

A mathematical model on community dynamics of Batesian mimicry with a general attack probability

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1 Introduction

Batesian mimicry is a similarity between an unpalatable species (model-species) and a palatable species (mimic-species) in coloration and patterns. As many examples of Batesian mimicry have been reported in various taxa, Batesian mimicry is a widespread phenomenon in nature[1]. In Batesian mimicry, once a predator eats an unpalatable model-species, it learns the distastefulness and then avoids not only the unpalatable model-species but also the palatable mimic-species. Therefore, the mimic-species can avoid predation because of the similarity to the model-species. This mechanism has been supported by many empirical studies [1].

Many theoretical studies on Batesian mimicry have been conducted so far. However, while they focused mainly on the evolution ([2] for example), they have not paid less attention to the community dynamics. In general, evolution occurs through the process of population and community dynamics. Therefore, it is needed to understand the community dynamics in detail as a basic process causing the evolution of Batesian mimicry.

Previous studies on the community dynamics of Batesian mimicry constructed and analyzed mathematical models [3, 4, 5]. In these models, the predation rates of the model-species and mimic-species are determined by their population densities. This is because predators learn the taste of prey and then become more likely to attack or ignore it, and because the opportunity to learn the taste of prey is more frequent as the population density of prey is large. Thus, in these mathematical models, it is needed to give the relationship between the predation rates and the population densities of the model-species and mimic-species.

In previous studies, the relationship about the predation rates is assumed to be a specific mathematical function as we see in the next section. However, the empirical basis of the specific function form describing the predation rates is not enough. In general, the qualitative properties of these mathematical models vary depending on the properties of the function form. This means that theoretical predictions derived in the previous studies can depend on the specific assumption about predation rate, and in that case, the predictions are neither robust nor appropriate. Here, it is required to find theoretical predictions that are independent from the specific assumption about predation rate.

In this paper, we constructed a mathematical model, in which we did not assumed a specific mathematical function, but a general mathematical function with biologically plausible conditions. Then, we analyzed the mathematical model and discussed the result comparing with the typical pattern of geographical distribution in Batesian mimicry. This paper is organized as follows: in section 2, we construct the mathematical model and make four plausible assumptions. In section 3, we show some theorems about the existence and stability of the equilibria. In section 4, we discuss the result.

2 Mathematical model

2.1 Mathematical model on community dynamics

We proposed a mathematical model on the population densities of a model-species $x(t)$ and mimic-species

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$y(t)$ at time t as follows:

$$\begin{aligned} \frac{dx}{dt} &= r_1 x \left(1 - \frac{x}{K_1} \right) - \psi_1(x, y, P), \\ \frac{dy}{dt} &= r_2 y \left(1 - \frac{y}{K_2} \right) - \psi_2(x, y, P), \\ x(0) &= x_0 > 0, \quad y(0) = y_0 > 0, \quad r_1, r_2, K_1, K_2, P > 0. \end{aligned} \quad (1)$$

Here, r_1 and r_2 represent the intrinsic growth rates of the model-species and mimic-species, and K_1 and K_2 represent the carrying capacities of the model-species and mimic-species, respectively. P represents the population density of their predator. $\psi_1(x, y, P)$ and $\psi_2(x, y, P)$ represent the predation rates of the model-species and mimic-species respectively, that is, the numbers per unit time of eaten model-species and mimic-species.

