FoxNet: an individual-based modelling framework to support red fox management

Bronwyn A. Hradsky[1,2ǂ], Luke Kelly[1,3], Alan Robley[4], Brendan A. Wintle[1,2]

[1]Quantitative and Applied Ecology, School of BioSciences, University of Melbourne, Australia

[2]NESP Threatened Species Recovery Hub, University of Melbourne, Australia

[3]ARC Centre of Excellence for Environmental Decisions, School of BioSciences, University of Melbourne, Australia

[4]Arthur Rylah Institute, Department of Environment, Land, Water and Planning, Heidelberg VIC 3084 Australia

ǂCorresponding author. hradskyb@unimelb.edu.au

Running title: FoxNet – an IBM framework to support fox management

Summary

1. Invasive predators are a key driver of biodiversity decline, and effective predator management is a globally important conservation issue. Red foxes (*Vulpes vulpes*) pose a significant threat to wildlife, livestock and human health across Eurasia, North America and Australia. Despite worldwide investment in red fox management, decision-makers still lack flexible tools for predicting management efficacy.

2. We have developed FoxNet, an individual-based modelling framework that can be customised to predict red fox population dynamics, including responses to control and landscape productivity. High-resolution models can be run across northern- and southern-hemisphere landscapes. We present three case-study models to verify FoxNet outputs, explore key sensitivities, and demonstrate the framework's utility as a management-planning tool.

3. FoxNet models were largely successful in reproducing the demographic structure of two very different fox populations, and accurately generated the relationship between home-range size and fox-family density for home-range sizes between 1.0 and 9.6 km^2. They also captured the rapid decline and seasonally-driven recovery of a fox population following poison-baiting.

4. An exploration of alternative baiting scenarios for a woodland reserve predicted that current management suppresses fox density by ~70%. Frequent baiting is required to combat recolonization; baiting at higher densities or establishing a buffer zone would further reduce fox densities. Predictions were sensitive to home-range and litter-size assumptions, illustrating the value of region-specific data on fox movement and biology.

5. *Synthesis and applications:* FoxNet provides a versatile modelling framework for guiding management of a globally-significant pest species. Customised models can be used to answer critical questions about the location, spread and timing of predator control. FoxNet's ability to reproduce field observations from diverse landscapes indicates its immediate relevance to management. Future extensions could include competitor and prey species to predict trophic responses to fox control and explore the effects of habitat disturbance on predator density.

Keywords: agent-based model, biodiversity conservation, carnivore, invasive species, population dynamics, predator control, spatially-explicit population model, *Vulpes vulpes*

Introduction

Invasive mammalian predators are among the leading causes of global biodiversity decline (Bellard *et al.* 2016; Doherty *et al.* 2016). Understanding the effectiveness of predator control is therefore a key conservation issue across urban and natural landscapes (Bonnell & Breck 2017; O'Donnell *et al.* 2017). One of the world's most widespread predators, the red fox *Vulpes vulpes*, is invasive or overabundant across much of its range (Larivière & Pasitschniak-Arts 1996). Red foxes (hereafter 'foxes') pose a significant threat to numerous birds and mammals (Kamler & Ballard 2002; Doherty *et al.* 2016), impact livestock (Baker *et al.* 2008), and host zoonoses (Muller *et al.* 2015; Budgey *et al.* 2017). Thus, there is substantial investment in the design and deployment of fox management programs across Europe, North America and Australia (McLeod 2004; Shwiff *et al.* 2011; Muller *et al.* 2015). For example, Australia spends more than $16 million AUD on fox management annually (McLeod 2004).

A range of techniques have been used to study fox management, including field experiments (Thomson *et al.* 2000; Bino *et al.* 2010; Lieury *et al.* 2015), mathematical models (Harding *et al.* 2001; McLeod & Saunders 2001) and individual-based models (IBMs; Thulke *et al.* 1999; Smith & Wilkinson 2003; Rushton *et al.* 2006; Budgey *et al.* 2017). IBMs (also known as agent-based models) can be used to investigate how individual behaviours and local interactions create spatial and temporal patterns in population dynamics (Grimm et al. 2005). They represent the components of a system as unique, autonomous 'agents' (or 'individuals') which use adaptive behaviours, such as seeking food resources, to achieve goals (Grimm et al. 2005). IBMs have considerably advanced our understanding of fox management, demonstrating that lethal approaches are more effective than fertility control for suppressing foxes and eradicating diseases, and that fox density, immigration, and the timing and configuration of intervention influence control efficacy (Smith & Wilkinson 2003; Rushton *et al.* 2006; Eisinger & Thulke 2008; Budgey *et al.* 2017).

Nonetheless, several factors limit the broader relevance of previous fox management IBMs. First, the proportion of individuals 'treated' (i.e. poisoned, immunised or sterilised) within the management area is pre-determined by the modeller. This prevents comparison of different management designs (e.g. the intensity of bait deployments) and ignores issues such as spatial variation in bait uptake (Carter & Luck 2013). Second, most IBMs have been developed for specific landscapes, and do not support customisation of demographic parameters, which vary widely among fox populations (Devenish-Nelson *et al.* 2013). Finally, existing models fix the distribution and number of fox territories from the outset of implementation, preventing exploration of the dynamic nature of fox territories (Bino *et al.* 2010; Hradsky *et al.* 2017b). Recent advances in modelling carnivore territories based on resource acquisition and individual interactions (e.g. Carter *et al.* 2015) provide opportunities for more sophisticated explorations of these dynamics.

Poison baiting with 1080 (sodium fluoroacetate) is the primary fox management approach in Australia (Saunders *et al.* 2010). Baiting at large scales (>500 km^2) and high densities (≥5 baits km^{-2}), greatly reduces fox densities, with populations remaining low for several months (Thomson *et al.* 2000; Berry *et al.* 2014). In contrast, patchy or smaller-scale control may result in little detectable change in fox density (Bengsen 2014; Newsome *et al.* 2014), or even increase fox activity or abundance through compensatory immigration (Lieury *et al.* 2015; Towerton *et al.* 2016). Considerable uncertainty remains about the efficacy of large-scale fox management for biodiversity conservation (Walsh *et al.* 2012; Robley *et al.* 2014; Towerton *et al.* 2016), and the design of more effective management is hampered by a lack of tools for predicting the effects of control.

The aim of this study was to develop a spatially-explicit IBM framework to facilitate predictive modelling of fox populations under spatially- and temporally-variable management regimes. Our modelling framework, FoxNet, can be customised to heterogeneous landscapes and northern- and southern-hemisphere scenarios. We “evaludated” (i.e. evaluated and validated) FoxNet using a hierarchically-structured approach to analyse processes at an individual- and population-level (Augusiak *et al.* 2014; Kubicek *et al.* 2015). Case-study models are presented to demonstrate different aspects of FoxNet’s generality and application to management problems, including output verifications or sensitivity analyses for key parameters. Additional demonstrations, worked examples, and implementation verifications are provided in the User Guide (Appendix S1).

