A simulation to identify the optimal area to survey in the early stage of invasion by *Solenopsis invicta*

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Abstract

Efforts to eradicate invasive alien species commonly use simulations to calculate the cost-effectiveness of surveys. Although eradication of *Solenopsis invicta* in the early stages of an invasion is important, few simulations are available to calculate the cost-effectiveness of surveys when a single colony has been detected. In the case of *S. invicta*, it is difficult to determine from the status of the detected colony whether new queens have dispersed, so it is necessary to consider dispersal as a probabilistic event and calculate its probability. We therefore first constructed a mathematical model in which we used Bayesian statistics to estimate the probability of dispersal as a function of the results of the survey. This mathematical model revealed that the efficacy of the survey and the associated cost differed greatly between cases depending on whether dispersal was or was not confirmed. Next, we developed a simulation that incorporated this mathematical model to inform the determination of the survey area when a single colony had been detected. The simulation showed how ecological parameters and geographical information could be used to identify an efficacious survey area, even in heterogeneous landscapes such as international ports where invasions occur sporadically. Finally, we used this simulation to assess the efficacy of a survey in the case of an *S. invicta* outbreak at the Port of Tokyo, Japan. The results suggested that the survey covered a sufficiently wide area but that it could have been designed in a more efficacious manner.

Introduction

Species that migrate to regions geographically separated from their original habitats with the transfer of people and goods are called alien species (Mack et al. 2000). Alien species that have a negative impact on the regions to which they are introduced are specifically termed “invasive alien species” (IAS). By displacing native species, IAS can change ecosystems (Mack et al. 2000; Clavero and García-Berthou 2005; Essl et al. 2011; Blackburn et al. 2019) and damage the economy (Pimentel et al. 2005). Economic losses caused by IAS have been increasing and were estimated to have reached a range of US\$46.8 billion to US\$162.7 billion in 2017 (Diagne et al. 2021). Some ant species are so invasive that five of them are included among the world’s 100 worst IAS (Lowe et al. 2000). Invasive alien ants cause damage across various ecosystems in regions they invade (Holway et al. 2002), because they outcompete native ants that play ecological roles as, inter alia, scavengers, predators, prey, plant pollinators, and seed dispersers (Hölldobler and Wilson 1990).

Solenopsis invicta is one of the most notorious IAS because it causes substantial economic losses (Gutrich et al. 2007) in addition to ecological damage and adverse health effects (Jemal and Hugh-Jones 1993; DeShazo et al. 1999). The cost of damage and control is estimated to be about US\$6 billion every year in the United States (Lard et al. 2006). In Australia, A\$300 million was spent between 2000 and 2016 on eradication programs, and the annual control cost was somewhere between A\$11 and A\$12 million (Spring et al. 2017). *Solenopsis invicta* was introduced from South America (Caldera et al. 2008) to the United States in the 1930s and has expanded its range worldwide: to Australia in 2001 (Wylie et al. 2016), to Taiwan in 2003 (Chen et al. 2006), and to China in 2004 (Lu et al. 2008). Cases of discovery have been

reported in recent years at ports in South Korea (Lyu and Lee 2017) and in Japan in 2017 (Hashimoto 2019). One of the ecological differences between *S. invicta* and other invasive alien ants is that *S. invicta* disperses not only over short distances by budding but also over long distances by nuptial flights (Holway et al. 2002).

In the management of invasive species, it is common practice to predict the distribution by using models and simulations to calculate the cost-effectiveness of decisions made to control the pests (Savage and Renton 2014). Various models and simulations have been constructed for *S. invicta*. Species distribution models (SDMs) were initially used to predict the possible habitat and the range of expansion of *S. invicta* in the United States (Korzukhin et al. 2001). Subsequently, SDMs have been used to make predictions on a worldwide scale (Morrison et al. 2004). In East Asia, SDMs have been developed by using local climatic and land parameters in places where invasions have been confirmed, for example in China (Xiong et al. 2008) and Korea (Sung et al. 2018; Byeon et al. 2020). SDMs are useful for predicting further spread in regions that have already been invaded and for preliminary assessment of regions vulnerable to invasion (Roura-Pascual and Suarez 2008). In Australia, simulations that have reproduced past spread events have been constructed to predict the spread of *S. invicta* as a new approach that is different from SDMs (Schmidt et al. 2010; Keith and Spring 2013; Keith et al. 2019). However, these models predict only the long-term expansion of distributions over a wide range on the basis of information from areas where *S. invicta* has already spread. In addition, it should be noted that the accuracy of spread models decreases as the period of simulation increases (Helms and Bridge 2017). These simulation models are therefore not suitable for predicting the expansion of the distribution of a species over a small area in the early stages of an invasion during a short period of time.

To prevent the global spread of *S. invicta*, it is important not only to reduce its distribution in areas where it is already widespread but also to thoroughly eradicate it in areas where it is in the early stages of invasion. Early detection of invasive species, including *S. invicta*, is an effective approach to control them. The eradication costs required when a species has spread for several generations are much greater than the costs required to eradicate the population immediately after establishment (Reaser et al. 2020). For example, *S. invicta* ants were eradicated from New Zealand because thorough monitoring was conducted immediately after they invaded (Bissmir 2006; Sheree 2009). In other words, the control of *S. invicta* in the early stages of an invasion is a very cost-effective way to prevent the spread of their distribution globally. It is therefore very important to survey and eradicate when a single colony of *S. invicta* is detected in areas such as Korea and Japan, which are in the early stages of invasion. However, the spatial and temporal ranges of the existing models that have been introduced for predicting the spread of *S. invicta* are too large to be used in the case of detection of a single colony. The spatial range of a simulation required for a single detected colony is a few kilometers, and the time frame is a few years. In addition, to our knowledge, most of the existing simulations assume that the probability that dispersal will occur is always 1. That assumption leads to an inaccurate calculation of the effect of the survey.

