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Invasive species management in two-patch environments: Agricultural damage control in the raccoon (Procyon lotor) problem, Hokkaido, Japan[*]

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Abstract

We develop discrete-time models for analyzing the long run equilibrium outcomes on invasive species management in two-patch environments with migration. In particular, the focus is upon a situation where removal operations for invasive species are implemented only in one patch (controlled patch). The new features of the model are that (i) asymmetry in density dependent migration is considered, which may originate from impact of harvesting as well as heterogeneous habitat conditions, and (ii) the effect of density-dependent catchability is well-taken to account for the nature that the required effort level to remove one individual may rise as the existing population decreases. The model is applied for agricultural damage control in the raccoon problem that has occurred in Hokkaido, Japan. Numerical illustrations demonstrate that the long run equilibrium outcomes highly depend on the degree of asymmetry in migration as well as the sensitivity of catchability in response to a change in the population size of invasive species. Furthermore, we characterize the conditions under which the economically optimal effort levels are qualitatively affected by the above two factors and aiming at local extermination of invasive species in the controlled patch is justified.

Key Words: Catchability, Density dependent migration, Local extermination, metapopulation, Removal effort

[*] We are responsible for any remaining errors.

"The problem of invasive species and their control is one of the most pressing applied issues in ecology today (Hastings et al., 2006)."

1   Introduction

The invasive species have increasingly been acknowledged as a global threat, since they could fundamentally destroy indigenous ecosystem after its establishment (Shigesada and Kawasaki, 1997; Perrings et al., 2000a). Although there are several unique characteristics accompanied with invasive species that contribute to social damage, one critical feature is that they tend to spread or disperse very quickly once they succeed in invasion. Such quick dispersion partly reflects the fact that native species do not possess defensive skills against newcomers in many cases (Perrings et al., 2000b).

Many governmental attempts have been made to eradicate the established invasive species. Unfortunately, however, only a few succeeded, and most of them failed especially when the habitat is sufficiently large (Bomford and O'Brien, 1995). That is, the management official ends up halting eradication attempts (Myers et al., 1998; Bomford and O'Brien, 1995; Clout and Veitch, 2002). When the invasive species are widespread in a large habitat, catchability could be decreasing in the population size of invasive species. This implies that the cost of removing the last 1-10% population becomes prohibitively expensive, and thus achieving extermination appears to be extremely difficult (Myers et al., 1998; Bomford and O'Brien, 1995). In summary, we call such a problem "the issue of density-dependent catchability."

Given the historical fact, many researchers and practitioners sometimes recommend "area-wise control," which includes attempts for local extermination. Such regimes in invasive species management are that removal operations for invasive species are made only in some part of the whole habitat where some important industry or ecological

asset is located such as agriculture. Real world examples in which area-wise control is undertaken as a management strategy include: raccoon (*Procyon lotor*) problems in Hokkaido, Japan, Crown-of-thorns starfish (*Acanthaster planci*) problems in Okinawa, Japan, and many other instances in various places as well. As an example from native species control problems, sika deer management program is well-known, which has been enforced since 1998 in Hokkaido, Japan. In this program, Hokkaido is divided into several regions and area-wise control strategies are undertaken (Matsuda et al., 1999).

Whereas area-wise controls have recently emerged as a management scheme in invasive species management, a series of literature, which analyze the management strategy in this vein, mainly focus upon a situation where invasive species are reproduced and removals are implemented in a single closed system (Eisewerth and Johnson, 2002; Perrings, 2005; Hastings et al., 2006; Olson and Roy, 2002). However, such a framework is not appropriate when removal efforts are locally implemented.

It is noted by several papers that a meta-population model is more appropriate since (i) local removals potentially impact the inter- and intra-species competition, and (ii) habitat conditions may simply be heterogenous (Delong and Lamberson, 1999; Holt, 1985; Hastings, 1982). As a result, density dependent migration may become asymmetric (Armstrong and Skonhoft, 2006; Tuck and Possingham, 1994). Although there may be several works which consider area-wise controls, none of them, to the best of our knowledge, explicitly examine the effect of a meta-population structure, density-dependent catchability and asymmetry in migration in the invasive species management. Thus this paper seeks to tackle these issues. At this point, several open questions come to mind:

1. What would be an appropriate measure for effectiveness of removal efforts from the long run perspective?

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2. Is there any situation where it is better to aim at local extermination even with a meta-population?

3. How do the degree of asymmetry in migration and the density-dependent catchability affect the long-run equilibrium outcome?

4. How does an economically optimal effort level change with the above two factors?

The goal and contribution of this research are to develop a simple framework of discrete-time models for analyzing the long-run consequences of removal operations for a meta-population, and to answer a set of the aforementioned questions in the context of invasive species management. In particular, an ecological model with two-patch environments is proposed, considering the key features of invasive species controls: (i) asymmetry in density dependent migration, and (ii) the effect of density-dependent catchability, i.e., required effort level to remove one individual could rise as the existing stock decreases.

While we do not obtain analytical characteristics due to non-linearity in the form of density-dependent catchability, we demonstrate that it could be utilized for a real world case study of invasive species management. For the purpose of illustration, the model is applied to agricultural damage control in the raccoon problem that has occurred in Hokkaido, Japan. In this application, we consider two economic functions so as to measure the effectiveness of removal effort levels: 1. agricultural damage originating from roaming raccoons and 2. removal costs which are formulated as a function of removal efforts. We first investigate the long run equilibrium outcomes of ecological variables and the associated economic functions, and then discuss an economically optimal effort level.

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2   Model

Management officials seek to balance the cost of removal operations and damage that originates from roaming invasive species. Therefore, management officials are sometimes determined to implement removal operation only in some part of the whole habitat areas of invasive species as noted in the previous section. This may be due to the fact that the whole habitat areas could be too huge to be covered by removal operation, or the budget in every period may not be sufficient to do so.

