# Multiscale modelling of invasive species control: the cane toad in Australia

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# Abstract


The cane toad is an invasive species in Australia that has the potential to affect many native species negatively. Several recent studies seek to stop their spread in the Kimberley-Pilbara semi-arid region where rainfall is strongly seasonal and toads have to rely on artificial water points for refuge during dry seasons. Modelling is a crucial tool to explore control strategies and predict their impact. However, due to the lack of data on large-scale spread and control of cane toads in a region with similar characteristics, modelling cane toads in the Kimberley-Pilbara region requires utilising data on an individual scale.

Our project involves an application component of cane toad modelling and a methodological component of modelling and computation. In the application domain, we seek to estimate the large-scale impact of some control methods when deployed in the Kimberley-Pilbara region. To achieve this aim, we need to overcome the challenge of making macroscale predictions from microscale data. Therefore, in the computation domain, we seek to model a large number of agents in relatively large spatiotemporal scale while still capturing details in individual behaviour.

To address the research aims mentioned above, we develop a multiscale model of cane toad control in the Kimberley-Pilbara region, which consists of two agent-based models at different scales. The microscale model allows us to use available data regarding the movement and ecology of cane toads to model how toads move and colonise a new water point and how control methods affect this process. The macroscale model allows us to use the simulation results of the microscale model to represent toad spread and control in the large, real landscape of the Kimberley-Pilbara region and make predictions to support decision-making.

We conclude that multiscale agent-based modelling, with the integration approach employed in this project, can overcome the computation cost of large ABMs and is an effective tool to model cane toad control and a class of modelling problems with similar characteristics. Future studies should aim to formally identify this class of problems. Using the model, we predict that cane toads will colonise the Kimberley-Pilbara corridor in approximately 87 years, and the most effective and robust approach to stop their spread involves an exclusion strategy near either ends of the corridor, potentially supplemented with traps or a corridor-fence depending on practical constraints. These results strengthen an argument made in previous studies of toad control in this region: prompt action is needed to stop toads from spreading further, and exclusion is a potential tool for spread prevention.

# Declaration

I certify that:

- This thesis does not incorporate without acknowledgement any material previously submitted for a degree or diploma in any university; and that to the best of my knowledge and belief it does not contain any material previously published or written by another person where due reference is not made in the text.
- Where necessary I have received clearance for this research from the University's Ethics Committee and have submitted all required data to the School.
- The thesis is 25279 words in length (excluding text in images, table, bibliographies and appendices).

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# Chapter 1

# Introduction

For as long as humans have been spreading around the world, human activities have led to the introduction of species to environments and regions beyond their native range. Due to their relatively novel characteristics and often the lack of natural predators or competitors, such introduced species have the potential to greatly harm local ecosystems, in some cases leading to the extinction of native species. The domestic cat (*Felis catus*) is a well-known example of an invasive species that has had extensive global impacts [53]. In Australia alone, cats have had catastrophic impacts on native mammals in the 'critical weight range' [42] and they continue to kill millions of birds each year [89]. Their impacts serve as a pertinent reminder of how a species, which is often introduced as a companion animal, can go on to cause environmental impacts.

Species can also be deliberately introduced for bio-control purposes. One infamous example is that of the cane toad (*Bufo marinus*), which was introduced to Queensland, Australia in 1935 as biological pest control [24]. Since its introduction, the toad has spread through several states and exceeded 200 million in population [17], causing significant damage to local ecosystems and becoming a notorious invasive species. At the present, the invasion front has already reached the Kimberley region in Western Australia and is advancing towards the Pilbara region. The climate of this transitional region is semi-arid with strongly seasonal rainfall, and thus toads will be heavily reliant on natural and artificial water bodies to survive in dry seasons [27].

Control programs are important to reduce the ecological damage of invasive species, and models can be useful to devise effective control programs. In invasive species control programs, decisions must be made regarding the specifics of each program, such as the exact control method, the frequency of deployment or the distribution of resources over an area. Such decisions can be explored using mathematical or computational models – simplified representations of real-world processes and relationships. After a model is formulated, a large number of experiments, each with different parameters, can be simulated to compare different scenarios and variations in strategy. In addition, the results can provide insights into the modelled system and estimates of how different strategies will play out in real life, as long as the model is well parameterised or fit to data. In short, models allow us to make decisions in invasive species management with more certainty and information about the trade-offs between different choices.

Models have been employed to understand the spread of cane toads and explore different control approaches. One area of spread is range prediction, and there have been many attempts to predict the toad's range by modelling their physiological constraints [44], climatic conditions of their home range [76] and environmental and anthropogenic factors of their current range in Australia [82]. Another area where models have contributed is to investigate the role of evolution in the increasingly enhanced dispersal capability of toads at the invasion front and the potential trade-offs [11]. Models built to evaluate control strategies are less common. Florance et al. [27] employed modelling to investigate the toad's reliance on water bodies in arid regions and explore the effect of blocking the toad's access to such water points. Later studies have followed up by exploring the potential of a "waterless barrier", created by excluding toads from artificial water points in the Kimberley-Pilbara corridor to prevent toads from spreading further into the Pilbara [80, 75]. On the other hand, despite having been studied quite extensively [15, 90, 54], the impact of traps on cane toads at population level has not been modelled.

Agent-based models (ABMs) can provide new insights into the spread and control of cane toads. In an ABM, a system is represented as its components and their behaviour. Cane toads' behaviour has been studied extensively through radio-tracking, field research and laboratory experiments [64, 48, 51], and this information can be used to parameterise an ABM. Despite this, in most studies of their spread and possible control approaches, cane toads have been modelled collectively as an expanding population. There are challenges in using an ABM to model toads, namely that of computational cost. To support management of cane toads in Australia, estimating the large-scale impact of a control strategy when deployed in the actual landscape is important. However, toads are very small vertebrates that can reach high densities [50], so modelling millions of toads at the same time will be computationally infeasible and ineffective. As such, new computational methods need to be developed to address this problem.

Our project involves modelling the control of cane toads in the Kimberley-Pilbara region, while addressing the associated computational problem. Specifically, we seek to answer two questions. The first question is methodological and regards the computation aspect of our project: How to effectively represent a large number of agents on a relatively large spatiotemporal scale while still capturing important details of individual behaviour? The second question regards the application of the model – cane toad control – and provides context and purpose for the methodological question: What is the large-scale impact of trapping and corridor-fencing on the spread of cane toads in the Kimberley-Pilbara corridor, especially when combined with the waterless barrier??

To address the research questions, we develop a multiscale model of cane toad control in the Kimberley-Pilbara region, which utilises data at different scales to make broad-scale predictions (overview in Chapter 3). The model consists of two agent-based models – a microscale model of toad individual behaviour in relatively small areas (details in Chapter 4), and a macroscale model of population-level spread and control in the Kimberley-Pilbara corridor (details in Chapter 5). The microscale model allows us to use available data on the movement and ecology of cane toads to model how toads move in an abstract landscape and colonise a new water point, and how control methods affect this process. The macroscale model allows us to use the simulation results of the microscale model to represent the spread and control of cane toads in the large, real landscape of the Kimberley-Pilbara region and make predictions to aid decision-making. Together, the system of models illustrates how individual behaviours lead to and affect population-level dispersal dynamics. By running experiments with both models, we answer the application research question (Section 6.1). By reflecting on the model design and evaluating its computational advantages, we present a potential solution to the computation research question (Section 6.2).

According to our model, toads will colonise the Kimberley-Pilbara region without fail, most likely in under 100 years. Among the investigated control methods, trapping and corridor-fencing cannot reliably stop toads, and the only way to halt their spread in the region is by restricting their access to a number of water points to create a "waterless barrier". The best locations to deploy this barrier are at the ends of the corridor. Despite not working on their own, trapping and corridor-fencing show promise when used alongside exclusion. Finally, although a wetter climate and uncertainty in water point capacity might result in faster spread and reduced protection from control strategies, they can be accounted for by excluding more water points or supplementing an exclusion strategy with traps or a corridor-fence.

Our model addresses the computation research question through two mechanisms: reusing simulation results of the microscale model across macroscale simulations and employing approximation in the integration. Reusing simulation results involves running the microscale model in advance, aggregating the outcomes and using the aggregated statistics to model toad spread between water points in the macroscale model. Approximation involves running the microscale model with a discrete, sparse grid of parameters and employing interpolation to approximate the values in between grid nodes. With these mechanisms, we reduce the number of required microscale simulations by a factor of roughly $10^3$ and overcome the limitation of computational cost associated with large ABMs (Section 6.2).

The rest of the report is structured as follows. In Chapter 2, relevant background information – including the spread and control of cane toads in Australia, current approaches in modelling cane toads, and modelling at multiple scales – is presented, followed by research questions formulated from the gaps in knowledge and methodology. In Chapter 3, we outline our modelling aims, present an overview of the multiscale model and go through the available input data that inform our model. In Chapter 4, we review approaches to modelling important microscale processes, describe the microscale model in detail and present the experiments that we run with it. Chapter 5 follows a similar structure, presenting the macroscale processes, model and experiments. In Chapter 6, we discuss our findings and answers to the research questions, and evaluate our methodology in its capacity to provide these answers.

# Chapter 2

# Literature review

## 2.1 Application domain – Cane toad control

### 2.1.1 The cane toad invasion

Human activities have introduced species to new habitats outside their natural range, whether as unintentional stowaways on a cargo ship or as domestic pets moving across borders with their host families. Occasionally, introduced species proliferate, spread quickly across the new landscape and displace and endanger endemic wildlife. At the point when they start to impact local ecosystems negatively, such species are often called invasive species. Invasive species control is crucial to reduce the ecological damage of such biological invasions. Depending on the stage of spread and the area affected, control can take many forms: eradication, which involves removing an invasive species completely from an area; suppression, which involves reducing the population of an invasive species to keep at a low level; or spread prevention, which involves stopping them from spreading into an area. To improve the effectiveness of control and allocate resources where they are most needed, it is also important to understand an invasive species's behaviour and impact.

Cane toads were introduced to Australia in 1935 in an attempt to control the cane beetle [24]. The attempt, however, was unsuccessful, and the toads quickly started to spread through Queensland and Northern Territory. In the last decade, the invasion front has reached Western Australia [22] and New South Wales [57], with the total population of cane toads exceeding 200 million [17]. According to many studies, the invasion front is moving at a speed many times faster than its initial rate [64, 63] thanks to a combination of spatial assortment and dispersal-facilitating environmental factors [82]. There have been many attempts to predict the species' eventual range with varying conclusions [76, 82, 44], but recent studies seem to agree that the toads will continue their march in Western Australia towards the western coast and afterwards further south [22]. As such, at the moment many attempts to prevent or slow down the spread of cane toads tend to focus on this region.

### 2.1.2 Impact on native wildlife

Cane toads, with their rapid rate of reproduction and unique characteristics, have greatly disrupted native species and ecosystems in various ways. The most direct and significant form of damage is the toxins present in all life stages of cane toads, which poison and kill native predators [73]. Although some predator species have adapted to the poison by changing their behaviour or physiology [60, 62, 65], many others are still at risk, especially those at the invasion front. In addition, the toads and toad tadpoles compete against native species – especially native anurans – for resources and prey on small invertebrates [73, 74]. At population level, there is evidence that the arrival of cane toads leads to a sharp decline in some species [47, 21], most often due to the ingestion of the cane toad's toxins. Conversely, there are species that experience an increase in population thanks to the decrease in toad-eating predators [21].

In long-colonised regions, many of the steep fluctuations that coincided with the arrival of cane toads have since then stabilised, and some affected species have recovered [73]. Moreover, some recent studies seek to mitigate the toad's impact through taste-aversion training [85]. By exposing vulnerable, toad-naive predators to smaller, non-lethal toads or nausea-inducing, toad-tasting baits, they are conditioned to avoid toads altogether as a food item when they arrive – almost like a vaccination process. However, it is undeniable that cane toads have a diverse and cascading impact on local species and, in some cases, a potential to endanger endemic species and upset existing ecosystems.

### 2.1.3 Control approaches

Given the possible impact the cane toads can have, decades of effort have gone into finding effective ways to eradicate them and, where that is no longer possible, to contain the invasion. As a result, a variety of approaches have been proposed.

The most basic methods to suppress the population of cane toads involve manual collection by local communities and toad traps [59], which have proved useful to eradicate some satellite populations [88]. Toad traps involve a wire-mesh box with one-way trapdoors, baited with both insect-attracting light and acoustic lure – recorded advertisement calls [90, 54]. This type of traps has been found to be more labour-effective than hand capture as they can be left operating on their own [55]. Crossland et al. [15] also developed another type of traps that targets the tadpole phase of toad metamorphosis – since toad tadpoles often consume eggs of their own species, a submerged box can be baited with toad toxins to lure tadpoles. These traps have been shown to be successful at capturing a large number of tadpoles and reducing the presence of toads afterwards [15, 52]. However, there have been no attempts to assess the broad-scale impact of deploying cane toad traps. The idea of fencing to exclude toads from conservation areas was also suggested [6], but the potential of fences as a spread prevention method has not been investigated.

From field surveys and laboratory experiments, several studies have shown that cane toads at the invasion front might have evolved improved dispersal capacity compared to those from established populations [64, 63, 51], possibly at the cost of competition and breeding [41, 28]. This finding motivated genetic backburning as a management method – to relocate slow-dispersing toads from long-colonised regions ahead of the invasion front to mix genetically with fast-dispersing toads when they arrive [66]. By slowing down the advancing speed of the invasion front, barriers can be made more effective. Other intervention approaches include using pheromones to suppress the growth of eggs and tadpoles [13], releasing pathogens to impair adult toads [72], and genome engineering to render toads sterile or less toxic [81].

In semi-arid regions of Australia, annual rainfall is often limited to a wet season lasting several months, and during dry seasons there is little to no rainfall [10]. In these regions, artificial water points (AWPs) are built by pastoralists in the form of troughs, dams or water tanks to provide water for grazing livestock. As toads need frequent access to water for hydration, without rainfall they rely almost exclusively on these AWPs [27, 48]. Moreover, as the main breeding ground of toads, water points also serve as invasion hubs where satellite populations are formed and later merge into the main population. Capitalising on this, access to such points can be restricted using mechanisms (such as fences, reinforced tank, etc.) to exclude toads from their only water source and prevent them from establishing in the area [27, 49]. The exclusion of toads from all AWPs can in turn exclude toads from a significant proportion of Australia's arid landscape otherwise habitable to them [27]. A later study conducted by Tingley et al. [80] took this idea further and examined the exclusion of toads from AWPs in one particular area as a way to create a barrier to halt the invasion. The coastal strip of land connecting the Kimberley and Pilbara regions in Western Australia was identified as a suitable location where this approach is most effective. Since this area contains a narrow corridor of artificial water bodies, the reinforcement or closure of relatively few AWPs can create a wide "waterless" barrier impassable to toads and thus protect the far-side region from future incursions. According to several studies, this approach alone can potentially halt the invasion at a reasonable cost [80, 75, 31].

Despite the wealth of possible control methods, it should be noted that there has been no significant progress in stopping the cane toad invasion. Although some localised control methods such as fencing and trapping have been proven to be effective in some field trials, little has been done to explore the impact and cost of deploying them on a larger scale. Other approaches such as genetic backburning and the waterless barrier require significant funding and commitment from the state government, relevant departments and private landowners, and as such need further investigation and risk assessment before they can be considered. Here, modelling can be a useful tool to both estimate the population-level impact of fencing and trapping and assess the risks associated with methods such as the waterless barrier.

## 2.2 Methodological background – Modelling

### 2.2.1 The different forms of models

A model is an attempt to represent the real world in some way, often by making assumptions, abstractions and simplifications with the purpose of highlighting a particular mechanism or interaction. By focusing on only certain aspects of a system or process, models provide a valuable platform to learn more about its dynamics and make predictions about its behaviour [26]. A diagram of a leverage, for example, is a model of said system. Although properties such as materials and weight might not be represented and the components might be abstracted as thin lines and circles, the diagram still allows us to predict what would happen if a force is applied on one end and even compute the torque at the other end.

Models that allow us to make quantitative analyses and deductions are categorised as quantitative models. There are different types of quantitative models. Quantitative models can use mathematical language, such as functions or equations, to express real-life processes, in which case they are often called mathematical models [3]. A mathematical model can be validated with empirical data and used to make quantitative predictions. For example, the growth of a population is often expressed as an exponential or logistic function, depending on whether resources are infinite or not. These models can be validated using recorded annual population levels of a country and, if found to be accurate, used to estimate the population level at some point in the future. Such models are rigorous and precise by nature and are effective at describing systems as a whole – humans as a population, water as a volume of fluid, etc. Quantitative models can also come from analysing large databases and extracting patterns from them, in which case they are often called statistical models [18]. For example, from a large number of records of height and weight, regression analyses can be run to find the best-fit model, and eventually a linear model is found to best describe the relationship between height and weight. Afterwards, this linear model can be used to predict someone's likely height knowing their weight, or vice versa. Statistical models are good to quantify the uncertainty within one variable, to estimate the relationships between multiple variables, and to make statistical predictions of a system. Finally, computational models follow an algorithmic or mechanistic approach, using variables and procedures to represent real-life processes [77]. Such models are mainly used to study systems that cannot be described using mathematical expressions or relationships – including complex systems. Similar to other types of models, by substituting different sets of parameters, computational models can be used to investigate different scenarios and explore uncertainty in parameters.

Complex systems are systems which consist of many interacting components and exhibit behaviours qualitatively different from those of its components [68]. For example, although brain neurons are relatively simple in their structure and behaviour, the brain as a whole is capable of thinking, processing images and storing memories – feats that can never be attributed to a single neuron. As such, the output of a complex system is almost impossible to derive just by analysing its components, and often agent-based models (ABMs) – an example of computational models – are used to represent such systems [4]. In an agent-based model, only a system's constituting components and their behaviour are modelled, and the outcome is obtained by observing the system as a whole. Due to ABMs' nature, only by "running" the models and letting the agents' behaviour play out can the outcomes be observed. Even when a system might be described analytically, ABMs are still a useful alternative if data on component-level behaviour are readily available to parameterise the model. An example of an ABM is the termite construction model [46], which models termites as individual agents with behaviours such as moving, picking up an available building block and putting it down. Although the termites themselves follow simple rules, the system as a whole is capable of constructing complex structures with rooms, doorways and corridors without any master plan. In an agent-based model, the same modelling principles of abstraction and simplification still apply: the termite model might choose to ignore the presence of other termites except the builders and the queen and treat all building materials as homogeneous cubes. Inaccurate as it is, the model still provides insight into how pheromones might drive the construction of termite nests and allows us to predict how their shape might change in the presence of strong wind [46].

### 2.2.2 A powerful tool in ecology and invasive species control

The different types of models, presented in the previous section, have proved useful in various scientific fields of study. Here we briefly introduce their prevalence in the area of ecology and their value in invasive species control.

In the field of ecology, models are a common tool to describe ecological relationships, such as between climatic conditions and forest coverage or between fish population and fishing activities. A famous quantitative model is the predator-prey model – also called the Lotka–Volterra model – which takes the form of two differential equations, one to describe the population of predators and the other prey. This model describes how different processes such as predation, growth and mortality interact, often cancelling out and resulting in an equilibrium [38]. Recently, ABMs (also called Individual-Based Models in the field of ecology) have gained popularity in ecological studies [19] thanks to their ability to represent rich life-history and heterogeneity between individuals [32]. Instead of differential equations, an ABM would represent the predator-prey relationship mentioned above by modelling predators and prey individually, each exhibiting relevant behaviours such as grazing, hunting, breeding and dying of natural causes [30]. However, the disadvantages of this bottom-up representation involve the need for data on individual-level characteristics and behaviours as well as the computational cost of simulating each entity separately. The increased computational cost is particularly relevant in ecological systems with large populations of interacting entities.

In the study of invasive species control, models can provide useful insights. In order to allocate control efforts and estimate the impact of control, understanding the population and spread dynamics of a species is crucial [1] and models are often used to study such dynamics [14]. Moreover, due to the long-term nature of management strategies, it is often costly or infeasible to test them in real life. As such, models provide a useful platform to investigate and optimise long-term strategies. For example, Baker et al. [2] developed mathematical models of detectability, population dynamics and dispersal of the cherry guava on Lord Howe Island from removal records. These models were then used to find the best management strategy, which reduced the duration and total effort of the program significantly. In a recent study, FoxNet, an agent-based model was built to reproduce the population dynamics of the invasive red fox in different landscapes [40]. Foxes are simulated both individually and as family units, and their behaviour depends on their age, status and time of year. Habitat cells contain food and potentially baiting stations. To validate, simulations of fox populations at real sites were run using data from field studies as input parameters, and model outputs are compared against field estimates – in fact, the outcomes of the models were found to closely match field estimates. Different baiting regimes were then compared by varying density and frequency of baits. FoxNet proved how a well designed ABM, when parameterised with ecological data, can replicate real-world outcomes and help tune control programs.

## 2.3 Modelling cane toads

### 2.3.1 Previous cane toad models

Models have been widely used in understanding and predicting the spread of cane toads. Urban et al. [82] used statistical regression to model the relationship between the occurrence data of cane toads in Australia and environmental variables, which include both bioclimatic variables like habitat requirements and anthropogenic factors such as land use and road cover. The resulting model can then be used to predict the species's eventual range. In another study [83], the same authors used regression to fit invasion speed to environmental factors and patch connectivity in each cell, and quantified how invasion speed might have been influenced by represented factors from their regression coefficients. This study provided an example of how occurrence data can be transformed into invasion speed using the $\alpha$-hull algorithm. Another approach was employed in the model of Kearney et al. [44], which attempts to predict the future range of the cane toad in Australia under different climate conditions using a mechanistic, biophysical model. This model computes the range of environmental factors such as temperature and rainfall habitable to toads from their biophysiological processes such as heat exchange, metabolism and locomotion, and as such has the advantage of not relying on patchy occurrence data. However, there have been few attempts to model the toad's dispersal in a stepwise fashion to represent and predict how they slowly spread across connected habitat patches in Australia. Computational models can be suitable for this purpose.

Compared to range prediction, there have been relatively few models that explore potential control methods against cane toads. To estimate the impact of excluding toads from water points, Florance et al. [27] modelled the toads' annual dispersal distance as a function of their body temperature and the number of rainy days, similar to Kearney et al.'s method [44], then used this distance to create geographical buffers around permanent and artificial water points. In arid regions, since water points act as refuges for cane toads during dry seasons, the resulting area represents where toads can physiologically disperse to, and removing water points reduces this area. Following up on this idea, studies on the waterless barrier are backed by a discrete generation point-process model [80, 75]. A point-process model represents processes as events happening at a point in a mathematical space. In this model, the number of colonisers at any point in each generation depends on its distance to already-colonised water points and their capacity as well as the toad's dispersal ability. As long as a water point has two or more colonising toads, it will be colonised in the next generation and remain so indefinitely. The waterless barrier is then created by making a number of water points unavailable for colonisation. The model relies on several assumptions, some of which are: that in dry seasons toads cannot move and cannot survive without water points, that toads can only reproduce in and colonise permanent or semi-permanent water points, and that the possibility of long-distance dispersal – such as toads hitch-hiking on vehicles and establishing a satellite population – is not significant. Such assumptions are not always true and thus need to be assessed and accounted for in future studies.

