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A mathematical model of population dynamics for Batesian mimicry system

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We analyse a mathematical model of the population dynamics among a *mimic*, a corresponding *model*, and their common *predator* populations. Predator changes its search-and-attack probability by forming and losing its search image. It cannot distinguish the mimic from the model. Once a predator eats a model individual, it comes to omit both the model and the mimic species from its diet menu. If a predator eats a mimic individual, it comes to increase the search-and-attack probability for both model and mimic. The predator may lose the repulsive/attractive search image with a probability per day. By analysing our model, we can derive the mathematical condition for the persistence of model and mimic populations, and then get the result that the condition for the persistence of model population does not depend on the mimic population size, while the condition for the persistence of mimic population does depend the predator's memory of search image.

Keywords: population dynamics; hybrid model; mimicry; search image; memory

AMS Subject Classification: 92D25; 92D40; 92B99; 91E40

1. Introduction

Batesian mimicry is such a phenotype that a prey species (*mimic*) resembles some warning signals of another species (called *model* species) which is more or less unpalatable for the predator due to its physiological or morphological defence. To reduce the predation pressure, the mimic species benefits from the predator's learning ability to avoid eating the unpalatable species after it eats the model species by chance [3, 11, 14, 16]. In general, the predator–prey interaction is affected by the predator's learning ability to create the search image for its prey and its memory, which have been attracting observational/experimental/theoretical researches in behavioural, psychological, and evolutionary ecology [6, 10, 18–20]. Mimicry is naturally one of the main subjects in such research.

The efficiency of mimicry significantly depends on the frequency of predator's encountering the model individuals, because the lower frequency makes the smaller probability for the predator to

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create the repulsive search image, that is, the smaller mimic benefit. The frequency is determined by the model and the mimic population densities. Therefore, the efficiency of mimicry depends on the population dynamics among the model, the mimic, and their predator, too. In this paper, as a theoretical problem, we consider the population dynamics of model–mimic system, involving the predator’s memory of the search image for its prey.

Tsoularis and Wallace [24] and Tsoularis [21–23] considered a type of mathematical model with the predator’s learning and forgetting and discussed its effect on the predation rate, making use of numerical calculations of the mathematical model, ‘learning automaton’ as it is called by themselves. They mainly discussed the predation efficiency from the viewpoint of its optimality as foraging strategy. Some other researchers have considered mathematical models with Monte Carlo numerical simulation, too, mainly to discuss some evolutionary aspects of mimicry, for example, mimic polymorphism [20], Batesian–Müllerian dichotomy [7–9], coexistence of co-mimic or other palatable species [6,18,19], etc.

In this paper, we analyse a mathematical model of the population dynamics among a mimic, a corresponding model, and their predator populations. The mathematical model was constructed and preliminarily analysed in [17]. Predator changes its search-and-attack probability by forming and losing its search image. Our mathematical model consists of the daily population dynamics with ordinary differential equations, the seasonal population dynamics with difference equations, and the annual population dynamics with difference equations. Analysing our model system, we can get the result that the condition for the persistence of model population does not depend on the mimic population size, while the condition for the persistence of mimic population does depend on the model population size and the predator’s memory of search image. From these results, we can give a mathematically explicit conclusion about the important role of the predator’s memory of search image for the establishment of persistent model–mimic system.

2. Base modelling

We analyse a mathematical model consisting of the daily population dynamics with ordinary differential equations, the seasonal population dynamics with difference equations, and the annual population dynamics with difference equations (see Figure 1). Each predation season is composed with the daily dynamics repeated in T days.

The predator population size is assumed to be kept constant, given by P , independently of the model and the mimic population sizes. This means that the predator is assumed to be a generalist

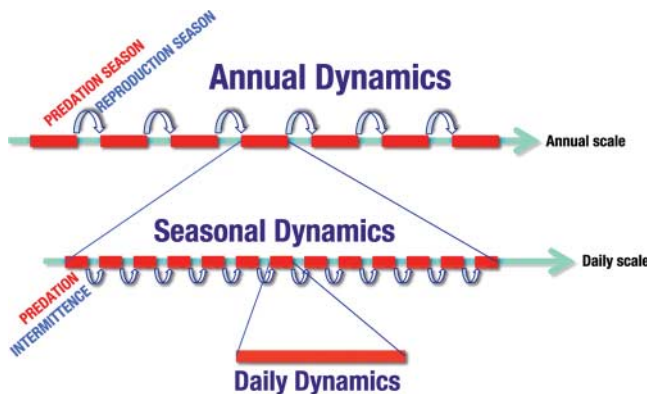


Figure 1. Multi time-scale structure of population dynamics in our model.

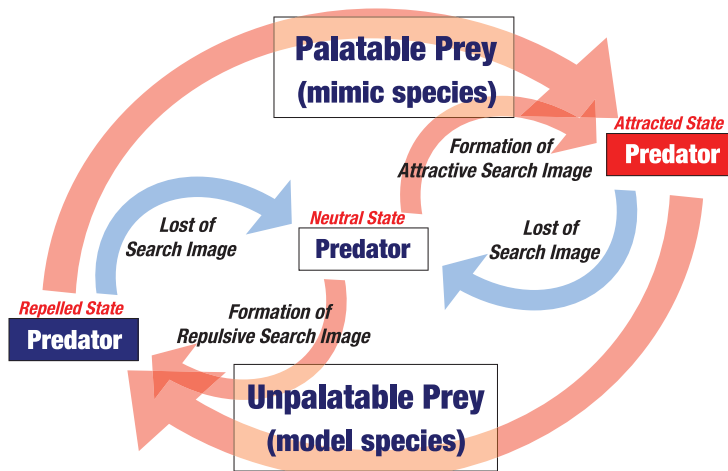


Figure 2. Pradator's state transition due to eating the model or the mimic prey.

and have some other prey to keep the stationary population size, so that it can survive and sustain its population even if the model and the mimic population go extinct.

The reproduction of model and mimic populations is assumed to occur in the period between the subsequent predation seasons. There is no reproduction of model or mimic within the predation season, so that the model and the mimic populations monotonically decrease during the predation season due to the predation.

Differently from the previous models of population dynamics about model–mimic system with either ordinary differential or difference equations system (e.g. [2,25]), our model can be regarded as a *hybrid* system of them (for a similar modelling, see [15]). However, our system could not be considered to be more complicated than the previous ones, because our modelling resulting in a hybrid model is neither for increasing the complexity towards the reality nor for introducing any new factor into the theoretical discussion, but rather for a mathematically tractable structure led from a simplification of natural scheme in the population dynamics of model and mimic species. We do not know any other mathematically tractable population dynamics model analysis about model–mimic system involving the effect of predator's behavioural change linked its memory of search image.

2.1. Daily dynamics

We assume that the predator cannot distinguish the mimic from the model, so that the predator searches and attacks them with a common probability. Once a predator eats a model individual in a day, it comes to omit both the model and the mimic species from its diet menu, and then not to search for nor attack them in the same day. In contrast, if a predator eats a mimic individual, it comes to increase the search-and-attack probability for both the model and the mimic (see Figure 2).

