APARP Project GMS1520: Estimating the success of vertebrate pest eradication and control programs

Final report

Peter A Caley[1], David S.L. Ramsey[2], Simon C Barry[1]

[1]CSIRO Computational Informatics/Biosecurity Flagship, GPO Box 664, Canberra, ACT 2601

[2]Arthur Rylah Institute, Department of Environment & Primary Industries, 123 Brown Street, Heidelberg, Victoria, 3084

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Contents

Figures

Tables

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Executive summary

This report details work completed in developing and applying innovative quantitative techniques to estimate the progress of vertebrate pest control programs. The report outlines new techniques in the development of quantitative methods for combining possibly disparate types of monitoring data to make better inferences on the effectiveness of vertebrate pest control programs. First, the report describes the application of the Approximate Bayesian Computational (ABC) methods to the analysis of monitoring data arising from vertebrate pest control operations, using the red fox incursion in Tasmania as a case study. Second, a fully Bayesian spatial detection model was developed to estimate population density from detection/non-detection data in situations where the sampled population is not individually identifiable. The methods underlying this model were developed after the application of ABC type analysis to these data proved unsatisfactory.

Applying the ABC method to data on red fox carcass discoveries in Tasmania illustrates how it can provide inference on model parameters in addition to measures of management success, such as the probability of eradication or whether eradication can be achieved under the current management regime. This includes the likely distribution of the population if still extant, its demographic parameters, and likely timing of introductions. We also demonstrate how the technique can be used to inform management decisions by forecasting the probability of population extinction in future years, along with the probability of a further carcass being detected either as road kill or after being shot by hunters. Combining these two measures can provide an estimate of when management authorities will either know that eradication is not yet attained (e.g. a future carcass detected) or the population is extinct.

We first tested the Bayesian spatial detection model on known (simulated) populations, then applied it to estimate the distribution and abundance of foxes in the Grampians National Park from remote camera surveys collected during the ‘Grampian Ark’ project. The resulting density estimates appear reasonable, although the confidence intervals are wide, reflecting the sparseness of the data arising from the intensive fox control operations in place. The new computational method appears to work efficiently, but the resulting parameter estimates were highly skewed and requires data with many sampling occasions, which may limit its use in certain situations. Further investigation of this new model is ongoing.

1 Introduction

During a vertebrate pest eradication program it is critical to have timely provision of information to support decision making. This information would inform management decision points such as:

1. What is the most likely size of the pest population under control, and what are its underlying demographic parameters?

2. Are the current management actions achieving the aim of driving a pest population into decline [a necessary criteria for eradication (Bomford and O'Brien 1995b)?

3. What is the likelihood that the target population has been successfully eradicated, given the available monitoring information?

Measuring the underlying parameters of a low density pest population presents special challenges, especially when the information available is from a diverse range of sources (e.g. public sightings, camera traps, road kills, DNA forensics) spread across space and time. The space-time complexity makes explicit traditional probability (likelihood) calculations near impossible, especially if the data are sparse (as is often the case in the early stages of invasions). Indeed, the problem is not amenable to formal likelihood-based statistical inference other than for grossly simplified non-spatial models of the process (see Caley and Barry under review and references therein).

There is a need to develop robust techniques for synthesizing such data within operational timeframes to enable pest managers to make the best decisions possible. Ideally techniques should be able to incorporate prior knowledge of population parameters, but also be appropriately conditioned on available data.

This project aimed to:

- develop methods and demonstrate how disparate types of data collected (perhaps) haphazardly in space and time can be used to make quantitative inferences about the underlying vertebrate pest population under control;
- demonstrate how the proposed inferential techniques may be used to monitor and inform vertebrate pest control programs in real time;
- communicate the technique to stakeholders.

We focus initially on the application of Approximate Bayesian Computational (ABC) methods to the kinds of sparse data often available during the early or late stages of vertebrate pest eradication programs. Where ABC methods are unsuccessful or unnecessary, we explore alternative conventional Bayesian methods.

2 Estimating the success of vertebrate pest eradications using Approximate Bayesian Computation

2.1 Methods

2.1.1 BACKGROUND ON APPROXIMATE BAYESIAN COMPUTATION

Approximate Bayesian Computation (ABC) is a powerful method combining Monte Carlo-type simulation, Bayesian statistics and data for making inference on dynamic processes that may be difficult or impossible to observe directly. ABC methods are a relatively recent methodological technique made possible by increasing computing power. The approach differs from pure Monte Carlo simulation techniques in that the observed data (e.g. sightings, bait take etc) actively constrain the simulations so that model inference is conditioned on the observed data. In addition, the Bayesian nature of ABC inference allows straightforward incorporation of prior knowledge (belief) of population parameters. The method has recently come to prominence with increasing desktop computer power, though has been applied predominantly in the field of population genetics (Csillery *et al.* 2010). In particular, being "likelihood-free", ABC methods are useful for inferring posterior distributions where likelihood functions are computationally intractable or too costly to evaluate (Toni *et al.* 2009). They have recently been proposed as having application to making inference during biological invasions (Rasmussen and Hamilton 2012).

A brief outline of the rationale and process of ABC is as follows:

- Let θ be the model parameters generating the observed data D. In our first case-study (detailed below) the model describes the spatial and temporal distribution of foxes and the data are spatially-referenced observations of road-killed and hunter-killed foxes. Managers are particularly interested in estimating the model parameters as a means of making inference about the population under control.

- A stochastic (i.e. chance) process often underlies the likelihood computation, and this process may be complex, making explicit probability (likelihood) calculations difficult or impossible. Thus, calculating the probability of the data given the parameters [written $P(D\,|\,\theta)$] may be intractable, either quickly enough or theoretically, to enable standard likelihood-based inferential approaches.

- The ABC approach side-steps the need to compute the likelihood (hence is sometimes referred to as a "likelihood free" methods). The steps for a simple implementation of ABC are as follows. First, a set of model parameters θ are generated from the prior distribution [denoted $\pi(\theta)$]. Next, a data set [denoted D'] is simulated from a stochastic model using θ. The "distance" measure between the simulated data and the observed data is then calculated. Formally we denote the function to calculate this distance as ρ and the distance between the simulated and observed data as $\rho(D',D)$. Now let ε be a measure of the discrepancy between the observed and simulated data for which the model simulation will be "accepted". That is, if $\rho(D',D)<\varepsilon$, accept the chosen model parameters, then repeat the process generating new model parameters from $\pi(\theta)$ until there are enough accepted parameter sets to describe the posterior distributions of the model parameters.

It should be noted that as the measure of allowable discrepancy becomes very large ($\varepsilon \to \infty$), the process simply generates samples from the prior distributions. That is, the inference is not informed by the data in any way. Alternatively, if we only accept simulated data that exactly matches the observed data (i.e. $\varepsilon = 0$), then the process generates samples from the posterior distribution of interest [i.e. $f(\theta \mid D)$]. The problem with this approach is the probability of exactly generating the observed data becomes near-impossible for problems of even moderate complexity. Hence, the choice of ε reflects tension between computability and accuracy. It should also be noted that the distance function could apply to the raw data, or some summary measure of the observed data (denoted S) or the simulated data (denoted S') (Beaumont 2010).

2.2 Case study – Incursion of the red fox in Tasmania

The apparent incursion of the European red fox (*Vulpes vulpes*) into Tasmania has caused considerable alarm due to predicted severe negative impacts on biodiversity. Indeed, Tasmania is home to several small mammal species that are extinct on the Australian mainland other than within predator-free exclosures, with the introduced red fox inferred to be one of the main drivers of extinctions of these mainland populations (Johnson 2006; Saunders *et al.* 2010). The evidence for the incursion is varied, including sightings, footprints, carcasses, and DNA extracted from scats (Berry *et al.* 2007; Sarre *et al.* 2012). Some of the data are contentious. An early scientific overview concluded that ``an unknown number of foxes have been deliberately and/or accidentally introduced to Tasmania since 1998 and that some of these and possibly their progeny are still living in the wild in Tasmania'' (Saunders *et al.* 2006). This resulted in an eradication program being instigated. This ongoing program to eradicate the purported fox incursion costs several million dollars annually, so there is practical interest in knowing the probability that eradication has been achieved and theoretical interest in methods of estimation. There is also a need to use the available data to infer what the most likely geographic distribution of the fox population is, if it is extant. Here, we are not interested in debating the credibility of the evidence, but rather in exploring the information available from the simple citizen-derived sighting records of fox carcasses considered by Tasmanian authorities to be credible. In particular, we choose to analyse the irrefutable evidence that fox carcasses have indeed been found in Tasmania – it were these data that alerted the authorities to the possibility that an incursion was underway. These “citizen science” type data will also be available at minimal cost for the foreseeable future and will most likely remain an important basis for making inference on the incursion.

2.2.1 CARCASS DISCOVERY DATA

Data on the discovery of fox carcasses were taken from publicly available data provided by the Fox Eradication Branch of the Tasmanian Department of Primary Industries, Parks, Water and Environment (http://www.dpiw.tas.gov.au/) and span the years 2001 to 2006 (Table 1).

Table 1. Details of fox carcasses found in Tasmania. Further details can be found at http://www.dpiw.tas.gov.au/.

Year	Location	Type
2001	Symons Plains—the “Bosworth fox”	Hunter kill
2003	Burnie—“Burnie road kill”	Road kill
2005*	Lillico Beach	Road kill
2006	Cleveland	Road kill

*Although officially reported as February 2006, this carcass was first sighted in December 2005

2.2.2 SPATIO-TEMPORAL MODEL OF THE INVASION PROCESS

Purpose & type

In order to make inference about the likely demography, distribution and status of an invading fox population based on carcass discoveries, we require a spatio-temporal model containing the processes of interest. The purpose of the population spread model is to underpin inference on the spatio-temporal distribution of foxes in Tasmania, both now and into the future. To do this, the model needs to be simple enough that it is tractable computationally, and must marginalize to the process under question—are there foxes and where are they? In summary, the model must be “adequate” or “fit for purpose”.

We use a cellular automata model with each cell representing a 5 km x 5 km area which is deemed to be suitable or not to be colonized by a breeding fox population. This cell size is reasonable in terms of the typical home range size of a fox. This size cell is reasonably larger than the typical home range size of a fox (5 - 7 km^2) (Carter *et al.* 2012). Clearly this is a major abstraction of the fox population, but we argue it is adequate within the modelling framework used.

Assumptions include:

1. Introduced foxes are effective reproductive units from the first year of introduction (e.g. a least one male-female pair);
2. A female fox will always find a mate in each year (i.e. once occupied, a cell is capable of reproducing in each year);
3. The number of road kills in a cell is trivial in terms of cell population dynamics (i.e. has no effect on cell reproductive performance); and
4. The hazard of being hit on a road is constant for all major roads (predominantly highways).

Clearly some of these assumptions can be removed or relaxed (e.g. getting traffic volume data to underpin the hazard rate on roads). The ABC method requires that estimable parameters are assigned prior distributions. The details of these priors are given below.

Habitat suitability

The prior distributions of habitat suitability are based on previous empirical studies conducted in mainland Australia (Saunders *et al.* 1995 and references therein). The following land use classifications were deemed suitable to sustain a fox population—grazing of native pastures, forestry, plantations, modified pastures, cropping, horticulture, irrigated pastures and cropping, irrigated horticulture, intensive animal and plant production, rural residential, urban intensive uses and land in transition. Land use classifications deemed unsuitable were nature conservation (predominantly south-west Tasmania), managed resource protected areas, other minimal uses, and mining and waste. For the purposes of the model, we assumed foxes were unable to colonise unsuitable habitat. This produced a fox habitat suitability map with 48% of Tasmania deemed suitable for foxes, and a spatial distribution very similar to that of Saunders *et al.* (2006) and Sarre *et al.* (2012).

