Bayesian inference of eradication of incipient Tephritid fruit fly populations, with application to Mediterranean fruit fly

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Contents

Chapter 1

Introduction

1.1 Control and monitoring of Tephritid fruit flies

Biological invasions are incursions of incipient populations of plants or animals that are non-native to a given region. In the midst of the ongoing globalisation of trade, the salience of biological invasions is increasing around the world. Biological invasions are salient because they pose severe economic and environmental risks. On the economic side, they threaten "wholesale loss of agricultural, forestry, and fishery resources" (**?**). On the environmental side, they threaten to disrupt native ecological processes – outcompeting potentially endangered natives, and creating globally homogenous, "cosmopolitan" ecological systems.

Tephritid fruit flies (*Diptera Tephritidae*) are of particularly high economic significance. Species in this genus have the potential to destroy a wide variety of horticultural produce, in extremely large amounts. Females lay eggs in plant tissue (often fruits). Eggs develop into larvae, which then feed on the plant tissue. Potential costs of Tephritid fruit fly incursions include losses to significant crop losses; materials and labour allocated to their eradication or suppression; knock-on effects to agricultural produce as a consequence of pesticide usage (Suckling et al. [2016]). Economic costs of successful fruit fly invasions in Australia have been estimated to be as high as hundreds of millions of dollars (Suckling et al. [2016], Hancock et al. [2000]).

Governments have a responsibility monitor and eradicate potential biological invasions. In particular, the Australian government is legally bound by the Biosecurity act 2015 to ensure a very low level of risk for animal and plant invasions. A core element required for controlling this risk is the development of capacities for monitoring and controlling pest outbreaks. Monitoring biological species is difficult and costly. As such,in the public interest, the cost of increasing monitoring intensity must be traded off against the cost of failing to detect an incipient invasion.

The manager's role is made more difficult when a pest population is *subdetectable*. Populations may be subdetectable because they can persist at low rates; because they are *taxonomically cryptic* (i.e. hard to distinguish from well known native species); because they are *behaviourally cryptic* (i.e. behave in ways that help them avoid detection by predators; see Kery [2002]); or because

the population is suppressed by efforts to eradicate them. Matters are made worse when tests to detect the presence of a population have extremely low sensitivity for other reasons. For example, monitoring traps for fruit flies have very low attractiveness. One study of Mediterannean fruit fly found that only 0.02% of 38.8 million flies were recaptured after release, in a standard surveillance setup in Adelaide (Meats and Smallridge [2007]).

Suppose an outbreak of an invasive pest has occurred. Monitoring for the pest must then be intensified and localised to the area of suspicion. If the pest has since been eradicated, governments are incentivised to declare eradication quickly. This is because suspension of pest free area status is economically costly to local producers. On the other hand, if eradication has *not* occured, declaring eradication prematurely could (a) lower the manager's credibility, and therefore value of local produce, and (b) cause larger costs longer term due to local establishment of the pest.

A necessary prerequisite for minimising the probability of failing to detect an existing invasion is to understand what can be inferred about the state of the population from what has been observed in surveillance. In particular, it is desirable to understand the likelihood that extinction has occurred, given that the species has not been detected over a certain period of time.

PFA status is economically valuable to producers in the relevant region. Firstly, there may be offshore markets which require that produce is supplied from a PFA for a given pest. Secondly, in some markets, PFA status may allow the

supplier to receive a price premium for goods sold. In other words, PFA status increases the value of local produce on international markets.

1.1.1   Problems this work seeks to address

As mentioned above, the manager seeks to minimise resources spent on surveillance, while minimising the chance that an eradication is declared when none has occurred. The general problem this thesis is concerned with is to infer whether or not an invasive species has been extinguished based on survey records.

The present work attempts to address two gaps related to Tephritid fruit flies. First of all, I attempt to develop a model for understanding the evidential properties of survey records in arbitrary trapping grids. Second of all, I attempt to address the issue of evaluating existing PFA reinstatement dates. These are the date- and location-dependent lengths of time for which a pest must not be observed before eradication can be declared.

I seek to develop a method that can (a) evaluate proposed zero-catch criteria from a statistical point of view; (b) help to formulate new zero-catch criteria based on thresholds for the posterior probability of eradication; and (c) flexibly inform decision making, so that decision makers can weigh the cost of eradication probabilistically against the cost of further eradication attempts.

Chapter 2

Literature review

TODO: Write introduction to this chapter

2.1 Literature background

In this subsection, I will describe a number of models that have been applied to the problem of inferring species absence. I group these models into less and more elaborate models. The core difference between frequentist and Bayesian methods is in their treatment of the variables that describe the presence or absence of the species. Frequentist methods assume that the species is either absent or present with probability one. In this framework, surveillance activities are considered to be random experiments with fixed parameters. On the other hand, Bayesian methods assume that species absence is uncertain (i.e. random).

TODO: Write a section on the fruit fly literature (namely Meats 2005, and the debate between Carey et al and others in the 1990s) and relevant gaps.

2.1.1   Simple models

TODO: Consider deleting or reducing this section on simple models. Elaborate models are the focus of the thesis. TODO: If keeping, write an introduction for this section.