The increasing spread rate of toads at the invasion front, mentioned in Section 2.1.1, is further studied with modelling. In one such study, an spatial explicit agent-based model was used to explore the trade-offs between dispersal and other processes in an abstract asexually reproducing invasive species [11]. In this model, individuals are simulated on a 20 x 15 000 grid and characterised by three pseudo-genes representing the proportion of resources allocated to dispersal, reproduction and competition. Adult individuals reproduce offspring that inherit their traits, and then die afterwards. Mutations happen with a small probability, and offspring disperse and then compete before reaching adulthood. More recently, the impact of the dispersal-competition trade-off on the strength of a spread-barrier was studied using a ABM [66] similar to one used by Burton et al. [11]. In this model, sexually hermaphroditic individuals disperse along a one-dimensional space and compete to reproduce, and genes and heritability are represented in more detail. The population spreads towards a barrier which kills any individuals advancing into it, and the barrier is considered "breached" if more than 5 individuals advance past it. As predicted, the barrier was found to be less effective against fast-dispersing individuals on the invasion front. In addition, the model was also used to examine the impact of a genetic backburn, which was found to be effective at increasing the strength of a barrier as long as long-distance dispersal is unlikely. Although the two models mentioned in this paragraph are built to explore characteristics found in cane toads, it should be noted that both are models of a non-specific organism in an abstract space.

### 2.3.2 ABMs to model cane toads

As noted in the previous section, there have been no ABMs that specifically model cane toads in Australia. This section presents the reasons why ABMs can be a good choice to model cane toads control, including the availability of individual-level data and the heterogeneity between toads.

To produce accurate, and hence useful, models of a particular species in a particular landscape, data are often needed for several purposes. Most mathematical and computational models require some form of validation data, which are compared against the model's output to make sure the model is a good representation. For example, range-prediction models can be validated using occurrence or distribution data. Data can also be used as input for model parameters, although the exact data depend on the type of model and the level of detail.

The focal point of one of the most well-documented biological invasions, the cane toads themselves have been extensively studied at organism level, including their biophysical characteristics, morphology and even their genomics [8, 61, 45, 25]. Moreover, their behaviour and movement patterns have been of particular interest, presumably because those aspects directly influence the species's dispersal rate across the landscape. For example, several studies have tracked individual toads using radio-tracking devices and produced traits and aggregated statistics characterising the toads' movement [70, 64, 9], and roads have been found to facilitate toads' dispersal [71, 7]. Many field studies have confirmed their reliance on water sources and how their activities tend to centre around such sites [48, 8]. Similarly, in terms of control, many studies have investigated the toads' reaction to different types of baits [90, 54]. From this, several variations of cane toad traps have been devised, often with experimental results from field trials. Such knowledge can be utilised in a cane toad model either as parameters or as basis to make informed assumptions.

The cane toad invasion can be considered a complex system, with individual-level behaviours of toads, such as moving, hydrating and breeding, giving rise to system-level outcomes, such as the species's dispersal dynamics across a heterogeneous landscape. As such, and given the wealth of knowledge about the individual-level behaviour of toads, an agent-based model is a potential method to model the spread and control of cane toads. In addition, male and female toads have been found to exhibit different movement patterns [64] and react differently to baits [54, 90], and being able to represent heterogeneity between individuals is another strength of ABMs. However, toads have rarely been modelled at individual level. All ABMs mentioned in Section 2.3.1 are models of an abstract invasive species built to confirm theories and observations made with the cane toads. Conversely, models of the spread of cane toads in Australia have been mainly developed from the top down, representing cane toads collectively as a slowly advancing population.

### 2.3.3 The computational cost of large ABMs

Modelling cane toads using ABMs has its own challenges. In this section, we discuss the importance of computational performance of an ABMs, how this is especially relevant to modelling cane toads, and finally how multiscale modelling techniques might hold part of the solution.

The computational performance of an ABM implementation is of great importance, especially in models with a large number of agents. The main reason is that agent-based models are often simulated many times to determine the effect of stochasticity, explore parameter space, analyse sensitivity of parameters and compare different scenarios [36]. There have been several approaches to improve performance and scalability of ABMs. The simplest involves minimising model complexity and avoiding or reusing expensive computations [36]. Many ABMs also utilise the concept of super-agents, where one agent represents a group of real-world entities [69]. This approach has the potential to greatly improve the performance of an ABM; however, it is not suitable in models where the density of agents and the interactions between them are important [58]. As such, it is not suitable for modelling toad control at the invasion front, since density and interaction between toads strongly influence the colonisation of new water bodies and the overall advancement of the invasion front. Another approach involves the parallel execution of agent simulation code across multiple processing units [34]. Thanks to the increasing prevalence of parallel computing units, this approach has become more common in recent years [37, 20, 78, 23]. However, the performance gain from parallelism is still limited by the available computing power while also requiring complex restructuring of the model software.

In order to support the decision-making process of cane toad control in Australia, models need to be parameterised and validated with real data, and simulations need to be run on the real landscape, similar to FoxNet [40]. However, this requirement poses a further computational challenge to modelling toads at individual level. The Kimberley-Pilbara region where a potential waterless barrier is actively considered spans hundreds of kilometres. Given that cane toads can reach a very high density [50], modelling toads individually means that at some point in the simulations there might be millions of toads present. Moreover, as mentioned before, both dispersal and invasive species management are long-term processes, and thus their outcomes can take many years to observe. To meaningfully simulate that many agents, each with their own state and behaviour, on a large spatial and temporal scale can be prohibitively costly in terms of computational power. Hence, there is a strong need for a model which can bridge that gap between the microscale behaviour and the macroscale dynamics.

Interconnected processes spanning multiple scales are not unique to the cane toad invasion or ecology – they are everywhere. For example, in the field of biology which involves processes of different scales, proteins, cells, tissues and organs are all common subjects for modelling. The land use and traffic of a city depend on its governing body, organisations and citizens. In meteorology, different weather systems at different scales interact to influence the weather in our local areas as well as climatic conditions globally. As such, many studies have explored ways to represent this gap between scales in different contexts, and the collective approach is recently coined into the field of multiscale modelling [39]. A review by [16] outlined many cost-effective computational techniques for multiscale models, including multiscale ABMs, and such techniques can be useful in formulating and simulating an agent-based cane toad model. Examples include separating processes that happen at different timescales by integrating a second model and only running microscopic simulations for small spatial domains and where appropriate.

## 2.4 Research questions

### 2.4.1 Computation domain

As explained in Section 2.3.2, agent-based modelling and simulation is the method of choice. ABMs are suitable for this project because of the availability of data at individual level, the need to represent heterogeneity between individuals, and the need to observe system-level outcomes. Moreover, regarding the control of cane toads in Australia, toads have never been modelled individually before, which means an attempt to formulate an agent-based model of toads might provide new insights into cane toad control and serve as a reference for future models. However, as mentioned in Section 2.3.3, ABMs can be prohibitively expensive when applied to cane toads. Hence, the following methodological question needs to be addressed:

- RQ1: How to effectively represent a large number of agents (e.g. millions) on a relatively large spatiotemporal scale (e.g. thousands of square kilometres and several decades) while still capturing important details of individual behaviour?

RQ1 is exploratory and qualitative in nature. As the main methodological contribution, RQ1 is tackled throughout the project by exploring the model design space (including implementation) and addressing smaller questions – in the context of cane toad modelling and the purpose of the model – including, but not limited to:

- What aspects of individual behaviour and interaction are most relevant in modelling cane toad control? (one example of such aspects is agent movement)
- How can such aspects be represented on a small spatiotemporal scale?
- How can such aspects be represented effectively and efficiently on a large spatiotemporal scale? (some examples can be agent movement and the effect of certain control methods on this movement)

### 2.4.2 Application domain

Even though the project ultimately aims to make contributions to computer science and in particular scientific modelling, the application domain – invasive species control and in particular cane toad control – not only motivates and justifies the methodological research question but also guides its answer by highlighting the most important aspects of the real-world system to be modelled as well as the appropriate level of complexity. As such, we have decided to identify relevant research questions in the application domain to serve as the purpose of the model, and which this project also strives to address. From reviewing the current literature surrounding cane toad control and modelling as well as personal communications with a cane toad control expert, we have identified a direction that has not been explored, yet merits investigation:

- RQ2: What is the large-scale impact of trapping and corridor-fencing on the spread of cane toads in the Kimberley-Pilbara corridor, especially when combined with the waterless barrier?

Similar to RQ1, RQ2 is answered by addressing smaller questions:

- RQ2a: Without intervention, how long will it take for cane toads to colonise the Kimberley-Pilbara corridor?
- RQ2b: How does each control method (traps, corridor-fence, and exclusion), when employed individually, impact the spread of cane toads in the Kimberley-Pilbara corridor?
- RQ2c: How does combining control methods impact the spread of cane toads in the Kimberley-Pilbara corridor, compared to employing them individually?

Each small question requires overcoming certain computational challenges. RQ2a requires being able to represent how spread on a large scale emerges from individual-level behaviour of a large number of toads. Similarly, RQ2b and RQ2c require being able to represent how modifications to individual behaviour by control methods can impact and stop large scale spread. These mini-questions are answered by constructing a model of toad spread in the Kimberley-Pilbara region, running experiments with this model and interpreting the results.

# Chapter 3

# Multiscale model of cane toad control – overview

This chapter provides an overview of the proposed methods. We start by describing the modelling aims in Section 3.1, which drive the design of our model in order to sufficiently answer the research questions. This is followed by an overall description of the multiscale model, a system consisting of two models of different scales, in Section 3.2. Finally, in Section 3.3 we present the available input data that inform parameters and assumptions in our model.

## 3.1 Modelling aims

In general, the project involves constructing a model of cane toad control, devising and running experiments with the model, and interpreting and discussing the results. The results and the whole process would then provide answers to the research questions outlined in Section 2.4. To achieve the end goal of answering the research questions, the design of the model must meet several requirements, both in terms of computation and application domain:

- The model must be able to provide quantitative estimates regarding the spread of cane toads in the Kimberley-Pilbara region given different courses of action, including a do-nothing scenario and different control regimes.
- The model must be devised from and parameterised with real-world data whenever possible. Where data are not available, assumptions must be made based on existing knowledge or practices.
- The model must be flexible enough to take into account uncertainty in parameters, especially those assumed without data, and provide the range of outcomes resulting from variations in such parameters.

- The model must be computationally efficient, so that the necessary experiments can be completed in reasonable time, both for this project and for potential users of the model.

Beyond answering the research questions within the scope of this project, the model itself should also be a contribution in the form of a useful tool for stakeholders and policy-makers to explore different scenarios regarding cane toad control in general and in the Kimberley-Pilbara region. Those scenarios might include, but are not limited to, different control strategies, practical constraints (e.g. only certain water points are available to manage; fences cannot be monitored and maintained more frequently than monthly, etc.) and what-if scenarios (e.g. faster locomotion ability, different climate conditions, addition of water points, etc.)

## 3.2 Models of different scales

We construct a system of two spatially explicit agent-based models: a microscale model of toads' individual behaviour in relatively small areas, and a macroscale model to represent population-level spread in the Kimberley-Pilbara corridor. By meeting the requirements previously outlined in Section 3.1, the system itself forms a potential solution to the computation research question stated in Section 2.4.1 and provides the tool to address the application research question stated in Section 2.4.2.

The microscale model is a spatial abstraction that allows us to input fine-grained movement rules for toads and observe the probability of colonisation of water points under different initial states. In this model, toads are modelled individually as moving agents that spread from colonised water points across a relatively small landscape, potentially colonise new water points and are hindered by control mechanisms. The microscale model is parameterised using known ecological characteristics of toads and mainly simulates scenarios where individual-level behaviour matters, such as at the invasion front and when environmental conditions permit the dispersal of toads. The outcomes of the microscale model are aggregated and used to parameterise the large-scale model.

The macroscale model uses the real Kimberly-Pilbara landscape and allows us to make estimates regarding the spread of toads in the region and impact of control on this spread by utilising the output of the microscale model – the colonisation probability between water points. In the macroscale model, water points in the Kimberley-Pilbara corridor are modelled as a connected network of nodes, and the large-scale spread of cane toads through this region as transmission through the water point network. Variations in rainfall between subregions of the corridor are modelled, parameterised using weather records of weather stations situated along the corridor. The links between water points indicate the chance of toads spreading from one water point to another, and this chance depends on variables such as the distance between them, the capacity of the colonised water point, and the climate in each subregion. Control methods either reduce the chance of toads spreading from one water point to another (trapping and fencing), or remove this chance entirely (exclusion).

In this project, representing the system in two separate models has several benefits. By separating and integrating the two models efficiently – such as only representing toads in small spatial domains and reusing the microscale simulation results across the large landscape – we address the computational challenge of modelling a large number of agents. Furthermore, this approach facilitates the analysis of the microscale model in isolation, as its outcomes can be easily extracted.

The models are described in detail in their respective chapters, Chapter 4 and Chapter 5, following the ODD protocol [33]. ODD is a standard format for describing agent-based models. It is intended to facilitate the communication and replication of ABMs by providing a clear structure and encouraging rigorous descriptions of model details. Nowadays, the protocol is used widely in ecology and other fields [84].

The models are implemented in NetLogo [87], a programming language and modelling environment for agent-based modelling. Visualisations of the data and the results are produced using R [67], a programming language and environment for statistical computing. NetLogo source code and R scripts can be found in Appendix A.

## 3.3 Input data

This section describes the available input data, including the sources, the format and any processing steps if applicable. Their usage in the models is explained in the respective model description (Chapters 4 and 5).

### 3.3.1 Movement and ecology

As mentioned in Section 2.3.2, cane toads have been studied extensively. In particular, studies that record toad movement through radio-tracking are crucial to this project. We use data from [64]. Specifically, we use aggregated statistics of movement such as daily movement rate (Table 3.1) to generate the movement of cane toad agents in our model. Moreover, the gender of the tracked cane toads is recorded in this dataset, allowing us to model the heterogeneity between male and female cane toads. Finally, this study was undertaken in the wet-dry tropics of the Northern Territory, a region with strongly seasonal rainfall relatively similar to the Kimberley-Pilbara corridor.

Table 3.1: Statistics from radiotracking to model toad movement

| | **Male** | **Female** |
|---|---|---|
| No. days tracked | 52.3 (35.5) | 33 (24.1) |
| Mean movement rate (m/day) | 46.2 (31.3) | 150.2 (117.1) |
| Movement rate range (m/day) | 0.3 - 82 | 0 - 370 |
| Meander ratio | 0.64 (0.32) | 0.62 (0.30) |

In addition to movement, other ecological characteristics of toads are also essential to modelling spread. Life cycle and behaviour of cane toads are detailed in [50] – their breeding rate is estimated to be 30 000 eggs per clutch, the time it takes for them to reach maturity ranges from 6 to 12 months, and juvenile toads mostly stay close to the water source where they spawn. Sex ratio is often assumed to be 1 male – 1 female in several papers [35, 12]. Finally, the distance at which toads can detect water is often assumed to be 100 m, and the number of colonisers leaving a water point in a generation, although unknown, is estimated to be in the range of $10^3$ to $10^6$ [80]. This existing volume of knowledge about cane toads helps inform parameters and assumptions in both models.

### 3.3.2 Control methods

There have been several field experiments on the exclusion of toads from water points as a control method [27, 49]. These experiments have confirmed the effectiveness of exclusion – following the installation of the exclusion mechanisms (for example, a ring of fence around a dam), toads that are attracted to excluded water points die while trying to get in, and the population of toads in the area surrounding excluded water points often drop to zero a few days afterwards. Regarding the failure rate of such exclusion mechanisms, an observation from [49] indicates that some of the fences used in the study were damaged by kangaroos at some point in a 175-day period, and thus they can fail without maintenance and allow toads to colonise the water point. As there are no concrete data, we assume that the exclusion at each water point has a 5% chance of failing every year. A similar assumption is made in previous models of exclusion [80, 75].

There have been several studies on trap characteristics [54, 56, 90] and effectiveness [55]. We use data from [55, 56] to model traps in the microscale model. Specifically, from the study, the daily capture rate of traps is approximately 3% of the population in the deployed area, the effective range of the bait is roughly 120 m and the maximum capacity of traps is estimated to be 30.

Except for the use of restricting access to water points, there have been no studies on the impact of fencing on cane toad movement when deployed on a larger scale, such as across the Kimberley-Pilbara corridor – the method we are investigating, from here on defined as corridor-fencing. As such, we need to make reasonable assumptions regarding their effectiveness. We assume the erected fence always prevents toad movement, but every 100-metre fence section has a 0.5% chance of being damaged by external factors every day. This results in an expected lifespan of roughly 200 days for each fence section before it is damaged.

### 3.3.3 Water point distribution

As detailed in Section 2.1.3, cane toads are heavily dependent on atmospheric and ground moisture and thus, in arid regions such as the Kimberley-Pilbara region, rely on permanent water sources during dry seasons for shelter and hydration [48]. Therefore, the distribution of water points in this region is very important to our model, as it determines the rate of spread as well as the effectiveness of control mechanisms in each particular area.


Figure 3.1: Water points form a corridor between Kimberley and Pilbara regions in Western Australia. The points on the map represent water points, with the colour representing the type of water point – blue for natural water points, red for dwellings, dark green for irrigation areas and light grey for other types of artificial water points. Irrigation areas are typically much larger than other water points and their data include area measurement, and the size of their corresponding point reflects the area (not to scale).

We use data from the most recent model of cane toads in this region, provided to us by one of the authors of [75] (B. Phillips, personal communication). The data were aggregated from several sources, including Geoscience Australia [29], Department of Water, WA and Department of Agriculture and Food, WA, and verified by land managers in this region. The dataset contains 566 water points, each with location (in coordinates) and type (natural, dam, tank, irrigation, dwelling, etc.). Water points of the type "irrigation area" also have size measurements in the form of area and perimeter. These data are used to initialise the environment in the macroscale model.

### 3.3.4 Rainfall

Due to their reliance on rainfall during wet seasons to disperse, rainfall pattern has a direct impact on the rate of spread and the maximal distance at which toads can travel before having to seek shelter or die of desiccation [8].


Figure 3.2: Weather stations in the Kimberley-Pilbara region. Source: Bureau of Meteorology

We use rainfall records of weather stations in this region (Figure 3.2) from the Bureau of Meteorology. The data are available in the form of daily measurements of rainfall in millimetres. Not all the data can be used – the rainfall records at some stations are patchy, sometimes missing entire seasons or years, and data from such stations are removed.

Wet seasons in the modelled region span from December to March. To correctly capture the pattern of rainfall in each wet season, we use "Rain Year" in place of Year and define it to run from July of the previous year to June of that year. For example, the Rain Year of 2020 includes rainfall records from July 2019 to June 2020. The next steps involve computing the number of days that toads can freely disperse – from here on defined as active days. We assume active days to be rainy days (rainfall $\geq 1$ mm) and the three days after each rainy day – following previous studies on cane toads [44, 27] – and mark such days in the dataset. Finally, for each station we aggregate the number of active days for each Rain Year from 2000 to 2020 and from this list compute the following statistics: mean, max, min, and standard deviation. These statistics, shown in Table 3.2, are used to randomly generate the number of active days recorded at a station during a Rain Year in the macroscale model (Section 5.4.3).

Table 3.2: Statistics on active days per Rain Year at weather stations in the studied region

| **Code** | **Name** | **Longitude** | **Latitude** | **Max** | **Min** | **Mean** | **Std. dev.** |
|---|---|---|---|---|---|---|---|
| 3003 | BROOME AIRPORT | 122.24 | -17.95 | 121 | 49 | 85.3 | 18.3 |
| 3066 | PORT SMITH | 121.81 | -18.52 | 126 | 49 | 76.9 | 20.22 |
| 3030 | BIDYADANGA | 121.78 | -18.68 | 127 | 44 | 80.2 | 22.8 |
| 3028 | ANNA PLAINS | 121.49 | -19.25 | 126 | 30 | 71.7 | 26 |
| 4019 | MANDORA | 120.84 | -19.74 | 111 | 25 | 59.3 | 25.9 |
| 4068 | WALLAL DOWNS | 120.64 | -19.78 | 109 | 15 | 53.3 | 26.2 |
| 4028 | PARDOO STATION | 119.58 | -20.11 | 98 | 28 | 61.6 | 20.8 |

# Chapter 4

# The microscale model of movement, colonisation and control

## 4.1 Introduction

Because the spread of an invasive species through a landscape is a phenomenon emerging from the movement of individual specimens, a model of individual movement can be helpful in estimating and studying large-scale spread. Individual movement is especially useful when modelling invasive species spread prevention, as there often exists no precedent of controlling an invasion on a similar landscape – thus no data. Modelling cane toad control in the Kimberley-Pilbara corridor falls in this category. However, there exist data on a smaller scale, such as the movement of individual toads as well as the behaviour and impact of control methods when deployed in a small area. Therefore, we need a model which can make use of small-scale data of toads and turn these data into useful information and insights (Section 3.2), from which broader predictions can be made. Chapter 5 goes into details about how such information and insights are utilised in the macroscale model.

Specifically, we aim to construct a model with the purpose of answering the following questions: How likely is an uncolonised water point to be colonised by toads leaving a colonised water point at a certain distance away? In addition, to what extent does trapping and fencing impact this spread? Finally, how does the outcome change with different modelling approaches and under uncertainty in the parameters that are unknown and assumed?

The modelled system involves a small number of water points, the toads migrating between them, and control methods that disrupt this spread. The process of colonising a new water point begins at the colonised water point from which toads emigrate. Assuming no interference, the emigration rate depends largely on the water point's capacity. From there, toads disperse across the landscape, potentially arriving at new, uncolonised water points. Although the exact process for toad movement is unknown, studies involving radio-tracking of toads provide certain statistics to model this movement. If breeding happens successfully at the new water points, they become colonised and after some time start to emit colonisers themselves. Control methods include traps and fences. Traps, baited with insect and acoustic lure, capture some toads at a certain rate. Fences stop toad movement completely but can be rendered ineffective due to natural phenomena, wildlife, and human activity.

The model is an agent-based model, with entities represented as interacting agents with their own state and behaviour. These entities include toads, water points, traps and fence sections. In simple terms, colonised water points emit toads; toads move randomly, detect new water points and colonise them; traps capture toads, and fence sections stop toad movement but have a chance to break, allowing toads to breach. The model spans up to hundreds of square kilometres in space and less than 200 days in time. To model spread, the model makes use of data on the movement and ecology of cane toads, presented in Section 3.3.1. Modelling control requires data on the effectiveness and robustness of traps and fences, presented in Section 3.3.2.

The rest of the chapter is structured as follows. Section 4.2 reviews potential approaches in modelling certain microscale processes central to the model, with respect to the assumptions that the model makes regarding cane toad ecology. This is followed by a detailed description of the final microscale model, following the ODD protocol [33] in Section 4.3. Next, the experiments which are run using the model are detailed in Section 4.4. The goals of these experiments include fitting model parameters to field observations, exploring uncertainty in unknown parameters, informing assumptions, and generating data for the macroscale model. The results are presented in Section 4.5. Finally, Section 4.6 contains a discussion on the implications of the results and the model in the context of the project.