It is reasonable to consider the occurrence of dispersal of *S. invicta* as a probabilistic event because dispersal does not always occur in discovered colonies, and it is difficult to determine from the condition

of the colony whether new queens have dispersed. When the occurrence of dispersal is considered to be a probabilistic event, Bayesian theory says that the results of the survey i.e., whether a new colony is confirmed or not, change the probability of occurrence of dispersal as well as the appropriate size of the survey. In the field of ecology, mathematical models that use Bayesian estimation based on the results of a survey that say individuals are absent to update the probability of an event have been used mainly to estimate the likelihood of a species' extinction (Solow 1993; Roberts and Solow 2003) and to declare the eradication of a pest (Barclay and Hargrove 2005; Regan et al. 2006). In estimating the extinction of a species, the time and probability of extinction are calculated from the variation in the sighting records of the species (Rivadeneira et al. 2009; Thompson et al. 2017). In the management of invasive species and pests, the probability of successful eradication is estimated from the numbers of null traps (Barclay and Hargrove 2005; Sakamoto et al. 2017) in addition to sighting records (Rout et al. 2009). However, to our knowledge, there is no model that uses Bayesian estimation to update the probability of dispersal from the results of a survey. It is therefore necessary to construct a new mathematical model by using Bayesian estimation that considers the dispersal of *S. invicta* as a probabilistic event and changes the probability of occurrence of dispersal depending on the results of the survey.

In this study, we developed a new simulation to determine the optimal survey area when a colony of *S. invicta* was detected in an early stage of the invasion. We first constructed a mathematical model that used Bayesian estimation to predict the number of colonies established in an area not yet surveyed when the dispersal of new queens could not be confirmed. Next, we developed a simulation that was based on the mathematical model and that used geographic data to predict the time when a colony of *S. invicta* would be detected. Finally, the simulation was used to assess the efficacy of a survey conducted in Japan, where the early stage of an invasion by *S. invicta* is ongoing.

Materials And Methods

We focused only on dispersal from the nest associated with the flight of monogyne queens because flight with a large dispersal range has a larger impact than budding on the design of the survey area. A colony of *S. invicta* containing a queen introduced from another region was defined as the first generation. From this first generation colony, N new queens disperse by flight and then build nests (Fig. 1a). The colonies established by new queens were defined as the second generation (Fig. 1a). However, if dispersal has not occurred, no new queen will be dispersed, and therefore no second generation colony will be established. The estimated probability of the dispersal's occurring was defined as the dispersal probability. We constructed a simulation to determine the optimal survey area when a first generation colony was detected. The dispersal probability, $P(D)$, was calculated by Bayesian estimation as a function of the survey area and its result. As the area expands when the absence of colonies is confirmed, the predicted number of colonies in the areas where no surveys have been conducted (hereinafter called the residual area) decreases (Fig. 1b). The reduction in the predicted number of colonies in the residual area was defined to be the effect of expanding the survey area.

Mathematical model

Dispersal probability

Table 1 shows the parameters used in this model. In our mathematical model, we assumed that all probabilities of establishment of a new queen for each site in the space were equal. The sum of the probabilities of establishment of a new queen for each site was p_e , and the ratio of the survey area to the total space was r . The costs of the survey were assumed to increase linearly with the size of the survey area, and r , the measure of the size of the survey area, was used as the metric of the cost. The prior probability that the dispersal had not occurred was $P(f)$. The prior probability was fixed at 0.5, i.e., the prior distribution was non-informative (see Supplementary information S1 for details). Also, we assumed that colonies were always detected when they were present in the survey area. There were two conditions under which no colonies would be detected in the survey area: no dispersal had occurred, or dispersal had occurred, but no colonies were established in the survey area. The probability that no colonies were present in the survey area, $P(S)$, was therefore calculated as follows:

$$P(S) = P(f) + (1 - P(f))(1 - rp_e)^N, \quad (1)$$

where N represents the number of new queens that dispersed. The maximum value of N was assumed to be 10,000; in the extreme case, 3-year colonies had 5000 propagules (Markin et al. 1973), and we assumed that dispersals had occurred at most twice. Dispersal from the second generation was not assumed, because very few flights of new queens occur from 1-year colonies. The conditional probability of no dispersal when no colonies were present in the surveyed area, $P(f|S)$, was given by Bayesian estimation as follows:

$$P(f|S) = \frac{P(S|f)P(f)}{P(S)} \quad (2)$$

$$P(f|S) = \frac{P(S|f)P(f)}{P(f) + (1 - P(f))(1 - rp_e)^N} \quad (3)$$

The dispersal probability was

$$P(D) = 1 - P(f|S). \quad (4)$$

When colonies were present in the survey area, $P(D) = 1$.

Residual number of colonies

When no colonies were detected in the survey area, the expected number of colonies in the area not surveyed (residual area) was represented by $E_1(N)$. $E_1(N)$ was the number of new queens multiplied by the dispersal probability and the conditional probability of establishment in the residual area when no colonies were detected in the survey area:

$$E_1(N) = NP(D) \frac{p_e - rp_e}{1 - rp_e} \quad (5)$$

Because $E_1(N)$ varied as a function of N , we set the maximum value of $E_1(N)$ as the residual number of colonies in a certain r .

$$R_1(r) = \max_{1 \leq N \leq 10000} E_1(N). \quad (6)$$

When second generation colonies were detected in the survey area, the expected value and the residual number of colonies were as follows:

$$E_2(N) = Np_e(1 - r) \quad (7)$$

$$R_2(r) = \max_{1 \leq N \leq 10000} E_2(N). \quad (8)$$

Evaluation indicators

The reduction in the residual number of colonies per size of surveyed area (hereinafter called the reduction per size) was calculated on the basis of the finite difference of R_1 and R_2 , as shown in the following equations. The reduction per size of R_1 and R_2 was used as a metric of the cost-effectiveness of the survey.

$$-\frac{R_1(r+h) - R_1(r)}{h} \quad (h = 0.0001) \quad (9)$$

$$-\frac{R_2(r+h) - R_2(r)}{h} \quad (h = 0.0001) \quad (10)$$

In addition, the size of the survey area required to reduce the residual number of colonies to a certain value was calculated from the inverse functions, R_1^{-1} and R_2^{-1} .