Locations of purported introductions

Introductions were assumed to result in a breeding pair of foxes which are assumed to form a functional “occupied” cell. Based solely on the rumoured/alleged release locations of foxes (Saunders *et al.* 2006), in each simulation we introduced foxes to cells near Longford, Oatlands, and St Helens. Clearly the distance from a major road that the introduced population first establishes could have a large effect of the timing of the observed road kills. To account for this, for any one simulation, first, the distance from a major road of the introduction was drawn from a uniform prior distribution on 0 to 25 km. An introduction cell with this setback from a major road was then selected with equal probability from the set of grid cells located within 30 km of the townships at the centre of the rumoured release locations. Note that we do not include the possibility of self-introduction at a major port, for which one case has been documented, and could have been occurring repeatedly.

Timing of introductions

The year of first introduction is rumoured to be 2001, although "accumulated evidence also indicates that such an act may have also occurred in 1999 and 2000" (Saunders *et al.* 2006). We backdate the rumoured date to include the possibility that foxes were introduced as early as 1995, and use a uniformly distributed prior on the period 1995—2001.

Dispersal

Two dispersal kernels were used, one to reflect what could be considered "natural" dispersal behaviour within an established fox population, and the second "invasion" dispersal behaviour to accommodate the hypothesis (untested) that the invading low density (and persecuted) fox population could have different dispersal characteristics due to the low density off conspecifics. The natural spread kernel is based on a Weibull distribution fitted to the data of Coman et *al*. (1991), who found that the great majority (70%) of red fox cubs were recaptured within 2 km of their original tagging location. For those that dispersed further, dispersal distances ranged up to 30 km with a mean of 11 km. The invasion kernel is circular, though with a flat density out to 30 km in all directions surrounding the occupied cell.

Survival & reproduction

The cell survival parameter (q) is the probability that an occupied cell will retain a breeding fox population from year-to-year. A uninformative prior (Uniform [0,1]) was chosen, reflecting uncertainty as to the effectiveness of the fox eradication program (e.g. no confirmed bait take by a fox as of end 2012), and the behaviour of the invading fox population, and the fact that past introductions have apparently failed (Statham and Mooney 1991). The cell reproduction number (λ) which is the number of new occupied cells generated by occupied cell is similarly uncertain. Predation by Tasmanian devils (*Sarcophilus harrisii*) on fox cubs has been hypothesized anecdotally as a reason for failure of past introductions of foxes, though with the spread of devil facial tumour disease (DFTD) since about 1995 and associated major decline in devil abundance across much of northern and eastern Tasmania by 2006 (McCallum *et al.* 2007), this hypothesized effect may be weakened considerably. A uninformative prior (Uniform [0,2]) was used for λ (i.e. somewhere between zero and the expected number of female foxes per litter assuming a 50:50 sex ratio). The net reproduction rate (NRR) for this simple system assuming survival before reproduction is (using the formula for the sum of a Geometric series):

$$\begin{aligned} NRR &= \lambda q + \lambda q^2 + \lambda q^3 + \ldots \\ &= \sum_{n=0}^{\infty} \lambda q^n - \lambda \\ &= \frac{\lambda}{1-q} - \lambda \\ &= \frac{\lambda q}{1-q}. \end{aligned}$$

A *NRR* of one or greater is a prerequisite for population growth.

Probability of road-kill

Roads are a strong attractant for scavenging species such as foxes. For example, Snow *et al.* (2012) estimated the annual survival rate for San Clemente island foxes (*Urocyon littoralis*) was about 20% lower for individuals living near roads. We used the record of fox control on Philip Island (Kirkwood *et al.* 2005) to help inform a prior on the probability that an occupied cell with a road passing through it will generate a road kill in any year. Over the 25-year period 1979/90–2004/05, there were 1,000 foxes recorded as being removed from Phillip Island, of which 35 were road kills. The fox population was thought to number at least 120-140 (removals of known cohort members) from 96/97 to 99/00. The island is about 100 km^2, which would be the equivalent of four 5 km x 5 km square cells, which could reasonably be assumed occupied in each of the years. So, the rate of road kill is 0.35 cell^{-1} year^{-1}. The corresponding probability of at least one road kill will be about 0.30 cell^{-1} year^{-1}. The population density of foxes in Tasmania is postulated as lower than that on Phillip Island, which also has a much higher density of roads, so the 0.30 was considered an upper bound. We were conservative on the low side, and used a Beta (10,90) distribution which has a mean of 10%, though considerable probability mass between 5% and 15% .

Probability of shot-kill

The hunting “observational” process in Tasmania is substantial, with in excess of 4,000 deer hunting licenses issued annually (DPIPWE – February 2011) to hunt the fallow deer (*Dama dama*), whose range overlaps extensively with the habitat considered suitable for foxes, though we note a lack of overlap on the northern coastal fringe. Elsewhere hunting of small introduced game species (e.g. European rabbits *Oryctolagus cuniculus*, European hares *Lepus europaeus*) is a popular pastime across Tasmania (author’s personal observation). In addition, permits are issued for the control of native species that can cause browsing damage to agriculture, such as wallabies (*Macropus spp.*) and brushtail possums (*Trichosurus vulpecula*). For the 2012–2013 season Wallaby licenses alone number nearly 7,000 (DPIPWE – February 2013). Spotlight shooting, which is a recognized method to obtain fox carcasses, is a core method for much of this hunting. This effectively extends the hunting observational process to all of Tasmania other than the nature conservation estate. Despite the widespread nature of hunting in Tasmania, its effort is undoubtedly uneven in time and space. To allow for this, at the start of each simulation run, the probability of a cell being subject to potential hunting was randomly assigned using a 50% probability—that is hunting could occur on half the cells. This is an arbitrary choice on our part, and it’s main role is to accommodate the possibility that a fox population is extant in a cell not subject to “observation” by shooting.

Generating a prior on the probability of shooting generating a shot fox from an occupied cell subject to hunting was difficult. Field *et al.* (2005) estimated the probability of detecting foxes within a 1 km segment of a spotlight transect ranged between 6 and 18% depending on vegetation, but translating this to a typical annual probability of successfully shooting a fox within a 5km x 5km cell is difficult. We could again use the Phillip island data, although the intensity of spotlight searching effort was very high there—much higher than would be typical for a hunted area in Tasmania. In the end we settled on a Beta (10,90) distribution (same as the probability of a road kill), which again is possibly conservative on the low side.

Ordering of events

The ordering of events applied to occupied cells were survival, road or hunter kill, then reproduction.

Estimating time to next carcass discovery or extinction

The trajectories for accepted simulations (see below) with an extant fox population as of the end of 2012 were projected stochastically out to 2022 using the parameters and state variables (e.g. spatial location of occupied cells as of 2012) unique to that simulation. These projections were used to estimate the time to the next fox carcass being detected, or the population going extinct, or either of these outcomes occurring.

ABC computations

The simplest ABC algorithm (ABC rejection sampler) in our case would involve: (1) Sampling a set of model parameters $\theta*$ from the prior distributions $\pi(\theta)$ specified above; (2) Simulating a dataset D' of road-killed and hunter-killed foxes using the spread model described; (3). Accepting the parameters $\theta*$ if a measure of the distance between the observed and simulated data is less than some arbitrary tolerance value ε (i.e. $\rho(D, D') \le \varepsilon$ where *d* is some distance function); (4) Repeating step one until a sufficient number of parameter combinations are accepted to characterise the posterior distributions of the parameters of interest. Whether or not the posterior distributions are correctly characterized depends on the tolerance between the observed data and accepted simulations. As mentioned previously, as $\varepsilon \to 0$, the correct posteriors are found with near certainty. The problem, of course, is that the probability of exactly reproducing the observed data may be so low that generating a sufficient number of samples for the posteriors may be computationally prohibitive. This is especially the case using rejection sampling which is inefficient due to repeatedly sampling areas of the parameter space that have a low probability of generating the observed data. Efforts to speed up the process generally involve the use of statistically sufficient summary statistics (if they exist) as a basis for estimating the discrepancy between D and D', and the implementation of more efficient samplers. Toni *et al*. (2009) provide more details.

Our measure of discrepancy was the sum over the observation period (conditional on the time of introduction) of the absolute difference between the number of observed and simulated carcasses, calculated separately for road kills and hunter kills. Approximate posterior distributions were generated using an ABC sequential Monte Carlo (ABC SMC) sampler (Toni *et al.* 2009)— a "particle filter". Starting with 1,000 particles (parameter combinations), the allowable discrepancy over the observation period between the simulated and observed road kill data was set to 2, 1, and then finally zero. We explore inference arising from road kill data only with that arising from both road kills and hunter kills. When including hunter kills, the allowable discrepancy for the hunter-killed data was set to 0 from the start. Hence for the final selection of accepted particles (and hence posterior distributions of parameters), the acceptance criteria was that the simulated road kills were exactly the same in number (*n*=3) and timing (years 2003, 2005 and 2006) as was the simulated hunter kill (*n*=1, year=2001). No restriction was put on the location of simulated carcass discoveries (although this is clearly influenced by the choice of introduction location). To do so would require a much broader prior distribution of possible introduction locations. Higher ε weren't considered as this resulted in particles with trivial results (e.g. immediate extinction) to be overly represented early in the particle filtering process. Normal distributions were used as perturbation kernels for all parameters. We confirmed that the ABC SMC sampler was generating very similar posterior distributions to an ABC rejection sampler—our choice of the SMC sampler was to speed up computations.

Software & hardware

All calculations was undertaken within the R computing environment (R Development Core Team 2011) using the "raster" (Hijmans 2013) and "simecol" (Petzoldt and Rinke 2007) packages. Ten computer processor cores were utilised to run ten independent ABC SMC simulations with the random number generator for each processor seeded with a different starting value using the set.seed() R function. Approximately 5,000 hours of processor time were required to generate 1,000 accepted simulations.

2.3 Results

A key point when interpreting the following results is that the posterior distributions of the parameters of interest are a probabilistic measure of belief in what value the parameter may take.

Model of road kills and hunter kills

The approximate marginal posterior distribution of the distance from the introduction site to a major road showed weak though consistent trends, with a slight preponderance for the releases being 5-10 km from a major road as opposed to either nearer or further (Figure 1). There was no correlation between the release distances (e.g. a distance release at one location is correlated with a closer release elsewhere). The most likely year of introduction was strongly skewed towards either 2001 (46% probability) or 2000 (36% probability), with the year 1999 somewhat plausible (12% probability) and earlier years unlikely (Figure 2a).

The parameter space of accepted simulations shows an unsurprising strong dependence between the yearly cell reproduction number and yearly survival (Figure 2b). In future, it may be possible to put tighter priors on survival and reproduction, although this may not change the inference much. The estimated probability of a road kill is significantly changed from the prior (Figure 2c), with a modal value of about 13%. The estimated probability of a hunter kill is only slightly changed from the prior (Figure 2d). There was negligible difference in the inferred mode of dispersal ("invasion" 51% vs. "natural" 49%), hence we have no support for discarding either.