2.1.1.1   McArdle 1990

I start by discussing the most basic approach to program design. This is the frequentist approach described by McArdle [1990]. I emphasise this method because (a) it is conceptually simple and therefore easy to describe, and (b) it is emblematic of other methods in the literature, which are similarly general and simple. First, let the *rarity* of the species $p \in [0, 1]$ be the probability that a species is detected in any given sampling unit. (Sampling units can be arranged spatially or temporally; e.g. a survey that involves checking w weeks at k locations would have wk sampling units.) Then, the number of surveys in which the species is detected is given by $X \sim \text{Binomial}(T, p)$. Accordingly, the probability of *not* detecting the species in T surveys is given by

$$\alpha = \Pr(X = 0) = 1 - (1 - p)^T.$$

The last formula allows us to compute any of the 3 quantities α, p, and t,

assuming the other two are given.

Given this framework, the problem of program design becomes the following. We decide *a priori* what the smallest "rarity" p worth detecting is. McArdle supposes that if a species if sufficiently difficult to detect (while, nonetheless, $p > 0$) then it cannot be considered a member of an ecological community, and therefore not worthy of being deemed "present". Write the smallest rarity worth detecting as p_0. Then, we choose a minimum detection probability α that we are willing to accept. For example, we might wish to have chance $\alpha > 0.95$ of detecting a species, given that it is present. Then, with the above formula, we can rearrange to get the smallest number of survey units T such that detection probability α is achieved.

Statisticians will recognise that the above is essentially power analysis for data modelled as identically and independently distributed Bernoulli trials. This analogy can be made more concrete. For any fixed rarity p, we can derive the probability of observing n or more negative surveys. This is the p-value. We can then reject the hypothesis that there is the rarity is greater than p_0, the rarity worth detecting.

2.1.1.2 Limitations of McArdle's method

Applying the above model to the problem of program design is not straightforward. Firstly, the model is fairly restrictive. It assumes that the probability of detecting the pest population is constant over time. Secondly, in the case of pest populations, it may be difficult to determine the smallest value of p

that is "worth" detecting. When a pest species is cryptic, the detectability (p in this model) can be extremely small even when the population is relatively large. Further, invasive potential of the pest may be large, so that even small populations bear a large cost to the decision maker.

2.1.1.3 Similar models

There are several other models in the literature, mirroring McArdle's method in their conceptual simplicity and generality. (See Boakes et al. [2015] for a relatively complete review.) Bayesian models are given by ... and Barnes et al. These methods have the advantage that the posterior distribution is derived analytically. This means that posterior probabilities can be computed extremely efficiently. However, each model assumes a constant growth rate. However, in real contexts, growth rates are highly variable and uncertain (Caley and Barry [2014]). It therefore may be unreasonable to assume that

TODO: How have simple models been used to address the Tephritid fruit fly problem specifically? Cite Meats and Smallridge (2006) and Lance and gates (1994).

2.1.2 Elaborate models

2.1.2.1 Justification for elaborate models

Recently, more elaborate models have appeared in the literature for specific eradication inference problems. Here, I discuss the motivation and justification for these models.

2.1.2.1.1 Motivation As discussed above, simple models, such as McArdle's method, are attractive for their simplicity, generality, and efficiency of computation. However, these virtues may come at the cost of biological plausibility. This is particularly the case when we have a significant degree of prior information about the species and region in question. For high stakes problems, we would like to be able to leverage existing domain knowledge about the location and species. This might mean using process models that are fine grained, scientifically plausible, and based on multiple sources of scientific knowledge and evidence. We would also like to be able to incorporate our uncertainty about the processes in question.

TODO: Flesh out the following list into paragraphs.

- They make strong assumptions about priors which are not defensible in general.
    - Assumption of a fixed, and either constant or declining population size (Caley et al. [2015], p. 2).
    - For example, McArdle's model assumes that there is a value of p small enough to be not worth detecting.
- They assume that we can estimate a sighting rate, which is constant as a function of the locations of the individuals.

Another issue with simpler models is their relative inflexibility with respect to the structure of the model. For example, the method of Barnes et al assumes that we know the probability of detecting a specimen drawn randomly from the

population. However, in the case of fruit flies, this quantity is difficult to study empirically. This is because the capture probability is highly dependent on the spatial layout and types of monitoring traps. In turn, the layout and type of trap are highly dependent on time and place in which the monitoring is taking place. For example, countries (and states within countries) differ in the types of traps used and the spatial density of traps. Also, spatial layouts of trapping networks vary from place to place, but it is usually the case that the precise locations of the traps are known to the decision maker who is responsible for monitoring.

The literature on elaborate computational models is fairly narrow. I know of only two attempts to biologically realistic models to infer probability of eradication from the survey record. These papers provide inspiration for the model I develop in the following chapter – although there are also some marked differences, as the reader will see. Here, I will discuss the contributions of each of these papers.

2.1.2.2   Paper 1: Keith et al

The first instance of an elaborate Bayesian model for inferring pest eradication is given by Keith and Spring [2013]. The authors use an agent-based Bayesian model to infer the distribution of fire ant nests in Brisbane. They obtained data on the locations and month of discovery for $n = 7{,}068$ nests. They also observed whether data were passively or actively discovered (e.g. by members of the public or through a targeted search).

The model explicitly models the location of each agent (ant nest). Typically, when a Bayesian model is agent based, this means that there is an unknown number of parameters in the model. The upshot of this is that typical Markov Chain Monte Carlo (MCMC) methods, such as the Metropolis Hastings sampler, fail. This is because they do not allow the dimension of the parameter vector to vary between draws. To get around this problem, a generalised Gibbs sampling algorithm is used. This gets around the problem by adding a step to the Gibbs sampler in which we move between coordinate spaces.

