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Graphical Abstract

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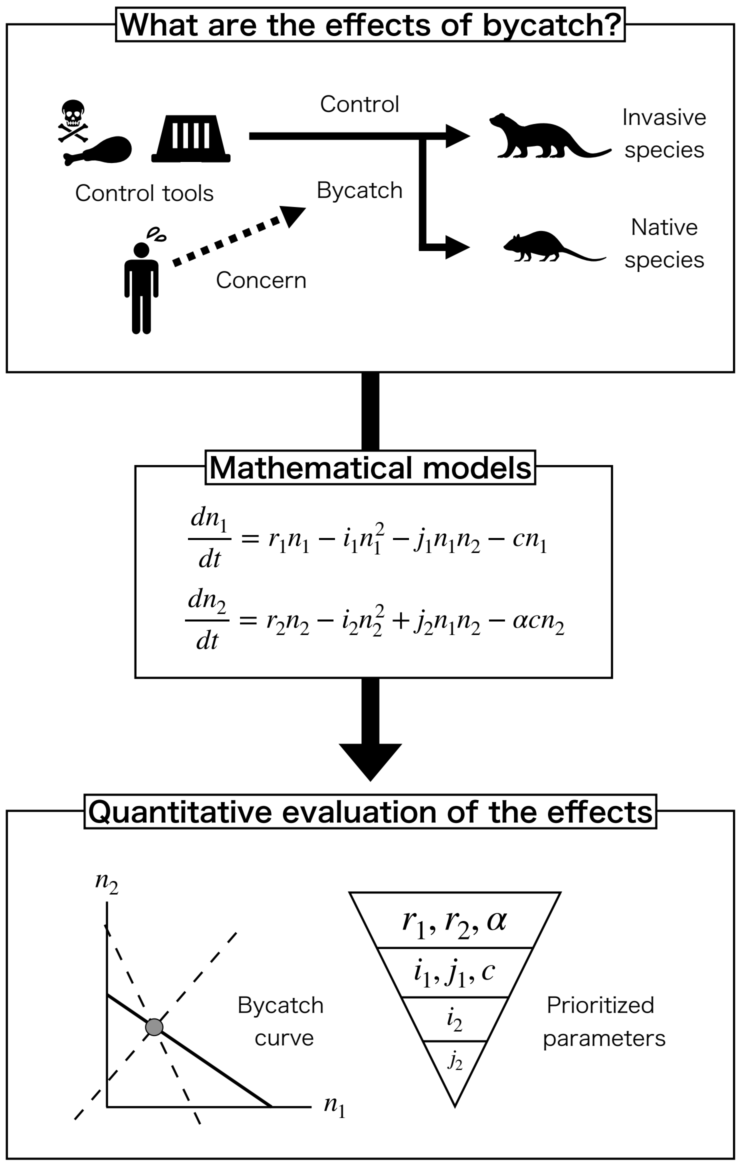

Highlights

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- Bycatch curve was defined to show the density changes of native and invasive species
- Parameter priority was determined for estimation in actual control programs
- With intrinsic growth rates and specific killing rate, control success is determined
- With some parameters, the simple model gives approximate density changes of species
- With sufficient parameters, the basic model gives eradication goals in detail

Quantitative evaluation of the effects of bycatch on native species using mathematical models

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Abstract

Traps and poison bait are used to control invasive species and protect native species. However, the traps can kill native species and the poison bait may increase their mortality. As it interferes with conservation efforts, it is necessary to evaluate the effects of such bycatch. However, there are few theoretical methods for quantification of these effects.

This paper presents a method for quantitatively evaluating the effects of bycatch on native populations, using a mathematical model that represents the population dynamics of native and invasive species.

The mathematical model suggested the conditions under which only invasive species will be eliminated even if bycatch occurs. We also present the concept of the "bycatch curve", which shows the population density according to the killing rate. In addition, a mathematical simulation is presented using parameters estimated for the Amami-Oshima system.

These theoretical results allowed us to determine the parameters that should be prioritized for estimation in actual control programs.