Methods

THE FOXNET MODELLING FRAMEWORK

FoxNet is a customisable framework for running red fox population models, based in Netlogo (version 6.0.2; Wilensky 1999). It has four main types of agent: *habitat-cells*, *foxes, fox-families* and *bait-stations.* It progresses in weekly, fortnightly or four-weekly time-steps, with 52 weeks per year. A detailed User Guide and description of FoxNet following the revised Overview, Design Details (ODD) protocol (Grimm *et al.* 2010) are provided in Appendix S1.

FoxNet forms a landscape of square habitat-cells, which can be generated within FoxNet or imported via a GIS extension. Habitat-cells specify the layout of habitat types and monitoring regions(s). Their size is user-specified; 0.01 km^2 provides a good compromise between computational efficiency and intra-home-range variation, given fox home-range size varies from less than 0.5 km^2 to more than 9 km^2 (Trewhella *et al.* 1988). To facilitate scenario customisation, the productivity of each habitat-cell in the primary habitat type is calculated from the size of an average fox home-range for that location (input by the user) and the daily food requirements of an adult fox (378 g/day; Lockie 1959); an approach similar to Carter *et al.* (2015). For example, if input fox home-range size was 2 km^2, the productivity of each 0.01 km^2 habitat-cell in the primary habitat type would be 1.89 g day^{-1}. The productivity of other habitat types is specified relative to this primary habitat type.

Foxes are mobile agents whose behaviour is determined by their age, status (cub, subordinate, disperser or alpha) and the time of year (Larivière & Pasitschniak-Arts 1996). Each alpha fox is a member of a fox-family – another agent, which is used to establish and update the territory of its family-members (foxes within a family share a semi-exclusive territory; Sargeant 1972). A fox-family must contain at least one alpha fox, and may also include the alpha's mate, cubs and subordinate offspring (Baker *et al.* 1998).

Bait-station agents indicate the habitat-cells where baits are laid. They can be positioned at regular, random or customised locations, and only affect foxes who can access that habitat-cell.

Baiting occurs at user-specified intervals (maximum frequency of once each time-step), lasts one time-step by default, and is lethal or non-lethal (i.e. foxes may die or survive after encountering a bait).

FoxNet repeats a series of processes consecutively each time-step (Fig. 1):

1. Year and week counters are updated (by 1, 2 or 4 weeks, as applicable). Key seasonal events are linked to week-of-year, making FoxNet customisable to northern- and southern-hemisphere scenarios.
2. The age of each fox is updated by the appropriate number of weeks. Cub foxes become subordinates if they reach the age-of-independence. If it is the dispersal season, subordinate male and females have user-specified probabilities of becoming dispersers.
3. Natal succession occurs, i.e., if a fox-family is missing an alpha fox, one of the family's subordinates that is the appropriate sex and ≥24 weeks old becomes the alpha (Baker et al. 1998).
4. Fox-families acquire/replace habitat-cells to maximise the productivity and efficiency of their territory. This enables fox-families to take over unoccupied productive habitat-cells (Sargeant 1972) and respond to changes in resource availability (Bino et al. 2010; Hradsky et al. 2017b). If the productivity of a fox-family's territory is less than an adult fox's minimum food requirements (<295 g/day; Winstanley *et al.* 2003), the fox-family fails, causing all adults to become dispersers and cubs to die.
5. If applicable, baits are laid at bait-stations and the cost of baiting is calculated. Foxes belonging to a fox-family with a territory that overlaps an active bait-station are at risk of dying. Risk scales directly with the number of bait-stations and bait efficacy, and inversely with territory size and fox abundance (Appendix S1). Each bait-station only affects one fox each time-step.
6. New disperser foxes leave their natal family and move in a random direction for a random distance drawn from a sex-specific exponential distribution, scaled by their home-range-size

(Trewhella et al. 1988). Disperser foxes then explore an area three times the radius of an average home-range (Soulsbury et al. 2011) where they (1) are exposed to any active bait-stations; (2) attempt to join a fox-family that lacks an alpha fox of the appropriate sex; (3) try to establish a new fox-family. If unsuccessful, they remain a disperser until the next time-step.

7. If it is the breeding season, fox-families that contain an alpha male *and* an alpha female fox breed, producing a Poisson-distributed number of cubs. If an alpha fox is absent, all family-members become dispersers and attempt to join other nearby fox-families, promoting the persistence of the population at low densities.
8. Stochastic background mortality of foxes occurs, based purely on their age.
9. Cub foxes belonging to fox-families without any adults die, reflecting their dependence on food-provision (Baker *et al.* 1998). This allows baiting to affect reproductive success. Fox-families that no longer have any family members are removed.
10. Model outputs are updated and plotted. Outputs can include age structure, population structure, dispersal distances, density or number of neighbours of foxes within the monitoring region(s), the number of foxes with territories overlapping a monitoring transect, and/or bait-take rates.
11. If baits were deployed at bait-stations at step 5, un-eaten baits are removed to mimic the degradation of the poison to non-toxic levels (Saunders *et al.* 2000).
12. The time-step counter increases by one.
13. The model checks if any fox agents are alive. If all foxes are dead, the model stops.

FOXNET CASE STUDIES

Case-study models were run in R v3.5.1 (R Core Team 2016) using RNetLogo (Thiele 2014), with 30 iterations of each parameter set. Unless otherwise specified, models were run for 15 years to remove founding effects before experiments commenced. Input parameters were extracted from field studies (see Appendix S2 for sources) and were not calibrated to improve output fit. Output verification (Augusiak *et al.* 2014) was conducted through quantitative comparison of model outputs and field estimates as per Bennett *et al.* (2013)

i. Bristol, England and *Northern Hemisphere*

The fox population at Bristol is dense (>6 foxes km^2) and socially complex. Parameters from field studies (Appendix S2) were used to build a FoxNet model with a homogenous 1600 km^2 landscape (Appendix S3 Fig S3.1). The number of foxes in each demographic group and the proportion of foxes in each age class were output for a central 116 km^2 area in April and compared to field estimates by Harris and Smith (1987). Harris and Smith (1987) only provide point estimates without uncertainty bounds and so we could not test whether modelled output bounds lay within their observation error. Instead, we verified demographic group outputs by calculating the probability of the field observation coming from the modelled distribution, and verified age-structure outputs by fitting a linear regression to mean model outputs against field observations and checking whether the regression differed from 1:1. Harris and Smith (1987) reported net annual emigration of 17.6% male cubs, 5.9% female cubs and 3.4% of adult females, and so we ran a second 'emigration' version of the model with a customised code to incorporate these rates as mortality at the start of each dispersal season.