Simulation

Table 2 shows the parameters used in this simulation. A spatial distribution map of the probability of establishment of a new queen was created by using the nesting and landing probabilities. From this map of the probability of establishment and the mathematical model described above, we calculated the relationship between the survey area and the residual number of colonies. How to design the survey area on the basis of the residual number of colonies is explained with an example in Fig. 2.

Distribution map of nesting probability

The spatial distribution of the nesting probability was described by using a two-dimensional grid of cells. The nesting probability was defined as the probability that one new queen landing in cell i succeeded in nesting. We set green belts, bare lands, and disturbance sites as danger zones where new queens tended to nest successfully (Tschinkel and King 2017). In this study, the nesting probabilities of cells in the danger zone, other locations, and non-nesting locations such as the ocean were set to 0.005, 0.0005, and 0, respectively (Tschinkel and King 2017). The map in Fig. 2a is an example of an area where a danger zone was located.

Distribution map of landing probability

The spatial distribution of the landing probability was described by using a two-dimensional grid of cells with the same size as the map of nesting probability. The probability of landing in a cell was defined as the probability of one new queen's landing in that cell. The landing probability in cell i was calculated by using the Weibull distribution (Savage and Renton 2014) as follows:

$$P_{\text{landing}}(i) = \frac{W(d_i, \kappa, \lambda)}{2d_{iH}} Ca, \quad (11)$$

where d_i represents the distance between the first generation colony and cell i , and Ca is the size of a cell. The parameters of the Weibull distribution were calculated as follows (Savage and Renton 2014):

$$\kappa = \frac{\ln(\ln(100)/\ln(2))}{\ln(\delta_{99}/\delta_{50})} \quad (12)$$

$$\lambda = \delta_{50} \ln(2)^{-\frac{1}{\kappa}} \quad (13)$$

where δ_{50} and δ_{99} represent the 50th and 99th percentiles of the flight distance, which we set to 540 m and 2000 m, respectively, on the basis of the tradeoff model in the work of Helms and Godfrey (2016). An example of a distribution map of the landing probability is shown in Fig. 2b.

Distribution map of probability of establishment

The probability of establishment of cell i was calculated as follows:

$$P_{\text{establishment}}(i) = P_{\text{dispersal}}(i)P_{\text{landing}}(i). \quad (14)$$

Figure 2c is an example of a distribution map of the probability of establishment based on Fig. 2a and Fig. 2b.

Determination of survey area

The survey area consisted of survey sections. The shape and size of each survey section were determined by external factors: geographical features, the number of available resources, and differences in land managers (Hoffmann 2011). In the simulated example of the application of the mathematical model, the survey sections were arranged in a regular pattern (see Fig. 2d), but in the validation of the model in the Aomi area, the actual survey sections were used (see below). The probability of establishment in each survey section was determined by summing the probabilities of the cells in that section. The survey area was determined by the number of survey sections to be surveyed, starting from the section with the highest probability of establishment. We, therefore, arranged the survey sections in the order of highest probability of establishment and calculated the cumulative probability of establishment (Tables 3 and 4).

By substituting the total probability of establishment in all cells into p_e and the cumulative probability of establishment in a survey area into rp_e , we obtained the residual number of colonies (R_1 and R_2). For example, dividing the section of the survey area as shown in Fig. 2d led to the relationship between the residual number of colonies and the size of the survey area shown in Fig. 2e. We set the threshold of the residual number of colonies to stop the survey at 0.5 colonies. If no colonies were detected during the survey in the first section, then the estimated residual number of colonies was below the threshold, and the survey was finished. If colonies were detected during the survey in the first section, the survey was extended to the fourth section (Fig. 2d), when the residual number of colonies was below the threshold (Fig. 2e). The reduction in the residual number of colonies per size of the survey area is shown in Fig. 2f as an index of cost-effectiveness.

Survey in the Port of Tokyo

In 2019, a colony of *S. invicta* was discovered at Aomi in the Port of Tokyo (Ministry of Environment Japan 2020). The simulation developed in this study was used to assess the efficacy of the survey at Aomi. An aerial photograph surrounding Aomi, which was taken in 2019 is a part of the Digital Japan Basic Map (ortho photo) project of the Geospatial Information Authority of Japan, was obtained from Tellus (SAKURA internet Inc. 2019). The aerial photograph was used to manually map green belts and bare lands as danger zones. Although image analysis was not the subject of this study, a paper on automatic detection of the colony of *S. invicta* by using Landsat images may be of interest (Savage and Renton 2014). The survey sections were designed on the basis of information (Ministry of Environment Japan 2020) about the actual survey (see Appendix S2).

Analysis

R version 4.0.0 was used for all numerical calculations and image analyses (R Core Team 2020). The aerial photograph was handled as raster data by using the “raster” package version 3.1-5 (Hijmans et al. 2011).

