

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

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Chapter 1

Introduction

1.1 Control and monitoring of Tephritid fruit flies

Biological (pest) invasions are incursions of incipient populations of plants or animals that are non-native to a given region.¹ Such invasions can have high economic significance when the invading species is considered a *pest* (i.e., harmful to human concerns). In the midst of the ongoing globalisation of trade, the salience of biological invasions is increasing around the world. Invasions pose severe economic and environmental risks. On the economic side, they may threaten “wholesale loss of agricultural, forestry, and fishery resources” (Mack et al. [2000]). On the environmental side, they may threaten to disrupt native ecological processes – e.g. by threatening the extinction of endangered natives, and creating globally homogenous, “cosmopolitan” ecological systems (Ibid.).

Tephritid fruit flies (*Diptera Tephritidae*) are a genus of insects of particularly high economic significance. Species in this genus have the potential to destroy a wide variety

¹Note that, for the purpose of this work, the term *population* will be used to mean a group of animals living together in a group. This is to be distinguished from the statistical use of the term.

of horticultural produce in large amounts. Females lay eggs in plant tissue (often fruits) which is then destroyed in the process of their development. 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]). Potential costs of Tephritid fruit fly incursions include crop losses; labour and materials associated with eradication and suppression; and knock-on effects to agricultural produce as a consequence of pesticide usage (Suckling et al. [2016]).

Some locations in Australia and the USA are internationally recognised exclusion zones for some species of fruit fly. In some of these places *spot infestations* of the relevant fly species can be common (Meats and Clift [2005]). Spot infestations are small invasions, usually met with efforts to eradicate. Eradication methods include spraying of pesticide and release of sterile insects that disrupt the flies' breeding cycle. Currently, it is widespread practice that inference of absence for such invasions is informal. In particular, pest absence is declared according to rules of thumb (Ibid.). These rules are in the form of **zero-catch criteria**. The idea is that, if zero flies are detected for some pre-specified length of time (the zero-catch criterion) we may infer with confidence, and therefore declare, that they have been eradicated from the region (see chapter 2).

There are issues with the zero-catch criteria currently used. Firstly, they are only minimally sensitive to variability between situations. For example, outbreaks two locations with the same temperatures will have the same zero-catch criteria, even though they may differ in other significant ways. Secondly, they do not explicitly or transparently take into account the low sensitivity of fruit fly traps, which has been the subject of some study (see chapter 2). Thirdly, they are based on a simplified model of fruit fly biology which does not account for variation in development times (both within and between fly

populations).

The primary goal of the present work is to develop a rigorous statistical framework for inferring pest absence after a suspected outbreak. The hope is that such a framework can be useful (a) to evaluate existing zero-catch criteria, and (b) to develop improved criteria. A secondary goal of the framework is to provide situation-specific estimates of the probability of eradication. These may be useful to the regulator, who wishes to weigh the cost of eradication probabilistically against the cost of a successful biological invasion.

The method I propose involves spatially explicit, agent based modelling of the relevant fruit fly population. This proposal is inspired by similar recent works using Bayesian models to infer probability of pest absence from real data (see chapter 2).

1.2 Outline of this work

I begin this work in chapter 2 by reviewing relevant literature. In particular, I discuss two bodies of literature. The first is on the existing literature on quantitative analysis of zero-catch criteria for tephritid fruit flies. I explain zero-catch criteria in greater detail, then discuss some ways in which they have been analysed and evaluated in academic literature. The second is on existing Bayesian models for inferring of pest absence. Two example cases from the literature are discussed as inspiration for the model developed in the present work. As far as I know, these are the only such models for this problem (inferring extirpation of a pest population) presented to date. In chapter 3, I develop, and justify, a framework for modelling tephritid fruit fly invasions. Model details are discussed at an abstract level. The focus in this chapter is to present a skeleton of the method. I.e., the basic structure of the model, and core quantities of interest, are discussed. But the

model is not fully specified or fit to data. Finally, in chapter 4, I apply the methodology to the specific case of Mediterranean fruit fly, a tephritid species of particularly high economic significance in the USA and Australia. A prior distribution is defined, and inference is performed to evaluate and derive zero-catch criteria for an hypothetical case.

Chapter 2

Literature review

2.1 Introduction

The present work responds to two literatures. Firstly, it responds to the literature on zero-catch criteria for tephritid fruit flies. In particular, I propose a methodology for rigorous, model-based evaluation and revision of zero-catch criteria. Secondly, this work responds to the literature on Bayesian inference of eradication of pest populations in general. Thus far, Bayesian models of pest extirpation have been developed for at least two scenarios. However, tephritid fruit flies raise some unique challenges, which the present work discusses. Further, the question of zero-catch criteria is not broached. In this chapter, I discuss each of these literatures, and how they inform the present work, and the problem this work seeks to address. I begin by discussing fruit fly zero-catch criteria, and how they have been analysed in the literature. I then move on to discuss the Bayesian models that inspire the approach I take in chapter 3 and 4.

2.2 Zero-catch criteria

As mentioned in chapter 1, inference of pest absence is typically performed based on rules of thumb, referred to here as *zero-catch criteria* (following Meats and Clift [2005]). In some fruit fly exclusion zones that are at high risk of invasion, a network of monitoring traps are laid out year round. These traps are checked periodically (typically every 7-14 days). These are minimum periods of time over which a fly is not detected. If we do not detect a fly for the specified (temperature-dependent) number of weeks, then we may infer and declare that the incipient population has been eradicated.

The reader may wonder why declaring eradication is considered important. The primary reason is that pest free area (PFA) status is economically valuable to producers in the relevant region. This is because there may be offshore markets which require that produce is supplied from a PFA for a given pest. Even in lieu of such a requirement, PFA status may allow the supplier to receive a price premium for goods sold. As such, PFA status increases the value of goods sold.

Zero-catch criteria vary according to the species and the international market for the relevant produce (Meats and Clift [2005]). However, it is typical that they are based on the assumed length of a generation. For example, for Mediterranean fruit fly the criterion is 12 weeks, or 4 weeks and 1 generation, whichever is longer. The length of a generation is typically a constant based on the number of “degree days” that pass. Briefly, the degree days associated with a sequence of days of length n is the sum of average temperatures for each day, minus the development threshold for the relevant species. Here, the development threshold is the lowest temperature at which we assume the species is capable of developing.¹ Degree day methods are simple but ignore important aspects of fly biology

¹It may help to consider an example. Suppose over 3 days we observe minimum temperatures $\min_1 =$

such as humidity, host availability, and differential effects of temperature on different lifestages of fly – e.g. larvae, adult, etc. (Collier and Manoukis [2017]). Importantly, they are considered to be relatively arbitrary (see Meats and Clift [2005] and Collier and Manoukis [2017]).