The simplest framework for the analysis of such a situation is applying an ecological model in two-patch environments (Holt, 1985). The area in which removal operations are implemented is denoted as controlled patch, and the other areas in which no removal operation is implemented are denoted as uncontrolled patch.

2.1   Ecological model

Consider the following system of population dynamics over time in the two-patch environments in which removal operations are implemented only in one patch:

$$
\begin{aligned}
X_{1,t+1} &= F(X_{1,t}) - M(X_{1,t}, S_{2,t}) \\
&= X_{1,t} + r_1 X_{1,t}(1 - X_{1,t}/K_1) - m(\beta X_{1,t}/A_1 - S_{2,t}/A_2),
\end{aligned}
\tag{1}
$$

and

$$
\begin{aligned}
X_{2,t+1} &= F(S_{2,t}) + M(X_{1,t}, S_{2,t}) \\
&= S_{2,t} + r_2 S_{2,t}(1 - S_{2,t}/K_2) + m(\beta X_{1,t}/A_1 - S_{2,t}/A_2),
\end{aligned}
\tag{2}
$$

$$
S_{2,t} = X_{2,t} - H_{2,t},
\tag{3}
$$

where

$X_{1,t}$ is invasive species population in uncontrolled patch at period t;

$X_{2,t}$ is invasive species population in controlled patch at the beginning of period t;

$r_i, i = 1, 2$ is the intrinsic growth rate of habitat i;

$K_i, i = 1, 2$ is the carrying capacity of habitat i;

$A_i, i = 1, 2$ is the area of habitat i;

$m(> 0)$ is a parameter representing the general magnitude of migration between habitats;

$\beta(> 0)$ is a parameter to take account of the fact that the migration may be due to different habitat potentials within the two sub-populations caused by harvesting in controlled patch and by heterogeneous habitat conditions;

$H_{2,t}$ is population removed in controlled patch at period t;

$S_{2,t}$ is escapement in controlled patch at period t.

In the above model, we simply ignore heterogeneity in the density and in the migration probability within the habitat. In addition, we assume that the per capita migration rates in habitats 1 and 2 are respectively $m'\beta A_2$ and $m'A_1$, which is proportional to the area of destination. The numbers of migrants from habitat 1 to 2 and from 2 to 1 are respectively $m'\beta A_2 X_1$ and $m'A_1 S_2$. Replacing $m'A_1 A_2$ by m, we obtain equations (1) and (2). Parameter β plays a key role in determining the long run equilibrium outcomes, which represents the degree of asymmetric migration in two-patch habitats.

The above system of difference equations is similar to the one of the continuous time model employed in Armstrong and Skonhoft (2006). However, there are some distinct points to be noted. First, we choose the discrete-time setting for the purpose

of applications since the time series data on raccoon population, economic damage, and estimated biological parameters are collected in the discrete manner. In fact, most basic statistics and data are yearly based in the raccoon problems. We also believe that the discrete-time formulation is more convenient for the purpose of applying the model to case studies in general.

Second, a stock-recruitment model is employed to take account of density-dependent catchability (Tuck and Possingham, 1994; Clark, 1990). This must be distinguished from a straightforward discretization of the continuous-time model as adopted in the application of fishery models. The discretization scheme as in fishery literature causes a problem that the effect of density-dependent catchability is not well-taken, whose standard specification can be found in Conrad (1999). Such a choice of discretization is more likely to yield the result that extermination is desirable. On the other hand, the stock-recruitment model enables us to incorporate the density-dependent catchability well as demonstrated in what follows.

To capture the effect of density-dependent catchability, a continuous-time submodel representing a production function is introduced in each intra-period as follows.

$$
\begin{aligned}
\dot{h} = dh/d\tau &= (X_{2,t} - h(\tau))q(X_{2,t} - h(\tau))e(\tau) = p(X_{2,t} - h(\tau))e(\tau), \\
&= (X_{2,t} - h(\tau))b(X_{2,t} - h(\tau))^{\theta-1}e(\tau) = b(X_{2,t} - h(\tau))^{\theta}e(\tau),
\end{aligned}
\tag{4}
$$

where

τ denotes an instant of time in an intra-period such that $t \leq \tau \leq t + \triangle, 0 < \triangle < 1$, and $\triangle$ denotes the length of time in removal operation implemented in that period t;

$e(\tau)$ is the effort level devoted at instant τ for $t \leq \tau \leq t + \triangle$;

$h(\tau)$ is the stock size removed by operations at instant τ for $t \leq \tau \leq t + \triangle$;

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$X_{2,t} - h(\tau)$ is the existing population of invasive species (escapement) at instant $\tau, t \leq$

$\tau \leq t + \Delta;$

$q(\cdot) = b(X_{2,t} - h(\tau))^{\theta-1}$ is density-dependent catchability, b is some coefficient to be

adjusted for measurement units and $\theta \geq 0$ is the sensitivity of catchability;

$p(\cdot) = b(X_{2,t} - h(\tau))^{\theta}$ is catch per unit of effort (CPUE)

with the boundary conditions that

$$h(t) = 0, \quad h(t + \Delta) = H_{2,t}, \quad t = 0, 1, \ldots, \infty. \tag{5}$$

Combining the specifications of equations (4) and (5), we analytically derive a production function of $H_{2,t}$, which is analogous to solving an initial value problem of the first-order ordinary differential equation (4) with the boundary conditions (5). Solving for $H_{2,t}$ yields

$$H_{2,t} = X_{2,t} - \left[X_{2,t}^{1-\theta} - (1-\theta)b \int_t^{t+\Delta} e(\tau)d\tau \right]^{\frac{1}{1-\theta}}, \tag{6}$$

where $E_t = \int_t^{t+\Delta} e(\tau)d\tau$ represents the total effort level of removal operations devoted by the management officials in period t, and the second term in the right-hand side is the escapement level in period t, i.e.,

$$S_{2,t} = \left[X_{2,t}^{1-\theta} - (1-\theta)b \int_t^{t+\Delta} e(\tau)d\tau \right]^{\frac{1}{1-\theta}} = X_{2,t} - H_{2,t}. \tag{7}$$

This type of sub-continuous model in an intra-period for the production function is first introduced by Clark (1990), and many other researchers implicitly adopt such specification as well (Moxnes, 2003; Reed, 1979). With this approach, the effect of density-dependent catchability and CPUE that has actually occurred in each intra-period is well-taken in the sense that required effort level of catching one individual

may rise as the existing population decreases.