We used similar inputs (Appendix S2) to verify that FoxNet models reproduced the relationship between home-range size and fox-family density observed across 22 northern hemisphere fox populations (Trewhella *et al.* 1988). We varied the home-range size input from 0.45 to 9.6 km^2 (the minimum and maximum values recorded by Trewhella *et al.* (1988)) and ran models for 5 y as fox-family densities stabilised within this time. We fitted a linear regression to the relationship between 1/home-range-size and fox-family density for the FoxNet outputs and field observations, and tested whether data source influenced the regression intercept or slope.

ii. Carnarvon, Western Australia

An arid Australian rangeland at Carnarvon supports a low density of foxes (~0.5 foxes km^{-2}) with a monogamous mating system (Marlow *et al.* 2000). A destructive sample across 200 km^2 in December provided a snapshot of population age structure and abundance (Marlow *et al.* 2000). We used parameters from field studies (Appendix S2) to build a model of this population and verified age-structure outputs using a linear regression of mean output values against field observations, as for the Bristol case-study above.

We then built a model with the same input parameters but a 13,628 km^2 landscape to reproduce a management experiment described by Thomson *et al.* (2000). We imported the landscape as a raster with land, ocean and an asymmetric monitoring region (Appendix S3 Fig S3.2). We wrote a customised baiting code to deploy 5 poison baits km^{-2} across a 3180 km^2 zone in August, followed by baiting of the outermost 5 km of the zone in May and the outermost 10 km in February and May of the third year. We determined whether the range of output fox densities in a core ~1000 km^2 baited region over 96 weeks overlapped Thomson *et al.*'s (2000) field estimates, for three modelled levels of bait efficacy. Only foxes >12 weeks old were included in the output densities, as field survey methods were unlikely to detect young cubs.

iii. Mt Clay Reserve, Victoria, Australia.

Government agencies have been poison-baiting foxes at Mt Clay State Forest and Narrawong Flora Reserve (hereafter 'Mt Clay Reserve') in south-eastern Australia since 2005 as part of the Glenelg Ark program to protect threatened native mammals (Robley *et al.* 2014). The program has reduced fox activity but some foxes persist in the 4703-ha reserve and surrounding farmland, and priority native species have not shown a substantial positive response (Robley *et al.* 2017). Poison baits are buried at 45 stations at 1-km intervals along roads within the reserve, and replaced fortnightly (Robley *et al.* 2014). Alternative baiting designs, including changes to baiting density and frequency, need to be explored to enhance conservation management (Robley *et al.* 2017).

We customised a FoxNet model with parameters from field studies and imported a 4971 km^2 landscape which delineated forest, farmland and ocean (Appendix S2; Appendix S3 Fig S3.3). We applied the following alternative baiting programs:

i. Current management: baits deployed fortnightly at 1-km intervals along roads.
ii. Variation in baiting frequency: baits replaced every fortnight, four weeks, quarter, or once a year (in January, April, July or September).
iii. Variation in bait density: a grid of baits across the reserve, with 0.5 – 8 baits km^{-2}.
iv. Variation in baited area: a 1 bait km^{-2} grid across the reserve and a 1 – 10-km surrounding buffer.

Modelled fox density in the reserve was sampled fortnightly, with values calculated across 10 years of baiting, after a 2-year transition phase. Field estimates were not available for validation, but we analysed model output sensitivity to fox home-range area, litter size, female dispersal rates, bait efficacy and the relative productivity of forest and farmland by independently varying each parameter by ±20% and ±50% (Appendix S2).

Results

i. *Bristol, England* and *Northern Hemisphere*

The numbers of non-breeding female, alpha male and subordinate male foxes output by the initial Bristol model were consistent with field estimates (Table 1). However, the modelled numbers of fox-families, breeding females and cubs were approximately 4%, 10% and 9% higher than field estimates, respectively, and the itinerant population was also substantially larger than observed (Table 1). This led to the overall modelled population size being approximately 24% larger than the field estimate. Including additional mortality to mimic net emigration reduced, but did not entirely reconcile, these differences, with the modelled population remaining 16% larger than the field estimate (Table 1).

The population age structure output by the initial Bristol model entirely overlapped field estimates (Fig. 2a) with no evidence that the regression of modelled outputs against field estimates differed from 1:1 (mean ± 1.96 se: $\beta_0 = 0.17 \pm 0.22$; $\beta_1 = 0.99 \pm 0.01$). Including net emigration had little effect on modelled age structure (Fig. 2a) but caused the slope of the regression to become slightly higher than 1:1 ($\beta_0 = -0.71 \pm 0.95$; $\beta_1 = 1.06 \pm 0.05$).

The relationship between fox home-range size and fox-family density was very similar for model outputs and field observations from 22 northern hemisphere studies (Fig. 3). There was no evidence that data-source influenced either the intercept (0.15 ± 0.29, $p = 0.32$) or slope (-0.24 ± 0.27, $p = 0.09$) of the relationship. Model outputs showed much less variation than field data, likely because FoxNet does not currently include stochastic environmental variation in mean survival, fecundity or home-range size.

ii. Carnarvon, Western Australia

The output age structure for Carnarvon followed a similar pattern to field estimates, with no evidence that the regression of mean modelled outputs against observations differed from 1:1 ($\beta_0 = 1.49 \pm 5.11$; $\beta_1 = 0.88 \pm 0.24$). However, model outputs included proportionally more 1–2 y and 2–3 y old animals and fewer 3–4 y old and >6 y old animals (Fig. 2b). This is likely because the field observations were not from a stable population: there were more animals in the 3–4 y old age class than the younger age classes (Fig. 2b). The output density of adult foxes (mean, min–max: 0.42, 0.34–0.49 foxes km^{-2}) marginally overlapped the field estimate of 0.46–0.52 foxes km^{-2}.

Modelled bait efficacies of 0.3 and 0.5 did not result in sufficient suppression of the Carnarvon fox population. However, a bait efficacy of 0.7 (i.e. a ~13 % chance of death per time-step for a fox with one bait on its territory) produced a decline comparable to Thomson *et al.*'s (2000) observations (Fig. 4). Recovery rates were also consistent with observations: remaining very low for six months then increasing sharply with the dispersal of young foxes in autumn. Modelled densities were 45 (30–54)% lower than field data for week 40, but approached observed values by weeks 82–87 (Fig. 4).

iii. Mt Clay Reserve, Victoria, Australia

For an unbaited Mt Clay model scenario, output fox densities over a 10-year period fluctuated between 1.01 (0.81–1.12) and 2.61 (2.15–2.84) foxes km^{-2} (excluding cubs <12 weeks of age). Densities were lowest pre-breeding and peaked in early summer each year with the recruitment of subordinates (Fig. 5a). These patterns are corroborated by a field study from 300-km away that found fox densities fluctuate between 1.2 foxes km^{-2} immediately prior to breeding and 3.0 foxes km^{-2} in early summer (Coman *et al.* 1991). The model predicted that the current baiting regime reduces average maximum fox density by 73% and dampens annual fluctuations, with a small peak associated with recruitment, and a larger peak around autumn dispersal (Fig. 5a).

