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Rabies disease dynamics in naïve dog populations in Australia

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Abstract

Currently, Australia is free from terrestrial rabies but an incursion from nearby Indonesia, where the virus is endemic, is a feasible threat. Here, we aimed to determine whether the response to a simulated rabies incursion would vary between three extant Australian dog populations; free-roaming domestic dogs from a remote indigenous community in northern Australia, and free-roaming domestic and wild dogs in peri-urban areas of north-east New South Wales. We further sought to predict how different management strategies impacted disease dynamics in these populations.

We used simple stochastic state-transition models and dog demographic and contact rate data from the three dog populations to simulate rabies spread, and used global and local sensitivity analyses to determine effects of model parameters. To identify the most effective control options, dog removal and vaccination strategies were also simulated.

Responses to simulated rabies incursions varied between the dog populations. Free-roaming domestic dogs from north-east New South Wales exhibited the lowest risk for rabies maintenance and spread. Due to low containment and high contact rates, rabies progressed rapidly through free-roaming dogs from the remote indigenous community in northern Australia. In contrast, rabies remained at relatively low levels within the north-east New South Wales wild dog population for over a year prior to an epidemic. Across all scenarios, sensitivity analyses revealed that contact rates and the probability of transmission were the most important drivers of the number of infectious individuals within a population. The number of infectious individuals was less sensitive to birth and death rates. Removal of dogs as a control strategy was not effective for any population modelled, while vaccination rates in excess of 70% of the population resulted in significant reductions in disease progression.

The variability in response between these distinct dog groups to a rabies incursion, suggests that a blanket approach to management would not be effective or feasible to control rabies in Australia. Control strategies that take into account the different population and behavioural characteristics of these dog groups will maximise the likelihood of effective and efficient rabies control in Australia.

Highlights

- Rabies transmission in three Australian dog populations was modelled
- Disease progression was rapid in free-roaming dogs within indigenous communities
- Low contact rates amongst free-roaming domestic dogs in NSW inhibited rabies spread
- Rabies spread in wild dogs was prolonged; an epidemic peaked 1 year post incursion
- High vaccination rates with limited dog removal proved the best control option

Keywords

Canis familiaris, dingo, disease modelling, free-ranging, SEIR, state-transition

Introduction

Terrestrial rabies, a preventable viral zoonosis, is responsible for approximately 59,000 human deaths annually (Hampson *et al.*, 2015). In developing continents such as Africa and Asia, rabies virus is usually transmitted to humans in saliva via the bite of an infected dog (*Canis familiaris*) (Warrell and Warrell, 2004). Although rabies is not currently in Australia, an incursion of a canine rabies biotype from

Indonesia, where recent outbreaks have occurred in humans and domestic dogs (Tenzin and Ward, 2012), is a realistic and imminent threat (Murray *et al*., 2012). Because current Australian policies prevent prophylactic vaccination of animals against rabies (Animal Health Australia, 2011), all Australian dogs will be susceptible to rabies infection.

Most available models of rabies spread tend to simulate control strategies that have not yet been applied to rabies virus affected regions (e.g. Zinsstag *et al*., 2009; Brunker *et al*., 2012; Zhang *et al*., 2012). Because Australia has never had endemic rabies (there has likely only been one incursion, in 1867 (Pullar and McIntosh, 1954) and the disease did not persist), model outputs from rabies endemic regions may not be representative of an Australian rabies outbreak scenario. Consequently, it is imperative that Australia develop models using local dog behavioural and population dynamic parameters, in conjunction with known rabies epidemiological parameters, to aid preparation for a terrestrial rabies outbreak (Sparkes *et al*., 2015).

As well as being free of rabies, Australia differs from other countries in the assemblage of functional categories of dogs present. Australia's dogs can be separated into three groups or populations based on the extent and type of association with humans and their ability to roam: a) restrained domestic dogs, that rely solely on humans for food and shelter; b) free-roaming domestic dogs, that are owned but allowed to roam freely at some point; and c) wild dogs, including dingoes, that are not reliant on humans for resources and always free to roam. Although classified into distinct categories here, these dog functional groups exist along a continuum and individuals from the functional groups interact (e.g. Dürr and Ward 2014; Sparkes *et al*., 2014). Although wild dogs are very seldom tamed and restrained, some of the other dogs may move between different groups during their life (e.g. usually restrained dogs escaping through an open gate, working dogs being retired or restrained when not working, hunting dogs being restrained except when hunting). Previous research (e.g. Coman and Robinson, 1989; Meek, 1999; Claridge *et al*., 2009; Allen *et al*., 2013; Dürr and Ward, 2014) reinforces behavioural differences between these functional groups, hence, it is reasonable to expect each may respond differently to a rabies incursion.

