that under the parameter values for case 1,

$$a_{23} < \frac{1 - \beta_2 p / r_2}{1 - \beta_3 p / r_3} \quad \text{and} \quad a_{32} > \frac{1 - \beta_3 p / r_3}{1 - \beta_2 p / r_2} \quad (12.11)$$

are satisfied, and *f. polytes* and *f. cyrus* can coexist at the positive equilibrium point when *P. aristolochiae* is absent.

**[Result C2-2]** Now let us choose the parameter values for case 2 as  $r_1 = 0.5$ ,  $r_2 = 1.0$ ,  $r_3 = 1.0$ ,  $K_1 = 50$ ,  $K_2 = 50$ ,  $a_{23} = 1$ ,  $a_{32} = 0.3$ ,  $p = 0.5$ ,  $\alpha = 0.6$ ,  $\beta_2 = 0.8$ ,  $\beta_3 = 0.7$ ,  $n_{10} = 0.01$ ,  $n_{20} = 1$ , and  $n_{30} = 34$ . This case corresponds to an expectation of the population dynamics of butterflies after introducing the model *P. aristolochiae* into Taketomi-jima Is. The different choices between this and case 1 are  $r_2 = r_3 = 1.0$ ,  $\beta_2 > \beta_3$ , and the smaller initial value for *f. polytes*, since the above parameters satisfy condition (12.9) and only *f. cyrus* remains when *P. aristolochiae* is absent. Figure 12.6a shows that the introduction of the model yields the stable coexistence of *P. aristolochiae*, *f. polytes*, and *f. cyrus*. Further Fig. 12.6b shows the positive dependence of the RA and the AI.

**[Result C2-3]** The above results imply that the qualitative properties obtained for case 1 still hold true for case 2.



**Fig. 12.6** Simulation results on temporal changes of all related quantities  
 (a) The blue line denotes the population density  $n_3$  of the non-mimic *f. cyrus*, the green line is the density  $n_2$  of the mimic *f. polytes*, the purple line is the RA, the orange line is the AI, and the ocher line denotes the density  $n_1$  of the model *P. aristolochiae*, respectively. Parameter values used in numerical simulations are as follows, and the stability condition for the positive equilibrium is satisfied with these parameter values:

$r_1 = 0.5, r_2 = 1.0, r_3 = 1.0; K_1 = 50, K_2 = 50; a_{23} = 23, a_{32} = 0.3; p = 0.5; \alpha = 0.6, \beta_2 = 0.8, \beta_3 = 0.7; n_{10} = 0.01, n_{20} = 1, n_{30} = 34$  (initial values)

(b) Numerical simulation results of the positive dependence of the RA on the AI. Parameter values used in the numerical simulation are all the same as in Fig. 12.6a

**12.4.1.3 Case 3:  $r_2 = r_3$  and  $\beta_2 = \beta_3 (= \beta)$**

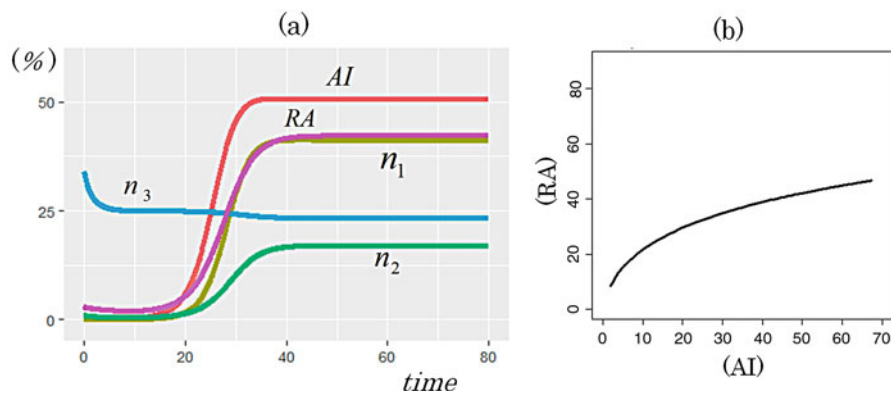
Now consider case 3. We adopt the parameter values  $a_{23} = 1.1, a_{32} = 0.1, \beta = 1$  and the same values for the remaining as case 2. Similar case 2, the parameters satisfy condition (12.9). Figure 12.7 shows the similar property as Fig. 12.6.