Decreasing baiting frequency from fortnightly to 4-weekly or quarterly intervals would increase maximum fox density to 122% or 255% of current levels (Fig. 5b). Baiting once per year would mean that maximum fox densities remained at 91–95% of unbaited levels (Fig. 5b).

The current baiting regime deploys 0.96 baits km^{-2} patchily across Mt Clay. A regular grid with 1 bait km^{-2} would only require one extra bait-station but would reduce maximum fox density to 92%

of current levels due to more even coverage. Grids with higher bait densities would achieve greater reductions (Fig. 5c). At 8 baits km^{-2}, maximum fox density would be reduced to 37% (0.27 foxes km^{-2}) of current densities (Fig. 5c).

Establishing a 1000-m baited buffer around Mt Clay would reduce maximum fox density within the reserve to 58% of the current baiting scenario, or 63% of the "1 bait km^{-2} but no buffer" scenario (Fig. 5d). Larger reductions would occur with a wider buffer, although returns diminish with increasing buffer width (Fig. 5d).

Output maximum fox densities for Mt Clay were relatively robust to changes in the proportion of dispersing females, the relative productivity of forest and farmland, the efficacy of baits, and increases in home range area, with no more than a 26% change in maximum density for the ±50% change scenarios (Fig. S4.1). Outputs were more sensitive to the estimates of litter size and decreases home-range area, which affected both fox density in the unbaited landscape and the population's capacity to recover from baiting. A 50% decrease in mean litter size reduced maximum fox density to just 0.05 (0.00–0.17) foxes km^{-2} in the year prior to baiting, and often resulted in extinction post-baiting (Fig. S4.1); however, an average of 1.87 cubs per breeding female is unrealistically low compared to observed litter sizes of 2.8–6.74 cubs worldwide (McIlroy *et al.* 2001). In contrast, a 50% decrease in mean home-range area (to 1.07 km^2) increased maximum fox density to 4.66 (3.96–5.14) foxes km^{-2} in the year prior to baiting; densities remained nearly twice the baseline scenario after baiting (Fig. S4.1). This values falls within the lowest 20th percentile of fox home-ranges sizes observed in south-eastern Victoria (Hradsky *et al.* 2017b; B. Hradsky, unpublished data).

Discussion

Our modelling framework, FoxNet, provides a new tool to support management of a globally-significant pest species. The case-study models reproduced numerous field observations from northern- and southern-hemisphere environments, indicating considerable promise in generality and predictive accuracy. Our exploration of fox densities under alternative baiting strategies demonstrates FoxNet's value for answering critical questions about the optimal design of predator control at scales relevant to policy and on-ground management.

MODEL VERIFICATION

Models generated using the FoxNet framework reproduced the structure of fox populations from two highly contrasting landscapes. The Bristol model generated a dense fox population with an age structure and breeding population largely consistent with observed values, but a higher number of itinerant foxes. Incorporating emigration did not fully reconcile this difference. Discrepancies in the order of 5 – 16% potentially lie within the error margins of Harris & Smith's (1987) field estimates; however other possible causes are discussed below. The Carnarvon model generated a sparse population with an age structure similar to that observed by Marlow *et al.* (2000), but with more young foxes and fewer old foxes, likely due to a historic legacy in the field data: a stable population would not have more animals in an older age class than a younger one. This highlights the need to consider whether populations are at equilibrium or in transition when analysing data, fitting and evaluating models, and designing management responses.

FoxNet models accurately predicted *fox-family* density from home-range size data across an order of magnitude. This accuracy contrasts favourably with the approximately 10 - 20% discrepancy between mean model outputs and field estimates for *fox* densities for the Bristol and Carnarvon case-studies. Fox densities within FoxNet models fluctuate substantially each year, peaking with the recruitment of cubs (as shown for the Mt Clay model), while the number of fox-families remains relatively constant. Small discrepancies in the timing of seasonal events such as births or dispersal

(Marlow et al. 2016) and seasonal variation in mortality rates (Storm et al. 1976; Harris & Smith 1987) could therefore explain the differences between modelled fox densities and field estimates. Ideally, model performance would be evaluated over several years to capture seasonal and annual variation due to climate and other interacting factors. The FoxNet framework could be easily adjusted to include intra-annual and sex-specific survival dynamics where data are available.

Based on realistic assumptions about bait efficacy, the Carnarvon model reproduced the response of a fox population to pulse baiting, including population decline and recovery. In the short-term, modelled population recovery was somewhat slower than observed (Thomson *et al.* 2000), indicating an opportunity to improve model fit via experiments that explore compensatory fecundity and immigration hypotheses (Marlow *et al.* 2016; Zakharov *et al.* 2016).

DESIGNING STRATEGIES FOR INVASIVE PREDATOR MANAGEMENT

The Mt Clay case-study demonstrates FoxNet's utility for planning fox control. For this relatively small nature reserve, the model showed that frequent baiting was required to combat recolonization from the surrounding landscape. The current baiting strategy was predicted to suppress maximum fox population densities by approximately 70%. This concurs with annual motion-sensing camera surveys conducted between 2013 and 2015, which detected foxes at 66–91% fewer sites at Mt Clay than an unbaited reserve (A. Robley, unpublished data). The model indicated that foxes remained present within Mt Clay at low densities, which is again supported by the detection of foxes at 8–28% of baited sites in annual surveys (A. Robley, unpublished data).

Reducing the frequency of bait replacement at Mt Clay from fortnightly to every four weeks would result in a ~20% increase in maximum fox density, while annual baiting would be largely ineffectual. By contrast, increasing the number of bait-stations would substantially reduce fox densities, relative to the current regime. For example, maximum fox densities could be maintained at <0.4 foxes km^{-2} by increasing bait density to 4 baits km^{-2} or by baiting at 1 bait km^{-2} across the reserve and a 2000-m buffer. To maintain fox densities at consistently low levels, it is more effective to bait a buffer zone than increase bait density, as this dampens the annual peak caused by dispersing individuals. These results are immediately useful for supporting management decisions in the case-study location and could be easily adapted to other scenarios.

Aspects of fox demography such litter size vary substantially between populations (Devenish-Nelson *et al.* 2013); however, model outputs for Mt Clay were robust to most tested parameters. A strength of the modelling and evaluation framework is that it provides clarity about which uncertainties are most important to resolve in order to improve management decisions and design adaptive management strategies (Runge *et al.* 2011). For example, the sensitivity of the model to home-range size indicates that this is a key research priority. For the Mt Clay case-study, home-range data were available for 18 foxes in comparable habitat, providing a high degree of confidence in the estimate. Predicted fox densities under the current baiting regime were more sensitive to a decrease in home-range size than an increase, because smaller home-ranges resulted in a denser population and less effective bait saturation. Similarly, the population could not persist if fecundity was (unrealistically) low even in the absence of baiting; however, increasing fecundity had less effect as carrying capacity is limited by the number of available territories. Knowledge about the level of parameter precision required to discriminate between management options is crucial when designing monitoring or experiments to address knowledge gaps that impact management (Wintle 2018).

