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**Eradicating invasive ant species in the early  
stage of invasion: A theoretical strategy for  
efficient monitoring**

Dissertation for the Doctor of Philosophy

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# Abstract

Invasion by the red imported fire ant, *Solenopsis invicta* Buren, has detrimental impacts on public health, agriculture and biodiversity. For un-invaded countries, it is crucial to detect/destroy all related nest during early invasion once an incursion is found. However, the surveillance effort, such as monitoring range and frequency, for thorough detection remains elusive. Previous theoretical work that address the optimum monitoring effort either (i) focus on mid to late stage of invasion, thus, are not applicable to early invasion; (ii) substantially abstract the ant biology, thus the implications are inapplicable to actual monitoring; or (iii) utilize abstract parameters, which requires substantial additional work to translate their analysis into application. Here, I use mathematical modeling and derive the most efficient effort in actual numerical values in order to assist eradication planning and execution: it is to conduct monitoring twice within 4 or 6 km radius from the nest of origin depending on its age while shifting the locations of bait traps and setting them at intervals of 30 m in each monitoring. This study is applicable to sedentary colonial organisms such as ants. I assumed the climatic condition of mainland Japan, but monitoring range increases in warmer regions because queen ants disperse farther. Additionally, colony growth accelerates under warm climate, which increases the importance of early monitoring. Detection of the nest of origin is crucial in applying our results; it is achieved by comparing ages of the detected nests. If multiple nests—all similar in age—were found, 6 km radius from all the nests should be monitored. I assumed the use of bait traps for surveillance, but applying detector dogs and remote sensing may ensure detection. The cost-efficacy analysis of our study is applicable only when the interval between bait traps is less than 60 m, because the monitoring cost decreases nonlinearly above that. Our results are incorporated in guidelines issued by governmental organization. This is the first theoretical study that provides

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actual numerical values of monitoring effort in detail.

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# Chapter 1

## Introduction

### 1.1 Red imported fire ant: What are they?

Red imported fire ant, hereafter referred to as RIFA, is a member of the genus *Solenopsis* in the sub-family of *Myrmicinae* in the family of *Formicidae*—Ants. They are typically red to brown in color, which the body size of workers ranges from 2.4 to 6 mm [1]. A single nest could contain several hundred thousand workers depending on the social structure and habitat. In this section, I will answer the question “why does RIFA exert such an impact on infested areas?” by synthesizing information about their ecology and biology.

#### 1.1.1 Ecology

RIFA is native to central South America, and prevails as an invader primarily in areas with mild-temperate or subtropical climates [2,3]. RIFA workers forage from 15 to 43 °C, with maximal rates between 22 and 36 °C [4]. Exposure to temperatures above 42 °C is potentially lethal [5], while the metabolic rate is highest at 32 °C [6].

RIFA colonies typically form nest mounds, and actively relocate them at a frequency of at least once per year [7]. They often prefer narrow, disturbed habitats such as roadsides and forest edges of open land [8–11]. They are tolerant to disturbance, which in case of flood individuals link together and form a raft that can float on the water surface for days [2,12,13].

RIFA is omnivorous and is attracted to sources of protein, sugars, lipids, and moisture. These typically include dead mammals, insects, earthworms, and solid

food matter such as seeds [14–17]. Yet, RIFA also forages on live vertebrates and hatchlings too. Additionally, RIFA preferably forages on liquid such as sweet substances from plants or honeydew-producing homopterans [18–20].

In their native range, their abundance is regulated by competition with other ant species [21] and the presence of co-evolved predators [22] and enemies [23]. Porter et al. (1997) [22] synthesized that these include 18 species of parasitic phorid flies [24–26], 10 or more microorganisms [27, 28], at least 3 species of nematodes [27, 29], a parasitic wasp [30, 31], a parasitic ant [32], plus dozens of other symbionts of undetermined importance [33]. One example is the parasitic nematode *Tetradonema* sp. [29, 34], which parasites and sexually reproduces in the gaster of worker ants. Infected individuals seem to suffer higher mortality than non-infected ones, where the worker infection levels may reach 25 % of the workers [34].

In contrast, only few natural enemies have been discovered in their introduced range [22]. These include endoparasitic fungus [35, 36], a microsporidian obligate parasite [37, 38], a neogregarine parasite [39], a strepsipteran parasite [40], and phorid flies in the genus *Pseudacteon* [41]. Several of these species are proposed as potential biocontrol agents, yet, their effects on RIFA population regulation have partly been equivocal [42–44]. Other than pathogens and parasites, some vertebrate species—such as the black widow spider—are known to predate on queens and workers [45–47].

### 1.1.2 Social structure and life cycle

A colony of RIFA consists of two castes, one or more queen(s), and workers. Biology of RIFA such as the size of queens and workers, colony propagation, and density of nests substantially differ depending on the number of queen.

‘Monogyny’ refers to the social structure which workers tolerate only a single queen in a colony, whereas ‘polygyny’ refers to multiple queens accepted in a colony [48]. In a monogynous colony, workers kill the second reproductive [48]. Queens and workers of polygynous colonies are smaller than those of monogynous ones. Eggs laid per queen are less in the polygynous form, but the overall number of eggs produced in the colony is typically higher due to the presence of multiple queens. In the reproductive season—between spring and autumn—newborn queens of monogynous colonies leave the nest for mating flights and establish a nest

independently [48]. In contrast, newborn queens of polygynous colonies leave their natal nest accompanied by workers and establish a new colony relatively close to the maternal one [48, 49].

Interestingly, unlike many of the invasive ant species [50], RIFA population occurs in both monogynous and polygynous forms in their introduced range [51, 52]. The monogynous form appears responsible for the initial and rapid invasion of most of the southeastern United States. Regional-scale patterns of spread may be driven both by human-assisted transport and by the winged dispersal of female alates, which can travel kilometers from natal nests during mating flights [53–55]. Likewise, range expansion for the polygyne form of RIFA is 10–40 m/year in central Texas [55]. In contrast to colony reproduction by budding, winged dispersal of female alates enables new bridgeheads to be established in areas distant from the colony of origin [50].

According to Holway et al. (2002) [50], although the monogyne form of *S. invicta* is considered highly invasive [53, 56, 57], the polygyne form may locally be a bigger problem [58]. Monogyne colonies defend territories against neighboring conspecifics [59, 60], whereas polygyne colonies exhibit reduced intraspecific aggression [61, 62] and maintain high densities of interconnected nests [55, 58, 63–65]. In Florida, population densities of polygyne *S. invicta* are two times higher than those of the monogyne form [65]. Likewise, in Texas, colonies of the polygyne form can recruit up to twice as many workers to bait compared to colonies of the monogyne form [66].

### 1.1.3 Invasion process

I here synthesize the RIFA biology and ecology by summarizing information on their invasion process. Their primarily introduction routes are trade (see also section 1.2.4). After introduction, they typically relocate their nest to a preferable habitat—which I refer to as “settle in the wild” in this thesis—and the nest of origin grows. These nests form nest mounds with underground tunnels expanding like many other ant species. Obviously, there is an incipient stage for monogyne nests: a period concomitant with the nest establishment, when the newborn worker ants allocate resource to widen the nest rather than foraging, which is typically several days to two weeks. After several years, the nest include sufficient number of adults and the queen produce new queens, which disperse either by wing or on foot (see



the first and second paragraph of this section). Most of the new queens fail—they are usually preyed on by other insects, vertebrates and birds—but 1% or so establish new nests, and the RIFA expand their range.

## 1.2 Invasion by the red imported fire ant: why does it matter?

Introduction of most exotic species fail or have minor effects on their host communities [67,68]. Nevertheless, some exotics succeed and substantially alter community structure [67,69] with concomitant losses of ecosystem services and capitals [70].

RIFA is one of the most harmful of the invasive ant species. They exert impacts on public health, native biodiversity, and agriculture, which the estimated costs of control, medical treatment, and damage to property in the United States exceeded \$1 billion annually by the beginning of the twenty-first century [71]. In this chapter, I briefly review the economic and ecological impacts of RIFA introduction.

### 1.2.1 Public health and properties

The threat of RIFA on public health is growing year by year due to their rapid range expansion. In rural areas, the collision of farm equipment with RIFA nest mounds injures farmers and damage farm equipment [72,73]. In urban areas, RIFA build mounds in sunny, open areas such as yards, playgrounds, ball fields, parks, golf courses, and along road shoulders, which human could easily get in contact with them [8,74]. Studies report that 30 % to 60 % of subjects in infested urban areas could be stung each year by imported fire ants—RIFA and the congener black imported fire ant *Solenopsis richteri* [75,76]. Likewise, visitors and travelers could also frequently be stung. In one study, 55 of 107 previously unexposed subjects were stung within three weeks of arrival in an endemic area of Texas, which 8 developed fire ant venom-specific antibody [77].

Staying indoors may not be an effective prevention of getting in contact with RIFA, because these stings occur in indoor as well. RIFA agilely seek sites for colony survival during periods of environmental stress, such as food shortages or heavy rainfall. Inhabited dwellings can often be suitable sites in search of additional food and shelter, causing problems in homes, businesses, and other buildings [78,79]. Perhaps one of the most unexpected stings occurred in a medical facility, where a 67 year-old bedbound female patient was found stung all over the neck, chest, left arm, stomach, and back. An ant trail that led from

the floor to the patient’s bed was identified and was immediately eliminated, but “*fire ant-induced wheal and flare reactions too numerous to count were seen*” [80].

Clinical reactions to fire ant stings range from mild discomfort to life-threatening anaphylaxis [81], which surveys report 0.6 % to 6 % of stung individuals may have anaphylactic reactions [80]. Systematic reactions including anaphylaxis usually occur in individuals previously sensitized to fire ant stings. Yet, subjects with no previous exposure have had anaphylactic reactions after their first stings, because RIFA venom is cross-reactive with vespid venom [82]. Other than local and systematic reactions, symptoms such as seizures and mononeuritis [83,84], serum sickness, nephrotic syndrome, and worsening of pre-existing cardiopulmonary disease [80,85] have also been reported. A survey conducted in 1984 showed that 83 of 2,506 responses reported fatal reactions in the United States [81].

Damage to properties is another concern. Because RIFA is attracted to electric fields, they interfere with mechanical or electrical infrastructure and cause short circuits. These include malfunction of traffic signals [86], power distribution systems, communication systems, traffic signals, airport runway lights, air conditioners, computers, well pumps, and irrigation systems [87–89]. Additionally, RIFA tunneling under road surface may cause formation of potholes as documented in North Carolina and Florida [89,90]. Expenditures to repair potholes in Florida highways in RIFA infested areas averaged \$ 322/mile in late 20th century [91].

### 1.2.2 Native biodiversity

Biodiversity—the diversity within species, between species and of ecosystems [92]—provides numerous services to human society. These services include material goods: food, timber, medicines, and fiber; underpinning functions: flood control, climate regulation, and nutrient cycling; and nonmaterial benefits: recreation, education, and positive effects to mental health [93]. Conservation is crucial because ecological benefits from diverse natural ecosystems could exceed 10 times the cost of maintaining them [94].

RIFA introduction may have destructive effects on biodiversity [95]. RIFA often become the dominant ant species in infested areas due to their aggressive foraging behavior, high reproductive capability, and lack of predators and co-evolved competitors [22,23,29,96,97]. In central Texas, for example, they have

eradicated colonies of the harvester ant *Pogonomyrmex barbatus* [98], and several other species [58]. The extirpation of native ant communities is itself a loss to the biodiversity. Yet, it could have impact in larger scale, since native ant communities are often playing particular roles in ecosystem functions via altering physical and chemical environment below ground [99].

Impact of RIFA introduction may be pervasive. Studies show that arthropods including ticks, spiders, predatory beetles and horn flies [53, 100–102]; endangered cave invertebrates [103]; and vertebrates such as mammals [104], birds [105–110], reptiles and amphibians [105, 108, 111–115] but see [95] can also be susceptible to RIFA introduction. In contrast, some studies suggest minor or no impact [116–122], or even positive effects on some ant species [100, 123], or positive correlation with species diversity [124, 125], and impacts of RIFA introduction on native biodiversity partly remains controversial [122, 126, 127].

### 1.2.3 Agriculture

The estimated impact of RIFA infestation on agriculture exceeded \$ 90 million annually for Texas agricultural producers in 1999 [128]. These impacts are reported for nine damage categories: crop yield loss; livestock loss; equipment repair cost; replacement cost; farmstead cost; medical cost; veterinary cost; control cost, and equipment cost [128], which sum of crop yield losses, equipment repairs, and control material expenditures accounted for 73.3 % of all the damages [128].

Damages on crop yield include damages to seeds, seedlings, and root systems of a variety of agricultural crops [73, 87, 129–131] such as corns, soybeans [90, 132], fruits, vegetables, and nuts. Besides crops, costs to nursery/flower and cattle production could incur greater costs than other crops in some regions [128, 133, 134]. Notably, effects are likely not limited to agricultural systems; only 18 of 96 crop and non-crop seed species tested with RIFA colonies in a laboratory experiment were resistant to damage [135]. In general, RIFA incur damages to variety of crops and non-crops, and there are only few exceptions—such as cotton and sugarcane crops—which evidence suggests that RIFA may be beneficial by feeding on insects that feed on these crops [101, 136, 137].

#### 1.2.4 History of invasion

Introduced from the sub-Amazonian South America almost a century ago [138], RIFA has rapidly spread throughout the southern United States. Due to globalization of the economy, they have been introduced into California, Caribbean, Australia, New Zealand, Taiwan, Hong Kong, Macao, and China by early 21st century [139]. An assessment of genetic variation at molecular markers showed that the source of all but one of these introductions is the southern United States [139]. The sole exception is the population in Taiwan, which was introduced from California [139].

Recent studies suggest that RIFA introduction to un-introduced regions may accelerate. A study revealed that there is a positive feedback loop between the introduction and establishment stages of the invasion process, in which initial establishments promote secondary introductions [140]. This ‘bridgehead effect’ is increasing the risk of RIFA establishment especially in the East Asia, where Japan and South Korea are now having increasing importation from countries such as China.

The route of RIFA introduction includes commercial importation of untreated soil, sea containers, used cars and machinery, bark, and hay [141], see Table 1.1 for full list of the route along with likelihood of introduction). Table 1.1 seems to imply that marine transportation, and thus ports, is a major channel of introduction. Nevertheless, Australia and New Zealand for instance, have had introductions via airports, thus air transportation shall equally be monitored [142–144].

Their current global distribution is not precisely known, but a rough geographical distribution map is available at websites such as antmaps.org (<http://antmaps.org/?mode=species&species=Solenopsis.invicta>). See also [145, 146].

#### 1.2.5 Potential range of establishment

Future range expansion of RIFA covers nearly half of terrestrial land mass (see [147]). In the New World, large areas of Mexico and Central America, many Caribbean islands that have not yet been invaded, and Northern South America are at risk. In the Old World, regions surrounding Mediterranean Sea, Black and Caspian Seas are susceptible, while most of Europe and northern Asia is too

Table 1.1: **Likelihood of RIFA introduction via each examined pathway [141].**

| Route                                                                                                                                                                                                                                                                                                                                                                                                                                                                     | Likelihood of introduction |
|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|----------------------------|
| <ul style="list-style-type: none"> <li>• Commercial importation of untreated soil that undergoes no inspection or post-arrival quarantine</li> </ul>                                                                                                                                                                                                                                                                                                                      | Very high                  |
| <ul style="list-style-type: none"> <li>• Sea containers – wharf-inspected</li> <li>• Sea containers – transitional facility-inspected</li> <li>• Packaging materials: sea – wharf-inspected</li> <li>• Vehicles</li> <li>• Used car parts</li> <li>• Used machinery</li> <li>• Non-wooden building materials</li> <li>• Untreated and non-manufactured wooden building</li> <li>• Material</li> <li>• Bark</li> <li>• Hay</li> <li>• Used electrical equipment</li> </ul> | High                       |
| <ul style="list-style-type: none"> <li>• Sea vessels</li> <li>• Personal effects (unaccompanied baggage)</li> <li>• Animal containers</li> <li>• Packaging materials: air</li> <li>• Packaging materials: sea –transitional facility-inspected</li> <li>• Nursery stock (dormant bulbs)</li> <li>• Manufactured wooden building materials</li> <li>• Treated wooden building materials</li> </ul>                                                                         | Moderate                   |
| <ul style="list-style-type: none"> <li>• Aircraft</li> <li>• Accompanied baggage: air</li> <li>• Accompanied baggage: sea</li> <li>• Air containers</li> <li>• Nursery stock (raised from seeds or cuttings)</li> <li>• Soil imported under MAF Soil Import Health Standard</li> <li>• Straw</li> <li>• Air courier cargo</li> <li>• International mail</li> </ul>                                                                                                        | Low                        |
| <ul style="list-style-type: none"> <li>• Transportation on a person</li> <li>• Nursery stock (tissue culture)</li> <li>• Beehives</li> </ul>                                                                                                                                                                                                                                                                                                                              | Negligible                 |

cold. Most of Africa, Middle East, India, South Asia, and Australia are within the potential range, as southern Japan, southern South Korea, and northern New Zealand are also susceptible.