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Keywords: Bycatch, Conservation, Control programs, Invasive species, Native species, Parameter priority

1. Introduction

Invasive species have a serious impact on native populations and can threaten their survival (Courchamp, Chapuis, et al., 2003). Mongooses and rats appear in “100 of the World's Worst Invasive Alien Species ” (Lowe et al., 2000), and their introduction into a closed system such as an island, where population immigration and emigration can be neglected, subjects native species to greater predation and competition over a shorter period of time than in an open system, such as the mainland (Hays & Conant, 2007; Shiels et al., 2014). Control programs in closed systems must be based on prompt and accurate surveys (Courchamp, Chapuis, et al., 2003).

There are two main types of control methods: traditional and biological methods (Courchamp, Chapuis, et al., 2003). Traditional methods include fencing, shooting, poisoning, and trapping. Traps are mainly used for mongooses (Hays & Conant, 2007), while traps and poison bait are employed for rats (Shiels et al., 2014). However, these methods may increase the mortality rate of native species. This unintended increase in mortality is called bycatch, and has already been recognized in marine systems (Hall et al., 2000; Lewison et al., 2004; Davies et al., 2009). However, it is also becoming increasingly problematic in terrestrial systems. For example, on Amami-Oshima Island, Japan, traps have been used to control the small Indian mongoose [*Herpestes* *auropunctatus*] (Watari, Takatsuki, et al., 2008; Fukasawa, Hashimoto, et al., 2013; Watari, Nishijima, et al., 2013), but as the mongoose population declined, the mortality of native species, such as the Amami spiny rat [*Tokudaia osimensis*] and the Ryukyu long-haired rat [*Diplothrix legata*], increased due to bycatch (Fukasawa, Miyashita, et al., 2013), which made it difficult to continue the control program (Watari 2011). In New Zealand, rats and possums have been eradicated by poison bait, such as brodifacoum and compound 1080 [*sodium monofluoroacetate*] (Innes & Barker, 1999; Howald et al., 2007). These methods have increased the mortality of native species, and also caused secondary poisoning of predators of invasive species (Rmpson & Miskelly, 1999; Powlesland et al., 1999; Eason et al., 2002), rising concerns about their use (Veitch & Clout, 2001; Courchamp, Chapuis, et al., 2003; Towns et al., 2006; Howald et al., 2007).

To prevent the unintended death of native species, it is necessary to evaluate bycatch by conducting detailed surveys, examining control plans, and predicting outcomes (Cromarty et al., 2002; Courchamp, Chapuis, et al., 2003). Bycatch has been quantified by field monitoring (Taylor & Thomas, 1993; Dowding et al., 1999; Empson & Miskelly, 1999; Powlesland et al., 1999; Eason et al., 2002) and statistical estimation (Armstrong et al., 2002; Watari, Nishijima, et al., 2013; Alderman et al., 2019), but there are few options available for theoretical evaluation. Some studies have proposed that it is necessary to kill all invasive species to prevent a negative impact on native species (e.g., Cromarty et al., 2002), whereas others have argued that invasive species should merely be minimized in consideration of bycatch (e.g., Eason et al., 2002; Courchamp et al., 2003; Howald et al., 2007). However, there is no method for determining the most appropriate control strategy.

We constructed differential equation models to resolve these problems. Our models are similar to previous differential equation models of consider bycatch (Pascoe, 1997; Anderson & Seijo, 2010; Clark, 2010). However, previous bycatch models were constructed for resource management and economic applications in the context of marine systems; by contrast, our model was designed for conservation applications in terrestrial systems, and provides a means to quantify the consequences of bycatch and determine the most appropriate control strategy.