EXTENDING THE FOXNET FRAMEWORK AND ITS APPLICATIONS

The FoxNet framework provides a substantial advance over previous IBMs of fox population control, as it captures the dynamic nature of fox territories and densities, and the effects of bait layout, home-range size and fox density on the efficacy of control. The case-study models confirm that FoxNet is a useful tool for predicting the structure and density of fox populations under different landscape contexts and management strategies. As the FoxNet framework allows foxes to update their territories in response to changes in habitat productivity, it could also be used to explore the effects of disturbance events such as fire on fox populations (Hradsky et al. 2017a), facilitating the development of integrated threat management programs. Future extensions could refine seasonal and density-dependent variations in fecundity, and include competitor or prey species to predict cross-trophic responses to management. FoxNet would require further work to capture daily interactions between individuals and so be applicable to disease-spread scenarios (see Thulke & Eisinger 2008). With revision of the territory-formation processes, FoxNet could also be adapted to other invasive carnivores such as feral cats.

IBMs capture important variation in processes at scales relevant to management and are increasingly used to improve efficiency in on-ground conservation planning (Stillman *et al.* 2015; Pacioni *et al.* 2018). FoxNet's realistic predictions make it immediately applicable to the spatial design and optimisation of predator control programs. By providing important insights into the effectiveness of management, FoxNet has the potential to be a valuable addition to the conservation practitioners' toolbox.

Author contributions

All authors conceived the study. BH was the main developer of FoxNet and led the writing of the manuscript. All authors contributed to FoxNet design and manuscripts, and gave final approval for publication.

Acknowledgements

Many thanks to Neil Carter for early discussions on IBM structure, Casey Visintin, Jian Yen and Nick Golding for help with parallel computing, and Michael Bode, Volker Grimm and an anonymous reviewer for constructive feedback. BH was funded by the Australian Government's National Environmental Science Program through the Threatened Species Recovery Hub, the Victorian Government and Parks Victoria. LK received support from the Victorian Government and ARC Centre of Excellence for Environmental Decisions.

Data accessibility

FoxNet code and outputs are available via CoMSES Net https://www.comses.net/users/2413/.

Supplementary Material

Appendix S1. FoxNet User Guide and ODD.

Appendix S2. Input parameters and data sources for the case-study models.

Appendix S3. Landscape layouts for the case-study models.

Appendix S4. Sensitivity analysis for the Mt Clay model.

References

Augusiak, J., Van den Brink, P.J. & Grimm, V. (2014) Merging validation and evaluation of ecological models to 'evaludation': A review of terminology and a practical approach. *Ecological Modelling,* **280,** 117-128.

Baker, P.J., Boitani, L. *et al.* (2008) Terrestrial carnivores and human food production: impact and management. *Mammal Review,* **38,** 123-166.

Baker, P.J., Robertson, C.P.J. *et al.* (1998) Potential fitness benefits of group living in the red fox, *Vulpes vulpes*. *Animal Behaviour,* **56,** 1411-1424.

Bellard, C., Genovesi, P. & Jeschke, J.M. (2016) Global patterns in threats to vertebrates by biological invasions. *Proceedings of the Royal Society B: Biological Sciences,* **283**.

Bengsen, A. (2014) Effects of coordinated poison-baiting programs on survival and abundance in two red fox populations. *Wildlife Research,* **41,** 194-202.

Bennett, N.D., Croke, B.F.W. *et al.* (2013) Characterising performance of environmental models. *Environmental Modelling & Software,* **40,** 1-20.

Berry, O., Tatler, J. *et al.* (2014) Slow recruitment in a red-fox population following poison baiting: a non-invasive mark–recapture analysis. *Wildlife Research,* **40,** 615-623.

Bino, G., Dolev, A. *et al.* (2010) Abrupt spatial and numerical responses of overabundant foxes to a reduction in anthropogenic resources. *Journal of Applied Ecology,* **47,** 1262-1271.

Bonnell, M.A. & Breck, S.W. (2017) Using resident-based hazing programs to reduce human-coyote conflicts in urban environments. *Human-Wildlife Interactions,* **11,** 146-155.

Budgey, R., Learmount, J. & Smith, G.C. (2017) Simulating control of a focal wildlife outbreak of *Echinococcus multilocularis*. *Veterinary Parasitology,* **237,** 47-56.

Carter, A. & Luck, G.W. (2013) Fox baiting in agricultural landscapes: preliminary findings on the importance of bait-site selection. *Wildlife Research,* **40,** 184-195.

Carter, N., Levin, S. *et al.* (2015) Modeling tiger population and territory dynamics using an agent-based approach. *Ecological Modelling,* **312,** 347-362.

Coman, B., Robinson, J. & Beaumont, C. (1991) Home range, dispersal and density of red foxes (*Vulpes vulpes* L.) in central Victoria. *Wildlife Research,* **18,** 215-223.

Devenish-Nelson, E.S., Harris, S. *et al.* (2013) Demography of a carnivore, the red fox, *Vulpes vulpes*: what have we learnt from 70 years of published studies? *Oikos,* **122,** 705-716.

Doherty, T.S., Glen, A.S. *et al.* (2016) Invasive predators and global biodiversity loss. *Proceedings of the National Academy of Sciences of the United States of America,* **113,** 11261-11265.

Eisinger, D. & Thulke, H.H. (2008) Spatial pattern formation facilitates eradication of infectious diseases. *Journal of Applied Ecology,* **45,** 415-423.

Grimm, V., Berger, U. *et al.* (2010) The ODD protocol: A review and first update. *Ecological Modelling,* **221,** 2760-2768.

Grimm, V., Revilla, E. *et al.* (2005) Pattern-oriented modeling of agent-based complex systems: Lessons from ecology. *Science,* **310,** 987-991.

Harding, E.K., Doak, D.F. & Albertson, J.D. (2001) Evaluating the effectiveness of predator control: the non-native red fox as a case study. *Conservation Biology,* **15,** 1114-1122.

Harris, S. & Smith, G.C. (1987) Demography of two urban fox (*Vulpes vulpes*) populations. *Journal of Applied Ecology,* **24,** 75-86.

Hradsky, B.A., Mildwaters, C.A. *et al.* (2017a) Responses of invasive predators and native prey to a prescribed forest fire. *Journal of Mammalogy,* **98,** 835-847.

Hradsky, B.A., Robley, A. *et al.* (2017b) Human-modified habitats facilitate forest-dwelling populations of an invasive predator, *Vulpes vulpes*. *Scientific Reports,* **7,** 12291.

Kamler, J.F. & Ballard, W.B. (2002) A review of native and nonnative red foxes in North America. *Wildlife Society Bulletin (1973-2006),* **30,** 370-379.