This kind of role of predator's search image in the predator–prey relationship has attracted many researchers in behavioural ecology (for a general review, see [10]). Although our assumptions including those given in the following sections would seem oversimplified in contrast to the reality, we expect that our assumptions do not lose the principal nature of model–mimic population dynamics, in order to theoretically elucidate some important issues in the establishment of persistent model–mimic system.

In the k th day of predation season, the predator frequency without any search image for the model/mimic prey, that is, at the neutral state in terms of the search-and-attack probability, is given by $p_k^0(t)$ ($k = 1, 2, \dots, T$) at time t after the beginning of the predation period ($t = 0$) in the k th day of predation season. $p_k^0(t)P$ gives the corresponding predator population density at time t . In the same way, the predator frequency with the higher search-and-attack probability after eating a mimic prey is given by $p_k^+(t)$, and that with *zero* probability after eating a model prey by $p_k^-(t)$. It is satisfied that

$$p_k^0(t) + p_k^+(t) + p_k^-(t) = 1, \tag{1}$$

for any $t \in [0, \tau]$, where τ is the length of predation period in which the daily dynamics undergoes in each day. The model and the mimic population sizes are given by $m_k(t)$ and $x_k(t)$ at time $t \in [0, \tau]$ in the daily dynamics.

In our model, the daily dynamics is governed by the following ordinary differential equations (for the detail of modelling, see [17]):

$$\begin{aligned} \frac{dm_k(t)}{dt} &= -P \left\{ p_k^0(t) + \frac{p_k^+(t)}{c^+} \right\} m_k(t), \\ \frac{dx_k(t)}{dt} &= -P \left\{ p_k^0(t) + \frac{p_k^+(t)}{c^+} \right\} x_k(t), \\ \frac{dp_k^0(t)}{dt} &= -\{m_k(t) + x_k(t)\} p_k^0(t), \\ \frac{dp_k^+(t)}{dt} &= p_k^0(t)x_k(t) - \frac{p_k^+(t)}{c^+} m_k(t), \\ \frac{dp_k^-(t)}{dt} &= \left\{ p_k^0(t) + \frac{p_k^+(t)}{c^+} \right\} m_k(t), \end{aligned} \tag{2}$$

where parameter c^+ is positive and less than 1, the inverse value of which indicates the increase factor of predation rate by the formation of *attractive* search image due to the predation of the mimic prey.

2.2. Seasonal dynamics

The model and the mimic population sizes at the end of k th day in the predation season are given by $m_k(\tau)$ and $x_k(\tau)$. They give the initial population sizes for the next day: $(m_{k+1}(0), x_{k+1}(0)) = (m_k(\tau), x_k(\tau))$. This is the boundary/continuity condition for the dynamics of mimic and model populations in the predation season. We ignore the death rate due to any other reasons except for the predation in each day of predation season.

As for the frequencies in the predator population, we introduce the probability of losing the search image, say, the forgetting probability. The predator loses its search image with a probability between subsequent days in the predation season. The predator with the higher predation probability loses its *attractive* search image with probability $1 - \sigma^+$ per day, where σ^+ means the probability per day to keep the attractive search image ($0 \leq \sigma^+ \leq 1$). The predator with the zero predation probability loses its *repulsive* search image with probability $1 - \sigma^-$ ($0 \leq \sigma^- \leq 1$) per day. So the parameter σ^- means the probability per day to keep the repulsive search image. With these assumptions, we give the relation between the predator frequencies at the end of k th

day and those at the beginning of $(k + 1)$ th day as follows:

$$\begin{aligned}
 p_{k+1}^0(0) &= p_k^0(\tau) + (1 - \sigma^+)p_k^+(\tau) + (1 - \sigma^-)p_k^-(\tau), \\
 p_{k+1}^+(0) &= \sigma^+p_k^+(\tau), \\
 p_{k+1}^-(0) &= \sigma^-p_k^-(\tau).
 \end{aligned}
 \tag{3}$$

Hence, if model and mimic populations do not exist, the frequency p^0 asymptotically approaches 1 in a geometric manner day by day.

These conditions for the model/mimic populations and the predator frequencies essentially govern their seasonal dynamics through each predation season of T days.

2.3. Annual dynamics

Let us consider the n th predation season. The initial population sizes of model and mimic are given by $m_1(0)$ and $x_1(0)$ from the definitions for the daily dynamics. These initial population sizes simultaneously define the initial population sizes for the n th predation season, now rewritten by $M_{n,0}$ ($= m_1(0)$) and $X_{n,0}$ ($= x_1(0)$).

In our model, the reproduction of the model and the mimic populations is given by what is called Beverton–Holt model (e.g. see [1]). Since the reproduction season is now assumed to be between subsequent predation seasons, their population sizes $(m_T(\tau), x_T(\tau))$ at the end of n th predation season determine $(M_{n+1,0}, X_{n+1,0}) = (m_1(0), x_1(0))$ at the beginning of $(n + 1)$ th predation season with the following reproduction functions:

$$\begin{aligned}
 M_{n+1,0} &= \frac{r_M m_T(\tau)}{1 + \beta_M m_T(\tau)}, \\
 X_{n+1,0} &= \frac{r_X x_T(\tau)}{1 + \beta_X x_T(\tau)},
 \end{aligned}
 \tag{4}$$

where r_M and r_X are, respectively, the intrinsic growth rate, β_M and β_X the intra-specific density effect coefficient. r_M/β_M and r_X/β_X are, respectively, the carrying capacity for the model and the mimic populations.

We assume that the predator completely loses the search image in the period between subsequent predation seasons. Thus the initial condition for the predator’s frequencies according to the state of search-and-attack probability is given by

$$(p_1^0(0), p_1^+(0), p_1^-(0)) = (1, 0, 0)
 \tag{5}$$

on the first day of any predation season, independently of their values at the end of previous season.

3. Complete model

3.1. Mathematical nature of daily dynamics

To complete our modelling, we first consider some mathematical nature of daily dynamics for the base model given in the previous section.

From Equation (2), we can easily find that $d(\log m_k)/dt = d(\log x_k)/dt$ for any $t \in [0, \tau]$. This means that the ratio $x_k(t)/m_k(t)$ is constant independently of t , so that $x_k(t)/m_k(t) = x_k(0)/m_k(0)$

for any $t \in [0, \tau]$ and any $k = 1, 2, \dots, T$. Moreover, from the boundary/continuity condition that $(m_{k+1}(0), x_{k+1}(0)) = (m_k(\tau), x_k(\tau))$, we lastly have

$$\frac{x_k(t)}{m_k(t)} = \frac{x_k(0)}{m_k(0)} = u_n := \frac{x_1(0)}{m_1(0)}, \tag{6}$$

for any $t \in [0, \tau]$ and any $k = 1, 2, \dots, T$ in the n th predation season. The ratio u_n is an invariant constant for the population dynamics in the n th predation season. Let us remark that, from the definition, $x_1(0)/m_1(0) = M_{n,0}/X_{n,0}$, which is the ratio at the beginning of the first day in the n th predation season.

Further, from Equation (2), we can find that $d(m_k + p_k^- P)/dt = 0$ for any $t \in [0, \tau]$, too. Thus, we have

$$m_k(t) = m_k(0) - \{p_k^-(t) - p_k^-(0)\}P, \tag{7}$$

for any $t \in [0, \tau]$.

