

Prediction of range expansion and optimum strategy for spatial control of feral raccoon using a metapopulation model

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Abstract A meta-population model is often used to predict spatial distribution of the target species in a regional landscape. Parameters necessary to build a metapopulation model can be obtained from a set of two distribution maps of the same region surveyed in two different periods. Such an approach is suitable to predict range expansion based on the information obtained in the early stage of introduction, where detailed information is lacking.

Range expansion of the feral raccoon (*Procyon lotor*) in Kanagawa Prefecture, Japan was predicted by a meta-population model. Habitat suitability was evaluated from the relation between vegetation and raccoon distribution. Colonisation kernels were estimated from two distribution maps based on surveys conducted in 2001 and 2004. The reliability of the model was evaluated by comparing actual history and simulation.

The optimum strategy for spatial control was identified using this simulation model. The current raccoon population was divided into isolated subpopulations by cluster analysis. One or several subpopulations were hypothetically removed in the simulation of range expansion, and the future reduction of the whole distribution range was calculated. All combinations of subpopulation removal patterns were examined and the most cost-effective removal pattern was identified.

Habitat analysis showed that raccoons preferred landscape with forest patches. Raccoons colonised up to a distance of 2.8km at 50% probability per three years. Results of simulation corresponded to actual history. It was predicted that raccoons will spread over the whole Kanagawa Prefecture by the year 2019, and will reach central Honshu Island in about 2064.

There were five isolated populations in 2004. The benefit / cost ratio changed according to time after subpopulation removal (time horizon). The most cost effective strategy short term was to eradicate isolated small marginal populations. The most cost effective strategy, mid term, was to eradicate all populations located in the marginal front and the most cost effective strategy long term, was to completely eradicate the whole population. For all time horizons, eradication of the central subpopulation was the worst strategy.

Keywords: Kanagawa Prefecture; Japan; metapopulation model; raccoon; *Procyon lotor*

INTRODUCTION

In the early stage of introduction of alien species, we usually have to predict range expansion based on limited information (Fig. 1). The most easily available information is the presence of the focal alien species in a region. The next step will be a distribution map of the species. Information on habitat preferences can also be obtained in the early stage of research. Estimation of population density and other population parameters, such as population growth rate and mortality, on the other hand, require much effort.

A distribution map describes presence or absence of the target species. There is a metapopulation model dealing with presence and absence of local populations in a fragmented landscape (Hanski 1998). Distance-dependent colonisation and extinction probability in a habitat

patch are essential parameters, but detailed information such as population density, fecundity, mortality and longevity of individuals is not required

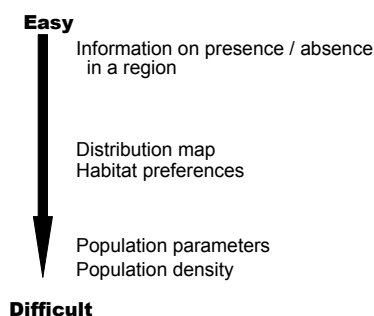


Figure 1 Availability of information as research progresses

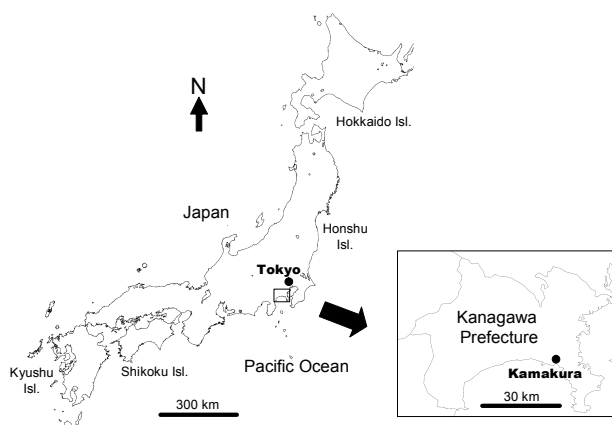


Figure 2 Location of study region.

in the metapopulation model. One set of distribution maps surveyed in two different periods provides enough information for the modelling. Habitat suitability is identified using a land cover map and a distribution map of the target species. The colonisation kernel and the probability of extinction from a habitat patch are determined from two distribution maps obtained at two different periods.