2. Methods

We constructed mathematical models to describe the dynamics of native and invasive populations. As predation by invasive species, such as mongooses and rats, is a major factor in the decline of native species (Courchamp, Chapuis, et al., 2003; Hays & Conant, 2007; Shiels et al., 2014), this study assumed that the density of native species is negatively correlated with that of invasive species. In addition, this study focused on a closed system. Based on these assumptions, a simple Lotka-Volterra model with logistic growth was used to model changes in the population density of two species in the absence of control (Volterra 1926; Pearl & Reed, 1977; Berryman 1992; Lotka 2002),

$$\begin{aligned}\frac{dn_1}{dt} &= r_1 n_1 - i_1 n_1^2 - j_1 n_1 n_2,\\ \frac{dn_2}{dt} &= r_2 n_2 - i_2 n_2^2 + j_2 n_1 n_2.\end{aligned} \tag{1}$$

The upper and lower equations represent the native and invasive populations, respectively, where n_1, n_2 are the population densities, r_1, r_2 are the intrinsic growth rates, i_1, i_2 are the intraspecific interaction coefficients, and j_1, j_2 are the interspecific interaction coefficients. All parameters are positive and carrying capacities can be expressed as $k_1 = r_1/i_1,\ k_2 = r_2/i_2$. The functional response was assumed to be mass-action because invasive species, such as mongooses and rats, are often omnivorous and their interactions are approximately random (Hays & Conant, 2007; Shiels et al., 2014).

A term representing bycatch is used in our model:

$$\begin{aligned}\frac{dn_1}{dt} &= r_1 n_1 - i_1 n_1^2 - j_1 n_1 n_2 - c n_1,\\ \frac{dn_2}{dt} &= r_2 n_2 - i_2 n_2^2 + j_2 n_1 n_2 - \alpha c n_2,\end{aligned} \tag{2}$$

where c is the killing rate of native species, and α is the "specific killing rate" of invasive species, which generally satisfies $1 \leq \alpha$. α and c satisfy $0 \leq \alpha c \leq 1$, as it is obviously not possible to kill more individuals of an invasive species than exist. These linear terms reflect the fact that traps and poison bait are often arranged uniformly in spatial terms (Powlesland et al., 1999; Alderman et al., 2019).

3. Results

Model (2) behaves in three distinct ways depending on the population parameters. Based on the results of Gause & Witt (1935), we reformulated the model (2) using $r'_1 = r_1 - c,\ r'_2 = r_2 - \alpha c$:

$$\frac{dn_1}{dt} = r'_1 n_1 - i_1 n_1^2 - j_1 n_1 n_2, \tag{3}$$
$$\frac{dn_2}{dt} = r'_2 n_2 - i_2 n_2^2 + j_2 n_1 n_2. \tag{4}$$

These equations describe three behaviors:

$$\begin{cases} \text{(a) Native species become extinct and only invasive species survive,} \\ \qquad \text{if} \quad i_2/j_1 \leq r'_2/r'_1 \\ \text{(b) Both native and invasive species survive,} \\ \qquad \text{if} \quad -j_2/i_1 < r'_2/r'_1 < i_2/j_1 \\ \text{(c) Invasive species become extinct and only native species survive,} \\ \qquad \text{if} \quad r'_2/r'_1 \leq -j_2/i_1 \end{cases} \tag{5}$$

If the system is in state (a) and the native population is threatened with extinction, the condition $i_2/j_1 \leq r'_2/r'_1$ is considered to be satisfied because the predation pressure on native species j_1 is sufficiently greater than the density dependence of invasive species i_2. In this case, extinction of native species must be avoided by increasing the killing rate c; this paper considers the case where the killing rate c is increased from state (a).

Increasing c yields two different results depending on whether the specific killing rate α satisfies the following inequality:

$$\alpha > r_2/r_1. \tag{6}$$

When (6) holds, r'_2/r'_1 decreases monotonically with respect to c, and the dynamical system reaches (b) at $c = c_\beta$ and (c) at $c = c_\gamma$. c_β and c_γ are expressed as:

$$c_\beta = \frac{r_2 j_1 - r_1 i_2}{\alpha j_1 - i_2}, \quad c_\gamma = \frac{r_2 i_1 + r_1 j_2}{\alpha i_1 + j_2}. \tag{7}$$

As these values are given explicitly, they can be used as target values for the control program. On the other hand, when the population parameters do not satisfy (6), r'_2/r'_1 increases monotonically or remains unchanged with respect to c, and the system maintains state (a). Thus, to prevent the extinction of native species, we have to ensure that $\alpha > r_2/r_1$ is valid.