As is hopefully clear from the discussion so far, zero-catch criteria are relatively informal. They assume, implicitly, that, if we have not detected a population in a certain fixed number of generations, then they must not be present at a sustainable population density. Meats and Clift [2005] provide point estimates of the probability that the zero-catch criteria get it wrong by declaring an outbreak when flies are still present at a sustainable level. However, crucial to the authors’ analysis is the assumption that the zero-catch criteria are generally correct. For example, they assume that the implied acceptable rate of fly detection corresponds to the lowest viable population density for the fly species in question. The justification given is that the criteria are formulated on the basis of a significant degree of practical experience. However, it is debatable whether it is possible to learn optimal zero-catch criteria by experience. In particular, in the case of Mediterranean fruit fly, there is a long-standing debate about whether spot-infestations in California are due to repeated eradications, or instead due to repeated flare-ups of one continuous low-lying population (Carey et al. [2017]). As such, it is unclear whether existing zero-catch criteria should be taken at face value, as these authors do. Further, it is not possible to evaluate criteria using the authors method as it is based on the assumption that the zero-catch criteria are correct.

Some attempts have been made to evaluate zero-catch criteria using agent based mod-

6, $\min_2 = 8$, and $\min_3 = 7$, and maximums $\max_1 = 22$, $\max_2 = 18$, $\max_3 = 19$. Assume flies don’t develop when the ambient temperature is below 10°C. Then the accumulated number of degree days in this period is $\sum_{i=1}^3 \left(\frac{\min_i + \max_i}{2} - 10 \right) = 10$.

els (see, e.g. [Collier and Manoukis \[2017\]](#)). These are complex computational models of fly dynamics. Such studies involve simulating the time to extirpation of outbreaks in various locations. The idea is to determine the time taken for the pest population to be eradicated under control measures. However, this method does not use information in survey records to inform this process.

2.3 Bayesian models for inferring absence of a pest population

The problem of inferring the presence or absence of a difficult-to-detect species has a literature of its own. Models date back to at least the 1990s, using relatively simple and general models to infer pest absence (see [Boakes et al. \[2015\]](#) and [Caley and Barry \[2014\]](#) for reviews). Such methods are attractive for their simplicity, generality, and efficiency of computation. Unfortunately, these models make strong assumptions about priors which are not defensible in general. For example, most assume a fixed, and either constant or declining population size ([Caley et al. \[2015\]](#), p. 2). This is not reasonable for the study of invasive species, for which the population growth rates are uncertain, and indeed may be increasing.

Another issue with simpler models is their relative inflexibility with respect to the structure of the model. For example, many models (see, e.g., [?, ?, ?](#)) assume 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 dependent on the spatial layout and types of monitoring traps that are deployed. Spatial density and trap type vary between situations. For example,

countries (and states within countries) differ in the types of traps used and the spatial density of traps. As such, while we may be able to learn about the probability of capture **per trap**, it is not possible to learn about the probability that a fly is captured in general.

In contrast, a class of elaborate models for inferring species extinction have recently appeared in the literature on inferring pest extirpation from survey records. In particular, two attempts have recently been made to develop 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.

2.3.1 Red fire ants

The first instance of a 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 standard Metropolis-Hastings sampling, fail. This is because they do not allow the dimension of the parameter vector to vary between draws. As discussed in chapter 4, this is a general problem faced by agent based Bayesian models. To get around this problem, the authors use a technique they call generalised Gibbs sampling. This gets

around the problem by adding a step to the Gibbs sampler in which the Markov chain moves between coordinate spaces.

2.3.2 Red foxes

The second instance of a 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 form of approximate Bayesian computation (ABC) to sample from the posterior. 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. The authors use the sum of the observations over the observation period as the matching statistic. They kept samples only if the y simulations were an exact match

with the data.

2.4 Gaps

Above, I have discussed the two models in the literature for inferring eradication of an incipient biological invasion. The current work seeks to address two gaps in the literature.

Firstly, 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 surveillance system is relatively simply. Traps are placed at fixed, known locations, and checked periodically, at regular time intervals. Further, prior research investigating the efficacy (i.e. sensitivity) of these traps exists (see chapter 3). If used carefully, this information can be leveraged through the model's priors to learn from the zero-sighting record efficiently. Since the authors discussed above used noninformative priors for key parameters, leveraging such information represents the first attempt to use prior literature to set informative priors for such a model.

2.4.1 Fruit fly literature gaps

Complex models have not been developed to study the problem of inferring fruit fly eradication from zero-sighting records. Such models, if developed, could perform a range of useful functions. For example, when used with zero-catch data, such models could be used (a) to evaluate rules of thumb for PFA reinstatement; (b) to rigorously devise new recommendations for PFA reinstatement, that are sensitive to specific features of the outbreak; and (c) to provide the decision maker with precise probabilistic estimates of

the probability of eradication given any particular length of time for which flies were not detected. Further, such models, when used with real surveillance datasets, could also be used to learn about crucial properties of fruit fly species, such as their field population growth rates, and trap capture rates.

The present work builds on the work of [Lance and Gates \[1994\]](#). In that work, the authors first estimate the probability of detection in a single trap, as a function of distance between trap and fly, based on their own experimental data. Then, they use the estimated curve to derive a point estimate of the probability of capturing one or more flies. This is done under the assumption of a uniform prior distribution for the locations of flies. Under these assumptions, the authors examine the likelihood of zero detections for various population sizes. This allows the authors to estimate how large the population needs to be before it is detected with a high degree of certainty. This work generalised that work in two ways. Firstly, a prior distribution is defined on the population size. This allows us to infer the posterior probability of eradication. Secondly, a more realistic prior is set for fly locations. In real cases, if we suspect the presence of a fly population, we will typically have some information about its whereabouts. I discuss ways for using this information to infer the probability of eradication more efficiently in chapter 3.

2.5 Conclusion

Chapter 3

General framework proposal

3.1 Introduction

3.2 The scenario

In the following, I describe a general probabilistic model of an ecological system. The size, location, and number of captures, for a biological population, are explicitly modelled. It is assumed that the data given are a number of captures (or, alternatively, sightings or detections), and that we wish to infer posterior distributions for the parameters governing size and/or locations.

3.3 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 \[1990\]](#)). It is typical, instead,

to assume that each fly has identical probability of being detected (captured). However, incorporating the spatial component allows us to leverage a useful source of prior information about trap efficacy. 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 – one one hand, we get the total proportion of flies recaptured; on the other hand, we also get the mean proportion of flies captured **per trap**, given distance between that trap and the release point. The first kind of data can be useful when the experimental setting is similar to the real-world setting for which we want to perform inference. This will be approximately the case when the types of traps, their number, and the spacing between them, are the same. However, this will often not be the case. In particular, studies vary significantly in the types and number of traps used. For example, [Lance and Gates \[1994\]](#) used Jackson traps spaced 1.6 km apart, as is standard in California. Meanwhile, [Meats and Smallridge \[2007\]](#) used Lynfield traps, spaced 0.4 m apart, as is standard in Adelaide. Further, we may wish to infer eradication of pest populations in trapping systems that are genuinely novel or untested. 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 ([DPIPWE \[2011\]](#)).