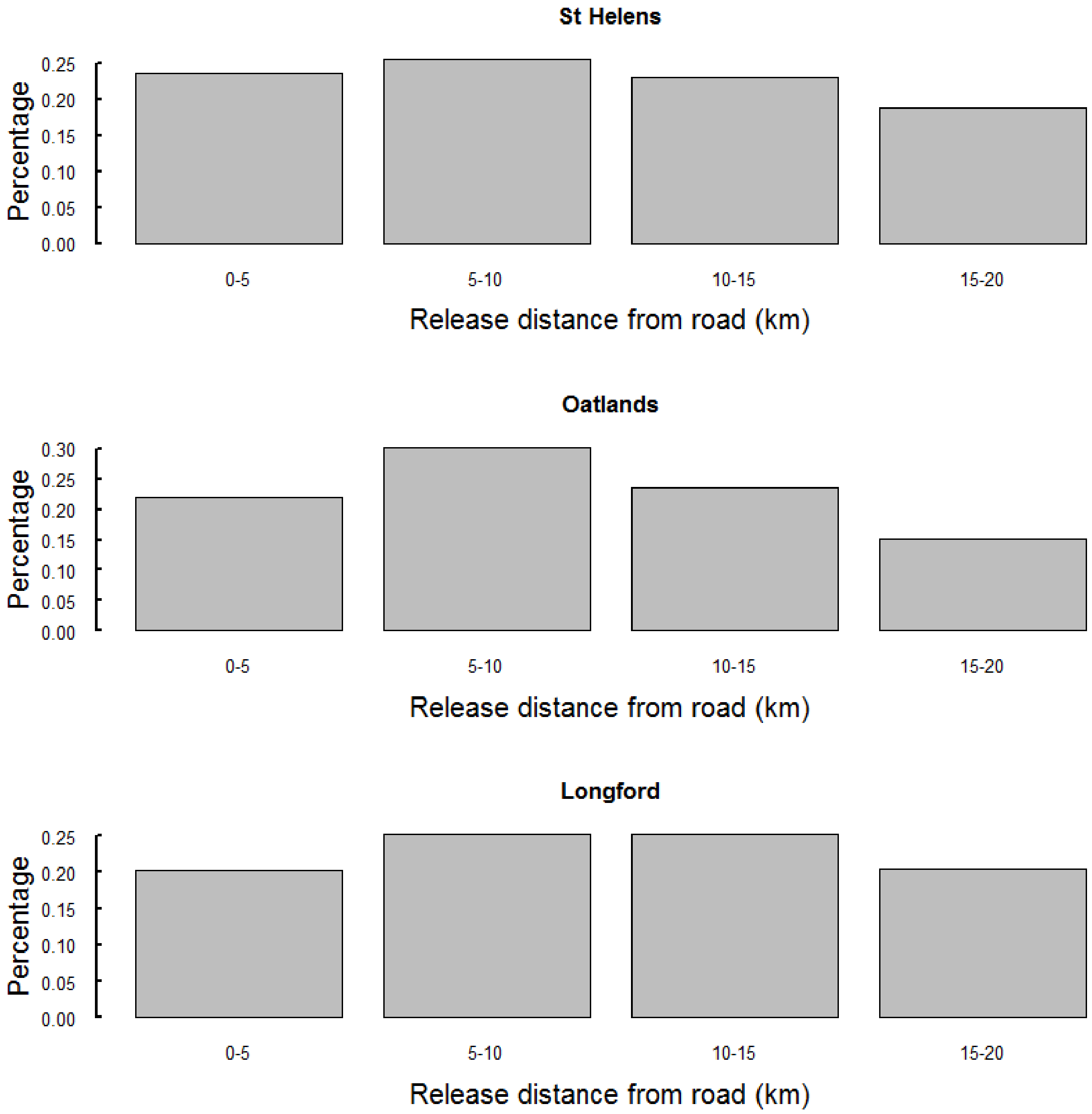

Figure 1. Distribution of setbacks from major roads for model fitted to road kill and hunter kill data as of end 2012.

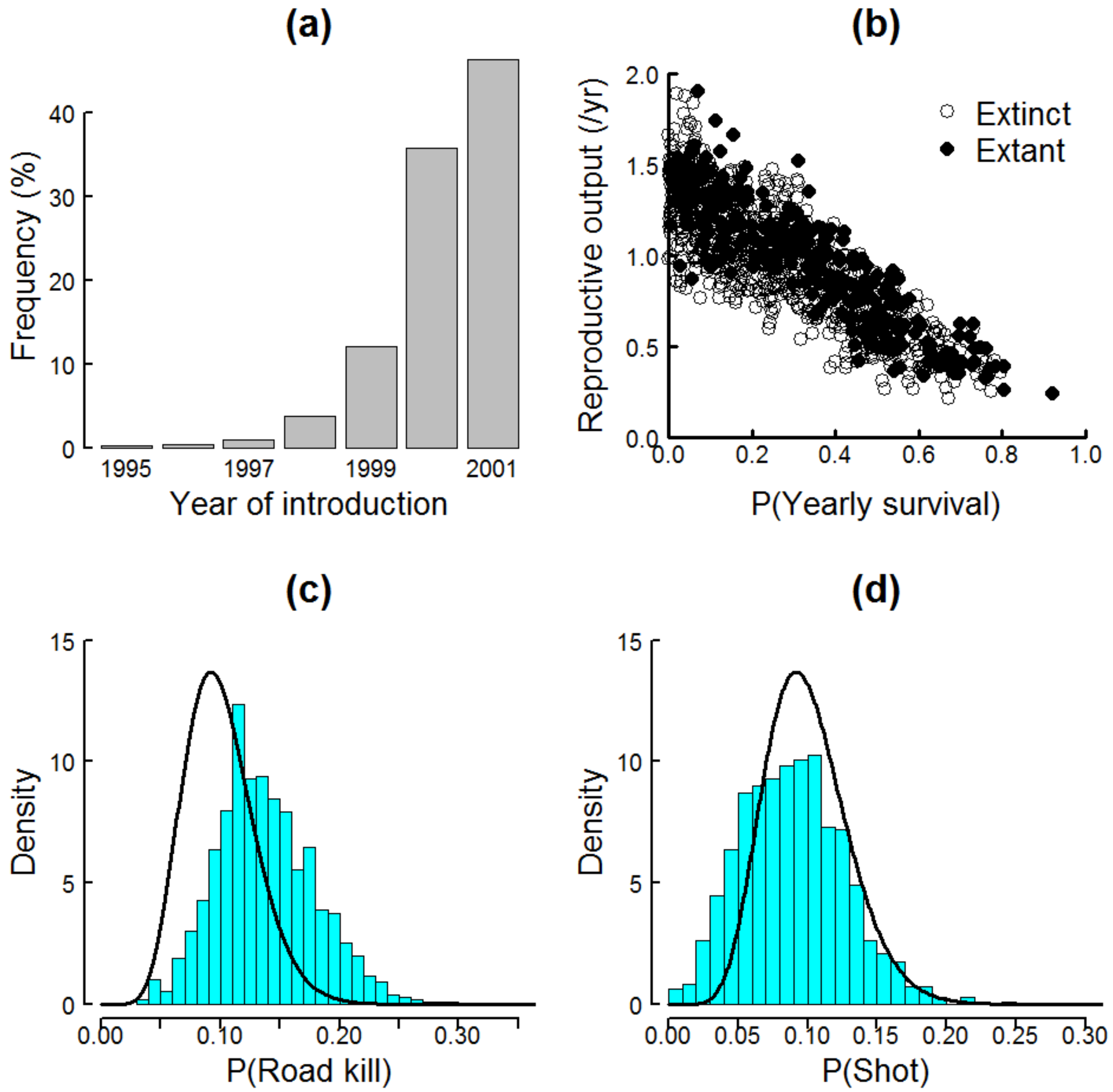

Figure 2. Approximate posterior distributions based on accepted simulation runs for (a) Year of introduction; (b) Relationship between reproductive output per year and probability of yearly survival, with open circles indicating populations extinct at the completion of 2012; (c) The probability density of being a road kill (bars) and the prior based on a Beta distribution (solid line); (d) The probability density (given hunting occurs in an occupied cell) of generating a hunter kill (bars) and the prior based on a Beta distribution (solid line).

The trajectories of accepted simulation runs can broadly be characterized as small populations with low reproductive rates at risk of extinction, although for a small proportion of accepted simulations the population was widespread and increasing (Figure 3).

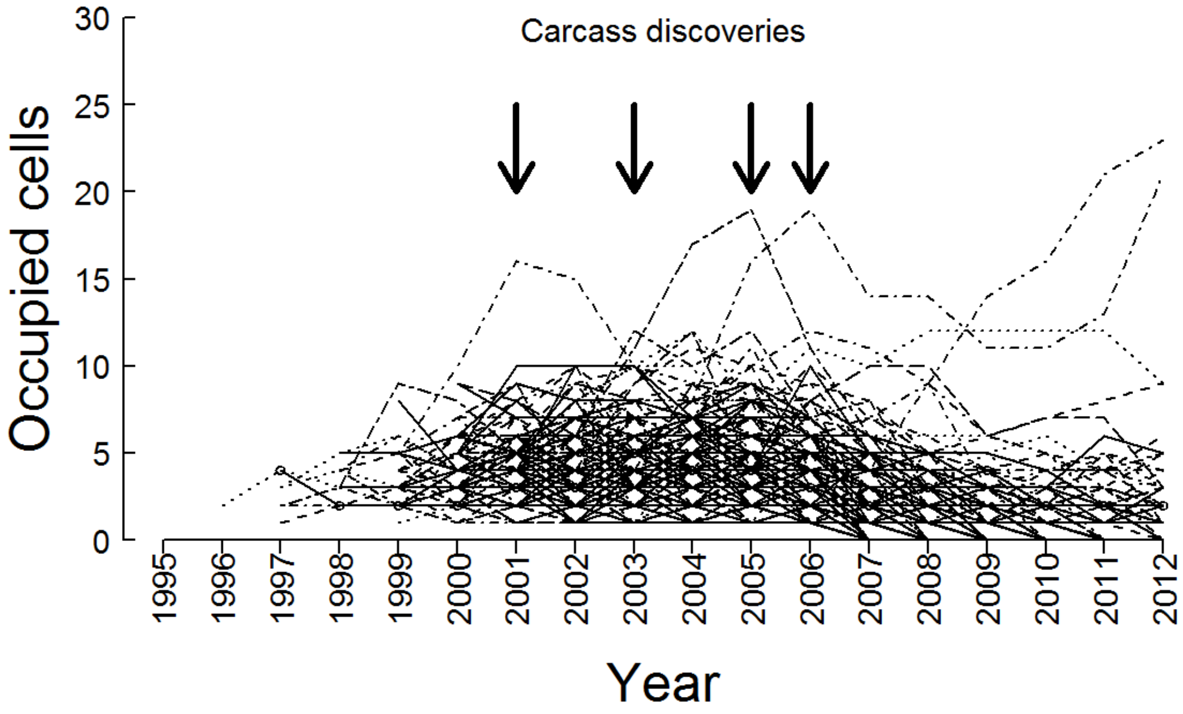

Figure 3. Population trajectories of 300 accepted simulations [for clarity] with arrows indicating year of carcass discoveries. The 2001 arrow is a hunter kill with the remainder road kills.

The inferred population size as of the end of 2012 is most likely zero (extinct) (*c.* 70% probability), or very small (1–5 occupied cells) with about 25% probability. There is about 5% chance the population occupies either a small (6–10) or moderate–large (>10) number of cells as of 2012 (Figure 4).