With these features, the arguments in [17] give the following result about the mathematical nature of daily dynamics:

In the daily dynamics given by Equation (2) for the n th predation season, the system has the nature to asymptotically approach the equilibrium state as follows:

$$(m_k(t), x_k(t), p_k^0(t), p_k^+(t), p_k^-(t)) \xrightarrow{t \rightarrow \infty} \begin{cases} E_0(0, 0, p_k^{0*}, p_k^{+*}, p_k^{-*}) & \text{if } m_k(0) \leq \{1 - p_k^-(0)\}P, \\ E_+(m_k^*, u_n m_k^*, 0, 0, 1) & \text{if } m_k(0) > \{1 - p_k^-(0)\}P, \end{cases} \tag{8}$$

for $k \geq 1$.

3.2. Equilibrium state approximation (ESA)

To complete our modelling, we introduce a mathematical approximation for the state at the end of each day in the predation season. Let us assume that the state $(m_k(t), x_k(t), p_k^0(t), p_k^+(t), p_k^-(t))$ approaches the equilibrium state given by Equation (8) *sufficiently fast*. In other words, we assume that the state at the end of k th day $(m_k(\tau), x_k(\tau), p_k^0(\tau), p_k^+(\tau), p_k^-(\tau))$ is *sufficiently near the equilibrium state* given by (8). Then, as a mathematical approximation, we hereafter use the equilibrium state given by (8) as the state at the end of k th day (i.e. at $t = \tau$).

With this equilibrium state approximation (ESA), we reset up the relation between the predator frequencies at the end of k th day and those at the beginning of $(k + 1)$ th day as follows ($k \geq 1$):

$$\begin{aligned} p_{k+1}^0(0) &= \lim_{t \rightarrow \infty} \{p_k^0(t) + (1 - \sigma^+)p_k^+(t) + (1 - \sigma^-)p_k^-(t)\}, \\ p_{k+1}^+(0) &= \lim_{t \rightarrow \infty} \{\sigma^+ p_k^+(t)\}, \\ p_{k+1}^-(0) &= \lim_{t \rightarrow \infty} \{\sigma^- p_k^-(t)\}, \end{aligned} \tag{9}$$

instead of Equation (3). Thus, the boundary/continuity condition for the dynamics of mimic and model populations in the predation season of our complete model is consistently given by

$$\begin{aligned} m_{k+1}(0) &= \lim_{t \rightarrow \infty} m_k(t), \\ x_{k+1}(0) &= \lim_{t \rightarrow \infty} x_k(t). \end{aligned} \tag{10}$$

At last, in our complete model, the daily and seasonal dynamics are given by Equation (2) with Equations (1), (9) and (10), while the annual dynamics is by Equation (4) with Equation (5), substituting $\lim_{t \rightarrow \infty} m_T(t)$ and $\lim_{t \rightarrow \infty} x_T(t)$, respectively, for $m_T(\tau)$ and $x_T(\tau)$.

In our modelling, the ESA by Equations (9) and (10) is not simply an *approximation*, but is one of the important steps in constructing our complete model. If we consider the daily dynamics of base model (2) with (3), the extinction of model or mimic population within a predation season never occurs even when the predator’s overgrazing makes the population very small. Subsequently in this case, the extinction never occurs in any finite year. This is one of the mathematical nature for many models with differential equations, which could sometimes be regarded as a mathematical *approximation* or a mathematical *idealization* to the reality. On the other hand, this mathematical treatment ignores some biologically practical aspects, for example, the demographic or environmental stochasticity, the Allee effect, etc. For our model, we have chosen the ESA as a part of modelling to introduce such effect of demographic or environmental stochasticity or Allee effect which could cause the population extinction in a finite time due to sufficiently small population size, as shown in the following sections.

4. Analysis

4.1. Daily dynamics

From Equations (8) and (9), as far as the mimic population persists, we have

$$(p_{k+1}^0(0), p_{k+1}^+(0), p_{k+1}^-(0)) = (1 - \sigma^-, 0, \sigma^-). \tag{11}$$

In contrast, once the mimic population goes extinct in the k th day with the equilibrium state E_0 in Equation (8), which may be regarded as the consequence of predator’s overgrazing, we have

$$\begin{aligned} p_{k+1}^0(0) &= p_k^{0*} + (1 - \sigma^+)p_k^{+*} + (1 - \sigma^-)p_k^{-*}, \\ p_{k+1}^+(0) &= \sigma^+p_k^{+*}, \\ p_{k+1}^-(0) &= \sigma^-p_k^{-*}. \end{aligned}$$

Subsequently in this case, since both mimic and model populations have gone extinct, the system (2) gives no change of the predator frequencies during the subsequent day. Thus, we have

$$\begin{aligned} p_{k+1}^{0*} &= p_k^{0*} + (1 - \sigma^+)p_k^{+*} + (1 - \sigma^-)p_k^{-*}, \\ p_{k+1}^{+*} &= \sigma^+p_k^{+*}, \\ p_{k+1}^{-*} &= \sigma^-p_k^{-*}. \end{aligned}$$

Therefore, the predator frequencies geometrically approach $(1, 0, 0)$ day by day after the extinction of mimic and model populations, because of the predator’s losing the search image.

With Equation (8), the arguments in [17] give the following result about the persistence of mimic and model populations:

The mimic and the model populations persist in the k th day if and only if $m_k(0) > (1 - \sigma^-)P$ for $k > 1$ and $m_1(0) > P$. Then, $(p_k^{0*}, p_k^{+*}, p_k^{-*}) = (0, 0, 1)$ and $m_k^* = m_k(0) - (1 - \sigma^-)P$ for $k > 1$ and $m_1^* = m_1(0) - P$. If and only if $m_k(0) \leq (1 - \sigma^-)P$ for some $k > 1$ or $m_1(0) \leq P$, the mimic and the model populations go extinct in the k th or the first day of predation season, and then we have the equilibrium state E_0 with $0 < p_k^{0*} < 1, 0 < p_k^{+*} < 1$ and $0 < p_k^{-*} < 1$. After their extinction, $(p_k^{0*}, p_k^{+*}, p_k^{-*})$ asymptotically approaches $(1, 0, 0)$ as k increases.

As for a special case without the model population, when the system contains the mimic and the predator, we can easily show that *the mimic population goes extinct in the first day of predation season* (Appendix 1).

We remark that, if the predator is absent, the population sizes of mimic and model are kept constant throughout the predation season, due to ignoring any factors of their death other than the considered predator’s predation. This means that the predation has the important role for the above-mentioned dependence of mimic persistence on the model population.