The optimum spatial control strategy for an actively spreading alien species needs to be determined in the early stage of introduction and it can be determined using the metapopulation model. The site of the first introduction is usually at the centre of the distribution range, where population density is usually high and damage to economic activities and native biodiversity are also obvious. Although a management programme is often conducted in such high density area, the alien species will continue to spread. In order to reduce future damage, we need to know what the priority areas for eradication are.

Raccoons (*Procyon lotor*) are native to North America, and were brought to Japan as pets. They are now naturalised in several locations in Japan (Japan Wildlife Research Centre 1998). The raccoon is a mesopredator and the major predator of bird eggs in fragmented landscapes in its native range (Schmidt 2003). In Japan, naturalised raccoons become the largest tree climbing predators and the largest predators in suburban and urban area, and can cause considerable ecological impacts (Ikeda 2002).

A precise model to predict raccoon population dynamics in fragmented habitat of its native range is available (Broadfoot *et al.* 2001). However, it requires several population parameters and the initial population size in each habitat patch. These values are currently hard to obtain for populations in Japan, and this approach was hence not taken in this study.

In this study, the range expansion of feral raccoon was predicted based on two distribution maps (Kanagawa Prefecture 2001, records of 1999 to

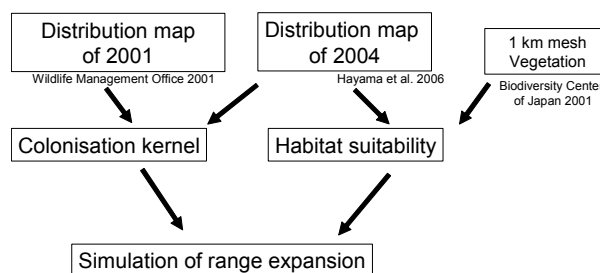


Figure 3 The procedure for simulation of range expansion based on two snapshots of raccoon distribution map and environmental data.

2001, an early version of Hayama *et al.* 2006, record of 2003 to 2004) using a metapopulation model and the optimum strategy for spatial control was identified using this model.

METHODS

History of feral population in Kanagawa Prefecture

A TV animation programme with a raccoon character was broadcasted in Japan in the 1970s, and many raccoons were imported from North America as pets. Since then naturalised raccoons have been found in several regions in Japan where land cover is a mixture of urban and forest areas. The raccoon was naturalised in Kamakura City, Kanagawa Prefecture, around 1988 and several female raccoons with young were found in 1990 (Fig. 2, Nakamura 1991).

Raccoon resource use and habitat preferences in Kanagawa

The raccoon is a middle size omnivorous mammal. In its native range of North America, it needs cavities in trees, snags, logs, rock piles, underground burrows for shelter and dens, and thus it usually requires forest and shrub lands and avoids industrial areas (Anon 1995, Broadfoot *et al.* 2001). The mixture of forest and other land covers (residential areas and farmlands) results in high population density due to high food availability in residential areas and farmland, and den site availability in forest (Hoffman and Gottschang 1977, Oehler and Litvaitis 1996).

As a preliminary analysis, habitat suitability for raccoons in Kanagawa Prefecture was assessed using the 2.85 x 2.3km grid map of raccoon distribution in 2004 (an early version of Hayama *et al.* 2006, Fig. 3). Percentages of forest cover, farmland and town were calculated based on 1km mesh vegetation data (Biodiversity Centre of Japan 2001) using free GIS

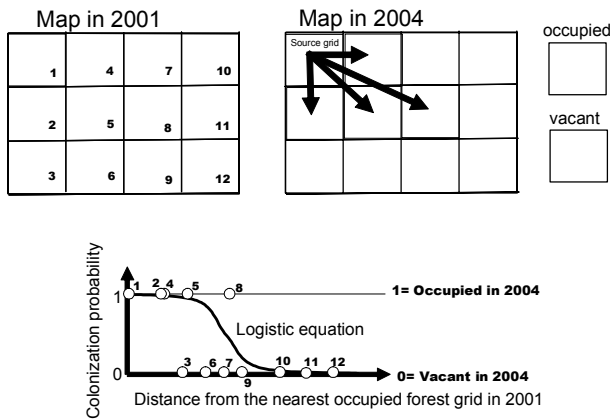


Figure 4 Colonisation kernel was determined using two distribution maps surveyed in 2001 and 2004 (above).