### 1.3 Previous eradication efforts

Once a wild population is established, eradicating RIFA becomes increasingly difficult due to winged dispersal of alate queens. No country except for New Zealand has successfully eradicated RIFA so far. Likewise, some countries are now setting their pest management goals to suppression of RIFA populations rather than complete eradication.

Important aspects of RIFA eradication include preventing introductions, preventing spread of established nests, and detecting/destroying introduced nests. Therefore, key activities include planning, processes and systems to support eradication; surveillance; treatment; communication and engagement; and science, research and development [148]. In this section, I will answer the questions “what are the countermeasures to prevent RIFA establishment?” and “what measures are effective in eradicating RIFA once they have established?” by integrating information on how governments have been controlling them.

#### 1.3.1 Case study of successful eradication in New Zealand

In March 2001, 9 months to 2 years old RIFA nest was found at Auckland Airport [141, 149]. The nest was immediately destroyed. Visual surveillance—operators stopping every two meters and inspecting the presence of a nest—within 500 m from the detection location was conducted. Bait traps were deployed every 10 m within 1 km radius. Additionally, high-risk areas within 5 km radius were surveyed with bait traps.

A further incursion was found at the Port of Napier in February 2004 [150]. Approximately 200 workers were found in attractant bait traps during surveillance activity undertaken as part of the Ministry of Agriculture and Forestry national invasive ant program. Bait traps were then deployed every 10 m within 2 km radius, which the same surveillance was also conducted the following year.

The latest incursion happened in 2006 at a forest product facility in Whirinaki [150–152]. The nest consisted of approximately 30,000 workers, and covered 2 m<sup>2</sup>. Four rounds of surveillance involving visual surveys and bait traps were conducted. Bait traps were deployed at a minimum density of four pots per equivalent 10 m × 10 m grid within a 2 km radius of the nest [152]. Over the three-year program, more than 900,000 bait traps were collected. For areas diffi-



cult to access by foot, aerial treatments using insecticidal ant baits were applied at a rate of 2 m/ha. Six rounds of bait surveillance were applied to these areas by helicopter over the three-year period. Regular supplementary monitoring of the area by visual survey was conducted out to 200 m from the original nest site. Following the three-year surveillance program, MAF Biosecurity New Zealand declared the successful eradication of RIFA from Whirinaki in 2009 [152]. Movement controls—such as a permitting system for movements of risk goods out of the controlled area—were lifted after eradication was declared. Public awareness about RIFA was raised by communications activities such as regular advisories via email and hand delivered mails in the 2 km movement controlled area [152].

### 1.3.2 Planning, processes and systems to support eradication

Typical goals of eradication programs include: eradicate and/or suppress local RIFA populations; enforce/reinforce detecting systems; increase public understanding and community vigilance; and establish protocols for international collaboration to prevent international spread of RIFA [148, 153, 154]. Planning refers to detailed description of these eradication goals and criterion, as well as resource distribution to execute the plan.

Crucial to successful implementation of these goals are range of supporting functions such as information management and data analysis [148]. These refer to monitoring and analyzing RIFA spread patterns and colony relatedness in order to assess the risk of RIFA establishing in certain areas. Typically, historical data along with expert knowledge is used, but more recently, mathematical and computational models are also used to estimate future spread [3, 147, 155, 156]. Recording and representing data are conducted by government webpages [157] and/or geographical information systems [158]; see also section 1.3.1.

A built-in review process of eradication program, management strategies, and policies is another crucial supporting function. The review process ensures the program remains updated to current pattern of infestation [148]. It also monitors procedures and protocols for quality assurance. Technical expertise and scientific research are expected to provide the basis for the continual refinement. Evaluation/validation of surveillance tools and treatment by scientists are included in the review process as well [148].

To establish a robust eradication plan, international collaboration may play

a crucial role in three ways: firstly, provisioning advices; secondly, information exchange between biosecurity experts (e.g. [159]); and finally, establishing biosecurity protocols to prevent further introduction and re-invasion [160]. Because human-mediated dispersal is the predominant cause of international RIFA spread, and risk of introduction is increasing due to the bridgehead effect [140], establishing biosecurity protocols may become one of the central concerns in future eradication planning for un-invaded countries.

### 1.3.3 Surveillance

One of the central tasks in eradication programs is surveillance—detecting RIFA nests. There are generally four surveillance methods proposed to be useful: visual surveillance by field teams; odor detection dogs; remote sensing surveillance; and community surveillance [148]. Planning the combination of these methods ensue eradication planning.

Visual surveillance by field teams is the primary method used in many eradication plans [148, 161, 162]. Operational staff may or may not use GPS systems [52], in which they visually inspect ground by walking on foot. Techniques employed may include food lures such as soybean oil-absorbed corn grits, cookies, or hot-dogs [161–164]. The weakness of this method is the detection errors—overlooking small nests—which may be complemented by the use of odor detection dogs [165]. Odor detection dogs, or alternatively ‘RIFA sniffing dogs’, can detect a nest 40 m away. They usually retire after six to eight years. These dogs are currently used to assist targeted surveillance, and to confirm the extinction of RIFA following treatment of isolated infestations in relatively small areas.

For surveillance of larger areas, remote sensing may be more an efficient method [148]. In suitable weather conditions, RIFA nest mounds are approximately 10°C hotter than surrounding ground. The use of thermography camera-mounted helicopters and image sensory technologies [166] are implemented for detection in several countries such as Taiwan and United States [165, 166]. To complement these surveillance methods undertaken by national programs, the community, industry, and other areas of government are encouraged to search and report RIFA. In such cases, the required action for national programs is to establish web pages and contacts to gather information.

### 1.3.4 Treatment

Treatment, or destruction of nest mounds, requires structured approaches. It could be either physical, that is, to pour gallons of boiling water into a nest mound [167], or chemical, such as the use of insecticides [162, 163]. Notably, because the treatment requires elimination of the queen that inhabits deep in the soil, chemical treatment could be more effective in application.

Chemical treatment generally falls into three use types: firstly, individual ant mound treatments; secondly, surface treatments; and thirdly, broadcast granular bait-formulated products [162]. The first treatment predominantly uses fast-acting contact insecticides to treat individual nests, whereas the third generally uses slow-acting ingredients for large areas, and the second falls somewhere in between depending on the active ingredient (see Table 1.2 for examples of each treatment).

Table 1.2: **Example of nest treatment.** [162]

| Type of treatment  | Example                                                                                                                                                                                                                                                                                                                                                                                 |
|--------------------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Individual mound   | Liquid mound drench; granules applied to the mound surface and watered in; granules or dusts applied to the mound surface; liquid or aerosol mound injections; fast-acting granular or some liquid bait formulations.                                                                                                                                                                   |
| Surface            | Liquid sprays or granular formulations broadcast over the entire treatment area. Time till eliminating a colony depends on the active ingredients: pyrethroid insecticides applied to the surface eliminate surface ant activity within an hour but colonies nesting below the soil surface may be unaffected; granular fipronil applications eliminate colonies slowly over 4-6 weeks. |
| Broadcast granular | Use of carrier such as defatted-corn grits coated with a food lure such as soybean oil, in which the active ingredient is dissolved. Attracted foraging ants carry the bait back to the colony where the insecticide-containing oil is shared and consumed by colony members.                                                                                                           |

These three treatments can be used in a combination, for example, using broadcast granular treatment followed by individual mound treatment (see [168]).

### 1.3.5 Communication and engagement

In Australia, for example, public reporting accounted up to 70 % of new detections within a four-year period [148]. This demonstrates the importance of fostering collaboration between communities in order to promote shared responsibility. The major issue is to increase public understanding of the risks of RIFA infestation especially when RIFA is not highly prevalent. This includes pre-invasion and post-treatment periods. Channels for communication are traditionally emails, e-news, mass media advertising including television and radio, signage, mail-outs, school education programs, and public displays [148]. Likewise, a combination of these with more modern interactive communication channels—such as social media including Facebook and Twitter, and webinars—may promote communication in a cost-effective manner.

### 1.3.6 Science, research and development

Genetic information about the introduced RIFA nest(s) plays a crucial role in planning and executing RIFA eradication. It reveals whether a colony is monogyny/polygyny, and how long it has been present. These information together determine the potential distribution of related colonies. Additionally, genetic analysis reveals: whether the colony belongs to an existing population or is the result of a new incursion; and what the invasion bottleneck is, if any [148]. The bottleneck analysis, including generation sequencing, determines the level of genetic instability or genetic viability of a population, which implies how suitable the habitat is for the introduced population. Apart from genetic analyses, regular assessments of surveillance and treatment methods, and also improving detection tools based on up-to-date scientific knowledge ensure best practice in RIFA eradication [148].

## 1.4 Aim of the thesis

Because RIFA invasion may incur destructive effects, and is difficult to eradicate once it has established, detection during the early stage of invasion is an important aspect of eradication. However, monitoring effort sufficient for eradication in the early stage of invasion remains elusive. The aim of this thesis is twofolds: (i) provide a framework that relates monitoring effort with detection rates; and (ii) use the framework and exemplify the monitoring strategy for eradication. Notably, because we focus on early invasions—RIFA is introduced to an un-invaded region—it is ethically not feasible to build such a framework by field-experiments. We instead focus on building a theoretical framework that provides monitoring efforts in actual numerical values.

## 1.5 Structure of the thesis

In the remaining part of this chapter I provide an overview of this thesis.

In Chapter 2, I first synthesize information about previous theoretical models on monitoring effort in general (section 2.1), then about those on RIFA (section 2.2). These include economic optimization models, mathematical models, statistical models and simulation models. I conclude that although these are of certain interest, there is very less, if any, research that provide explicable and actually applicable monitoring strategies. I point out the importance of (i) considering the RIFA biology in depth; (ii) not requiring model fitting; and (iii) providing implications in actual numerical values to assist decision makers plan RIFA eradication during early invasion.

In Chapter 3, I introduce a mathematical model that provides the monitoring effort in actual numerical values. The model is the one provided in Ujijama and Tsuji (2018) [169], which further discussions that were not considered in the paper is given in section 3.4.

Chapter 4 provides general discussions about our work and directions for further research. Our model put several assumptions in order to formulate the RIFA biology and monitoring into equations. I explicitly state these limitations to avoid misuse of our model, then, discuss some possible extensions to relax these assumptions. I further refer to the limit of active surveillance, and suggest resource allocation towards promoting passive surveillance.

## Chapter 2

# Previous theoretical work on monitoring strategies

### 2.1 Theoretical work on invasive species detection

A crucial aspect of RIFA eradication is thorough nest monitoring and destruction during early invasion [170]. Therefore, formulating structured surveillance strategies—in particular bait trap-based monitoring strategies—in the early stage of invasion is one of the central concerns [170]. Contributions of scientific knowledge to formulating these strategies generally fall into two types: chemical studies on active ingredients [171–173] and theoretical studies on bait delivery [162, 170]. Exploration of more effective active ingredients with less side effects has led to decades of chemical studies (see [171]). Effectiveness, in terms of RIFA eradication, connotes efficacy and speed of action [173], which recent progress is summarized elsewhere [171, 172].

In this section, I synthesize information on previous theoretical work, and point out the remaining issues. Because models targeting RIFA is scarce, I first briefly synthesize research on invasive species in general. I conclude that although these research are of certain interest, they do not meet our needs in determining an efficient monitoring strategy for RIFA eradication in their early invasion, because of three reasons: (i) the biology of social insects—which RIFA, and in general, ants are included—substantially differ from that of the non-social species, thus these models are not applicable for RIFA; (ii) most of these models assume mid to late stage of invasion such that the species already expanded their range, but

our focus is to identify a monitoring strategy to eradicate RIFA before range expansion; and (iii) majority of these models do not consider spatial structure or at the best a coarse resolution, thus they do not address the question of “where to” monitor to eradicate the subject species in the early invasion.

To my knowledge, theoretical work on detection of invasive species generally fall into three types: (i) models to unravel the population density of a species; (ii) models to find the optimal surveillance effort in sub-divided populations; and (iii) spatial models to control the spread of a species.

The first type of research builds the theoretical basis of how to estimate the species’ abundance from the number of species caught per trap. Assume that a trap is set in an area where the focal species is present [174–176]. If the species moves around—for instance to search for resource or mates—then the species will get caught by the trap at some moment—unless it does not advertently avoid them. By assuming some movement patterns to the species—such as random walk or Levy walk— [174], the probability of trapping can be calculated, in which it can be used to inversely-estimate the local abundance of the species. The spatial-scale of analysis can be enlarged. Although these models are useful in estimating the population size of the focal species, it does not provide insights into the required monitoring effort—such as where and how frequent the monitoring has to be conducted—to eradicate the species.

The second are more relevant to our question. These models assume that an invasive species occupy some habitat patches, where staffs visit and conduct monitoring [177–181]. They assume an existence probability that the species is present in a patch, a detection probability of the monitoring; a cost for monitoring, and a punishment cost of failing to detect the species. The species may or may not disperse between habitat patches. By plotting the punishment cost and cost for monitoring, these studies “find out” the optimum effort to balance damage of infestation and cost of monitoring [178–181]. Although their theories are mathematically interesting, their application to actual monitoring is limited because they do not give implications to how wide the monitoring range has to be. Furthermore, there results are highly sensitive to the punishment cost, but this is usually unpredictable with sufficient accuracy in un-invaded regions, which limits the application of their theory.

The third are perhaps most relevant to our question in the sense that they



explore spatial pattern of survey and destruction to control the spread of invasive species. These studies typically use computer simulations to replicate the (geometrical) pattern of spread, and interfere with them by a hypothetically monitoring [182–184]. They perform several patterns of interference varying the spatial configuration, and find out a strategy to best suppress the range expansion of the species [182, 184]. Although these studies bring valuable insights due to their explicit spatial-structured model, the application of their theory into actual monitoring is limited because they assume that the distribution of the species is priorly known, which is typically itself the target of the monitoring. Additionally, they do not provide analysis about how frequent and wide the monitoring has to be to eradicate the species.

Overall, these studies assume species such as weeds and moths, which the goal of deploying traps is to capture the individual *per se*. Nevertheless, in many social insects including RIFA, the individuals captured by traps are the workers and not the queens, which eradication depends on the removal of the queens. Additionally, the distribution of RIFA nests are quite discrete—unlike the assumptions of the above models—due to the long-distance flight by the queens. I synthesize models specifically for RIFA in the following section.

## 2.2 Theoretical work on fire ant detection

Although bait trap-based monitoring is now conducted for decades, bait delivery—such as width of monitoring area; spatial and temporal frequency to deploy them; and their spatial patterns—are, in general, determined empirically [162, 185, 186]. The formulation of strategies based on empirical knowledge is, itself, not much of a problem. However, the lack of strong evidence could be, when there is a need to explain the risks and potential countermeasures to the public. In this context, theoretical work may help providing a more clear and concise evidence for the explanation.

To my knowledge, theoretical works on bait delivery are scarce, which generally fall into three types: (i) models to find the optimal sampling strategies under the restriction of resource; (ii) constructive approaches to monitor the efficacy of monitoring; and (iii) models to find the optimal resource allocation among surveillance methods.