3.4 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) whether or not any flies were detected (i.e. caught in traps). Defining notation, at each time point t , we must define a

joint distribution over (a) the number of flies N_t , (b) the $N_t \times 2$ matrix of fly locations \mathbf{L}_t , and (c) an indicator variable y_t which is 1 if any fly was caught at time t .¹ I.e., the model is in essence a joint distribution $p(\{N_t, \mathbf{L}_t, y_t\}_{t=1}^T)$. Recall that our goal is to evaluate zero-catch criteria for declaring eradication. Therefore, to evaluate zero-catch criteria, we want to infer $\Pr(N_T = 0 \mid \{y_t\}_{t=1}^T = \mathbf{0}_T)$, where T is the established zero-catch criteria, based on degree day calculations. Call this quantity **the probability of eradication conditional on no detection**. To derive new zero-catch criteria, we want to find the smallest T such that $\Pr(N_T = 0 \mid \{y_t\}_{t=1}^T = \mathbf{0}_T) < 1 - \alpha$, for some threshold α . Here, α represents our risk tolerance. Call this quantity **the time to eradication**.

A Bayesian framework is assumed for inference. As such, to infer the above quantities, we must specify a joint **prior** distribution over $\{N_t, \mathbf{L}_t\}$, and a likelihood, i.e. a distribution for $\mathbf{y} \mid \{N_t, \mathbf{L}_t\}_{t=1}^T$. Instead of defining a joint prior directly on $\mathbf{N} = \{N_t\}_{t=1}^T$, I define a prior distribution over the parameters that govern the process by which the population grows or decays over time. As such, an assumed stochastic growth model structures the prior over \mathbf{N} .

3.4.1 Population size

As mentioned above, a prior distribution must be set for the population size N_t at each time point $t \in \{1, \dots, T\}$. A natural way to do this is to define a stochastic model of the population's change. Explicitly, I recommend to define a prior over N_1 directly. Then, for each $t \in \{1, 2, \dots, T\}$, define a prior on N_t , conditional on the previous values $\{N_i\}_{i=1}^{t-1}$, as well as parameters governing the growth. A simple example, which I employ in chapter 4, is the Poisson branching process with exponential growth or decay. This is a model of

¹It is assumed that the frequency of time points t corresponds to the frequency at which surveillance traps are checked.

the form

$$N_t \mid \{N_{t-1}, R_t\} \sim \text{Poisson}(N_{t-1} \exp\{R_t\}),$$

where a continuous prior distribution is defined over the R_t terms, which may have support over the whole real line.² This model has the attractive property that, when we condition on $\{R_t\}_{t=1}^T$ but marginalise out $\{N_t\}_{t=1}^{T-1}$, N_T has mean $\mathbb{E}(N_1) \exp\{\sum_{t=1}^T R_t\}$.³ This is attractive because the exponential growth model is popular in biology and ecology. Given this, in many cases, it should be relatively simple to set informative prior hyperparameters for the latent variable R_t . We might do this through expert elicitation, or through review of the relevant literature, in which population change may already be expressed in terms of growth rates.⁴

It may be worth noting that we could choose to factor in covariate information for the growth process. For example, for a given pest species, we might understand the growth of populations over time as a function of weather or rainfall. I do not discuss this possibility further in this thesis.

It may also be worth noting that there are no a priori assumptions on the population dynamics for the growth model. In principle, it should be 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 is outside the scope of this thesis, and I do not explore it further. However, this highlights key benefits of the modelling

²Alternatively, the logistic growth model, with an additional “carrying capacity” parameter, could be used.

³Note, however that $N_T \mid \{R_t\}_{t=1}^T$ is not Poisson distributed, and has variance strictly larger than its mean.

⁴For example, see [Papadopoulos et al. \[2002\]](#).

approach taken here, namely its flexibility and modularity.

3.4.2 Fly locations

As mentioned previously, I propose to explicitly model the location of each fly. As a consequence, at each time t , a prior distribution must be set on each of the N_t flies. Accounting for prior beliefs about the location of each fly introduces substantial complexity to the model. However, this can be simplified significantly, as I hope to demonstrate here.

Note that, in typical situations, we will not be interested in inferring the posterior distributions of fly locations. As such, this is a nuisance parameter.

I first discuss the option of setting an uninformative 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. Firstly, when an outbreak is suspected, it is typical that information about location is available. On one hand, 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. On the other hand, if an outbreak is known or suspected, then flies must have been detected somewhere. Most likely, the locations of these detections will be known to the analyst. When the fly species has low dispersal

distances (as e.g. medfly does) these detection locations are highly informative. Therefore, an informative prior, utilising this information, formally or informally, is recommended.

It is assumed the flies are typically clustered in space. This may be justifiable in practice. For a small, seed population, a population with low density will die out due to the allee effect. However, when this assumption is not realistic, an alternative prior on locations should be considered.

Let L_c be a bivariate random variable describing the centre of the population. Let $L_{i,t}$ be a bivariate random variable describing the location of fly i at time t . It seems natural to assume that $E(L_{i,t} | L_c) = L_c$, for any (i, t) . This model assumes that the centre of the population does not move over time. Further, we can specify that $(L_{i,t} \perp\!\!\!\perp L_{i',t'}) | L_c$, for $(i, t) \neq (i', t')$. I.e., conditional on the centre of the population, the fly locations provide no information about each other. This gives the computational advantage that we do not need to track flies locations across time. At each time period, they scatter independently.

The benefit of these assumptions is priors can be set on the parameters governing L_c and $L_{i,t} | L_c$ separately. The prior on $L_{i,t}$ describes the distribution of fly dispersals. Information on this quantity, for a given species, will often be available in scientific literature.

3.4.3 Probability of capture (likelihood)

Recall from above that the number of captures (and therefore the data for this model) at time point t is written as y_t , for $t \in \{1, \dots, T\}$. Recall that it is assumed that the trap locations are each fixed and known with certainty. Then, it is assumed that the probability that 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. Then, the probability that fly i is caught at any trap is simply

$$p_{i,t} := 1 - \prod_{k=1}^K (1 - p(d_{i,k,t})).$$

Going further, the probability that any fly (out of N_t flies) is caught at any trap is

$$p_t := 1 - \prod_{i=1}^{N_t} (1 - p_{i,t}).$$

Therefore, conditional on \mathbf{L}_t and N_t , we can define

$$y_t = \begin{cases} 1 & \text{one or more flies caught at time } t \\ 0 & \text{otherwise.} \end{cases}$$

For each time point t , y_t has the Bernoulli distribution with mean p_t .

The probability of capture function $p(\cdot)$ should be based on prior analysis of release-recapture data, already discussed, and may be deterministic or random. For example, we might regress captures on distance, from release-recapture data, and allow coefficients to vary randomly. Then, the posteriors would form the priors for the present model.

Two things should be noted here. Firstly, y_t is not the number of captures per se, but rather is binary as defined above. This simplification can be made because we are only interested in the case where no flies are detected. This is because the primary application of the model is to evaluate and derive zero-catch criteria. To extend the model to the case where we observe non-zero captures, we can simply define y_t to be the sum of Bernoulli trials for $i \in \{1, \dots, N_t\}$, each with mean $p_{i,t}$.

Secondly, this model of captures takes for granted the common assumption that there

is no interference between traps (see ?). This assumption is essentially that the probability that a fly is captured at a given trap is not affected by the presence of other traps. The justification is that $p(\cdot)$ is typically estimated to decrease quickly as a function of distance. This is because traps are generally ineffective as attractants. Therefore, it is typically the case that $p(d_{i,k,t})$ is very small for all but at most one trap. Therefore, the effect of discounting the possibility of being caught there is negligible.