When the system is in state (b) and equilibrium, we are able to visualize the density changes of two species caused by the control program. Nullclines in (2) (when the system is in equilibrium) satisfy:

$$\begin{aligned} r_1 - i_1 n_1 - j_1 n_2 - c &= 0, \\ r_2 - i_2 n_2 + j_2 n_1 - \alpha c &= 0. \end{aligned} \tag{8}$$

Eliminating c from these equations, a single curve is obtained:

$$n_1 = \frac{(\alpha r_1 - r_2) - (\alpha j_1 - i_2)n_2}{(\alpha i_1 + j_2)}. \tag{9}$$

When c is varied, the fixed point of coexistence moves along the curve. Thus, this curve represents the change in density of invasive and native species when the killing rate c is modified in the control plan. We defined this curve as the "bycatch curve" (Fig. 1). If $\alpha > r_2/r_1$ and $j_1 > i_2$ hold, the bycatch curve passes through the first quadrant and satisfies $c = c_\beta$ at the fixed point that intersects with the n_2 axis, and satisfies $c = c_\gamma$ at the fixed point that intersects with the n_1 axis. The bycatch curve can be adapted even though the interaction term is more complex, but the fixed point of coexistence must be stable.

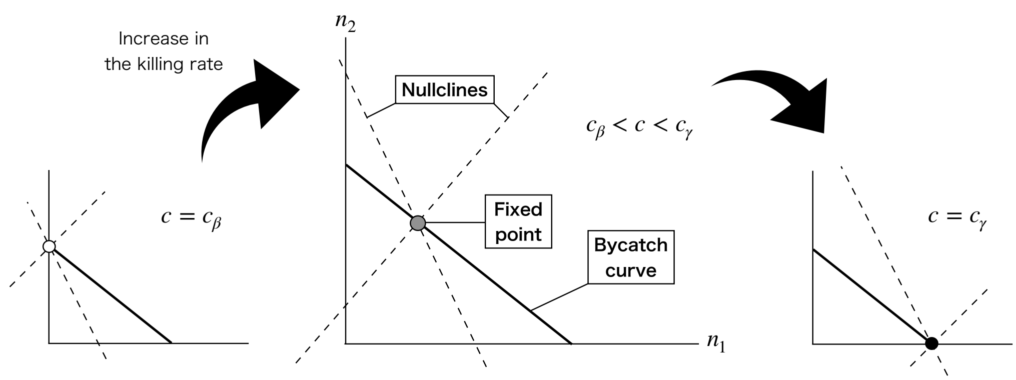

Figure 1: Concept of the bycatch curve (9). When (6) is satisfied, it represents the trajectory of a fixed point with variation of the killing rate c on the phase plane, and c_β, c_γ are the targets of the control.

Using this model, we performed an example simulation assuming that the Amami spiny rat is a native species and the small Indian mongoose is an invasive species. From Bayesian estimations conducted in previous studies (Fukasawa, Hashimoto, et al., 2013; Watari, Nishijima, et al., 2013), the values of the population parameters were set to $r_1 = 8$, $i_1 = 0.4$, $j_1 = 0.4$, $r_2 = 0.5$, $i_2 = 0$, $n_1(0) = k_1 = 20$. Assuming that the the control gradually increases, c is set to increase linearly $c = 0.01 \cdot t$ (where t is year). As j_2 and $n_2(0)$ were not estimated in previous studies, j_2 was set to 0.01 assuming a conversion rate of about 1/40, and $n_2(0)$ was set to 0.01 because the number of initially introduced individuals was very small. In the absence of control ($c = 0$), the system is in state (a) because $i_2/j_1 = 0$ and $r_2/r_1 = 0.0625$ satisfy the condition $i_2/j_1 < r_2/r_1$. If the specific killing rate α exceeds the threshold $r_2/r_1 = 0.0625$, the system can be transitioned to state (b) or (c) by increasing the killing rate c. When $\alpha = 1, 2, 3$, the goals of the killing rate $c_\beta = 0.50/\alpha$, $c_\gamma = 0.28/(0.4\alpha + 0.01) \sim 0.70/\alpha$ are, respectively:

$$\begin{cases} \alpha = 1: \ c_\beta = 0.50, \ c_\gamma \sim 0.70 \\ \alpha = 2: \ c_\beta = 0.25, \ c_\gamma \sim 0.35 \\ \alpha = 3: \ c_\beta = 0.17, \ c_\gamma \sim 0.23 \end{cases} \tag{10}$$

As the linearly increasing c becomes 0.20 in 20 years and 0.40 in 40 years, the simulation results (Fig. 2: left) are interpreted as follows:

$$\begin{cases} \alpha = 1: \text{The control is very low,} \\ \qquad\quad \text{and only the native species goes extinct.} \\ \alpha = 2: \text{The control is not sufficient,} \\ \qquad\quad \text{and the native species goes extinct before the invasive species.} \\ \alpha = 3: \text{The control is sufficiently high,} \\ \qquad\quad \text{and only the invasive species goes extinct.} \end{cases} \tag{11}$$

It seems that $\alpha = 1, 2$ cannot protect native species, but $\alpha = 3$ facilitates their conservation. In the case of $\alpha = 3$, it may be assumed that the number of invasive species has not decreased in the middle of the eradication period (e.g., 20th year), and that eradication cannot be achieved; this is reasonable when comparing the killing rate at that time (0.20) with the target ($c_\gamma \sim$ 0.23).

4. Discussion

It has been suggested that the negative impact of bycatch on native species is smaller than that of invasive species (Innes & Barker, 1999; Hays & Conant, 2007; Jones et al., 2016), but there is no real theoretical basis for this opinion. This paper suggested that only the invasive population will become extinct by increasing the killing rate if $\alpha > r_2/r_1$ and $j_1 > i_2$ hold. When we