The first are a series of mathematical analysis to solve the optimization problem of spatial sampling strategies under restricted resource [187, 188]. The aim of these studies is to propose a model that constructs an occurrence map of species from imperfect data [187], which the model is as follows: (i) an initial arbitrary sampling is hypothetically performed; (ii) a parameter that denotes the “information value” is updated; (iii) the sampling rule—determining where to perform sampling—is updated; (iv) sampling is performed; (v) go to step (ii) until the resource is zero. The output of the study is a set of fitted parameters that consists the “sampling rule” in step (iii). They conclude that these parameters, and thus the hypothetical sampling rule, substantially improved classical sampling methods in the simulation. Although these studies are certainly mathematically interesting, the application of their theory to actual monitoring is limited due to four reasons: (i) they do not provide detailed descriptions of how bait delivery should be conducted (ii) the model is not biologically realistic, they assume the dispersal distance of fire ants is 100 m, but monogynous queens disperse up to several kilometers; (iii) the parameters fitted are abstract, and substantial additional work is required to translate them into actual monitoring efforts; and (iv) perhaps most of all, practitioners typically ask the required resource for complete detection, but they maximize detection under a given resource, therefore the question is reversed in these studies.

The second are more biologically realistic models that incorporate actual ant biology such as growth and diffusion of nests [189–191]. These studies apply constructive approaches that “*enable inferences to be made about the locations of undiscovered individuals over time to identify trends in invader abundance and spatial extent*” [191]. They create hypothetical ant distributions by agent-based simulations [189, 191] or by statistical methods [190], fit the model with spatial-temporal distribution data, then hypothetically perform monitoring to assess the efficacy. They conclude that if slightly larger area [189, 191] or remote habitats [190] were surveyed and treated in Australia in the early 21st century, the RIFA invasion in Australia could have been controlled. Although these studies are certainly useful in predicting the spread of RIFA, their application is limited to eradication in the mid to late stage of invasion, because these models require a large data set of spatial-temporal ant distribution for model fitting [190]. Additionally, they do not provide detailed descriptions of how a structured bait delivery should be conducted.

The third are perhaps the most applicable to eradication in the early stage of invasion. These studies use either statistical or optimization models to analyze the trade-off between cost and efficacy of monitoring activities [192–195]. The strength of these models is that they consider two or more surveillance methods—such as bait traps, detecting dogs, and remote sensing—in their framework to optimize resource allocation among methods [193–195]. For example, Spring and Cacho (2015) [192] simulated a hypothetical spread with a concomitant hypothetical monitoring, then, statistically estimated a curve for the probability of eradication as determined by the eradication efforts. They conclude that there must be a means of searching large area each year with sufficient sensitivity to the eradication probability, because it is the dominant term. Ward, Anderson, and Barron (2016) [194] compared the efficacy of bait trap, visual surveillance, and detecting dogs in terms of detection probability. They assumed that detection probability is a half-normal function of distance from the searched point, and fitted the function with several monitoring data in a bay. They conclude that the use of all surveillance methods combined increases the probability of eradication. Baker et al. (2017) [195] developed a framework to relate monitoring methods with detection probability. They built a difference equation that describes the population growth, then, assigned a Sigmoid-function for the probability of erad-

ication as determined by the growth. Dispersal of ants is not considered. They conclude that the use of growth regulator and toxins, along with several detector dog, may be more cost-effective than the use of lure deployment. Although these studies certainly provide interesting insights, their application may be limited because they assign arbitrary detection probabilities or functions [192, 195]; neglect dispersal [195]; or require model fitting by using experimental data of actual infestation [194, 195], which makes the model less applicable to individual incursions. Secondly, the statistical analyses of these studies obscure the causal relation between the RIFA biology, bait delivery, and monitoring efficacy, which makes it less understandable to the public.

To assist the formulation of structured monitoring strategies in the early stage of invasion, we need a model that provides detailed description of how bait delivery should be conducted. This includes actual numerical values of monitoring range, frequency, and trap density, which has never been fully addressed in the above studies. Therefore, a model that is (i) relating the RIFA biology with structured surveillance strategies and monitoring efficacy; (ii) not requiring fitting using prior infestation data in order to consider early invasion; (iii) spatially explicit to incorporate dispersal is required to provide useful insights. Incorporation of RIFA biology in terms of growth rate, foraging area, and dispersal is particularly crucial in reflecting the nature of RIFA biology. In the next chapter, I introduce and discuss a theoretical framework to shed light on the required monitoring effort for RIFA eradication.

## Chapter 3

# Theoretical strategy for monitoring

### 3.1 Purpose of this study

Because of the bridgehead effect [140], un-invaded countries in the RIFA potential-distribution [147] are now facing increasing risk of introduction. Establishing global biosecurity protocols to prevent human-mediated international dispersal—such as deploying insecticide to containers before shipping them—is the primary means to prevent incursion. Deploying insecticide to containers that arrived may also be effective. Yet, some nests may survive and invade, therefore a strategy of structured surveillance is in need. Structured surveillance, in the effort of detecting all related nests of the nest of origin, is one of the most crucial activities when an incursion is found in an un-invaded area. Nevertheless, the surveillance effort—such as the range, frequency and density of deploying bait—that is required for complete eradication remains elusive. The purpose of this study is to theoretically derive the most efficient surveillance effort in terms of numerical values in order to assist decision makers plan RIFA eradication in the early stage of invasion.

## 3.2 Assumptions

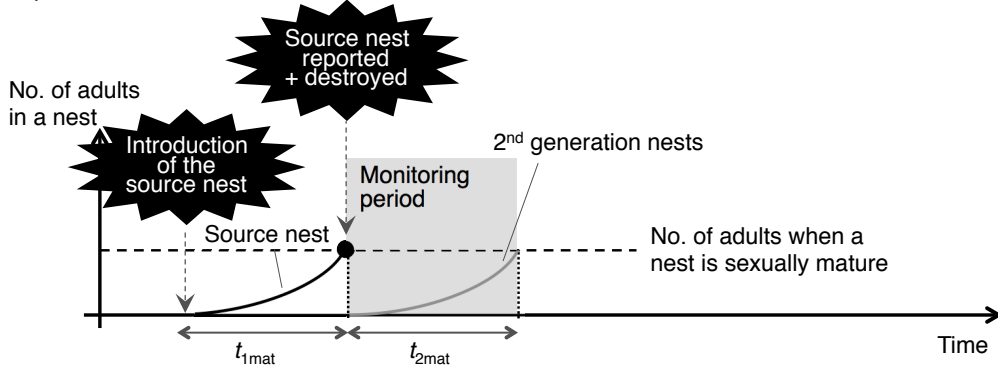
We assume that the red imported fire ant was introduced to an un-invaded region and settled in the wild [196]. The nest was found some time after the nest started producing alate queens and monitoring started then. We assume that monitoring is conducted with highly attractive bait traps, such as soybean-oil-absorbed corn grits and hotdogs [171, 197]. We also assume that, with such a bait trap, a fire ant nest is detected at 100% probability when the bait is placed in the foraging territory around the fire ant nest [171, 198] (see section 3.4.3 for further discussion), except when the nest is at the incipient stage. For ease of application, bait traps are set in lattice patterns. We set the origin of the coordinate axes to the location where the first-generation nest (here called the “source nest”) is found. Assume that the existence probability distribution of a next-generation nest at location  $(x, y)$  varies with the dispersal capability of an alate queen, i.e. the location of a nest is determined solely at the time of independent founding after the nuptial flight and nest relocation [7] is thereafter not considered. The fire ant has two social forms: monogyne and polygyne. A long-distance nuptial flight, followed by independent colony founding, takes place only when the colony is in the monogynous form [199]. Here, we assume the monogynous form, because in this form the colony expands its range faster [48, 200] and is thus more difficult to eradicate than the polygynous form [201].

We will consider two cases: the optimistic case, in which the source nest is found instantly after it starts producing queens and second-generation alate queens have dispersed only for a short period (Fig. 3.1a); and the pessimistic case, in which detection of the source and the second-generation nests is delayed, such that the second-generation nests have started producing queens and third-generation alate queens have dispersed for a short period (Fig. 3.1b).

The optimistic case corresponds to the situation in which the source nest has remained undetected for a while and the nest has matured to form a mound that someone has discovered by chance.

The pessimistic case corresponds to the situation in which the source nest and second-generation nests have been undetected for a while and the second-generation nests have matured to form mounds, one of which has been noticed by chance. The source nest is assumed to be found approximately at the same time as the second-generation nest, because it is large and easy to detect once

a Optimistic case



b Pessimistic case

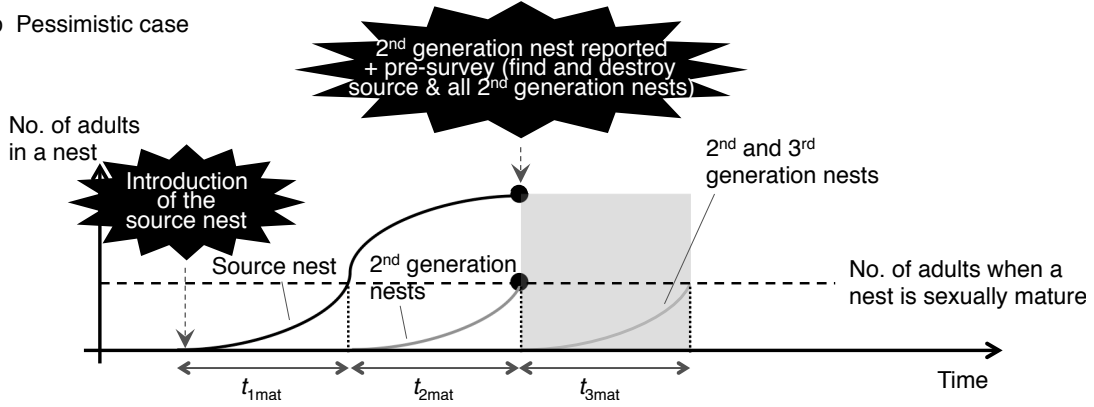


Figure 3.1: **Two types of incursion.** In each panel, the horizontal and vertical axes denote time and number of adults in the nest, respectively. Black, gray and light gray curves denote the transition in the number of adults in the source nest, second-generation nests, and second and third-generation nests.  $t_{1mat}$ ,  $t_{2mat}$ , and  $t_{3mat}$  are the time till the source, second generation and third-generation nests, respectively, become sexually mature. Black dots indicate the detection and destruction of the focal nests: in the upper panel the source nest is found and destroyed with a concomitant monitoring; whereas in the lower panel the second generation (or source) nest is found, a pre-survey to destroy all the second generation (and source) nest is conducted, and monitoring period starts. The lightly shaded region denotes the monitoring period. (a) Optimistic case. (b) Pessimistic case.

the searchers have been alerted. It is natural to assume that a pre-survey is conducted immediately after the detection in the effort to find and destroy all second generation nests. The monitoring effort of the pre-survey is that in the optimistic case; which the center of monitoring is set to the location of the source nest. In the pessimistic case, the aim of the monitoring is to detect all the second and third generation nests that may have established at  $t = t_{2\text{mat}}$ . Note that the monitoring period should be no more than two to three years in both cases, because the next-generation nests will become sexually mature and produce alate queens in two to three years [202], depending on the food density and climatic conditions [8]. In other words, monitoring has to be intense enough to be able to detect all of the dispersed nests within two to three years.

We assume the surveillance effort is characterized by two parameters: monitoring range, which is the radius of monitoring area from the source nest; and bait interval, which is the geographical interval between each bait. Under these model settings, we assess two monitoring strategies: non-shift, which there is only one monitoring at  $t = 3$  years and bait locations are not shifted; and shift, which there are two monitoring in total at  $t = 2.5$  and 3 years and the locations of bait are shifted for half the interval in a subsequent monitoring (Fig. 3.2). In the non-shift strategy and the first monitoring in the shift strategy, baits are located at  $(x_i^t, y_j^t) = (i \times l_b, j \times l_b)$  ( $i, j = 0, \pm 1, \pm 2, \dots, \pm 2 \times r_m/l_b$ ) at time  $t$ , where  $l_b$  is the spatial interval of baits and superscripts of  $x$  and  $y$  denote time. Considering the shift strategy, in the subsequent monitoring conducted at time interval  $t_{\text{int}}$  after the first, the baits are located at  $(x_i^{t+t_{\text{int}}}, y_j^{t+t_{\text{int}}}) = (x_i^t + l_b/2, y_j^t + l_b/2)$ .

The radius of the detectable area  $r(t)$  is defined as

$$r(t) = r_c(t) + r_s(t), \quad (3.1)$$

where the nest radius  $r_c(t)$  and foraging radius  $r_s(t)$  are

$$r_c(t) = \sqrt{\frac{S(t)}{\pi d}}, \quad (3.2)$$

$$r_s(t) = \sqrt{\frac{\beta \cdot S(t - t_s)}{\pi}}, \quad (3.3)$$



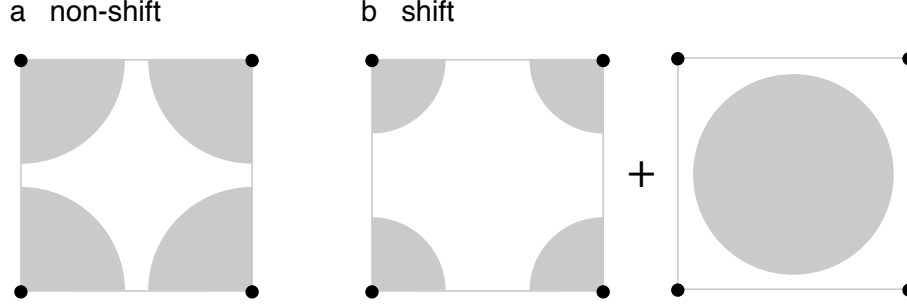


Figure 3.2: **Two types of monitoring strategies.** For every graphic the black dots denote bait and gray area denote the detectable area, which the radius is a sum of foraging radius and nest radius. A nest is detected if it is located within the detectable area, therefore the sum of this area over repeated monitoring, if any, is the total detectable area. In the analysis, we consider the trade-off between (a) monitoring once by non-shift; and (b) monitoring twice but by shifting bait.

and the number of adults in a nest  $S(t)$  is

$$S(t) = \frac{220,000}{1 + 83e^{-1.26t}}. \quad (3.4)$$

Parameters and constants are summarized in Table 3.1.

Here,  $\beta$  is a ratio to convert the number of adults in a nest to territorial area,  $t_s$  is the age of a nest when adults start searching for resource and  $S(t)$  is obtained empirically [8]. See Table 3.1 for the values of parameters and constants.  $d$  is deduced from equation (3.2) and the assumption that the radius of a fully-grown—that is  $S(t) = 220,000$ —nest is 15 to 20 m including underground tunnels, depending on the soil conditions (K. Tsuji personal communication 11 September 2017).  $\beta$  is deduced from equation (3.3) and the results of a survey that the territorial area is approximately 1/1000 times the number of adults in a nest [59]. Worker ants start searching for resources two to four weeks—that is roughly 1/17 of a year—after the nest is established.

Given the above model design, the detection rate  $D(t)$  is defined as

$$D(t) = A_m \times O(t), \quad (3.5)$$

where  $A_m$  ( $0 \leq A_m \leq 1$ ) and  $O(t)$  denote the thoroughness and effectiveness of monitoring, respectively, and time  $t = 0$  when the nest of origin was found and

Table 3.1: **Parameters and constants.**

| Parameters and Constants                                            | Symbol      | Value  | Dimension          |
|---------------------------------------------------------------------|-------------|--------|--------------------|
| <b>Parameters</b>                                                   |             |        |                    |
| Monitoring range                                                    | $r_m$       | -      | (m)                |
| Radius of a nest                                                    | $r_c(t)$    | -      | (m)                |
| Radius of foraging territory from the edge of a nest                | $r_s(t)$    | -      | (m)                |
| Number of adults in a nest                                          | $S(t)$      | -      | (-)                |
| Spatial interval of traps such as baits                             | $l_b$       | -      | (m)                |
| <b>Constants</b>                                                    |             |        |                    |
| Age of nest of full sexually-maturity                               | $t_{1mat},$ | 3      | (years)            |
|                                                                     | $t_{2mat},$ |        |                    |
|                                                                     | $t_{3mat}$  |        |                    |
| Interval between the first and second monitoring                    | $t_{int}$   | 0.5    | (years)            |
| Number of adults per square meter in a nest                         | $d$         | 200    | (m <sup>-2</sup> ) |
| Ratio to convert the number of adults in a nest to territorial area | $\beta$     | 1/1000 | (m <sup>2</sup> )  |
| Age of nest when adults start foraging                              | $t_s$       | 1/17   | (years)            |

destroyed.  $A_m$  is the ratio of the monitoring area to the entire area where related nests may exist. Thus,

$$A_m = \iint_{-r_m \leq x, y \leq r_m} P(x, y) dx dy, \quad (3.6)$$

where  $P(x, y)$  is the existence probability distribution of related nest, and  $r_m$  is the monitoring range in the direction of the x- and y- axes from the origin; that is, the monitoring area is the square of  $r_m$ .  $P(x, y)$  denotes the probability that a second- or third- generation queen establishes a nest at location  $(x, y)$  (see appendix A for derivation).