NOTE: Delete the next paragraph?

If the researcher has cause to believe that interference may be non-negligible, a simple correction can be applied. Without loss of generality, suppose we are interested in a single fly in a single trapping period. Let q_k be the probability that that fly is captured at trap k , calculated using the distance function above. Let q_0 be the probability that the fly is not captured at all. The set $\{q_k\}_{k=0}^K$ are probabilities of exhaustive and mutually exclusive events. Therefore, we can redefine the probabilities of trap-specific capture (or no capture) as $q'_k = q_k / \sum_{i=0}^K q_i$.

Finally, the reader should note that it is assumed that this is homogenous across time. I.e., the population size N_t and locations of flies \mathbf{L}_t tell us everything we can know about whether a fly is captured at time t .⁵

3.5 Conclusion

⁵As such, it is assumed implicitly that temperature has no effect on fly behaviour. This is a strong assumption, against which there is some evidence (see [Bali et al. \[2021\]](#)).

Chapter 4

Case study: Mediterranean fruit fly (*C. Capitata*)

4.1 Introduction

In the previous chapter, I proposed a model for evaluating and proposing zero-catch criteria in specific situations, for various locations, seasons, and species of fruit fly. In this chapter, I illustrate the method by applying the model to an hypothetical outbreak. Mediterranean fruit fly is chosen for its economic significance, and Adelaide is chosen because of the availability of research on trapping sensitivity performed there. The analysis is primarily illustrative. As before, modelling is performed with a view to evaluating existing zero-catch criteria, and toward developing new criteria.

4.2 Medfly (*Ceratitidis capitata*)

Mediterranean fruit fly (*Ceratitidis Capitata*) or *medfly* are a particularly salient species of tephritid fruit fly. Medfly has 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 ([Sciarretta et al. \[2018\]](#)). 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 species.

Medfly are very hard to detect at low levels. As with other fruit fly species, monitoring is typically performed with the aid of traps fitted with chemical attractants. These traps are relatively ineffective. 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 sterilised flies. If this is an accurate reflection of trap sensitivity, then it is possible that very large populations will be undetectable for significant periods of time. Further, medfly are known to disperse only small distances (?). This means that, if they are in a location that is not heavily monitored, they may evade detection for long periods.

4.3 Data

4.3.1 Zero-sighting surveillance data

As mentioned above, I do not use real data to estimate parameters. Instead, I model a hypothetical situation. The situation is intended to simulate the conditions described in

codes of practice for use of zero-catch criteria (see [DPIPWE \[2011\]](#)). The general 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 that no flies are detected at any point in this period.

It is preferable to specify a location, so that real weather data can be used to inform the model's hyperparameters (see [4.4.1.1](#)). Therefore, it is assumed that the outbreak takes place in Adelaide. Adelaide is a key location for fruit fly outbreaks. Further, for medfly, evidence from trap sensitivity studies is available from experiments performed in Adelaide, but no other Australian city.

The zero-catch criteria is 12 weeks, or 28 days and one generation, whichever is longer ([Meats and Clift \[2005\]](#)). In a typical Australian summer, a Medfly generation takes 28-34 days ([DPIRDWA](#)). Therefore, the period I look at is over 12 weeks.¹ I.e., in the terminology of [3](#), we set $T = 12$. To evaluate this criteria, we want to find the probability of eradication after $T = 12$ weeks, i.e. $\Pr(N_{12} = 0 \mid \mathbf{y} = \mathbf{0}_{12})$.

It is assumed that general surveillance traps are spaced in a 400×400 metre grid, year round. We assume that a fly is caught at the centre of the grid (without loss of generality). Then, 16 *supplementary* traps are placed within a 200 metre of the location of the first detection (see figure [4.1](#)). These traps are checked weekly for 6 weeks ($t \in \{1, \dots, 6\}$) before being removed. Following this, we continue to monitor with only the original general surveillance traps. It is assumed that no fly is caught at any point in this period. Pest free area status is reinstated after 12 weeks. After this, we continue to observe no

¹See also [PIR \[2017\]](#), who state that the suspension period is 12 weeks in an Adelaide summer.

fruit flies indefinitely.

As mentioned previously, it is assumed that trap locations have fixed, known locations. In particular, we assume that monitoring is intensified for the first 6 weeks ($t \in \{1, \dots, 6\}$). 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.² See ?.

It is assumed that the outbreak starts on November 1, 2020. The year 2020 is chosen rather than 2021, so that weather data is available for at least 1 year from the start of the monitoring period. (The time of writing is May, 2022.) Data on historical daily temperature averages (the mean for each day) were obtained from the Bureau of Metereology.

4.4 Model

I now propose a model for the case discussed above. This discussion builds on 3, where I outlined the model in broad generality. There, I discussed the model while leaving some key situation-specific hyperparameters and distributions unspecified. For example, the prior distribution on the initial population size N_1 , and the relationship between probability of capture and distance between fly and trap $p(d)$ were unspecified. Here, hyperparamters and distributions are proposed and justified.

As in the previous chapter, the model is broken into priors and likelihood in the following way. Firstly, (1) The size of the population (number of individuals); (2) the locations

²It is typical to wait until at least 2 flies have been detected near each other for an outbreak to be declared. To illustrate the method in a simplified setting, I suppose that one fly detection is sufficient.

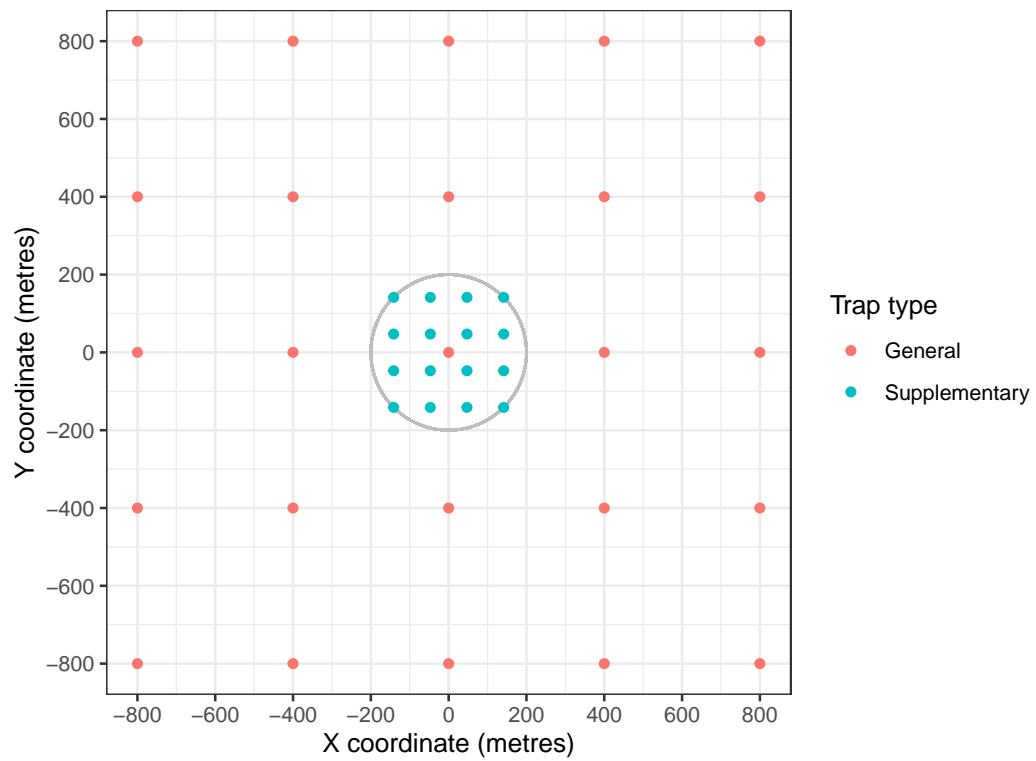


Figure 4.1: Illustration of the hypothetical trapping grid. Grey circle represents 200m radius disc surrounding the site of the most most recently detected medfly specimen.

of individuals and traps; and (3) number of individuals caught in traps, conditional on (1) and (2). To structure discussion, I discuss these elements in turn, beginning with prior distributions.