## 4.2 Modelling microscale processes

In this section, we go through some important processes that influence the spread of cane toads at microscale: population and emigration; movement; colonisation of water points; and control methods. With each process, we first review the approaches previous studies have taken in modelling it, and afterwards talk about our approach and the rationale behind our decision.

### 4.2.1 Population and emigration

Ecological models often represent the population of a species and how it varies due to processes such as breeding, predation, migration and natural deaths. Population size often determines the rate of spread of a species – the higher the population, the more individuals leave their habitat in search of a new one. The population in a particular area depends on the carrying capacity of the habitat – the highest level of population the habitat can sustain with its resources. Different habitat patches can have different carrying capacity – for example, a larger water body is able to sustain a larger number of cane toads with food, moisture and sheltering sites.

Emigration refers to the behaviour of toads leaving their habitat water point in search of a new one. In previous models of the spread of cane toads, the number of toads emigrating from a water point was often assumed to depend on its maximum capacity instead of the current population at the water point. Due to the breeding and maturing rate of toads (mentioned in Section 3.3.1), colonised water bodies – water points with at least one toad from each gender – are assumed to reach carrying capacity after one generation. Moreover, before reaching adulthood, juvenile toads don't disperse far from their spawning site. As such, modelling the exact population at each water body is not particularly useful, as before a water point starts to emit mature colonisers it has no significant impact, and afterwards its impact is governed mainly by its carrying capacity.

We employ a similar approach in our model. The state of each water point is represented only by its colonisation status, and the number of colonisers emitting from it depends on its capacity, which is a permanent attribute of each water point. The relationship between capacity and colonisation probability is explored in an experiment, described in Section 4.4.2.

The temporal pattern of emigration – regular vs stochastic, sparse vs dense – can also be an important element in modelling spread. From observation (B. Phillips, personal communication), emigration pattern depends heavily on rainfall, with toads often staying around a water point for days before leaving en-masse after a rainfall event. However, there has been no formal study on this. In our model, varying the pattern of coloniser emission does not have a significant impact on outcome, so we decide to model colonisers leaving daily.

### 4.2.2 Movement

Toad movement is the most important microscale process in modelling dispersal. In an arid region with heavily seasonal rainfall, the dispersal of cane toads relies entirely on finding a new sheltering and breeding site (usually water bodies) within a limited time period – the wet season [79, 8]. When the dry season comes, toads are less active and mainly shelter close to water points due to the need for hydration, and toads far from a water source risk dying of desiccation [48].

There have been attempts to model the process that drives toad movement, most notably the study of Schwarzkopf and Alford [70]. In this study, toads are modelled as a three-stage process where toads decide whether to move, whether to move to a new site or return to its location, and where to move to in the form of the distance and heading of their movement. This model was found to match real movement with reasonable similarity.

We employ a similar approach to the toad movement model described in [70], assuming that toads take a persistent random walk with a certain distance and heading, until they land on another water point. However, we choose not to model the sedentary behaviour of toads by dropping the possibility of toads not moving or moving around their sheltering site – the first two stages in the aforementioned model. Many studies have found great variability among individuals, with the pattern of movement ranging from remaining mostly at one site to moving in almost straight lines. Moreover, as mentioned in Section 2.1.3, toads at the invasion front often move at greater speed and straightness compared to toads in established regions. As we are modelling the invasion front, we are only interested in toads that disperse some distance away and contribute to the spread of the population. We assume that the change in heading at each timestep is drawn from a certain distribution, and this distribution is unique to each individual cane toad. Finally, we only model days in which the conditions are sufficient for toads to move across the landscape – defined as active days in Section 3.3.4.

Studies involving radio-tracking of toads at the invasion front provide certain aggregated statistics to calibrate our movement model. We use data from [64], particularly the following statistics: mean rate of movement, meander ratio and number of days tracked (Section 3.3.1). The magnitude of the movement can be directly parameterised using mean rate of movement. Although heading of toads at each timestep cannot be simply extracted from aggregated data, the two other statistics – meander ratio and number of days tracked – can be used to fit the parameters that determine the change in heading. This experiment is detailed in Section 4.4.1.

### 4.2.3 Colonisation of water points and modelling gender

Reproduction of cane toads requires a pair of cane toads – one male, one female – to be present at a water point. Although male and female cane toads have different characteristics and behaviour, in general gender was not modelled in previous models of the spread of cane toads through water points. In the model used in [80], a water point is considered colonised if at least two toads of arbitrary gender arrive at the water point in a generation. The follow-up version of the model retains this assumption [75].

In our model, a water point can only be colonised if both genders are present. According to the movement dataset, there is a noticeable difference between male and female cane toads in terms of movement rate. As such, we believe the previously employed requirement – two toads of any gender – would overestimate the likelihood of colonisation, and in turn the rate of spread, significantly. Conversely, requiring both genders for colonisation would bring the modelling results closer to reality. This ability to represent heterogeneity and its impact is also an advantage of using an agent-based model. To quantify this, we conduct an experiment comparing different requirements, detailed in Section 4.4.3.

Traps have been found to have different capture rates of male and female cane toads depending on the bait. Therefore, as a side effect, representing gender enables us to investigate this trade-off between capturing male and female toads. This experiment is described in Section 4.4.5.

Although it is known that toads can detect water sources and move towards them to seek shelter, there has been no study on the exact mechanism of this homing behaviour and the distance at which toads can detect water sources. Given the lack of data, previous models by cane toad experts have assumed that toads can detect water points from 100 m away (Section 3.3.1). We make the same assumption in our model and run sensitivity analyses to explore the impact of this uncertainty (Section 4.4.4).

### 4.2.4 Control methods

The next step after modelling the spread of cane toads involves predicting how that spread is altered under various control methods. Among the control methods devised against cane toads, the methods we decided to model include trapping and fencing. As mentioned in Section 2.1.3, traps are wire-mesh boxes baited with light and sound to capture toads. Fences consist of cloth or compressed panels held together by metal wires and posts and are installed to stand 60 – 90 cm above ground to stop toads' movement.

We model traps to affect all toads in a radius around them, with each toad having a probability to be captured. To our knowledge, there have been no previous models of cane toad traps. However, in a previous individual-based model of invasive species control [40], an approach similar to ours was employed – individuals with a territory overlapping a bait station are at risk of dying from that station. Baiting stations are comparable to traps in behaviour, as individuals exposed to them have a chance to be affected and die. However, the range of baiting stations, as modelled in FoxNet [40], depends on the foxes' exploration and habitat range, which can vary between foxes. On the other hand, the range of traps in our model depends on the range of the acoustic bait within the trap that lures toads towards it (120 m, Section 3.3.2), which is fixed and not dependent on the toads.

We model a fence as small sections that completely stop toad movement. However, each section has a chance to be damaged, and toads can move freely through a damaged fence section until it is repaired. This approach not only accounts for external factors such as natural phenomena, wildlife and human activity (such an incident with cane toad fences was mentioned in [49]) but also allows a variable that can be controlled – the frequency at which the fence is monitored and repaired. We also considered a simpler approach – allowing every toad which comes into contact with the fence a small chance to breach – but in the end, considering the lack of concrete data on the failure process of cane toad fences, opted for the former approach for its advantages.

Some data are available regarding cane toad traps but none are available for cane toad fences (Section 3.3.2). We make assumptions about the chance of a fence section being damaged and run sensitivity analysis on this unknown and uncontrollable variable (Section 4.4.5). Moreover, in the same experiment, we explore how the impact of those control methods changes depending on key controllable parameters regarding their deployment, such as trap density, trap location and fence repair interval.

## 4.3 Microscale model description

In this section, we describe the model as implemented, following the ODD framework [33]. The model's components and parameters are explained in sufficient detail so that it can be replicated. This model is used to run the experiments detailed in Section 4.4.

### 4.3.1 Overview

#### Purpose

This model is constructed with the purpose of estimating the spread of cane toads between a small number of water sources in one wet season and the impact of microscale processes, including deployment of control methods such as trapping and fencing, on this spread.

#### Entities and state variables

In the model, there are four types of agent: toads, water points, traps and fence sections. Toads are mobile agents characterised by their gender, speed and location. Water points are immobile agents characterised by their location, capacity and colonisation status (uncolonised, colonised and emitting). Traps are immobile agents characterised by their location and capture count. Fence sections are immobile agents characterised by their location and status (whether they are broken).

Table 4.1: Attributes and variables of agents in microscale model

| Type of agent | Permanent attribute | State variable |
|---|---|---|
| Toad | gender, speed, heading deviation | location, heading |
| Water point | location, capacity | colonisation status |
| Trap | location | capture count |
| Fence section | location | status |

#### Scales

The model is spatially explicit. The modelled space represents an abstract region between two arbitrary water points, mapped to a grid. The size of each grid-cell is 0.01 $km^2$ (100m x 100m) – this aligns well with the assumed water detection radius of toads (100m) (Section 4.2.3) and range of advertisement calls (120m) used as bait in traps (Section 4.2.4) for optimising purpose. As locations of toads and water points are represented as real-valued coordinates, the grid size has no significant impact on the model except fence sections, which are modelled to be one grid-cell in length.

Simulations run in discrete time for 160 timesteps, each timestep indicating a day. The duration of 160 days serves as an upper bound of active days during wet seasons – from data, the highest number of active days is 127 (Section 3.3.4).

#### Process overview

Here we provide a brief summary of how important processes are scheduled in the model. Details regarding those processes can be found in Section 4.3.3.

At every timestep:

1. Toads move if they are not at an uncolonised water point and not impeded by fence sections
2. Traps capture nearby toads with a probability
3. New water points are colonised if the colonisation conditions are met
4. Traps are reset if the timestep matches reset interval
5. All fence sections are fixed if the timestep matches fix interval

### 4.3.2 Design concepts

The model revolves around the spread of a population – cane toads – through individual behaviours and the impact of environmental elements, such as water points and human-set traps, on this spread. Individual toads have basic objectives to survive and to breed, although these objectives are not always directly reflected in their behaviour. Toads can sense nearby water sources and move towards them, hence displaying adaptive behaviour; otherwise their movement is stochastic. Interactions between agents include implicit breeding between toads at water points, capture by traps, and fence sections impeding toad's movement. As a whole, the population of cane toads exhibits a collective behaviour of colonising new water sources at a certain probability. There is no learning in this model.

### 4.3.3 Details

**Input data**

The model requires no input at runtime.

**Initialisation**

Here we provide details on how agents, model parameters and variables are initialised at the beginning of each simulation.

Water points are created using the model parameters wp-distribution and distance. Wp-distribution determines the number of water points in the model. By default it takes the value of "one-to-one", simulating the spread between two water points, one colonised and one uncolonised. When only modelling and studying toads' movement (Section 4.4.1), it is set to "one-source". In "one-to-one" scenarios, the parameter "distance" determines the distance between the two water points.

Toads are created at emitting water points at every timestep. Toads' heading are random (0 to 360 degrees). The number of toads created is determined by toads-per-wave, which represents the emitting water point's capacity (Section 4.2.1). Toads' gender is randomly initialised to Male or Female with a 1:1 ratio. Toads' speed is drawn from a normal distribution depending on their gender – this distribution is described in movement data

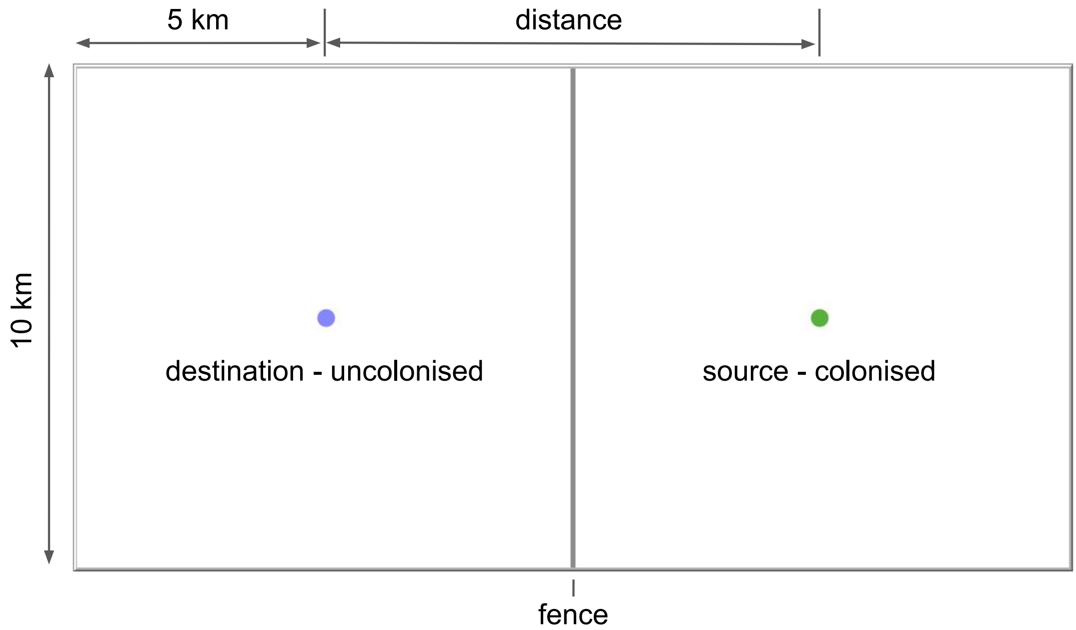


Figure 4.1: Model visualisation showing one-to-one scenario with a fence

from [64] (Section 3.3.1). Toads' heading deviation, controlled by their attribute angle-dev, is drawn from a uniform distribution with the mean determined by mean-angle-dev. This value is fit to the recorded meander ratio in field survey with an experiment (Section 4.4.1). Finally, the distance at which toads are able to detect and move towards water points is assumed to be 100 m (Section 4.2.3).

Traps share the same attributes – there is no variation among traps other than their location and capture count. Their capture rate, range and capacity are taken from field studies (Sections 3.3.2 and 4.2.4). In the same studies, traps are often reset (i.e. removing captured toads) daily. Regarding deployment of traps, we assume they will be deployed in a square area of 200m x 200m centred on the water point and in density of 1 per 100m, meaning traps are placed 100m away from each other.

Fence sections are created in a straight line formation between two water points (Figure 4.1) and have one state variable representing whether they are damaged or not. We assume that fence sections have the same chance to be damaged (0.5% every day) and are all repaired periodically, with repair frequency determined by fence-fix-interval.

### Submodels

Here we provide details regarding processes within the model. This includes:

- Toad movement – how toads move at each timestep and how this movement changes with the presence of nearby water points and fence sections
- Water point colonisation – how colonisation status of water points changes

Table 4.2: Model parameters and initial value of state variables

| | | | |
|---|---|---|---|
| | | **Toads - global** | |
| male-speed-mean (m/day) | 46.2 | male-speed-dev | 31.3 |
| female-speed-mean (m/day) | 150.2 | female-speed-dev | 117.1 |
| mean-angle-dev (degrees) | 20 | water-detection-radius | 100 (m) |
| | | **Toads** | |
| gender | 50% male, 50% female | speed (m/day) | drawn from a normal distribution with speed-mean and speed-dev |
| location | at emitting water point(s) | angle-dev (degrees) | drawn from a uniform distribution with mean mean-angle-dev |
| heading (degrees) | random, 0 - 360 | | |
| | | **Water points- global** | |
| wp-distribution | one-to-one | distance (km) | as per scenario, 0 - 20 |
| toads-per-wave | 20 - 100, default 60 | days-per-wave | 1 |
| | | **Water points** | |
| colonised? | 1 True, 1 False | emitting? | like colonised? |
| | | location | as per scenario, depending on distance |
| | | Traps - global | |
| trap-range | 120m | trap-reset-interval | 1 day |
| male-capture-rate (%/day) | 3 | female-capture-rate (%/day) | 3 |
| trap-density (traps/100m) | 1 (default) | trap-radius | 100m |
| max-capture | 30 | | |
| | | **Traps** | |
| Captures | 0 | Location | laid out in uniform distribution around water bodies, from trap-density and trap-radius |
| | | **Fence - global** | |
| fence-break-prob (%/day) | 0.5 | fence-fix-interval (days) | 30 (default) |
| | | **Fence sections** | |
| broken? | false | location | form a line in the middle, between 2 water points |

- Trap – the procedure of trap captures and capacity
- Fence – how the broken status of fence sections change

**Toad movement** At every timestep,

- if there is an uncolonised water point within water-detection-radius, move towards it a distance determined by speed; otherwise
- heading is drawn from a normal distribution with previous heading as the mean and toad-angle-dev as the deviation, then
- move a distance specified by the toad's individual speed towards heading. If the path is blocked by a fence section, stop where the fence section is. If the path crosses an uncolonised water point within water-detection-radius, change heading towards it.

**Water point colonisation** At every time step, each uncolonised water point performs a check. If there are at least one toad from each gender at the water point, it is colonised (Section 4.2.3). Once a water point is colonised, it remains colonised. If there is no more uncolonised water point, the model stops.

**Trap** At every timestep, if a toad is within the range of a trap, it has a chance to be captured. Captured toads are removed from the model, and the capture count of the trap is increased by one for each toad captured. Each trap has a capacity, and can no longer capture toads if captures reach capacity. The capture count of traps is reset periodically.

**Fence** As mentioned in Toad movement submodel, toads cannot move past a fence section. At every timestep, each section of the fence has a chance to be damaged (fence-break-prob). Toads can cross damaged sections freely. The entire length of the fence is repaired periodically with the repair frequency determined by fence-fix-interval.

## 4.4 Experiments on microscale processes

In this section, we describe experiments run using the microscale model. The overall aims of these experiments include finding a reasonable range of values for unknown parameters by fitting to field data (Section 4.4.1) and exploring the impact of uncertainty in model parameters on the outcomes (also called sensitivity analyses, Sections 4.4.4 and 4.4.5). Moreover, the experiment in Section 4.4.3 evaluates the impact of a modelling decision – modelling gender – by comparing it against a previous approach. Finally, some experiments generate outputs that are later used to parameterise the macroscale model, such as those described in Sections 4.4.2 and 4.4.6. The results of these experiments are presented in Section 4.5.

### 4.4.1 Fitting movement angle parameter to observed meander ratio

This experiment investigates the correlation between the model parameter that determines toads' heading and the observed meander ratio, ultimately fitting the parameter to field data. As described in Section 4.2.2, the toads' heading at every timestep is controlled by an attribute representing the straightness of their movement. This attribute is different for each toad and is drawn from a distribution with a mean mean-angle-dev. Although this model parameter cannot be directly assumed from data, it can be fit to data, specifically the meander ratio recorded in [64]. This meander ratio is calculated as the total displacement divided by total distance moved during the study. In the study, the meander ratio was observed to be around 0.64 for male cane toads and 0.62 for female cane toads.

In this experiment, we run simulations with different values of mean-angle-dev and observe the average meander ratio of toad agents. As the purpose is to record a characteristic of the movement of toad agents and not colonisation, there is no uncolonised water point – only one colonised water point emitting toad agents. The simulations are run for 53 timesteps, the mean number of days male toads are tracked in [64]. At the beginning of the simulation, 10 000 male toad agents are created, and afterwards no more are created. Other parameters take the default values detailed in Section 4.3.3. For this experiment only, we only run one simulation for each value of mean-angle-dev, as running more simulations is analogous to simply simulating more toad agents. From the results of this experiment, we choose the value for mean-angle-dev that reproduces a meander ratio comparable to that observed in [64].

### 4.4.2 Estimating toad spread between two water points

This experiment estimates the microscale spread between two water points, and how important model parameters – distance, capacity and duration – affect this spread. These parameters depend on real-life distribution and size of water points. We run simulations with two water points – one colonised and emitting colonisers, the other uncolonised. The distance between those two water points ranges from 2 to 20 km (i.e. 2, 4 ... 18, 20 km). Similarly, the capacity of the emitting water point (controlled by model parameter toads-per-wave) ranges from 20 to 100 toads per day (i.e. 20, 40 ... 100). We run 1000 simulations for each parameter combination, resulting in 50 000 simulation runs in total. We observe whether the uncolonised water point is colonised, as well as simulation duration, which indicates the time needed for the uncolonised water point to be colonised or the maximum value – 160 days – if it remains uncolonised.

For each simulation result, we then generate further results by varying the number of days toads are allowed to move (active days) in the range from 40 to 160 (40, 60, 80, etc.) and comparing this number against the simulation duration. If the number of active days is lower than simulation duration, it means for that scenario the uncolonised water point is not yet colonised so the simulation outcome is set to "uncolonised". If the number of active days is equal to or higher than simulation duration, the outcome is the same as the original outcome. For example, if the uncolonised water point is colonised in 125 days, then at 40, 60, 80, 100 and 120 days the outcome is "uncolonised", and at 140 and 160 days the outcome is "colonised". This post-processing step allows gathering results regarding different numbers of active days from only one simulation run.

Finally, we aggregate the results to get the colonisation probability of each combination of parameters. The final output takes the form of a 3-dimensional matrix and represents a function of colonisation probability with respect to distance, capacity and active days of the emitting water point. In addition to showing the relationship between these parameters and spread, figures are produced to illustrate the behaviour of the model to the reader. The results provide a baseline to compare against those of later experiments and also be used to parameterise the macroscale model.

### 4.4.3 The impact of modelling gender

This experiment quantifies the impact of modelling gender on the outcome of the model. As mentioned in Section 4.2.3, we hypothesise that modelling gender would result in lower spread rate due to the more selective colonisation requirement and the fact that male cane toads move at a slower rate. We run simulations similar to those in Section 4.4.2 (one emitting – one uncolonised) but with two different requirements for colonisation, and observe the colonisation probability under each requirement. In one set of simulations, colonisation requires at least one male and one female. In the other set, colonisation only requires two toads of any gender. Compared to the experiment in Section 4.4.2, distance between the two water points ranges from 5 km to 35 km instead to accommodate the higher spread rate of the any-gender scenario. Capacity is set at 100 toads per day. Each combination of requirement and distance values is run 1000 times.

### 4.4.4 Exploring sensitivity to detection radius

This experiment explores the sensitivity of the model outcome with regard to detection radius (the distance at which toads can detect water), which is an unknown model parameter (assumed to be 100 m in other experiments). We run simulations similar to those in 4.4.2 (one emitting - one uncolonised), however varying the detection radius in the range from 100 m to 1.6 km and observe the colonisation probability. The distance between the two water points takes the values of 10, 12 and 14 km to explore the potentially different effects of increasing detection radius in different settings, while capacity is fixed at 100 toads per day. Each combination of detection radius and distance values is run 1000 times.

### 4.4.5 Control methods – sensitivity and deployment

This set of experiments explores the sensitivity of the model outcome with regard to unknown parameters in modelling control methods. These parameters can be uncontrollable, such as the break probability of fence sections, or controllable, such as trap density, trap site and fence repair interval.

As traps are well parameterised with data from field studies, experiments with traps only involve controllable deployment parameters, namely the trapping density and site. We vary trap density – from 1 to 3 per 100m – and the deployment site – at the emitting water point, at the uncolonised water point, and at both – and compare the results between those scenarios and against a scenario with no traps. The distance between two water points is fixed at 8km and capacity is fixed at 60 toads per day.