$O(t)$  is the observable ratio defined as: the ratio of the detectable area to the area of a  $r_m$  m  $\times$   $r_m$  m grid. Therefore it is defined as follows:

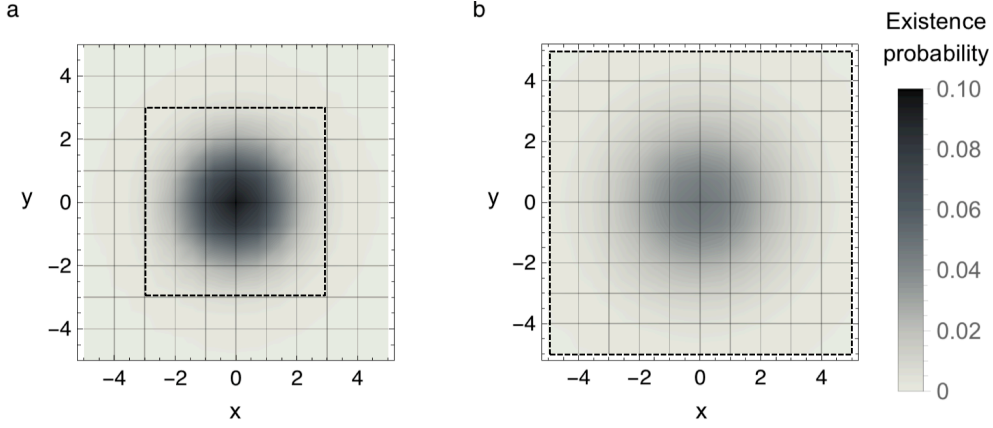


Figure 3.3: **Existence probability distribution**  $P(x, y)$ . Assuming that an alate queen has dispersed from the origin  $(0, 0)$ , the maps show the two-dimensional distributions of the existence probability of a next-generation nest at coordinates  $(x, y)$ . The square area surrounded by the broken line denotes the monitoring range, which is a radius of  $r_m$  around the origin. Above give examples of when  $r_m = 3$  km in the optimistic case and  $r_m = 5$  km in the pessimistic case. (a) Distribution of second-generation nests in the optimistic case. (b) Distribution of third-generation nests in the pessimistic case.

$$O(t) = \begin{cases} \pi \left( \frac{r(t)}{l_b} \right)^2 & 0 \leq r(t) < \frac{l_b}{2} \\ \pi \left( \frac{r(t)}{l_b} \right)^2 - \frac{4r(t)^2 \left( \arccos \frac{l_b}{2r(t)} - \frac{l_b}{2r(t)} \sin \left( \arccos \frac{l_b}{2r(t)} \right) \right)}{l_b^2} & \frac{l_b}{2} \leq r(t) < \frac{l_b}{\sqrt{2}} \\ 1.0 & r(t) \geq \frac{l_b}{\sqrt{2}} \end{cases} \quad (3.7)$$

where  $l_b$  is the spatial interval between bait traps. In the second row, the second term represents the overlap of the detectable area. The derivation of  $O(t)$  when the bait locations are non-shift is included in that of when the locations are shifted, which I provided in appendix C.

### 3.3 Results

First we assume that the locations of bait are not shifted and monitoring is conducted once at  $t = 3$  years.  $O(t)$ , which is the observable ratio, increases logistic-function-like until the value reaches 1.0 (Fig. 3.4a), because it is dependent on the radiuses of the nest and territory (Fig. 3.4b), while these are dependent on the number of adults in the nest, which is a monotonically increasing logistic function (Fig. 3.4c).

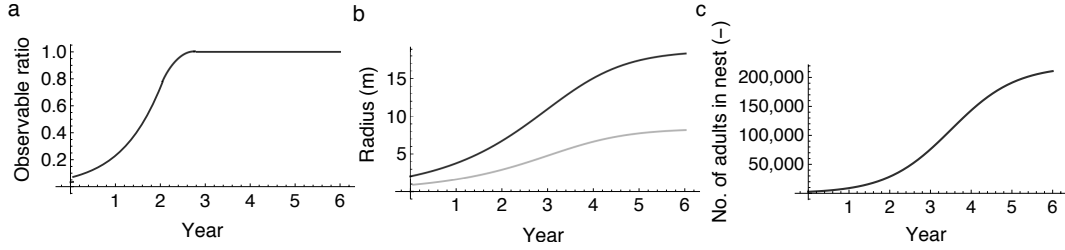


Figure 3.4: **Characteristic traits of the nests.** (a) Observable ratio  $O(t)$  when  $l_b = 20$  m. (b) Radius of a nest  $r_c(t)$  (black line) and radius of foraging territory  $r_s(t)$  (gray line). (c) Number of adults in a nest  $S(t)$ .

Three-year detection rate, which is the probability of detecting all potentially established nests within three years, is derived. When trap locations are not shifted and there is only one monitoring at  $t = 3$  years, traps must be deployed at a minimum density of four pots per equivalent  $20 \text{ m} \times 20 \text{ m}$  grid within 4 km radius of the source nest in the optimistic case (Fig. 3.5a). Whereas, this becomes  $20 \text{ m} \times 20 \text{ m}$  grid within 6 km radius in the pessimistic case (Fig. 3.5b). Expanding the monitoring range increases the detection rate especially up until a range of 3 km in the optimistic case and 5 km in the pessimistic case, because the existence probability of RIFA is substantially low farther than that (Fig. 3.3).

Compared to the non-shift method, the shift method allows the bait interval to be one-half times longer. When trap locations are not shifted, bait must be deployed at a minimum density of four pots per equivalent  $30 \text{ m} \times 30 \text{ m}$  grid within 4 km radius of the source nest in the optimistic case (Fig. 3.6a). Whereas, this becomes  $30 \text{ m} \times 30 \text{ m}$  grid within 6 km radius in the pessimistic case (Fig. 3.6b).

The cost of monitoring, which is substituted by the number of deployed traps,

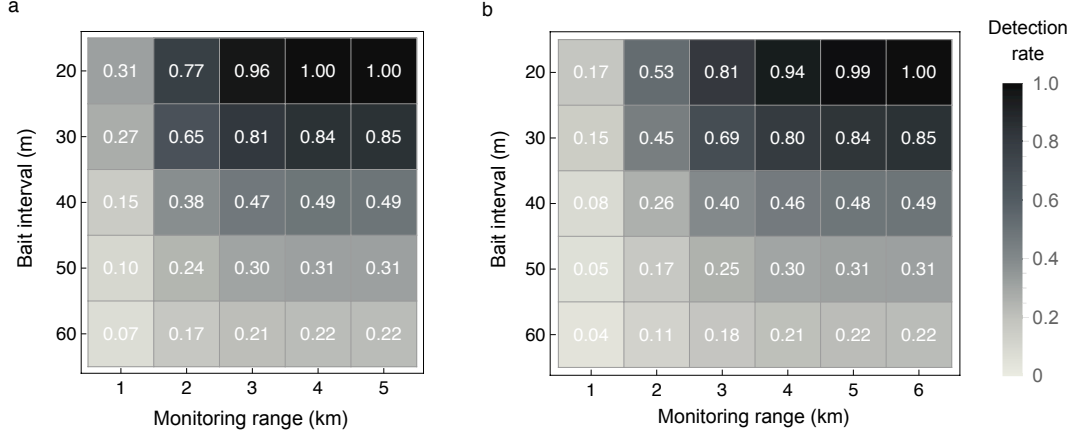


Figure 3.5: **Three-year detection rates when bait traps are not shifted.** Each number at a given bait interval and monitoring range denotes the detection rate rounded to two decimal places. (a) Optimistic case. (b) Pessimistic case

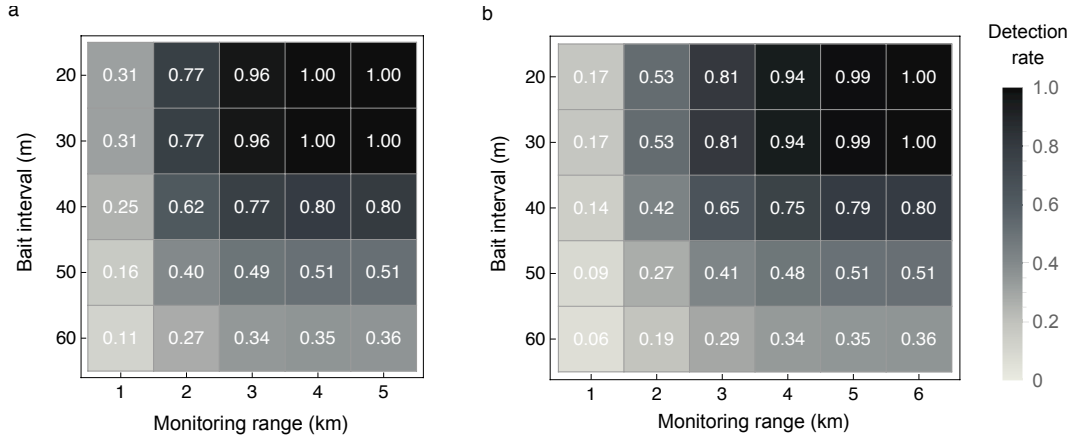


Figure 3.6: **Three-year detection rates when bait traps are shifted.** Each number at a given bait interval and monitoring range denotes the detection rate rounded to two decimal places. (a) Optimistic case. (b) Pessimistic case.

is less when trap locations are shifted compared to when they are non-shifted (Table 3.2). Note that we ignore the combination of monitoring range and bait interval that detection rate does not become 1.00, because the purpose of surveillance is to completely detect all the potentially established nests.

Table 3.2: **Number of traps required to conduct monitoring.** “–” shows the parameter set for which the three-year detection rates subceed 1.0. The values are calculated based on the following assumption: monitoring is conducted only once when non-shift, and twice when shift.

| Bait Interval                                                     | Monitoring Range |        |        |
|-------------------------------------------------------------------|------------------|--------|--------|
|                                                                   | 4000 m           | 5000 m | 6000 m |
| Non-shift bait trap-location (one monitoring at $t = 3$ year)     |                  |        |        |
| Optimistic case                                                   |                  |        |        |
| 20                                                                | 160801           | 251001 | 361201 |
| 30                                                                | -                | -      | -      |
| Pessimistic case                                                  |                  |        |        |
| 20                                                                | -                | -      | 361201 |
| 30                                                                | -                | -      | -      |
| Shift bait trap-location (two monitoring at $t = 2.5$ and 3 year) |                  |        |        |
| Optimistic case                                                   |                  |        |        |
| 20                                                                | 321602           | 502002 | 722402 |
| 30                                                                | 143291           | 223558 | 321602 |
| Pessimistic case                                                  |                  |        |        |
| 20                                                                | -                | -      | 722402 |
| 30                                                                | -                | -      | 321602 |

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### 3.4 Discussion

We used mathematical modeling to study the efficiency of monitoring strategies to detect and eradicate invasive ants in the early stage of their invasion. Our results suggests that bait traps must be deployed at a minimum density of four pots per equivalent  $20 \text{ m} \times 20 \text{ m}$  grid within 4 km or 6 km radius when the source nest was found early or lately, respectively. However, this could be widened to  $30 \text{ m} \times 30 \text{ m}$  grid when trap locations are shifted for a repeated surveillance. In such cases, the total number of deployed traps decreases from 160,801 to 143,291, and 361,201 to 321,602 when the source nest was found early or lately, respectively.

Here, I address four questions on our results: (i) Can we not directly derive the required bait interval?; (ii) Incursions do not happen only in mainland Japan, what is the monitoring effort for other regions?; (iii) What if bait traps were not as highly-attractive as is assumed in this study?; and (iv) Considering the pattern of deployed traps, would applying close-packing structures—and thus triangular lattices—not be more efficient than shifting bait?

#### 3.4.1 Direct derivation of bait interval

We calculated the detection rate as a function of bait interval and other parameters in section 3.3, but it would be convenient to have an equation to directly derive the bait interval required for the detection rate to be 1.0 until an arbitrary time. The equations below give the required interval when we assume that the entire area in which the object species may exist is monitored. The actual interval must be shorter than them. Equation (3.8) covers the case in which trap location is not shifted or the objective species frequently relocates its nests, whereas Equation (3.9) covers the case in which trap location is shifted (see appendix D for derivation).

$$l_b = \sqrt{2}r(t), \quad (3.8)$$

$$l_{b,\text{shift}} = r(t) + \sqrt{2 \cdot r(t + t_{\text{int}})^2 - r(t)^2}. \quad (3.9)$$

See Table 3.1 for the parameter list. Note that  $t + t_{\text{int}} \leq 3$  if the object species is *S. invicta*, in order to avoid the reproduction of next-generation queens. Substitute  $d = 200$ ,  $t_s = 1/17$ ,  $\beta = 1/1000$  and assume  $t = 3$  for Equation (3.8)

and  $t = 2.5$  and  $t_{\text{int}} = 0.5$  for Equation (3.9). Then,  $l_b = 22.3$  and  $l_{b,\text{shift}} = 31.0$ . These values are confirmed as reasonable from our findings that the detection rate was 1.0 up to  $l_b = 20$  in Fig. 3.5 and up to 30 m in Fig. 3.6. In applying these equations to species other than *S. invicta*, the species-specific functions of  $r(t)$  and  $S(t)$  have to be empirically determined. In practice, growth of the colony's territorial area may often be easier to monitor than that of colony size, because estimating accurately the colony size requires excavation of the whole nest in which the radius is 15 m or larger depending on soil condition. Note that the territorial area may change on a daily basis [203], thus it is important to collect data for several days and use the average value.

### 3.4.2 Different environments and monitoring intervals

We assumed the environmental condition of mainland Japan, which relaxing this assumption may affect the results in two aspects: the colonial traits  $d$  and  $\beta$ , which are the density of adult ants in a nest and a ratio to convert the number of ants into territorial area respectively; the other is the dispersal of queen ants. I leave the later for section 4.2, here I discuss the influence of the colonial traits on the required-bait-interval (Equation (3.8), (3.9)). I also discuss the effect of varying the temporal interval between the two monitoring in the bait-shift case, which I denoted as  $t_{\text{int}}$ .

$d$ , the density of adult ants in a nest, converts the number of adult ants in a nest  $S(t)$  to the surface area of the nest—although the nest is technically “underground”. Note that this “surface area” includes the nest mound and the underground-tunnels. Therefore, the higher  $d$  is, the dense the ants are compound in one nest, or alternatively, the shorter the tunnels are. In this context, biologically,  $d$  may reflect the soil condition in which the harder the soil is, the higher  $d$  is. This is actually true in the nature. Considering Equation (3.8), (3.9), when  $d$  increases, the radius of a nest shortens, thus the detectable area shrinks, therefore bait interval has to be shorter (Fig. 3.7a).

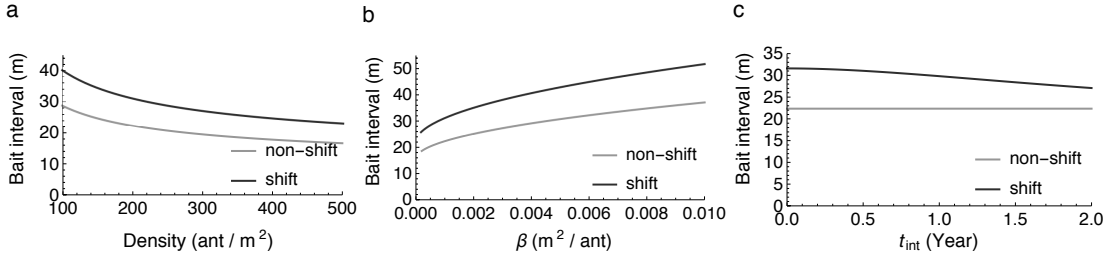
Similarly,  $\beta$ , which converts  $S(t)$  into the territorial area, may imply how wide the foraging workers search for resource. The larger  $\beta$  is, the wider the detectable area is, therefore bait interval can be widened (Fig. 3.7b).