Here, we are modelling the risk of an adverse event (namely an undetected pest invasion). In such cases, we might consider examining a worst case scenario. In this case, this could be done by specifying priors such that we assign high density to cases where (a) the growth rate is very close to zero, so that the fly population is capable of persisting at below-detectable levels indefinitely, or (b) flies are located far away from surveillance traps. Given these considerations, it should be trivial to identify worst-case scenarios where we can almost never be certain that flies are eradicated, given any length of time. However, such results are likely unreasonable, and do not accurately reflect our prior state of information. Nonetheless, I attempt to err on the side of pessimism about the while making the prior distribution as realistic as possible.

4.4.1 Prior distributions

4.4.1.1 Population size N_t

In this case, N_1 is the first week after the most recent fly detection. I have chosen to set $N_1 \sim \text{Geometric}(1/20)$. This is chosen as it is a discrete distribution with right skew, and a relatively large amount of mass in the region of $x = 0$, corresponding to the situation where flies are already eradicated (see figure 4.2).³ The mean of the geometric distribution is chosen arbitrarily. The primary goal is to have a small population on average, with non-zero risk of a population size greater than 50. However, it is not clear, without prior

³The geometric distribution is also a natural choice for this latent variable; I do not explore this further here.

domain knowledge, whether this distribution is empirically reasonable. Population counts do not exist for past outbreaks. This issue is discussed further in section 4.7.

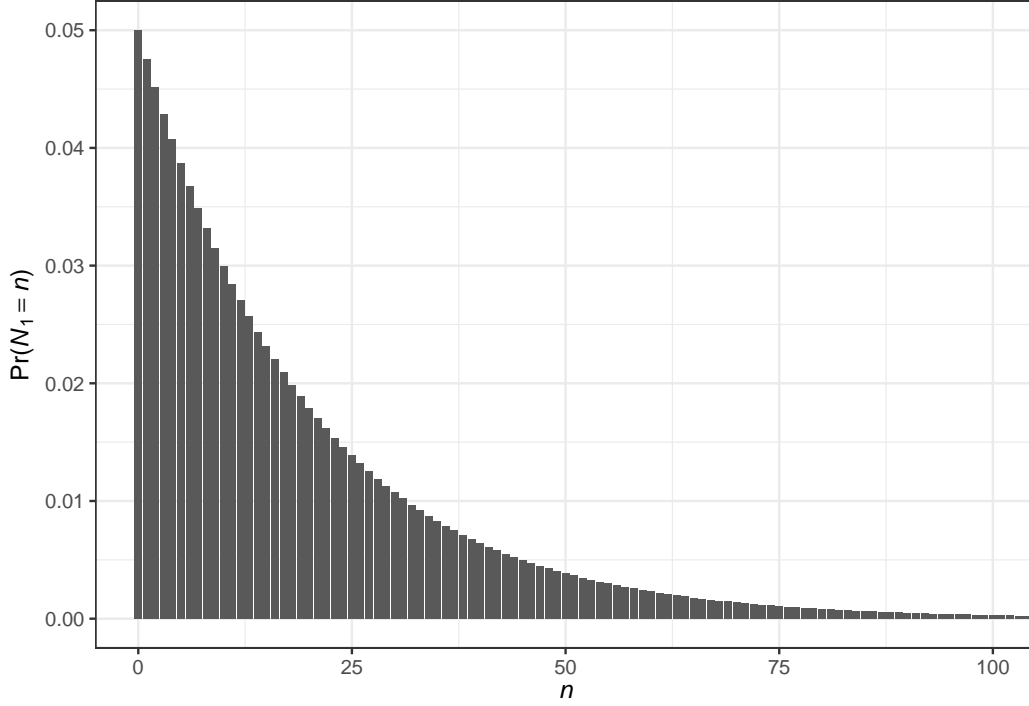


Figure 4.2: Prior distribution of initial population size N_1 .

As for N_t , for $t \in \{2, \dots, T\}$, I assume the Poisson branching process with exponential growth, discussed in 3. To recap, it is assumed that, for $t \in \{2, \dots, T\}$, $N_t \mid \{N_{t-1}, R_t\} \sim \text{Poisson}(N_{t-1}e^{R_t})$.

It is assumed, primarily for convenience, that $R_t \sim N(\mu_t, \sigma_t^2)$. Choices for the hyperparameters $\{\mu_t\}_{t=2}^T$ are informed by the results of ?. The authors transform observed captures C_t as $\ln(C_t/C_{t-1})$, and fit a simple model to the resulting values from field data on Medfly captures.⁴ In particular, they estimate the mean *daily* growth rate, conditional

⁴Notably, temporal autocorrelation is ignored.

on mean daily temperature, for each day t , to be

$$E(R_t \mid \text{Temp}_t) = \alpha \text{Temp}_t^2 + \beta \text{Temp}_t + \gamma,$$

where $\alpha = -0.000386$, $\beta = 0.0279$, and $\gamma = -0.374$. To get the daily mean growth rates, observed daily temperatures are plugged into this formula. Then, weekly mean growth rates μ_t , are derived by summing over daily growth rates within each week. The dataset used by ? is small, consisting of only 24 observations. Ideally, we would quantify uncertainty about these estimates. However, this is difficult, as the authors do not provide data, or an analysis of the variance of residuals for their model. I do not explore this further here, though it should be considered in real applications.