Finally, we note mathematical results in a compact way in Sect. 12.4 as follows, Let us define the right-hand sides of the inequality in (12.9), (12.10), and (12.11)

as

$$a_{23}^c = \frac{1 - \beta_2 p / r_2}{1 - \beta_3 p / r_3} \quad \text{and} \quad a_{32}^c = \frac{1 - \beta_3 p / r_3}{1 - \beta_2 p / r_2}. \tag{12.12}$$

It is easy to check that  $a_{23}^c = a_{32}^c = 1$  for case 3 and  $a_{23}^c < 1, a_{32}^c > 1$  for case 1 and 2. Since the condition  $a_{23} > a_{23}^c$  implies that *f. polytes* goes extinct under the competition with *f. cyrus* ( $n_2(t) \rightarrow 0$ ) when *P. aristolochiae* is absent, both cases 1 and 2 enlarge the possibility for the extinction of *f. polytes* when *P. aristolochiae* is absent. The results obtained in Sect. 12.4 show that *f. polytes* can coexist with *f. cyrus* under the invasion of *P. aristolochiae* even *f. polytes* has disadvantageous property as case 1 (relatively small intrinsic growth rate) or case 2 (relatively small survival rate under that predation). Note that the same result can be obtained the case where  $\frac{\beta_2}{r_2} > \frac{\beta_3}{r_3}$ .



**Fig. 12.7** Simulation results on temporal changes of all related quantities

(a) The blue line denotes the population density  $n_3$  of the non-mimic *f. cyrus*, the green line is the density  $n_2$  of the mimic *f. polytes*, the purple line is the RA, the orange line is the AI, and the ochre line denotes the density  $n_1$  of the model *P. aristolochiae*, respectively. Parameter values used in numerical simulations are as follows, and the stability condition for the positive equilibrium is satisfied with these parameter values:

$r_1 = 0.5, r_2 = 1.0, r_3 = 1.0; K_1 = 50, K_2 = 50; a_{23} = 23, a_{32} = 0.1; p = 0.5; \alpha = 0.6, \beta_2 = \beta_3 = 1.0; n_{10} = 0.01, n_{20} = 1, n_{30} = 34$  (initial values)

(b) Numerical simulation results of the positive dependence of the RA on the AI. Parameter values used in the numerical simulation are all the same as in Fig. 12.7a

## 12.5 Summary and Discussions

Based on new experimental results, we presented an extension of the model for population dynamics of the mimetic butterfly *P. polytes* in Sakishima Islands, Japan (Sekimura et al. 2014). We introduced here difference in the predation rate between two female forms *f. polytes* and *f. cyrus* by parameters  $\beta_2, \beta_3$ , respectively. The new model system (12.1), (12.2), and (12.3) still includes three major effects: (a) self-density effect by carrying capacity; (b) mimetic effect, that is, the probability that a predator attacks prey on an encounter is proportional to the relative frequency of the mimic among the model and the mimic; and (c) intraspecific competition between two forms *f. polytes* and *f. cyrus* for resources such as nectar and, indirectly, the male. As to growth rate and predation rate, we took account two cases ( $r_2 < r_3$ ) and ( $r_2 = r_3$ ) into consideration and assumed the inequality  $\alpha < \beta_2, \beta_3$  among predation rates of the model *P. aristolochiae*, *f. polytes*, and *f. cyrus*, respectively.

Using mathematical analysis and computer simulations of the system equations, we extended the possibility of the logical relationship on the population dynamics

of the mimetic butterfly *P. polytes* in Sakishima Islands. In particular, we discussed both temporal change in the relative abundance (RA) and variation in the RA in Sakishima Islands. We estimated conditions for existence of equilibrium solutions of butterfly populations by making a comparison between experimental results and mathematical analyses of the model equations. Our results show that one of key factors to understand field data is the carrying capacity  $K_1$  of the model in each island. The positive dependence of the RA on the AI originates from the result that changes of both the relative abundance (RA) and the advantage index (AI) with respect to the carrying capacity  $K_1$  are positive.

The results in Sect. 12.4 have shown that both cases with respect to production rate: ( $r_2 < r_3$ ) and ( $r_2 = r_3$ ) could be possible to reproduce experimental data on the population dynamics of the mimetic butterfly *P. polytes* in Sakishima Islands. The first case: ( $r_2 < r_3$ ) means that the mimicry of *P. polytes* requires a kind of genetic change in production rate of the mimetic form *P. polytes* to reproduce the data. On the other hand, the second case ( $r_2 = r_3$ ) means that in order to reproduce the data, changes in ecological factors such as intraspecific competition coefficients ( $a_{23}$ ,  $a_{32}$ ) and predation rate  $\beta_2, \beta_3$  are required for the mimicry of *P. polytes* without any genetic change. We think that it is not enough to determine at the moment which case is the real case that occurred in Sakishima Islands, because experiments on butterflies in both the field and the laboratory are somewhat subtle. We hope that much reliable experiments will be done to understand the reality in the future.

Finally, we hope that the mathematical analysis and computer simulations in the paper provide the theoretical basis on the female limited polymorphism of *P. polytes* in Sakishima Islands.

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