$t_{\text{int}}$  is the interval between the two rounds of monitoring when shifting bait locations. Note that the second monitoring is conducted at  $t = 3$  years and the



first is at  $t = 3 - t_{\text{int}}$  years. Because detective rate  $D(t)$  reaches one at around two and a half years, varying  $t_{\text{int}}$  within half a year seems not to affect the results (Fig. 3.7c). Increasing  $t_{\text{int}}$  for more than half a year slightly decreases the required-bait interval because the coverage of the first round will decrease due to smaller territorial area of RIFA. Obviously, varying  $t_{\text{int}}$  does not affect the monitoring cost because monitoring cost is estimated based on human days (see also section 4.3), which is not affected by “when” the second round is conducted.

Although I here used a reductionist approach—to estimate the influence of the components ( $d$  and  $\beta$ ) on the required-bait-interval—in application, this is not as helpful as it may seem. This is because, as noted in section 3.4.1, simply monitoring the growth of the colony’s territorial area is much practical—the bait interval consists solely of the territorial area (see Equation (3.8), (3.9))—and requires less additional effort than to individually monitor  $d$ ,  $\beta$  and estimate their influence.



**Figure 3.7: Required-bait-interval in different environments and monitoring intervals.** In each figure, the light and dark gray lines denote the bait interval required for thorough detection when bait is not shifted and shifted, respectively. In section 3.3 we assumed that  $d = 200$ ,  $\beta = 1/1000$  and  $t_{\text{int}} = 0.5$ . (a)  $d$ : Density of ants in a nest. (b)  $\beta$ : Ratio to convert number of adults into territorial area. (c)  $t_{\text{int}}$ : Interval between two monitoring in the bait-shift case. The second round is conducted at  $t = 3$  years, and the first is at  $t = 3 - t_{\text{int}}$  years.

### 3.4.3 Trap efficacy

Technically, the aim of this study is to investigate the detection rate when monitoring effort—monitoring area and spatio-temporal intensity of monitoring—is varied. Therefore, we assume that the rate of capture of RIFA when the trap is placed in the foraging territory around the nest (here called the “trap efficacy”)

is 1.0. There are two justifications for this assumption: (1) to maintain the model mathematically solvable; and (2) to focus on the aim of this study.

(1) To maintain the model mathematically solvable

When introducing a trap efficacy  $p$  ( $0 \leq p \leq 1$ ), it is easily deduced that the observable ratio  $O(t)$  will satisfy  $O(t) < 1$ . For simplicity, assume that traps are set in patterns shown in Fig. 3.8.

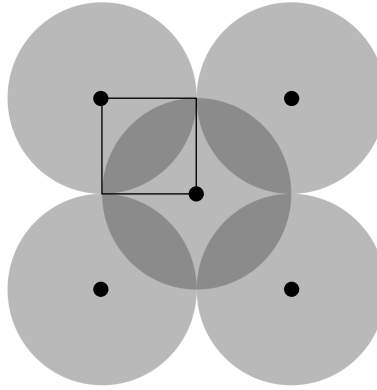


Figure 3.8: **Location of traps in a thought experiment.** Black dots denote traps. Detectable areas are shown in grey, and the dark grey areas are the overlapping areas of detectable areas. Note that this pattern of bait deployment is not equivalent to the shift nor non-shift in our study, and is a pattern just for a thought experiment to prove that the introduction of a trap efficacy makes the model mathematically unsolvable.

The entire monitoring area could be divided into grids which all of them are equally covered by the detectable area (one of these areas is the square region surrounded by the black line in Fig. 3.8). Focusing on the square region, we can define  $O(t)$  as the ratio of the area covered by the detectable area to the square area, which the area covered is schematically shown in Fig. 3.9a. If the trap efficacy satisfies  $p = 1$ , the observable ratio satisfies  $O(t) = 1$  because the detectable area covers the entire square region. However when  $p < 1$ , from Fig. 3.9b, it is shown that  $O(t) < 1$ .

This thought experiment implies that the observable ratio, and thus the detection rate, will never reach 1.0 if we incorporate such a “trap efficacy” that is below 1.0. The implication holds true even when considering more realistic or complicated situations such as Fig. 3.10.

Thus if we incorporate trap efficacy, because the detection rate will never

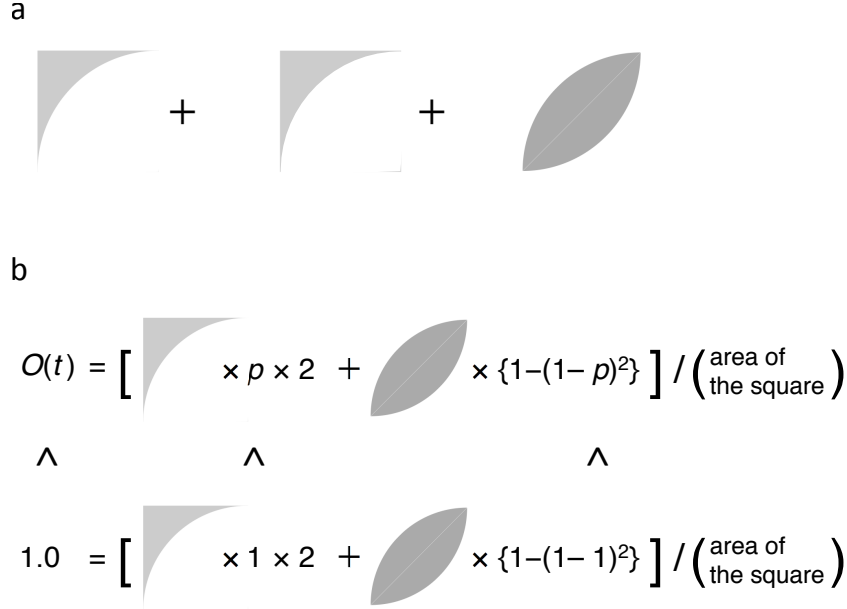


Figure 3.9: **Graphical representation of the observable ratio in the thought experiment.** Detectable areas are shown in gray, where the dark gray areas are the overlapping part.

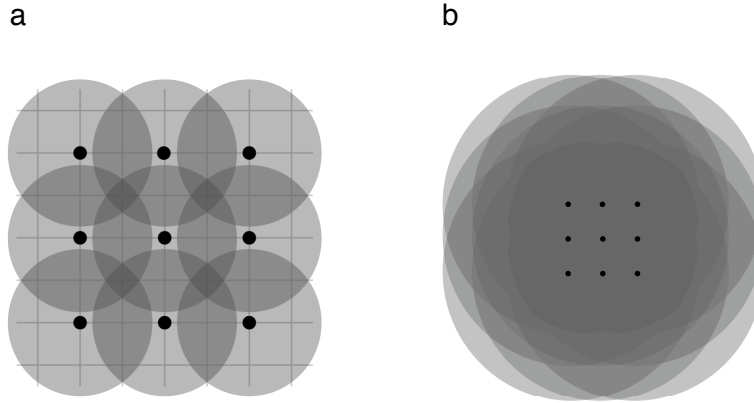


Figure 3.10: **Examples of further realistic situations.** (a) Detectable areas when the radius of the detectable area is relatively small. (b) Detectable areas when the radius of the detectable area is large such that neighboring detectable areas are overlapping.

reach 1.0, the available implication from the model would be “decrease the bait interval as less as possible to increase detection rate”, which is not an insightful implication.

Furthermore, we will not be able to formulate the detection rate if we incorporate trap efficacy. As we showed in the above discussion, it is required to formulate every overlapping and non-overlapping areas in order to formulate the observable ratio. However, this becomes extremely difficult even in a relatively simple situation such as Fig. 3.10a. In a focal square region, the number of overlapping area increases when the radius of detectable area increases, or bait interval decreases (Fig. 3.10b). If we incorporate trap efficacy, the results will imply that the bait interval needs to be decreased, which means that the number of overlapping area infinitely increases, which makes it impossible to formulate the observable ratio.

However, for a very limited situation we can analyze the outcomes of which a trap efficacy is incorporated. Ending the analysis at a timing which  $O(t) = 1$  when  $p = 1$ , there will be only one overlapping area per square region. The outcome is as following.

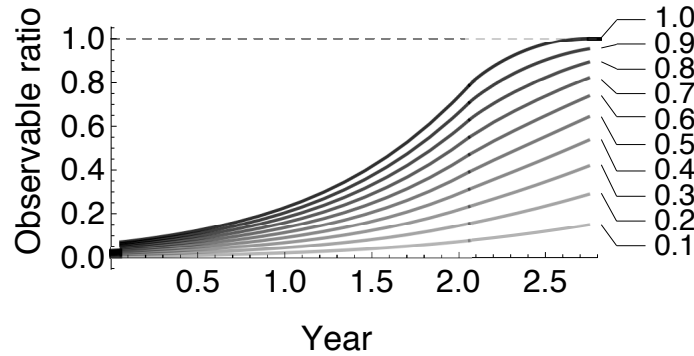


Figure 3.11: **Observable ratio when incorporating trap efficacy, location of baits is not shifted.** Observable ratios are shown in curves. The numbers on the right side of the curve denotes the trap efficacy of which the observable ratio is calculated. Parameter set shown in Table 1.1 is applied for calculation. The light gray dashed line denotes  $O(t) = 1$ .

Fig. 3.11 shows that the observable ratio increases depending on the trap efficacy. We previously showed that the observable ratio satisfies  $O(t) < 1$  if  $p < 1$ , thus we can only conclude that “the observable ratio, and the detection rate,

increases depending on the trap efficacy, but will not reach 1.0” if we incorporate such trap efficacy.

(2) To focus on the aim of the study

Again, technically, the aim of this research is to show how wide the monitoring area has to be, and how frequent monitoring should be on a spatio-temporal scale to eradicate RIFA in the early invasion. The focus of this study is to investigate the monitoring range and spatio-temporal pattern of traps required for thorough monitoring. From the above discussion it is shown that a thorough monitoring is not achievable if we incorporate “trap efficacy”. Furthermore, incorporating trap efficacy simply decreases the observable ratio, and no other helpful insights are obtained by the extension. In order to focus on the issue, it is necessary not to incorporate unhelpful assumption—which is an Occam’s razor point of view.

#### 3.4.4 Triangular lattices for bait deployment

We translate the RIFA detection probability into a mathematical problem in terms of the coverage of the observable area. Therefore, a key aspect of maximizing monitoring efficiency is to find out how to cover the largest area possible with least overlap. In this context, a triangular close-packing structure (Fig. 3.12), and thus the application of triangular lattices, may seem to be the most efficient pattern to deploy bait. Here, I compare the efficiency of deploying bait in a triangular lattice with that of the square lattices (Fig. 3.13a,b), which I conclude that the triangular is more efficient than the non-shifted square lattice, but less than the shifted square lattice.

I will assume that the one side of a triangular lattice is  $l_b$ , the interval between baits (Fig. 3.14). Then, the observable ratio of the triangular lattice is as follows:

$$O(t) = \begin{cases} \frac{2\pi}{\sqrt{3}} \left( \frac{r(t)}{l_b} \right)^2 & 0 \leq r(t) \leq \frac{l_b}{2} \\ \frac{4}{\sqrt{3}} \left( \frac{r(t)}{l_b} \right)^2 (\pi - 3(\theta - \cos \theta \sin \theta)) & \frac{l_b}{2} < r(t) \leq \frac{l_b}{\sqrt{3}} \\ 1 & r(t) > \frac{l_b}{\sqrt{3}} \end{cases} \quad (3.10)$$

here,  $\theta$  is the angle shown in Fig. 3.14.

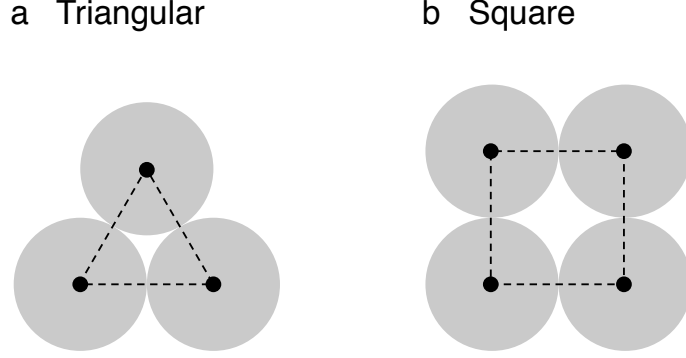


Figure 3.12: **Close-packing in two dimension.** In each graphics, the black dots, area surrounded by the broken lines, and gray areas denote baits, a unit area, and observable areas, respectively. (a) Triangular close-packing; the observable areas cover  $\pi/(2\sqrt{3}) \approx 0.906$  of the unit area. (b) Square close-packing; the observable areas cover  $\pi/4 \approx 0.785$  of the unit area.

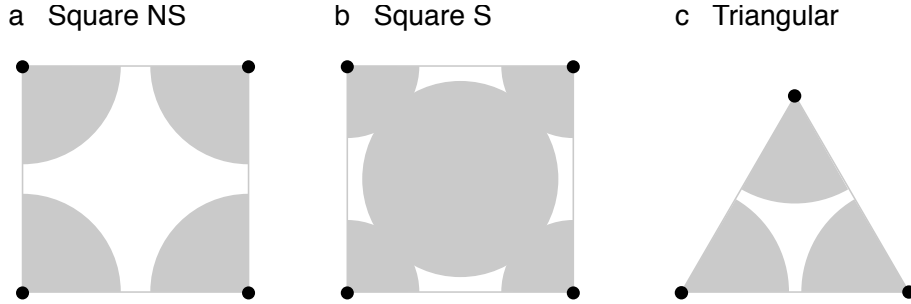


Figure 3.13: **Example of the observable area in each bait pattern.** In each graphics, the black dots and gray areas denote baits and observable areas, respectively. (a) Square lattice; monitoring is conducted only once, which the locations of bait are non-shifted. (b) Square lattice; monitoring is conducted twice, which the locations of baits are shifted in the repeated monitoring. (c) Triangular lattice; monitoring is conducted only once.

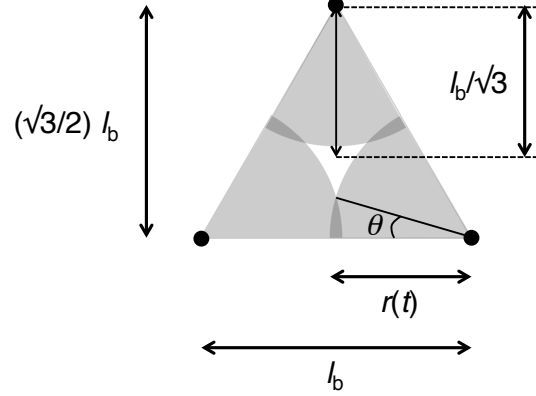


Figure 3.14: **Schematic of the triangular lattice.** The black dots and gray areas denote baits and observable areas, respectively. Distance from every bait to the center of the unit area is  $l_b/\sqrt{3}$ .

Plotting the observable ratio of both the triangular and square lattices reveals that triangular lattices are more effective than square lattices without bait-shift, but are less effective than those with shift (Fig. 3.15). This happens because the area close to the center of a unit area is left uncovered for a while in both the triangular and square lattices without bait-shift, whereas it is covered relatively early when the bait locations are shifted. The cost of monitoring of triangular lattices is slightly higher than that of the square lattice without shift (Table 3.3) due to the decrease in vertical interval—it decreases from  $l_b$  to  $\sqrt{3}/2 l_b$  (see Fig. 3.14). Whereas, the cost of monitoring of triangular lattices is much less than that of the square lattice with bait-shift, simply because there are two monitoring when bait locations are shifted.