4.2. Seasonal dynamics

Let us consider the case that the mimic and the model populations persist till the k th day of predation season ($k > 1$). Then, from Equations (7)–(11), we have the following daily recurrence relation about the initial model population sizes of subsequent days:

$$m_{j+1}(0) = m_j(0) - \{1 - p_j^-(0)\}P \quad \text{for } j = 1, 2, \dots, k - 1. \tag{12}$$

Since $p_1^-(0) = 0$ and $p_j^-(0) = \sigma^-$ for $j > 1$ from Equation (11), this recurrence relation gives the following general form of $m_j(0)$:

$$m_j(0) = m_1(0) - \{1 + (j - 2)(1 - \sigma^-)\}P \quad \text{for } j = 2, 3, \dots, k. \tag{13}$$

Therefore, since the necessary and sufficient condition that the mimic and the model populations persist in the T th day (= the last day) of the predation season is given by $m_T(0) > (1 - \sigma^-)P$ from the result in the previous section, we get the following result about the seasonal dynamics:

The mimic and the model populations persist through the n th predation season if and only if

$$M_{n,0} = m_1(0) > m_c := \{1 + (T - 1)(1 - \sigma^-)\}P. \tag{14}$$

Otherwise, the mimic and the model populations simultaneously go extinct in the k_e th day of the n th predation season, where k_e is given by

$$k_e = \left\lceil \left[\frac{M_{n,0}/P - 1}{1 - \sigma^-} + 1 \right] \right\rceil. \tag{15}$$

The symbol $\lceil x \rceil$ means the smallest integer not less than x . The critical size m_c defines the lower bound for the initial population size according to the persistence of mimic and model populations through the predation season. We remark that the critical size m_c is determined by the predation pressure given by P , the length of predation season T , and especially the faculty to keep the repulsive search image given by σ^- .

In the case that the mimic and the model populations persist throughout the n th predation season, the model population size m_T^* at the end of the predation season is given by

$$\begin{aligned} m_T^* &= m_T(0) - (1 - \sigma^-)P = m_1(0) - \{1 + (T - 1)(1 - \sigma^-)\}P \\ &= M_{n,0} - m_c. \end{aligned} \tag{16}$$

As a consequence, the extinction of only one of mimic and model never occurs in the seasonal dynamics of our model, while it is likely that both of them go extinct in a predation season.

A numerical example of the seasonal dynamics governed by Equation (2) with Equations (9) and (10) is shown in Figure 3.

We note that the condition of extinction depends on the initial value of model population in the predation season and the strength of predation pressure related to the predator’s memory of repulsive search image. In short, the above-mentioned mimic extinction in the seasonal dynamics is due to the extinction of model population by the high predation pressure with sufficiently poor memory of repulsive search image. The extinction of model population is necessary for that of mimic population.

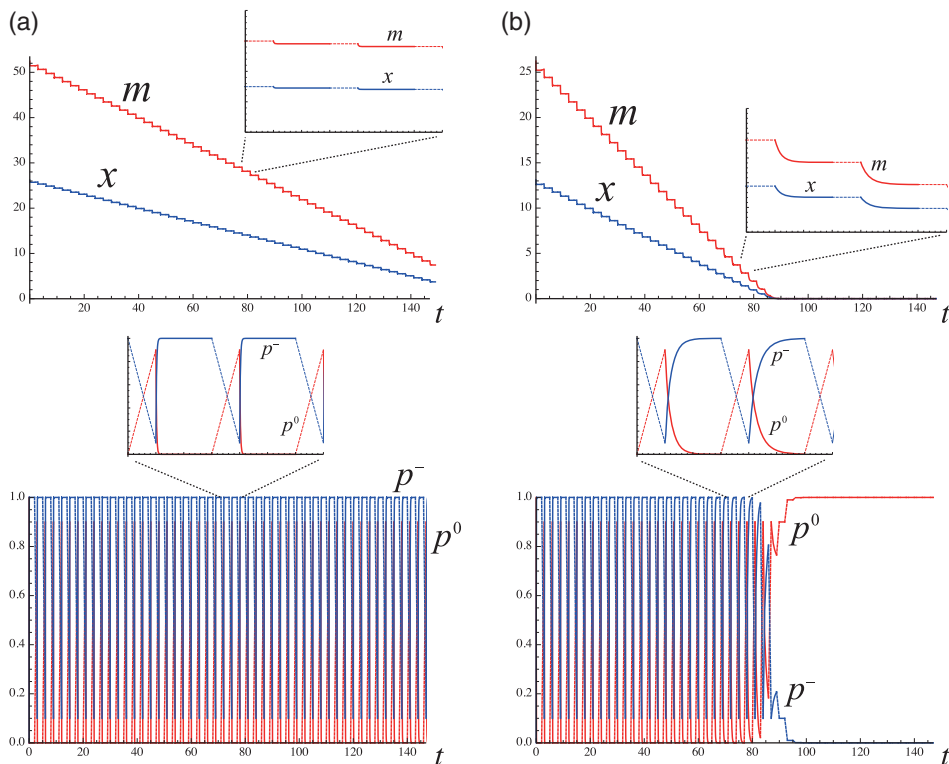


Figure 3. A numerical example of the seasonal dynamics governed by Equation (2) with Equations (9) and (10). (a) $(m_1(0), x_1(0)) = (52.4469, 26.2234)$; (b) $(m_1(0), x_1(0)) = (26.2234, 13.1117)$. Commonly, $T = 50$, $\tau = 2.0$, $c^+ = 0.1$, $\sigma^+ = 0.5$, $\sigma^- = 0.1$, $P = 1.0$, $m_c = 45.1$. The mimic and the model populations persist through the predation season in (a), while they go extinct at a day in (b).

4.3. Annual dynamics

From Equation (4) with Equations (9) and (10), the model and the mimic populations at the beginning of $(n + 1)$ th predation season, $M_{n+1,0}$ and $X_{n+1,0}$, are now given by the following reproduction functions:

$$\begin{aligned}
 M_{n+1,0} &= \frac{r_M m_T^*}{1 + \beta_M m_T^*}, \\
 X_{n+1,0} &= \frac{r_X x_T^*}{1 + \beta_X x_T^*},
 \end{aligned}
 \tag{17}$$

where

$$x_T^* = u_n m_T^* = \frac{x_1(0)}{m_1(0)} m_T^* = \frac{X_{n,0}}{M_{n,0}} m_T^*$$

from Equation (6). Then, from Equations (8), (14), (16) and (17), making use of the result obtained in the previous section, we have the following difference equations to determine the annual dynamics in terms of the model and the mimic population sizes at the beginning of

predation season:

$$\begin{aligned}
 M_{n+1,0} &= \frac{r_M[M_{n,0} - m_c]_+}{1 + \beta_M[M_{n,0} - m_c]_+}, \\
 X_{n+1,0} &= \frac{r_X[M_{n,0} - m_c]_+ X_{n,0}}{M_{n,0} + \beta_X[M_{n,0} - m_c]_+ X_{n,0}},
 \end{aligned}
 \tag{18}$$

where the symbol $[\]_+$ is defined as follows:

$$[x]_+ := \begin{cases} x & \text{for } x > 0, \\ 0 & \text{for } x \leq 0. \end{cases}$$

We note that the annual dynamics of model population is independent of that of mimic population, while the latter depends on the former.