2.1.2.3 Paper 2: Caley et al

The second instance of an elaborate Bayesian model for inferring eradication is given by Caley et al. [2015]. Caley and co-authors develop a Bayesian model of fox sightings in Tasmania. Their goal is to infer the posterior probability that foxes had been eradicated, given a record of fox carcass sightings. They obtained data on fox carcass sightings from two sources, namely hunter kills and road kills. These separate "observation processes" were modelled separately, so that posterior detection rates were allowed to differ between the sighting types. Detection rates were assumed to be constant across time and location for each type of sighting. Notably, uninformative priors were set for detection rates (i.e. the probability of detecting a fox was set to be uniform on $[0, 1]$). This was because the fox sighting mechanism has not been studied empirically (indeed, it is not clear how it could be studied at all). Data consisted of a single sighting count for each location (with Tasmania divided geographically into grid cells)

and each year between 2001 and 2013. Data were all zeroes with the exception of exactly four unit observations (sightings of exactly one fox).

The authors use a simple rejection algorithm to sample from the posterior. I will refer to this algorithm as exact Bayesian computation (EBC), to be distinguished from approximate Bayesian computation (ABC). ABC works by first drawing samples of the parameter vector θ from the prior distribution $\pi(\theta)$, then second, drawing simulated data y_{sim} from the likelihood, then keeping the proposed θ if and only if y_{sim} is an approximate match with the observed data. EBC is the same, except that samples are only kept if y_{sim} is an *exact* match with the observed data.

The authors point to the complexity of the likelihood to justify the use of ABC over more standard Monte Carlo methods such as Metropolis Hastings or Gibbs sampling. Based on their description of the model, however, it is not clear that Metropolis-Hastings would not suffice.

2.2 Gaps

TODO: Write a paragraph in this section outlining the gaps in the fruit fly literature.

Above, I have discussed the two elaborate computational models in the literature for inferring eradication of an incipient biological invasion. The current work seeks to address two gaps in the literature. Firstly, elaborate Bayesian models have not been explored for inferring eradication of Tephritid fruit flies. Fruit flies

pose an interesting case study, because the regulator has fine grained information about the detection system. In particular, the regulator knows the locations of each of the traps. Further, prior research investigating the efficacy of these traps exists. If used carefully, this information can be leveraged through the model's priors to learn from the zero-sighting record efficiently.

Fruit flies are interesting for a few reasons:

- A body of research exists to understand trap efficacy.

- The surveillance program is predictably structured

- The intensity of the surveillance program changes in a predictable way.

Second, no such model has addressed the question of PFA status reinstatement. Instead, they discuss inferring eradication from an actually observed record.

TODO: Write conclusion of this chapter

Chapter 3

Model development

NOTE: In this section I discuss the model abstractly without setting any priors or doing any inference. I am unsure whether to keep this chapter or to integrate it with the following chapter. On one hand, if I discuss general properties of the model in the next chapter, then that chapter becomes very long and complicated. On the other hand, it may be hard to understand the material in this chapter because of how abstract it is.

TODO: Write introduction to this chapter TODO: Write outline of this chapter

3.0.1   The scenario

TODO: Write a general description of the zero catch scenario

3.1   Structure of the model

At the most basic level, I propose to define a joint distribution over (a) the number of flies in a population, (b) the location of each fly, and (c) the number of flies that are detected (caught in traps). Defining notation, at each time point t, we must define a joint distribution over the number of flies N_t, the $N_t \times 2$ matrix of fly locations $\mathbf{L}_t$, and the number of flies detected y_t. I.e., the model is a joint distribution $p(\{N_t, \mathbf{L}_t, y_t\}_{t=1}^T)$. Our goal is, primarily, to infer the posterior distribution of the population size at the last time point N_T, conditional on $\mathbf{y} = \{y_t\}_{t=1}^T = \mathbf{0}_T$. To make this possible, we must specify a joint **prior** distribution over $\{N_t, \mathbf{L}_t\}$, and a likelihood, i.e. a distribution for $\mathbf{y} \mid \{N_t, \mathbf{L}_t\}_{t=1}^T$. In the next sections, I discuss general strategies for each of these. I leave the task of illustrating this process for a specific case to the final chapter.

3.2   Why make the model spatially explicit?

The value of including a spatial component in the model may be questioned. This is relatively unusual in standard approaches (see, e.g., McArdle [1990]). The answer is that the spatial component allows for the use of a useful source of prior information. There exists a moderately large literature of **release-recapture** studies for various species of fruit fly (**?**).

Release recapture studies give us two kinds of data – namely, data on capture rates as a function of distance, and more general capture rates. Experimental

data on marginal capture rates (irrespective of distances) can be useful when
the trapping setup is similar to the setup we want to draw inference about.
However, this will often not be the case. For example, studies vary in the
number and type of traps used. Further, we may wish to infer eradication of pest
populations in trapping systems that are unlike those in studies. For example,
after an outbreak has occurred, and eradication measures have been stopped,
it is common to set up supplementary trapping units to intensify monitoring
and increase the likelihood of detecting flies, conditional on their presence in
the area (sup [2011]).

3.2.1 Population size

A natural way to set a prior on the population size at each time point t is to set
a prior on the population size at the initial time point, and then assume that
the population sizes at other time points are given by some (deterministic or
stochastic) function of the population size at $t-1$, and the value of a covariate
vector X_t, which includes variables relevant to population growth.