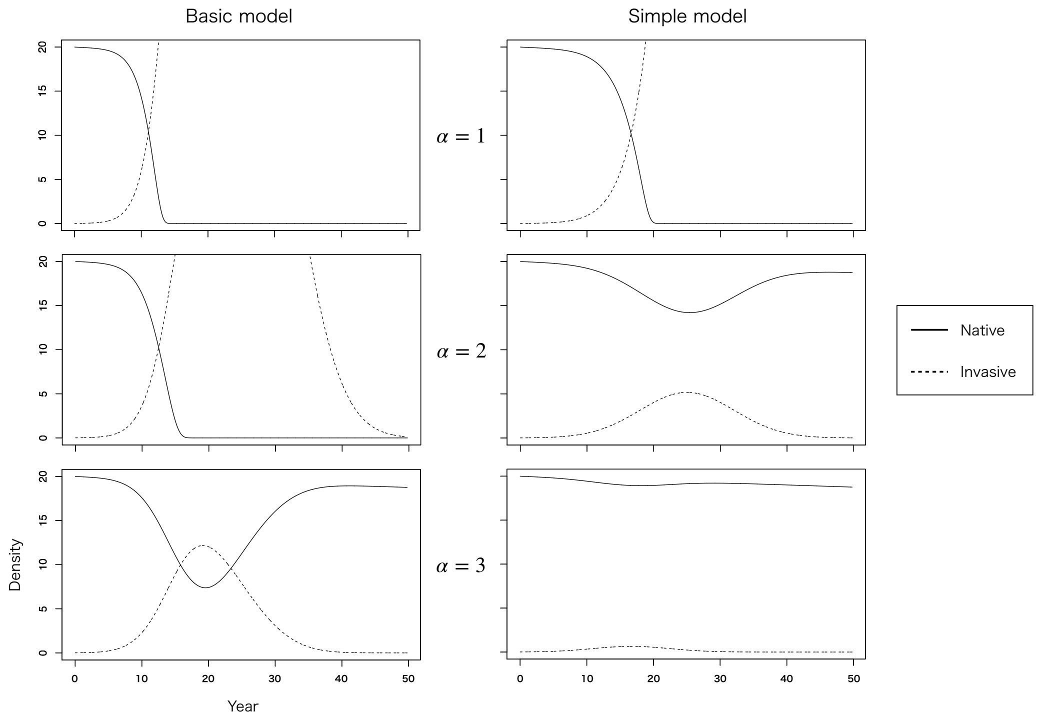

Figure 2: Example simulation using model (2) [Left] and model (12)[Right]. The value of the parameters and initial conditions were set to $r_1 = 8,\ i_1 = 0.4,\ j_1 = 0.4,\ r_2 = 0.5,\ i_2 = 0,\ j_2 = 0.01,\ c = 0.01 \cdot t,\ n_1(0) = 20,\ n_2(0) = 0.01$, where t is year.

can configure α to satisfy $\alpha > r_2/r_1$, this opinion is theoretically supported. When this condition is satisfied, c_β and c_γ are important values for the killing rate. As c_β is the minimum killing rate at which native species survive and c_γ is the minimum killing rate at which invasive species go extinct, the former can serve as the first goal of eradication, and the latter as the ultimate goal. In addition, using the bycatch curve, we can visualize the path of a fixed point on the phase plane as the killing rate changes. As this concept represents only the equilibrium state, it may not provide detailed information on the behavior of the system in the non-equilibrium state. However, it can be a useful indicator when implementing long-term plans in which there is sufficient time for the system to reach equilibrium.

To apply these results in real projects, information on population parameters is necessary. For example, there are classically static and dynamic approaches for estimating intraspecific i and interspecific interaction coefficients j (MacArthur & Levins, 1967; Seifert & Seifert, 1976; Shenbrot & Krasnov, 2002). When estimating these interactions for invasive species, it is necessary to use a dynamic approach that can be adapted to non-equilibrium conditions, rather than a static approach that assumes equilibrium conditions (Shenbrot & Krasnov, 2002). In statistical estimations, Bayesian estimation is considered to be useful because it can take into account uncertainty (Watari, Nishijima, et al., 2013; Alderman et al., 2019).

It may be ideal to estimate all parameters, but it is difficult to evaluate the interactions of invasive species when we do not have time to collect enough data or the density of native species is low at the outset of the project. In these cases, a simple approach would be useful. The model (2) assumes that invasive species have negative density dependence and benefit from predation on the native species, but if the invasive species is still increasing and the native species is already low-density, these effects are expected to be smaller than those of other terms. The model (2) is then simplified as follows:

$$\begin{aligned}\frac{dn_1}{dt} &= r_1 n_1 - i_1 n_1^2 - j_1 n_1 n_2 - c n_1,\\ \frac{dn_2}{dt} &= r_2 n_2 - \alpha c n_2.\end{aligned} \tag{12}$$

This model has the solutions:

$$\begin{aligned} n_1(t) &= \frac{e^{A(t)}}{e^{A(0)}/n_1(0) - \int_0^t i_1 e^{A(\tau)} d\tau},\\ n_2(t) &= n_2(0) e^{\int_0^t (r_2 - \alpha c) d\tau},\\ A(\tau) &= \int (j_1 n_2(\tau) + c - r_1) d\tau. \end{aligned} \tag{13}$$

Here, the eradication goals of invasive species αc_β and αc_γ correspond to the intrinsic growth rate of invasive species r_2. Model (12) enables us to broadly understand the population dynamics with only six parameters, r_1, r_2, i_1, j_1, c, α, but it should again be noted that this approach is justified only if $i_2 \sim 0$ and $j_2 \sim 0$ hold.