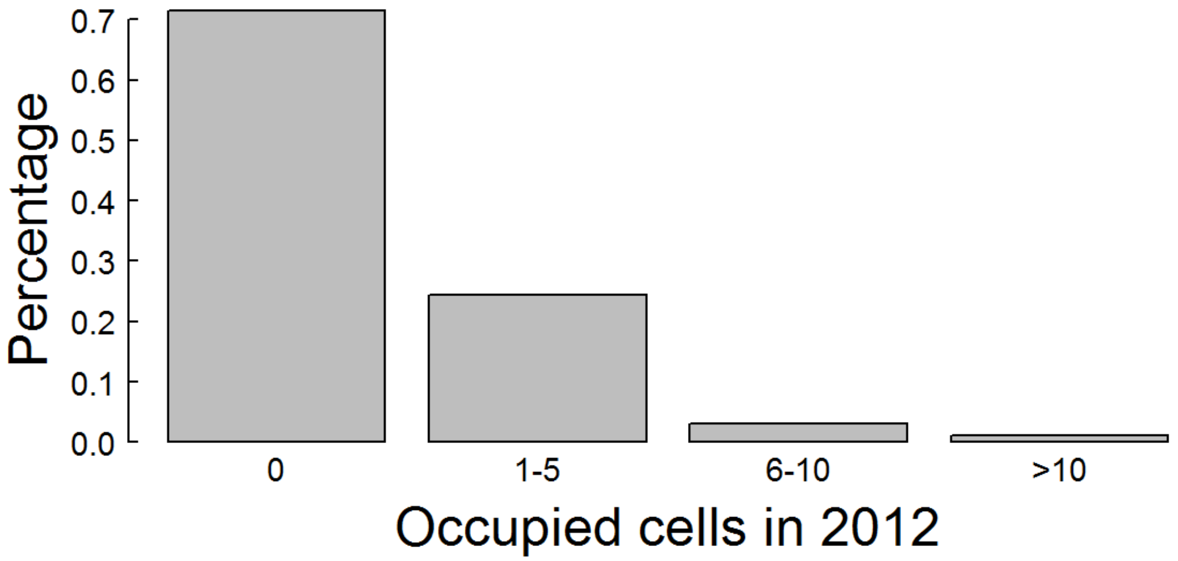

Figure 4. Frequency distribution for the number of occupied cells at the end of 2012 out of 1256 habitable cells.

The posterior distribution of cell occupation at the end of 2012 is characterised by very low occupancy probabilities (Figure 5), as most surviving populations were highly restricted (Figure 4). Cells with higher probabilities of occupancy tended to be located away from major roads (Figure 5). Specific differences between posterior distribution of foxes inferred by our ABC results and that of the recent analysis of Sarre *et al*. (2012) include a virtual absence of possible occupation to the south-east and south-west of Hobart—areas where fox DNA positive predator scats have reportedly been found.

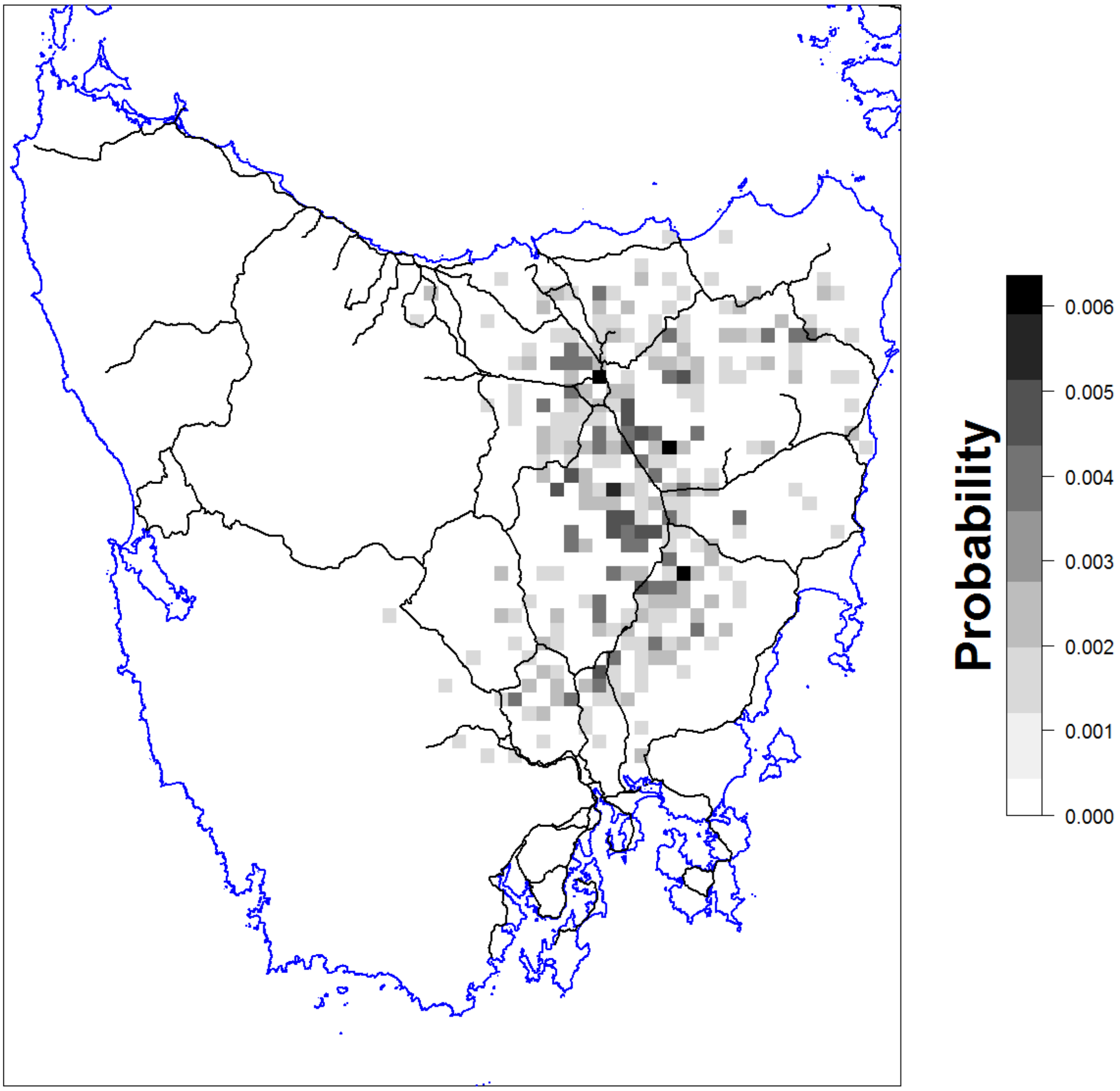

Figure 5. Approximate posterior distribution of the distribution of cells occupied by the red fox in Tasmania as of the end 2012 based on hunter kill and road kill observation process. Solid lines are major roads. A smoother distribution could be generated by increasing the number of accepted simulation runs.

The posterior distribution for the net reproduction rate suggests that either the population most likely has low demographic vigour, with only 4% of accepted simulations having a life time reproductive rate above one, or control operations are suppressing population growth (Figure 6). The lack of any clear evidence one way or the other on bait take by foxes means either explanation is possible. The interpretation of this would be that there is a 96% probability that the population will become extinct eventually under the current management regime, which may or may not involve foxes being removed from the population by poisoned baits.

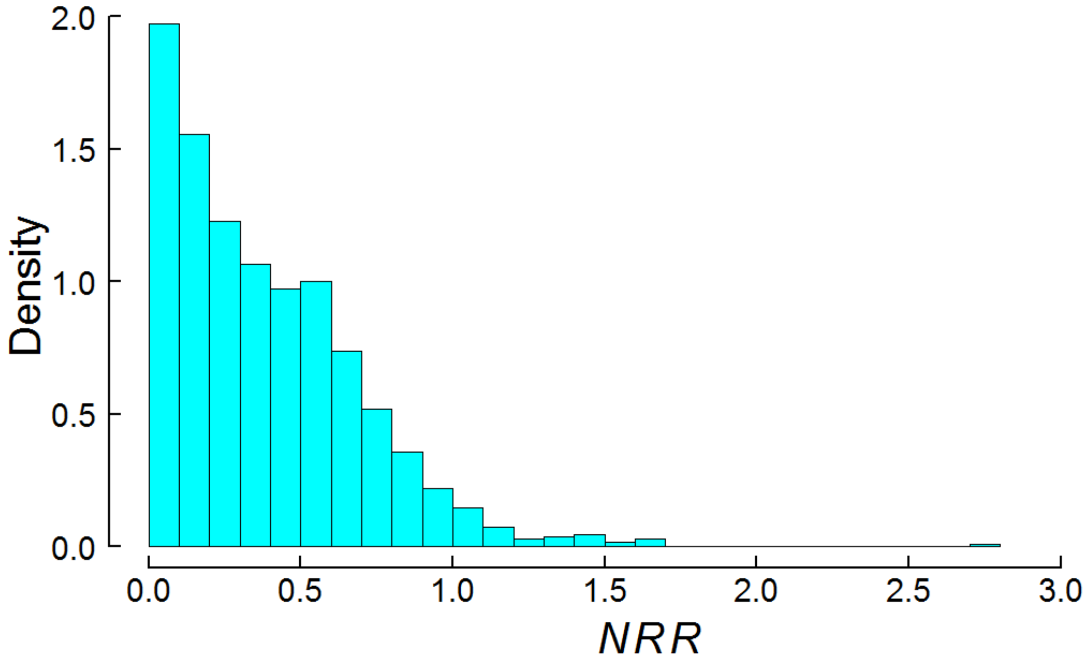

Figure 6. Approximate posterior distribution of the Net Reproductive Rate (*NRR*) of cells occupied by foxes.

Estimated time to next detection or extinction

Conditional on the model's assumptions and prior beliefs, the probability that a further carcass is found in 2013 is estimated to be about 5% and the probability that the population has become extinct increases to *c.* 75% (Figure 7). Extending this into the future, by 2022, it is estimated that there is nearly 100% certainty that either the population has become extinct, or it has been detected by either a road or hunter kill (and hence it is apparent that further control is necessary) (Figure 7). That is, within 10 years, either extinction will be achieved with probability of about 90%, or it will be apparent that attempts to cause population extinction have failed. This inference, as previously stated, is conditional on a model fitted to road-kill and hunter-kill data only.

Although the posterior distribution can be used now to make inference about future events, as further data are collected (e.g. if 2013 passes without a subsequent road- or a hunter-kill) then the model will require updating if updated inference is required.

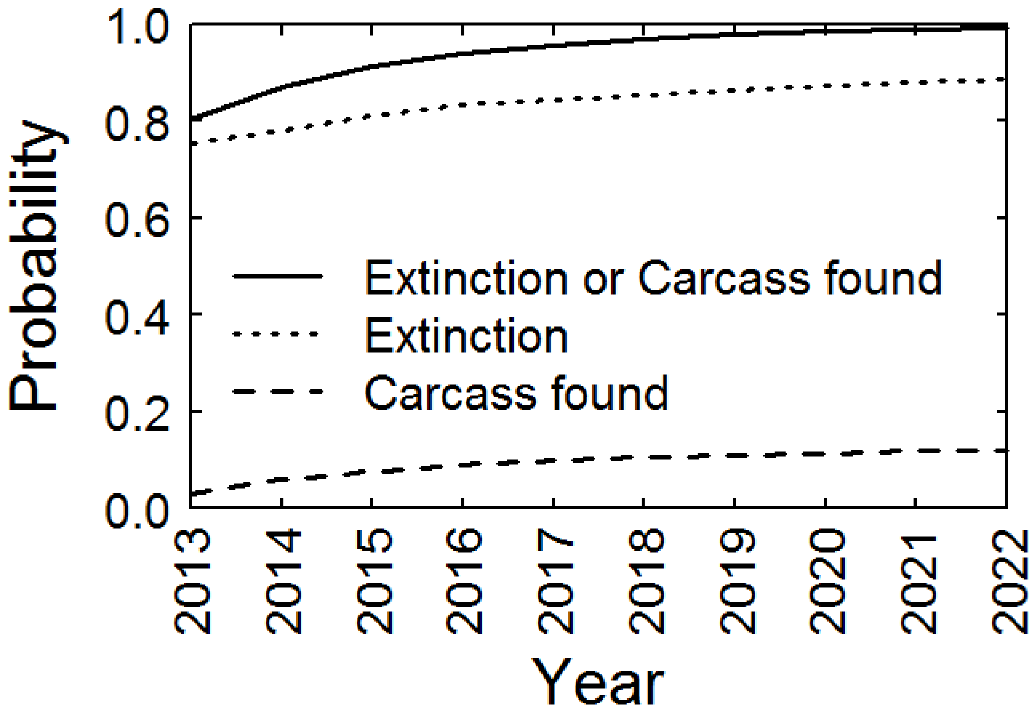

Figure 7. Probability of population extinction (dotted line), cumulative probability of at least one new road kill (dashed line), and the combined probability of either population extinction or at least one further road kill (solid line). Results based on 30 simulation runs on each of the 1,000 accepted runs finishing in 2012.