Traps have also been found to capture male and female toads at different rates depending on the characteristic of the bait [54]. To investigate this trade-off, we run simulations involving two types of traps: one that captures more females at the expense of capturing less males (female-capture-rate 5%, male-capture-rate 1%) and vice versa. All other parameters are similar to the previously described experiment, except trap density is fixed at 2 per 100 meters.

All parameters regarding fences are unknown, including the break probability of each section and repair interval. We run simulations with break probability ranging from 0.1% to 1% and repair interval ranging from 7 days to 90 days and compare the results between those scenarios and against a scenario with no fence. The distance between two water points is fixed at 8km and capacity is fixed at 60 toads per day.

### 4.4.6 Estimating the impact of control on spread

This set of experiments estimates the impact of control methods on microscale spread between two water points, with certain assumptions regarding unknown control parameters. We run simulations similar to those in Section 4.4.2, with one emitting and one uncolonised water point 2 to 20 km away from each other, and with the emitting water point's capacity ranging from 20 to 100. However, control methods are enabled.

There are 3 scenarios in total: fence-only; trap-only and fence-trap. To explore the range of impact, in each scenario we also alter two parameters involving control deployment: trapping density is either 1 or 2 (traps per 100m), and fence repair interval is either 7 or 30 (days). Fence break probability is set at a conservative value of 0.5%.

## 4.5 Microscale results

In this section, results of the experiments previously described in Section 4.4 are presented, interpreted and supported by figures when appropriate.

### 4.5.1 Fitting movement angle parameter to observed meander ratio

The results show an inverse relationship where higher deviation leads to lower meander ratio. In practice, a lower meander ratio results in less straight movement (Figure 4.3). When deviation ranges from 20 to 22, the target meander ratio (0.64) is achieved.

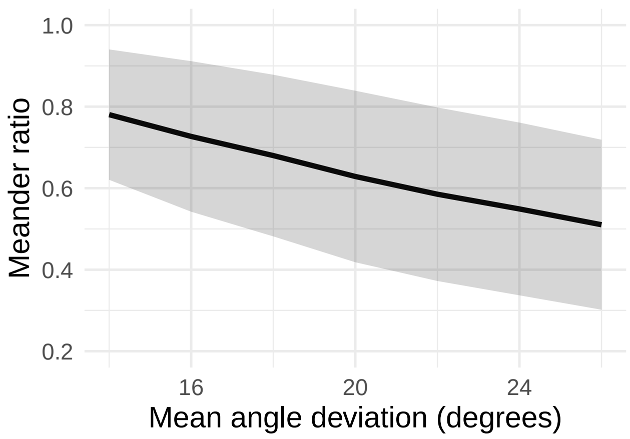


Figure 4.2: Inverse correlation between angle deviation and meander ratio

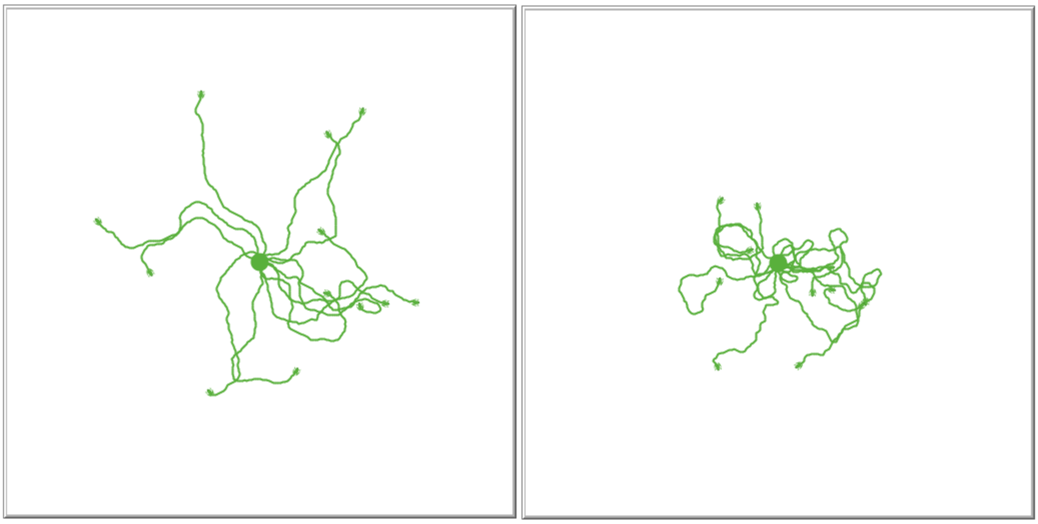

Figure 4.3: Toads move relatively straighter and disperse further with lower angle deviation. The pictures show toad movement with an angle deviation of 16 (left) and 24 degrees (right). For the purpose of illustration, the speed and deviation of all toads in this simulation are set at the mean values, so there is no stochastic variation in attributes between toads.

### 4.5.2 Estimating toad spread between two water points

The results show that spread is most dependent on distance and active days. Specifically, at 160 active days, colonisation probability is relatively high (more than 50%) regardless of capacity as long as the distance is less than 8 km (Figure 4.4). As distance increases, colonisation probability starts to drop off quickly; at a distance above 14 km, colonisation probability is less than 5%. Decreasing active days has a similarly significant effect – assuming a capacity of 100 toads per day, toads can only colonise a water point more than 10 km away at 160 active days. At 40 active days (minimum value), colonisation probability is extremely low save for the shortest distance (2 km). In other words, the distance toads can spread is strongly limited by the number of active days.

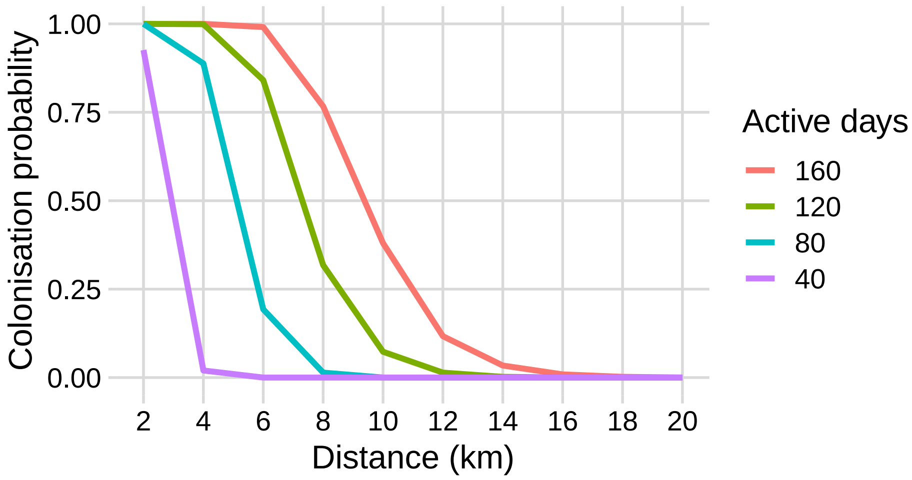


Figure 4.4: Relationship between number of active days and colonisation probability at a given distance (active days = 160)

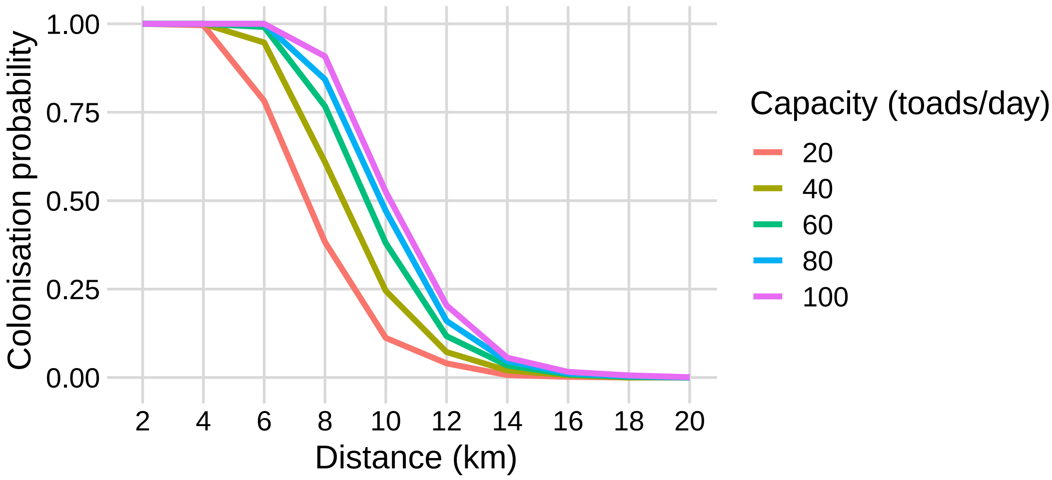


Figure 4.5: Linear increase in capacity has limited impact on spread (active days = 160)

Spread does not change significantly with small variations in capacity. For example, increasing the capacity of the source water point from 60 to 100 toads per day only increases colonisation probability by at most 15%; and at the lowest level of capacity (20 toads per day), toads can still colonise water points more than 8 km away (Figure 4.5). A closer examination reveals that capacity correlates with distance on log scale (Figure 4.6). Specifically, doubling the capacity of the source water point allows toads to colonise a water 10 km further with comparable probability.

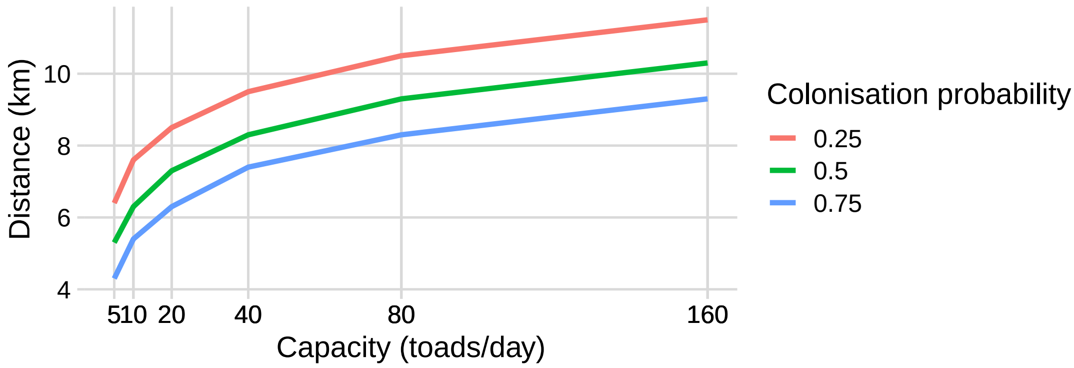


Figure 4.6: Source capacity and colonising distance correlate on log scale.
The lines represent the capacity-distance combination with colonisation probability of approximately 0.25, 0.5 and 0.75. (active days = 160)

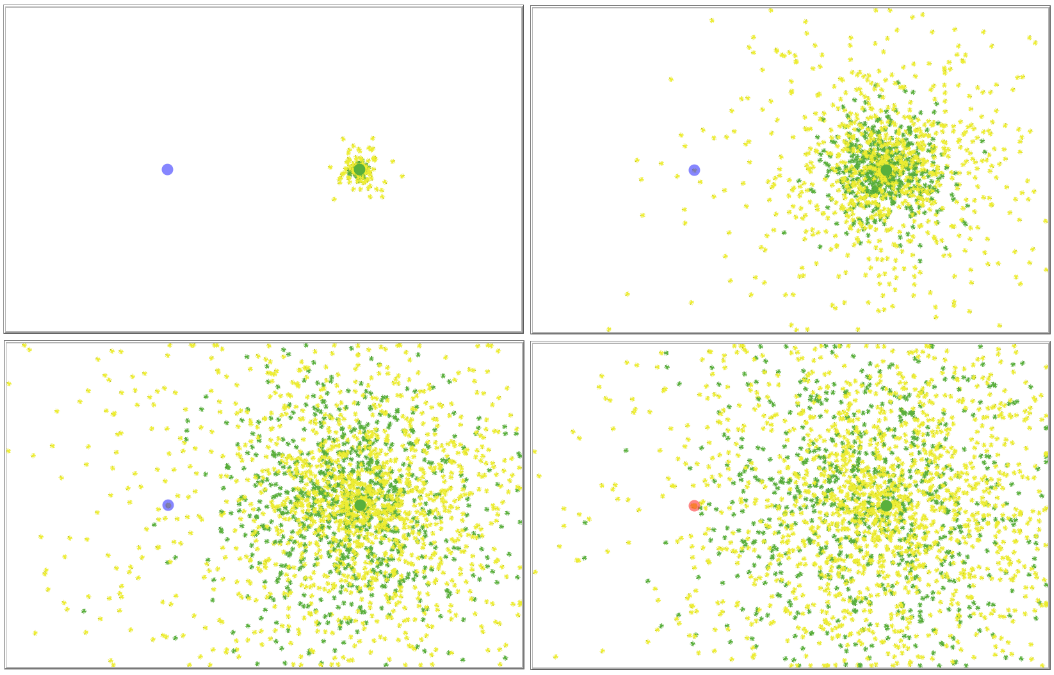

Figure 4.7: Toads disperse and colonise a water point in a simulation run.
T = 5 (top left), 36 (top right), 83 (bottom left) and 111 (bottom right). The circles represent water points – green is colonised, blue is uncolonised. Small points represent toads – yellow indicate females, green indicate males.

### 4.5.3 The impact of modelling gender

The results show that requiring both genders for colonisation greatly reduces the colonisation probability of a new water point. Specifically, while scenarios requiring both genders only end in certain colonisation at a close distance of 5km, without this requirement a water point 15km away is still at almost complete risk of colonisation (Figure 4.8). At a distance of 15km, the uncolonised water point already has a very low chance (approximately 5%) of

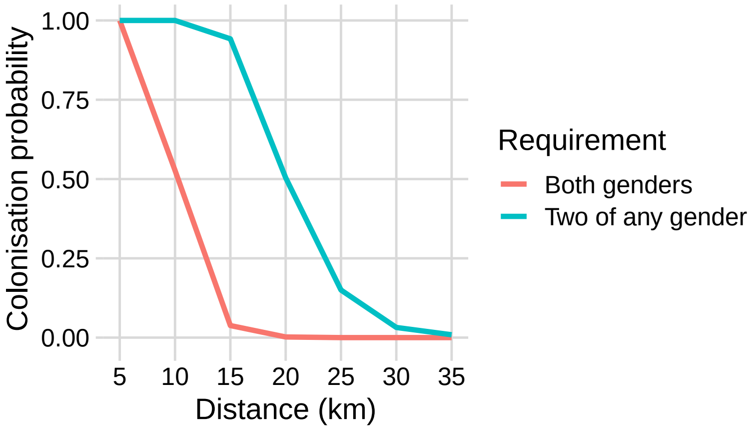


Figure 4.8: Requiring both genders for colonisation greatly reduces spread

being colonised if both genders are required. However, when two toads of any gender are enough to colonise a water point, colonisation probability only drops to a similar level at a distance of 30km. This difference means toads can spread more than 10km further away with the same probability when the presence of both genders is not required.

### 4.5.4 Exploring sensitivity to detection radius

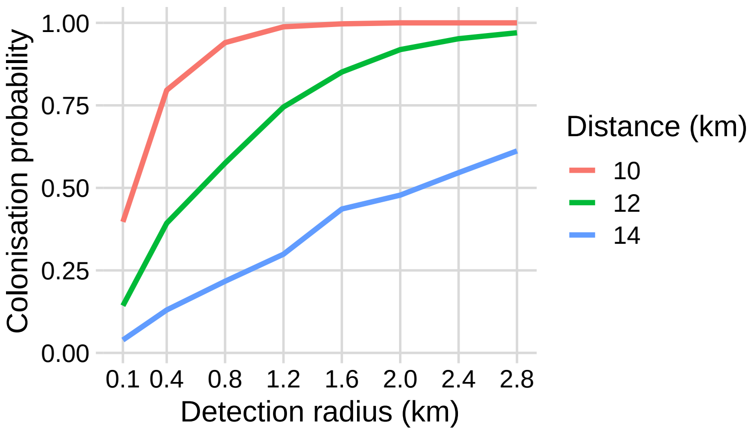


Figure 4.9: Detection radius impacts colonisation probability proportionately

The results show that, as expected, water detection radius of toads correlates with the probability of colonising the new water point. The extent of this correlation, however, depends almost linearly on the colonisation probability at the base detection radius – increasing the detection radius has a relatively weaker impact when the colonisation probability is already low. Specifically, colonisation probability doubles when detection radius is raised to 400 m – at distance 10km this increase is 37%, while at distance 14km it amounts to less than 10% (Figure 4.9). In all cases, the impact of increasing detection radius levels off when colonisation probability gets close to 1.

### 4.5.5 Control methods – sensitivity and deployment

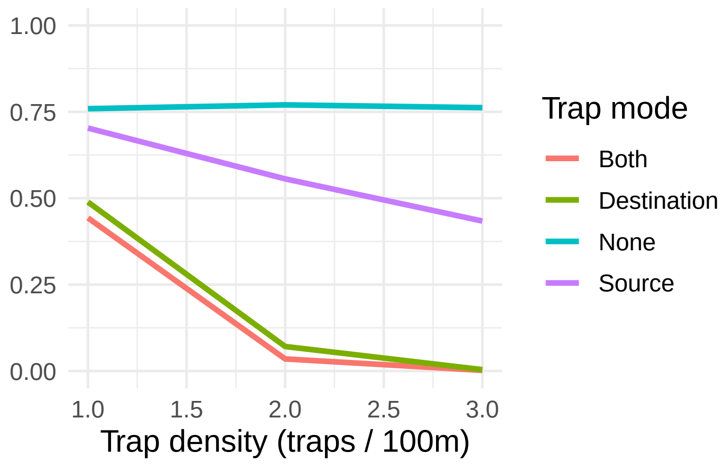


Figure 4.10: Traps are much more effective at higher density

The results show that trapping at low density (1 trap / 100m) has negligible impact (Figure 4.10). However, at higher density, trapping significantly reduces the probability that the trapped water point becomes colonised. Regarding the site, our simulations show that trapping at uncolonised water bodies (i.e. the destination of a colonisation trajectory) is more impactful. Specifically, in the settings of this experiment, trapping with the density of 2 or more traps per 100m at the destination can reduce the colonisation probability by up to 60%. Meanwhile, trapping at emitting water points has relatively small impact, only slightly reducing colonisation probability compared to a no-trap scenario especially at lower densities. However, this behaviour is most likely due to how we model emigration and does not accurately reflect real-life impact of trapping at a colonised water point (Section 6.2.2). Given this inaccuracy caused by a modelling decision, only destination-trapping is investigated in the macroscale model.

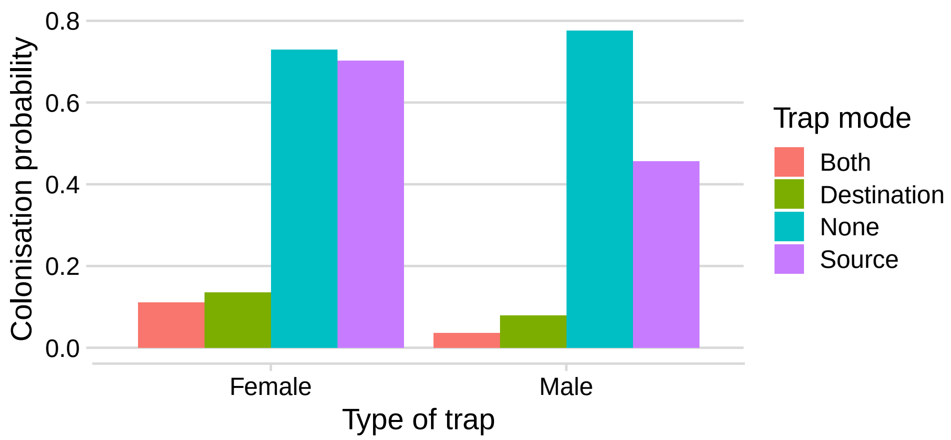


Figure 4.11: Trapping males is slightly more effective at preventing colonisation

Regarding the trade-off between capturing males and females, the results show that for the purpose of preventing colonisation at uncolonised water points, capturing males has a stronger impact than capturing females (Figure 4.11). This difference is most likely due to the fact that females move faster and so are relatively more abundant as colonisers than males. Males move slower and so, at a certain distance, arrive at the destination late in the simulation and in low abundance. Therefore, they are less likely to be replaced if captured.

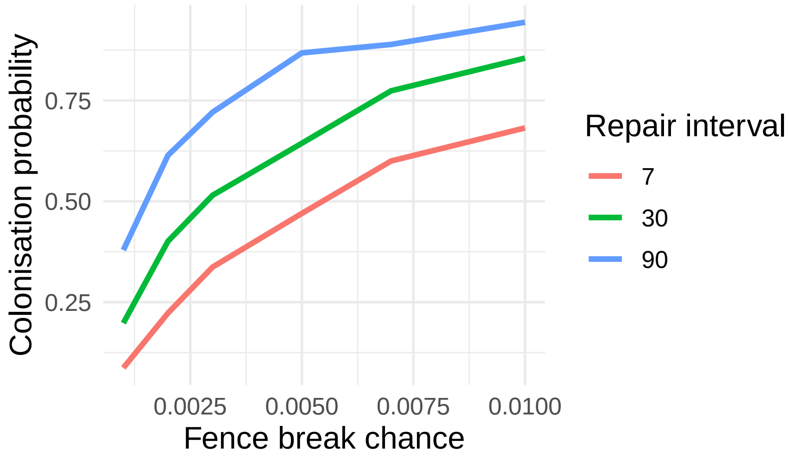


Figure 4.12: Fencing only effective with low break chance and frequent maintenance

From the results, a fence is only impactful given a very low break chance. Above a certain threshold in break chance, the addition of a fence does not affect spread to any meaningful degree. In our experiment, this threshold is around the 0.5% per day mark (Figure 4.12). For example, if 100-meter fence sections break for only 0.2% of the time every day on average (e.g. an expected lifetime of roughly 500 days), then under monthly maintenance a fence can reduce colonisation probability by almost 50%. Note that the exact threshold and impact are dependent on the other parameters of our experiment – for example, distance and water point capacity – and might change slightly in other scenarios.

Monitoring more frequently does result in reduced chance of toads spreading to the other side of the fence. However, in the simulated scenario, the impact is relatively limited. In the range of parameters that we are investigating, a three to four-time increase in maintenance frequency often has an impact equivalent to reducing break chance by half.