To formulate the number of eaten prey per unit time, we resolve the process of predation into the three steps: encounter, attack, and catch (Fig. 1). Based on this scheme, the number of eaten model-species (mimic-species) per unit time can be given by the multiplication of the following three terms:

- (i) **Encountered number:** This is the number of encounter between the model-species (mimic-species) and the predator individuals per unit time. The number is assumed to be $c_1 x P$ ($c_2 y P$) where c_1 (c_2) represents a positive proportionality constant.
- (ii) **Attack probability:** This is the probability of attack by a predator when the predator encounters a model-species (mimic-species). This probability for the model-species at time t is denoted by $\phi(x(t), y(t))$. For simplicity, we assumed that predators cannot distinguish the model-species and mimic-species. Therefore, the probability for the mimic-species is also given by $\phi(x(t), y(t))$.
- (iii) **Catching probability:** This is the probability of success in catching by a predator when the predator attacks an encountered model-species (mimic-species). This probability is denoted by q_1 (q_2). For simplicity, we assumed that the model-species and mimic-species die if they are caught by a predator.

Based on the above assumptions, the number of eaten model-species and mimic-species per unit time are given as follows:

$$\begin{aligned} \psi_1(x, y, P) &= c_1 x P \cdot \phi(x, y) \cdot q_1, & \psi_2(x, y, P) &= c_2 y P \cdot \phi(x, y) \cdot q_2, \\ c_1, c_2 > 0, & & 0 < q_1, q_2 \leq 1. \end{aligned}$$

By setting $\alpha \equiv c_1 q_1$ and $\beta \equiv c_2 q_2$, we get

$$\psi_1(x, y, P) = \alpha x P \phi(x, y), \quad \psi_2(x, y, P) = \beta y P \phi(x, y), \quad \alpha, \beta > 0. \quad (2)$$

Substituting Eqs. (2) into Eqs. (1), we obtain the following mathematical model:

$$\begin{aligned} \frac{dx}{dt} &= r_1 x \left(1 - \frac{x}{K_1} \right) - \alpha x P \phi(x, y), \\ \frac{dy}{dt} &= r_2 y \left(1 - \frac{y}{K_2} \right) - \beta y P \phi(x, y), \\ x(0) &= x_0 > 0, \quad y(0) = y_0 > 0, \quad r_1, r_2, K_1, K_2, \alpha, \beta, P > 0. \end{aligned} \quad (3)$$

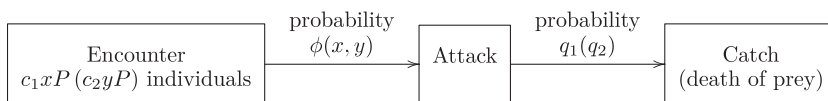


Fig. 1 Scheme of encountering, attacking and catching of predators.

2.2 Assumptions of attack probability

In the previous subsection, we constructed mathematical model (3) using the attack probability $\phi(x, y)$. Previous studies assumed the attack probability $\phi(x, y)$ to be specific functions ([4, 5] used $\frac{y}{x+y}$, and [3] used $\left(\frac{y}{x+y}\right)^s$ where $s > 0$). However, the empirical basis of these used functions is unsatisfactory. Here, instead of assuming the attack probability to be a specific function, we only make the following four assumptions on the qualitative properties of the attack probability:

- (i) The attack probability decreases when the population density of model-species increases, that is,

$$\frac{\partial \phi}{\partial x} < 0 \quad \forall x > 0 \quad \forall y > 0. \quad (4)$$

- (ii) The attack probability increases when the population density of mimic-species increases, that is,

$$\frac{\partial \phi}{\partial y} > 0 \quad \forall x > 0 \quad \forall y > 0. \quad (5)$$

- (iii) The attack probability is zero if only the model-species exists, that is,

$$\phi(x, 0) = 0 \quad \forall x > 0. \quad (6)$$

- (iv) The attack probability is equal to one if only the mimic-species exists, that is,

$$\phi(0, y) = 1 \quad \forall y > 0. \quad (7)$$

The above assumptions are not only plausible in Batesian mimicry, but also satisfied by the functions used in previous studies[3, 4, 5].