Analysing the first equation of (18), we can obtain the following result about the persistence of model population (Appendix 2):

If and only if the following conditions are satisfied, the model population persists in any predation season, and $M_{n,0} \rightarrow M^* = m_c + \lambda_+ = (r_M - 1 - m_c/\lambda_+)/\beta_M$ as $n \rightarrow \infty$:

$$r_M \geq (1 + \sqrt{\beta_M m_c})^2, \tag{19}$$

$$M_{1,0} \geq m_c + \lambda_- = \frac{(r_M - 1 - m_c/\lambda_-)}{\beta_M}, \tag{20}$$

where

$$\lambda_{\pm} := \frac{1}{2\beta_M} \{r_M - (1 + \beta_M m_c) \pm \sqrt{D}\}, \tag{21}$$

$$D := \{r_M - (1 + \sqrt{\beta_M m_c})\} \{r_M - (1 - \sqrt{\beta_M m_c})\}.$$

Otherwise, the model population goes extinct in the n_e th predation season with $M_{n_e,0} \leq m_c$, where

$$n_e := 1 + \left\lceil \frac{\log\{(1 - [M_{1,0} - m_c]_+/\lambda_+)/ (1 - [M_{1,0} - m_c]_+/\lambda_-)\}}{\log\{(1 + \beta_M \lambda_+)/ (1 + \beta_M \lambda_-)\}} \right\rceil. \tag{22}$$

The symbol $[x]$ is the same as before. λ_{\pm} is positive whenever the condition (19) is satisfied. Parameter dependence of the persistence of model population is shown in Figure 4, where we also used the following condition mathematically equivalent to conditions (19) and (20) in order to draw the boundary curve:

$$M_{1,0} > m_c \quad \text{and} \quad r_M \geq \frac{M_{1,0}(1 + \beta_M M_{1,0} - \beta_M m_c)}{M_{1,0} - m_c}. \tag{23}$$

Furthermore we can prove that, even if the mimic population is absent, the seasonal and the annual dynamics for the model population is the same as shown above (see Appendix 3). Let us note

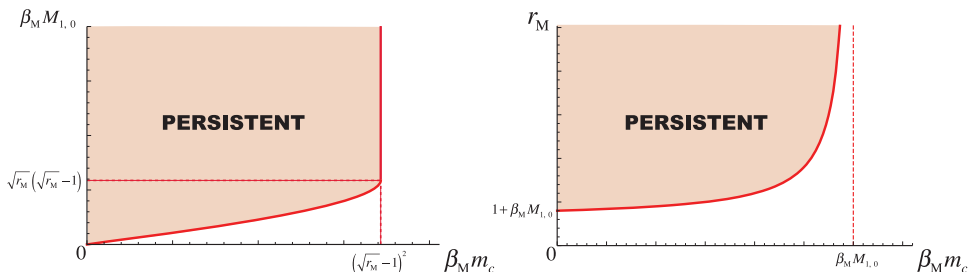


Figure 4. Parameter dependence of the persistence of model population. Boundary curves are given by (19) and (20), or by (23).

that the above condition for the persistence/extinction of the model population is independent of any parameter of mimic. This means that the extinction of model population in our system can be regarded as the consequence of high predation pressure which depends on the faculty of predator’s memory of repulsive search image. In our model, it is independent of the presence of mimic population. In contrast, the persistence of mimic population depends on the model population, as we will see in the following analysis.

As for the mimic population governed by the second difference equation of (18), let us consider it here with $M_{n,0} \equiv M^* = m_c + \lambda_+$ for any n . This is because the model population dynamics is independent of the mimic one. Besides, as we have already seen, if the model population goes extinct, then so does the mimic population. So we now focus the mimic population dynamics when the model population has reached its equilibrium state according to the annual dynamics governed by the first difference equation of (18). Hence, instead of the second difference equation of (18), let us consider here the following annual dynamics of mimic population:

$$X_{n+1,0} = \frac{r_X X_{n,0}}{1 + m_c/\lambda_+ + \beta_X X_{n,0}}. \tag{24}$$

From this difference equation, we can obtain the following result about the persistence of mimic population:

Only when the model population persists at its equilibrium state, if and only if the following condition is satisfied, the mimic population persists in any predation season:

$$r_X > 1 + \frac{m_c}{\lambda_+} = r_M \left(1 - \frac{M^*}{r_M/\beta_M} \right), \tag{25}$$

and then

$$X_{n,0} \longrightarrow X^* = \frac{1}{\beta_X} \left\{ r_X - \left(1 + \frac{m_c}{\lambda_+} \right) \right\} = \frac{\beta_M M^*}{\beta_X} + \frac{r_X - r_M}{\beta_X} \tag{26}$$

as $n \rightarrow \infty$. Otherwise, the mimic population goes extinct, that is, $X_{n,0} \rightarrow 0$ as $n \rightarrow \infty$ for any $X_{1,0} > 0$.

Differently from the case of model population, there is no condition for the initial value $X_{1,0}$. Since $\lambda_+ > 0$ whenever the model population persists, the condition (25) indicates it necessary for the mimic population persistence that the intrinsic growth rate r_X is greater than 1. Parameter dependence of the condition (25), for the mimic population persistence is shown in Figure 5, where we used also the following condition mathematically equivalent to the condition (25) in order to draw the boundaries:

$$r_X > 1 \quad \text{and} \quad \begin{cases} r_M < \beta_M m_c + 2r_X - 1 \\ \text{or} \\ r_M > \frac{r_X}{r_X - 1} \beta_M m_c + r_X. \end{cases} \tag{27}$$

Additionally, from conditions (23) and (27), we can easily prove that, if the following condition is satisfied, the mimic population necessarily persists when the model population persists:

$$\beta_M M_{1,0} \leq r_X(r_X - 1). \tag{28}$$

On the other hand, if

$$0 < r_X(r_X - 1) < \beta_M M_{1,0}, \tag{29}$$

the persistence of mimic population depends on some other parameters of mimic and model populations (see Figure 5).

We note that, unless the condition (25) is satisfied, the mimic population tends to go extinct, though its extinction never occurs at any finite time as long as the model population persists. As

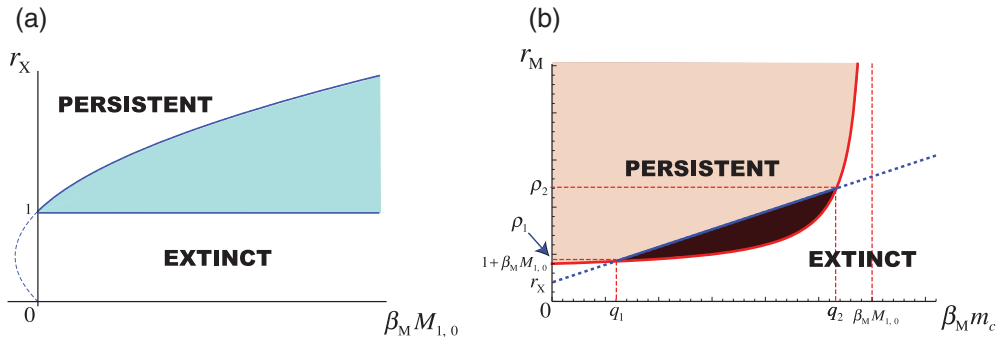


Figure 5. Parameter dependence of (a) the persistence of mimic population when the model population persists; (b) the coexistence of mimic and model populations for the light colored region in (a). In (a), the light colored region is given by (29). For the persistent region in (a), the mimic population can persist whenever the model population can. For the extinct region in (a), the mimic population eventually goes extinct even when the model population persists. For the light colored region in (a), the persistence of mimic population depends on some other parameters as shown in (b). In (b), boundary curves are given by (23) and (27). For the light colored region in (b), the mimic population can persist with the persistent model population. For the dark colored region in (b), the model population persists while the mimic goes extinct. As $r_X \rightarrow 1 + 0$, the persistent region in (b) for the mimic population disappears. For the extinct region in (b), the model and the mimic populations go extinct. q_1 and q_2 are respectively the smaller and the larger of $1 + \beta_M M_{1,0} - r_X$ and $(1 - 1/r_X)\beta_M M_{1,0}$. ρ_1 and ρ_2 are respectively the smaller and the larger of $\beta_M M_{1,0}/(1 - 1/r_X)$ and $\beta_M M_{1,0} + r_X$.