Logistic regression was used for colonisation kernel (below). We call a grid “occupied” if raccoon is present and “vacant” if raccoon is absent.

software (Koike 2004). Land cover of the grid was divided in two categories 1) without forest (farmland, residential or industrial areas only), and 2) with at least 10% forest cover. Since the population started to spread from Kamakura City, and has not yet expanded to the entire prefecture, only the area within 20km from Kamakura City was analysed. We call a grid “occupied” if raccoon is present and “vacant” if raccoon is absent. The fraction of grids occupied by raccoon was 82% for the grids with forest, and 60% for the grids without forest. Raccoons significantly preferred the grids with forest ($P < 0.05$, Fisher’s exact test).

Based on this information, grids with at least some forest (forest cover $> 10\%$) were considered as raccoon breeding habitat. Other areas (towns or farmlands without forest) were considered as habitats where raccoons may stay temporarily and feed, but where they do not reproduce.

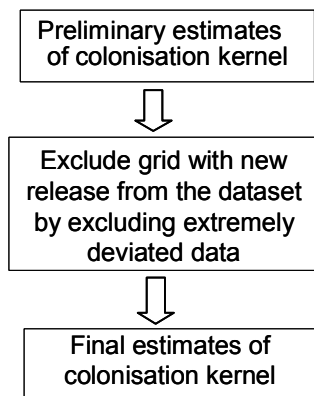


Figure 5 Removing new releases from the analysis is necessary to identify the colonisation kernel accurately.

Colonisation kernel

Each grid (2.85 x 2.3km) was considered as a habitat patch for the metapopulation model (Fig. 4). Raccoons colonise from an “occupied” grid where a raccoon population is present to a “vacant” grid where raccoon is absent. Among occupied grids, grids with at least some forest were considered as source grids where raccoons breed and where new individuals disperse from. Grids without any forest were not considered as source grids. The probability that raccoons colonise a vacant grid, $P(x)$, decreases with the distance from the nearest source grid, x . A logistic function is often used to approximate this (Komuro and Koike 2005),

$$P(x) = \frac{e^{kx+l}}{1 + e^{kx+l}} \quad (1)$$

where k and l are regression coefficients. This function defines a colonisation “kernel” around a given source grid.

In this study, the occupied forest grids in 2001 were considered as source grids, and success or failure of colonisation was judged from the distribution map in 2004. The centre-to-centre distance from the nearest source grid (occupied in 2001) to a given grid (destination grid) was calculated for all grids. One record in the dataset corresponded to one destination grid. Variables in the dataset were presence (value=1) or absence (value=0) of raccoons in 2004, and the distance from the nearest source grid. Logistic regression (SPSS 10.0J) was used to obtain the colonisation kernel (Fig. 4), assuming presence or

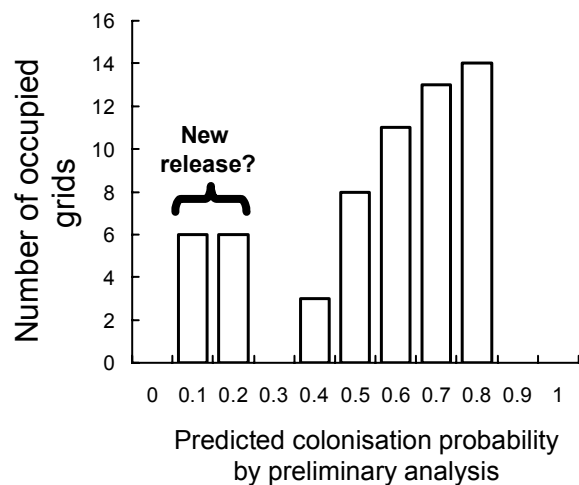


Figure 6 Colonisation probability in 2004 was predicted based on the distribution map in 2001, using the preliminary “colonisation kernel”. Several grids had a low colonisation probability, although they were occupied in 2004. This presence of raccoons was considered to be the result of new releases, and such grids were excluded from the final estimation of colonisation kernel.