For clearer understanding, refer to Figure 1 in which catchability and CPUE are graphically shown as a function of the existing population of invasive species in an intra-period. The initial poulation prior to any removal operation is $X_{2,t}$. As time goes on in each intra-period, removal efforts are made, and the existing population of $X_{2,t} - h(\tau)$ gradually decreases. At the same time, CPUE is monotonically decreasing, while marginal change in catchability depends on whether or not the sensitivity of catchability, θ, is larger than unity. If it is larger than unity, catchability decreases in the existing population, otherwise it increases. A series of these events that occurs in each intra-period during removal operations are graphically described in Figure 1.

A parameter of our interest is the sensitivity of catchability, θ, which represents the index for the percent change of catchability in response to 1 % change in the existing invasive species stock. Put differently, it represents how CPUE depends on the existing population of invasive species. As Figure 1 shows, if $\theta > 1$, CPUE is convex in the existing population, otherwise concave.

Here, it must be noted that if the sensitivity of catchability is larger than unity, i.e., $\theta > 1$, extermination of invasive species is impossible, otherwise possible. This fact may be noticed by checking the second term in the right hand side of equation (6), that is, the escapement level is

$$\left[X_{2,t}^{1-\theta} - (1-\theta)b \int_t^{t+\Delta} e(\tau)d\tau \right]^{\frac{1}{1-\theta}} = \left[X_{2,t}^{1-\theta} - (1-\theta)bE_t \right]^{\frac{1}{1-\theta}} .$$

This term is positive for any finite effort level of E_t when θ is larger than unity. In other words, when $\theta > 1$, the required effort level for extermination is infinite, which implies infeasibility of eradication. However, even though $\theta < 1$, it does not imply that extermination is easy. In this case, as the sensitivity of catchability is approaching one,

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extermination gets more difficult and costly actions. The sensitivity of catchability, θ, and adjustment parameter, b, in the production function are identified from the field data, which we describe in the calibration section.

The decision that must be made by the management officials is to set an annual effort level for removal operations, $E_t, t = 0, 1, \ldots$. In real world, this is measured by aggregate days for which traps had been set in the field. It is common that the government officials announce the target of total effort level they seek to achieve in each period. In this paper, it is assumed that the government sets effort levels to some constant and keeps the level all over the remaining periods, since it works as a benchmark analysis for the population dynamics.

We also admit that an optimal removal effort via dynamic programming or optimal control can be derived under the assumptions that the current estimates of population level in two patches are accurately measured. However, we do not take this approach, and leave a topic to be addressed in the future. As is often the case with invasive species management, the population estimates especially outside the controlled patch are unavailable or not collected by the government agency. Therefore, even though it is possible to derive an optimal feedback strategy of removals, as in the sense of Tuck and Possingham (1994), it is quite difficult to be implemented due to the informational obstacles in reality. Thus, constant annual effort is assumed along the line of the above argument, i.e., $E_t = E$ for all $t = \{0, 1, 2, \ldots\}$, but the government can choose the level of E.

2.2 Bionomic steady state

Under the assumption of constant effort level $E_t = E$, there may exist a steady state at which $X_{i,t+1} = X_{i,t}, S_{2,t+1} = S_{2,t}, H_{2,t+1} = H_{2,t}, i = 1, 2, t = \tau, \ldots, \infty$ for some $\tau > 0$. For simplicity, we drop the subscript of t to denote a set of the variables at the

steady state in what follows, i.e., X_1, X_2, S_2, H_2. The bionomic steady state can now be characterized by the following system of equations:

$$r_1 X_1 (1 - X_1/K_1) = m(\beta X_1/A_1 - S_2/A_2),$$

$$X_2 = S_2 + r_2 S_2 (1 - S_2/K_2) + m(\beta X_1/A_1 - S_2/A_2),$$

$$S_2 = X_2 - H_2,$$ (8)

$$(X_2 - H_2)^{1-\theta} = \left(X_2^{1-\theta} - (1-\theta)bE \right).$$

The system derives from equations (1), (2), (3) and (6), and possesses four unknowns of X_1, X_2, S_2, H_2 and four equations.

Unfortunately, it is impossible to solve the steady state equilibria in the analytic form. However, we confirm that there are two equilibria in which (i) all variables are zero, and (ii) they are interior. The stability of such a interior equilibrium is checked by formulating the Jacobian matrix, following the starndard procedure (Edelstein-Keshet, 1988). We have identified that it is stable in most plausible parameter spaces.

2.3   Economic model

We introduce two economic functions which work for measuring the effectiveness of some constant removal effort level: which are (i) costs of removal operation and (ii) social damage that accrued from roaming invasive species. While removal cost is easy to measure, what is social damage may be difficult to reach consensus. Social damage in control patch could mainly be divided into the following two types; (i) agricultural economic loss and (ii) ecological one. Whereas there does not exist a good measure of ecological loss, data on agricultural economic damage has been collected by Hokkaido government, Japan (Hokkaido-government, 2006). Thus, we adopt the agricultural economic loss as a proxy representing social damage.