Results

Mathematical model

When the ratio of the survey areas (r) was fixed, the dispersal probability when dispersal was not confirmed decreased as the number of new queens increased (Fig. 3a). When the number of new queens (N) was fixed, the dispersal probability decreased as the ratio of the survey area increased (Fig. 3b). In both cases, the dispersal probability decreased rapidly as the probability of establishment in the whole space (p_e) increased. The expected number of colonies in the area not surveyed showed a single peak (as shown in Fig. 3c) when dispersal was not confirmed (E_1) by the number of new queens (N). As p_e increased, the height of the E_1 peak hardly changed, but N at the peak position decreased, and the tail became narrower (explained in detail in Supplementary information S3). As r increased, the peak value of E_1 and the value of N at the peak decreased (Fig. 3d).

The residual number of colonies when dispersal was not confirmed (R_1) was always smaller than the number when dispersal was confirmed (R_2), independent of r (see Fig. 4a). The reduction per size in R_1 decreased as r increased, whereas the reduction per size in R_2 remained constant, regardless of r (see Fig. 4b). In other words, because r was smaller than the value of the abscissa at the intersection point of the two lines in Fig. 4b, the cost-effectiveness of the R_1 survey was higher than that of the R_2 survey. The difference between R_1 and R_2 increased with r up to the value of r at the intersection point in Fig. 4b, and then in the region to the right of the intersection point in Fig. 4b the difference approached 0 as r increased (Fig. 4a). $R_2^{-1} - R_1^{-1}$ was calculated to obtain the difference in the survey area required to reach a certain value of R_1 and R_2 (see Fig. 4c). In other words, Fig. 4c shows the difference in cost required to obtain the same effect size. The difference between R_2^{-1} and R_1^{-1} increased as the residual number of colonies decreased up to the intersection point in Fig. 4b, and then it decreased. It should be noted that R_1 converged to almost the same curve regardless of the value of p_e as r increased in Fig. 4d (see Supplementary information S3).

Case study: Survey in the Port of Tokyo

The results of the survey at Aomi in the Port of Tokyo were compared with the results of the simulation described in the Materials and Methods. Fig. 5a is an aerial photograph of the area around Aomi and the danger zones there, and Fig. 5b shows the distribution of the probability of establishment. Fig. 5c is an enlarged view of the 1200m square region centered on the detection point in Fig. 5c. Fig. 5d shows the actual survey sections (details in Supplementary information S2), and the relationship between the cumulative survey area and the residual number of colonies is shown in Fig. 5e and Table 4. Both the residual number of colonies when dispersal was not confirmed (R_1) and the number when it was confirmed (R_2) decreased as the survey area expanded, but R_1 was always smaller than R_2 . When Section 4 and subsequent sections were surveyed, the difference between R_1 and R_2 was almost 0 (Fig. 5e). Fig. 5f shows the cost-effectiveness of each survey section, which was the reduction in the ratio of the number of residual colonies to the size of the survey section (the reduction per section size). The cost-effectiveness of R_1 decreased as the survey area expanded, and cost-effectiveness remained at a low value after Section 5. The cost-effectiveness of R_2 remained high up to section 4 but was low after section 5.

Discussion

In this study, we developed a simulation to help determine the best way to survey the area around a detected colony of *S. invicta* in the early stage of an invasion. To develop this simulation, we first constructed a mathematical model by using Bayesian estimation, which considered the occurrence of dispersal as a probabilistic event. In the field of ecology, methods for estimating the probability of extinction or eradication from the information of absence using Bayesian estimation began with Solow (1993) and have been applied in various ways: decision-making theory (Regan et al. 2006; Rout et al. 2009), spatially explicit models (Anderson et al. 2013; Ward et al. 2016), Bayesian updating (Thompson et al. 2019), and multinomial mixture models (Sakamoto et al. 2017). In both the estimation of extinction

and the declaration of eradication, the probability that the population has reached zero in the process of population decline is calculated. In the case of a decreasing population, there is an assumption that there are few members of a population just before eradication or extinction. In the case of an increasing population, the range of the numbers of new queens was too wide (1–10,000) in this study to estimate dispersal probability, because the dispersal probability varies as a function of the number of new queens (Fig. 3a). In addition, estimating the number of new queens is more difficult than confirming dispersal on the basis of the status of a colony. The mathematical model developed by Yackel Adams et al. (2018) to determine the probability of the existence of an initial population of an invasive alien snake also suffers from the fact that the range of expected density is wide. However, because there was a single peak associated with the expected number of colonies being established in the area not yet surveyed, $(E_1(N))$, (Eq. 5, Fig. 3c), the maximum value of $E_1(N)$ could be calculated, even though the number of new queens was unknown. We used the maximum value of $E_1(N)$ as an index of the residual number of colonies (R_1) to evaluate the implications of the survey. The demonstration by our mathematical model that the method of estimating the probability of an event from the results of a survey that say individuals are absent by using Bayesian estimation could also be used to monitor population growth may expand the range of application of this method.

The mathematical model revealed two phenomena associated with the residual number of colonies. First, the cost-effectiveness of a survey decreased as the survey area increased when dispersal was not confirmed. Because the residual number of colonies when dispersal was confirmed (R_2) decreased linearly with r (Fig. 4a), the reduction per size in R_2 was a constant, independent of the surveyed area (Fig. 4b). However, because the residual number of colonies when dispersal was not confirmed (R_1) decreased rapidly in a manner similar to an exponential decay (Fig. 4a), the reduction per size in R_1 decreased as the surveyed area increased (Fig. 4b). In other words, even if the size of the survey area was the same, the effectiveness of the survey varied as a function of the size previously surveyed when dispersal was not confirmed. From the standpoint of efficiency, the survey area should correspond to the intersection of the R_1 and R_2 curves (see Results) in Fig. 4b. Alternatively, if an acceptable number of colonies is set as a threshold value, the survey area should be designed so that the residual number of colonies is below the threshold value. Second, even when dispersal has not been confirmed, assuming a dispersion probability of 1 would overestimate the residual number of colonies. The value of R_2 was always larger than R_1 (Fig. 4a), and the survey area required to reduce the residual number of colonies when dispersal was confirmed was also always larger than the area when dispersal was not confirmed (Fig. 4c). In other words, the effects of the survey and the necessary costs differed when dispersal was confirmed and when it was not. To design a cost-effective survey area, it is therefore necessary to adopt a calculation method based on whether or not dispersal is confirmed. Although confirming dispersal is not important if all possible ranges of dispersal can be surveyed, the range of dispersal associated with nuptial flights of *S. invicta* is too wide to survey the whole range of dispersal.