The choice for σ_t^2 is necessarily more arbitrary than the choice for μ_t . As mentioned above, ? do not provide an analysis for the variance of residuals for their model. Therefore, it is difficult to meaningfully quantify prior beliefs about the variance of the growth rate. Increasing the variance increases the prior probability that populations die out, due to runs of “bad luck”. Therefore, smaller variances are more pessimistic. With this in mind, I have chosen to set the standard deviation for daily growth to $\sigma_t = \sigma = 0.1$. In my view, this is roughly consistent with the plot provided by the authors (see figure 4.3). However, as this choice is arbitrary, it should be treated with skepticism.

```
knitr::include_graphics('references/ksplot.png')
```

4.4.1.2 Spatial location

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

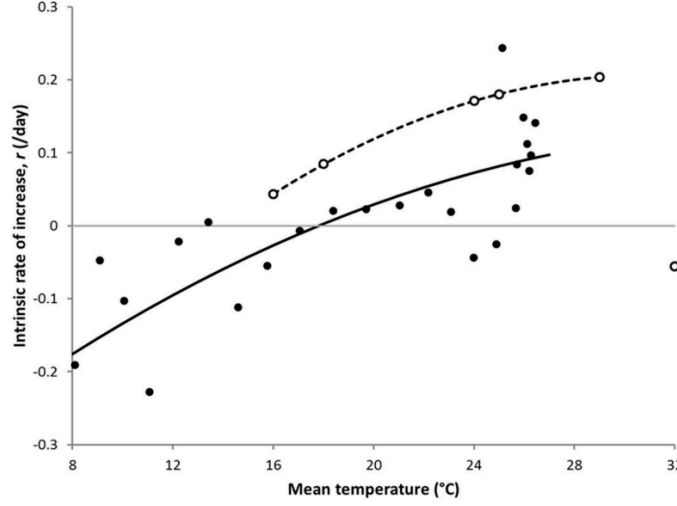


Figure 4.3: Relationship between population increase $\ln(C_t/C_{t-1})$ and mean daily temperature. Taken from @ks2019. The solid line is fit to field data (black points); the dashed line is fit to lab data (white points).

chapter, prior distributions must be set for the location of the population centre, and for dispersals of individual flies from that centre.

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

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

where Normal_2 is the bivariate normal distribution, $\mathbf{0}_2$ 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 close to the centre of the grid, where a fly was detected most recently (we suppose). 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.⁵ This makes

⁵For details about how this prior was arrived at, see appendix.

sense, as the setting of supplementary traps close to the centre, as is standard, belies a prior belief that other flies are likely to be located in the vicinity of the first capture.

4.4.1.2.2 Individual fly dispersals Let $L_{i,t}$ denote the location of fly i at time t , as in the previous chapter. I assign this quantity the prior distribution

$$L_{i,t} \mid L_c \sim \text{Normal}_2(L_c, 12.5^2 I_2),$$

where the notation is defined as in the previous section above. The variance is chosen so that ~95% of flies are within 30 metres of the population centre. Here, 30 metres is chosen arbitrarily. It reflects a belief that flies typically do not disperse very far. This is a pessimistic (“worst case”) assumption. When flies are spread further from their population centre, it is more likely that at least one is close to a trap. As such, large populations of flies are less likely to go undetected.

The normal distribution is chosen for a few reasons. Firstly, it is conceptually simple and intuitive to parameterise. This helps with expert elicitation. Secondly, the location has a simple marginal distribution, thanks to the fact that a normal random variable with a normal mean is itself normal.⁶ Thirdly, the distance between a normal random variable and its mean has a known distribution. In particular, if $X \sim \text{Normal}_2(\boldsymbol{\mu}, \sigma^2 I_2)$, then $\|X - \boldsymbol{\mu}\|^2 \sim \Gamma(1, \sigma^2/2)$, where $\Gamma(a, b)$ is the gamma distribution with shape a and scale b . In this case, for any fly i we have $\|L_{i,t} - L_c\| \mid L_c \sim \Gamma(1, 12.5^2/2)$. Similarly, the *marginal* squared distance between fly i and the origin is $\|L_{i,t}\|^2 \sim \Gamma(1, (12.5^2 + 160^2)/2)$. Knowing this allows us to easily compare and calibrate the distribution against experimental results.

⁶This is just the standard conjugacy of the multivariate normal mean for the multivariate normal likelihood, when the covariance matrix is fixed.

This, in turn, makes elicitation of priors simpler and more intuitive. (It allows us to visualise, for example, the distribution of distances to the origin and to the population centre.)

There is evidence suggesting that Medfly dispersal distance is in fact distributed as a power law (see, e.g., [Meats and Clift \[2005\]](#) and [Plant and Cunningham \[1991\]](#)). In particular, the distributions estimated by these authors have far heavier tails than the distribution proposed above. As mentioned above, the normal prior implies that squared dispersal distances are gamma random variables, the square roots of which are Nakagami distributed. The Nakagami distribution, parameterised as above, has a far thinner right tail than a power law. As such, the present priors may heavily underestimate our best guess about the dispersal distances of individual flies. In further work, we might investigate whether this has a large effect on the results through sensitivity analysis (see section [4.7](#)).

It may also be worth noting that, in real cases, the assumption of zero mean and spherical covariance matrix ($\sigma^2 I_2$) may not be reasonable. Dispersals may have non-zero mean (due to wind direction) and the distance and/or direction of individual dispersals may be correlated.⁷ Further, it may not be reasonable to assume, as I have done here, that the fly population cannot move across time. Ideally, the importance of these assumptions should be checked based on the case at hand (e.g. properties of the situation or species in question). Extending the model in various ways to meet these problems is beyond the scope of this work, but warrants further investigation.

⁷These claims are argued for Medfly by [Baker et al. \[1986\]](#).

4.4.2 Likelihood

The likelihood is the distribution of $y_t \mid \{N_t, \mathbf{L}_t\}$. Here, it is

As mentioned previously, results of trap sensitivity studies are used to inform the likelihood of capture. In particular, I use the results of ?. These authors estimate that the probability of capture for any given fly in any given trap is given by the power law

$$p(d) = \begin{cases} ad^{-b}, & d > 1 \\ a & 0 \leq d \leq 1. \end{cases}$$

Here, $a = 0.4702111/2$, $b = 1.37$, and d is the distance between the fly and the trap at the start of the period.⁸ Thresholding is introduced because (a) the function does not yield valid probabilities for small enough d . This function is used for convenience as it is provided by the authors of the study, and data is not publicly accessible. In the context of a more detailed analysis, it may be beneficial to consider uncertainty in the probability of capture by specifying hyperprior distributions for a and b . I do not explore this further here, as the model is intended to be illustrative only.

Finally, an adjustment is made to $p(d)$, before the formulae from the previous chapter are used. In $p(d)$ we have the probability of capture over the lifetime of the individual. However, for any given week, we wish to know the probability of reporting capturing a fly over that week. It is assumed that the lifetime is roughly 4 weeks. The correction is reported in detail in the appendix.

⁸Note that these are transformed from the values reported by the authors. The function is (a) transformed from percentage to proportion scale, (b) halved, as the traps only capture *male* medflies, which consist of approximately half of the population, and (c) converted from kilometre to metre scale.

4.5 Sampling

Recall that we are interested in inferring the probability of eradication conditional on no detections, namely $\Pr(N_T = 0 \mid \mathbf{y} = \mathbf{0}_T)$, for any cutoff T . As such, we must infer the distribution of $N_T \mid \mathbf{y} = \mathbf{0}_T$. Note that this is distinct from the distribution of $N_t \mid \mathbf{y} = \mathbf{0}_T$, where $t < T$. At time t , we do not know that we will not get another detection up to time T . Rather, we only know that we have not detected any flies yet **up to now** (i.e. time t). Therefore, conditioning on the event $\mathbf{y} = \mathbf{0}_T$ means that we condition on information not yet available to us.