3 Estimating the density of vertebrate pests using detection/non-detection data from unmarked populations

3.1 Background

Many methods for sampling vertebrate pests are based on detection/non-detection (presence/absence) data where the identity of individuals detected remains unknown. Usually, such data are subject to analysis to estimate the probability of occupancy for a sample location, corrected for imperfect detection (occupancy analysis) (MacKenzie *et al.* 2004). While estimates of occupancy are useful in many contexts they are still a fairly crude representation of the dynamics of the population. Indeed, many problems in vertebrate pest ecology require estimates of population density or abundance (e.g. harvest quotas, disease/damage thresholds). Traditionally it has been assumed that it is difficult or impossible to estimate animal density from presence/absence data unless certain restrictive assumptions were made or supplementary information was collected. However, previous studies have estimated local population density from presence-absence data assuming a functional relationship between detection probability p and local density N, the so-called Royle/Nichols (RN) model (Royle and Nichols 2003). This estimator requires a similar design to traditional occupancy study that assumes independence between sample units. That is, individuals detected at a particular sample unit cannot be detected at other sample units. If animal home ranges overlap multiple sample units then detections among neighbouring sampling units are correlated and estimates of population abundance using this model are biased high. This is a particular risk in studies of animals with large home ranges, such as many carnivore species. When sampling locations cannot be assumed to be independent, then estimation of density in unmarked populations is problematic. In this instance, recapture or resighting information on individuals is required for estimation to proceed (e.g. Borchers and Efford 2008; Royle and Young 2008).

Recently Chandler & Royle (2013) developed a model for spatially-referenced count data that estimates animal density in unmarked populations using a spatial model of the detection process. Unlike other estimators for count data, such as the N-mixture model (Royle 2004), the Chandler and Royle model (hereafter CR model) does not require sampling locations to be independent (i.e. i.i.d sampling). The core of the model is the use of spatially correlated count data to infer a spatial point process representing the number and locations of animal home range centres. Hence, the CR model is an extension of existing spatial capture-recapture models (e.g. Borchers and Efford 2008; Royle and Young 2008) applied to data from unmarked populations.

However, many of the sampling designs used for carnivore surveys only yield detection/non-detection data rather than counts. Methods such as tracking stations, bait-take, camera-traps, and scat-surveys may only be able to indicate the presence of an individual on a particular sample occasion rather than a count. Hence, it would be advantageous to be able to infer density from detection/non-detection data rather than rely on estimates of occupancy. Here we extend the model of Chandler & Royle (2013) to enable density estimation for detection/non-detection data where sample locations are not independent (i.e. spatially-correlated detections). As the model is spatially-explicit, a by-product of the estimation process is the likely locations of home range centres within the sampled area. We report on the performance of the extension of the CR model using simulation and illustrate its use with a practical example estimating the abundance of foxes in the Grampians National Park from detection/non-detection data from remote camera surveys.

3.2 Methods

The model is based on that proposed by Chandler & Royle (2013) but modified to handle detection/non-detection data and uses the same general notation where possible. Their model is based on a Bayesian analysis of the latent encounters of spatially referenced individuals with sampling devices using data augmentation and Markov Chain Monte Carlo (MCMC) sampling. For a more in-depth description of the CR model applied to count data, the reader is referred to Chandler & Royle (2013).

3.2.1 SAMPLING DESIGN

The sampling design consists of an array of J sampling devices having locations at $\mathbf{X}=(x_{j1}, x_{j2})$, ($j$= 1, 2, … J) and set for K occasions (k = 1, 2, … K). The array of devices is laid out in such a way that individuals could potentially be detected at multiple devices (e.g. a 'grid' pattern). Individuals may be detected at any of the **X** on any given occasion and hence, are considered to be 'passive' in that they record the presence of an individual but do not capture it. Devices such as camera traps, tracking plots or bait stations are all sampling devices that have been used to produce detection/non-detection data. As will be shown, the non-independence of devices induces spatial correlations in detections that can be used to infer the parameters of a spatial detection process. Hence, the spatial placement of devices with respect to the home range size of individuals becomes important. The observations at each device denoted h_{jk} take binary values indicating detection of at least one individual on device j at occasion k. Hence $h_{1\cdot}$ =(01001) indicates detections on occasions 2 and 5 for device number 1. The resulting data are a $J \times K$ matrix of detections **h**.

3.2.2 SPATIAL DETECTION MODEL

The conceptual model underlying the detection process is a spatially-explicit, individual-based model of detections in devices located in 2-dimensional space. This model is structurally similar to the models underlying the detection process given in Efford (2004) and Ramsey *et al.* (2005). Consider a population of N individuals that are potentially at-risk of being detected with each individual $\mathbf{z}_i$ (i=1, 2, …, N) defined by a centre of activity $\mathbf{s}_i = (s_x, s_y)$, its nominal home range centre. The locations of home range centres are unknown but are considered to be fixed for the duration of sampling. Individuals move about their home range centres according to some probability distribution (e.g. bivariate normal) and in the process can potentially be exposed to detection (see below) (Figure 8). We also assume that home range centres are distributed randomly over the area of interest A according to a random uniform distribution (e.g. Efford 2004; Royle *et al.* 2009). That is,

$\mathbf{s}_i \sim \text{Uniform}(A)$. Eqn 1

Structurally, this is similar to assuming that the home range centres are distributed according to a homogeneous spatial Poisson process with constant intensity (density) over the area of interest A. However, it is important to note that equation 1 implicitly allows for any configuration for the locations of home range centres. Thus, inference is concerned primarily with estimating the locations of the unknown home range centres and hence, the abundance N (and density) of individuals within the region A (e.g. Royle *et al.* 2009).

Encounter process

Individuals can only encounter devices that occur within their home range. If we consider the situation with only one animal and one device, the probability of detecting the individual declines as a function of the distance d between the device and the home range centre. Assuming movements around the home range centre occur with bivariate normal probability then the probability of detection is given by the half-normal function:

$$p_{ij} = g_0 e^{-d_{ij}^2 / 2\sigma^2}$$
$$d_{ij} = \left\| \mathbf{x}_j - \mathbf{s}_i \right\| \quad , \qquad \text{Eqn 1}$$

where g_0 is the per occasion probability of detection when the home range centre and device location coincide (i.e. *d*=0) and σ is the spatial scale over which the detection probability declines with increasing distance between the home range centre and the device (e.g. Efford 2004; Ramsey *et al.* 2005).

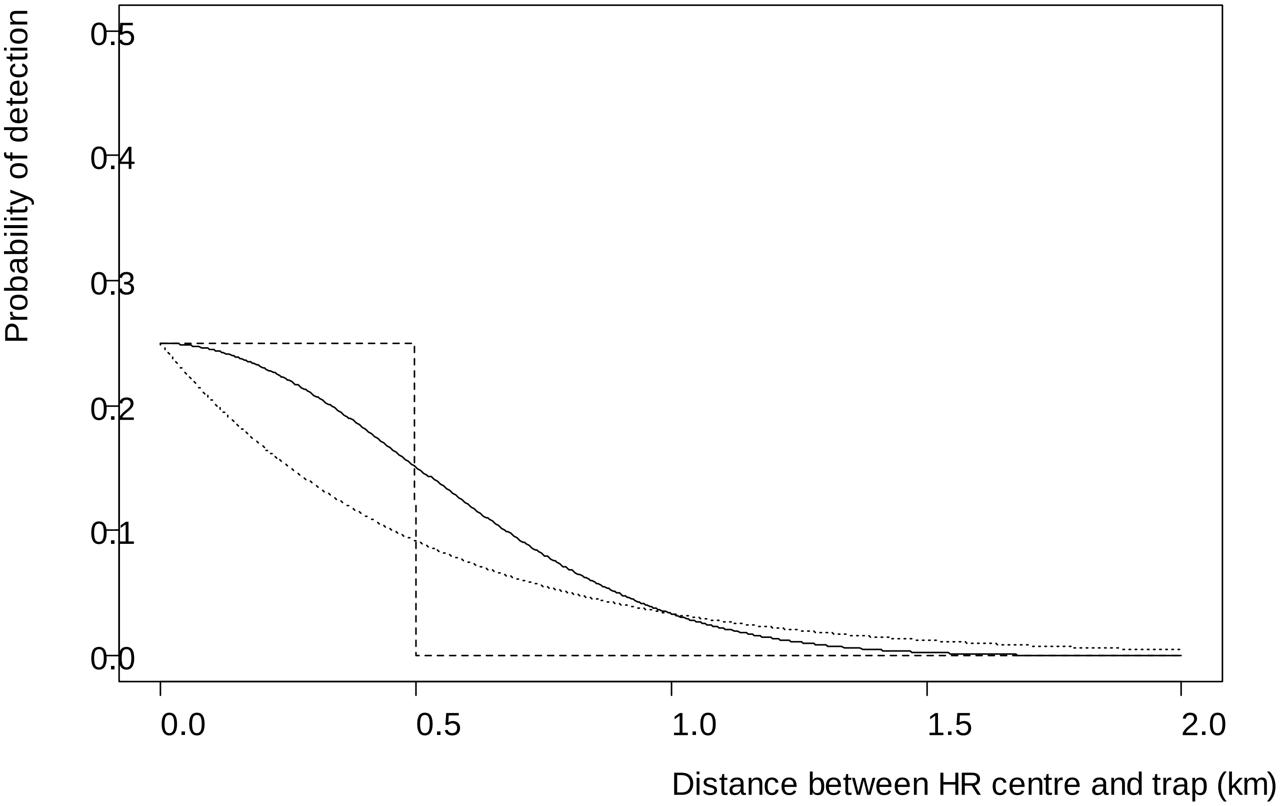

Figure 8. Shape of possible detection functions showing the decline in the probability of detection for an individual with increasing distance between the detection device and the individuals home range centre. Solid line – half normal detection function (equation 1), dashed line – uniform detection function; dotted line – exponential detection function. For all three curves the parameters were g_0 = 0.25; σ = 0.5.