The operation cost for removal is taken from the standard specification of renewable resource management, i.e,

$$C_t = cE_t, \tag{9}$$

where c is constant marginal cost per unit effort. On the other hand, agricultural damage is assumed to be a class of the following power function of the escapement level at period t, i.e.,

$$D_t = D(S_{2,t}) = aS_{2,t}^d, \tag{10}$$

where parameters of a and d are estimated from available data.

Given the above economic functions of removal costs and social damage out of invasive species, we propose that the social welfare in the long run equilibrium may be a good measure of economic effectiveness from a long run perspective. As noted in the previous section, a stable equilibrium exists when government officials set some constant annual effort of E. In this case, it is guaranteed that all ecological variables of $(X_{1,t}, X_{2,t}, S_{2,t}, H_{2,t})$ converges to X_1, X_2, S_2, H_2 in the long run, independently of the initial population levels as far as the parameters and effort level are unchanged. Of course, the steady state depends on the annual constant effort E, that is, the equilibrium can be reexpressed as $X_1(E), X_2(E), S_2(E), H_2(E)$. Thus, welfare in the long run equilibrium is written as

$$W(E) = -C - D(S_2) = -cE - aS_2(E)^d. \tag{11}$$

One of the aims in this research is to suggest an economically optimal level of constant annual effort, that is,

$$E^* \in argmax_{E \in \mathbb{R}_+} W(E), \tag{12}$$

which is equivalent to finding an effort level that minimizes the social welfare loss in an

interior equilibrium.

3 Model calibration and parameter estimations

Figure 2 displays the locations of controlled and uncontrolled patches on raccoon management in Hokkaido, Japan. The more densed colored and less colored patches in an area framed by a black line in that figure correpsond to controlled and uncontrolled patch, respectively. In this section, the model introduced in the previous section is calibrated to capture the population dynamics with density dependent migration for the purpose of application to raccoon problems in Hokkaido, Japan.

3.1 Biology

In this subsection we introduce how to determine a set of parameters necessary for the numerical analysis of population dynamics, based on the result of field research as well as life table of raccoons in Hokkaido. We mainly focus on an intrinsic growth rate, r, and carrying capacity, K, in each patch.

With respect to the intrinsic growth rates, the governmetal reports provide some benchmark method from life table of raccoons (Hokkaido-government, 2006). For this calculation of intrinsitc growth rate, several assumptions in life table must be made: sex ratio of male and female, pregnancy rate, litter size, natural death rate and child death rates of adults and juveniles within a single year. We adopt the same values for these parameters and calculation method noted in Hokkaido report (Hokkaido-government, 2006), and finally obtain $r = 0.61$, which is employed in a simulation throughout the rest of the paper.

With respect to carrying capacity of K, our decision is based on the recent field research conducted by Maesaki et. al. (2001). They report that the range of estimation

in density per km^2 is approximately $0.5 \sim 4.1$. Given this field survey, we adopt $4/km^2$ for the carrying capacity. Since we know the areas of controlled and uncontrolled patch, which are $A_2 = 9,506km^2$ and $A_1 = 38,527km^2$, multiplying these with density yields the approximation of carrying capacities of uncontrolled and controlled patches as $K_1 = 154,112$ and $K_2 = 38,028$, which are used in numerical analysis.

With respect to the remaining two parameters in the population dynamics, that is, β and m, associated with migration, there are no available data or field research that can be used for identification. Instead, we suppose some range of values for these parameters, and describe how they affect the resulting outcomes in the discussion. At this point, we simply note that three values for β are assumed $\beta = \{0.5, 1.0, 1.5\}$, and the rate of migration between two patches, $m = 875$, as a starting point.

3.2   Social damage

A series of annual reports issued by Hokkaido government suggest that agricultural damage is a main factor that motivates her to implement removal controls of raccoons. Therefore, this paper takes agricultural damage or loss as a proxy for social damage as mentioned previously.

Figure 3 illustrates the relationship between agricultural damage (unit: ten thousand yen) and estimated escapement, i.e., $X_{2,t} - H_{2,t}$ collected as data over the last ten years in the controlled patch (Hokkaido-government, 2006). Surprisingly enough, the curvature is not convex, but concave in the sense that marginal agricultural damage appears to be decreasing in the escapement level. This result is opposite to the usual assumption that a series of past economic literature have adopted. This result may be due to several reasons. First, it has been remarked that the way of collecting data on agricultural damage is subject to measurement errors. For instance, farmers, who suffer from roaming raccoons in an early stage, may tend to over-report the agricultural

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damage due to psychological or cognitive reasons. Second, raccoons are well-known to posseess opportunistic and omnivorous feeding habits (Ikeda et al., 2004). They therefore may seek to obtain another source of preys if agricultural products for their forage become scarce to a certain degree. In any event, the evidence for the relationship between agriculutral damage and the escapement of raccoons remains scarce and the reasons must be further investigated.

We estimate the damage function of $D_t = D(S_{2,t}) = a S_{2,t}^d$ by running the following regression:

$$\log(D) = \log(a) + d \log(esc) + \epsilon,$$

where esc represents the escapement level of population estimated in the controlled patch as an independent variable.

The OLS regression results are reported in Table 1. As expected, escapement is not so significant even at the 10% level. However, agricultural damage seems to be dependent on the escapement level from practical consideration, and we will use these estimated values of $\hat{a} = 538.30, \hat{d} = 0.2169$ in numerical illustration.

3.3 Catchability and catch per unit of effort (CPUE)

There are not sufficient data to estimate CPUE and catchability in controlled patch, although some estimates of (i) population prior to removal operations, (ii) the number of populations removed, and (iii) total effort devoted within a single year are available in specific years. For example, such estimates in 2006 are given as follows: Population estimate prior to removal operation, population removed and total effort are $X_{2,2006} = 4,907$, $H_{2,2006} = 1,140$ and $E_{2006} = 64,360$ trap days, respectively. Based on these limited data, the best thing one can do is to introduce several plausible scenarios that may be the case in reality, and identify the catchability and CPUE depending on each

scenario.