Clearly, the posterior distribution of N_t depends on integrals over the locations of each fly. These integrals are intractable. Therefore, we resort to sampling to approximate $\Pr(N_T = 0 \mid \mathbf{y} = \mathbf{0}_T)$. A simple rejection sampler is used.

There is a key difficulty with sampling with such methods for this case. This model is *agent based*, insofar as the individual properties of a random number of individuals (agents) are explicitly represented. In this case, at any time t , there is a location $L_{i,t}$ for each of N_t flies. Since N_t is itself unknown, this means that the number of parameters (namely the number of $L_{i,t}$ terms) is unknown.⁹ As mentioned in chapter 2, this introduces a difficulty, as standard Markov chain Monte Carlo techniques, such as basic Metropolis-Hastings, fail when this is the case.

To get around this problem, I have used a simple rejection sampler. This sampler is intuitive, simple to implement, and relatively efficient for this problem (for the case discussed here, roughly 25% of samples are *not* rejected). However, other methods exist that may be worth exploring, for analogous problems where the rejection rate of ABC is

⁹This 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]).

higher.¹⁰

4.5.1 Sketch of the algorithm

Here I present an algorithm for drawing *at least* S independent samples from the distribution of $N_t \mid \mathbf{y} = \mathbf{0}_t$, for all t up to some arbitrary cutoff T . Note that this quantity is distinct from $N_t \mid \mathbf{y} = \mathbf{0}_T$. At time t , we do not know that we will not get another detection up to time T . We only know that we have not detected any flies yet **up to now** (i.e. time t).

- Set a number of time periods T that is arbitrarily large, so that it covers all time points of interest.
- For each sample j :
 - Draw the number of flies and their locations for all time points from their prior distributions.
 - Draw an indicator variable determining whether a fly is captured for each time point $\mathbf{y} = \{y_t\}_{t=1}^T$.
 - Store the first (smallest) t such that $y_t = 1$. Call this quantity τ_j . If $\mathbf{y} = \mathbf{0}_T$, set $\tau_j = \infty$.
- Stop when the number of samples with $\tau_j = \infty$ is S .

For any number of weeks c , we can extract the subset of draws such that $\tau_j > c$. This can be treated as a set of independent posterior draws from $N_j \mid \mathbf{y} = \mathbf{0}_j$. Depending on how often we observe $\tau_j = \infty$, we may end up with a much larger number of samples

¹⁰The best known “trans-dimensional” Markov sampler is the reversible jump MCMC of [Green \[1995\]](#), generalised by [Keith et al. \[2004\]](#).

than S . But we end up with exactly S samples such that $\tau_j > \infty$, and therefore S draws of $N_T \mid \{y_t\}_{t=1}^T = \mathbf{0}_T$, where T is the final time point we consider.

4.5.2 Sampling results

At least 10,000 samples were taken. The acceptance rate for sampling was approximately 0.25. This relatively high level of acceptance is due to the low likelihood of captures, across most of the high prior density region of the model space.

4.6 Results

Results are shown in 4.4. The blue and red lines show the prior and posterior probability of eradication for each (weekly) time point after the monitoring period begins on November 1. Under the model, the posterior probability of extinction after $T = 12$ weeks is approximately 0.443.¹¹ The first week for which the posterior probability of eradication is greater than 95% is after 35 weeks, much later than the PFA date.

4.7 Discussion

Here, I discuss the results of the model, and subject the model to scrutiny. Methods of model validation are discussed.

4.7.1 Problems with growth and capture models

The model depends heavily on the models of population growth and trap sensitivity employed. However, the propriety of each of these models may be questioned. In the case

¹¹Unfortunately, it is not straightforward to visualise the prior or posterior density of this quantity.

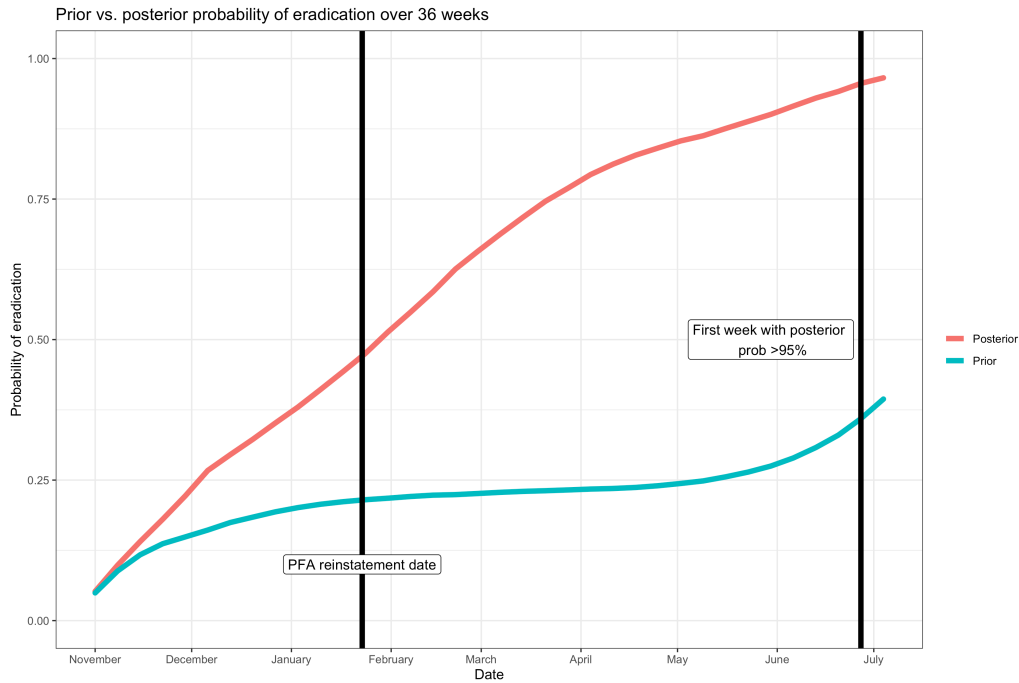


Figure 4.4: Prior vs. posterior probability of eradication over 36 weeks.

of population growth, estimates have been used from a published model. This model was fit to data from an orchard in Thessaloniki, Greece (?). It is not clear that this model is ecologically valid for Adelaide, as important climactic variables, such as humidity, may differ. Further, we may also question the premise of estimating population growth rates from trapping data. This is because the relationship between population size and number trapped is confounded by fly behaviour. It may be the case that flies are less active in some populations, so that the sensitivity of traps varies across time. In future work, detailed, black-box simulation models of medfly population processes, such as MED-FOES, should be considered (Manoukis and Hoffman [2014]).

In the case of trap sensitivity, we might question the heavy reliance of the model on the results of only one study. There is a significant body of release-recapture literature

for Medfly (see [Andress et al. \[2013\]](#) for a thorough review). This literature spans across continents, between USA, Australia, and Europe. For this case study, I have referenced only [Meats and Smallridge \[2007\]](#). This is because it is the only study that has been performed in Australia. However, estimates of trap efficacy are lower than is typically observed in other studies. It is not clear whether this is due to (a) some feature of the methodology or materials used, such as low quality sterilised flies; or (b) the efficacy of traps used in Australia. In lieu of further studies, we may wish to perform meta analysis across studies to derive a more plausible prior distribution of capture probabilities $p(d)$ at each distance d .