already shown in the seasonal dynamics, the mimic population goes extinct in a predation season only when so does the model population. Thus, the mimic’s extinction in the above result means the long-term tendency to go extinct. In such case, the mimic population size decreases not only day by day in the predation season but also year by year in annual scale. This is the case that the mimicry would not be the adaptive strategy for the species which has the faculty to mimic the model species. So in such cases, the model–mimic system could not be established also in the evolutionary context. Such mimic extinction in our model can be caused by too small (intrinsic or net) growth rate of mimic population that could be regarded as the cost of mimicry. Only mimic species with sufficiently smaller cost of mimicry in terms of the growth rate can coexist with the model, and can establish the persistent model–mimic system.

Consequently, for our model, the establishment of persistent model–mimic system (as a population dynamics) requires that the conditions (19), (20), and (25) are simultaneously satisfied, being shown as a parameter region in Figure 5.

4.4. Equilibrium population size ratio

When the model population is persistent under those conditions (19) and (20), we can show, from Equation (6), that the ratio of their population sizes approaches a constant as $n \rightarrow \infty$:

$$\frac{X_{n,0}}{M_{n,0}} = \frac{x_k(t)}{m_k(t)} = u_n \rightarrow \frac{X^*}{M^*} = \frac{\beta_M}{\beta_X} \cdot \frac{[r_X - 1 - m_c/\lambda_+]_+}{r_M - 1 - m_c\lambda_+}, \tag{30}$$

where $[\]_+$ is defined as before. Numerical illustrations of m_c -dependence of the equilibrium population size ratio are given in Figure 6.

We can easily prove that $m_c/\lambda_+ (= \beta_M\lambda_-)$ is monotonically increasing and $m_c + \lambda_+$ is monotonically decreasing in terms of m_c . Since m_c defined in Equation (14) is monotonically decreasing between its minimum P and maximum TP in terms of σ^- , the results of our analysis indicate that the persistence of model and mimic populations depends on the predator’s memory of repulsive search image. Moreover, as shown in Figure 6, it is likely that the predator’s memory of repulsive

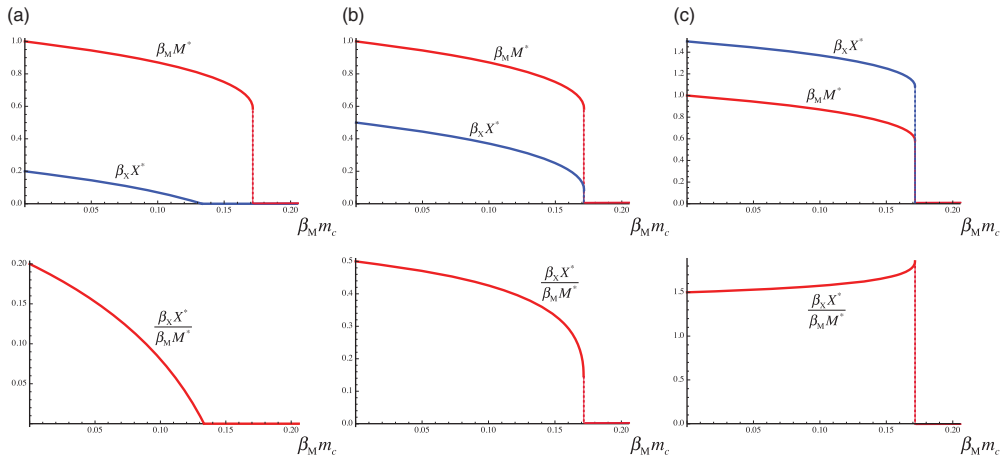


Figure 6. m_c -dependence of equilibrium population sizes at the beginning of predation season, that is, for the annual dynamics (18). (a) $r_X = 1.2$; (b) $r_X = 1.5$; (c) $r_X = 2.5$. Commonly, $r_M = 2.0$. In case of (a), the mimic population is extinct for a range of m_c in which the model population is persistent. In cases of (b) and (c), the mimic population is persistent as long as the model population is.

search image could determine the population size ratio between the mimic and the model populations. We note that the equilibrium population size ratio is not always decreasing in terms of m_c as indicated by (26) and illustrated by Figure 6(c) in case of $r_X > r_M$.

4.5. Establishment of persistent model–mimic system

For our model, when and only when the conditions (19), (20), and (25) are simultaneously satisfied, the model–mimic system can be persistently established as a population dynamics, that is, both the model and mimic populations are persistent to coexist. Since the right-hand sides of inequalities in those conditions (19), (20), and (25) are monotonically increasing in terms of m_c , the establishment of persistent model–mimic system is harder as the value of m_c gets larger. We note that the dependence of those conditions on the predation pressure (i.e. on P) and the predator’s memory of repulsive search image (i.e. on σ^-) is only through m_c .

Since m_c is monotonically increasing in terms of P and decreasing in terms of σ^- , this result means that

the stronger predation pressure or the weaker memory of repulsive search image could make the establishment of persistent model–mimic system harder. In other words, it is necessary for the establishment of persistent model–mimic system that their common predator has so strong memory of repulsive search image as to provide the model and the mimic populations with sufficiently weak predation pressure.

5. Concluding remarks

From the result of our model, we conclude that, as the predator’s memory of repulsive search image is stronger, it is more likely for the model population to persist, and the equilibrium model population size gets larger. This is because the stronger memory of repulsive search image is to repel the predator longer from the model population so as to make the predation pressure weaker for it. This feature can be adopted to the persistence and the equilibrium size of mimic population, too.

Then, as for the establishment of persistent model–mimic system, we derive the conclusion that it is necessary that their predator has so strong memory of repulsive search image as to provide

the model and the mimic populations with sufficiently weak predation pressure. This conclusion may be regarded to be consistent with the result of Speed and Turner [20] with a Monte Carlo numerical simulation model that the mode of forgetting has a more significant effect on mimetic relationships than the rate of learning.

In our model, the effect of the predator's memory of repulsive search image on the population dynamics is represented by parameter σ^- . It is likely that the memory would be closely related to the strength of stimulus given by the model to its predator. For example, the model's higher unpalatability (e.g. stronger toxicity) for its predator could make the predator's repulsive search image decline slower, to be kept longer or be more hardly lost. This argument implies that the species of low unpalatability could not become the model for a mimic species from an evolutionary viewpoint, so that such a low unpalatable species could not belong to any persistent model–mimic system. Model species of a persistent model–mimic system would be required to be unpalatable highly enough.