The scenarios we will assume with respect to catchability and CPUE are:

1. (Eradication is Infeasible (EI)), In this scenario, we set $\theta_{EI} = 1.1, b_{EI} = 1.78 \times 10^{-6}$.

2. (Eradication is Difficult, but Feasible (EDF)), $\theta_{EDF} = 0.9, b_{EDF} = 9.48 \times 10^{-6}$.

3. (Eradication is Possible, (EP)), $\theta_{EP} = 0.5, b_{EP} = 2.69 \times 10^{-4}$.

Utilizing the above three estimates in 2006 and production function of equation (6) gives the parameter values of each scenario, that is, θ and b.

First, it must be recalled that the sensitivity of catchability, θ, tells us whether extermination is feasible or not. Since we never know its true value with the current removal technology and methods for our case study, it is good to assume several possibilities. Therefore, we first set $\theta_{EI} = 1.1, \theta_{EDF} = 0.9, \theta_{EP} = 0.5$, and each scenario is named EI, EDF, EP, respectively, after the degree of difficulty in achieving extermination corresponding to the value of the sensitivity of catchability. Once we set the sensitivity of catchability and given the estimates of $X_{2,2006}, H_{2,2006}, E_{2006}$ in 2006, we can calculate adjustment parameter, b, from equation (6). Rearranging equation (6) yields

$$b = \frac{X_{2,t}^{1-\theta} - (X_{2,t} - H_{2,t})^{1-\theta}}{(1-\theta)E_t}, \tag{13}$$

which enables us to identify the values of b_{EI}, b_{EDF}, b_{EP} as listed above.

In the result section that follows, we will compare the long run equilibrium outcomes across each scenario, which plays an important role in determining the economically optimal level of constant annual effort associated with asymmetric migration between two patches.

4 Result

We present numerical results in this section, using the parameter values and functional forms for key variables calibrated from the data in the raccoon problem, Hokkaido, Japan. The baseline parameters are summarized in Table 2.

Throughout this section, we treat the long run equilibrium outcomes under the constant annual effort. We have confirmed that all the equilibrium outcomes presented in this section are invariant with an initial population level. In other words, the same equilibrium outcomes, independently of initial population levels, are reached as far as the parameters and effort levels keep unchanged.

Figure 4 provides a set of 9 panels (3×3), which displays equilibrium outcomes of an ecological model, depending on each scenario and parameter set. The horizonal axis in each panel represents the constant annual effort level measured by total days for which traps has been set in the field, while the vertical axis denotes ecological variables of X_1, X_2, S_2. The panels in the 1st, 2nd and 3rd rows measure X_1, X_2, S_2, and the 1st, 2nd and 3rd columns correspond to the scenarios of EP, EDF and EI, respectively. Each panel provides a comparison of three lines, each of which is corresponding to the parameter of asymmetric migration: $\beta = \{0.5, 1.0, 1.5\}$: $\beta = 0.5$ (line without dots), $\beta = 1.0$ (solid line with dots), $\beta = 1.5$ (thin line with dots).

As can be seen from Figure 4, the parameter of asymmetric migration, β, affects the long-run equilibrium. In general an increase in β yields more raccoon population in controlled patch, X_2, and less population in uncontrolled patch X_1. This result follows our intuition.

On the other hand, difference in S_2 due to asymmetric migration of β depends on the annual effort level of E. If E is sufficiently small, then difference in S_2 is obvious (See the effort level of $0 \sim 300,000$ in the 3rd row panels of Figure 4). However, once E gets sufficiently large, then the difference becomes small or negligible (See the effort level of

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$300,000 \sim 600,000$ in the 3rd low panels of Figure 4, and also refer to Table 3). Such a trend for sufficiently large effort levels arises due to the two different reasons depending on each scenario. In EP, local extermination is simply achieved, i.e., $S_2 = 0$, for all $\beta = \{0.5, 1.0, 1.5\}$ when sufficiently large efforts are devoted. In fact, the effort levels required for extermination are 310,000, 420,000, and 510,000, depending on parameter values of $\beta = \{0.5, 1.0, 1.5\}$ (Confirm this from the row of EP in Table 3 and also from Figure 4).

In terms of EDF and EI, CPUE gets very low in an equilibrium as effort level is sufficiently increased and the existing population in controlled patch decreases. This feature in an equilibrium reflects the fact that effectiveness of one unit effort rapidly declines, and thus the difference in the population level prior to removal operation has negligible impacts on the resulting escapement level afterwards. Thus, difference in S_2 becomes small as effort levels are sufficiently large, although extermination is not achieved in EDF and EI (See the columns of EDF and EI in Table 3).

Here, it must be recalled that extermination is technically feasible in EDF and EP. For the range of effort levels we employed in numerical analysis, it is succeeded in EP when the effort level of E are set more than 310,000, 420,000, 510,000 depending on $\beta = 0.5, 1.0, 1.5$, respectively, and it is not achieved in EDF for all β (See Table 3). This suggests that even though extermination is technically possible, the difference in the sensitivity of catchability, θ, significantly affects the annual effort level at which eradication is succeeded in an equilibrium. In general, as the sensitivity of catchability is larger, the effort level that is required for extermination would increase as illustrated. In summary, analysis of an ecological model suggests that both the sensitivity of catchability and the degree of asymmetric migration are crucial in determining the equilibrium outcome especially on whether local extermination is succeeded or not in controlled patch.

We have looked at the ecological outcomes so far. In turn, we now present the economic consequence in what follows. Figure 5 provides a set of 9 panels (3×3), which displays equilibrium outcomes associated with social welfare defined in equation (11) where the 1st, 2nd and 3rd rows correspond to the equilibrium welfare when constant marginal cost is set as c is 200, 100, 50, respectively, while the 1st, 2nd and 3rd columns correspond to the scenarios of EP, EDF, and EI, respectively. Each panel provides a comparison of three lines, each of which corresponds to the parameter of asymmetric migration, $\beta = \{0.5, 1.0, 1.5\}$: $\beta = 0.5$ (line without dots), $\beta = 1.0$ (solid line with dots), $\beta = 1.5$ (thin line with dots).