We developed a practical simulation that made use of our mathematical model to determine the survey area when a colony of *S. invicta* was detected. Existing models, such as SDMs, have focused on

predicting the expansion of the distribution over a wide area and the long period of time. With the recent global expansion of the distribution in *S. invicta*, mathematical models such as those developed by Baker et al. (2017) and Ujijama and Tsuji (2018) have been constructed for the early stage of an invasion. The former predicts the optimal allocation of management resources by combining population dynamics with a detection model, but it does not include information on suitable habitats (Baker et al. 2017). The latter calculates the optimal placement of bait traps as a function of the territorial range of a colony (Ujijama and Tsuji 2018). However, that model provides only theoretical guidelines for the range and spacing of baits because the effects of a heterogeneous landscape are not considered. Our simulations, which use geographic information and information at the place where a colony is detected, can be expected to make highly accurate predictions. In addition, by incorporating our mathematical model based on Bayesian estimation, it is possible to calculate cost-effectiveness in a way that reflects the results of the survey. Our simulation is, therefore, more practical than existing simulations and mathematical models.

Analysis by using our simulation suggested that the survey area at Aomi in Japan was wide enough to reduce the number of colonies in the residual area. The danger zones with a high probability of nesting were scattered (Fig. 5a), and the spatial distribution of the probability of establishment was also heterogeneous (Fig. 5b). To increase cost-effectiveness, areas with a high probability of establishment should be prioritized for the survey. However, the shapes of the survey sections at Aomi were distorted, and even the areas with a high probability of establishment were divided (Fig. 5c). This inefficient design of sections may have resulted from physical obstacles: geographical fragmentation by buildings and difficulty of surveying locations owing to constant activity associated with roads and container yards. Although it is difficult to implement the theoretically optimal survey sections in an actual survey, the methodology of this study effectively enabled us to calculate the theoretical effect of each survey section by determining the actual limitations. The survey at Aomi, for example, revealed that the residual number of colonies was less than 0.5 in the survey of Section 1 (Fig. 5d), and the cost-effectiveness of surveying was low after Section 5 (Fig. 5e). These results indicated that the survey area at Aomi was adequate or somewhat overly wide if the goal was to reduce the residual number of colonies. An increase in the efficiency of the survey might have been better achieved by increasing the frequency of the surveys in Sections 1 to 4 rather than by expanding the survey area. In addition, coordination among multiple land managers might have helped to improve the cost-effectiveness of the survey at Aomi. In Australia, the CSIRO (Commonwealth Scientific and Industrial Research Organisation) plays a role in such coordination and provides centralized control (Hoffmann 2011). In Japan, it may be necessary to organize an institution to perform centralized control of management, even in regions where an invasion is in its early stages.

Our simulation is considered useful when only one colony is detected in a region where invasions occur sporadically, such as at international ports. However, other simulations will be required for regions where multiple colonies of the second generation have been detected. To improve the accuracy of this simulation, it is necessary to collect more information about the biology of *S. invicta*. As more information on the relationship between suitable habitat and the rate of successful nesting is revealed (Tschinkel and King 2017), nesting probabilities may become more accurate, and danger zones can be

designed on multiple levels. If the dispersal probability can be estimated from the state of the colony (e.g., the number of workers or nest size), the accuracy of the mathematical model will be improved by the estimation of the prior probability.

The mathematical model developed in this study can be applied to many other IAS. Our simulation was divided into two parts: one was the acquisition of the spatial distribution of the probability of establishment, and the other was use of the mathematical model to calculate the residual number of colonies. By replacing the former with existing simulations and mathematical models, it was possible to perform simulations that took into account the probability of dispersal of other IAS. The use of this kind of simulation in controlling pests would improve the accuracy of the simulation.

In conclusion, we have succeeded in developing a new simulation to support planning of the survey area when a colony of *S. invicta* is detected. This simulation solves the problem of overestimating the predicted number of colonies in the residual area when dispersal is not confirmed and provides a practical framework for determining the survey area. Assessment of the survey at Aomi on the basis of this simulation revealed that the survey area was sufficient to reduce the residual number of colonies, but that there was room for improvement from the standpoint of cost-effectiveness.

Declarations

Author contributions

Conceptualization: Shumpei Hisamoto, Koichi Goka, Yoshiko Sakamoto; Methodology: Shumpei Hisamoto; Formal analysis and investigation: Shumpei Hisamoto; Writing - original draft preparation: Shumpei Hisamoto; Writing - review and editing: Shumpei Hisamoto, Koichi Goka, Yoshiko Sakamoto; Funding acquisition: Koichi Goka; Supervision: Koichi Goka, Yoshiko Sakamoto.

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Data availability statements: Data are not yet provided. Upon acceptance data will be archived in Figshare. Data that support the findings of this study are provided from the corresponding author upon request from reviewers.