It may be worth noting that there are no a priori assumptions on the popula-
tion dynamics for the growth model. Thanks to the generality of the sampling
algorithm, it is simple to "plug in" elaborate growth models. For example, the
models of Lux [2018] or Manoukis and Hoffman [2014] could be used to generate
independent random draws from the population of Medfly. In this way, they
can structure our prior over the population size. In this case, inference would
proceed simple as in the case I outline here. This highlights a benefit of the

modelling approach taken here, which is its generality and modularity.

$$N_t = f(N_{t-1}, X_t)$$

3.2.2   Population location

I first discuss the option of setting a uniform prior. Setting an uninformative prior is fairly straightforward for this problem. In particular, we might assume that, beyond a certain distance from the outbreak centre (say, 1km) any existing population of Medfly is distinct from the population of interest. Therefore, we might set the prior distribution for the population location to be uniform on the surface of a disc with (e.g.) 1km radius around the outbreak centre.

Despite the fact that an uninformative prior is relatively straightforward to set, it is most likely not advisable in specific applications. It will typically be the case that prior information is available to the decision maker. In particular, fruit flies are heavily dependent on the availability of suitable fruit trees for survival and reproduction. Therefore, someone with local area knowledge will be able to determine the most likely locations for an existing population. Also, the supplementary zone is not chosen arbitrarily. The choice of supplementary zone will typically reflect the beliefs of the decision maker about the location of the fly population.

When prior information exists, setting the prior distribution to be uninformative may cause us to underestimate the likelihood of observing captures

in the supplementary surveillance zone. The overall effect will be to inflate $\Pr(N_T = 0 \mid \mathbf{y} = \mathbf{0}_T)$.

3.2.2.1 Individual fly dispersals

In release-recapture experiments, it is often the case that flies are released from a single point in the trapping grid (**?, ?**). In the simplest model of detection, we might assume that this happens in the real world. In that case, the distance between each trap and each fly would just be the distance between that trap and the population. In other words, flies would all be clustered at a single point. However, this may not be reasonable in practice. Instead, it may be more reasonable to assume that flies are dispersed around a central point.

To incorporate dispersion of flies, I assume the following. Let L denote the central point of the population, as above. Then, let $D_{i,t}$ denote the location of fly i at time t, relative to the population centroid L. For simplicity, it is assumed that $D_{i,t}$ is independent of $D_{i',t'}$, for any $(i',t') \neq (i,t)$. Thus, our belief is essentially that flies are shuffled around at each time point, so that a fly's location at $t-1$ tells us nothing about its location at t (except through the information both reveal about L). This simply means that we do not track the locations of flies across time – i.e., whether a fly lives across time periods, or instead dies and is replaced, are equivalent scenarios under this model.

3.2.3 Probability of capture (likelihood)

TODO: Flesh this out.

I assume that surveillance events occur at regular time intervals $t \in \{1, \cdots, T\}$. The probability that a fly i is caught in trap k at time t is given by $p_{i,k,t} = p(d_{i,k,t})$ where d is the distance between fly i and trap k at time t, and $p(\cdot)$ gives us the probability of capture as a function of distance.

Probability of capture is based on the distances between each fly and each trap. For the trap locations, I assume that the locations of traps are fixed and known with certainty (i.e. not random). This will be the case in real cases, where the decision making body also decides the locations of the traps.

- No interference.

TODO: Write conclusion of this chapter

Chapter 4

Case study: Mediterranean

fruit fly

TODO: Probabilistic graphical model of the entire model (with a box to demarcate the "internal" components from the components on which a prior distribution is set). TODO: Plot the trapping grid.

4.1 Introduction

TODO: Rewrite this intro in light of the model proposal chapter

In the previous chapter, I proposed to address a gap in the literature by providing an elaborate model for inferring the eradication of an incipient invasive population of Tephritid fruit flies. In this chapter, I present an illustrative model

of medfly surveillance after an hypothetical invasion. I use a simplified model of Medfly population dynamics. However, for various species of Tephritid fruit fly (medfly included) detailed models exist. A benefit of the proposed method is that it can easily incorporate almost any model of medfly dynamics.[1]

TODO:

- Note that this analysis is primarily illustrative. Performing a more specific analysis requires access to confidential data.

- Note that the method can be used for a real scenario - we only need to change the priors, data and locations of the traps.

- Note that I use a simplified model of Medfly dynamics for illustrative purposes - but the method can easily incorporate more complex ABS models, and cite those models.

TODO: Write one paragraph outlining this chapter

4.2 Background

4.2.1 Medfly are economically important

Mediterranean fruit fly (*Ceratitis Capitata*) or *medfly* are a particularly salient species of tephritid fruit fly. Medflies have high invasive potential, as it can adapt to a relatively large range of climates and environments, and is known to have the capability to infest the fruits of over 300 species of plants (Ibid.).

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[1]Note, though, that the sampling method I use may not be appropriate in all cases. When the model predicts that the population size "explodes", then the rejection rate for the sampling algorithm may become very high, causing the algorithm to be highly inefficient.

Recently, an incursion of medfly in Adelaide, South Australia, prompted a large scale eradication effort. This comprised in part of hiring 350 special-purpose staff that set over 13,000 additional traps, and collected over 350 tonnes of fruit. The scale of the response to this outbreak indicates the perceived economic significance of this fruit fly species.