Figure 5 enables us to identify an economically optimal level of constant annual effort from the long run perspective. It is the one which gives the highest value of $W(E)$ as defined in equation (12). For instance, when $c = 200$ and the scenario is EI, then an economically optimal effort level is zero. Because W is the highest at $E = 0$ (See the panel of the 1st row and 3rd column in Figure 5). It implies that any positive removal effort does not pay off compared to the case of $E = 0$ for all $\beta = \{0.5, 1.0, 1.5\}$ in the long run. As another example, focus on the case of EI when $c = 50$ (See the panel of the 3rd row and the 3rd column in Figure 5). Then it can be observed that an economically optimal effort level is about 220,000 for all $\beta = \{0.5, 1.0, 1.5\}$. This suggests that setting $E = 220,000$ pays off compared to any other effort level from the long run perspective, irrespective of the degree of asymmetric migration.

Close inspection of Figure 5 reveals that the qualitative features of $W(E)$ in EP are quite different from those in EDF and EI. In EP, the economically optimal effort level is located where local extermination is just achieved if constant marginal cost is sufficiently small, i.e., $c = \{100, 50\}$, otherwise zero effort is economically optimal (See the column of EP in Table 3, and the three panels of the 1st columns in Figure 5). Thus, in this situation the problem simply reduces to "Is the constant marginal cost of

c small enough that local extermination pays off?" When $c = \{50, 100\}$, it is optimal to aim at local extermination so that an economically optimal effort levels must be adapted with β. When $c = 200$, zero effort level is optimal.

Whenever the sensitivity of catchability is sufficiently small, the same qualitative feature with respect to $W(E)$ as in EP holds. In this case, economically optimal effort levels could be highly dependent upon degree of asymmetric migration, β. This reflects the fact that in EP, the effort level required for eradication increases as β rises (See Table 3).

In EDF and EI, the optimal effort levels are zero or some strictly positive effort level, which could be independent of parameters of asymmetric migration β. If $c = 50$, then the optimal effort level is located around $220,000 \sim 230,000$ and its levels appears to be independent of the degree of asymmetric migrations β in both scenarios (See the two panels of the 3rd row and 2nd, 3rd columns in Figure 5). Next, observe the two panels of $c = 100$ (See the two panels of 2nd row and 2nd and 3rd columns in Figure 5). In EDF, only when $\beta = 0.5$, it is optimal to set about $E = 200,000$, otherwise zero. In EI, the optimal effort level appears to be around $E = 150,000$ for all β. Finally observe the two panels of $c = 200$ (See the two panels of the 3rd row, and 2nd, 3rd columns in Figure 5). In these cases, the optimal effort level is zero irrespetive of β so that any positive level of removal effort cannot be justified in both scenarios (See the two panels in the 1st row and 2nd, 3rd columns in Figure 5).

From a series of the above numerial results in EDF and EI, we draw the following observations: whenever the sensitivity of catchability is sufficiently high and some positive effort is economically desirable for all β, then the economically optimal effort level could be almost independent of the degree of asymmetric migration. This is in sharp contrast with the case of EP.

In this result section, we choose the limited parameter set of constant marginal cost

$c = \{200, 100, 50\}$. However we can say what would happen if it takes other parameter ranges of c. If constant marginal cost of c takes the value larger than 200, the optimal effort levels simply remains zero for all scenarios. If c is less than 100, the qualitative features of optimal effort levels are almost identical to the ones with the cases of $c = 50$ in all scenarios. Therefore, our result presented in this section could be viewed as an exhaustive list of important results.

Finally we summarize the findings; it is demonstrated that only when the sensitivity of catchability is sufficiently small such as EP scenario, local extermination at controlled patch yields an optimal welfare in an equilibrium. Accordingly, the optimal effort level must change with β as illustrated above for local eradication. On the contrary, if the sensitivity of catchability is sufficiently large such as EDF or EI, it is never optimal to aim at local extermination, rather it could be better to aim at keeping low escapement level at the controlled habitat. In such a situation, an economically opitmal effort level could be almost independent of the degree of asymmetric migrations β (See the three panels of the 3rd row in Figure 5). It must be noticed that this feature is in contrast with that in the case of low sensitivity of catchability. Therefore, identifying the sensitivity of catchability in terms of current removal technology is important to determine a socially desirable goal as well as the relationship between an economically optimal effort level and the degree of asymmetric migrations.

5   Discussion

The Hokkaido government currently appears to set local extermination in controlled patch as her goal on this raccoon problem, and aims at implementing an annual effort level of $E = 80,000 \sim 100,000$ trap days. From our research, the current goal is justified only if the current technology or method for removal of raccoons exhibits a

sufficiently low sensitivity of catchability and the constant marginal cost per unit effort is sufficiently low. It is testable, and the estimate on the sensitivity of catchability really helps guiding where we should go on this problem.

Although we do not present all the patterns of numerical results, we confirm that migration parameter of m will not qualitatively impact on the equilibrium outcomes of both ecological variables and economic functions. In other words, for the wide range of m, only when the sensitivity of catchability is sufficiently small, local extermination is economically desirable. However, once θ is sufficiently high, then local extermination is never optimal and keeping the low escapement by setting the optimal effort level ranged between 150,000 and 230,000. Reflecting these numerical results with real practice on the raccon problems in Hokkaido, we recommed that effort level be increased up to about $150,000 \sim 230,000$ if the sensitivity of catchability with current technology is sufficiently high. On the contrary, if the current removal technology possesses a sufficiently low θ, the "strike level of removal effort" for local extermination must be carefully evaluated, which highly depends on the migration rate from uncontrolled areas.