### 4.5.6 Estimating the impact of control on spread

Employing control methods reduces toads' ability to spread, although the extent of this reduction varies between methods. Overall, the results show that trapping, at low density, have a lesser impact compared to fencing (Figure 4.14). The impact of traps is more pronounced when both methods are deployed together, in which case colonisation probability is significantly reduced. When deployed at higher density, traps have an impact on spread comparable to that of a weekly-maintained fence. Moreover, control methods are most effective at medium distance. When water points are too closely-packed (4 km apart

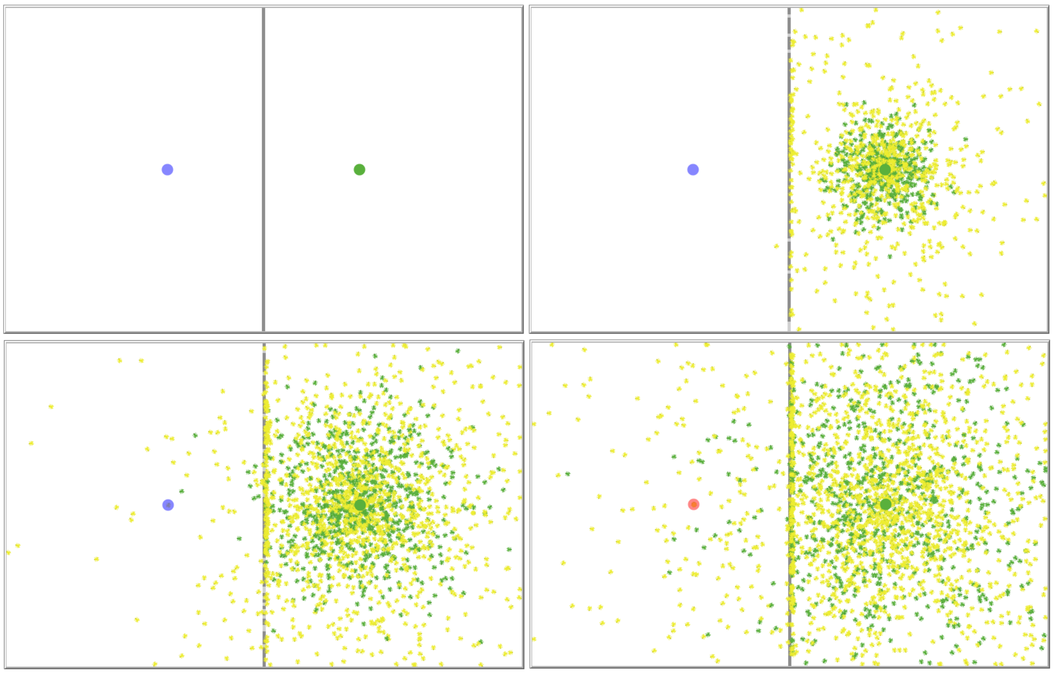

Figure 4.13: Toads breach a fence to colonise a new water point in a simulation run. T = 0 (top left), 30 (top right), 60 (bottom left) and 100 (bottom right). The line in the middle represents a fence, which stops most toads in their tracks. Occasionally a section of the fence breaks and lets toads through until it is repaired.

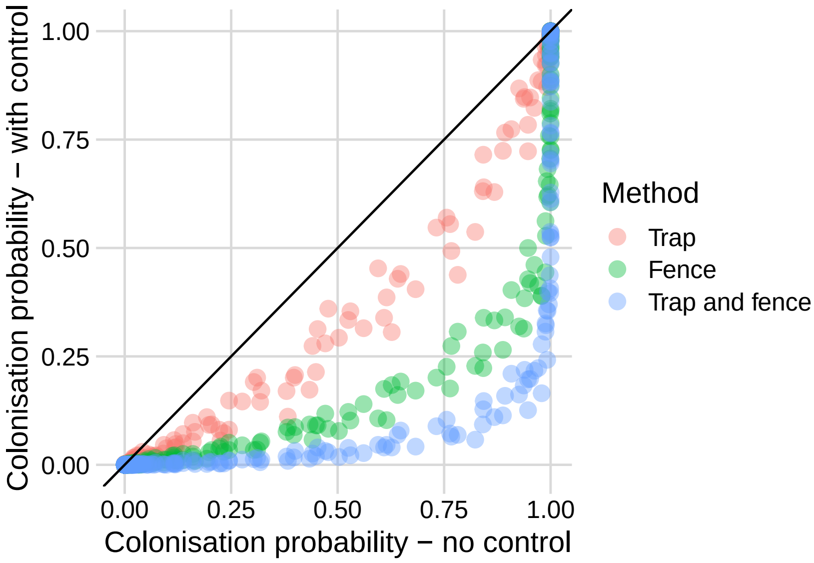


Figure 4.14: Trapping and fencing reduce colonisation probability to different extents. Each point represents a scenario with different parameters (capacity, distance and active days), and the axes represent the resulting colonisation probability without control and with control. In this graph, traps are deployed at low density (1 per 100m) and fences are repaired monthly.

or less), toads can easily spread between them despite the presence of control, and when water points are too far apart (more than 160 km apart), there is already little chance of spreading even without control (Figure 4.15).

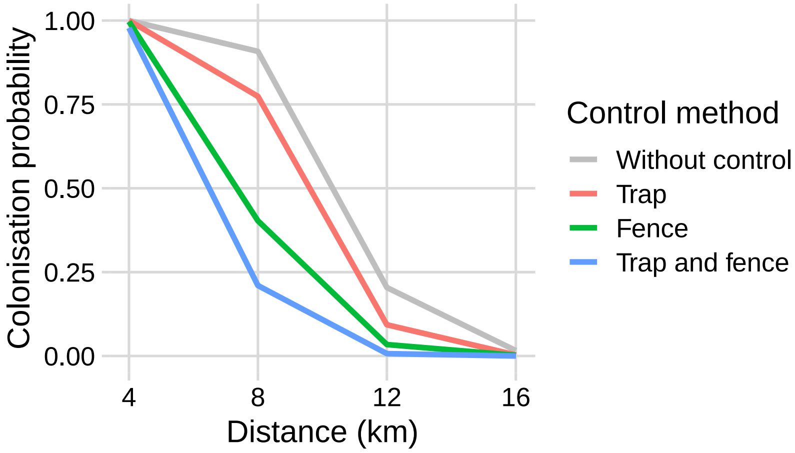


Figure 4.15: The impact of fencing and trapping is only noticeable at medium distance

## 4.6 Discussion of the microscale model

In this section, we summarise the results detailed in Section 4.5 and how they provide answers to the questions laid out at the beginning of the chapter (Section 4.1). We also discuss the contributions of the microscale model in the wider context of the project itself.

The model allows us to replicate individual movement of cane toads by fitting movement parameters to real-world data. This capacity is evident in the first experiment (Section 4.5.1) and is necessary in order to parameterise the model for use in other experiments. We found a range of values for an unknown model parameter (mean-angle-dev) that results in movement behaviour comparable to that recorded in field studies. Keeping in mind that we want to model the more dispersive individuals and avoid underestimating the spread of cane toads, we decide to use the lower bound of this range (20) for this parameter in subsequent experiments.

The first question we set out to answer with this model is: how likely is an uncolonised water point to be colonised by toads from another water point at a certain distance away? The results described in Section 4.5.2 give us a broad image as well as specific estimates on the spread of toads between water points and how this spread changes with variables such as the distance between water points, the number of active days in a wet season and the capacity of the source water point. This information allows us to answer the question both generally – a function that varies strongly with distance and active days, and quantitatively – for example, given 160 days with the right conditions and a capacity of 100 toads per day, toads' probability of colonising a water point is certain if it is within 6 km and extremely low if it is more than 14 km from where they emigrate.

The second question we set out to answer with this model is: to what extent does trapping and fencing impact this spread? The results described in Section 4.5.6 give us an answer: these methods reduce toads' spread only when the distance is more than 4 km; they often do not completely eliminate the probability of colonisation; and the impact of low-density trapping is likely to be insignificant. Finally, the model allows us to produce specific quantitative estimates of the impact on spread under some uncertainty due to unknown parameters. For example, at 160 active days, 100 capacity and distance of 8 km, the addition of a fence can reduce colonisation probability by approximately 50%.

The third question we set out to answer with this model is: how does the outcome change with different modelling approaches and under uncertainty in parameters? By running sensitivity analyses, we get a better idea about the impact of modelling approaches and parameter uncertainty on outcomes and thus are able to give an answer. For example, detection radius is one such unknown parameter and the results presented in Section 4.5.4 show that at short distances, the model can be very sensitive to variations in this parameter. Sensitivity analyses are especially relevant when modelling control methods, which often involves many unknown parameters. For example, the results in Section 4.5.5 show that a reduction in break chance could significantly improve a fence's effectiveness. Finally, knowing the range of outcomes also allows us to make better assumptions on model parameters.

Also relevant to the third question, the results in Section 4.5.3 show that modelling gender using gender-specific data can change the outcome significantly, especially when the difference between gender is large. This finding confirms our hypothesis that previous studies, by not requiring both genders for colonisation and not taking into account the difference in movement rate between genders, potentially overestimated the capability of cane toads to spread across water points.

In answering all the questions above, the microscale model constitutes one half of the multiscale model, and thus when integrated with the macroscale model, allows us to investigate how small-scale changes, such as varying water point capacity and control deployment specifics, can affect toad spread across a region. For example, the results in Section 4.5.2 and Section 4.5.6 illustrate the kind of data which can be used to parameterise the macroscale model, and the results in other experiments inform assumptions or models at larger scale. The next chapter is about the macroscale model, including a detailed description of how the two models are integrated.

# Chapter 5

# The macroscale model of spread and environment

## 5.1 Introduction

Invasive species control is specific to a geographical region – different landscapes might require different approaches to control. As such, in a model of control, representing the real landscape can help make more accurate estimates regarding control strategies. This landscape can be relatively much larger than the scale at which the invasive species is usually observed. Moreover, the impact of control programs often needs to be observed over a long time, often through many generations of the invasive species itself. In chapter 4, we argued that it is beneficial to represent the invasive species as individuals to study how changes at individual level affect spread dynamics. However, to apply this approach at a large spatial and temporal scale, as described above, is computationally challenging. Therefore, there is a need for a model of a larger scope in both space and time that can be integrated with an individual-scale model.

Specifically, we aim to construct a model with the purpose of answering the following questions: How long does it take for cane toads to spread to the Western end of the Kimberley-Pilbara corridor from the Eastern end? To what extent do control approaches – including exclusion from water points, trapping and corridor-fencing – impact this spread? Finally, how does the outcome change under uncertainty in parameters and environmental conditions?

The modelled system involves the spread of cane toads through a specific region in North-Western Australia, between the Kimberley and Pilbara regions, and the impact of control methods on this large-scale spread. Toads are already present in the Kimberley region and will make their way towards the Pilbara region. As mentioned in Section 2.1.3, due to the climate in this transitional region, cane toads rely heavily on artificial water points as sheltering and breeding sites. As a result, the coastal "corridor" of water points enables the spread of cane toads through the region and is central to any control effort that seeks to stop them. Control methods include exclusion, traps and a corridor-fence.

The model is an agent-based model, with water points represented as immobile, interacting agents. Toads are not represented either as individuals or populations – instead, their spread is marked by the colonisation status of water points. Colonised water points attempt to convert uncolonised water points in its range to a "colonised" state. Control methods are implemented at each water point – exclusion and traps – or at the links between them – as is the case with corridor-fencing. Excluded water points are not available for colonisation at all, but occasionally become available in a short period. Trapped water points have a reduced probability to be colonised and to colonise others. When a link is fenced, water points of both ends have a reduced probability to colonise each other. Finally, a control strategy is modelled by applying one or more control methods at a number of controlled water points in an area.

The rest of this chapter is structured into 6 sections, following a similar format to Chapter 4. Section 5.2 reviews common approaches in multiscale model integration and presents how we integrate the microscale results into our macroscale model. Section 5.3 reviews alternatives in modelling certain macroscale processes important to toad spread and presents our approach. This is followed by a detailed description of the macroscale model as implemented in Section 5.4. Next, the experiments run using the model are detailed in Section 5.5. The goals of these experiments include exploring uncertainty in the capacity of water points and in rainfall data, as well as making estimates of the macroscale spread of cane toads with and without control. The results are presented in section 5.6. Finally, Section 5.7 contains a discussion on the broader implications of the results and the model in the context of the project.

## 5.2 Integration in multiscale model

In this section, we review the approaches similar studies have taken in integrating models of different scales, and afterwards talk about our approach and the rationale behind our decision.

### 5.2.1 Potential approaches to integration

In a multiscale system consisting of two models, there are multiple approaches to integration. One approach involves the model of larger scale calling on the microscopic model to run simulations with certain initial states and return the results [16]. In this case, the two models are tightly coupled and the microscopic model is almost a submodel that is controlled and initiated on-demand by the model of larger scale. Conversely, the microscopic model can also be run first to supply the data unavailable at macroscopic level, which is only possible if the microscopic model itself is self-sufficient, or the space of initial states is simple enough to be exhaustively simulated. This approach has been employed in some previous cane toad studies, in which a microscopic model of toad movement is used to generate a dispersal kernel needed for a macroscopic model [80]. Finally, a multiscale system might incorporate a shared space where both models are run in parallel [86, 43]. This approach is only relevant in cases where both models exist independently and the integration only enables interaction between the scales or switches between them when necessary.

### 5.2.2 Our approach

#### Output as parameters

Our approach involves running the microscale model in advance and aggregating the outcomes to generate intermediate data, which are then used to parameterise the macroscale model. Due to the lack of data regarding spread between water points, our macroscale model relies heavily on microscale simulations. In addition, we intend to run a large number of macroscale simulations to explore different strategies in cane toad management, so running the microscale model every time we need to model toad movement between water points – i.e. many times per timestep – would be prohibitively expensive. Decoupling models and running them separately allow us to easily reuse simulation results as well as analyse them separately from the macroscale model.

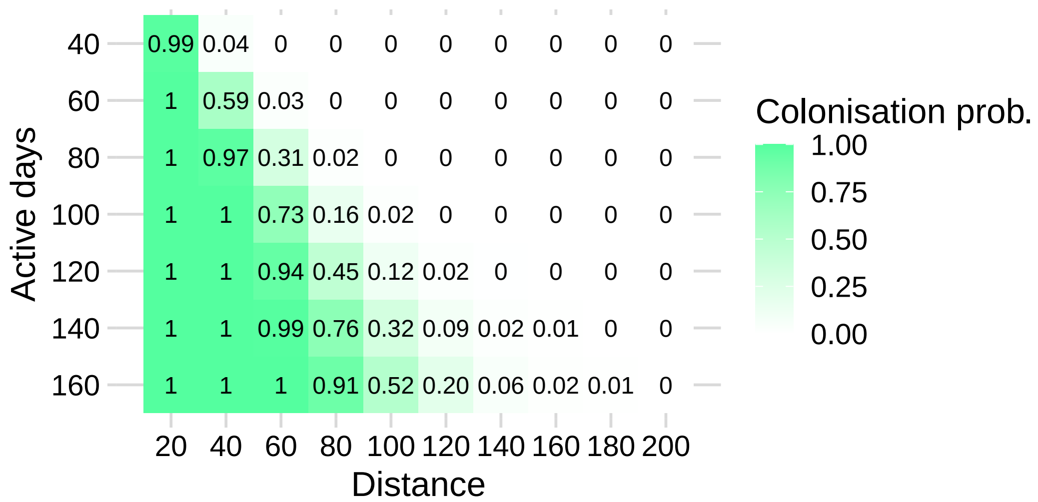


Figure 5.1: Function of colonisation probability as interface between models.
Only two variables, distance and active days, are present in this figure. Capacity ranges from 20 to 100. The values shown in the figure are from a capacity of 100 colonisers per day.

The intermediate data take the form of the probability that a colonised (source) water point successfully colonises an uncolonised water point (destination), which depends on variables of both water points such as the capacity of the source, the distance between them and the number of days which toads can move freely between them (Figure 5.1). The microscale model can be considered a multivariate blackbox function, and the intermediate data – aggregated from results of simulation runs with different sets of variables, such as those in Sections 4.5.2 and 4.5.6 – represent points that belong on the function surface, from which the function can be approximated. This approximated function serves as the main interface between the two models and its usage is described in more detail in the macroscale model description (Section 5.4).

#### Output to inform submodels

Besides serving as parameters for the macroscale model, the output of the microscale model is also used in the form of macroscale submodels. One such example is the relationship between capacity and distance. As mentioned in Section 4.5.2, linear variations in capacity have been found to have little impact on spread; instead, capacity correlates to spread in log scale. Due to the uncertainty in the capacity of water points and the need to explore the impact of this uncertainty, we need to simulate larger magnitudes of capacity. However, to simulate such a large number of agents in our agent-based microscale model would be too computationally demanding. Therefore, we decide to approximate the impact of larger capacities in the macroscale model itself, using the knowledge gained from microscale output. The exact approximation approach is presented in detail in the macroscale model description (Section 5.4.3).

Another example involves modelling the size of water points. Although the size of most water points in the dataset is unknown, some water points of a certain type – irrigation area – do have measurements of area. These irrigation areas are much larger in size than other types of water point such as tanks or dams, which potentially means that their capacity, as well as the chance of toads finding them, are relatively higher. To approximate the increased colonisation chance that comes with larger size, we use the results from the experiment with water detection radius (Section 4.5.4). The exact approximation approach is presented in detail in model description (Section 5.4).

## 5.3 Modelling macroscale processes

In this section, we go through some important processes that influence the spread of cane toads at macroscale: colonisation of water points, control methods and strategy, rainfall distribution and variation in water point capacity. With each process, we first review the approaches previous studies have taken in modelling it, and afterwards talk about our approach and the rationale behind our decision.

### 5.3.1 Colonisation of water points

Modelling the spread of cane toads through a large region is the first goal of the model, and is also a prerequisite before impact of control can be gauged. As mentioned in chapter 4, this spread emerges from several microscale processes. At a larger scale, however, the spread of cane toads occurs through one main process. Due to strong seasonal fluctuations in rainfall in the Kimberley-Pilbara corridor, the spread of cane toads through this region over many years is mostly centred around the colonisation of water points.

Previous models of toad spread resemble a point process model ([80, 75] and Section 2.3.1. In short, this method computes the number of toads arriving at a water point from all source water points and assumes it is colonised if this number reaches a value of 2 toads or more. However, this approach might not be suitable to model control methods which involve removing toads at the uncolonised water points, namely traps. By removing toads, there is no longer a clear link between the number of toads arriving at a water point and whether it is colonised or not – toads might be captured after arrival and fail to colonise the water point, or captured after having colonised the water point.

In our model, we adopt an approach similar to that described in the previous paragraph, in the sense that water points interact with each other and toads in the environment are not modelled. However, instead of transmitting colonisers, colonised water points directly affect uncolonised water points, turning them into "colonised" with a probability, with the assumption that toads from different water points colonise a new water point independently. It is akin to treating the cane toad invasion as an infectious disease, then modelling the transmission of the disease between hosts without modelling the pathogens. By no longer modelling the number of toads, this approach avoids the complexities and potential inconsistencies introduced by toad removal at uncolonised water points, as control methods directly impact the colonisation probability. This colonisation probability can be easily generated and provided by the microscale model.

In Section 5.5.1, we run experiments with default parameters and no control methods to estimate the time it takes for toads to colonise the region.

### 5.3.2 Control methods and strategy

Modelling the impact of control on the spread of toads is one of the main goals of the model. Control methods – exclusion, trapping and corridor-fencing – are modelled differently depending on the nature of the control method.

In previous models exploring the waterless barrier idea, exclusion is modelled as the removal of a water point from all interactions with other water points. In other words, it is treated as non-existent and does not contribute to the spread. The exclusion mechanism at each water point has a chance to fail in each generation, resulting in the water point being available again for colonisation and potentially contributing to spread for a small number of generations. Our model employs the same approach.

Other control methods, namely trapping and corridor-fencing, are modelled in the microscale model as microscale processes. Their impact on the larger scale of this model is reflected in the pairwise colonisation probability between water points. In the presence of traps or a corridor-fence, a different colonisation probability is used for computations.

A control strategy is modelled as the application of one or more control methods at a location (corridor-fencing) or at a number of water points (trapping and exclusion) in one particular area. This approach is similar to how previous studies modelled control [80, 75], although in those studies only one control method is considered. The model can then be used to explore the impact of different control strategies and find the control strategies that achieve the desired control outcome (Sections 5.5.2 and 5.5.3).

### 5.3.3 Rainfall distribution

As mentioned in Section 2.1.3, in a semi-arid region such as the Kimberley-Pilbara corridor, the amount of rainfall in wet seasons heavily influences the distance at which toads disperse. As such, the distribution of rainfall across space and time is therefore important in predicting the spread and the impact of control.

We assume cane toads are able to disperse three days following a rainfall event, an assumption consistent with previous studies [44, 27, 80]. Such days are defined in our model as active days, and the number of active days during an entire wet season impacts how far toads disperse between water points. We model the distribution of active days at each weather station using aggregated statistics from that station's data (Section 3.3.4) and draw from this distribution at each timestep. The number of active days at a water point is assumed to be equal to that at the closest station weather. In addition, to model periodic floods, we add uncharacteristically wet years every decade. During these years, the number of active days is higher than usual. We run sensitivity analyses on this wet-year mechanism in Section 5.5.5 to explore the robustness of control strategies in a wetter climate.

An alternative approach to generating weather from aggregated statistics involves applying the rainfall record to each timestep of the model, essentially simulating historical rainfall year-by-year [75]. However, for our project we decide the added value of implementing this approach does not justify the time cost. Moreover, generating the rainfall pattern (through active days) allows us to cover scenarios that did not occur in the past.

### 5.3.4 Variation in water point capacity

Although the typical capacity of water points is unknown, it can be assumed based on expert opinion and previous studies. However, the actual capacity might vary between water points, and the exact distribution of capacity in the landscape might impact the spread of cane toads and control strategies. We encode this uncertainty by drawing from a random distribution for capacity when initialising water points for each simulation, an approach used in previous studies. Moreover, in Section 5.5.4 we run sensitivity analysis on the mean capacity of water points, exploring scenarios in which it is significantly higher than assumed and how control strategies are affected.

## 5.4 Macroscale model description

In this section, we describe the macroscale model as implemented, following the ODD framework [33]. The model's components and parameters are explained in sufficient detail so that it can be replicated. This model is used to run the experiments in Section 5.5.

### 5.4.1 Overview

#### Purpose

This model is constructed with the purpose of estimating the spread of cane toads in the Kimberley-Pilbara corridor over many years and the impact of control strategies (the deployment of one or more control methods in an area) on this spread.

#### Entities and State variables

In the model, there are two types of agent – water points and weather stations. Water points are immobile agents characterised by their location, size, capacity, colonisation status and control status. Weather stations are immobile agents characterised by their location, the current number of active days and the statistics describing the distribution of active days at that station (mean, max, min and standard deviation).

Table 5.1: Attributes and variables of agents in macroscale model

| **Type of agent** | **Permanent attribute** | **State variable** |
|---|---|---|
| Water point | location, size, capacity, trapped?, fenced?, excluded? | colonised?, emitting?, exclusion-fail?, exclusion-fail-since |
| Weather station | location, mean-active-days, max-active-days, min-active-days, dev-active-days | active-days |

#### Scales

The model is spatially explicit. The modelled space represents the Kimberley-Pilbara corridor, approximately 400 km x 300 km in size. Simulations run in discrete time for at most 200 timesteps, each timestep indicating a year.

#### Process overview

Here we provide a brief summary of how important processes are scheduled in the model. Details regarding those processes can be found in Section 5.4.3.

At every timestep:

1. Weather stations generate active-days for the current timestep
2. Working exclusion mechanisms at water points have a chance to fail
3. Failed exclusion mechanisms get repaired after 2 timesteps
4. Water points colonised in previous timestep start to emit colonisers

5. Uncolonised water points are colonised with a probability by nearby emitting water points

### 5.4.2 Design concepts

The model revolves around the spread of cane toads by colonising water points in a region, the rainfall pattern which influences this spread, and control strategies aimed to deter this spread. Water points and weather stations are static, passive agents and do not have objectives. Interactions between agents include colonised water points attempting to colonise uncolonised water points, and weather stations determining rainfall patterns of nearby water points. As a whole, the collection of water points behaves like a network through which toads spread across the landscape. There is no sentient agent and thus no adaptation or learning in this model.