3 Result

In mathematical model (3), there are the following equilibria:

$$E_x = (K_1, 0), \quad E_y = \left(0, K_2 \left(1 - \frac{\beta P}{r_2}\right)\right), \quad E_+ = (x^*, y^*),$$

where x^* and y^* are real numbers satisfying the following equations:

$$x^* = K_1(1 - A\phi(x^*, y^*)), \quad (8)$$

$$y^* = K_2(1 - B\phi(x^*, y^*)), \quad (9)$$

$$A \equiv \frac{\alpha P}{r_1}, \quad B \equiv \frac{\beta P}{r_2}. \quad (10)$$

Here, it should be noted that a coexistence equilibrium E_+ does not always exist in the positive region. Furthermore, even if a coexistence equilibrium E_+ exists in the positive region, the number is not always one.

We provide Theorem 1 for the existence and stability of equilibrium E_x , Theorem 2 for the existence and stability of equilibrium E_y , Theorem 3 for the existence of equilibrium E_+ using Lemma 1 (in this paper, we use an "attractor" as an asymptotically stable point).

Theorem 1. *The model-only equilibrium $E_x = (K_1, 0)$ always exists on the positive x -axis. Furthermore, the equilibrium E_x is always a saddle point.*

Proof. The existence is proven from $K_1 > 0$. The Jacobian matrix at E_x is given as:

$$J|_{E_x} = \begin{pmatrix} -r_1 & -\alpha PK_1 \frac{\partial \phi}{\partial y}(K_1, 0) \\ 0 & r_2 \end{pmatrix}.$$

Therefore, the equilibrium E_x is a saddle point because $\text{Det} J|_{E_x} = -r_1 r_2 < 0$. \square

Theorem 2. *The mimic-only equilibrium $E_y = (0, K_2(1 - B))$ exists on the positive y -axis if and only if $B = \beta P/r_2 < 1$. When the equilibrium E_y exists, the stability is as follows:*

- (i) *The equilibrium E_y is a saddle point if $A < 1$.*
- (ii) *The equilibrium E_y is an attractor if $A > 1$.*

Proof. The existence is proven from $K_2 > 0$. Noting that $\frac{\partial \phi}{\partial y}(0, y) = 0$ for $y > 0$ from Eq.(7), the Jacobian matrix at E_y is given as:

$$J|_{E_y} = \begin{pmatrix} r_1(1 - A) & 0 \\ -\beta PK_2(1 - B) \frac{\partial \phi}{\partial x}(0, K_2(1 - B)) & -r_2(1 - B) \end{pmatrix}.$$

The inequality $-r_2(1 - B) > 0$ holds from $B < 1$. (i) From $r_1(1 - A) > 0$, $\text{Det} J|_{E_y} < 0$. Therefore, the equilibrium E_y is a saddle point. (ii) From $r_1(1 - A) < 0$, $\text{Tr} J|_{E_y} < 0$ and $\text{Det} J|_{E_y} > 0$. Therefore, the equilibrium E_y is an attractor. \square

Lemma 1. *A point (x^*, y^*) is a positive equilibrium if and only if a positive real number x^* satisfies the following two conditions:*

- (i) $\eta(x^*) > 0$,
- (ii) $\zeta(x^*) = 1$,

where

$$\eta(x) = \frac{BK_2}{AK_1}x + K_2 \left(1 - \frac{B}{A}\right), \quad \zeta(x) = A\phi(x, \eta(x)) + \frac{x}{K_1}.$$

Proof. Suppose that (x^*, y^*) is a positive equilibrium. From Eqs. (8) and (9),

$$\phi(x^*, y^*) = \frac{1}{A} \left(1 - \frac{x^*}{K_1}\right) = \frac{1}{B} \left(1 - \frac{y^*}{K_2}\right). \quad (11)$$

Rearranging Eq. (11) in terms of y^* , we get

$$y^* = \frac{BK_2}{AK_1}x^* + K_2 \left(1 - \frac{B}{A}\right) = \eta(x^*). \quad (12)$$