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References

- Anderson DP, Ramsey DSL, Nugent G, et al (2013) A novel approach to assess the probability of disease eradication from a wild-animal reservoir host. *Epidemiol Infect* 141:1509–1521.
<https://doi.org/10.1017/S095026881200310X>
- Baker CM, Hodgson JC, Tartaglia E, Clarke RH (2017) Modelling tropical fire ant (*Solenopsis geminata*) dynamics and detection to inform an eradication project. *Biol Invasions* 19:2959–2970.
<https://doi.org/10.1007/s10530-017-1499-9>
- Barclay HJ, Hargrove JW (2005) Probability models to facilitate a declaration of pest-free status, with special reference to tsetse (Diptera: Glossinidae). *Bull Entomol Res* 95:1–11.
<https://doi.org/10.1079/ber2004331>
- Bissmir S (2006) Red imported fire ant found at Whirinaki. *Biosecurity* 69:9
- Blackburn TM, Bellard C, Ricciardi A (2019) Alien versus native species as drivers of recent extinctions. *Front Ecol Environ* 17:203–207. <https://doi.org/10.1002/fee.2020>
- Byeon DH, Lee JH, Lee HS, et al (2020) Prediction of spatiotemporal invasive risk by the red imported fire ant (Hymenoptera: Formicidae) in South Korea. *Agronomy* 10:875.
<https://doi.org/10.3390/agronomy10060875>
- Caldera EJ, Ross KG, DeHeer CJ, Shoemaker DDW (2008) Putative native source of the invasive fire ant *Solenopsis invicta* in the USA. *Biol Invasions* 10:1457–1479. <https://doi.org/10.1007/s10530-008-9219-0>
- Chen JSC, Shen CH, Lee HJ (2006) Monogynous and polygynous red imported fire ants, *Solenopsis invicta* buren (Hymenoptera: Formicidae), in Taiwan. *Environ Entomol* 35:167–172.
<https://doi.org/10.1603/0046-225X-35.1.167>
- Clavero M, García-Berthou E (2005) Invasive species are a leading cause of animal extinctions. *Trends Ecol Evol* 20:110. <https://doi.org/10.1016/j.tree.2005.01.003>
- DeShazo RD, Williams DF, Moak ES (1999) Fire ant attacks on residents in health care facilities: A report of two cases. *Ann Intern Med* 131:424–429. <https://doi.org/10.7326/0003-4819-131-6-199909210-00005>
- Diagne C, Leroy B, Vaissière AC, et al (2021) High and rising economic costs of biological invasions worldwide. *Nature* 592:571–576. <https://doi.org/10.1038/s41586-021-03405-6>
- Essl F, Dullinger S, Rabitsch W, et al (2011) Socioeconomic legacy yields an invasion debt. *Proc Natl Acad Sci U S A* 108:203–207. <https://doi.org/10.1073/pnas.1011728108>
- Gutrich JJ, VanGelder E, Loope L (2007) Potential economic impact of introduction and spread of the red imported fire ant, *Solenopsis invicta*, in Hawaii. *Environ Sci Policy* 10:685–696.
<https://doi.org/10.1016/j.envsci.2007.03.007>

- Hashimoto Y (2019) Fire ant biology and invasion ecology. *pestology*(Pest Control Res 34:7–13. https://doi.org/10.24486/pestology.34.1_7
- Helms JA, Bridge ES (2017) Range expansion drives the evolution of alternate reproductive strategies in invasive fire ants. *NeoBiota* 33:67–82. <https://doi.org/10.3897/neobiota.33.10300>
- Helms JA, Godfrey A (2016) Dispersal polymorphisms in invasive fire ants. *PLoS One* 11:e0153955. <https://doi.org/10.1371/journal.pone.0153955>
- Hijmans RJ, van Etten J, Mattiuzzi M, et al (2011) Raster: Geographic data analysis and modeling. R Packag. version 2–0
- Hoffmann BD (2011) Eradication of populations of an invasive ant in northern Australia: Successes, failures and lessons for management. *Biodivers Conserv* 20:3267–3278. <https://doi.org/10.1007/s10531-011-0106-0>
- Hölldobler B, Wilson EO (1990) *The ants*. Harvard University Press, Cambridge
- Holway DA, Lach L, Suarez A V., et al (2002) The causes and consequences of ant invasions. *Annu Rev Ecol Syst* 33:181–233. <https://doi.org/10.1146/annurev.ecolsys.33.010802.150444>
- Jemal A, Hugh-Jones M (1993) A review of the red imported fire ant (*Solenopsis invicta* Buren) and its impacts on plant, animal, and human health. *Prev Vet Med* 17:19–32. [https://doi.org/10.1016/0167-5877\(93\)90051-T](https://doi.org/10.1016/0167-5877(93)90051-T)
- Keith JM, Spring D (2013) Agent-based Bayesian approach to monitoring the progress of invasive species eradication programs. *Proc Natl Acad Sci U S A* 110:13428–13433. <https://doi.org/10.1073/pnas.1216146110>
- Keith JM, Spring D, Kompas T (2019) Delimiting a species' geographic range using posterior sampling and computational geometry. *Sci Rep* 9:1–15. <https://doi.org/10.1038/s41598-019-45318-5>
- Korzukhin MD, Porter SD, Thompson LC, Wiley S (2001) Modeling temperature-dependent range limits for the fire ant *Solenopsis invicta* (Hymenoptera: Formicidae) in the United States. *Environ Entomol* 30:645–655. <https://doi.org/10.1603/0046-225X-30.4.645>
- Lard CF, Schmidt J, Morris B, et al (2006) An economic impact of imported fire ants in the United States of America
- Lowe S, Browne M, Boudjelas S, Poorter M De (2000) 100 of the world's worst invasive alien species: a selection from the global invasive species database
- Lu YY, Liang GW, Zeng L (2008) Study on expansion pattern of red imported fire ant, *Solenopsis invicta* Buren, in South China. *Sci Agric Sin* 41(4):1053–1063