absence in 2004 as dependent variable, and distance from the source grid as independent variable. The whole dataset was divided into two datasets according to vegetation; destination grids having at least some forest, and those that did not have any forest. Two colonisation kernels were obtained: colonisation with breeding between forest grids (from forest grid to forest grid), and temporal dispersal to non forest areas (from forest grid to other areas).

In some forest grids, raccoon was observed in 2001, but not in 2004. Extinction of a non viable population (e.g. release of only one individual), or failure to detect the presence of raccoons might cause such phenomenon. We included such data in the analysis, so that extinction and failure of detection were considered in the colonisation model to some extent.

A new release of one or more can cause a new colonisation into a highly isolated grid. If we include such data, the resulting colonisation kernel will have a very long tail, and indicate a very long dispersal distance. In Kanagawa Prefecture, raccoons caught in Kamakura City as a pest were sometimes released in forests in the northwest of the prefecture, because people refrained from killing raccoon (Kaneda, personal communication). In order to exclude such additional releases, we analysed the relation between predicted colonisation probability and actual colonisation (Fig. 5). The number of occupied grids should decrease where predicted colonisation probability was small (i.e. distant from source grid), however, there were several grids colonised in 2004 that had no source grid close to them (Fig. 6). Such grids were considered as new releases, and excluded from the final analysis.

Identifying subpopulations

Eradication of a small part of a large population will soon be replenished by individuals from surrounding areas. Thus we divided the whole population in the prefecture into several subpopulations based on isolation distance. Grids occupied by raccoons in 2004 were extracted and geographical distances between these grids were calculated for all combinations of grids. The resulting distance matrix was analysed by the cluster analysis of Minna de GIS (Koike 2004). The clusters of grids that were separated from each other by more than the calculated maximum distance of dispersal ability were defined as subpopulations.

Each subpopulation is expected to have an independent origin of released raccoons. However, since raccoons might be released several times at easily accessible sites (e.g. a forest edge close to an urban area), and feral raccoons caught in towns might

also be released in such sites, individuals of a given subpopulation might have various genetic origins. Genetic analysis was hence not used to divide subpopulations.

Simulation model

All grid cells were divided into two categories: with forest, and without forest. The time step used was three years. In each step, the distance from the nearest source grid, x , was calculated for all grids, and the probability to colonise the focal grid, $P(x)$, was evaluated. Presence or absence of raccoons during the next step was then determined stochastically according to $P(x)$. Since it was a Monte Carlo simulation, the results of the simulation differed from trial to trial. An already occupied grid could become empty depending on the probability of $1 - P(0)$ (representing extinction from the grid). Minna de GIS (Koike 2004) was used for simulation.

Evaluating the reliability of the range expansion simulation

A simulation of past range expansion was made to evaluate reliability of the model using the same grid (2.85 x 2.3km) as the actual distribution data. In this simulation, the initial population started from Kamakura City, where the first naturalisation was found, and spatial spread after 30 years was simulated. The simulated raccoon distribution was compared with the actual distribution of a subpopulation around Kamakura City. Reliability of the simulation was evaluated based on a similarity index, S_t , between the actual raccoon distribution in 2004 and the simulated distribution:

$$S_t = \frac{a_t}{a_t + b_t + c_t} \quad (2)$$

where a_t was the number of grids where raccoon was present both in the actual data and in the simulation, b_t was the number of grids where raccoon was not observed in the actual situation but was present in the simulation, c_t was the number of grids where raccoon was observed in the actual situation but was not present in the simulation, and t was the year after initial release in the simulation.