### 5.4.3 Details

#### Input

The model requires no input at runtime.

#### Initialisation

Here we provide details on how agents, model parameters and variables are initialised at the beginning of each simulation.

Water points are created from water point data (mentioned in Section 3.3.3), which contain the coordinates and type of each water point. If the water is an irrigation area, its capacity is set as the product of mean-capacity and its area in square kilometres. Otherwise, capacity is drawn from a Poisson distribution with a mean determined by mean-capacity. All variables concerning control are set to False. Most water points are set to be uncolonised and not emitting, except those in North-Eastern corner, which are set to colonised and emitting to simulate the invasion having reached the corridor. Links are created between water points that are close enough to colonise each other.

Weather stations are created from the aggregated water station data (mentioned in Section 3.3.4), which contain their location and statistics regarding the distribution of active days. The interval between wet years is set to 10 years by default.

Tables containing colonisation probability of water points are loaded from data (Section 5.2). These include one table of base spread without control and seven tables of spread under different controlled scenarios (fence, trap, fence and trap) and different intensity levels for each control method.

From a series of pre-generated locations evenly spaced along the corridor, at most one control location is active during each simulation. A number of water points closest to

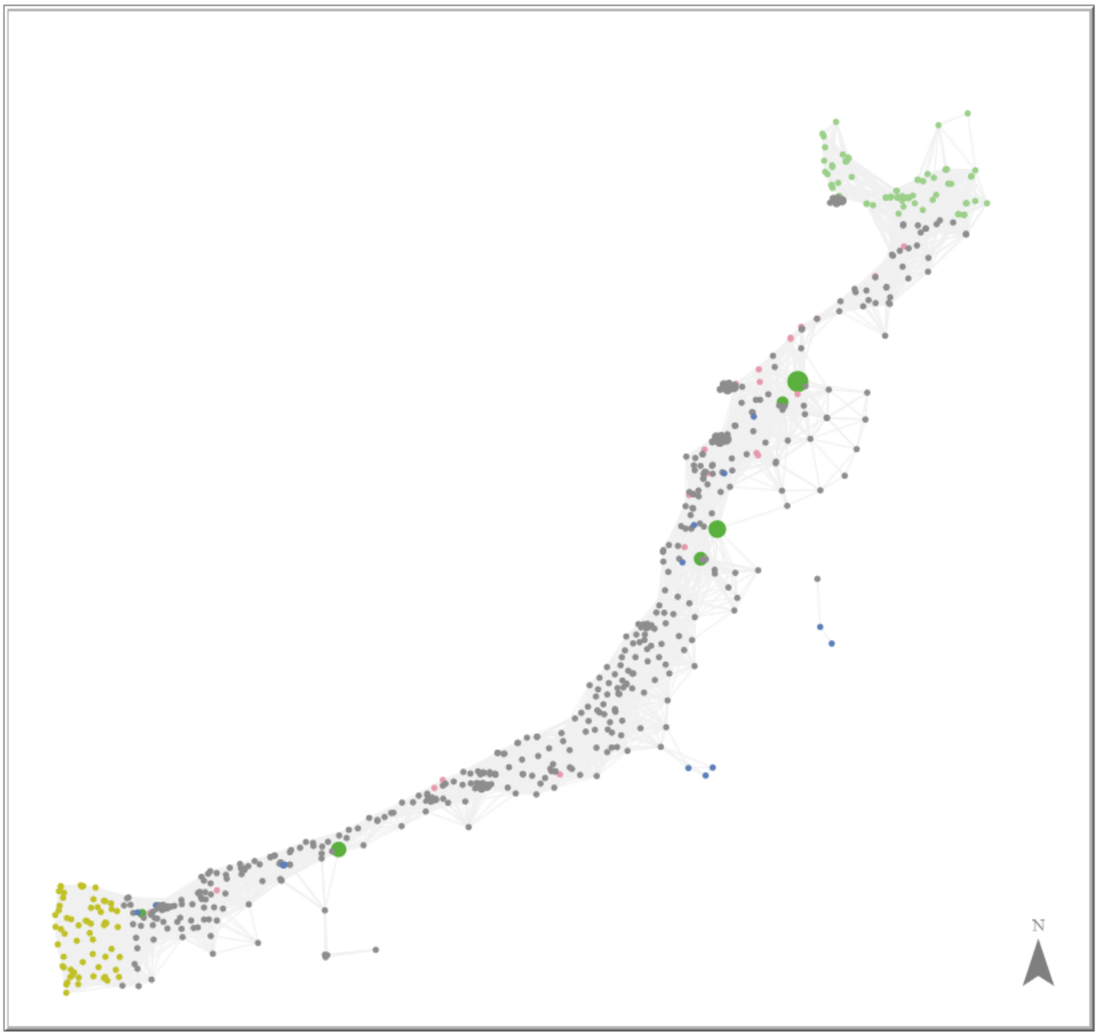


Figure 5.2: Model visualisation showing water points in the Kimberley-Pilbara corridor. The points represent water points, with the colour representing the type of each water point – blue for natural water points, red for dwellings, dark green for irrigation areas and light grey for other types of artificial water points. Water points are linked to nearby water points within colonisation distance. Grey cloud shapes are weather stations. At the beginning of the model, water points in the North-Eastern corners are initialised as colonised, marked visually by their light green colour. If the toads reach any of the water points in the South-Western corner, marked by their yellow colour, the region is considered to be completely colonised and the simulation ends.

this location are identified (no-controlled-wps), and control methods are enabled at those water points (excluded? and trapped?). If fencing is enabled, mark links (i.e. colonisation trajectories) that cross the corridor-fence (fenced? = true).

**Submodels**

Here we provide details regarding processes within the model, including:

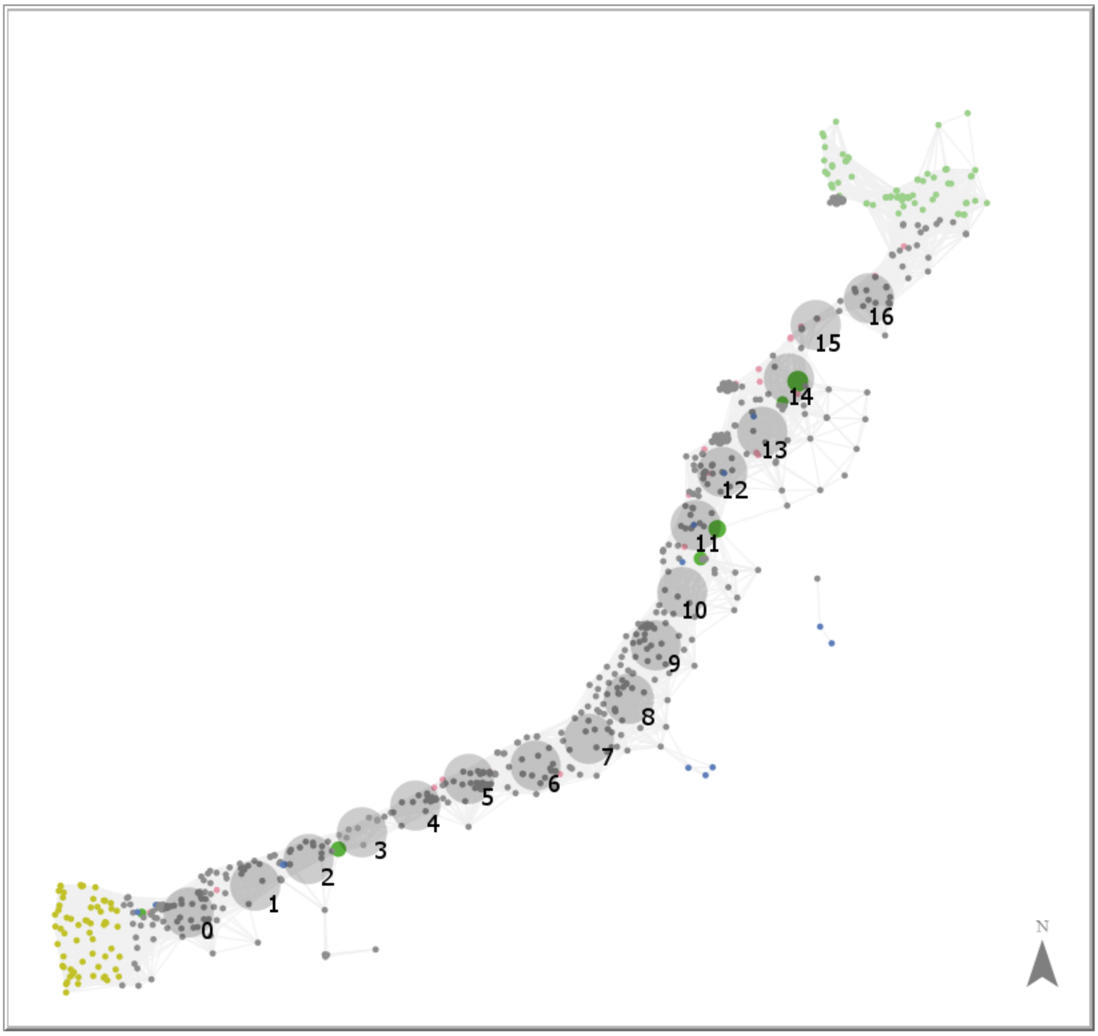


Figure 5.3: Control locations are evenly positioned along the corridor

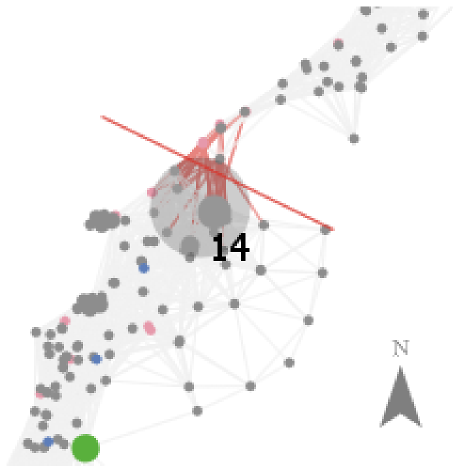


Figure 5.4: Corridor-fence affects all links that intersect it

Table 5.2: Model parameters and initial value of state variables

| | | | |
|---|---|---|---|
| | **Water points - global** | | |
| mean-capacity | 60 | exclusion-fail-prob | 0.05 |
| exclusion-repair-delay (years) | 2 | | |
| | **Water points** | | |
| location and type | from data | capacity | drawn from a Poisson distribution with mean mean-capacity |
| colonised? and emitting? | false | trapped? and excluded? | false |
| exclusion-fail? | false | exclusion-fail-since | -1 |
| | **Water point links** | | |
| fenced? | false | | |
| | **Weather stations - global** | | |
| wet-year-interval (years) | 10 | wet-year-extra-days | 14 |
| | **Weather stations** | | |
| location, mean-active-days, max-active-days, min-active-days, stddev-active-days | from data | active-days | 0 |
| | **Control - global** | | |
| no-controlled-wps | as per scenario | location | from data |
| active-control-loc | 0 - 16, as per scenario | exclusion? | as per scenario |
| trap | none / density 1 / density 2, as per scenario | fence | none / weekly repair / monthly repair, as per scenario |

- Active days: how the number of active days is generated and assigned to water points
- Colonisation probability: how colonisation probability is looked up and modified
- High capacity: how capacity above the limit is modelled by modifying the look-up distance
- Exclusion: how exclusion status of water points changes
- Trap and fence: how traps and the corridor-fence affect the colonisation process

**Weather stations and active days** At every timestep, the number of active days at a weather station is generated from a normal distribution described by its statistics (mean-active-days, max-active-days, min-active-days, stddev-active-days). However, if the current timestep falls on a wet year, a weather station's active-days is set at max-active-days + wet-year-extra-days instead. The number of active days (days in which toads are able to move) at a waterbody is modelled to be the same as the closest weather station. The number of active days of a colonisation trajectory – a directed edge between two water bodies – is equal to the number of active days at the destination.

**Colonisation probability** At every timestep, for each uncolonised water point, emitting water points in range attempt to colonise it one by one. Each source's probability of colonising a new water point depends on the source's capacity, the distance between them, as well as the number of active days of the uncolonised water point. Those three parameters determine where in the spread table the colonisation probability should be looked up. As the actual parameters in each case might fall between the values used to generate the spread table (Section 4.4.2), the colonisation probability for a set of parameters (capacity, distance, active-days) is computed using trilinear interpolation [5], a common approach to interpolate between 8 points in a 3-dimensional space. If a parameter is smaller than the lower bound of their range in the spread table, it is treated as the lowest. For example, water points less than 2 km away from each other have the same colonisation probability as if they are 2 km (lowest distance) away from each other.

If the water point has an area measurement, the probability is further augmented following the formula:

$$Pr_{colon}(..., radius) = Pr_{colon}(...) \cdot (1 + (radius/4)) \tag{5.1}$$

This formula is based on the relationship between water detection radius and colonisation probability in the microscale model (Section 4.5.4).

**High capacity** To approximate capacities that exceed the highest capacity in the spread table, when looking up colonisation probability in the spread table we compute an equivalent combination of capacity and distance. Specifically, the source's capacity is divided by 4 while distance is reduced by 2 km. This approximation is applied until capacity falls within the range of (20 - 100), and the resulting capacity and distance can then be used to look up the colonisation probability. This procedure is based on the relationship between capacity and distance (Section 4.5.2), specifically how a multiplication of capacity by 4 allows toads to spread approximately 2km) further with comparable probability. Formally:

$$Pr_{colon}(4 \cdot capacity, distance, ...) = Pr_{colon}(capacity, distance - 20, ...) \tag{5.2}$$

**Exclusion** Water points that are controlled with exclusion (excluded? is True) cannot be colonised. At every timestep, each of those water points has a chance (exclusion-failure-prob) to become available for colonisation (set exclusion-fail? to True). When this failure happens, the timestep is recorded (exclusion-fail-since), and after a number of timesteps (exclusion-repair-delay), the failure is reverted (set colonised?, emitting? and exclusion-fail? to False).

**Trap and fence** When a water point is attempting to colonise another, if the uncolonised water point is controlled with traps or the link between them is fenced, the colonisation probability is looked up in the corresponding spread table. The spread table is chosen based on the control status of the destination water point and the trajectory between the two water points following the rules described in Table 5.3.

Table 5.3: Spread table from control statuses of trajectory and destination

| **Trajectory - fenced?** | **Destination - trapped?** | **Spread table** |
|---|---|---|
| true | true | fence-trap |
| true | false | fence |
| false | true | trap |
| false | false | base |

## 5.5 Experiments on macroscale processes

In this section, we describe experiments run using the microscale model. The overall aim of these experiments is mainly to answer the application research questions, either by making predictions regarding the spread and control of cane toads in the studied region (Sections 5.5.1, 5.5.2 and 5.5.3) or by exploring how uncertainty affects such predictions (Sections 5.5.4 and 5.5.5). The results of these experiments are presented in Section 5.6.

### 5.5.1 Estimating toad spread in Kimberley-Pilbara corridor

This experiment estimates how long cane toads will take to spread through the Kimberley-Pilbara region. Parameters take default values described in Table 5.2 with no control methods. We run 2000 simulations and for each simulation observe the time it takes for the region to be colonised. The simulation results are aggregated to produce the mean and the range of outcomes. In addition, figures are produced to illustrate the behaviour of the model to the reader. The results of this experiment provide a baseline to compare against those of later experiments.

### 5.5.2 Evaluating different control methods and locations

This experiment explores the impact of deploying different control methods individually at various locations along the corridor. We run simulations similar to 5.4.1, however with one control method enabled at different locations. Specifically, we simulate 5 scenarios: exclusion, trapping at low density, trapping at high density, corridor-fencing with monthly maintenance, and corridor-fencing with weekly maintenance. For each scenario, the control location is varied between 17 pre-generated control locations running along the corridor. Moreover, the number of controlled water points ranges from 4 to 14. We run 1000 simulations for each combination and observe whether the region is colonised in 200 years. The results are aggregated to produce the probability of the region being colonised – we assume the region is well-protected from cane toads if this probability is less than 5%. In addition, we also measure simulation duration, which indicates the time it takes for the region to be colonised or the maximum value, 200 years, if the region remains uncolonised.

### 5.5.3 Estimating impact of combining multiple control methods

This experiment estimates the impact of control strategies in which several control methods are deployed. Specifically, we simulate 3 scenarios, each involving a unique combination of two control methods: corridor-fencing and trap, exclusion and corridor-fencing, and exclusion and trap. Moreover, we vary the effort in trapping and corridor-fencing: low / high density for trapping and monthly / weekly maintenance frequency for corridor-fencing. Similar to the previous experiment, the control location is varied between 17 pre-generated control locations running along the corridor and the number of controlled water points ranges from 4 to 14. We run 1000 simulations for each combination and observe whether the region is colonised in 200 years. The results are aggregated to produce the probability of the region being colonised.

### 5.5.4 Exploring sensitivity to capacity of water points

This experiment explores the sensitivity of the model with regard to the mean capacity of water points. As mentioned in Section 5.3.4, this parameter is unknown but potentially impactful, as it can enable toads to spread between water points further apart than predicted in the microscale level. We re-run the scenario to estimate toad spread with and without control methods (Sections 5.5.1, 5.5.2 and 5.5.3), while increasing the mean capacity of water points to explore the effect on spread and evaluate the robustness of control strategies. Specifically, mean capacity is set at 240 and 960 colonisers per day (i.e. default value, 60, multiplied by 4 and $4^2$). At the highest capacity of 960, the number of colonisers per generation is roughly $10^5$, closer to the assumption used in previous studies ([80] and B. Phillips, personal communication).

### 5.5.5 Predicting the impact of a wetter climate

This experiment explores the sensitivity of the model with regard to climatic conditions. As shown in Section 4.5.2, the number of active days in a wet season strongly influences colonisation probability between water points and can be similarly impactful on large-scale spread. Although this model input is informed by data, there is still a high degree of uncertainty due to climate change. We re-run the simulations to estimate toad spread with and without control methods (Sections 5.5.1, 5.5.2 and 5.5.3), while reducing the interval between wet years and increasing their intensity to explore the effect on spread and evaluate the robustness of control strategies. Specifically, wet-year-interval is set at 5 years instead of the default value of 10 years, and wet-year-extra-days is set at 28 days instead of the default value of 14 days.

## 5.6 Macroscale results

### 5.6.1 Estimating toad spread in Kimberley-Pilbara corridor

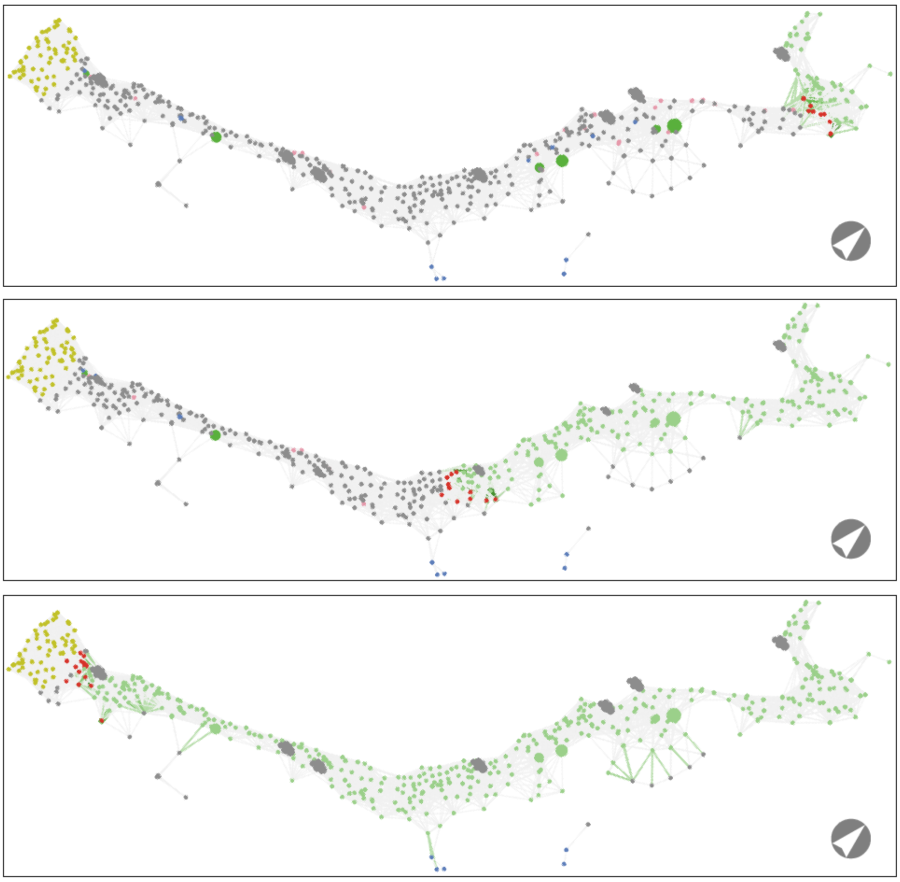

Figure 5.5: Toads spread towards South-Western side of the corridor.
T = 1, 45 and 90 from top to bottom. Images are rotated for presentation (North arrow at bottom right). Green links indicate toads spreading between colonised and uncolonised water points. Water points that become colonised in the current timestep – marked red in the model visualisation – do not emit toads (i.e. colonise others) until the next timestep.

According to our model, without any intervention, the Kimberley-Pilbara corridor will be colonised in 68 - 115 years. The mean estimated time is 86.7 years, with a relatively low standard deviation of 6.2 years.

### 5.6.2 Evaluating different control methods and locations

Between the three control methods, only exclusion can stop the invasion completely. When only exclusion is deployed, at some locations (locations 3, 4 and 15 in Figure 5.6), it takes as few as 9 controlled water points to achieve a region colonisation probability lower than 5%. Controlling more water points brings this probability down further while also making more locations viable (location 10, 14 and 16).

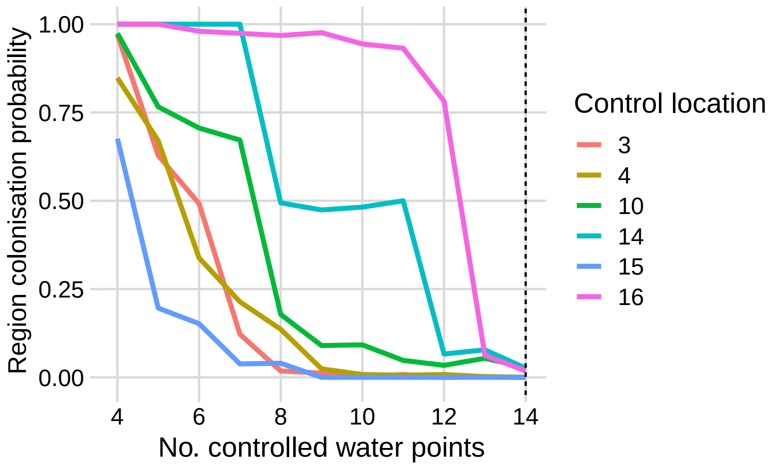


Figure 5.6: Removing a number of water points can potentially stop toads.
The coloured lines represent the control locations with low colonisation probability. All other control locations result in the colonisation of the region with near certainty (probability close to 1), even at a high number of controlled water points. Small fluctuations are due to stochastic processes.