Table 3.3: **Number of deployed baits in the optimistic case.** Monitoring radius  $r_m$  is 4 km. I assumed the monitoring area is a square with one sides  $r_m$ , as is assumed in Table 3.2.

| Bait Interval [m] | 3 years detection rate / Number of bait |                |               |
|-------------------|-----------------------------------------|----------------|---------------|
|                   | Triangular                              | Square (ns)    | Square (s)    |
| 20                | 1.0 / 184,631                           | 1.0 / 160,801  | 1.0 / 321,602 |
| 30                | 0.965 / 81,816                          | 0.848 / 71,289 | 1.0 / 143,291 |

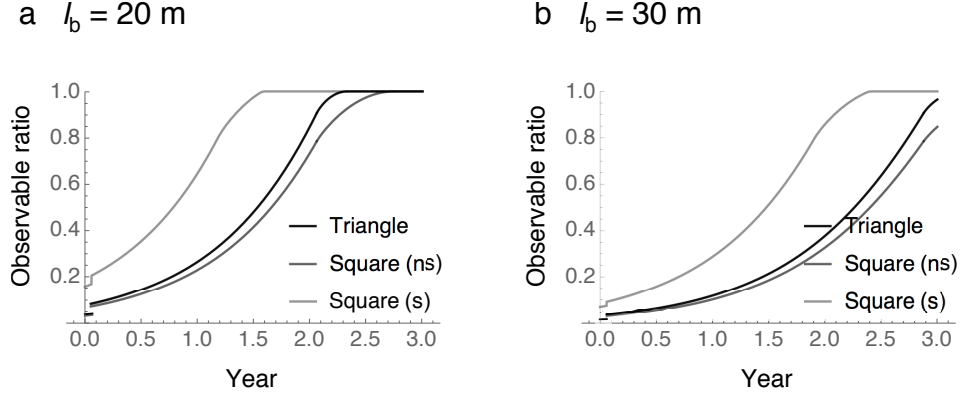


Figure 3.15: **Observable ratio.** In each graph, the darkest, second darkest, and lightest lines denote the observable ratio of triangular lattice, square lattice without bait-shift (abbreviated as “ns”), and square lattice with bait-shifted (abbreviated as “s”), respectively. (a) Bait interval: 20 m. (b) Bait interval: 30 m.

Notably, deducing from Table 3.3, the square lattice without bait-shift may seem the most “efficient” structure because it has the detection rate of 1.0 while it deploys only 160,801 bait traps, which the cost-efficacy–detection rate over the number of deployed bait–apparently seems the highest. However, this is not the case. This confusion ignores the fact that the cost-efficacy can not simply be compared between lattice structures because the square lattice with bait-shift performs two monitoring.

There are two points to be noted when comparing the cost-efficacy between lattice structures. The first is that the square lattice with bait-shift reaches the detection rate of 1.0 much earlier than the other two. It is not fair to compare the detection rates after one of them stopped increasing, therefore comparisons must be made at the timing when one of them—in our study most likely square lattice with shift—reached 1.0. The second is that the square lattice with shift conducts two monitoring, and there is a chance that RIFA is found in the first round (see Fig. 3.16). We can not ignore this probability when calculating cost-efficacy because the monitoring cost of both the first and the second round is considered in Table 3.3.

How should we calculate the cost-efficacy in such cases? For simplicity, in the following discussion I will assume that the first and second round of monitoring are conducted at  $t = t_1, t_2$ , which the detection rates are  $p_1$  and  $p_2$ , respectively



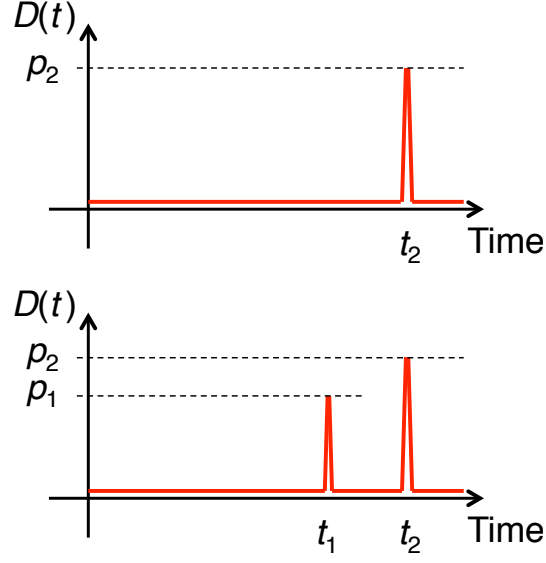


Figure 3.16: **Detection rates occurring.** In both panels, the red line represents the detection rate occurring as the monitoring is being conducted. In the upper panel there is only one monitoring at  $t = t_2$ , which the detection rate is  $p_2$ . In the lower panel there are two monitoring at  $t = t_1, t_2$ , which the detection rates are  $p_1$  and  $p_2$ , respectively.

(Fig. 3.16). Also, I will assume that the cost of monitoring is identical in the first and second round which is noted as  $C$ . Then, the cost-efficacy of monitoring when applying a square lattice without bait-shift is as Equation (3.11). By substituting the actual detection rates, I obtain the cost efficacy of applying square lattice without bait-shift in a comparable form, which implies that the square-lattice with bait-shift is the most efficient structure (Fig. 3.17).

$$(\text{Cost efficacy}) = \frac{p_1 + p_2}{2C}. \quad (3.11)$$

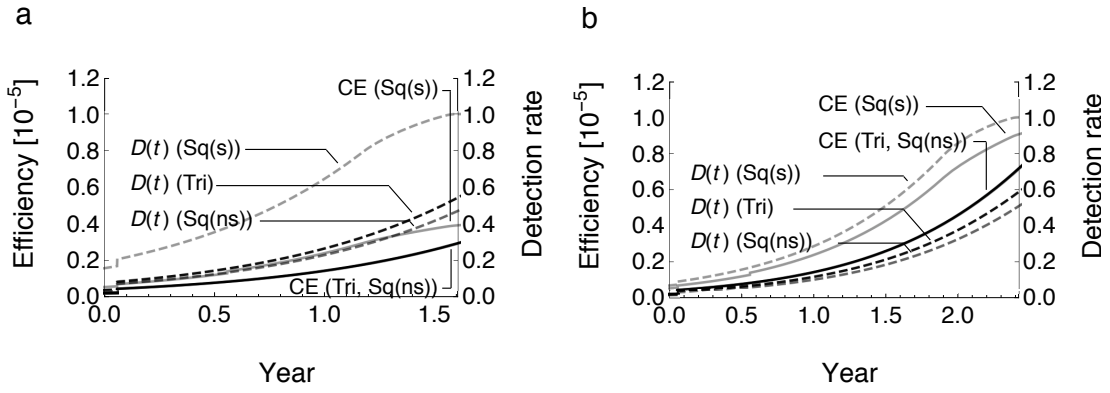


Figure 3.17: **Cost-efficiency when bait interval is 20 or 30 m.** In each graph, the solid lines denote the cost-effficacy (abbreviated as “CE” in the figures), whereas the dashed lines denote the detection rate (denoted as “ $D(t)$ ” in the figures). “Sq(s)”, “Sq(ns)” and “Tri” denote the lattice structures, Sq(s): square lattice with bait-shift, Sq(ns): square lattice but no bait-shift, and Tri: triangular lattice. Note that the units of the left vertical axis, which is the efficacy, is  $10^{-5}$ , and the right is simply numerical values from 0.0 to 1.2. I show the cost-efficiency until the detection rate of Square (s) is 1.0, as I noted the importance before. There seems to be only two solid lines in each graph because the cost-efficiency of triangular and square (ns) lattices are nearly overlapping. (a) Optimistic case. (b) Pessimistic case.

## Chapter 4

# Discussion and Conclusion

A crucial aspect of RIFA eradication for un-invaded countries is the complete detection of related nests, once an incursion is found. However, the required surveillance effort for this remains elusive; monitoring frequency and density of traps have typically been decided empirically. Here, we build a mathematical model and derive the most efficient surveillance effort in numerical values in order to assist decision makers plan RIFA eradication in the early stage of invasion.

### 4.1 Contribution

Our contribution is that we showed actual numerical values of monitoring effort to ensure eradication of RIFA in the early stage of invasion. We incorporated ant biology in details (such as Table 3.1), which has never been considered in depth. Additionally, no other studies have revealed the benefit of shifting trap locations in a repeated monitoring. The results of our study assist the planning process of eradication because it provides the details of monitoring effort that should be executed once an incursion is found. It should be noticed that no eradication planning knows the exact distribution of subject species in advance of surveillance; our proposal is useful in identifying related nests, if any (see also the “Planning” paragraph in section 4.2).

The detail of our contribution in the context of resolving the social challenge, that is RIFA eradication, is summarized as follows: (i) we show an equation to derive the surveillance effort that ensures certain detection of all related nests of the nest of origin; (ii) we derive this equation without loss of generality—the equation

applies to other monogynous ant species by choosing adequate parameters; and (iii) we propose and assess an efficient monitoring method—that is to shift trap locations for repeated monitoring. Therefore, by applying our research, government and organizations can derive the required monitoring effort and monitoring-cost in case of an incursion, which provide evidence for RIFA eradication planning.

The contribution of this study to innovation science fall into two points: (i) we provide governments a framework to compare and assess monitoring strategies; and (ii) by actually utilizing this framework we suggest an innovative monitoring strategy—that is to shift locations of bait traps in repeated monitoring which allows an increase in efficiency of monitoring. In other words, we assist government’s RIFA eradication planners by providing a framework to assess ideas of monitoring strategies and demonstrating the use of it. The framework differs from previous theoretical works in three aspects: (i) it provides detailed and applicable suggestions; (ii) it is applicable to individual incursions because it does not require complicated model fittings; and (iii) the suggestions are clear and logical because the causal relation between the biology and the suggestion is clear.

The first can be further broken down into two points: the former is that we provide monitoring effort in actual numerical values; and the later is that we incorporate RIFA biology in details. Several previous studies only provide abstract parameters [187,188], which requires substantial additional work to apply their results. For example in Peyrard et al. (2013) [187] a parameter that denotes the ‘*different “strength level” of invasion*’ is utilized, but the biological meaning of this is unclear. RIFA biology such as growth and dispersal of colonies is often neglected or underestimated [187,195], which our work considered it in depth.

The second is that our model does not require prior infestation data to calibrate the model, which becomes crucial for eradication planning in the early stage of invasion. Typical models require initial distributions and parameter fitting using actual spread data [189–191], which limits their use to mid- to late-stage of invasion. Our model requires no parameter fitting and is thus applicable to individual incursions in their early stages.

Finally, the third is that our model does not use statistical means, which is frequently used in other models [194,195], thus the causal relation is clear and the results are explicable. Recalling that decision makers may be obliged to explain the logic behind the estimation of the monitoring strategy, explicability

may become an important aspect of modeling monitoring.

In summary, our framework allows decision makers to know monitoring efforts in actual numerical values—not abstract parameters—in order to eradicate RIFA during early invasion.

## 4.2 Limitations

The application of our results is limited in four aspects: (i) species; (ii) circumstances; (iii) surveillance method; and (iv) planning.

**Species** Our model assumes a sedentary ground-dwelling colonial organism that has a foraging territory—such as ants. Therefore, ant species without a specific nest—such as *Prystomyrmex punctatus*, or those that nest on trees or ceilings of buildings—such as the African big-headed ant *Pheidole megacephala*—are not the subject of this framework. The later are not included because it is difficult to estimate their foraging territory. Nevertheless, some bees and wasps may be the subject of our model, if they have a fixed foraging territory around the nest, and if there are effective traps that could be deployed within these territories. Notably, we assumed that ants do not relocate their nest, but for those that often relocate—such as the Argentine ant *Linepithema humile*—the results of non-shift method should be applied. This is because shifting trap locations in a repeated monitoring will not contribute to increasing the detectable area if the species often relocate their nests (see Fig. 3.2b).

**Circumstances** Although it is true that RIFA may evacuate into dwellings when there is disturbance—such as heavy rain—, they prefer to form nest mounds in open, sunny, and soft ground. Therefore, our model design that the RIFA distribution and monitoring is conducted on the ground—there is no three-dimensional spatial structure—is biologically plausible. Additionally, it is worth noting that the average dispersal distance of fire ants depends on the air temperature: the hotter the farther. The monitoring area therefore should be expanded in tropical and subtropical regions. Colony growth rate also depends on temperature. We set the time limit of monitoring to three years, assuming the climate of mainland Japan, because independently founded colonies start to produce alate queens within three years under climatic conditions that are close to those at the northern end of the fire ants’ potential distribution [147]. The monitoring time limit should be shorter in warmer regions such as southeastern Asia.

**Surveillance method** We assumed the use of bait traps, but the type of trap deployed will vary with the object species. Actual detection rates are subject to the efficacy of individual bait traps; use of the appropriate trap therefore becomes important in applying these results to eradication programs. The efficacy of traps for certain species was not our target here, but it has been explored elsewhere

[204, 205]. Recall that one of the important conclusions of this study is the determination of the recommended monitoring range, that is a radius of 4 or 6 km from the source nest. If the traps used are not as highly attractive as is assumed in our model [198], or the trap efficacy decreases depending on the distance from the nest entrance [198], then, within this 4 or 6 km radius of the monitoring range, monitoring should be conducted not solely by traps but by a combination of visual surveillance [161], high-tech surveillance (such as drones with special cameras adopting image recognition technologies) and fire-ant-sniffing dogs [165, 194] to achieve thorough monitoring. Additionally, in application, not all area within the monitoring range may be suitable for bait trap-based survey. These include private lands, busy streets, roadways, and areas within the path of cars or tractors. Other surveillance methods stated above may suit better in these areas (see also section 4.5 “surveillance method” paragraph).

We showed that shifting trap location in the repeated monitoring increases the detection rate. This also holds true in the case of high detection error—further repetition may be recommended to increase detection rate—however this is a matter of degree. In practice, if a large nest mound was discovered during the repetition, this implies that alate queens may have dispersed from that nest, thus further monitoring should be conducted setting the newly-discovered nest as the center of monitoring range. Additionally, we assumed that bait traps are deployed in lattice patterns—because they are deployed so in application. But triangular-, hexagonal- or any other lattice patterns could be applied if traps could be deployed in such patterns easily. This may actually happen if drones with high-resolution GPS are utilized, yet, the trade-off between cost and efficacy should carefully be analyzed.

**Planning** Detection of the source nest is crucial, because setting the center of the monitoring range on a second- or third- generation nest would reduce the thoroughness of detection. To avoid this error, the age of the nest should be estimated before the nest is destroyed. Two parameters might be helpful in estimating nest age: one is the number of adults in the nest and the other is the age of the queen ant. Estimating nest age from the number of adults in the nest requires the estimation of a number of parameters such as intrinsic growth rate and carrying capacity; therefore, the utilization of queen age may be better (see [206]). Nevertheless, collection of the queen in a monogynous field

colony is also a difficult task. If multiple nests—all similar in size—were found and estimating the nest age turned out to be difficult, then monitoring should be conducted within 6 km radius from each of the nests.

Notably, in the pessimistic case “*The source nest is assumed to be found approximately at the same time as the second-generation nest, because it is large and easy to detect once the searchers have been alerted*” (section 3.2). This assumption seems biologically plausible since aged nest mounds grow up to 40 cm tall and is located on open and disturbed grounds. Yet, this assumption may not hold true in dry cold regions—such as the northern end of their potential distribution—where the nest mounds may be smaller. To relax this assumptions, a prior monitoring to identify the source nest (or alternatively the “1st generation nest”) shall be conducted immediately after a nest was reported. The monitoring should be: conducted 4 km radius from the nest; conducted twice, both in a (temporarily) short interval such as several days to a week or two, while shifting the locations of bait in the second monitoring. Refer to Equation (3.8) or (3.9) to determine the spatial interval between bait.

In summary, for certain detection of all related nests, careful surveillance such as the following is recommended: (i) age-analysis and destruction of the reported/found nest; (ii) detect the source nest (ii) monitor 4 km or 6 km around the source nest depending on the age; (iii) go back to step (i) if further nests are found.



### 4.3 Monitoring cost

The cost of monitoring is one of the central concerns in conducting surveillance, which our work considered it in terms of the number of deployed bait traps (hereafter referred to as “NDB”). This may seem to be an over-simplification, because monitoring costs would likely consist majorly of labor-cost. Here, I discuss two issues: (i) could the labor-cost be estimated from NDB; and (ii) are the costs of various monitoring strategies comparable based on NDB, which I conclude that the use of NDB as an index of the total cost seems to be a fair and accepted idea.