- Lyu DP, Lee HS (2017) The red imported fire ant , *Solenopsis invicta* Buren (Hymenoptera : Formicidae : Myrmicinae) discovered in Busan sea port , Korea. Korean J Appl Entomol 56:437–438.
<https://doi.org/10.5656/KSAE.2017.11.0.049>
- Mack RN, Simberloff D, Lonsdale WM, et al (2000) Biotic invasions: Causes, epidemiology, global consequences, and control. Ecol Appl 10:689–710. [https://doi.org/10.1890/1051-0761\(2000\)010\[0689:BICEGC\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2000)010[0689:BICEGC]2.0.CO;2)
- Markin GP, Dillier JH, Collins HL (1973) Growth and development of colonies of the red imported fire ant, *Solenopsis invicta*. Ann Entomol Soc Am 66:803–808. <https://doi.org/10.1093/aesa/66.4.803>
- Ministry of Environment Japan (2020) Proceedings of the expert meeting on fire ant control the 1st business year of Reiwa era.
https://www.env.go.jp/nature/intro/2outline/attention/file/20200204_shiryou.pdf. Accessed 25 Mar 2021
- Morrison LW, Porter SD, Daniels E, Korzukhin MD (2004) Potential global range expansion of the invasive fire ant, *Solenopsis invicta*. Biol Invasions 6:183–191.
<https://doi.org/10.1023/B:BINV.00000022135.96042.90>
- Pimentel D, Zuniga R, Morrison D (2005) Update on the environmental and economic costs associated with alien-invasive species in the United States. Ecol Econ 52:273–288.
<https://doi.org/10.1016/j.ecolecon.2004.10.002>
- R Core Team (2020) R: A language and environment for statistical computing
- Reaser JK, Burgiel SW, Kirkey J, et al (2020) The early detection of and rapid response (EDRR) to invasive species: a conceptual framework and federal capacities assessment. Biol. Invasions 22:1–19
- Regan TJ, McCarthy MA, Baxter PWJ, et al (2006) Optimal eradication: when to stop looking for an invasive plant. Ecol Lett 9:759–766. <https://doi.org/10.1111/j.1461-0248.2006.00920.x>
- Rivadeneira MM, Hunt G, Roy K (2009) The use of sighting records to infer species extinctions: An evaluation of different methods. Ecology 90:1291–1300. <https://doi.org/10.1890/08-0316.1>
- Roberts DL, Solow AR (2003) When did the dodo become extinct? Nature 426:245.
<https://doi.org/10.1038/426245a>
- Roura-Pascual N, Suarez A (2008) The utility of species distribution models to predict the spread of invasive ants (Hymenoptera: Formicidae) and to anticipate changes in their ranges in the face of. Myrmecol News 11:67–77
- Rout TM, Salomon Y, McCarthy MA (2009) Using sighting records to declare eradication of an invasive species. J Appl Ecol 46:110–117. <https://doi.org/10.1111/j.1365-2664.2008.01586.x>

- Sakamoto Y, Kumagai NH, Goka K (2017) Declaration of local chemical eradication of the Argentine ant: Bayesian estimation with a multinomial-mixture model. *Sci Rep* 7:1–8. <https://doi.org/10.1038/s41598-017-03516-z>
- SAKURA internet Inc. (2019) Tellus. <https://www.tellusxdp.com/>. Accessed 25 Mar 2021
- Savage D, Renton M (2014) Requirements, design and implementation of a general model of biological invasion. *Ecol Modell* 272:394–409. <https://doi.org/10.1016/j.ecolmodel.2013.10.001>
- Schmidt D, Spring D, Mac Nally R, et al (2010) Finding needles (or ants) in haystacks: Predicting locations of invasive organisms to inform eradication and containment. *Ecol Appl* 20:1217–1227. <https://doi.org/10.1890/09-0838.1>
- Sheree C (2009) Red imported fire ants eradicated from Napier. cabdirect.org
- Solow AR (1993) Inferring extinction from sighting data. *Ecology* 74:962–964. <https://doi.org/10.2307/1940821>
- Spring D, Croft L, Kompas T (2017) Look before you treat: increasing the cost effectiveness of eradication programs with aerial surveillance. *Biol Invasions* 19:521–535. <https://doi.org/10.1007/s10530-016-1292-1>
- Sung S, Kwon YS, Lee DK, Cho Y (2018) Predicting the potential distribution of an invasive species, *Solenopsis invicta* Buren (Hymenoptera: Formicidae), under climate change using species distribution models. *Entomol Res* 48:505–513. <https://doi.org/10.1111/1748-5967.12325>
- Thompson CJ, Kodikara S, Burgman MA, et al (2019) Bayesian updating to estimate extinction from sequential observation data. *Biol Conserv* 229:26–29. <https://doi.org/10.1016/j.biocon.2018.11.003>
- Thompson CJ, Koshkina V, Burgman MA, et al (2017) Inferring extinctions II: A practical, iterative model based on records and surveys. *Biol Conserv* 214:328–335. <https://doi.org/10.1016/j.biocon.2017.07.029>
- Tschinkel WR, King JR (2017) Ant community and habitat limit colony establishment by the fire ant, *Solenopsis invicta*. *Funct Ecol* 31:955–964. <https://doi.org/10.1111/1365-2435.12794>
- Ujiyama S, Tsuji K (2018) Controlling invasive ant species: A theoretical strategy for efficient monitoring in the early stage of invasion. *Sci Rep* 8:. <https://doi.org/10.1038/s41598-018-26406-4>
- Ward DF, Anderson DP, Barron MC (2016) Using spatially explicit surveillance models to provide confidence in the eradication of an invasive ant. *Sci Rep* 6:1–5. <https://doi.org/10.1038/srep34953>
- Wylie R, Jennings C, McNaught MK, et al (2016) Eradication of two incursions of the red imported fire ant in Queensland, Australia. *Ecol Manag Restor* 17:22–32. <https://doi.org/10.1111/emr.12197>