From this equation (12), $\eta(x^*) = y^* > 0$. Therefore, condition (i) is satisfied. Substituting this relation $y^* = \eta(x^*)$ into Eq. (8), we obtain $x^* = K_1[1 - A\phi(x^*, \eta(x^*))]$. This equation can be transformed into

$$1 = A\phi(x^*, \eta(x^*)) + \frac{x^*}{K_1} = \zeta(x^*). \quad (13)$$

Therefore, condition (ii) is also satisfied. The converse is equally true. \square

Theorem 3. *A coexistence equilibrium $E_+ = (x^*, y^*)$ exists in the positive region if any one of the following conditions are satisfied:*

- (i) $A \leq B$.
- (ii) $B < A < 1$.

Proof. (i) Suppose that $A \leq B$. Function $\eta(x)$ is positive if and only if $x > K_1(1 - A/B) \equiv \hat{x}$, and any equilibrium does not exist in $x \geq K_1$. Therefore, we focus only on x in the range (\hat{x}, K_1) . From Eqs. (5) and (6), $\zeta(K_1) = A\phi(K_1, K_2) + 1 > 1$. In contrast, $\zeta(\hat{x}) = 1 - A/B < 1$. Therefore, from intermediate value theorem, there exists $x^* \in (\hat{x}, K_1)$ satisfying $\zeta(x^*) = 1$ and $\eta(x^*) > 0$. Hence, from Lemma 1, coexistence equilibrium E_+ exists at least one in the positive region.

(ii) Suppose that $B < A < 1$. Function $\eta(x)$ is always positive for positive x . From Eqs. (5) and (6), $\zeta(K_1) = A\phi(K_1, K_2) + 1 > 1$. In contrast, from Eq. (7), $\zeta(0) = A < 1$. Therefore, from intermediate value theorem, there exists $x^* \in (0, K_1)$ satisfying $\zeta(x^*) = 1$ and $\eta(x^*) > 0$. Hence, from Lemma 1, coexistence equilibrium E_+ exists at least one in the positive region. \square

4 Discussion

Through the analysis in this paper, we clarified the behavior of mathematical model (3). Particularly, the following facts are revealed:

- The model-only equilibrium (E_x) is always unstable (Theorem 1).
- The mimic-only equilibrium (E_y) is stable in a parameter region (Theorem 2).
- A coexistence equilibrium (E_+) exists in a parameter region (Theorem 3).

Here, we focus on the instability of the model-only equilibrium (E_x), and call the theoretical prediction "model-only instability". Based on the prediction "model-only instability", we can make a prediction on the geographical distribution of a model-species and a mimic-species. Let us consider an examination of various habitats where a model-species or a mimic-species can exist. In general, environmental conditions in habitats are various, and depending on the environmental conditions, the equilibrium state in each habitats also varies. Therefore, if prediction "model-only instability" is true and the interactions between habitats can be ignored, then the habitats that can be observed are habitats where they coexist, habitats where mimic-species only exists without model-species, and habitats where neither the two species do not exist.

Actually, this expectation is consistent with several examples of Batesian mimicry in nature. [6] reported that more than ten cases of Batesian mimicry show the same pattern of geographical distribution, and that in the typical pattern of geographical distribution, the range of mimic-species is wider than that of model-species (Fig. 2). This means that the habitats where only the model-species exists are not observed, and is consistent with the prediction "model-only instability".

In this paper, we constructed and analyzed a mathematical model on the community dynamics of Batesian mimicry, and the derived prediction is consistent with the typical pattern of geographical distribution. The theoretical prediction is robust because our mathematical model did not assume a specific attack probability.



Fig. 2 Illustration of the distribution of a model-species (venomous snake, *Micrurus fulvius*) and a mimic-species (non-venomous snake, *Lampropeltis elapsoides*) in the southeastern United States. There are three types of area: the area where they coexist (black), the area where mimic-species only exists (stripe) and the area where both species does not exist (white). This figure was remade from [6, Figure 1].

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