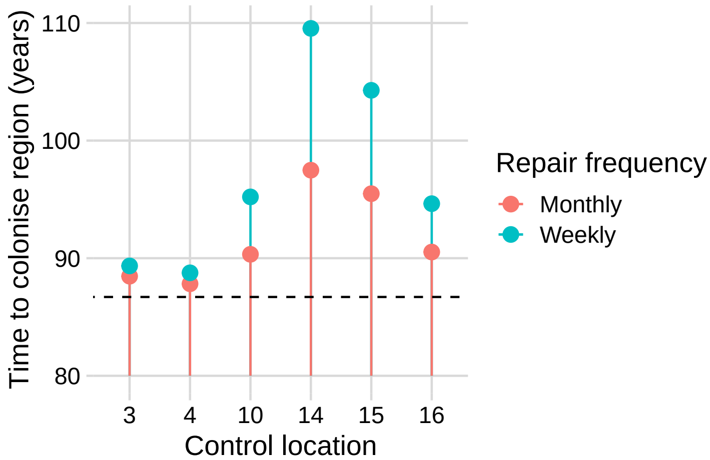


Figure 5.7: A corridor-fence can only slow the invasion without stopping it when deployed alone.
Only control locations 10, 14, 15 and 16 have noticeable impact – when deployed at other locations, the impact of a corridor-fence is minimal. Unlike other methods, one fence is deployed across the corridor and so its effectiveness does not scale with water points – only the location matters.

A corridor-fence and traps, when deployed by themselves, can only slow down the eventual colonisation of the region by a few years if deployed at the right location. Their impact is strongest at control locations 14 and 15; locations 3 and 4, while good for exclusion, are ineffective sites for a corridor-fence and traps. With monthly maintenance, corridor-fencing proves to be relatively more effective than trapping at low density. In some scenarios, fencing with monthly maintenance slows down the spread by more than 10 years (Figure 5.7), whereas the best outcome from low-density trapping is a 5-year increase (Figure 5.8).

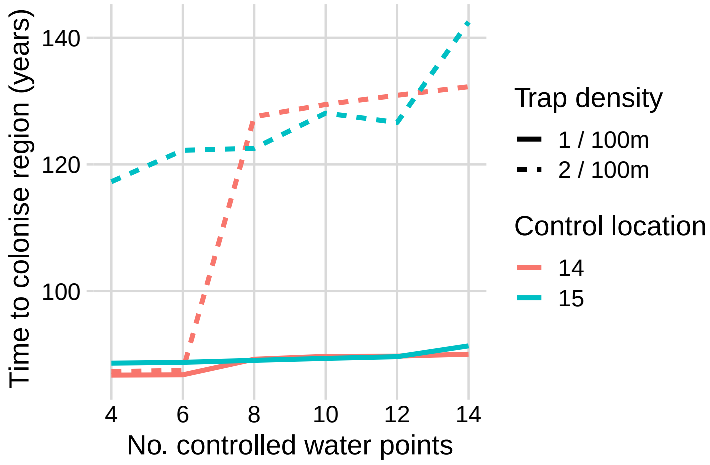


Figure 5.8: Traps can slow down the spread only when deployed densely.
Only control locations 14 and 15, shown in the graph, have noticeable impact – when deployed at other locations, traps' impact is minimal. Small fluctuations are due to stochastic processes.

Switching to weekly maintenance has a noticeable impact on the effectiveness of corridor-fencing, raising colonisation time by more than 20 years in some cases, but still does not stop toads from colonising the region. Increasing trap density to 2 per 100m makes trapping more effective compared to fencing, raising colonisation time by more than 30 years, although high-density trapping remains ineffective at stopping toads completely.

### 5.6.3 Estimating impact of combining multiple control methods

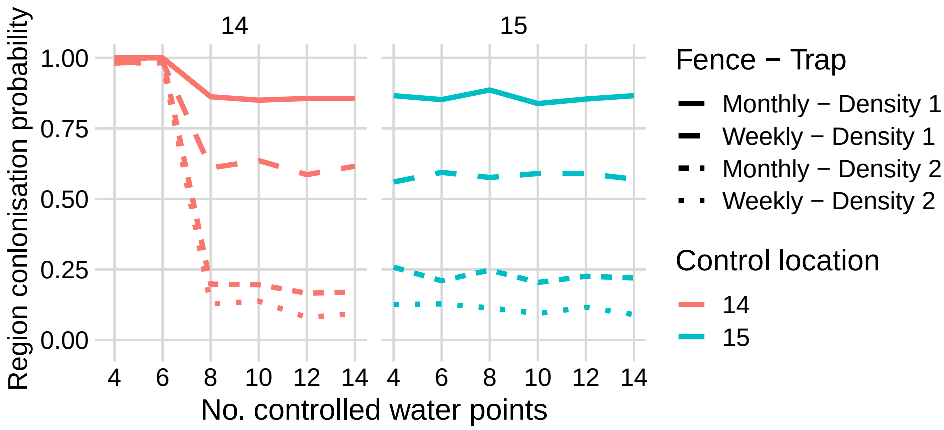


Figure 5.9: Fencing and high-density trapping together can hinder spread.
Only control locations 14 and 15 are shown here – other control locations are drastically less effective and so are not presented. Small fluctuations are due to stochastic processes.

Despite having no impact on region colonisation probability when deployed individually, corridor-fencing and trapping in conjunction provide some protection from colonisation, although this protection is still rather unreliable. With higher effort in both methods – weekly maintenance for the corridor-fence and high density for the traps – colonisation probability can be reduced to as low as 10% (Figure 5.9). While this outcome seems significant on paper, it does not mean the invasion is stopped in 90% of scenarios. In some simulations, although toads are unable to colonise the region within the time limit, they have already breached the control location and would go on to successfully colonise the region given more time. In such cases, combining a corridor-fence and traps only slows down the invasion. Without the removal of toads from colonised water points (which can be done with exclusion), water points that become colonised remain colonised, and it is only a matter of time before toads breach the controlled area.

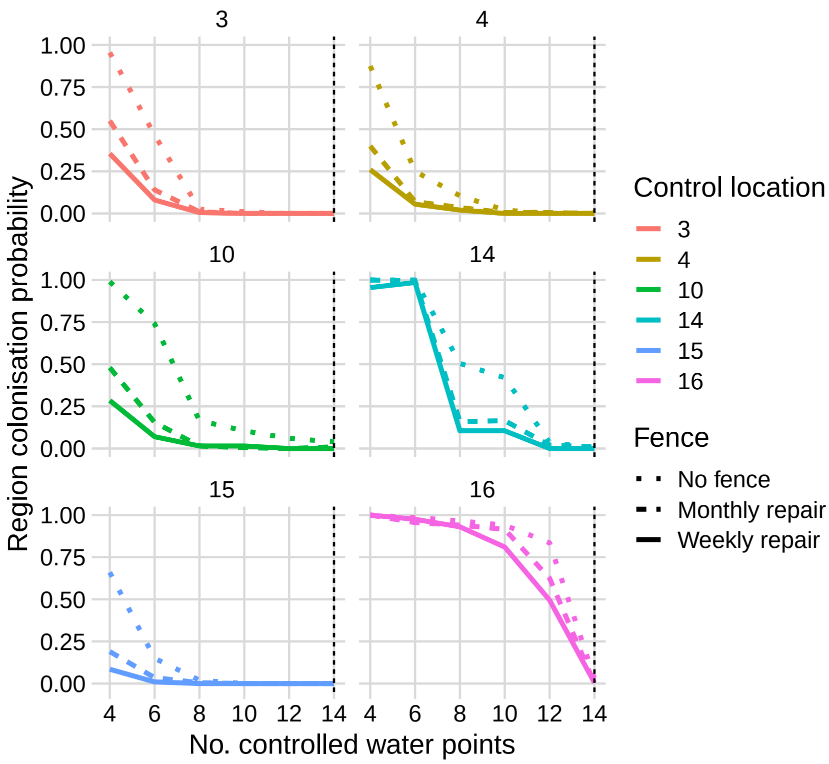


Figure 5.10: Supplementing exclusion with a corridor-fence improves overall effectiveness significantly in some cases

When used to supplement exclusion, corridor-fencing has a strong impact – from a different perspective, the removal of as few as 4 water points vastly improves the effectiveness of a corridor-fence (Figure 5.10). In certain scenarios, adding a corridor-fence is more effective at reducing the probability of the region being colonised compared to deploying exclusion at several more water points (control locations 10 and 14), and thus potentially allows securing the region (colonisation probability less than 0.05) with less water points controlled (control locations 10, 14, 15). It should also be noted that the difference between monthly and weekly maintenance is noticeable but much less significant compared to that between no-fence and monthly-repaired fence scenarios.

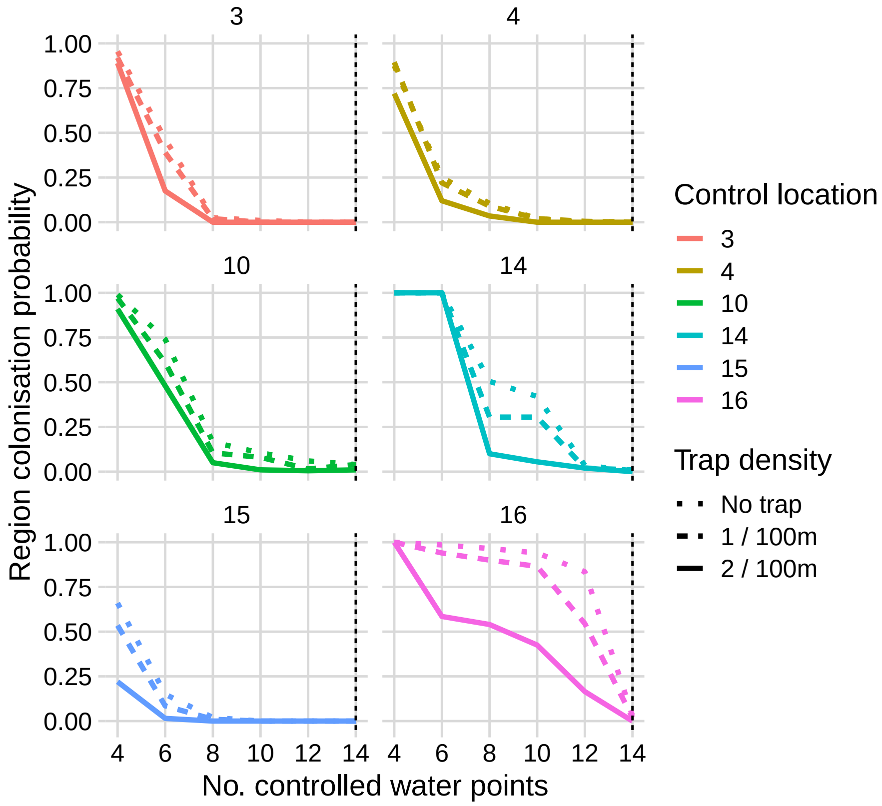


Figure 5.11: Supplementing exclusion with high-density traps improves overall effectiveness significantly in some cases

Supplementing exclusion with trapping also performs better than exclusion alone, although the improvement is often less than that of corridor-fencing. Specifically, unlike corridor-fencing, traps do not contribute significantly when a low number of water points (less than 8) are controlled (Figure 5.11). One exception is control location 16, where from only 6 controlled water points the addition of traps reduces region colonisation probability by almost 50%. In contrast, corridor-fencing performs poorly in this control location, barely influencing colonisation probability compared to no-fence scenarios, which suggests that different control methods might be better suited for different control locations. Finally, trapping only shows meaningful impact with higher density (2 traps / 100m).

### 5.6.4 Exploring sensitivity to capacity of water points

Increasing the mean capacity drastically reduces the expected colonisation time. Specifically, when mean capacity of water points is assumed to be 240 toads per day, according to the results the region is colonised in 47 - 70 years, and in 56.7 years on average. For the highest assumption of capacity (960 toads per day), this range is reduced further to 31 - 40 years, with the average time being 35.6 years.

A larger mean capacity allows toads to spread further than before and renders many

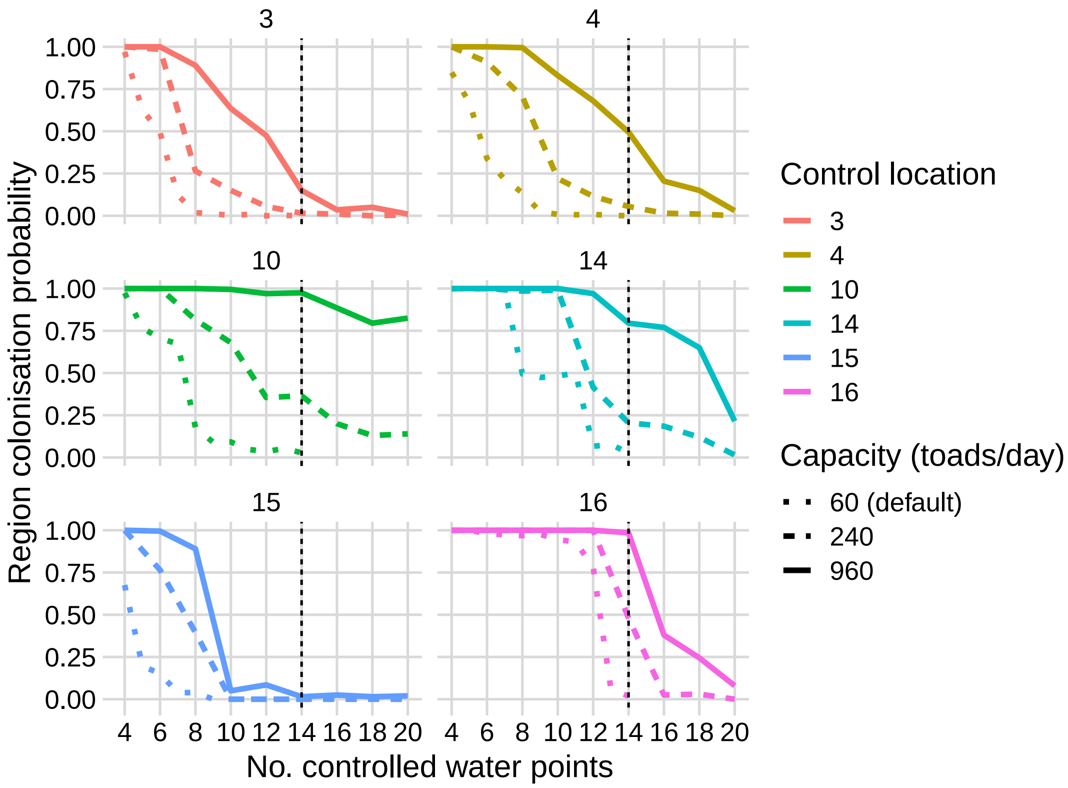


Figure 5.12: In exclusion-only scenarios, higher capacity leads to drastic changes in outcome. The coloured lines represent colonisation probability when exclusion is deployed alone; different types of line represent different assumptions about capacity. Small fluctuations are due to stochastic processes.

control strategies ineffective. Some control locations are more sensitive to this change than others and become ineffective at containing the invasion under the new assumptions. Specifically, although controlling 14 water points with exclusion alone at locations 10, 14 and 16 can contain the spread of toads through the region under the default value for capacity, with the highest assumption for capacity these strategies now almost always result in colonisation (Figure 5.12). Control location 15 is the most robust, with the region still protected from colonisation (colonisation probability less than 5%) even with the highest assumption of capacity, given that 14 water points are controlled. Finally, in scenarios where more water points are excluded to compensate (up to 20 from 14 water points), many control locations become viable again (locations 3, 4 and 16), while a few locations remain ineffective regardless (location 10 and 14).

Strategies that combine exclusion and another control method are also less effective in high-capacity scenarios. However, in many cases they are more robust compared to exclusion-only, resulting in less abrupt reductions in effectiveness (Figure 5.13). Specifically, when high-density traps are deployed together with exclusion, control locations 10 and 16 only result in colonisation in approximately 50% to 60% of the simulations under the highest value of capacity (instead of 100%, as is the case with exclusion-only), and this figure is 30%

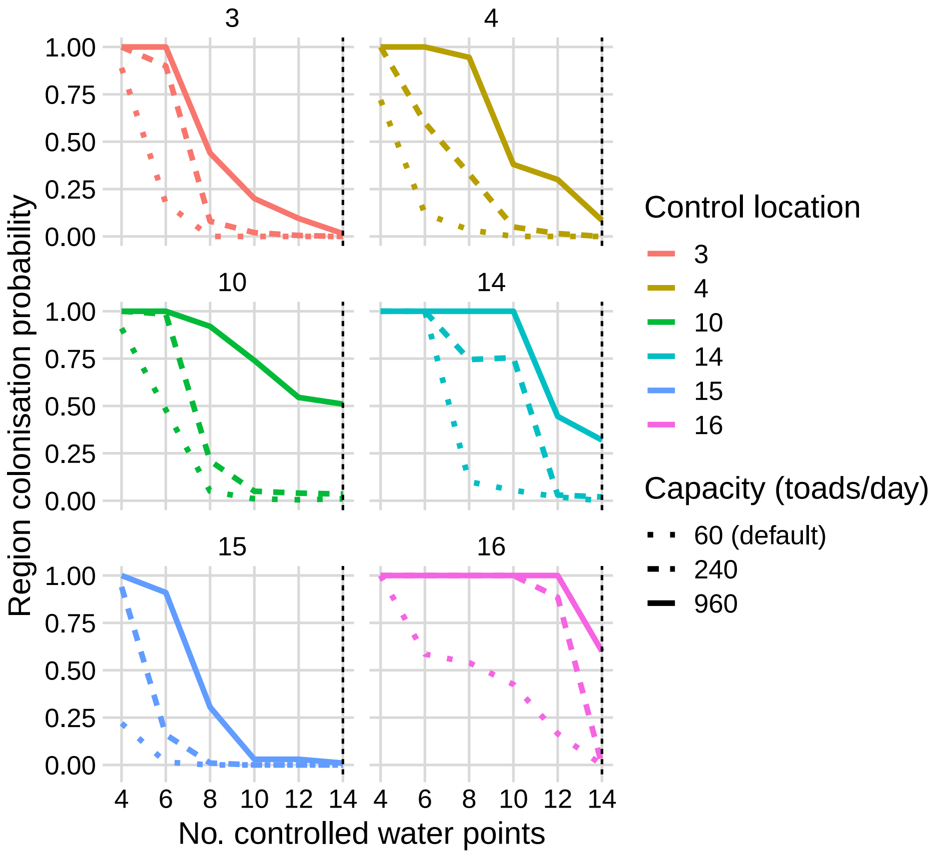


Figure 5.13: Scenarios which supplement exclusion with traps are relatively more robust to an increase in capacity.
The colored lines represent colonisation probability under a combination of exclusion and high-density trapping; dotted lines are the results under default assumptions, and solid lines are the results under higher assumption of capacity.

for control location 14 (instead of 75% with exclusion-only). Moreover, locations 3 and 4 experience noticeably less change and remain reasonably effective (colonisation probability less than 5% for 3 and less than 10% for 4). When capacity is only increased to 240 instead of 960 toads per day, all control locations remain effective at stopping toads from colonising the region. The combination of exclusion and a weekly-maintained corridor-fence performs similarly, with slightly higher colonisation probability under high-capacity assumption in some locations.

### 5.6.5 Predicting the impact of a wetter climate

Wetter climate can speed up the spread of cane toads to a small extent. When wet years occur twice as often and with stronger impact, toads can colonise the corridor in a minimum of 62 years. The expected colonisation time is 74.4 years, with a deviation of 4.2 years. The longest toads can take to colonise the region in a wetter-climate simulation is 90 years.

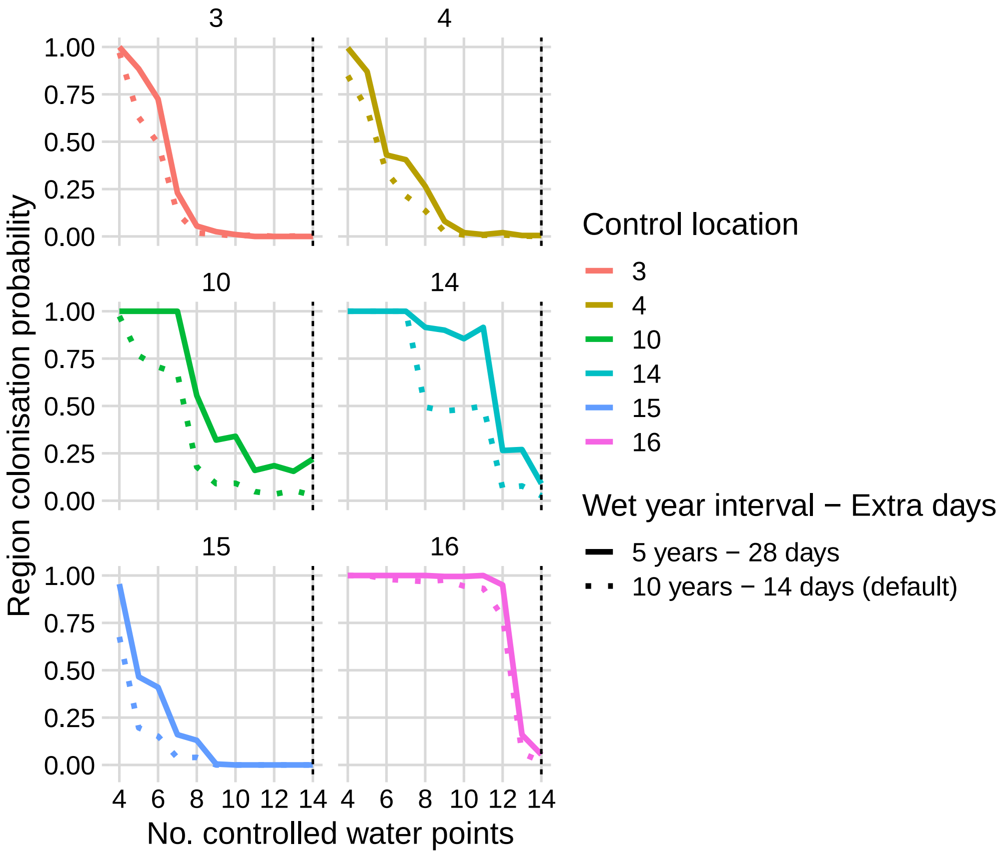


Figure 5.14: Most control locations remain reasonably effective under wetter climate with exclusion only. Small fluctuations are due to stochastic processes.

Similarly, wetter climate slightly reduces the effectiveness of control strategies. Most control locations remain reasonably effective (colonisation probability less than 25%), even with exclusion as the only control method deployed (Figure 5.14). However, some locations are affected more than others – specifically, the probability of colonisation increased to almost 25% for location 10 and approximately 10% for locations 14 and 16. When exclusion is combined with another control method, all control locations are more resistant to changes to climate and remain viable with 14 controlled water points (less than 2% colonisation probability, Figure 5.15).