Kubicek, A., Jopp, F. *et al.* (2015) Context-oriented model validation of individual-based models in ecology: A hierarchically structured approach to validate qualitative, compositional and quantitative characteristics. *Ecological Complexity,* **22,** 178-191.

Larivière, S. & Pasitschniak-Arts, M. (1996) *Vulpes vulpes*. *Mammalian Species,* **537,** 1-11.

Lieury, N., Ruette, S. *et al.* (2015) Compensatory immigration challenges predator control: An experimental evidence-based approach improves management. *The Journal of Wildlife Management,* **79,** 425-434.

Lockie, J.D. (1959) The estimation of the food of foxes. *The Journal of Wildlife Management,* **23,** 224-227.

Marlow, N.J., Thomson, P.C. *et al.* (2000) Demographic characteristics and social organisation of a population of red foxes in a rangeland area in Western Australia. *Wildlife Research,* **27,** 457-464.

Marlow, N.J., Thomson, P.C. *et al.* (2016) Compensatory responses by a fox population to artificial density reduction in a rangeland area in Western Australia. *Conservation Science Western Australia,* **10,** 3.

McIlroy, J., Saunders, G. & Hinds, L.A. (2001) The reproductive performance of female red foxes, *Vulpes vulpes*, in central-western New South Wales during and after a drought. *Canadian Journal of Zoology,* **79,** 545-553.

McLeod, R. (2004) *Counting the Cost: Impact of Invasive Animals in Australia*. Cooperative Research Centre for Pest Animal Control, Canberra.

McLeod, S.R. & Saunders, G.R. (2001) Improving management strategies for the red fox by using projection matrix analysis. *Wildlife Research,* **28,** 333-340.

Muller, T., Freuling, C.M. *et al.* (2015) Terrestrial rabies control in the European Union: Historical achievements and challenges ahead. *Veterinary Journal,* **203,** 10-17.

Newsome, T.M., Crowther, M.S. & Dickman, C.R. (2014) Rapid recolonisation by the European red fox: how effective are uncoordinated and isolated control programs? *European Journal of Wildlife Research,* **60,** 749-757.

O'Donnell, C.F.J., Pryde, M.A. *et al.* (2017) Controlling invasive predators enhances the long-term survival of endangered New Zealand long-tailed bats (*Chalinolobus tuberculatus*):

Implications for conservation of bats on oceanic islands. *Biological Conservation,* **214,** 156-167.

Pacioni, C., Kennedy, M.S. *et al.* (2018) Spatially-explicit model for assessing wild dog control strategies in Western Australia. *Ecological Modelling,* **368,** 246-256.

R Core Team (2016) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Robley, A., Gormley, A.M. *et al.* (2014) Long-term and large-scale control of the introduced red fox increases native mammal occupancy in Australian forests. *Biological Conservation,* **180,** 262-269.

Robley, A., Moloney, P.D. *et al.* (2017) Glenelg Ark: benefits to biodiversity from long-term fox control, 2005 to 2016. Technical Report Series 275. Arthur Rylah Institute for Environmental Research.

Runge, M.C., Converse, S.J. & Lyons, J.E. (2011) Which uncertainty? Using expert elicitation and expected value of information to design an adaptive program. *Biological Conservation,* **144,** 1214-1223.

Rushton, S.P., Shirley, M.D.F. *et al.* (2006) Effects of culling fox populations at the landscape scale: A spatially explicit population modeling approach. *Journal of Wildlife Management,* **70,** 1102-1110.

Sargeant, A.B. (1972) Red fox spatial characteristics in relation to waterfowl predation. *Journal of Wildlife Management,* **36,** 225-&.

Saunders, G., McLeod, S. & Kay, B. (2000) Degradation of sodium monofluoroacetate (1080) in buried fox baits. *Wildlife Research,* **27,** 129-135.

Saunders, G.R., Gentle, M.N. & Dickman, C.R. (2010) The impacts and management of foxes *Vulpes vulpes* in Australia. *Mammal Review,* **40,** 181-211.

Shwiff, S., Nunan, C. *et al.* (2011) A retrospective economic analysis of the Ontario red fox oral rabies vaccination programme. *Zoonoses and public health,* **58,** 169-177.

Smith, G.C. & Wilkinson, D. (2003) Modeling control of rabies outbreaks in red fox populations to evaluate culling, vaccination, and vaccination combined with fertility control. *Journal of Wildlife Diseases,* **39,** 278-286.

Soulsbury, C.D., Iossa, G. *et al.* (2011) Behavioral and spatial analysis of extraterritorial movements in red foxes (*Vulpes vulpes*). *Journal of Mammalogy,* **92,** 190-199.

Stillman, R.A., Railsback, S.F. *et al.* (2015) Making predictions in a changing world: the benefits of individual-based ecology. *Bioscience,* **65,** 140-150.

Storm, G.L., Andrews, R.D. *et al.* (1976) Morphology, reproduction, dispersal, and mortality of midwestern red fox populations. *Wildlife Monographs***,** 82pp.-82pp.

Thiele, J.C. (2014) R Marries NetLogo: Introduction to the RNetLogo Package. *Journal of Statistical Software,* **58,** 1-41.

Thomson, P.C., Marlow, N.J. *et al.* (2000) The effectiveness of a large-scale baiting campaign and an evaluation of a buffer zone strategy for fox control. *Wildlife Research,* **27,** 465-472.

Thulke, H. & Eisinger, D. (2008) The strength of 70%: revision of a standard threshold of rabies control. *Developments in biologicals,* **131,** 291-298.

Thulke, H.H., Grimm, V. *et al.* (1999) From pattern to practice: a scaling-down strategy for spatially explicit modelling illustrated by the spread and control of rabies. *Ecological Modelling,* **117,** 179-202.

Towerton, A.L., Dickman, C.R. *et al.* (2016) Control of the red fox in remnant forest habitats. *Wildlife Research,* **43,** 169-177.

Trewhella, W.J., Harris, S. & McAllister, F.E. (1988) Dispersal distance, home-range size and population density in the red fox (*Vulpes vulpes*) - a quantitative analysis. *Journal of Applied Ecology,* **25,** 423-434.

Walsh, J., Wilson, K. *et al.* (2012) Unexpected outcomes of invasive predator control: the importance of evaluating conservation management actions. *Animal Conservation,* **15,** 319-328.

Wilensky, U. (1999) Netlogo. Center for Connected Learning and Computer-Based Modeling, Northwestern University, Evanston, IL.

Winstanley, R.K., Buttemer, W.A. & Saunders, G. (2003) Field metabolic rate and body water turnover of the red fox *Vulpes vulpes* in Australia. *Mammal Review,* **33,** 295-301.

Wintle, B.A. (2018) Why, what, how much, and is it worth it? Questions to answer before spending a penny on monitoring. *Monitoring Threatened Species and Ecological Communities* (eds S. Legge, D. Lindenmayer, N. Robinson, B. Scheele, D. Southwell & B. Wintle). CSIRO Publishing.