Our result also implies that the higher predation pressure in the habitat of model species would be unfavourable for the establishment of persistent model–mimic system. From an evolutionary viewpoint, in the habitat under high predation pressure, the mimic species fails to invade so that the model–mimic system is hardly established.

In our result about the establishment of persistent model–mimic system, any relevance to parameters σ^+ or c^+ of the daily dynamics does not appear. Parameter c^+ representing the effect of attractive search image formation on the predation rate affects the speed of temporal variation of population sizes/frequencies in the daily dynamics. Furthermore, it affects the equilibrium values of p_k^{0*} , p_k^{+*} , and p_k^{-*} when the model and the mimic populations go extinct to be $(m_k^*, x_k^*) = (0, 0)$, too. However, as mentioned in the section to introduce ESA in our modelling, if the population sizes/frequencies temporally change sufficiently fast towards the equilibrium state in the daily dynamics, our result implies that the contribution of parameters σ^+ or c^+ to the condition for the establishment of persistent model–mimic system would be little even without the introduction of ESA (thus, with the seasonal dynamics with Equation (3) instead of Equation (9)). Our result emphasizes the importance of predator's memory of repulsive search image for the establishment of persistent model–mimic system.

In our model, the model population may become extinct in some cases, and then so the mimic population does, because the mimic population goes extinct in the absence of model population. The extinction of model population in our model can be regarded as the consequence of high predation pressure depending on the predator's memory of search image. It is taken for natural that the model population would be persistent against the predator in any established model–mimic system. In other words, the system in which the 'model' population became extinct in the history of evolution cannot be identified now as the model–mimic system. The mimic population with the model population under high predation pressure would be hard to persist, because the high predation pressure may limit the model population size at so low level that the mimicry would be maladaptive in such condition, as discussed, for example, in [4,5,13]. Extinction of the mimic population in our model could be regarded as corresponding to such extinction. If the model species of an established model–mimic system in a habitat could be observed in another independent habitat without any mimic species, it might be due to the higher predation pressure that makes the mimicry's invasion hard in the latter habitat.

In the framework of our mathematical model, we do not take account of non-mimic subpopulation belonging to the mimic species, although many mimic species have been observed to have such non-mimic subpopulation. Since the predator in our model is a generalist with some other prey species, such non-mimic subpopulation must have the predation pressure separately from that for the mimic subpopulation. This is because we assume that the predator may generally distinguish the mimic from the non-mimic, although the predator in our model cannot distinguish the mimic from its model. In such cases, the non-mimic may go extinct under the predation pressure.

If the non-mimic were more cryptic than the mimic against the predator, the reduced predation pressure may allow the non-mimic to persist. Although the net growth rate of mimic population must depend on the non-mimic subpopulation, we focus the persistence of mimic subpopulation in our mathematical considerations, so that the problem on the coexistence of mimic and non-mimic is out of the scope of this paper.

In this paper, we consider a mathematical model with a *hybrid* system of differential and difference equations. However, as seen from those mathematical results we obtained, our system could not be considered to be complicated, but be rather mathematically tractable, which has a structure led from a simplification of natural scheme in the population dynamics of model and mimic species. As most of the previous theoretical works about mimicry, numerical simulation-oriented modelling has been an easy choice of available theoretical consideration way in mathematical biology, and been useful to give some perspectives for the development of theory for some biological problems. However, it is frequently difficult to design a rational and satisfactory numerical scheme to derive results which could bring theoretically meaningful results, because of lack of biological data to estimate the parameter values used in numerical calculations. This is the case for the mimicry. In contrast, mathematical tractable model can give theoretically objective results, which is not affected by the lack of biological data, although they may be over-simplified or too abstract to bring some connection to observational/experimental research. Nevertheless, as history implies, such mathematical studies could be useful for developing the theoretical frameworks to understand the nature. We expect that our model would be so. Indeed, we do not know any other mathematically tractable population dynamics model about model–mimic system involving the effect of predator’s behavioural change linked its memory of search image.

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Appendix 1. Dynamics without model population

In this appendix, we consider the system (2), (4), (9) and (10) without the model population, that is, with $m_k(t) \equiv 0$ and $M_n \equiv 0$ for any k , any t and any n . In this case, the system consists of mimic and predator, and the daily dynamics is governed by

$$\begin{aligned} \frac{dx_k(t)}{dt} &= -P \left\{ p_k^0(t) + \frac{p_k^+(t)}{c^+} \right\} x_k(t), \\ \frac{dp_k^0(t)}{dt} &= -x_k(t)p_k^0(t), \end{aligned} \tag{A1}$$

$$\begin{aligned} \frac{dp_k^+(t)}{dt} &= p_k^0(t)x_k(t), \\ p_{k+1}^0(0) &= \lim_{t \rightarrow \infty} \{p_k^0(t) + (1 - \sigma^+)p_k^+(t)\}, \\ p_{k+1}^+(0) &= \lim_{t \rightarrow \infty} \{\sigma^+ p_k^+(t)\}, \end{aligned} \tag{A2}$$

with $(p_1^0(0), p_1^+(0)) = (1, 0)$. Since the unpalatable model population is absent, there cannot be any predator with lower search-and-attack probability, that is, $p_k^-(t) \equiv 0$ for any k and any t . This means that $p_k^0(t) + p_k^+(t) = 1$ for any k and any t .

From Equation (A1), we can find that

$$\frac{dx_k}{dp_k^+} = P \left(\frac{1}{c^+} - 1 \right) - \frac{P}{c^+} \frac{1}{1 - p_k^+},$$

and hence,

$$x_k(0) - x_k(t) = P \left(\frac{1}{c^+} - 1 \right) \{p_k^+(0) - p_k^+(t)\} + \frac{P}{c^+} \log \frac{1 - p_k^+(0)}{1 - p_k^+(t)}. \tag{A3}$$

Since $dx_k/dt < 0$ for any $p_k^+ \geq 0$ and $x_k > 0$, $x_k(t)$ is monotonically decreasing in terms of $t \geq 0$. On the other hand, since $x_k(t) \equiv 0$ is a specific solution for the first differential equation of (A1), $x_k(t)$ with any positive initial value $x_k(0) > 0$ is bounded from below, because of the uniqueness of solution. Therefore, $\lim_{t \rightarrow \infty} x_k(t) = x_k^* \geq 0$ exists with $x_k^* < \infty$. From Equation (A1) with the trivial boundedness such that $p^+ \leq 1$, making use of the analogous arguments, we find that $\lim_{t \rightarrow \infty} p_k^+(t) = p_k^{+*} \geq 0$ exists, too. At the same time, this means that $\lim_{t \rightarrow \infty} p_k^0(t) = p_k^{0*} \geq 0$ exists.

Now, from Equation (A3), since $p_1^+(0) = 0$, we have

$$x_1(0) - x_1^* = -P \left(\frac{1}{c^+} - 1 \right) p_1^{+*} - \frac{P}{c^+} \log(1 - p_1^{+*}). \tag{A4}$$

From the third differential equation of (A1), $x_1^* = 0$ or $p_1^{+*} = 1$. However, it is impossible that $p_1^{+*} = 1$, because the right-hand side of Equation (A4) is positively infinite when $p_1^{+*} = 1$ whereas the left-hand side is positively finite from the above arguments. Therefore, we find that $x_1^* = 0$.