Prediction of distant future

Raccoon distribution in the distant future was simulated taking the raccoon map of 2004 as the initial state. In surrounding areas outside Kanagawa Prefecture, there were several areas where raccoons

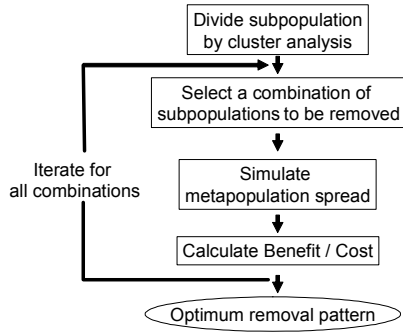


Figure 7 The procedure to identify the optimum pattern for eradication.

also naturalised; however, because reliable information was not available for them, we only considered the population in Kanagawa Prefecture.

The 2.5 x 2.5km grid on a transversal Mercator projection was used for this simulation, because the 2.85 x 2.3km grid from the distribution survey is an approximation of the grid defined by latitude and longitude, and will cause an accumulation of errors if the analysis is done for a large area.

Strategy for optimum spatial control

In the simulation, one or several subpopulations were removed completely at one time, and the resulting distribution change was calculated (Fig. 7). We considered a 110 x 171km area including Kanagawa Prefecture (Fig. 8), with 2.5km x 2.5km grids. The simulated removal was carried out for all combinations of subpopulations. Contribution of the removal after t years from the treatment, B_t , was calculated as:

$$B_t = N_t - R_t \quad (3)$$

where N_t was the number of grids occupied by raccoons after t years without any removal treatment, and R_t was the number of grids occupied after t years with removal treatment (Knowler and Barbier 2000).

The cost of eradication for one grid is not known, but the total cost of treatment should be proportional to the number of grids eradicated. It is difficult to calculate an absolute amount of money, but we can compare the cost of various eradication strategies using the number of eradicated grids instead of an amount of money. We optimised the benefit per cost ratio,

$$\text{Benefit / Cost} = \frac{B_t}{E} \quad (4)$$

where E is the number of eradicated grids.

The benefit/cost ratio (equation 4) means the reduced number of occupied grids in future, caused by the eradication of one grid. Eradication of one

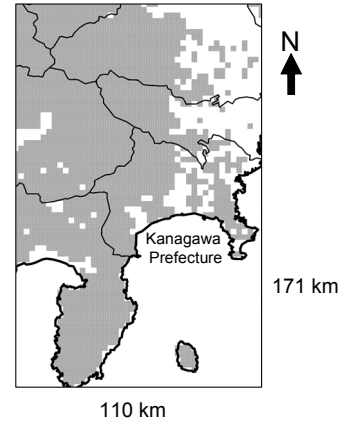


Figure 8 The area (171 km in south-north direction, 110 km in east-west direction) used to determine optimum spatial control strategy. Grey area represent grid with at least some forest, where raccoon can breed.

grid is an investment that will reduce the eradication effort necessary in the future. Compound interest for t years is expressed as

$$(1+r)^t = \frac{B_t}{E} \quad (5)$$

Annual yield (interest), r , was calculated as

$$r = \left(\frac{B_t}{E} \right)^{\frac{1}{t}} - 1 \quad (6)$$

For the calculation, the raccoon population of 2004 was divided into subpopulations. For all combinations of eradicated subpopulations, the benefit/cost ratio was calculated and the most cost effective eradication pattern was identified. Since the simulation was stochastic, it was iterated 50 times, and the average value of the cost/benefit ration was used. Minna de GIS (Koike 2004) was used for optimisation.

RESULTS

Colonisation kernel

Two colonisation kernels of forest-to-forest, and forest-to-other movements were similar (Fig. 9). Colonisation between grids with forest determines the ability for spatial spread of a raccoon population. The colonisation probability decreased to 50% at a distance of 2.8km from the source grid, and the colonisation probability was close to zero at 10km distance.