In this paper, we focus on agricultural damage as a reason for raccoon controls, and demonstrate a result that it is concave in the escapement level. What if it is convex? The answer for this question is that local extermination is simply more unlikely to be justified in our analytic framework, since reducing the population to zero is not so an attractive option, compared to the concave damage function.

This research takes the perspective that many of the management decisions of "area-wise controls" in an invasive species might be legitimately analyzed through a simple deterministic meta-population model with migration. In addition, we restrict our attention to the class of "constant annual effort" as a choice for the management officials. In reality, however, the model adopted in this research could be viewed as primitive, and it is totally possible to extend it into several directions for more real policy guidance:

(1) Multiple stochasticities such as growth uncertainty and implementation error could be incorporated into a model in which a Mote Carlo simulation may be of some use, (2) the optimal feedback strategy of removal controls can be derived through dynamic programming or optimal controls even under uncertainties as in the sense of Tuck and Possingham (1994), (3) the most important extension that must be made in the future is how we incorpolate loss of ecological services into the analytic framework of the mathematical model.

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Table 1: Estimates of parameters of agricultural damage

	Estimated Coefficients	Standard Errors	t stat
$\log a$	6.2884	0.9727	6.4643
d	0.2169	0.1226	1.7678

$R^2 = 0.3424$; Adjusted $R^2 = 0.2329$.

Table 2: The baseline parameters

Parameter	Description	Value
(r_1, r_2)	Intrinsic growth rates	(0.61,0.61)
K_1	Carrying capacity in uncontrolled patch	154,112
K_2	Carrying capacity in controlled patch	38,028
A_1	Area in uncontrolled patch	38,527
A_2	Area in controlled patch	9,506
m	Dispersion	875
(a, d)	Parameters in agricultural damage	(538,0.2169)

Table 3: S_2: Escapement in equilibrium

|			Constant Annual Effort, E (trap days)						
			0	100000	200000	300000	400000	500000	600000
S_2	EP	β = 0.5	35418	25637	562	1	0	0	0
		β = 1.0	38028	29462	16296	655	19	0	0
		β = 1.5	40286	32463	21954	4189	448	10	0
	EDF	β = 0.5	35418	13378	2022	698	319	159	81
		β = 1.0	38028	18051	4524	1621	757	389	207
		β = 1.5	40286	21451	6950	2610	1237	646	351
	EI	β = 0.5	35418	8874	2293	1070	620	397	269
		β = 1.0	38028	12367	3855	1839	1064	676	453
		β = 1.5	40286	15061	5183	2507	1448	915	610
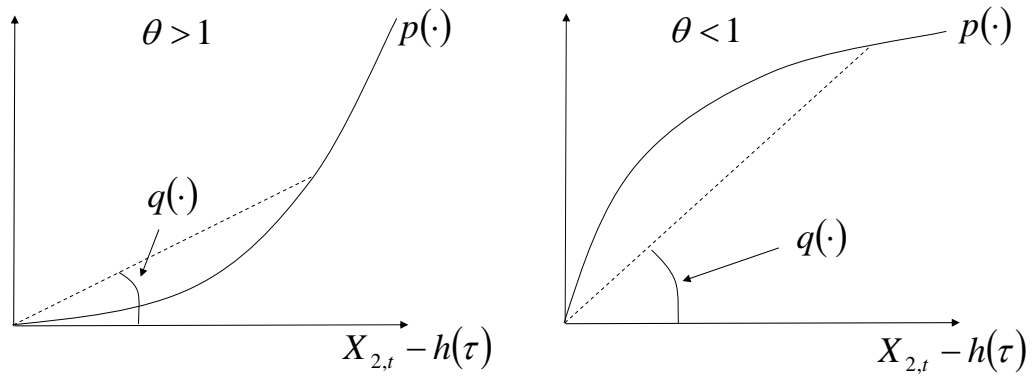
Figure 1: Catchability and CPUE as a function of the existing population size in each intra-period
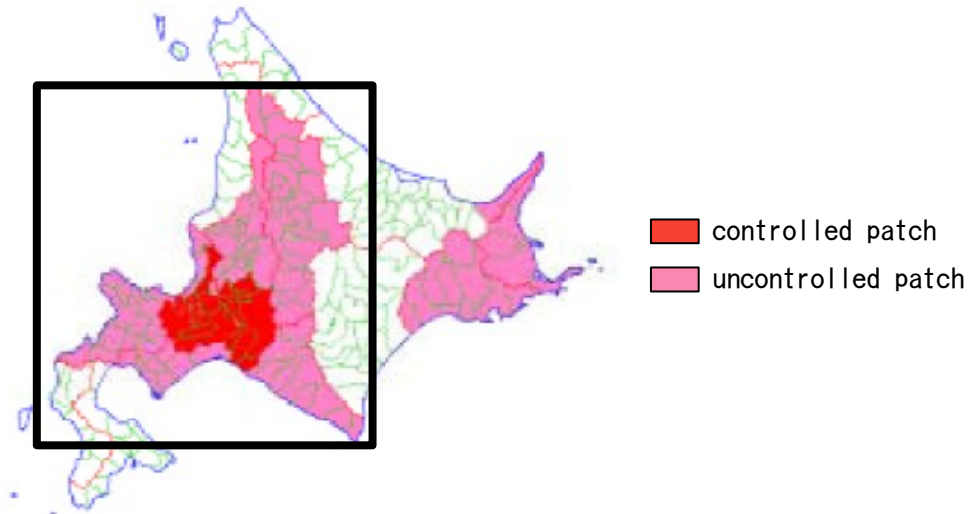