Consequently, in case of no model population, the mimic population goes extinct in the first day of predation season.

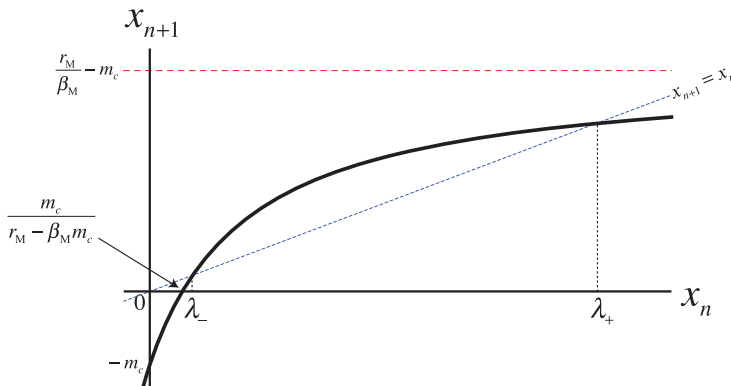


Figure A1. The function governing the discrete dynamics (A5) when the condition (19) is satisfied. λ_- and λ_+ are roots of (A6) and given by (21).

Appendix 2. Annual dynamics of model population

Substitute x_n for $[M_{n,0} - m_c]_+$ in the first difference equation of (18), and consider the following one-dimensional discrete dynamics for $x_n \in \mathbf{R}$:

$$x_{n+1} = \frac{r_M x_n}{1 + \beta_M x_n} - m_c. \tag{A5}$$

Making use of what is called cobwebbing method (for instance, see [12]), it is easily proved that $x_n < 0$ for some $n > 0$ even with any $x_1 > 0$ unless the following equation of λ has real positive roots:

$$\lambda = \frac{r_M \lambda}{1 + \beta_M \lambda} - m_c. \tag{A6}$$

Hence, the existence of real positive roots for the above equation of λ is necessary for $x_n > 0$ for any $n > 0$. If and only if the condition (19) is satisfied, the equation (A6) has two distinct real positive roots, λ_+ and λ_- given by Equation (21). When Equation (A6) has two distinct real positive roots, making use of cobwebbing method again, we can easily find that, if and only if $x_1 > \lambda_-$, we have $x_n > 0$ for any $n > 0$ and $x_n \rightarrow \lambda_+$ as $n \rightarrow \infty$ (see Figure A1). If $x_1 < \lambda_-$, then there is some $n > 0$ such that $x_n < 0$. These arguments give the necessary condition (20) for the persistence of model population.

Alternatively, since the difference equation (A5) is directly solvable, and we can obtain the following general solution:

$$x_n = \lambda_+ + (\lambda_+ - \lambda_-) \left\{ \frac{x_1 - \lambda_-}{x_1 - \lambda_+} \left(\frac{1 + \beta_M \lambda_+}{1 + \beta_M \lambda_-} \right)^{n-1} - 1 \right\}^{-1}, \tag{A7}$$

we can easily confirm the above-mentioned features of Equation (A5). Further, from this solution, we find that, when $x_1 < \lambda_-$, x_n is positive for n less than n_e given by Equation (22), and x_n is non-positive for $n \geq n_e$. Non-positive x_n corresponds to $M_{n,0} \leq m_c$ and subsequently to $M_{n+1,0} = 0$ in Equation (18).

Appendix 3. Dynamics without mimic population

In this appendix, we consider the system (2), (4), (9) and (10) without the mimic population, that is, with $x_k(t) \equiv 0$ and $X_n \equiv 0$ for any k , any t and any n . In this case, the system consists of model and predator, and the daily dynamics is governed by

$$\begin{aligned} \frac{dm_k(t)}{dt} &= -Pp_k^0(t)m_k(t), \\ \frac{dp_k^0(t)}{dt} &= -m_k(t)p_k^0(t), \\ \frac{dp_k^-(t)}{dt} &= p_k^0(t)m_k(t), \end{aligned} \tag{A8}$$

$$\begin{aligned}
 p_{k+1}^0(0) &= \lim_{t \rightarrow \infty} \{p_k^0(t) + (1 - \sigma^-)p_k^-(t)\}, \\
 p_{k+1}^-(0) &= \lim_{t \rightarrow \infty} \{\sigma^- p_k^-(t)\},
 \end{aligned}
 \tag{A9}$$

with $(p_1^0(0), p_1^-(0)) = (1, 0)$. Since the palatable mimic population is absent, there cannot be any predator with higher search-and-attack probability, that is, $p_k^+(t) \equiv 0$ for any k and any t . This means that $p_k^0(t) + p_k^-(t) = 1$ is satisfied for any k and any t .

From Equation (A8), we can find that $d(m_k + p_k^- P)/dt = 0$ for any $t \in [0, \tau]$. Thus, we have Equation (7) again for any t . Since $dm_k/dt < 0$ for any $p_k^0 > 0$ and $m_k > 0$, $m_k(t)$ is monotonically decreasing in terms of $t \geq 0$. On the other hand, since $m_k(t) \equiv 0$ is a specific solution for the first differential equation of (A8), $m_k(t)$ with any positive initial value $m_k(0) > 0$ is bounded from below, because of the uniqueness of solution. Therefore, $\lim_{t \rightarrow \infty} m_k(t) = m_k^* \geq 0$ exists. From Equation (A8) with the trivial boundedness such that $p^- \leq 1$, making use of the analogous arguments, we find that $\lim_{t \rightarrow \infty} p_k^-(t) = p_k^{-*} \geq 0$ exists, too. At the same time, this means that $\lim_{t \rightarrow \infty} p_k^0(t) = p_k^{0*} \geq 0$ exists.

If $m_k^* > 0$, then, from Equation (A8), it is necessary that $p_k^{0*} = 0$ so that $p_k^{-*} = 1$. In this case, from (7), $m_k^* = m_k(0) - \{1 - p_k^-(0)\}P$, which is valid when and only when $m_k(0) > \{1 - p_k^-(0)\}P$. In contrast, from (7), if $m_k^* = 0$, then $p_k^{-*} = p_k^-(0) + m_k(0)/P$ which is valid when and only when $p_k^-(0) + m_k(0)/P \leq 1$, that is, $m_k(0) \leq \{1 - p_k^-(0)\}P$.

Suppose that the model population persists till the k th day. Then, we have $(p_k^0(0), p_k^-(0)) = (1 - \sigma^-, \sigma^-)$ for $k \geq 1$. Therefore, if the model population persists through the k th day, we have the recurrence relation (12) with $j = k$. These arguments are the same as those for the system (2), (4), (9) and (10) with the mimic population. Consequently, the seasonal and the annual dynamics for the model population are not affected by the presence/absence of mimic population. In more detail, although its temporal variation in the daily dynamics is affected by the presence/absence of mimic population, its persistence in the seasonal and the annual dynamics is not.