Equation 1 states that each individual $\mathbf{z}_i$ with home range centre located at $\mathbf{s}_i$ is detected at a device $\mathbf{x}_j$ per occasion *k* according to

$$\mathbf{z}_{ijk} \sim Bernoulli\left(p_{ij}\right)$$

However, the full detection histories for each individual and device $\mathbf{z}_{ijk}$ are latent (unknown) and must be estimated. When there are many devices (and individuals), this can be time consuming. However Chandler & Royle (2103) showed that analysis can proceed without estimation of the full $\mathbf{z}_{ijk}$ array by conditioning on the trap-specific detections, which in this case have the same discrete Bernoulli distribution

$$h_{jk} \sim Bernoulli\left(P_j\right)$$

where the probability that at least one individual is detected in device *j* (P_j) is given by

$$P_j = 1 - \prod_{i=1}^{N} \left(1 - p_{ij}\right).$$

Furthermore, as detections at each occasion are assumed to be independent, we can aggregate the detections at each of the *J* devices by noting that:

$$n_j \sim Binomial\left(P_j, K\right)$$

where

$$n_j = \sum_{k=1}^{K} h_{jk} .$$

The estimation problem now reduces to one of estimating the latent $\mathbf{s}_i$ and hence *N*, the number of individuals in the population. Chandler & Royle (2013) fix the dimension of the estimation problem by considering the existence of *M* rather than *N* individuals in the population with *M* >> *N.* Estimation then proceeds using parameter-expanded data augmentation where a set of *M* latent indicator variables *w* are introduced so that the model now becomes

$$P_j = 1 - \prod_{i=1}^{M} \left(1 - p_{ij} w_i\right)$$

$$w_i \sim Bernoulli\left(\psi\right); i = 1, 2, \dots, M$$

This implies that when $w_i = 0$ then the probability that individual *i* is detected in any trap ($p_{i.}$) is also 0 and conversely, when $w_i = 1$, then individual *i* contributes their individual detection probability p_{ij} to the marginal trap total P_j. Hence the estimate of population size $\widehat{N}$ (the number of home range centres residing within the area *A* is given by

$$\hat{N} = \sum_{i=1}^{M} w_i$$

The spatial detection model given above was fit using a similar Metropolis-within-Gibbs algorithm as used in Chandler & Royle (2013). Prior distributions are required to be specified for g_0 (on the logit scale to avoid numerical problems), σ and ψ, which can either be uninformative or reflect prior knowledge. Prior information on home range size for many pest species of interest is likely to be available, which can be used to specify an informative or vaguely informative prior for the spatial scale parameter σ. This is illustrated for the estimation of fox abundance.

3.2.3 SIMULATION STUDIES

Single scenario

We explored the spatial detection model using simulation to evaluate the properties of the model under different sampling conditions. We conducted the simulations under similar conditions to that undertaken in Chandler & Royle (2013) so we could compare the simulation results for our presence/absence spatial detection model to the CR model for sample counts. Hence, we simulated detection/non-detection data using a 10 × 10 grid of sampling devices set in the centre of a 15 × 15 area with unit spacing (Figure 9). To illustrate the method, we initially simulated a single scenario with the number of home range centres (population size — $\widehat{N}$) set to 20 and the parameters of the half-normal detection function (Equation 1) set to 0.25 and 0.75 for g_0 and σ respectively and simulated detections over 20 occasions (Figure 9). We then fit the spatial detection model to the simulated data to determine whether estimation could recover the original parameters. Estimation was conducted using 50,000 iterations of the MCMC algorithm with the first 10,000 treated as a burn-in sample and discarded leaving 40,000 iterations to form the posterior distributions of the parameters. In addition to the parameters above, the MCMC algorithm also provides posterior samples of the locations of home range centres ($\mathbf{s}_i$). We constructed a density surface of the likelihood of the locations of home range centres from 10,000 posterior samples of $\mathbf{s}_i$ by fitting a 2D kernel density surface to the posterior samples using a Gaussian kernel with bandwidth set to 1.

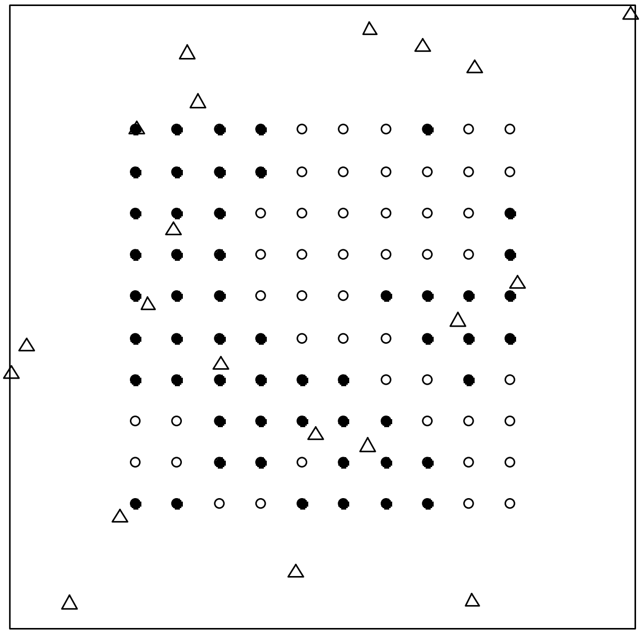

Figure 9. The pattern of detections resulting from a simulated sample of 20 individuals (open triangles – location of home range centres) by an array of 100 devices set on a 10 x 10 grid with unit spacing (open circles) over 20 occasions. Devices that detected an individual on any occasion are represented by closed circles. For this sample, the value of g_0 was set to 0.25 and the value of σ set to 0.75.

Extensive simulation study

In addition to the above, we also undertook more extensive simulations to explore the properties of the model under a wider range of conditions. Using the same 10 x 10 grid of sampling devices, we simulated scenarios with values of σ varied between [0.5, 0.75, 1.0] with two population sizes of [20, 50] individuals. In each case the value of g_0 was set to 0.25 and the number of occasions was varied between [5, 10, 20] occasions. This gave a total of 18 scenarios in all. We simulated 100 replicate populations for each of the above scenarios and fit the spatial detection model using the MCMC algorithm given in the supplementary materials. Each simulation consisted of 12,000 iterations of the MCMC chain with the first 2000 treated as burn-in samples and discarded leaving 10,000 iterations to form the posterior distributions of the parameters. We computed the mean and mode of the posterior distributions for each simulation and calculated their root-mean-square-error. The 95% coverage rates were also calculated as the proportion of simulations where the 95% credible intervals of the posterior distribution of *N* contained the true generating value.

3.3 Case study – estimating population density of foxes in the Grampians National Park

3.3.1 REMOTE CAMERA DATA

Remote cameras (n=77) were deployed in the central valley region (approximately 385 km^2) of the Grampians National Park (GNP) near Dunkeld, an area of high natural biodiversity (Figure 10). This area was divided into hexagons of 500 ha representing the area of a typical fox home range (Saunders *et al.*

1995). A random point within each hexagon was generated and the location used to place a camera. Two camera types were used, ScoutGuard SG550 infrared and ScoutGuard SG565 white-light cameras (HCO, Norcross, Georgia, USA) and were set to take one image a second while there was motion detected, with no quiet period. Each camera was attached to a tree at least 20cm above the ground and baited with a lure of chicken and tuna oil and set for an average of 28 days during February/March 2012.

For each camera, the detection or non-detection of foxes was recorded on each night. To define the area of interest *A* to conduct estimation, a convex polygon was drawn around the camera locations and then buffered by 2 km in each direction. This gave a total area for the region *A* of 617 km^2 (Figure 10). A vague uniform prior, U(-10,10), was placed on the logit of g_0, with a weakly informative prior used for the home range scale parameter σ. Home ranges of foxes in temperate areas of South-eastern Australia were estimated recently by Carter *et al*. (2012). Their estimates of range size averaged around 7 km^2 but varied from 2.5 - 11 km^2 with a standard deviation of 3.2 km^2. (Table 4, 95% MCP estimates of range size excluding the one "nomadic" individual). Assuming ranges are roughly circular, this equates to estimates of the scale parameter σ for the half-normal detection function varying from 0.36 – 0.79 km (mean=0.6, variance=0.02). We represented this information by constructing a gamma prior with shape parameter of 18 and a scale parameter of 0.033, which gave adequate coverage of the desired range (Figure 11). The upper limit of the parameter *M* used for data augmentation was set to 600.

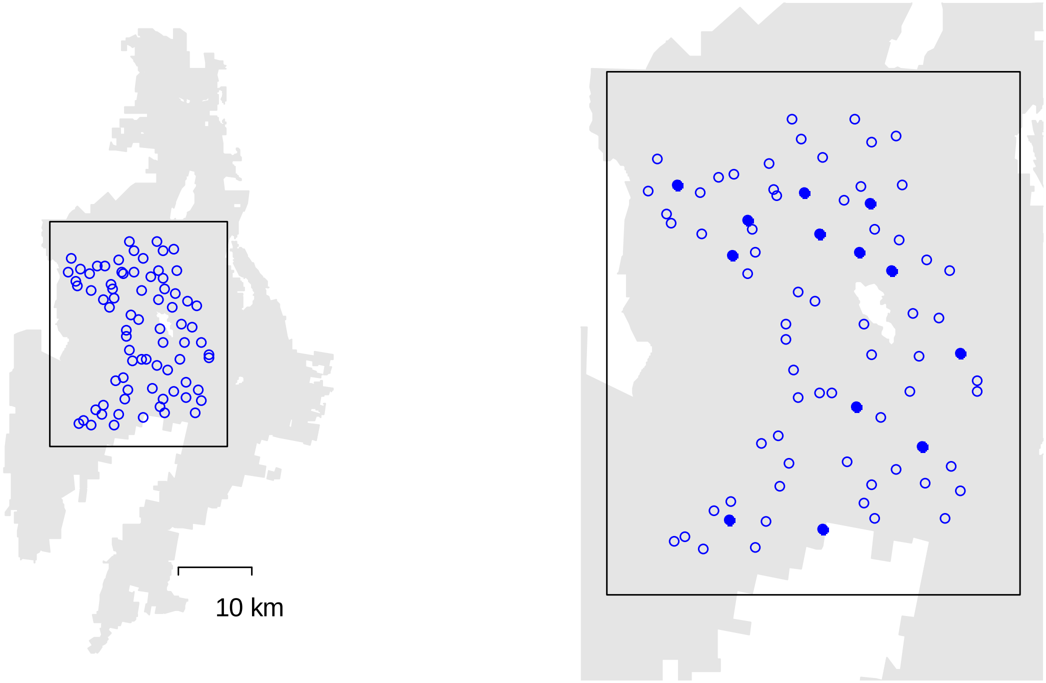

Figure 10. Location of Grampians camera survey for foxes. Camera locations are indicated by open circles. Filled circles indicate fox detections.

We drew 40,000 samples from the MCMC algorithm from each of three chains using diffuse initial values and discarded the first 10,000 leaving 30,000 samples from each chain to form the posterior distribution of the parameters. Convergence was assessed by calculating the Brooks-Gelman-Rubin convergence statistics $\widehat{\mathrm{R}}$ (Brooks and Gelman 1998) and by visual inspection of the chains. For each of the parameters, the number of home range centres ($\widehat{N}$) within the area A, and the parameters of the spatial detection function (g_0, σ), were calculated as the mode of the posterior distribution with associated 95% credible intervals. In addition we also estimated the likely locations of home ranges centres using 5,000 samples of the posterior distribution of the $\mathbf{s}_i$, by fitting a 2D kernel density surface to the locations using a Gaussian kernel with 1.5 km bandwidth.