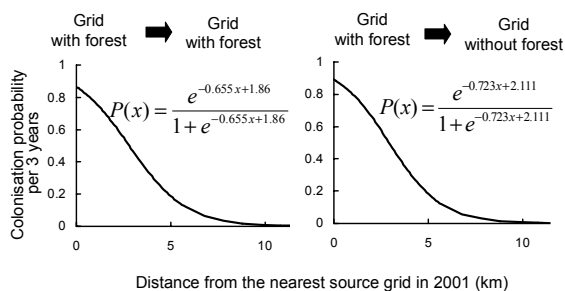


Figure 9 Colonisation kernels. Forest-to-forest colonisation represents true colonisation through breeding, and forest-to-other represents temporal use.

Subpopulation

Raccoons scarcely moved over a habitat-to-habitat distance longer than 10km in three years and an isolation distance of 10km was hence used to identify subpopulations. Five isolated subpopulations were found in Kanagawa Prefecture (Fig. 10). Kamakura City was at the centre of the largest subpopulation (A). The smallest subpopulation was in an isolated single grid (C).

Reliability of simulation

In the simulation that started from an original population at Kamakura City, the raccoon population spread continuously and reached the northern border of the prefecture after 30 years (Fig. 11). The similarity between simulated distribution and actual distribution of the subpopulation A was highest at 18 years after initial release (Fig. 12). It suggests that in this simulation the raccoon population should start to spread in 1986. This agreed with the actual history where naturalised raccoons were recognised in 1988

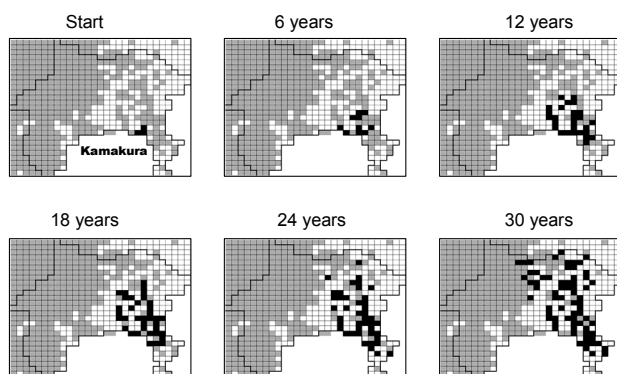


Figure 11 A result of simulation to reproduce past range expansion. Initial population was situated at the Kamakura City.

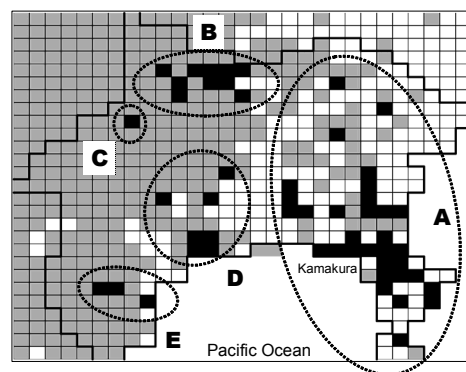


Figure 10 Subpopulation of Kanagawa Prefecture in 2004. Grey grids are habitat where raccoon can breed (forest), and black grids were occupied by raccoon as of 2004.

(Nakamura 1991), and the simulation model was considered to be reliable.

Future distribution of raccoons

There is a hilly suburban area between Kamakura and the northern border of the prefecture and a few isolated forests exist on steep hill-sides. Such suburban landscape may provide a corridor for raccoons. Most habitats in Kanagawa Prefecture are predicted to be occupied by 2019. Raccoons are predicted to reach central Honshu Island around 2064, and a large part of this island will be occupied after 200 years (Fig. 13).