Importantly, we do not model uncertainty in the parameters of either (a) the model of growth as a function of temperature, or (b) the model of probability of capture as a function of distance between fly and trap. This may cause us to *overestimate* the probability of eradication. For example, and intuitively, “the model” may conclude that, because there have been no captures, flies are eradicated; when it may have been the case that, in reality, traps are not as sensitive as we thought they were.

4.7.2 Arbitrary choices

The present model is based on a number of arbitrary choices. Some of the most important of these are (a) the variance of growth rate R_t ; (b) the distribution of the initial population size N_1 ; and (c) the distribution of dispersals. In principle, it should be possible to learn the distributions of the growth rates and dispersals from data. However, it is unlikely that the distribution of the population size N_1 can be calibrated empirically. For this distribution, it would be advisable to perform sensitivity analysis. This would see whether the model is sensitive to changes in our prior beliefs about the size of the initial

population. This is not performed here, as the present model is primarily illustrative, and this is beyond the scope of the work.

4.7.3 Simplifying assumptions

Simplifying assumptions of the model have already been mentioned throughout the text. For example, it is assumed that there is no interference between traps. This may cause us to overestimate the probability of capture for any given fly.

An important simplifying assumption is that traps are the only mechanism we have for detecting flies. Here, we have assumed that the only way that flies can be detected is with monitoring traps. However, when fruit fly outbreaks occur, coordinated efforts are made to inspect fruit for fly larvae. Further, the public are educated in fruit fly detection. As such, there are several pathways through which an incipient population of flies may be discovered. There is a potentially significant amount of information in this. When we condition only on failure to detect with traps, we ignore the fact that flies may or may not have been discovered through other means.

4.7.4 Limitations

A key limitation of the method used is that we do not get a posterior distribution over the probability of eradication. In general, it would be desirable to quantify uncertainty about the result. In future work, reparameterisations of the model should be investigated to allow for such an extension.

4.8 Conclusion

Chapter 5

Appendices

5.1 Appendix 1: Full model statement

Population size

Initial no. of flies:

$$N_1 \sim \text{Geometric}(1/20)$$

Number of flies:

$$N_t \mid N_{t-1} \sim \text{Poisson}\{N_{t-1} \exp(R_t)\}, \text{ where}$$

$$R_t \sim \text{Normal}(\mu_t, 0.07^2), \quad t \in \{2, \dots, T\}$$

Fly locations

Population location:

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

Fly locations:

$$L_{i,t} \mid L_c \sim \text{Normal}_2(L_c, 12.5^2 I_2) \quad i \in \{1, \dots, N_t\}, \\ t \in \{1, \dots, T\}$$

Detection model

Number of traps:

$$K \in \mathbb{N}_+$$

Trap locations:

$$L_k^{\text{trap}} \in \mathbb{R} \quad k \in \{1, \dots, K\}$$

Dist. btw. fly i and trap k at time t :

$$\delta_{i,k,t} := \|L_k^{\text{trap}} - L_{i,t}\| \quad i \in \{1, \dots, N_t\}, \\ k \in \{1, \dots, K\}, \\ t \in \{1, \dots, T\}$$

Individ. cap. prob.:

$$p_{i,t} = 1 - \prod_{k=1}^K (1 - p(\delta_{i,k,t})), \quad i \in \{1, \dots, N_t\}, \\ t \in \{1, \dots, T\}$$

Aggregate cap. prob.:

$$p_t = 1 - \prod_{i=1}^{N_t} (1 - p_{i,t}) \quad t \in \{1, \dots, T\}$$

Detection:

$$y_t \mid \{\mathbf{L}_t, N_t\} \sim \text{Bernoulli}(p_t), \quad t \in \{1, \dots, T\} \\ \mathbf{y} := [y_t]_{t=1}^T$$

5.2 Appendix 2: Population location prior

A trick is used to derive a prior for the case presented in chapter 4. 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).

Suppose we have K traps indexed by $k \in \{1, \dots, L\}$. Suppose also that we have a prior distribution over the population size N , given by $N \sim \text{Poisson}(\lambda)$, with $\lambda \sim \text{Exponential}(1/20)$. (This is the prior distribution for N_1 in chapter 4. 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. Suppose that the centre of the population is distributed uniformly over a 1600 m^2 trapping grid. 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.

Sampling was used to infer the posterior distribution. Under the above assumptions, the posterior resembles a bivariate normal distribution with mean $\mathbf{0}_2$ and variance $160^2 I_2$.

5.3 Appendix 3: Distance between a bivariate normal random variable and its mean is gamma distributed

Here I prove a claim made in chapter 4. This is the claim that $X \sim \text{Normal}_2(\boldsymbol{\mu}, \sigma^2 I_2) \implies \|X - \boldsymbol{\mu}\|^2 \sim \Gamma(1, \sigma^2/2)$, where $\Gamma(a, b)$ is the gamma distribution with shape a and scale b .

Let $X \sim \text{Normal}_2(\boldsymbol{\mu}, \sigma^2 I_2)$ so that $X_i \sim \text{Normal}(\mu_i, \sigma^2)$, $i \in \{1, 2\}$. Also, let $Z_i \sim \text{Normal}(0, 1)$, $i \in \{1, 2\}$. Then,

$$\begin{aligned} Y &= \|X - \boldsymbol{\mu}\|^2 \\ &= (X_1 - \mu_1)^2 + (X_2 - \mu_2)^2 \\ &= \sigma^2(Z_1^2 + Z_2^2). \end{aligned}$$

Therefore, $Y \sim \sigma^2 \chi^2(2)$, by the well known theorem that the sum of n independent standard normal random variables is distributed as $\chi^2(n)$. This distribution is equivalent to $\Gamma(1, 1/2)$, where Γ is defined as above. By the scaling property of the gamma distribution, we have $Y \sim \Gamma(1, \sigma^2/2)$.

5.4 Appendix 4: Probability of capture time adjustment

In chapter 4, I explain that we use estimates of the probability of capture over the lifetime of an individual fly. If these were used without correction for weekly capture probabilities, we would overestimate the probability of capturing any given fly. Here, I explain a correction used to adjust the probabilities of capture, when we are interested in the probability of capture over only one week.

Suppose there is just one fly. Let q be the probability that the fly is captured over its lifetime (4 weeks). Assume that each week, the fly is captured with daily capture probability p . We have

$$\begin{aligned}
 q &= \Pr(\text{fly caught in lifetime}) \\
 &= \Pr(\text{fly caught on week 1, 2, 3, or 4}) \\
 &= 1 - \Pr(\text{fly not caught on week 1, 2, 3, or 4}) \\
 &= 1 - (1 - p)^4 \\
 \implies p &= 1 - (1 - q)^{1/4}.
 \end{aligned}$$

Therefore, the probability that the fly is caught in any given week is $1 - (1 - q)^{1/4}$, where q is the lifetime probability of capture.

In chapter 4, it is assumed that Medfly lifetimes are four weeks long. Note, however, that we could substitute any proportion for $1/4$. Further, one could define the proportion as a random variable with a prior distribution, if we wish to model uncertainty about fly lifetime lengths.

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