Zakharov, E.S., Safronov, V.M. *et al.* (2016) The ecology of the red fox (*Vulpes vulpes* L.) in the middle Lena River basin. *Russian Journal of Ecology,* **47,** 392-398.

Table 1. Number of foxes in each demographic group for Bristol, UK, in early April. *p* is the probability of observing the field estimate by Harris and Smith (1987), given the distribution of FoxNet model outputs.

Demographic group	Field estimate	Original model outputs		Emigration model outputs	
	n	*mean (min–max)*	*p*	*mean (min–max)*	*p*
Territorial population					
Family groups	211	220 (213–226)	0.002	221 (216–228)	0.001
Breeding females	190	209 (199–215)	<0.001	210 (193–220)	<0.001
Non–breeding females	143	151 (124–183)	0.299	135 (103–165)	0.719
Alpha males	211	210 (201–218)	0.607	210 (201–217)	0.579
Subordinate males	44	44 (36–58)	0.481	38 (25–54)	0.779
Cubs	897	981 (918–1036)	0.003	991 (896–1052)	0.011
Itinerant population					
Itinerant females	0	145 (112–184)	<0.001	114 (84–146)	<0.001
Itinerant males	128	260 (227–288)	<0.001	172 (143–205)	0.002
Total population	1613	1999 (1907–2096)	<0.001	1870 (1781– 1945)	<0.001

Figures

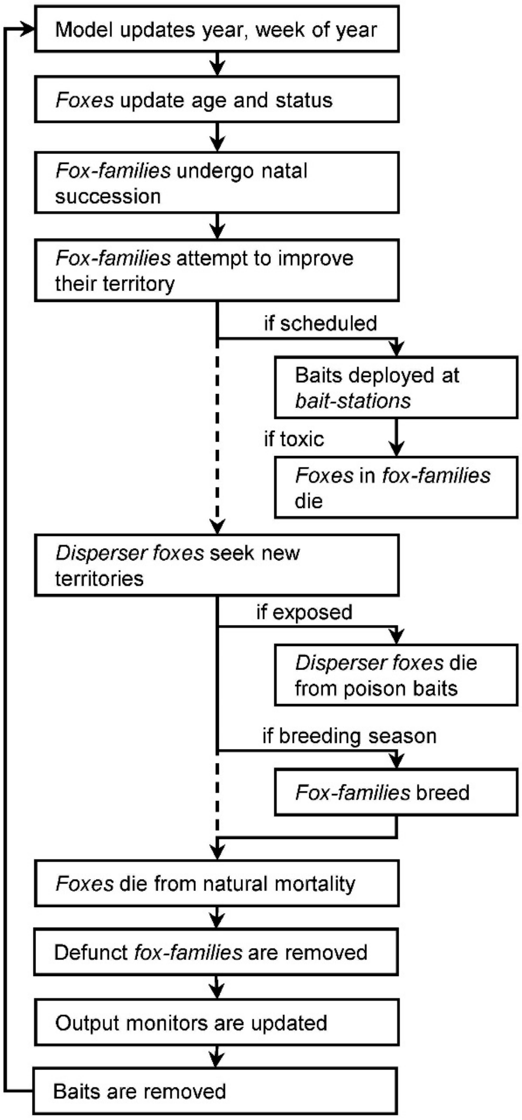

Figure 1. Key processes in the FoxNet modelling framework. The sequence is repeated each time-step (1, 2 or 4 weeks).

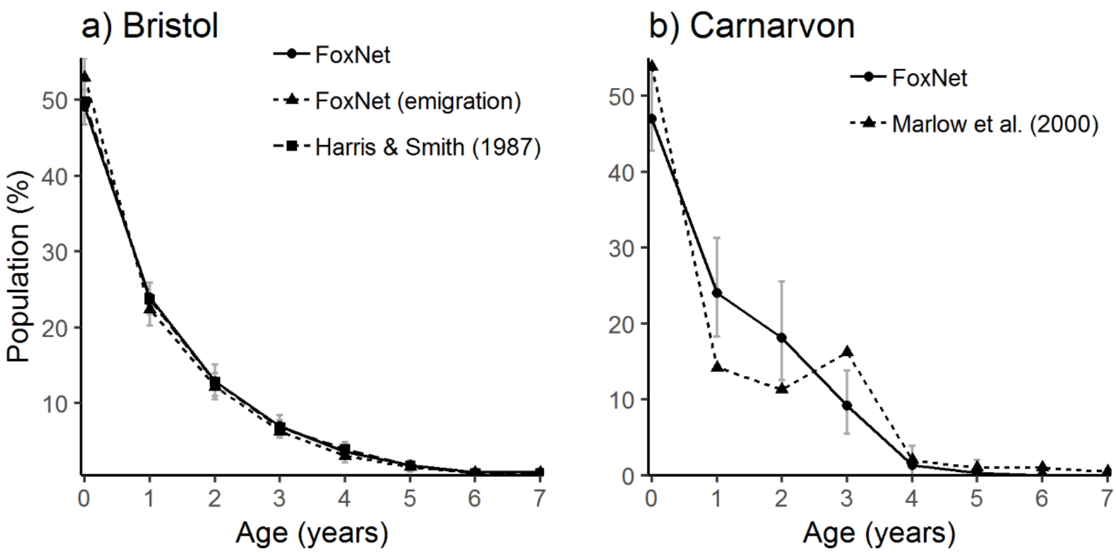

Figure 2. Age structure of fox populations in (a) Bristol, England, and (b) Carnarvon, Australia from FoxNet model outputs (mean (min–max), n = 30) and field point estimates.

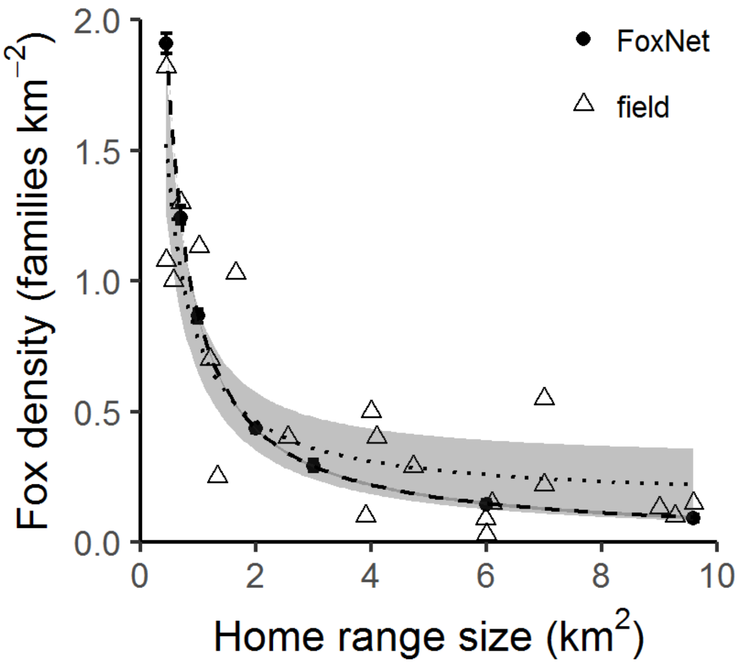

Figure 3. Relationship between fox home-range size and density from FoxNet outputs and field data collated by Trewhella *et al.* (1988). Curves are separate linear models fitted to the inverse of home-range size for FoxNet (dashed) and field (dotted) data, with shading indicating 95% confidence intervals.