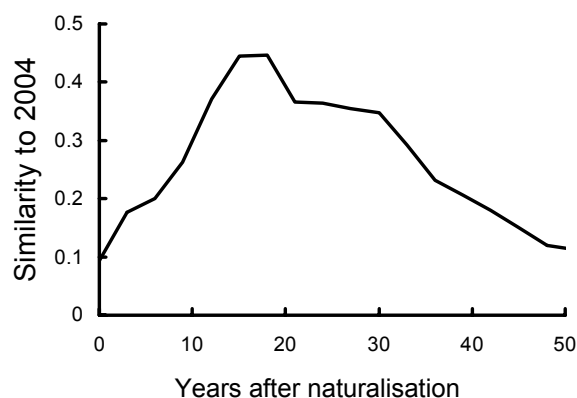


Figure 12 Similarity index (equation 2) between actual raccoon distribution (Hayama et al. 2006) and the result of a simulation of past range expansion (Fig. 11). Since an already occupied patch will go extinct stochastically with the probability of $P(0)=0.87$, the theoretical maximum similarity for the same distribution range is $P(0)^2=0.75$.

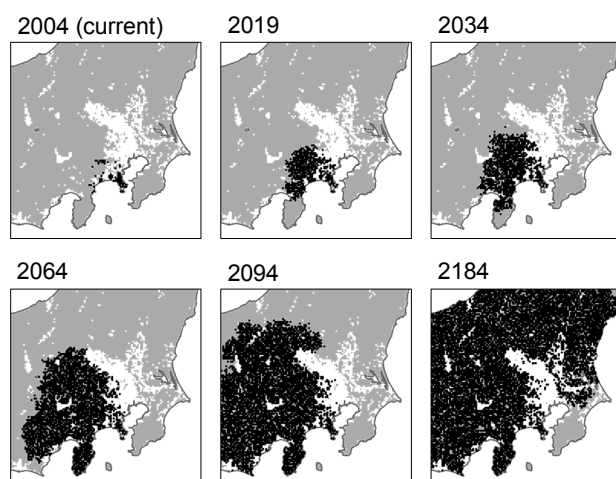


Figure 13 Long term prediction of raccoon range expansion.

Control strategy

The benefit/cost ratio was greatly different depending on the number of years since treatment (time horizon). Although all combinations of subpopulations were evaluated we illustrated typical four cases (Fig. 14); 1) eradication of a marginal isolated subpopulation (subpopulation C), 2) eradication of subpopulations at the front of spread (B, C, D and E), 3) eradication of central subpopulation (A), and 4) eradication of whole population (A, B, C, D, E). Other combinations produced intermediate results and did not produce an optimum benefit/cost for any time horizons.

The eradication of the marginal isolated subpopulation was the most cost effective treatment in the short term (less than 20 years), although the results fluctuated due to stochastic simulation. Eradication of subpopulations at the front of spread was the most cost effective strategy in the middle term (20–60 years). Eradication of all subpopulations was not cost effective in the short term, but, it was the most cost effective treatment in the long term (longer than 60 years). Eradication of the central subpopulation only was the worst strategy for all time horizons.

DISCUSSION

Prediction of range expansion

Prediction of the future distribution of invasive alien species is key information for decision making. Impact assessment should be based on future distribution ranges. If an invasive alien species is spreading, people living in the regions where the species will appear in the future should take

countermeasure as soon as possible, because they are potential victims. Simple simulation, using a metapopulation model, was reliable enough to predict the range expansion for an alien species.

There are many small naturalised populations of raccoons in various locations in Japan (Japan Wildlife Research Centre 1998). We did not include such populations in our simulation, and this means that the raccoons will spread sooner than in our simulation (Fig. 13). A nationwide distribution survey would be necessary for a more precise prediction.

Strategy for spatial control

According to the result in this study, isolated small populations (probably newly established) should be removed as the highest priority. It is possible to reduce the rate of spread efficiently with such treatment. The traditional control strategy of removing many individuals from the central population was the worst strategy, because such habitats will be re-populated with individuals from surrounding subpopulations. Contrary to this, in the case of coypus in the United Kingdom, removing individuals from the densest part of the population caused successful eradication (Baker 2006). However, coypus in the United Kingdom had a limited distribution range, and the dense part of the population might have worked as the source population for the marginal area. In the case of raccoons in Kanagawa Prefecture, on the other hand, the population is spreading rapidly, and eradication from the centre is not effective.