4.2.2 Medfly are cryptic

Medfly are very hard to detect at low levels. Monitoring for medfly is typically performed with the aid of lured traps (namely so-called Lynfield or Jackson traps). These traps are relatively ineffective for detecting medfly. For example, one study from the Adelaide metro area trapping grid found that only 0.02% of flies were recaptured from a release of 38.8 million flies. Further, medfly are known to have low dispersals across space. This means that low-lying populatons of flies may go undetected across generations. https://onlinelibrary-wiley-com.virtual.anu.edu.au/doi/pdfdirect/10.1111/j.1570-7458.2006.00415.x

4.3 Data

4.3.1 Zero sighting surveillance data

In this section, I do not use real data to estimate parameters. Instead, I model a hypothetical situation. The situation is as follows: We assume that at least one fly has been detected; eradication measures have since begun and then ceased; and we now proceed with intensified monitoring, while whatever population that

may exist is free to grow relatively unhindered. The goal of the analysis is to infer the probability of eradication for the incipient population, given no flies detected at any point in this period.

The data is a hypothetical survey record. The idea is to simulate a relatively realistic scenario. We observe the outcomes of a surveillance process. The surveillance process is generated by weekly checks of traps that are deployed uniformly in a given area (more about the trapping arrangement below). It is assumed that no specimens are detected at any point in the survey period. In other words, the sum of all detected counts in the period is zero.

4.3.2   Data on capture probability: release recapture studies

Above, I described the "data" under the model. This is the set of variables that we condition on to infer the posterior distribution. However, we can use data from other sources to inform our prior distribution over the model's parameters.

In cases where Bayesian models have been used, data has not been available on detection rates. For example, Caley and Barry [2014] and Keith and Spring [2013] set uninformative priors on the detection rates, and attempt to learn the detection rates for data. However, because of their global economic importance, tephritid fruit flies are relatively well studied. In particular, a number of fruit fly species have been studied with release recapture experiments. Release recapture experiments involve the release of a large number of (often sterilised) fruit flies.

These studies help us to learn both the dispersal patterns and tendencies of various species of fly, but also the effectiveness of various trap types and layouts.

4.4 Model

In this section, I discuss a model of medfly dynamics and detection.

4.4.1 Full model overview

I break the model into the following three components: (1) The size of the population (number of individuals); (2) the locations of individuals and traps; and (3) number of individuals caught in traps, conditional on (1) and (2).

The likelihood of a given number of captures is a function of latent variables, namely the number and locations of flies. Under the prior distribution, it is assumed that data at any given timestep are generated as follows. Firstly, nature draws a number of flies (i.e. a population size) which may or may not be based on the number of flies at the previous time step. Next, nature draws a location for each of the flies. Finally, nature draws a number of detections.

4.4.2 Population size

In this case, N_1 is the first week after the most recent fly detection. I have chosen to give N_1 the prior distribution $N_1 \mid \lambda \sim \text{Poisson}(\lambda)$, where $\lambda \sim \text{Exponential}(0.05)$. This distribution for N_1 is chosen as it is a discrete distribution with right skew, and a relatively large amount of mass $f_{N_1}(x)$ at $x = 0$,

corresponding to the situation where flies are already eradicated (see **?**)

```r
g = 1/20

init_pmf = function(n, g) g / (1+g)^(n+1)


x = 0:100


df = data.frame(x = x, y = init_pmf(x, g))


ggplot(df) +

  geom_bar(stat = 'identity', aes(x, y)) +

  xlab(bquote(italic(n))) +

  ylab(bquote('Pr('*italic(N)[1] == italic(n)*')'))
```

```r
# Prior probability that they're already eradicated
```

As for the population sizes at later time points, I assume that growth is exponential at an uncertain rate. In particular, it is assumed that, for $t \in \{2, \ldots, T\}$, $N_t \mid N_{t-1}, R_t \sim \text{Poisson}(N_{t-1}e^{R_t})$. Here, we can give any continuous distribution for R_t. I have chosen the vaguely informative prior $R_t \overset{\text{iid}}{\sim} \text{N}(0, 0.2)$. The symmetry of this prior means that we are indifferent about whether the population is growing or declining.

The growth rate prior has been chosen to place the vast majority of density below their estimated growth rate under optimal conditions. Medfly have been estimated to grow at 8% per day, in optimal lab conditions (Papadopoulos et al.
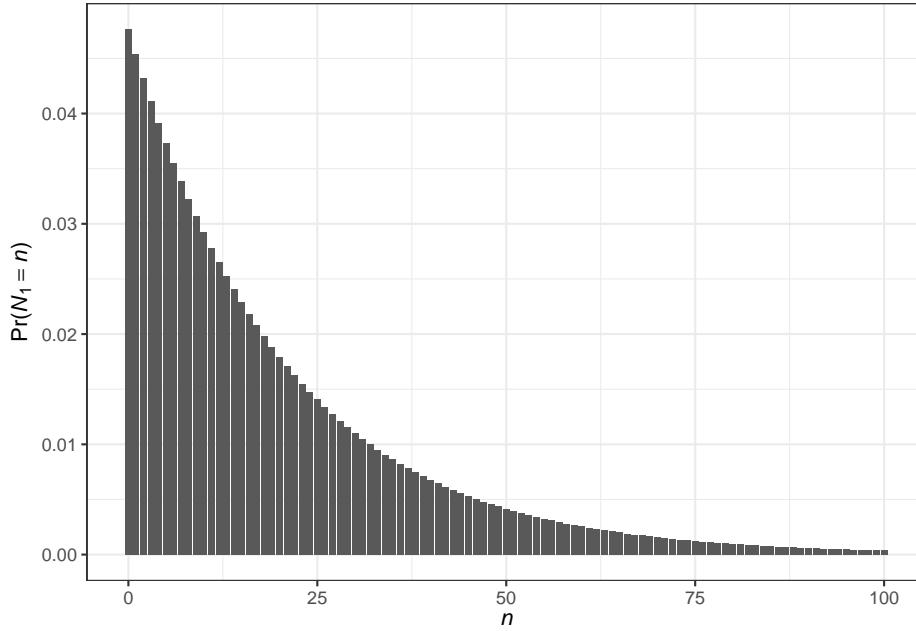
Figure 4.1: (#fig:prior_init_size)Prior distribution of initial population size