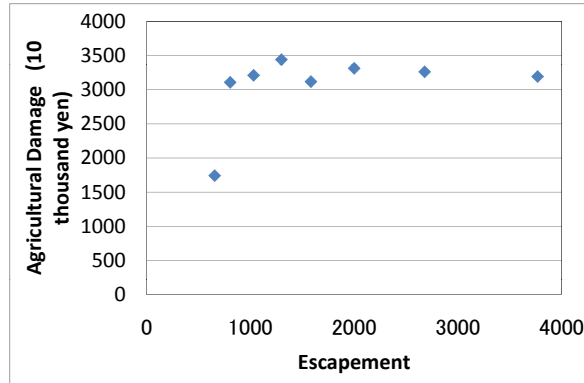Figure 2: Location map of controlled and uncontrolled patches in Hokkaido, Japan

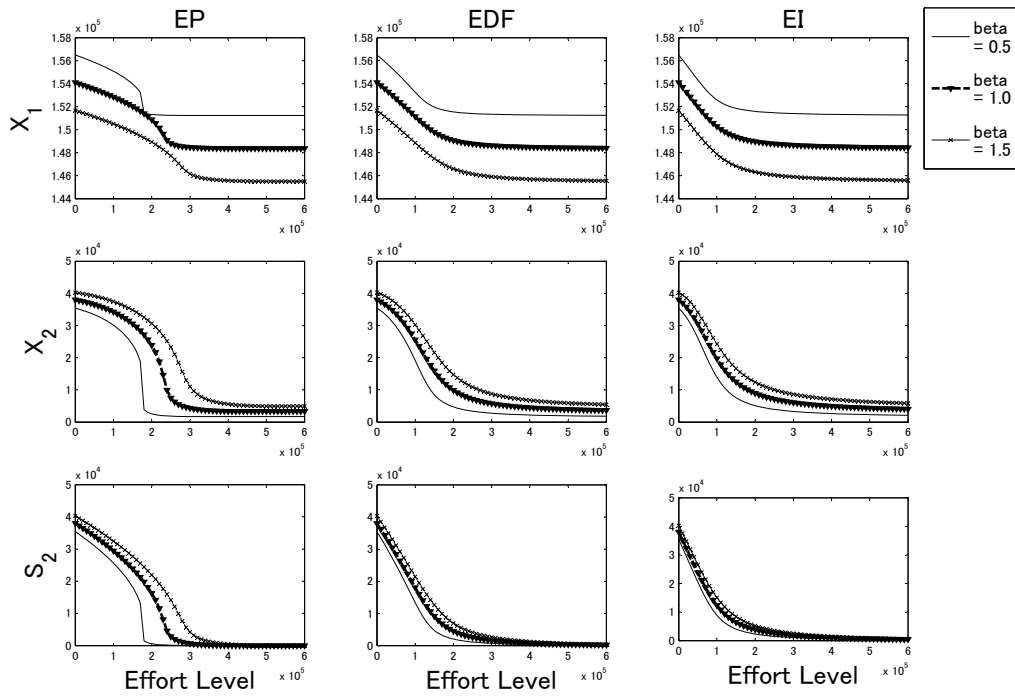Figure 3: Scatter plot between agricultural damage and estimated escaped population

Figure 4: Equilibrium outcomes of ecological variables as a function of constant effort, $\beta = 0.5$ (line without dots), $\beta = 1.0$ (solid line with dots), $\beta = 1.5$ (thin line with dots)
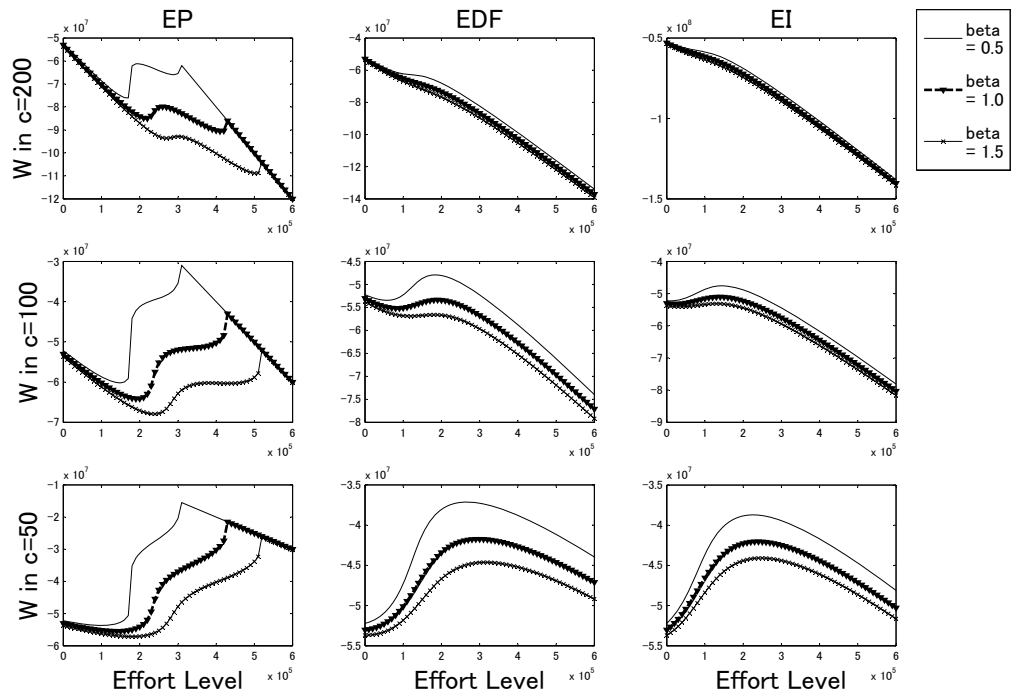
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Figure 5: Equilibrium outcomes of social welfare as a function of constant effort, $\beta = 0.5$ (line without dots), $\beta = 1.0$ (solid line with dots), $\beta = 1.5$ (thin line with dots)