Guideline of RIFA eradication [207], which is edited partly based on our research (K. Tsuji personal communication, May 22nd 2019), provides a table that relates the monitoring effort with labor cost. It estimates that monitoring 6 km around the nest of origin requires 282,679 traps and 1,413 person-day costs, whereas monitoring 4 km radius requires 125,511 traps and 628 person-day costs. Note that the estimated NDB differ from ours (Table 3.2) simply because our model assumed that the monitoring area is a square having a side of  $2r_m$ , while the guideline assumed that it is a circle having a radius of  $r_m$ . This is deduced by the fact that the monitoring area is  $113 \text{ km}^2 = 6 \text{ km} \times 6 \text{ km} \times \pi$  in Table 5. The estimates imply that it assumes a constant workload of 200 bait trap per person per day. In such cases, we can easily estimate labor-cost from NDB by dividing NDB with 200. Furthermore, the costs of various monitoring strategies are comparable based on NDB because workload per person per day is a constant—that is, independent from monitoring effort.

Table 4.1: **Estimate of the monitoring effort.** (translated by the author from [207]).

| Radius<br>[km] | Interval<br>[m] | Area<br>[km <sup>2</sup> ] | NDB     |         | Workload [person-day] |         |
|----------------|-----------------|----------------------------|---------|---------|-----------------------|---------|
|                |                 |                            | 1 year  | 2 years | 1 year                | 2 years |
| 6              | 20              | 113.0                      | 282,679 | 565,358 | 1,413                 | 2,827   |
| 6              | 30              | 113.0                      | 125,611 | 251,222 | 628                   | 1,256   |
| 4              | 20              | 50.2                       | 125,611 | 251,222 | 628                   | 1,256   |
| 4              | 30              | 50.2                       | 55,828  | 111,656 | 279                   | 558     |

Yet, assuming that the workload per person per day is independent from the monitoring effort may sound counter-intuitive, because increasing the interval between bait results in an increase of total distance a staff walks while deploying

200 traps.

This confusion is based on an assumption that staffs are paid by the distance they walk. This is not the case. The staffs are paid per day irrelevant from the distance they walk, as long as the work is completed within a day. Thus, the question is “in what monitoring effort would the workload per person not be completed within a day?”. Assuming that a staff deploys 200 bait per day—such as a 10 by 20 lattice—, the total distance a staff walks is  $199l_b$ , where  $l_b$  is the interval between bait. A person walks at a speed of 3 to 6 km/h, perhaps 2 km/h during bait deployment, and works 6 hours a day—therefore can deploy bait for at least 12 km a day. Thus, the maximum interval between bait, which a person can complete the workload within a day, is approximately 60 m ( $\approx 12,000 \text{ m}/199l_b$ ). Therefore, when  $l_b \leq 60 \text{ m}$  the workload per person is completed within a day, and the increase of interval does not affect labor cost.

Notably, shifting the locations of traps in a repeated monitoring does decrease the labor cost, that is, splitting monitoring into two days does not itself affect the labor cost. For example, assume that the monitoring area is a square having a side of 120 m, and a staff deploys 4 bait per person per day. When  $l_b = 20 \text{ m}$ , 36 bait is deployed, thus the workload is 9 person-day. Likewise, when  $l_b = 30 \text{ m}$  and location of trap is shifted, 16 bait is deployed per day, thus the workload over two days is 8 person-day.

## 4.4 Social challenge

This study addresses the social challenge of eradicating RIFA, which may potentially relate to, but not limited to, SDGs Goals 11, 15, and 17 [208]. Goal 11 is to “*Make cities and human settlements inclusive, safe, resilient and sustainable*”, which includes Goal 11.7: “*By 2030, provide universal access to safe, inclusive and accessible, green and public spaces, in particular for women and children, older persons and persons with disabilities*”. RIFA infestation substantially regulates human access to green and public spaces due to their habitat preference and toxic stings. Likewise, RIFA infestation may have adverse effects on achieving Goal 15: “*Protect, restore and promote sustainable use of terrestrial ecosystems, sustainably manage forests, combat desertification, and halt and reverse land degradation and halt biodiversity loss*” as I integrated information in section 1.2.2. Finally, preventing RIFA introduction to un-invaded countries will likely require international biosecurity protocols, that is “*Multi-stakeholder partnerships*” noted in Goal 17.16: “*Enhance the Global Partnership for Sustainable Development, complemented by multi-stakeholder partnerships that mobilize and share knowledge, expertise, technology and financial resources, to support the achievement of the Sustainable Development Goals in all countries, in particular developing countries*”. Furthermore, RIFA infestation impacts agriculture, and therefore potentially economy, thus eradicating them may be a crucial social challenge for sustainable development.

## 4.5 Future directions

The purpose of this study was to propose a theoretical strategy in actual numerical values in order to assist the decision makers plan and conduct eradication. I consider this goal is achieved, because our results and implications consist the Guideline of RIFA eradication issued by the Ministry of Environment ([207], K. Tsuji personal communication, May 22nd 2019). Yet, an additional work may further assist decision makers in their planning and execution.

Our work estimated monitoring efforts based on RIFA biology, which include dispersal of alate queens and foraging behavior of workers. However, human-mediated dispersal—such as inadvertent colony transfer via vehicles or transportation of containers—could cause long-distance dispersal, resulting in unexpected range expansion. Previous theoretical works (see Chapter 2) has never considered this type of spread in spatially structure models, perhaps because of the complexity of the issue.

One solution to predict this unexpected long-distance dispersal is to estimate transportation probabilities based on public transportation networks (Fig. 4.1). This network-analysis is conducted by assigning nodes to potential habitats and edges to transportation networks—such as roads, highways and railway—on GIS systems. By assigning certain rates that denote traffic density to the edges, then adaptively calibrating them, we can model the human-mediated RIFA dispersal in a simulation. A rough example of such a simulation model is the MoRIS of J. Gippet [209], which replicates and predicts human mediated dispersal.

Incorporating surveillance and eradication into simulation models is not difficult (see for example [192]). By incorporating hypothetical monitoring and statistically deriving the efficiency—which is the surveillance efficacy over cost—curve, we can reveal the trade-off between cost and monitoring efficacy. Another strength of this model is that it can perform pathway analyses. Pathway analyses refer to the analysis of route of spread. Unraveling the route of spread may become important when RIFA nests were sparsely distributed but turned out to be relatives. It may become important because determining the route of spread substantially helps in estimating the potential spread. This is an aspect of eradication that this thesis and our work [169] does not cover, which our work directs repetition of survey and age-analysis to detect all the related nests (see the “Planning” paragraph of section 4.2).

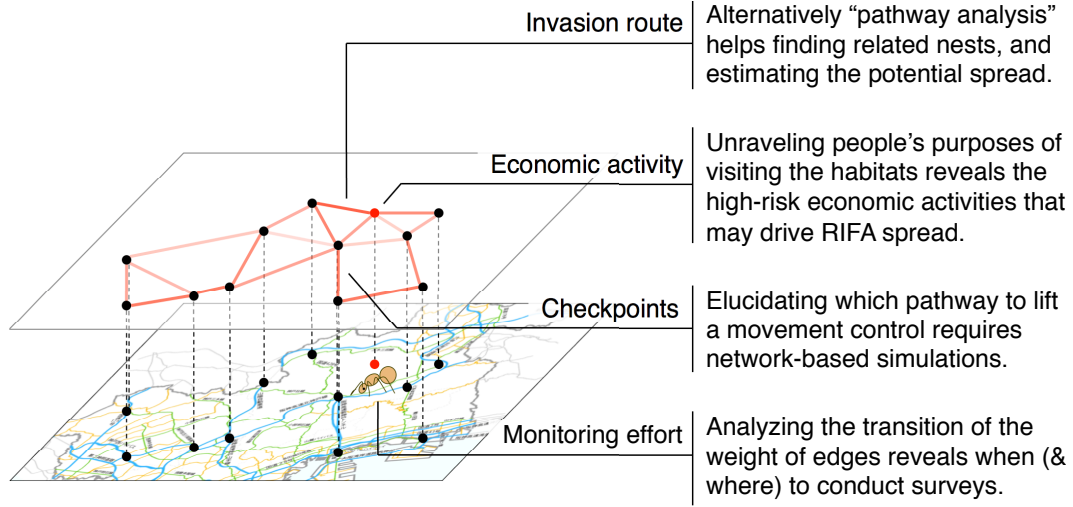


Figure 4.1: **Schematic of the simulation study.** The simulation analyzes the network-dynamics of the human-mediate dispersal of RIFA, which the nodes (black dots) are the potential habitats of RIFA and the edges (red lines) are the human-traffic. The edges has a weight that denotes the traffic-volume, which in the above figure I expressed it as the darkness of the red color. By performing pathway analyses, we may unravel the (i) invasion route; (ii) key economic-activity that accelerate the spread; (iii) location of where the checkpoints should be set; and (iv) the allocation of resource to monitoring methods. The picture of a map is from [210].

There are several questions that could be addressed by this simulation study: (i) what is the invasion route; (ii) where are the most effective routes to set checkpoints in the aim of preventing human mediated RIFA dispersal; (iii) what are the economic activities that are likely mediating RIFA dispersal; and (iv) how should we allocate monitoring efforts among preventions of local- and human mediated-dispersal.

The first question is already described above. The second question unravels the edge that achieves the highest cost-efficacy in preventing human-mediated dispersal if it is removed. Because the pattern of an individual’s movement is limited, there is likely a hub in terms of RIFA transportation. The simulation model may unravel such hubs and/or high-risk edges. The third question may especially be interesting. Because the nodes—that is, the potential habitats of RIFA—are often sunny, open, soft ground, we can expect that individuals are visiting there with some specific purpose. This includes agriculture, forestry, and perhaps recreation.

By characterizing the nodes and edges in terms of human economic activities, we can determine the high-risk activities along with high-risk materials that mediate RIFA dispersal. These information assist the planning process by determining the cause, which contribute to both increasing the efficacy and decreasing the cost of monitoring. The fourth is to determine the resource allocation. If long-distance dispersal was actually rare, or happens only in some specific period of the year, then it is not efficient to allocate much resource into setting and running checkpoints. The simulation study reveals when and where to monitor to prevent human-mediated dispersal. These questions—especially question (i) to (iii)—has never been addressed, but are crucial if human-mediated dispersal may take place, thus the impact of this model study will likely be substantial.

Our study had limitations in four aspects (see section 4.2); two of them—the study species and surveillance method—may be generalized in further works.

**Species** For eradication in the early invasion, the above discussions about human-mediated dispersal concomitant with our results generally covers invasive ground-dwelling ants—such as the Red imported fire ant *Solenopsis invicta* and Argentine ant *Linepithema humile*. Yet, detecting ant species that nest on trees, and wall or ceiling of buildings—such as the Little fire ant *Wasmannia auropunctata*; Yellow crazy ant *Anoplolepis gracilipes*; and African big-headed ant *Pheidole megacephala*—remains elusive. The difficulties in detecting these ants are threefold: first, their three-dimensional distribution makes bait traps and other surveillance methods less effective than it is on ground-dwelling species; second, their three-dimensional distribution substantially increases surface area that has to be surveyed; and third, housings and buildings usually require permission to survey. In these contexts, the idea of actively surveying these species *per se* may be an inefficient direction. One possible direction is to promote detection based on public science—or alternatively “citizen science”—, which refers to collecting distribution data based on reports from citizens. The idea of incorporating citizen science into eradication is not a preposterous idea; there are several species under survey based on citizen participation [211]. Additionally, for example in Australia, public reporting accounted up to 70% of new detections within a four-year period (see section 1.3.5). Many governmental organizations have a hotline for reporting detection [212], but perhaps an online channel based on a GIS system is much more convenient in both reporting and notifying the

distribution data. I suggest an eradication project to establish such an online channel, collect distribution-data based on citizen-participation, and performing pathway analysis on the data to predict potential establishments.

**Surveillance method** We assumed the use of bait traps in our study, yet, recently, detection dogs are receiving increasing interest in application. The strength of these dogs seems to be their high capability in detecting RIFA nests [165]. Nevertheless, their actual detection rate has scarcely been measured, which is likely influenced by the climate—it would likely decrease on windy days and areas—, locations—smelly areas such as seashores and roadsides may not be suitable—, and the dog’s working hours—the detection rate may decrease in time if the dogs get tired. The efficacy of these dogs needs to be measured to incorporate them into a resource allocation model, which determines the optimum use of these dogs. Once the efficacy is measured, the utilization of these dogs can be translated into a mathematical problem such as the traveling-sales-man. The above discussion is the same for other surveillance methods too, such as remote sensing using drones and IR cameras.

## Appendix A

# Derivation of the dispersal kernel

Dispersal kernel of nuptial flights in RIFA is poorly known, thus we assume a random walk type of dispersal. Then, the dispersal kernel will be a form of Gaussian distribution [213], and the dispersal kernel of the first generation  $P_1(x, y)$  is as follows,

$$P_1(x, y) = \begin{cases} \frac{x}{2\pi\sigma^2} \exp(-\frac{x^2 + y^2}{2\sigma^2}) & \sqrt{x^2 + y^2} \leq 5 \\ 0 & \sqrt{x^2 + y^2} > 5 \end{cases} \quad (\text{A.1})$$

Here,  $P_1(x, y)$  is a bivariate Gaussian distribution with mean  $\mu$  satisfying  $\mu = 0$ .  $P_1(x, y)$  is zero when  $\sqrt{x^2 + y^2} > 5$  since *S. invicta* females do not fly farther than 5 km [214]. The standard deviation  $\sigma$  depends on the average dispersal distance,

$$\iint (\sqrt{x^2 + y^2} P_1(x, y)) dx dy, \quad (\text{A.2})$$

which could be calculated based on laboratory experiment results [214]. *S. invicta* females are known to fly for an average of approximately 45 min, with flight speed approximately 0.6 m/s when the temperature is 26 °C, which is the average of highest temperature of June 2017 in Kobe city, Japan [215]. Thus the average dispersal distance is  $0.6 \text{ m s}^{-1} \times 3,600 \text{ s hour}^{-1} \times 45/60 \text{ hour} = 1620 \text{ m} = 1.62 \text{ km}$ . Solving the following equation,

$$1.62 = \iint (\sqrt{x^2 + y^2} P_1(x, y)) dx dy, \quad (\text{A.3})$$



the estimated value of the standard deviation is  $\sigma = 1.2926$ . The dispersal kernel of the second generation  $P_2(x, y)$  is

$$P_2(x, y) = \iint (P_1(x, y)P_1(x - x_1, y - y_1))dx_1dy_1. \quad (\text{A.4})$$

## Appendix B

### Derivation of detection rate $D(t)$

Consider the optimistic and pessimistic case. In the optimistic case, the source nest (“first generation nest”) is found instantly after it started producing queens, and second-generation alate queens have dispersed only for a short period (Fig. B.1a). In the pessimistic case, detection of the source and second-generation nest is delayed such that the second-generation nest started producing queens and the third-generation alate queens have dispersed for a short period (Fig. B.1b). Note that in the pessimistic case we assumed a pre-survey—in the effort to detect all the second generation nests—is conducted, and the purpose of monitoring is to detect all potentially established third-generation nests.

Now let us assume that monitoring is conducted. Traps such as baits are set in lattice patterns. Then for an arbitrary nest, four closest baits from the center of the nest could be selected, and there is a square with sides  $l_b$ , which is the spatial interval between baits (Fig. B.2a). In the square region, a nest would be detected if a bait was within  $r(t)$  from the nest. However, a nest would also be detected if the nest was within  $r(t)$  from the baits (Fig. B.2b). Thus, we call the area within  $r(t)$  from the baits the *detectable area*. Whether an established nest is detected or not solely depends on whether the nest is within the detectable area or not, and the probability is given by a simple ratio, *i.e.* the width of the detectable area over the width of the square region. We will call this ratio the *observable ratio*.