[2002]). Under an exponential growth model this is 56% per week. This can be taken as an extremely *pessimistic* upper bound on the growth rate. In real cases, flies may fail to establish due to food scarcity, predation, and/or unsustainably low population density.

In real cases, it will be desirable to attempt to estimate R_t from data. In particular, it is known that fruit fly population growth rates are highly dependent on temperature. Therefore, it would be wise to estimate and draw values of R_t conditional on weather measurements. Choosing an empirically realistic distribution for R_t is likely to improve the efficiency of inference from the survey record.

4.4.3 Spatial location

As mentioned in the previous chapter, the model is spatial, insofar as likelihood of detection depends on distances between traps and individual flies.

TODO: Explain that the centre of the grid is the site of the last detection.

4.4.3.1 Population location

The centre of of the population is assumed to be located at the two dimensional vector L. I have set the prior on L to be

$$L \sim \text{Normal}_2(\mathbf{0}_2, 160^2 I_2),$$

where Normal_2 is the bivariate normal distribution, $\mathbb{0}_2$ is the two-dimensional zero vector and I_2 is the 2×2 identity matrix. This prior reflects a prior belief that the centre of the population is highly likely to be found somewhere on a disc with. E.g., we believe that there is a 95% chance that the centre of the population is within $1.96 \cdot 160 \approx 320$ metres of the centre of the grid.[2] Recall that this makes sense because we believe that the flies are within the distribution.

4.4.3.2 Individual fly dispersals

I assume that, for any given fly, their prior distance from the central location is described by

$$D_{i,t} \sim \text{Normal}_2(\mathbf{0}_2, 12.5^2 I_2)$$

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[2]For details about how this prior was arrived at, see appendix.

where the notation is defined as in the previous section above. The variance of this distribution

The normal distribution is chosen for a few reasons. Firstly, it is conceptually simple and intuitive to parameterise. Secondly, the location of fly i at time t, namely $L + D_{i,t}$, has a simple marginal distribution, thanks to the fact that the sum of normal random variables is itself normal. Thirdly, for mean zero normal random variables, distances to the origin have a known distribution. For example, let

$$\mathbf{X} = (X_1, ..., X_p)^\top \sim \mathbf{N}_p(0, \sigma^2 I),$$

where I is the $p \times p$ identity matrix. Then the length of $\mathbf{X}$, $\|\mathbf{X}\|^{1/2} \sim$ Gamma(??????) **?** (see appendix). This allows us to compare and calibrate the distribution against experimental results (see appendix). This, in turn, makes elicitation of priors simpler and more intuitive.

It may be worth noting that, in real cases, the assumed prior distribution on dispersals may not be reasonable. For example, dispersals may have non-zero mean (due to strength and direction) or non-spherical covariance matrix (i.e. non-equal variances and/or non-zero covariances).[3] In applied cases, it may be possible to use information about wind directions to set more informative priors. This is beyond the scope of this work.

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[3]This is argued by Baker et al. [1986].