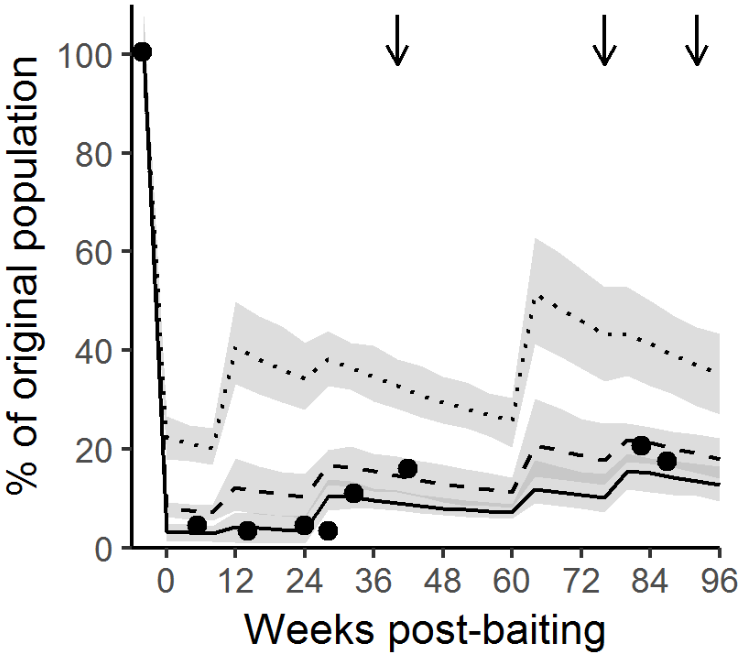

Figure 4. Effects of pulse baiting on relative fox density at Carnarvon, Western Australia. FoxNet outputs are for 0.3 (dotted line), 0.5 (dashed line) and 0.7 (solid line) bait efficacy, with shaded ribbons indicating minimum and maximum values from 30 replicates. Black dots show field data from Thomson *et al.* (2000); arrows indicate repeat baiting events.

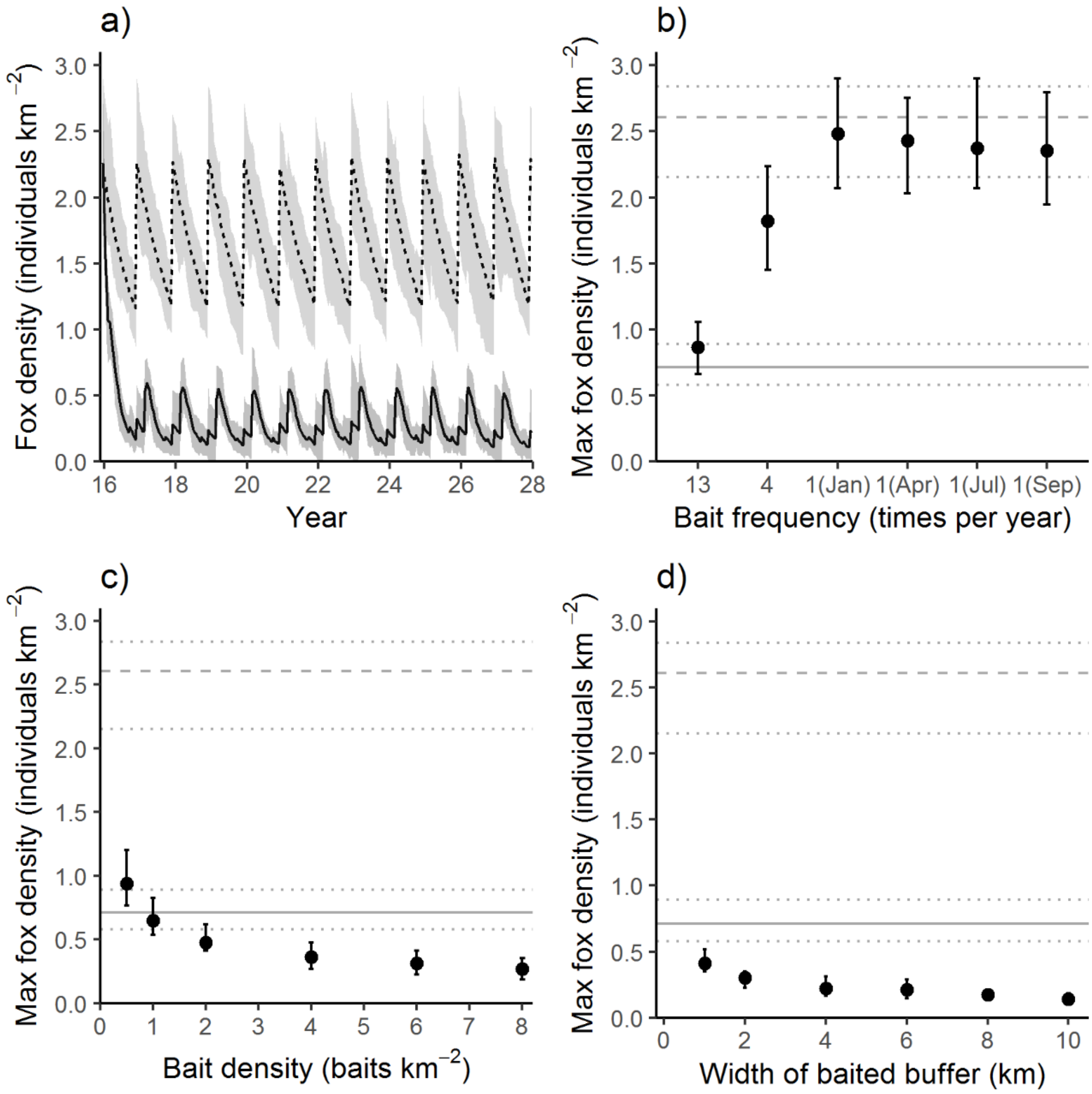

Figure 5. Modelled fox density at Mt Clay Reserve, Victoria. (a) fox density for 0–12 years post-baiting for unbaited (dotted line) and current baiting (solid line) regimes. (b) – (d) average maximum fox density over a 10-year period, under altered (b) bait frequency, (c) bait density and (d) baited buffer width. Grey horizontal lines in (b) – (d) indicate equivalent values from the unbaited (dashed) and current baiting (solid) scenarios. Ribbons and error bars indicate minimum and maximum values from 30 replicates.