Example simulations from (2) and (12) are shown in (Fig. 2). The actual killing rate imposed on invasive species in Amami is considered to be roughly $\alpha c = 0.02 \cdot t$ (Fukasawa, Hashimoto, et al., 2013). This result corresponds to the current Amami condition, where native species have disappeared around the area where the mongoose was introduced (Watari, Takatsuki, et al., 2008; Watari, Nishijima, et al., 2013). To avoid such a situation, it would have been necessary to sufficiently increase the killing rate and specific killing rate, as shown in (Fig. 2: bottom left). When $\alpha = 1$ (control is very low) or $\alpha = 3$

(control is sufficiently high), the final results do not differ between model (2) and model (12), but a large difference is observed when $\alpha = 2$. In this case, model (2) suggests extinction of native species (Fig. 2: middle left), but model (12) indicates survival of native species and overestimates the effect of control (Fig. 2: middle right), because it ignores the initial growth of invasive species by predation. As can be seen from this example, when using the model (12), it is essential to check if the assumptions $i_2 \sim 0$ and $j_2 \sim 0$ are sufficiently valid to ensure that the estimates do not differ significantly from the real system.

The results of this study suggest the parameters that should be prioritized for estimation (Fig. 3). We should start by measuring the intrinsic growth rate, r_1, r_2, and the specific killing rate α. Based on these parameters and inequality (6), we can determine whether the control program eradicates only invasive species. Next, it is recommended to estimate the interaction coefficients of the native species i_1, j_1 and killing rate c. These parameters, along with r_1, r_2, allow us to understand the approximate dynamics of the system by the model (12). Then, when we obtain the intraspecific coefficient of the invasive species, i_2, we can use the condition (5) to determine whether the system exists in state (a), and whether eradication is urgently needed. Finally, if the interspecific coefficient of the invasive species j_2 is acquired, it is possible to set detailed goals using the model (2) and bycatch curve (9).

In mathematical modeling studies, control of invasive species can lead to counterintuitive results (Courchamp, Langlais, et al., 1999; Courchamp,

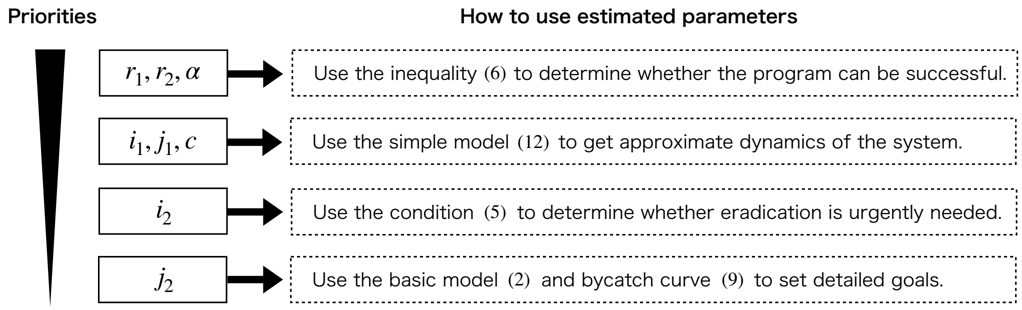

Figure 3: Parameters to be prioritized for estimation. r_1, r_2 are the intrinsic growth rates, i_1, i_2 are the intraspecific interaction coefficients, j_1, j_2 are the interspecific interaction coefficients, c is the killing rate of native species, and α is the specific killing rate of invasive species. Subscripts 1 and 2 denote native and invasive species, respectively.

Langlais, et al., 2000; Caut et al., 2007). Therefore, it is important to identify the characteristic interactions among species and model them in a flexible manner. For example, if secondary poisoning is a concern, it may be necessary to use a model that takes into account predators of higher trophic levels than the invasive species. In addition, if the invasive species is an opportunistic predator or its spatial distribution is not uniform, the interaction term must be improved. A descriptive approach using food webs is useful to identify interactions among species (Innes & Barker, 1999).

To resolve concerns about bycatch, it is necessary to prove the validity of the control plan with sufficient evidence. Therefore, we hope that the results of this study will not be used independently, but in combination with experimental data.

Declaration of competing interest

The author has no competing interest directly relevant to the content of this article.

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