4.4.4   Trap locations

```r
grid_size = 4

general_grid_1d = seq(-grid_size / 2, grid_size / 2) * 400

general_grid = expand.grid(general_grid_1d, general_grid_1d)

general_traps = as.matrix(general_grid)


d = 200 / sqrt(2)

supp_grid_1d = seq(-d, d, length.out = 4)

supp_traps = expand.grid(supp_grid_1d, supp_grid_1d)

all_traps = rbind(general_traps, supp_traps)


supp_indicator = rep(c('General', 'Supplementary'), c(nrow(general_traps), nrow(supp_t

traps_df = data.frame(all_traps, factor(supp_indicator, c('Yes', 'No')))


# Plot of traps
ggplot(traps_df) +

  geom_circle(aes(x0=0, y0=0, r=200), colour = 'grey') +

  geom_point(aes(Var1, Var2, col=supp_indicator)) +

  coord_fixed() +

  xlab('X coordinate (metres)') +

  ylab('Y coordinate (metres)') +

  labs(col = 'Trap type') +
```

```
scale_x_continuous(breaks = (-4:4)*200) +

scale_y_continuous(breaks = (-4:4)*200)
```
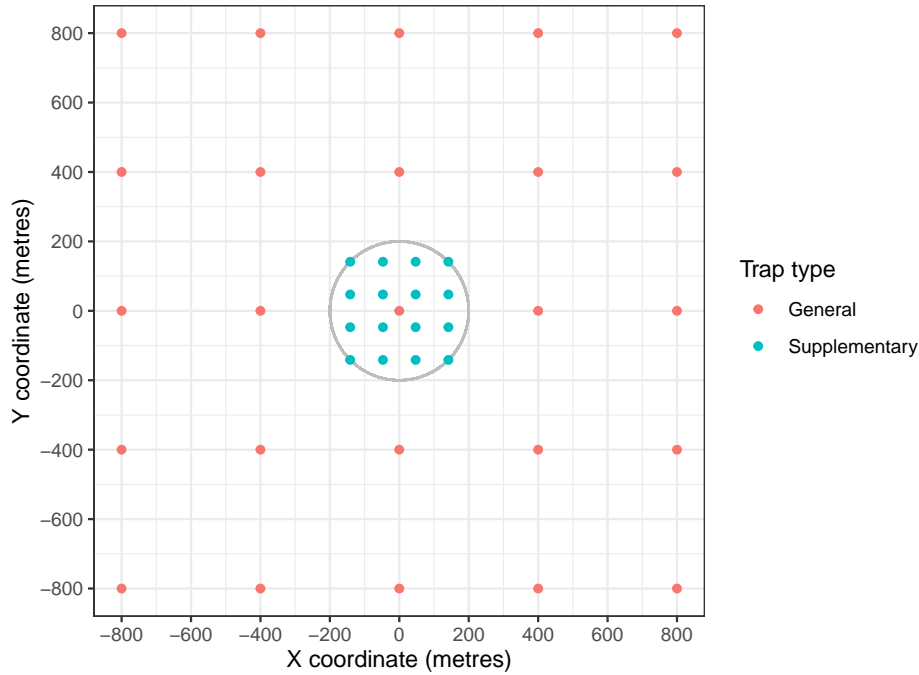

Figure 4.2: (#fig:trap_grid)Illustration of the hypothetical trapping grid. Grey circle represents 200m radius disc surrounding the site of the most most recently detected medfly specimen.

By intensified monitoring, I mean that **supplementary** monitoring traps have been placed alongside the previously existing grid of **general** monitoring traps. More precisely, it is assumed that **general** surveillance traps are placed year round in a 400×400 metre grid (DPIPWE, 2011, p. 50). The **supplementary** surveillance system consists of a set of 16 traps in a circular area, centred at the site of the first fly detection.[4]

---

[4]It is typical to wait until at least 2 flies have been detected near each other for an outbreak

4.4.4.1 Probability of capture

I assume that the probability of capture for a given fly in a given trap is

$$
p(x) = \begin{cases} ax^{-b}, & d > 1 \\[2em] a & 0 \geq d \geq 1 \end{cases}
$$

where $a = 0.4702111$, $b = 1.37$, and x is the distance between the fly and the trap at the start of the period. Thresholding is introduced because (a) the function does not yield valid probabilities for small enough x. In general, the use of a negative exponential function is not ideal here. This function is used for convenience as it is provided by the authors of the study, and data is not publicly accessible. For a more detailed analysis, it may be

The results of release recapture studies are highly variable, and gaining access to data may be difficult for older studies. In this case, it may be desirable to incorporate uncertainty about the probability function. This could be done, for example, by assigning prior distributions to the coefficients a and b. I do not explore this any further here, as this model exposition is intended for the purposes of illustration only.

---

to be declared. To illustrate the method in a simplified setting, I suppose that one fly detection is sufficient.

4.5 Computing the posterior distribution

In this section, I discuss the problem of computing the posterior distribution, given a survey record. Above, I stated that the model could be defined flexibly. Without restrictions on the form of the growth and detection models, the posterior may be analytically intractable. In other words, we will not be able to write out the posterior density or mass as a function of the data and prior distributions. Such situations are common in the Bayesian framework, because of the tendency for the posterior density or mass to depend, implicitly or explicitly, on analytically intractable integrals.

So far, we have talked about situations when sampling is required for inference. Further problems arise when the model is *agent-based*. In other words, when we include uncertainty about individual-level features in the model. In this case, the detection probability is random, even when the location and population size is known. In other words, the probability of detecting at least one individual is a function of the number of individuals, and also their individual (random) properties. This is a situation in which "the number of things you do not know is one of the things you do not know" (Richardson and Green, 1997).

4.5.1 ABC models

A simple rejection algorithm is used to draw samples from the posterior distribution.

Here, I have used EBC for intuitiveness, ease of implementation, and the fact

that it is relatively efficient for this problem. However, other methods exist that may be worth exploring, for analogous problems where the rejection rate of ABC is higher. There are at least two known methods for sampling from the posterior when the dimension of the parameter space is uncertain. These are the reversible jump MCMC sample (Green [1995]) and the generalised Gibbs sampler (**?**). These may be worth exploring for problems where the rejection rate is high for EBC.

Interestingly, the standard justifications for and against ABC do not apply to the case under consideration. Firstly, the standard justification for ABC is that it allows for inference when the likelihood function is "intractable" - i.e., unknown, uncomputable or otherwise difficult to work with. However, for the current model, the likelihood is known, and relatively simple to write out.

On the other hand, the standard drawback for ABC is that it ensures that we can typically only draw from the posterior approximately. Under standard conditions, we must define a criteria for similarity between simulated and observed data. This is typically done by specifying a summary statistic $S(\mathsf{y})$, and a similarity measure $\rho(S(\mathsf{y}), S(\mathsf{y}'))$ defined over the space spanning our data y. We reject a sample if we observe $\rho(\mathsf{y}_{\text{observed}}, \mathsf{y}_{\text{simulated}}) > \epsilon_0$, where ϵ_0.