The observable ratio obviously depends on  $r(t)$ , which differs among nests. However, the nest we shall consider is the one that is the most undetectable, since a monitoring strategy intense enough to detect the most undetectable nest

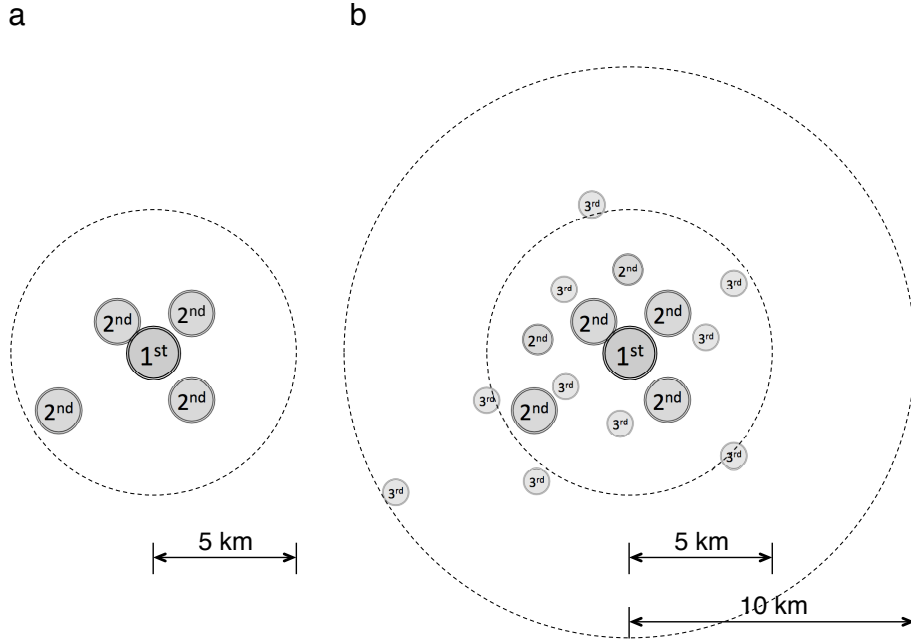


Figure B.1: **A possible distribution of the 1st, 2nd, and 3rd generation nests.** Circles with a number inside denote an area where fire ants from a nest would exist (with nests in the center of the circle). The radius of a circle is  $r(t)$  (see Table 1.1). The number scripted in the circle stands for the generation of the nest. (a) Optimistic case. (b) Pessimistic case.

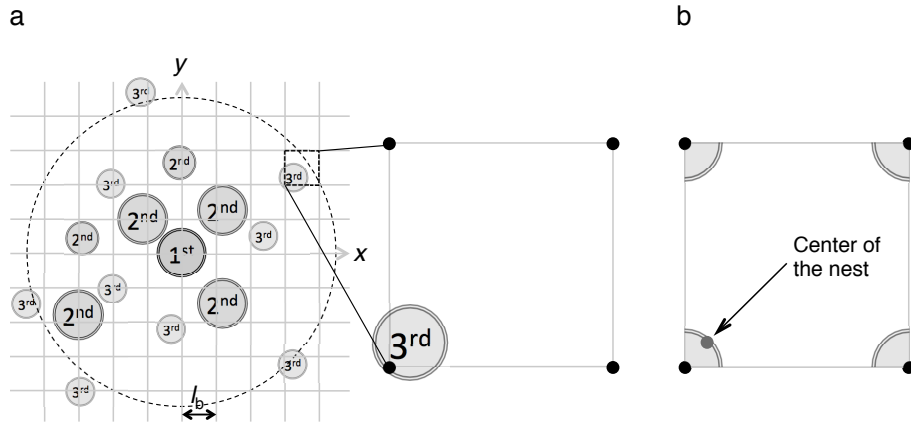


Figure B.2: **Definition of a detectable area.** (a) Bait traps are set in lattice patterns. A nest is inside a square region: sides are  $l_b$ , and there are baits on the corner. (b) Area within  $r(t)$  from baits is the detectable area, which a nest would be detected if it was established inside.

would likely succeed in detecting every other nest. The most undetectable nest is the smallest nest, which is the youngest nest, which is the nest established on  $t = t_{1\text{mat}}$  in the optimistic case and  $t = t_{2\text{mat}}$  in the pessimistic case. Here, the detection rate shall be defined as follows:

$$\begin{aligned}
 (\text{Detection rate}) = & \\
 & \iint ((\text{Probability of the youngest nest establishing on coordinate } (x, y)) \\
 & \times (\text{Probability of the youngest nest being detected after establishment})) dx dy,
 \end{aligned}
 \tag{B.1}$$

while the first and second terms on the right hand side of the above equation are the dispersal kernel and the observable ratio, respectively. The observable ratio is time dependent—not coordinate dependent—, therefore by applying the constant factor rule in integration we can separate it from the integrand. Thus, we obtain equation (3.5).

## Appendix C

# Detection rate when shifting bait locations

Assume that baits are located at  $(x_i^t, y_j^t) = (i \times l_b, j \times l_b)$  ( $i, j = 0, \pm 1, \pm 2, \dots, \pm 2 \times r_m/l_b$ ) during the first monitoring at time  $t$  (Fig. B.2a), where  $l_b$  is the spatial interval of baits and superscripts of  $x$  and  $y$  denote time. In the subsequent monitoring conducted at time interval  $t_{\text{int}}$  after the first, the baits are located at  $(x_i^{t+t_{\text{int}}}, y_j^{t+t_{\text{int}}}) = (x_i^t + l_b/2, y_j^t + l_b/2)$  (Fig. B.2b).

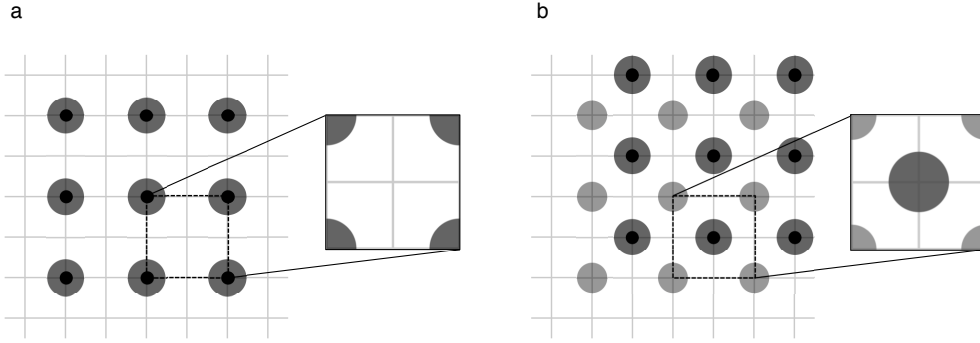


Figure C.1: **The overall detectable areas.** Black dots denote baits. Detectable areas in the first (light grey) and second monitoring (dark grey) are superimposed to show the overall detectable areas. (a) The first monitoring. (b) The second monitoring.

The detectable area will increase linearly while  $r(t) + r(t + t_{\text{int}}) < l_b/\sqrt{2}$  (Fig. C.2a). When  $r(t) + r(t + t_{\text{int}}) \geq l_b/\sqrt{2}$ , the detectable areas at time  $t$  and  $t + t_{\text{int}}$  overlaps, and the total detectable area is not a simple sum of the detectable area

at time  $t$  and  $t_{\text{int}}$ . When defining angles  $\theta$  and  $\phi$  as shown in Fig. C.2b, the overlapping area in Fig. C.2b is given as equation (C.1).

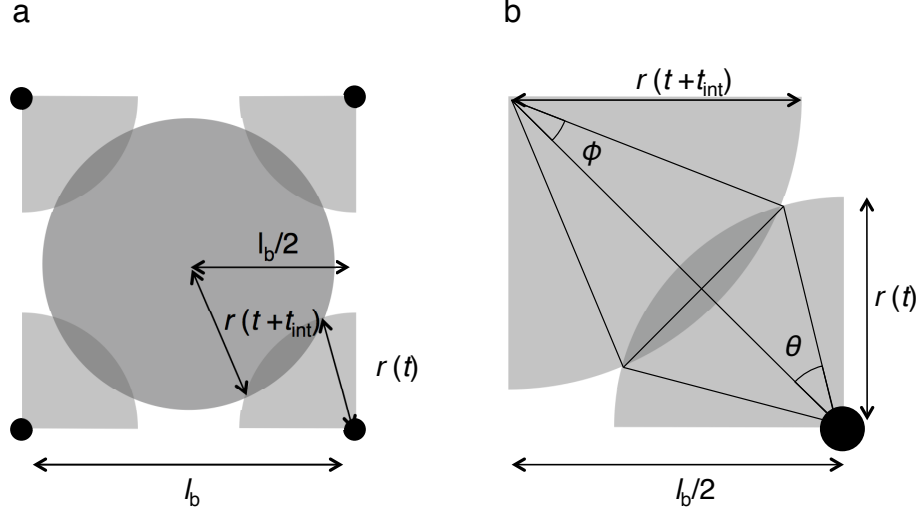


Figure C.2: **Definition of parameters.** Black dots denote baits. Detectable areas in the first (light grey) and second (dark grey) monitoring are superimposed to show the overall detectable areas. (a) The length of  $r(t)$  and  $r(t + t_{\text{int}})$ . (b) The angles.

$$\begin{aligned}
 & 2\left(\pi r(t)^2 \frac{\theta}{2\pi} - \frac{1}{2} r(t) \cos \theta r(t) \sin \theta + \right. \\
 & \left. \pi r(t + t_{\text{int}})^2 \frac{\phi}{2\pi} - \frac{1}{2} r(t + t_{\text{int}}) \cos \phi r(t + t_{\text{int}}) \sin \phi\right) \\
 & = r(t)^2 \theta - r(t)^2 \cos \theta \sin \theta + r(t + t_{\text{int}})^2 \phi - r(t + t_{\text{int}})^2 \cos \phi \sin \phi \\
 & = r(t)^2 (\theta - \cos \theta \sin \theta) + r(t + t_{\text{int}})^2 (\phi - \cos \phi \sin \phi),
 \end{aligned} \tag{C.1}$$

Here,  $0 \leq \theta, \phi \leq \pi/4$ . Since parameters  $\theta$  and  $\phi$  are introduced for temporal use, it shall be replaced with  $r(t)$  and  $r(t + t_{\text{int}})$ . Paying attention to the diagonal line in Fig. C.2b, they are given as equation (C.2), (C.3).

$$r(t) \cos \theta + r(t + t_{\text{int}}) \cos \phi = \frac{l_b}{\sqrt{2}}. \tag{C.2}$$

$$r(t) \sin \theta = r(t + t_{\text{int}}) \sin \phi. \tag{C.3}$$

Since  $0 \leq \theta, \phi \leq \pi/4$ , equation (C.3) is equivalent to equation (C.4).

$$\cos \phi = \sqrt{1 - \left( \frac{r(t)}{r(t + t_{\text{int}})} \sin \theta \right)^2}. \quad (\text{C.4})$$

Substituting equation (C.4) to equation (C.2) gives the relationship between  $\theta$ ,  $r(t)$  and  $r(t + t_{\text{int}})$ .

$$\begin{aligned} r(t) \cos \theta + \sqrt{r(t + t_{\text{int}})^2 - r(t)^2 \sin^2 \theta} &= \frac{l_b}{\sqrt{2}}, \\ r(t + t_{\text{int}})^2 - r(t)^2 \sin^2 \theta &= \frac{l_b^2}{2} - \sqrt{2} l_b r(t) \cos \theta + r(t)^2 \cos^2 \theta, \\ \sqrt{2} l_b r(t) \cos \theta &= \frac{l_b^2}{2} + r(t)^2 - r(t + t_{\text{int}})^2, \\ \cos \theta &= \frac{1}{\sqrt{2} l_b r(t)} \left( \frac{l_b^2}{2} + r(t)^2 - r(t + t_{\text{int}})^2 \right), \\ \theta &= \arccos \frac{1}{\sqrt{2} l_b r(t)} \left( \frac{l_b^2}{2} + r(t)^2 - r(t + t_{\text{int}})^2 \right). \end{aligned} \quad (\text{C.5})$$

Similarly,

$$\phi = \arccos \frac{1}{\sqrt{2} l_b r(t + t_{\text{int}})} \left( \frac{l_b^2}{2} + r(t + t_{\text{int}})^2 - r(t)^2 \right). \quad (\text{C.6})$$

Similarly, formulate the detectable areas at  $t = t + t_{\text{int}}$  that will protrude from the square region (that is, when  $r(t + t_{\text{int}}) > l_b/2$  and  $\theta < \pi/4$ ). Denote the angle as  $\omega$  ( $= \frac{l_b}{2r(t + t_{\text{int}})}$ ) when formulating the protruding areas. Then, when shifting bait locations, the observable ratio  $O(t)$  could be given as following (however, I will leave  $\theta$ ,  $\phi$  and  $\omega$  unconverted for simplicity.).

$$O(t) = \begin{cases} \frac{\pi}{l_b^2} (r(t)^2 + r(t + t_{\text{int}})^2) & r(t) + r(t + t_{\text{int}}) < \frac{l_b}{\sqrt{2}} \\ \frac{1}{l_b^2} \left[ \pi \{r(t)^2 + r(t + t_{\text{int}})^2\} \right. \\ \quad \left. - 4 \left\{ r(t)^2 (\theta - \cos \theta \sin \theta) \right. \right. \\ \quad \left. \left. + r(t + t_{\text{int}})^2 (\phi - \cos \phi \sin \phi) \right\} \right] & r(t) + r(t + t_{\text{int}}) \geq \frac{l_b}{\sqrt{2}} \\ \quad \cap r(t + t_{\text{int}}) < \frac{l_b}{2} \\ \frac{1}{l_b^2} \left[ \pi \{r(t)^2 + r(t + t_{\text{int}})^2\} \right. \\ \quad \left. - 4 \left\{ r(t)^2 (\theta - \cos \theta \sin \theta) \right. \right. \\ \quad \left. \left. + r(t + t_{\text{int}})^2 (\phi - \cos \phi \sin \phi) \right. \right. \\ \quad \left. \left. + r(t + t_{\text{int}})^2 (\omega - \cos \omega \sin \omega) \right\} \right] & r(t + t_{\text{int}}) \geq \frac{l_b}{2} \cap \theta < \frac{\pi}{4} \\ 1.0 & \theta \geq \frac{\pi}{4} \end{cases} \quad (\text{C.7})$$

The detection rate  $D(t)$  could be calculated based on equation (C.5), (C.6), (C.7) and (3.5).



## Appendix D

# Derivation of the maximum bait interval

When applying the model to other species, it would be convenient to have an equation to derive the maximum bait interval  $l_b$  required for the detection rate to be 1. Assume that the monitoring range covers the entire area the focal species may exist, i.e.  $A_m = 1$  in equation (3.5). Then,  $O(t) = 1$  is required for  $D(t) = 1$ . When  $O(t) = 1$ , the ratio of the detectable area in a square region with sides  $l_b$  is 1 (Fig. C.2a), which means that  $r(t) \cos \pi/4 = l_b/2$  if the location of baits is not shifted, and  $\theta = \pi/4$  in Fig. C.2b if the location of baits is shifted. Thus if the location of baits is not shifted,

$$l_b = \sqrt{2}r(t). \quad (\text{D.1})$$

If the location of baits is shifted, substitute  $\theta = \pi/4$  to equation (C.5) to obtain

$$\begin{aligned} \frac{1}{\sqrt{2}} &= \frac{1}{\sqrt{2}l_b r(t)} \left( \frac{l_b^2}{2} + r(t)^2 - r(t + t_{\text{int}})^2 \right), \\ \frac{l_b^2}{2} - r(t)l_b + r(t)^2 - r(t + t_{\text{int}})^2 &= 0, \\ l_b &= r(t) \pm \sqrt{r(t)^2 - 4\frac{1}{2}(r(t)^2 - r(t + t_{\text{int}})^2)}, \end{aligned}$$

thus considering the sign,

$$l_b = r(t) + \sqrt{2r(t + t_{\text{int}})^2 - r(t)^2} \quad (\text{D.2})$$

where  $r(t) = r_c(t) + r_s(t)$  and  $t_{\text{int}}$  is the temporal interval of monitoring. Equation (D.2) could be confirmed by increasing  $t$ .  $r(t)$  is a Sigmoid function and reaches a plateau in around 7 years (see Fig. 3.4). Thus if assuming  $r(t) \approx r(t + t_{\text{int}})$  when  $t > 7$ , then equation (D.2) implies that  $l_b = 2r(t)$ , which is obviously correct (assume  $r(t) = r(t + t_{\text{int}}) = l_b/2$  in Fig. C.2a).

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