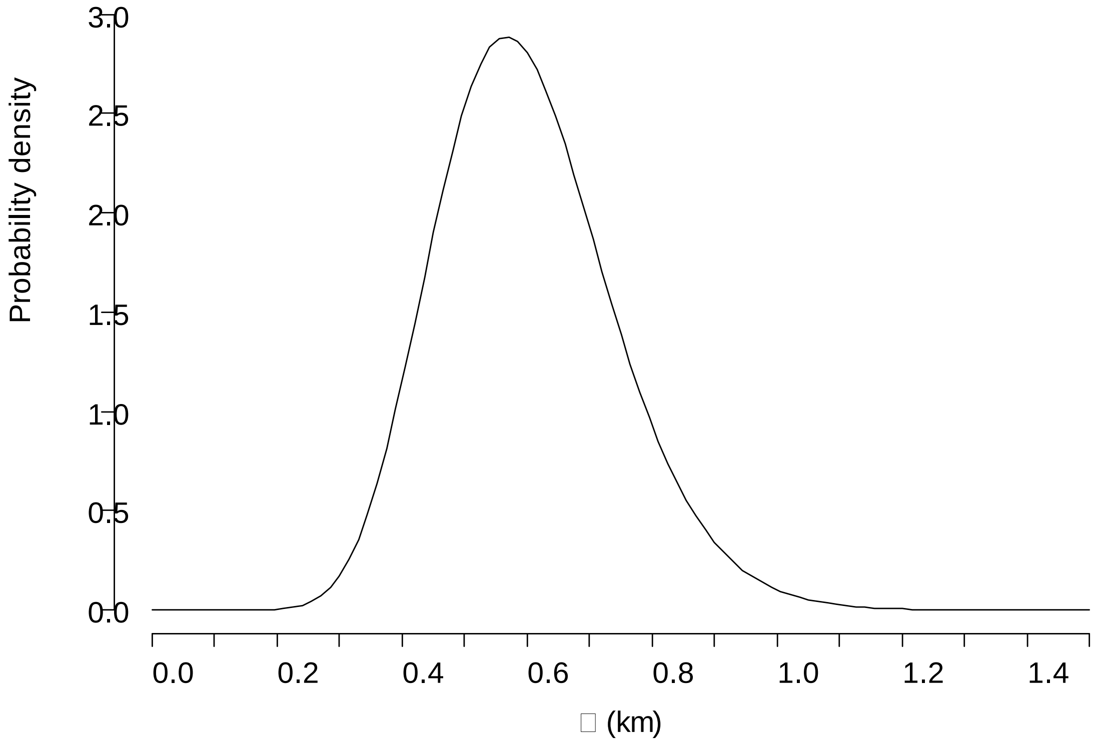

Figure 11. Gamma(18, 0.033) prior probability distribution used for the home range scale parameter σ for the Grampians fox data.

3.4 Results

3.4.1 SIMULATION STUDY

Single scenario

Visual inspection of the MCMC chain indicated the algorithm had converged after 10,000 iterations for each of the parameters of interest (Figure 12). The posterior estimates of the number of home range centres ($\widehat{N}$) was within 10% of the true generating value with the mean of the posterior distribution being slightly higher than the posterior mode (Table 2). This was due to the slightly skewed nature of the posterior distribution (Figure 13). Similarly, the estimates of the detection parameters also exhibited low bias being within 14% (g_0) and 10% (σ) of their true generating values (Table 2).

Table 2. Estimates of the posterior mean and mode of population size ($\widehat{N}$) and the parameters of the spatial detection function g0, σ and their true generating values used in the single scenario simulation.

Parameter	True value	Estimate (mean)	Estimate (mode)	95% CI
$\hat{N}$	20	21	18	11 - 37
g_0	0.25	0.22	0.22	0.14 – 0.30
σ	0.75	0.82	0.79	0.68 – 0.98

The density surface of the posterior distribution of s_i was successful at identifying the true locations of the home range centres of individuals that were likely to have been detected (Figure 14). Individuals on the periphery of the state-space (e.g. bottom centre-right corner of Figure 14) appear not to have been detected and hence, appear in an area of low likelihood.

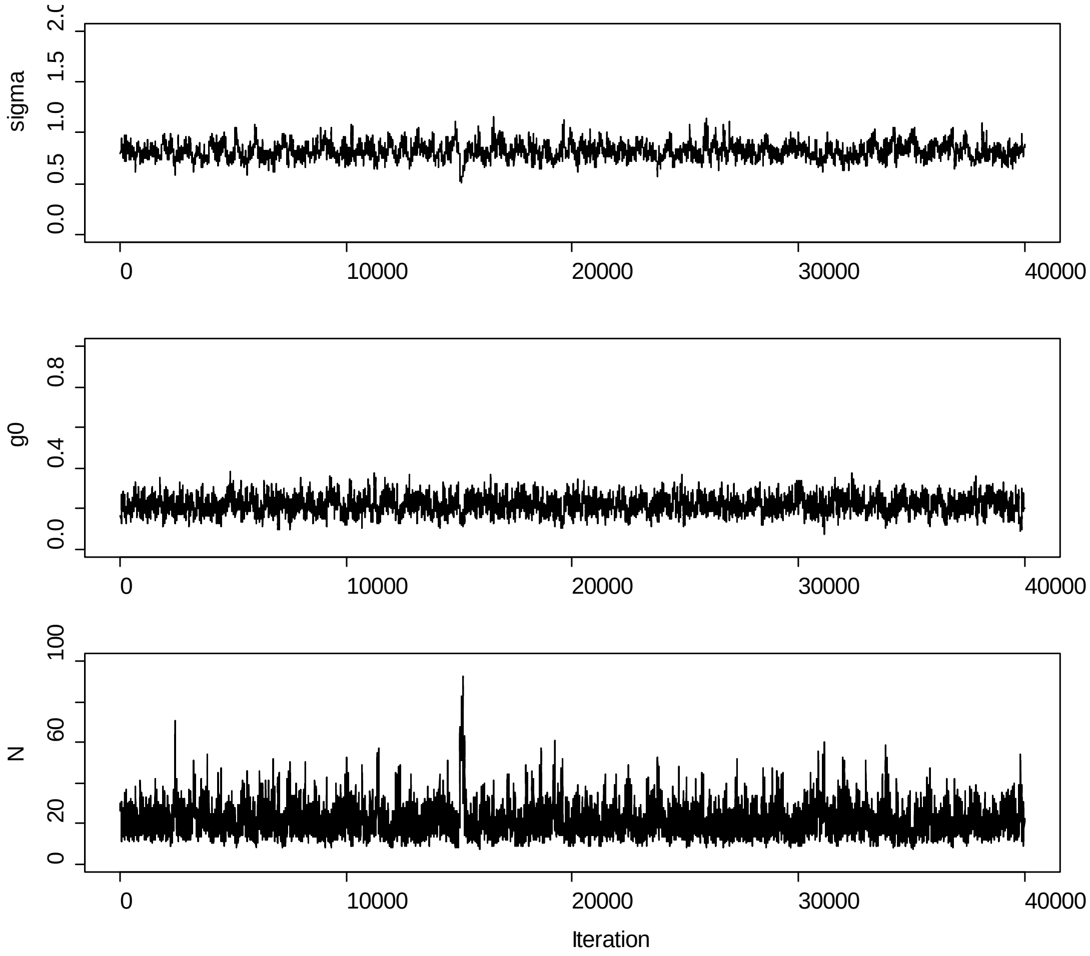

Figure 12. The MCMC chain histories for the three parameters from the spatial detection model following convergence.

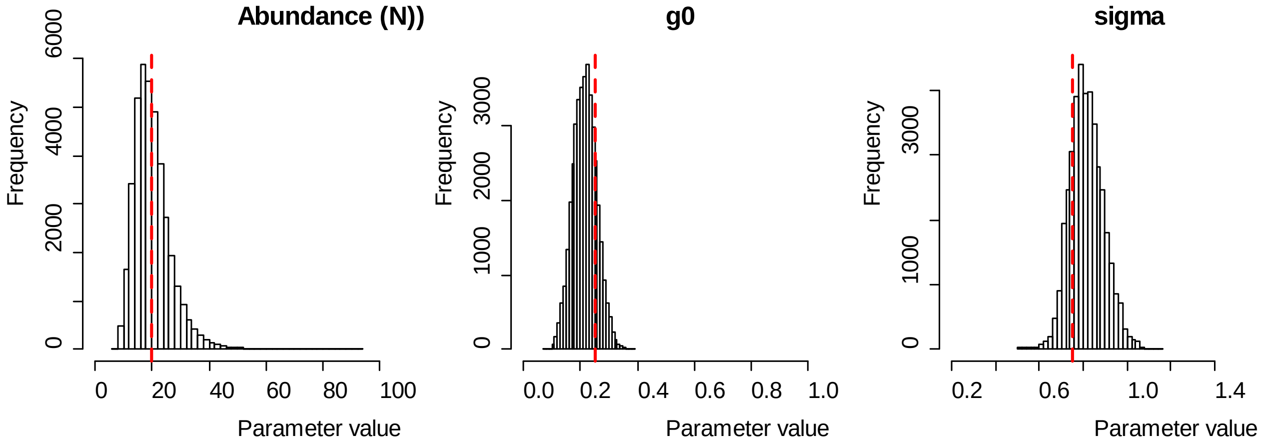

Figure 13. Posterior distributions of the parameters for population size N and the parameters of the half-normal detection function (g_0 , σ). The dashed red line indicates the true generating values for this particular scenario.

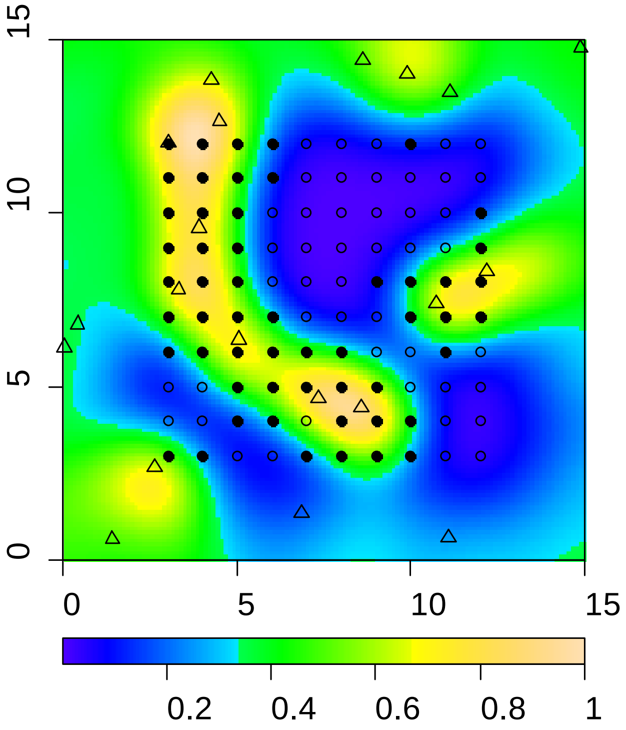

Figure 14. Density surface of the relative likelihood of locations of home range centres based of 10,000 samples of the posterior distribution of s_i for the single scenario.

Extensive simulation study

The mean of the posterior distribution used as an estimate of *N* for each of the scenarios, showed positive bias, especially when the number of occasions was low (*K*=5) (Table 3). The high bias of the mean was due to the skewed nature of the posterior distribution of $\hat{N}$. The posterior mode exhibited much lower bias and hence, is the preferred estimator for $\hat{N}$, a conclusion that was also reached by Chandler & Royle

(2013). However, the mode of the posterior distribution was only approximately unbiased for scenarios with either 10 or 20 occasions, and σ = 0.5 or 0.75 (Table 3). Coverage was also close to nominal for these scenarios. Scenarios with a low number of occasions (*K*=5) showed positive bias in the order of 10-50% and higher positive bias was generally exhibited in scenarios where σ was high (σ=1.0) (Table 3). Coverage was also usually less than nominal for these scenarios. In general, the performance of the spatial detection model was not as high as the model of Chandler & Royle (2013) using count data. This is not unexpected as detection/non-detection data are a degraded form of count data and hence, have lower information content. Due to logistical constraints, the number of simulated scenarios used here was less than those undertaken in Chandler & Royle (2013) (100 vs 200) and the number of MCMC samples were also less (12,000 vs. 32,000). Hence, the results used here should be treated as guide only and more extensive simulations are required to fully examine to properties of the spatial detection model.