10,000 samples were taken. The acceptance rate for sampling was 0.68. This high level of acceptance is due to the low likelihood of captures, across most of the high prior density region of the model space.

- How long did sampling take?

- What was the rejection rate?

4.6 Results

- The fly free period is 12 weeks or 28 days and one generation, whichever is longer (Meats and Clift [2005]). In summer, a Medfly generation takes 28-34 days (dpi). Therefore, the period I look at is over 12 weeks. However, this may be different based on the period that the manager is interested in.

The posterior probability of extinction after 12 weeks is approximately 0.684.[5]

4.7 Discussion

Here I discuss limitations and objections.

4.7.1 Drawbacks

- We do not get a posterior distribution over the probability of eradication.

TODO: Section on objections to/limitations of the model

- Objection: the model is subjective

- Objection: The model is too sensitive to priors.

    - Defence in Caley 2015

TODO: Write conclusion of this chapter

---

[5]Unfortunately, it is not straightforward to visualise the prior or posterior density of this quantity.

Chapter 5

Appendices

5.1   Appendix 1: Proof of ABC procedure

Here, I give a proof that the simple ABC rejection algorithm yields independent draws from the posterior distribution. Recall that the algorithm works by drawing samples of θ from the prior distribution with density $\pi(\theta)$. Then, for each draw of θ, we draw a data vector y_{sim} from the likelihood $l(\theta \mid y_{\text{sim}})$. Finally, we keep the sample if we observe that $y_{\text{sim}} = y_{\text{obs}}$ (where y_{obs} is the data vector we actually observed) and reject it otherwise. Then, the draws that we keep have distribution $f_{\text{ABC}}(\theta) = \pi(\theta) \cdot l(\theta \mid y_{\text{obs}})$, since our draws from the prior and likelihood are independent.[1]

---

[1] Credit is due to this StackExchange post.

5.2   Appendix 2: Full model statement

Population size

Initial no. of flies: $N_1 \mid \lambda \sim \text{Pois}(\lambda)$, where

$\lambda \sim \text{Exponential}(0.05)$

Number of flies: $N_t \mid N_{t-1} \sim \text{Poisson}\{N_{t-1}\exp(R)\}$, where

$R \sim \text{Normal}(0, 12.5^2)$, $t \in \{2, ..., T\}$

Fly locations

Population location: $L \sim \text{Normal}_2(\mathbf{0}_2, 160^2 I_2)$

Fly locations: $L_{i,t}^{\text{fly}} \mid L \sim L + \text{Normal}_2(\mathbf{0}_2, 30^2 I_2)$ $i \in \{1, ..., N_t\}$,

$t \in \{1, ..., T\}$

Detection model

Number of traps: $K \in \mathbb{N}_+$

Trap locations: $L_k^{\text{trap}} \in \mathbb{R}$ $k \in \{1, ..., K\}$

Dist. btw. fly i and trap k at time t: $\delta_{i,k,t} := \|L_k^{\text{trap}} - L_{i,t}^{\text{fly}}\|$ $i \in \{1, ..., N_t\}$,

$k \in \{1, ..., K\}$,

$t \in \{1, ..., T\}$

Individ. cap. prob.: $p_{i,t} = 1 - \displaystyle\prod_{k=1}^{K}(1 - p(\delta_{i,k,t}))$, $i \in \{1, ..., N_t\}$,

$t \in \{1, ..., T\}$

$\mathbf{p}_t := [p_{i,t}]_{i=1}^{N_t}$ $t \in \{1, ..., T\}$

No. of captures: $y_t \mid \theta \sim \text{Poisson-binomial}(N_t, \mathbf{p}_t)$, $t \in \{1, ..., T\}$

$\mathbf{y} := [y_t]_{t=1}^{T}$

5.3   Appendix 3: Population location prior

To update on detection location when the first fly is detected at a trap (say trap k) we can use a trick. The trick is to model the probability of the first detection being at trap k as the probability that a fly is detected at k in one period conditional on exactly one fly total being detected in that period. The benefit of this model is that it does not depend on how many weeks it took to get the first detection (which would require information about how long flies have been around before the first detection). See appendix for more details.

A mathematical trick can be used to derive a prior in some cases. Suppose we have K traps indexed by $k \in \{1, ..., L\}$. Suppose also that we have a prior distribution over the population size N, given by $N \sim \text{Poisson}(\lambda)$, with $\lambda \sim$

Exponential(1/20). Here we assume no change in population size over time. Now, we suppose that each trap k is "competing" to catch the first trap each week. We suppose that the trap at the centre of the grid was the first to catch a fly, and we want to use this information. Define the random variable

$$C_k = \begin{cases} 1 & \text{a fly is caught in trap } k \text{ before any other trap} \\ 0 & \text{otherwise.} \end{cases}$$

Under these assumptions, $L \mid C_k = 1$ is the distribution of L, given that a fly was caught in trap k before any other trap.

Whether or not we can analytically derive the posterior density depends on the probability of capture function $p(x)$. In the case we consider here, the function cannot be integrated, and so I resort to sampling. Under the above assumptions, the posterior resembles the convolution of a normal and a uniform distribution (see figure). See appendix for more details.

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