In reality, complete removal may be difficult for very large subpopulation. However, isolated small

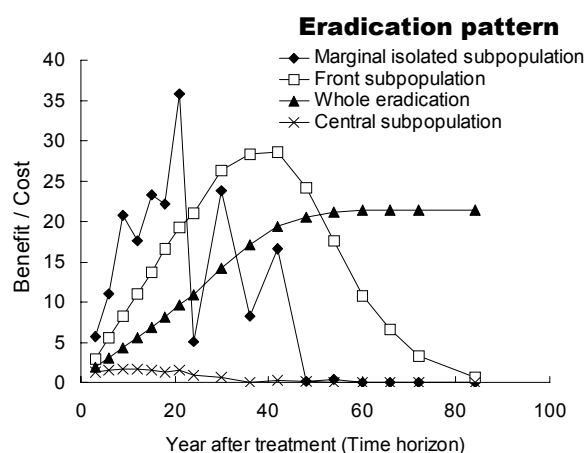


Figure 14 Benefit / cost ratio of four patterns of eradication. Benefit / cost ratio represents reduced number of occupied grids caused by eradication of one grid in 2004.

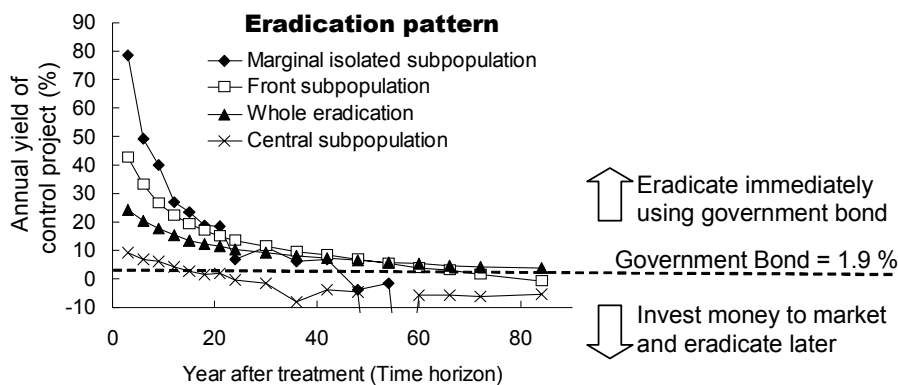


Figure 15 Annual yield of eradication project calculated from range expansion simulation.

subpopulations with one or several reproductive females may be removed easily. As shown in this study, such eradication programmes are very effective and they are highly recommended.

The annual yield of the raccoon control project suggested was higher than that for current government bonds of Japan (as of 2004) in many cases (Fig. 15). If the yield is larger than the interest of government bonds, eradication projects should be carried out immediately using funds from government bonds, to reduce government expenses in future. However in reality, the Japanese government can not issue a new bond to finance such eradication projects, because they already issued too many bonds as of 2004.

Since the geographical range used in the simulation was finite (Fig. 8), occupation of all habitats by raccoons reduced the effect of the initial removal treatment, and the benefit/cost ratio showed a humped shape along the time horizon (Fig. 14). The ratio increased with time, and then decreased in the distant future. If the habitat were to be infinite, the benefit/cost ratio might never decrease; however, the geographical area is always finite in the case of all islands and even for all continents, thus the humped shape in the graph has general relevance.

If an island, already occupied by an alien species, is considered, eradication of the alien species may be postponed from the financial point of view, because the annual yield of the eradication project is lower than that of government bonds. However, if we consider the extinction risk of native species caused by the alien species, the eradication project should be started immediately, given that extinction causes irreversible loss. Benefit should be evaluated not only by the reduction of area where an alien species is present, but by the reduction of the extinction risk of native species.

In this study removal treatment was assumed to

occur only once, however, simulation with iterative removal treatments may provide a more realistic tool to plan a control strategy. In addition, models based on precise population dynamic processes will be required to estimate the absolute eradication cost and to evaluate the best eradication technique. Nevertheless a basic spatial control strategy can be constructed using the meta-population model.

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