## 5.7 Discussion of the macroscale model

In this section, we summarise the results detailed in the previous section and how they provide answers to the questions laid out at the beginning of the chapter (Section 5.1). We also discuss the contributions of the macroscale model in the wider context of the project itself.

The first question we set out to answer with this model is: how long does it take for

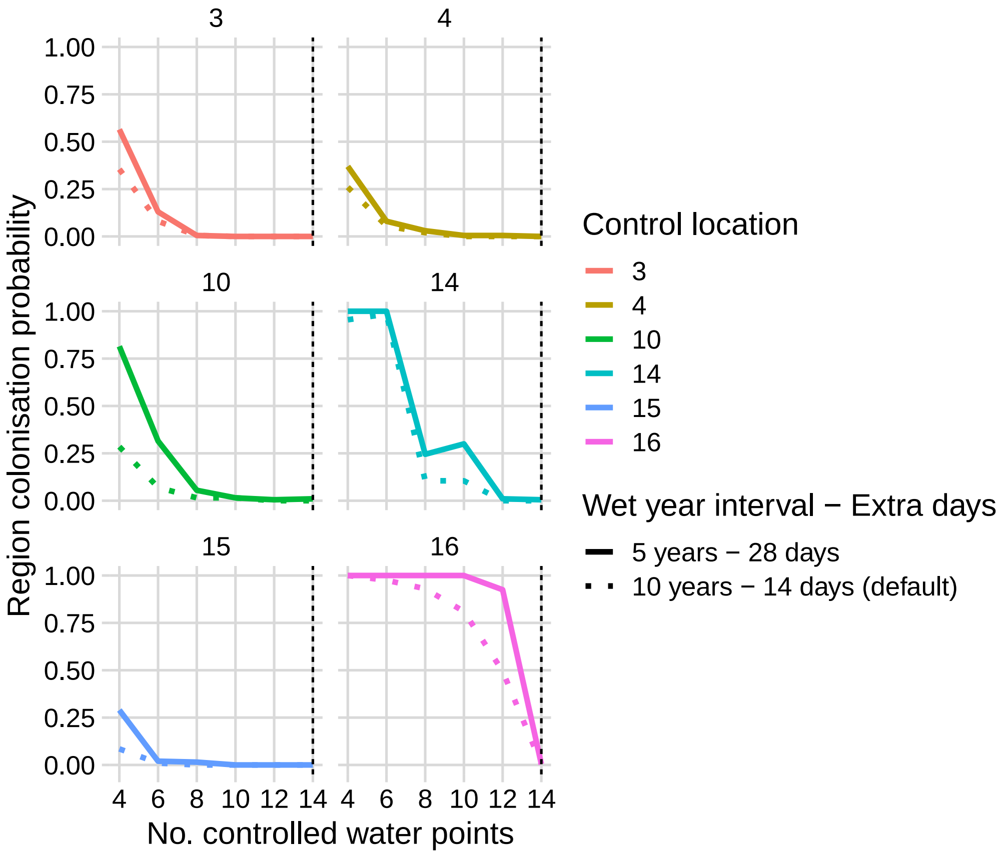


Figure 5.15: Supplementing exclusion with a corridor-fence reduces the impact of wetter climatic conditions. Small fluctuations are due to stochastic processes.

cane toads to spread to the Western end of the Kimberley-Pilbara corridor from the Eastern end? Our model predicts the colonisation of the Kimberley-Pilbara region in approximately 87 years (Section 5.6.1). At the soonest, toads will take 68 years to colonise the region. Furthermore, a low standard deviation means large variations across simulation runs are relatively uncommon, indicating stochasticity will not play a big part in the toads' spread.

The second question we set out to answer with this model is: to what extent does control approaches – including exclusion from water points, trapping and corridor-wide fencing – impact this spread? The results presented in Sections 5.6.2 and 5.6.3 allow us to answer this question. In our model, exclusion is generally the most effective as a control method, able to stop toads completely when deployed alone. Traps and corridor-fencing cannot stop the spread of toads; however, when deployed alongside exclusion, they can improve the effectiveness of the barrier and help achieve the target colonisation probability with less controlled water points.

The third and last question we set out to answer with this model is: how does the outcome change under uncertainty in parameters and environmental conditions? The results of sensitivity analyses on mean capacity and wetter climate in Sections 5.6.4 and 5.6.5 allow us to answer this question. Generally, a wetter climate, which allows toads more time to disperse between dry seasons, does slightly speed up the invasion in no-control scenarios but has a low impact on the outcome when control is applied. On the other hand, if the capacity of water points is many times larger than assumed, toads will spread across the region much faster and many control strategies, despite being adequate under current assumptions, will become ineffective. Along the corridor, there are control locations that are more sensitive to an increase in capacity than others. This sensitivity can be reduced by either combining exclusion with another control method such as trapping or corridor-fencing, or proactively employing exclusion at many more water points than needed.

In answering all the questions above, the macroscale model allows us to make useful estimates and comparisons regarding the spread and the control of cane toads in the Kimberley-Pilbara region. Moreover, it provides a tool to plan for uncertainty and change in climate. In the context of the project, together with the microscale model, it allows us to finally answer the research questions of the entire project regarding both cane toad control and modelling. In the next chapter, the answers to these research questions are presented, together with an overall evaluation of our multiscale model system.

# Chapter 6

# Discussion

In this chapter, we present our answers to the research questions of the project as well as any relevant findings from the experimental results, and discuss their implications in the fields of modelling and cane toad control. There are two research questions, each regarding one domain. In the application domain of cane toad control, we ask: what is the large-scale impact of trapping and corridor-fencing on the spread of cane toads in the Kimberley-Pilbara corridor, especially when combined with the waterless barrier? In the computation domain of modelling, we ask: how to effectively represent a large number of agents on a relatively large spatiotemporal scale while still capturing important details of individual behaviour? The application-domain question is answered in Section 6.1 by addressing smaller questions in a step-wise manner. In Section 6.2, we summarise our solution to the computation domain question and evaluate the strengths and limitations of our model with respect to answering the research questions as well as meeting the modelling aims set out in Section 3.1. Finally, we summarise the contributions and future directions in the form of a conclusion in Section 6.4.

## 6.1 The spread and control of cane toads

In this section, we present our findings regarding toad spread and control in the Kimberley-Pilbara corridor, which correspond to the three sub-questions regarding the application domain we formulated in Section 2.4.2:

1. Without intervention, how long will it take for cane toads to colonise the Kimberley-Pilbara corridor?

2. How does each control method (trapping, corridor-fencing, and exclusion), when employed individually, impact the spread of cane toads in the Kimberley-Pilbara corridor?

3. How does combining control methods impact the spread of cane toads in the Kimberley-Pilbara corridor, compared to employing them individually?

### 6.1.1 Spread without intervention

The first sub-question regarding the application domain is: without intervention, how long will it take for cane toads to colonise the Kimberley-Pilbara corridor? According to our model, toads will colonise the entire region and reach the South-Western end in approximately 87 years (Section 5.6.1), with 68 years being the earliest. Although small variations in capacity of water point do not have a significant impact (Section 4.5.2), significantly larger capacity can shorten the colonisation time drastically, with the region being colonised in 35.6 years on average (Section 5.6.4). Wetter climate also speeds up the spread through the region, although the difference is much smaller (Section 5.6.5).

Compared to previous studies [80, 75], our predictions indicate a much slower spread through the region. One potential reason is the inclusion of gender in our model and the large gap in movement rate between male and female cane toads. Moreover, our assumption regarding the typical capacity of water points (between $10^3$ and $10^4$ per year) is lower than that of previous studies (around $10^5$ and $10^6$ per year, [80] and B. Phillips, personal communication) – when mean capacity of water points is assumed at a comparable level, our model produces outcomes that are close to predictions of previous studies. The large gap between the predictions under different capacity assumptions highlights the need for future studies to narrow down the range of emigration rate of cane toads from water points, which would reduce a major source of uncertainty and allow models to make better estimates.

### 6.1.2 The effectiveness of control methods

The second sub-question regarding the application domain is: how does each control method, when employed individually, impact the spread of cane toads in the Kimberley-Pilbara corridor? According to our model, exclusion is clearly the most effective control method, able to stop the spread entirely, while trapping and corridor-fencing only slow it down and have little impact on colonisation probability. The inability to stop toads at large scale can be attributed to the ineffectiveness of fences and traps at short distances (Section 4.5.6) and the distribution of water points in the Kimberley-Pilbara corridor, with sections of the corridor consistently within 8 km of each other. In practice, traps only catch a portion of population and hence can allow some toads to survive and colonise a water point; meanwhile, a fence is likely to be damaged at some point and breached by some toads, and once a water point on the other side is colonised the fence is rendered useless. Compared to previous studies [80, 75], strategies that employ exclusion require managing less water points, most likely due to the slower spread discussed in Section 6.1.1. However, the optimal locations remain roughly similar, with best locations being at two ends of the corridor (locations 3 and 15 in this study). Finally, it should be noted that exclusion, when deployed alone, can be sensitive to changes in climate and capacity as shown in Sections 5.6.4 and 5.6.5. Therefore, it is advised to proactively account for this uncertainty by either supplementing exclusion with other methods or excluding toads from more water points than needed. The exact number of extra water points to control can vary depending on the location and the anticipated scenarios.

Although fences and traps are much less effective, we make several findings about them that might be of interest when considering those methods. Firstly, experiments with traps inform us that at low density traps have no significant impact (Sections 4.5.6 and 5.6.2), thus a higher density (i.e. 2 per 100m) should be considered to make a noticeable impact with traps. In practice, equivalent impact can also be achieved by a more effective trap design or supplementing traps with hand-collection. On a different note, we found that when trapping to prevent colonisation, traps that capture more males are more effective. This finding can be an important insight from an ecology point of view and worth investigating further, as it contradicts the usual tactic of prioritising females often employed in suppression trapping. Finally, fences can be much more effective if a break probability of less than 0.5% per day per section can be guaranteed, potentially by using a robust material. Experiments in fence variables inform us of the trade-off in break chance and repair interval (Section 4.5.5), and this information can help managers determine the suitable repair frequency to compensate for the level of robustness of the fence, given a target outcome and the relative costs of an improved fence and labour for maintenance.

### 6.1.3 Impact of combining control methods

The third sub-question regarding the application domain is: how does combining control methods impact the spread of cane toads in the Kimberley-Pilbara corridor, compared to employing them individually? Under the assumptions made in this model regarding fence durability, combining a corridor-fence and traps is not enough to reliably stop toads from colonising the region, due to the same reasons given in Section 6.1.2. However, when combined with exclusion, trapping and corridor-fencing are more effective and can reduce colonisation probability to different degrees (Section 5.6.3). Their increased effectiveness can be attributed to the "mostly waterless zone" created by excluding a number of water points, which results in the toad's increased reliance on long-distance spread to "hop" through this zone and colonise the entire region. The impact of employing a corridor-fence or traps alongside exclusion is even more noticeable in hypothetical scenarios involving wetter climate or higher capacity of water points – according to the results in Sections 5.6.4 and 5.6.5, a combined strategy is much more robust to such changes and remains relatively effective.

In many cases, the impact of adding a corridor-fence or traps to an exclusion-only strategy is comparable to the impact of excluding more water points. However, in practice some water points cannot be controlled for different reasons [75] – such as the nature of the water point or the cooperation of landowners – and in such cases, supplementing exclusion with another control method such as trapping or corridor-fencing remains a strong alternative.

## 6.2 Evaluation of methodology

Modelling cane toad control in the Kimberley-Pilbara region posed two challenges. Firstly, there are no data on large-scale spread and control in a similar region, so we needed to model toads at an individual scale where data are more available. Secondly, we needed to make predictions regarding impact of control strategies, which span a large spatiotemporal scale. We addressed these challenges in methodology by constructing a multiscale agent-based model consisting of a microscale model, which makes use of individual-level data, and a macroscale model, which represents spread and control at a larger scale. The two models were integrated by using simulation results of the microscale model to parameterise the macroscale model.

We assess this multiscale design, first as a tool to answer the application research question (Section 2.4.2) and then as a solution to the computation research question (Section 2.4.1). In particular, we assess the impact of the multiscale design and integration of two models, as well as modelling decisions within each model, on the capability of our model to meet the modelling aims set out in Section 3.1 and provide answers to the research questions.

### 6.2.1 A tool to model cane toad control

Our multiscale model achieves the modelling aims set out in Section 3.1. As demonstrated in Sections 5.6.1, 5.6.2 and 5.6.3, our model is capable of making estimates regarding the spread and control of cane toads in the Kimberley-Pilbara region. Furthermore, our model can help quantify the impact of uncertainty in parameters and data on the outcome, as demonstrated in Sections 5.6.4 and 5.6.5. Most importantly, the microscale model allows us to utilise small-scale data, such as movement and trap data (Sections 3.3.1 and 3.3.2), and informs multiple submodels in the macroscale model (Section 5.4.3). Incorporating more data reduces the number of assumptions we need to make, resulting in the entire model being more grounded and ecologically sound.

In addition, our model proves to be a useful tool for policy-makers and stakeholders to investigate the control of cane toads. Firstly, it allows them to explore what-if scenarios or actual changes, including and beyond those mentioned in this report. For example, our model can be used to estimate the impact of constructing new water points in the region on toad control by simply modifying the water point dataset, or to explore other variations in control methods such as different layouts for traps and fences. Moreover, it also provides insight regarding control methods, as discussed in Section 6.1 – one example is the ineffectiveness of traps when deployed at low density. Finally, with minor modifications, our model can potentially be used to explore the impact of constraints in control regimes, such as when water points of certain types cannot be excluded from toads.

Beyond cane toads, the model is also suitable to represent the spread and control of other invasive species with similar characteristics, such as a strongly seasonal dispersal cycle and a heavy reliance on habitat patches. The multiscale design even facilitates the adaptation of the model to a different invasive species. For example, the spread of another invasive species might rely on similar macroscale processes such as climate conditions and distribution of habitat patches, despite the individuals of that species having different characteristics and behaviours from cane toads. In that case, a new microscale model can be constructed, and the simulation results of this new model can still be used as parameters in the existing macroscale model to make predictions about the spread and control of that species in a real landscape.

### 6.2.2 A solution to modelling large number of agents with individual-level behaviour

Our solution involves a system of two models – a microscale model and a macroscale model. The microscale model represents microscopic processes on a small spatiotemporal scale using microscopic data – such as movement, colonisation and local control. Its purpose is to generate intermediate data – in this case the spread of toads between water points. Parameterised with these intermediate data, the macroscale model represents macroscopic processes happening on a large spatiotemporal scale – such as spread, region control and rainfall pattern. The macroscale model allows us to make predictions about such macroscopic processes – the spread and management of cane toads in the Kimberley-Pilbara region – and thus answer the application research questions.

As mentioned in Section 5.2, another common approach to integration in multiscale models is by incorporating the microscale model as a component of the macroscale model. In this approach, the macroscale model invokes the microscale model on-demand to run simulations from one or several initial states. In our context of modelling cane toad control, this approach would involve running a simulation in the microscale model every time toad movement is needed, or every time a water point might be colonised by toads from another nearby water point. We highlight the computational advantages of our approach by comparing it against this approach.

The first part of the research question involves the ability to represent a large number of agents on a large scale. Our solution achieves this goal through two mechanisms: the reuse of the microscale model's results across macroscale simulations, and the approximation of the integration function – colonisation probability (described in Sections 5.2 and 5.4.3). Specifically, our solution reduces the number of the microscale simulations needed by a factor of $10^3$. Therefore, we conclude that our solution achieves the first part of the research question satisfactorily. However, the level of effectiveness is dependent on the nature of the system we are modelling. The impact of each mechanism is explained in the next two paragraphs.

On one hand, reusing microscale results across macroscale simulations helps us avoid re-running the microscale model multiple times during a macroscale simulation. In our modelling context, the main process simulated in the microscale model (i.e. the colonisation of water points) are essential for the macroscale model (i.e. spread and control in the Kimberley-Pilbara region), and this process occurs a large number of times during each simulation of the macroscale model – approximately $10^3$ times. Moreover, we need to run a large number of macroscale simulations (i.e. comparing different control strategies and hypothetical scenarios) – in our case, we run $6{\cdot}10^5$ macroscale simulations in total. If microscale results are not reused and the microscale model is run on-demand, the number of microscale simulations needed would be a product of the number of macroscale simulations and the number of times the colonisation process occurs in a simulation (roughly $6{\cdot}10^8$), which would take a prohibitively long amount of time. A similar amount of computation would be required if the two models were not separated and microscale processes were run alongside macroscale processes. With our approach of running the microscale model in advance and reusing the results, we only need to run $4{\cdot}10^5$ microscale simulations in total for data-generation (experiments described in Sections 4.4.2 and 4.4.6). It should be noted that this approach, while avoiding re-running the microscale model multiple times, requires us to generate data for the entire parameter space in advance.

Covering the entire parameter space would be either computationally expensive, if the parameter is discrete, or downright impossible, if the parameter is continuous. To avoid this problem, we run microscale simulations with parameters taking uniformly-spaced, sparse values in a grid-like manner (described in Section 4.4.2 and illustrated in Table 5.1), then approximate the function in between those points (details in Section 5.4.3). With discrete parameters (i.e. active days and water point capacity), our approximation scheme reduces the number of microscale simulations needed by a factor of 20 for each parameters (thus $4{\cdot}10^2$ for both discrete parameters). With continuous parameters (i.e. distance between water points), approximation is always required. Although approximation comes at a cost of accuracy in the approximated function, the results in Section 4.5.2 show that the function of colonisation probability can be approximated without heavy loss in accuracy. It should be noted that approximating is only relevant because of the first mechanism – there is no need to approximate if microscale processes are simulated on-demand.

The second part of the research question involves the ability to capture important details of individual behaviour. Our solution achieves this goal through the microscale model, which plays a central role in determining the outcome of the whole system. As every parameter determines the outcome of the model – the probability that the uncolonised water point is colonised – a change in one microscale parameter can lead to a change in macroscale simulation results. For example, if in a future study toads are discovered to have evolved a greater rate of movement or a different pattern in choosing their direction compared to the observed behaviour in the dataset we use, the microscale model can be easily modified to reflect the new behaviour. Similarly, the parameters of traps and fences can be changed as more data become available – for example, if more effective traps are devised – and the impact would be carried to the macroscale model through the integration mechanism. Therefore, we conclude that our solution also achieves the second part of the computation research question satisfactorily.

Although in our project this technique is applied to one particular modelling problem of cane toad control, it is generally applicable to other modelling problems that have the following characteristics: microscale simulations must be run a large number of times for each macroscale simulation; macroscale simulations must be run a large number of times; the outcome of microscale simulations resembles a relatively simple function that can be easily approximated without heavy loss in accuracy. For instance, it would be useful in a multiscale model of an infectious disease – such as COVID-19 – in which the transmission between person to person is modelled on the microscale and occurs through droplets and aerosols.

## 6.3 Limitations and potential improvements

### 6.3.1 Limitations in computation approach

On the computation side, it should be noted that the advantages which come with our integration approach are dependent on the particular modelling setting of cane toad spread and control in the Kimberley-Pilbara region. As mentioned in Section 6.2.2, this setting is characterised by the need to run microscale simulations a large number of times for each macroscale simulation, the need to run a large number of macroscale simulations, and the colonisation probability function that can be easily approximated without heavy loss in accuracy. In modelling contexts with different characteristics, our approach might not yield the same advantages. One example is systems with a microscopic process involving complex decision-making of human agents through neural networks, such as models of disaster evacuation or land use with civilians as microscopic agents. In such systems, the technique might not be suitable due to the complexity of the interface between the two models, which often involves a multi-modal complicated function and a large parameter space. Another example is models in which the microscopic process is not central and only occurs a small number of times during a macroscale simulation, such as a model of tissue patches in which a small number of patches with abnormality are modelled at cell level. In future studies, it can be useful to quantify the tipping points in such meta-characteristics where a different approach becomes more advantageous.

Instead of approximation using interpolation, a function or distribution can be fit to the points generated by the microscale simulations and used in the macroscale model. This approach might improve accuracy and allow modelling outside of the range of parameter values used to generate microscale results (such as high water point capacity). However, fitting a distribution is an extra modelling task and can be computationally demanding. Depending on the setting, it might be more advantageous than the approximation approach we employ in this project.

### 6.3.2 Limitations in model design

Our decision to not model the population at colonised water points makes it difficult to estimate the impact of suppression trapping. According to the results in Section 4.5.5, trapping at an uncolonised water point is much more impactful compared to trapping at the source. However, this behaviour is most likely due to the assumptions we make with the microscale model – that the rate of colonisers leaving a water point is constant and only depends on the capacity of the water point, and the fact that the microscale model only simulates days when toads are more actively moving. In reality, trapping at source water points can suppress the population and thus reduce the number of emigrating toads, and can also continue during days when toads cannot disperse and remain sedentary. In our project, due to the inaccuracy when modelling traps at the source water point, we decide to only model destination trapping. In future studies, including a population model at colonised water points might enable us to estimate the impact of suppression trapping at those water points better.

The costs of deploying different control methods are not taken into account, which prevents us from comparing cost-effectiveness and identifying most cost-effective strategies. Given the focus and the scope of this study, we only compare different control strategies in effectiveness and do not include the cost factor in the model. However, incorporating cost is a natural direction to expand the model and would vastly improve its usability, as in practice cost poses an important constraint to control strategies.

Finally, the model was developed without involving the target audience - stakeholders in cane toad control in Western Australia. Although we did consult cane toad modelling experts who authored various studies on cane toads and the exclusion strategy (B. Phillips and R. Tingley), stakeholders might be able to provide further insights and constraints that impact the design and outcomes of the model [75].

## 6.4 Overall conclusion

In summary, the contributions of our project include the investigation and evaluation of an integration approach for multiscale models, the evaluation of multiscale modelling as a tool to study invasive species control, and practical insights regarding cane toad control in Australia. Through critical evaluation, we conclude that multiscale agent-based modelling, with our integration scheme, can overcome the computation cost of large ABMs in cane toad control and other modelling settings with similar characteristics. Furthermore, we conclude that our model is an effective tool to model the control of cane toads and other invasive species with similar characteristics, capable of answering key questions and exploring hypothetical scenarios. Regarding the chosen modelling context of cane toad control, by running experiments with our model, we predict that cane toads will most likely colonise the Kimberley-Pilbara corridor in less than 100 years. The most effective and robust approach to stop toads from reaching the Pilbara region involves an exclusion strategy near either ends of the corridor, potentially supplemented with traps or a corridor-fence depending on the relative cost and the availability of water points for exclusion. Wetter climate conditions or higher capacity of water points can shorten the colonisation time and render control strategies less effective, but the impact varies between locations.

Furthermore, we identify several areas in the project that merit future studies. On the computation side, further studies can evaluate the suitability of the integration method proposed in this project with regards to the meta-characteristics of different modelling contexts and explore other approximation schemes. On the application side of modelling cane toad control, extensions to the model can incorporate a population model at colonised water points, the relative costs of different control methods, and insights and constraints from stakeholders.

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# Appendix A

# Source repository

The NetLogo source code of the models, input data for the macroscale model, and R scripts used for data processing and result analysis can be found in this repository: `https://github.com/bda-pham/multiscale-canetoadcontrol`.