Xiong Y, Chen JD, Gu ZY, et al (2008) The potential suitability of Jiangsu Province, east China for the invasive red imported fire ant, *Solenopsis invicta*. Biol Invasions 10:475–481.
<https://doi.org/10.1007/s10530-007-9145-6>

Yackel Adams AA, Lardner B, Knox AJ, Reed RN (2018) Inferring the absence of an incipient population during a rapid response for an invasive species. PLoS One 13:e0204302.
<https://doi.org/10.1371/journal.pone.0204302>

Tables

Table 1 Parameters used in the mathematical model

Parameter	Meaning
$P(D)$	Dispersal probability
$P(f)$	Prior probability that the dispersal has not occurred
$P(S)$	Probability that no colony is present in the surveyed area
p_e	Sum of the establishment probabilities of a new queen.
r	Ratio of the survey area to the total space
N	Number of new queens that dispersed
$E_1(N)$	Expected number of colonies in the area not surveyed when no colonies are present in the survey area
$E_2(N)$	Expected number of colonies in the area not surveyed when colonies are present in the survey area
$R_1(r)$	Residual number of colonies when no colonies are present in the survey area
$R_2(r)$	Residual number of colonies when colonies are present in the survey area

Table 2 Parameters used in the simulation

Parameter	Meaning
$P_{nesting}(i)$	Nesting probability at cell i
$P_{landing}(i)$	Landing probability at cell i
$P_{establishment}(i)$	Probability of establishment at cell i
δ_{50}, δ_{99}	50th and 99th percentiles of flight distance
d_i	Distance between the first generation colony and cell i
$W(d_i, \kappa, \lambda)$	Probability of Weibull distribution

Table 3 Values of survey example in Fig. 2

Survey section ID	Probability of establishment	Cumulative probability of establishment	Cumulative size (km ²)	Residual number of colonies (R_1)	Residual number of colonies (R_2)
1	0.925×10^{-3}	0.00092	1.004	0.490	9.766
2	0.764×10^{-3}	0.00169	2.008	0.143	5.184
3	0.702×10^{-3}	0.00239	3.012	0.019	0.974
4	0.118×10^{-3}	0.00251	4.016	0.005	0.268

Table 4 Values of survey example in Fig. 2

Survey section ID	Probability of establishment	Cumulative probability of establishment	Cumulative size (km ²)	Residual number of colonies (R_1)	Residual number of colonies (R_z)
1	0.3690 $\times 10^{-3}$	0.000369	1.230	1.230	4.628
2	0.1876 $\times 10^{-3}$	0.000557	1.267	2.497	2.752
3	0.1369 $\times 10^{-3}$	0.000694	0.767	3.264	1.383
4	0.1081 $\times 10^{-3}$	0.000802	0.608	3.872	0.301
5	0.0102 $\times 10^{-3}$	0.000812	0.745	4.617	0.201
6	0.0021 $\times 10^{-3}$	0.000814	1.054	5.671	0.180
7	0.0008 $\times 10^{-3}$	0.000815	0.427	6.097	0.173
8	0.0003 $\times 10^{-3}$	0.000815	0.686	6.783	0.169
9	0.0003 $\times 10^{-3}$	0.000815	0.355	7.138	0.166

Figures

Figure 1

a The process of spread from an introduced colony of *Solenopsis invicta*. New queens disperse from the first introduced colony (first generation) and build a nest at their landing sites. Not all queens succeed in establishing a colony: most of them fail to build one. b Summary of this method. The residual number of colonies is reduced by increasing the area where the survey confirms the absence of colonies. Note that mounds are used to represent colonies in the figure, but colonies in a port do not necessarily build mounds

Figure 2

a Map of nesting probability. b Map of landing probability. c Map of probability of establishment. d Survey sections on the map of nesting probability. e Change in the residual number of colonies as a function of the survey area. The blue line represents the threshold of the residual number of colonies to stop the survey at 0.5 colonies. f Change in the reduction of R₁ and R₂ per size of survey area

Figure 3

a Change in dispersal probability as a function of the number of new queens (N) with the ratio of the survey area (r) fixed at 0.5. b Change in dispersal probability as a function of r with N fixed at 5000. c Expected number of colonies in the area not surveyed as a function of the number of new queens ($E_1(N)$) as p_e varies. d Change in $E_1(N)$ as a function of the number of r queens as r varies. Dotted lines link the maximum values of $E_1(N)$ at each value of r . Solid black line connects maximum values of $E_1(N)$.

Figure 4

a Change in the residual number of colonies (R_1 and R_2) as a function of the ratio of the survey area (r).
b Change in the reduction in R_1 and R_2 per size in R_1 and R_2 with r
c Difference between R_1^{-1} and R_2^{-1} as a function of the residual number of colonies.
d Change in R_1 as a function of r as p_e varies

Figure 5

The survey at Aomi in the Port of Tokyo. a Green pixel represents danger zone, and a blue dot is the detected colony. b Map of probability of establishment at Aomi. c Enlarged view of the map of probability of establishment at Aomi. d Actual survey sections at Aomi. Each survey section is detailed in Supplementary information S2. e Change in the residual number of colonies as a function of the survey

section. The blue line represents the threshold of the residual number of colonies to stop the survey at 0.5 colonies. f Reduction in the residual number of colonies per size in each survey section.

Supplementary Files

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