The estimates of the half-normal detection function (g_0 , σ) showed a similar pattern to the estimates of *N*. The posterior distributions of these parameters exhibited less skew than those for *N* and hence, there is less difference between the posterior mean and mode (Table 4). Higher bias was evident in estimates for both g_0 and σ for scenarios with a low number of occasions (*K*=5). However, when the number of occasions was high (*K*=10 or 20), estimates of both the mean and mode were approximately unbiased for all scenarios (Table 4).

Table 3. Estimates of the posterior mean and mode, RMSE of the mean and mode and 95% coverage of population size from the spatial detection model for scenarios with known population size of 20 or 50 individuals. Estimates were calculated from 100 simulated populations for each scenario. The value of g0 for all scenarios was 0.25.

σ	*N*	*K*	*Mean*	*RMSE*	*Mode*	*RMSE*	*Coverage*
0.5	20	5	46.8	35.9	21.5	12.7	0.97
	20	10	28.5	17.3	20.4	9.6	0.91
	20	20	23.2	8.0	20.3	6.5	0.96
	50	5	79.2	41.7	60.3	41.2	0.97
	50	10	67.2	32.1	54.4	28.9	0.93
	50	20	61.8	24.7	55.0	21.6	0.90
0.75	20	5	39.5	32.3	23.8	21.3	0.93
	20	10	29.5	17.6	22.1	10.9	0.92
	20	20	23.1	9.1	19.5	7.0	0.96
	50	5	76.3	39.7	58.1	36.5	0.98
	50	10	66.7	32.4	52.9	31.1	0.93
	50	20	63.1	26.8	52.1	22.4	0.96
1.0	20	5	47.8	39.0	29.0	26.8	0.89
	20	10	33.7	24.3	23.3	17.5	0.93
	20	20	29.0	17.6	22.1	10.6	0.90
	50	20	68.8	35.0	55.1	34.3	0.89

Table 4. Estimates of the posterior mean and mode of the parameters of the spatial detection function (g_0, σ) for each of the 12 simulated scenarios with known parameters. Estimates were calculated from 100 simulated populations for each scenario. The value of g_0 for all scenarios was 0.25.

			g_0		σ	
σ	*N*	*K*	*Mean*	*Mode*	*Mean*	*Mode*
0.5	20	5	0.25	0.17	0.58	0.47
	20	10	0.25	0.23	0.53	0.40
	20	20	0.26	0.25	0.50	0.50
	50	5	0.23	0.19	0.59	0.49
	50	10	0.25	0.22	0.50	0.41
	50	20	0.24	0.24	0.50	0.49
0.75	20	5	0.24	0.20	0.76	0.70
	20	10	0.25	0.23	0.72	0.59
	20	20	0.24	0.24	0.75	0.75
	50	5	0.24	0.22	0.78	0.70
	50	10	0.25	0.22	0.76	0.62
	50	20	0.24	0.24	0.74	0.73
1.0	20	5	0.23	0.21	0.91	0.88
	20	10	0.24	0.21	0.97	0.78
	20	20	0.24	0.24	0.98	0.98
	50	20	0.25	0.23	0.99	0.98

3.4.2 ESTIMATING POPULATION SIZE OF FOXES IN THE GRAMPIANS

The posterior estimate of *N* based on the mode of the posterior distribution was 63 foxes (Table 5). However the estimate was quite skewed with an upper 95% credible interval of 353 foxes. The relatively low precision of the abundance estimate was most likely due to the sparse nature of fox detections in the data (Figure 10). Corresponding estimates of density were 0.11 foxes km^{-2} (95% CI, 0.06 – 0.57) (Table 5). This is quite low for typical fox abundance in similar habitat, reflecting the fact that the site has been subject to intensive fox baiting since 1996 as part of the “Grampians ARK” project (Robley *et al.* 2012). The posterior estimate of σ was 0.43 which was lower than the mode of the prior distribution used (0.566) with the posterior mass shifted to the left, compared with the prior distribution (Figure 8). Hence, fox home ranges were estimated to be slightly smaller than assumed by the prior distribution with a most likely home range size of 3.5 km^2 (95% CI, 1.3 – 8.9) (Table 5). Daily detection by cameras was also low with the estimate of g_0 being only 0.037 indicating the probability of a camera detecting a fox when the centre of the fox home range and camera location coincides. This was similar to estimates of detection probability estimated from occupancy analyses applied to the same dataset (Robley *et al.* 2012).

Table 5. Parameter estimates of fox population size $\hat{N}$ (and density) as well as parameters of the detection function (g_0, σ) from the spatial detection model applied to detections in camera traps from the Grampians National Park.

Parameter	Estimate (mode)	SD	2.5%	97.5%
$\hat{N}$	63	84.1	37	353
Density (foxes/km^2)	0.11	0.136	0.06	0.57
g_0	0.037	0.026	0.012	0.114
σ	0.43	0.106	0.266	0.690

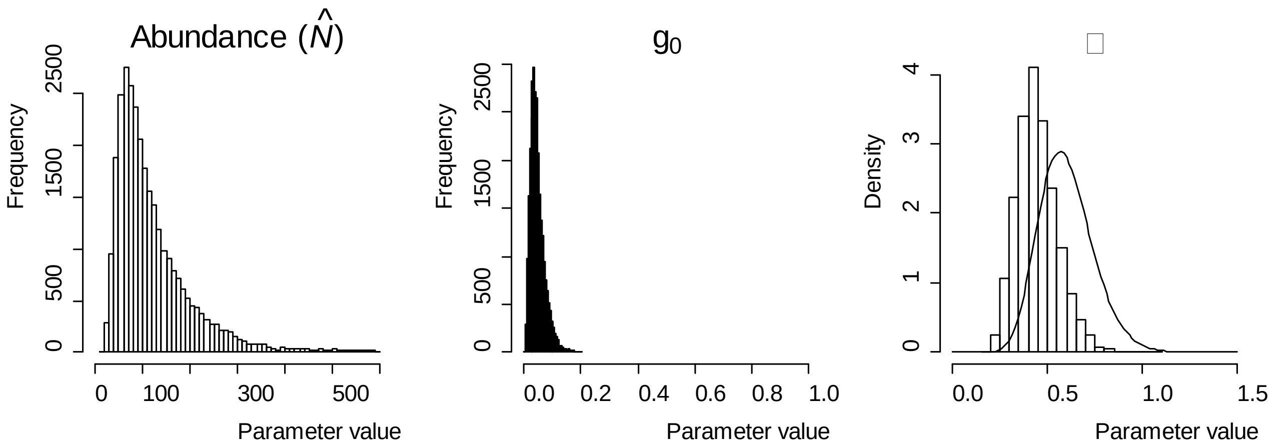

Figure 15. Posterior distributions of fox abundance $\hat{N}$, and the parameters of the half-normal detection function (g_0, σ) using the spatial detection model applied to fox detections in cameras in the Grampian National Park. The solid line overlaid on the posterior distribution for σ is the prior distribution used.

4 Discussion

Our application of the ABC method appears successful when applied to the sparse carcass discovery data associated with the red fox incursion in Tasmania. Our ABC model provides much more useful inference than the models based on the early work of Solow (1993a), which primarily make inference on whether the population is extinct but provide little additional inference about the population under control. The ABC approach also allows much more realistic processes to be considered than is the norm in the literature. For example, the original model of Solow (1993a) assumed a constant sighting rate, effectively meaning that the population was constant until extinction. Subsequent model elaborations such as declining sighting rate are considered by Solow (1993b) and Rout *et al*. (2009), and are a first step in addressing the issue of model plausibility but are not the complete solution. In particular the assumption of a constant or declining sighting rate may be sound for rare species in what is often terminal population decline. The use, however, of a model assuming a constant or declining population to underpin `rules of thumb' for ceasing eradication programs of invasive species may be unsound. Attempts at eradication of invasive species often fail, whether they be vertebrates [other than those undertaken on islands] (Bomford and O'Brien 1995a), plants (Rejmanek and Pitcairn 2002) or insects (Myers *et al.* 1998) so the model assumptions need be applicable to all possible scenarios. Invasive species, by definition, have potentially robust demographics that can lead to a rapid change in abundance that may or may not overlap with sighting mechanisms. The spatio-temporal approach we have taken here explicitly accounts for such a possibility, and allows the population to change stochastically. Inference on the likely distribution of the population if extant, demographic rates, locations and dates of introduction are examples of parameters for which the ABC method can provide inference.

Attempts at estimating population density from detection/non-detection data using ABC methods (APARP Project GMS1520 Progress Report) did not meet with initial success. Summary statistics of the spatial relationships among detections proved to be relatively uninformative about the spatial encounter process (spatial detection model). The parameter expanded data augmentation model developed by Chandler and Royle (2013) has overcome the problems inherent in the ABC model by including locations of home range centres explicitly in the state-space and sampling from their target distribution using a new MCMC algorithm. Since actual data likelihoods are specified in the model, approximate Bayesian techniques are not required. Although more work is required to determine the properties of the new model applied to detection/non-detection data under a variety of real-world conditions, the new method holds promise. Results from the limited number of simulation scenarios suggests that the spatial detection model performs fairly well with relatively low bias using sampling designs where spacing between detection devices is less than the length of a typical radius of an individuals' home range (assuming ranges can be approximated by a circular bivariate normal distribution) and the number of encounter occasions is high (i.e. 10 – 20). The non-independence of sampling devices allows multiple devices to be encountered by a single individual and produces spatially correlated detections that are informative for estimating parameters of a simple spatial encounter process.

To our knowledge, this is the first time that rigorous estimates of population density have been obtained from detection/non-detection data that does not require collection of any ancillary data (other than specifying prior distributions for parameters). The occupancy/abundance model of Royle and Nichols (2003) is related to the current model in that detection probability and occupancy are explicitly modelled by population abundance. However, the model of Royle and Nichols (2003) is usually not used to estimate population density as a parameter of interest as it requires that all sampling devices are independent, as well as the requirement to specify an effective sampling radius around each device with which to infer density. The last requirement is strictly subjective and has a major influence on population estimates. These requirements are distinct from those of the current model where the area of inference is explicitly included as the state-space in the estimation process. Estimation of population density is then trivial given the estimate of the number of home range centres present in the state-space. The current model should have wide applicability to a range of sampling situations that result in spatially correlated detection/non-detection data such as bait take, scat surveys, tracking stations and chew cards, to name a few.

Although the spatial detection model shows promise for inferring population density from detection/non-detection data, there are a number of limitations of the model that may preclude its use in some situations. In particular, the posterior distribution of the abundance can be highly skewed, especially if data are sparse (as in our Grampians fox data). This results in estimates of abundance with low precision, a finding that was also evident in the analysis of count data (Chandler & Royle 2013). In addition, it appears that estimates with low bias and high precision require a high number of detection occasions (i.e. 10 - 20), which may preclude its use in some situations. Further work is required to better define the limitations of the new model and this is the subject of ongoing investigations

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CONTACT US

t 1300 363 400
+61 3 9545 2176
e enquiries@csiro.au
w www.csiro.au

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FOR FURTHER INFORMATION

Computational Informatics/Biosecurity Flagship
Peter Caley
t +61 2 6216 7063
e peter.caley@csiro.au
w http://www.csiro.au/Organisation-Structure/Flagships/Biosecurity-Flagship.aspx

Division/Unit Name
David Ramsey
t +61 3 9450 8701
e David.Ramsey@depi.vic.gov.au
w http://www.depi.vic.gov.au/environment-and-wildlife/arthur-rylah-institute

Computational Informatics/Biosecurity Flagship
Simon Barry
t +61 2
e simon.barry@csiro.au
w http://www.csiro.au/Organisation-Structure/Divisions/Computational-Informatics.aspx