Although Dürr and Ward (2015) recently modelled rabies spread from data collected in two remote regions of northern Australia, only one of the three dog groups identified here (i.e. community free-roaming domestic dogs) was assessed. To our knowledge, no studies have attempted to model a rabies incursion in more than one of these functional groups. The differences between Australian dog groups makes it imperative that an explicit understanding of their likely responses to a rabies incursion is established, to ensure targeted and effective control strategies that encompass behavioural differences between the functional groups. It should also be noted that while rabies can infect any mammal, there are several variants of the virus and the arrival of the canine rabies biotype into Australia is the most likely scenario, rendering the spill over of rabies into other species such as the European red fox (*Vulpes vulpes*), a side issue (Sparkes *et al.* 2015).

In Australia’s national rabies preparedness strategy, the rabies AUSVETPLAN, control strategies hinge on vaccination and dog removal (Animal Health Australia, 2011). These strategies are based on models and experiences from rabies endemic countries (e.g. Shwiff *et al*., 2008; Hampson *et al*., 2009; Morters *et al*., 2013).

Although it has sometimes failed (Tenzin and Ward, 2012), vaccination has generally been more successful in controlling rabies, than dog culling programs (Rupprecht *et* *al*., 1995; Morters *et al*., 2013). Culling for rabies mitigation purposes usually targets dogs suspected to be infected and is not typically applied as a prophylactic, or as a reactive management action to control rabies. However, culling is commonly undertaken in Australia to reduce populations of wild dogs to protect livestock from predation (e.g. Fleming *et al*., 2001; Allen *et al*., 2014; Fleming *et al*., 2014). Hence, Australia's range of rabies control strategies among wild dogs would likely include the removal of suspected infected individuals, population reduction and oral vaccination (Animal Health Australia, 2011) or combinations of these. Although Dürr and Ward (2015) found culling of rabid dogs was likely an unsuccessful strategy for rabies eradication in Australia, they did not model proportional removals of susceptible individuals, nor population reductions.

Here, we developed simple models to describe the temporal response of dogs to a rabies incursion in Australia. We used two realistic incursion scenarios and sought to identify optimal management strategies for each scenario. Rather than treating all dogs homogenously, we modelled responses for three different dog populations: a) free-roaming domestic dogs from a remote indigenous community; b) free-roaming domestic dogs from peri-urban areas; and c) wild dogs.

Scenarios

The most likely incursion scenario, for Australia, would be the importation of an asymptomatic (latently infected) dog from a neighbouring island, as occurred in the 2008 rabies outbreak in Bali, Indonesia (Clifton, 2010). In Australia's case, a dog infected with rabies would likely originate from Indonesia.

Here, we propose two scenarios, a rabies incursion into 1) free-roaming domestic dogs within a remote Australian indigenous community in northern Australia and 2) a peri-urban free-roaming domestic and wild dog population in north-east New South Wales (NSW). Parts of mainland northern Australia lie less than 300km from rabies-endemic regions of Indonesia (Tenzin and Ward, 2012), while the largest human and dog populations are located in eastern NSW (West, 2008; Australian Companion Animal Council, 2010; Australian Bureau of Statistics, 2014). Therefore, these regions are likely at the highest risk areas for rabies introduction and spread, and are the focus of our scenarios.

Scenario 1- Incursion into an indigenous community, northern Australia
A dog– infected with rabies but prior to the onset of clinical signs– is introduced into a remote Australian indigenous community, via an Indonesian fishing boat (*sensu* Sparkes *et al*., 2015). Within a few days, the dog shows clinical signs of rabies and is abandoned or lost nearby or within the community. As in many northern Australian indigenous communities, free-roaming dogs are common, with 90.2% of the dog population free to roam (Sparkes *et al*., 2014), and the infected dog interacts with these community dogs. Due to the altered behaviour of the infected dog (Hampson *et al.*, 2009) and because dogs are territorial (Perez-Guisado and Munoz-Serrano, 2009), aggressive interactions occur between local dogs and the infectious intruder. Consequently, rabies is transmitted to resident community dogs, which soon begin to die from the infection.

Due to a lack of rabies awareness within the community, time to detect the initial rabies outbreak is prolonged (Dürr and Ward, 2015). Absence of veterinary facilities within the community further confounds detection. Following an increase in dogs biting humans, local medical staff seek assistance. An itinerant veterinary officer performs a necropsy on a symptomatic dog and sends samples to the Australian Animal Health Laboratory in Victoria, for testing. The rabies virus is positively identified and the Australian veterinary emergency plan for a rabies incursion (AUSVETPLAN) is triggered (Animal Health Australia, 2011).

Scenario 2- Incursion into north-east New South Wales

A dog– infected with rabies but prior to the onset of clinical signs– is illegally brought to the port of Ballina, north-east NSW from Indonesia on a vessel (e.g. yacht or fishing boat; Sparkes *et al*., 2015). Within a few days, the dog shows clinical signs of rabies and is abandoned or lost nearby or within the community. North-east NSW becomes the focus of the rabies epidemic for Scenario 2. The infected dog roams through private, peri-urban properties and public land (e.g. National Parks and State Forests), where it encounters other free-roaming domestic and wild dogs in the region. Some encounters result in aggressive confrontations and the dog is killed by wild dogs. The virus is transmitted to local wild dogs and free-roaming domestic dogs. As per Scenario 1, aggression towards humans results in the identification of rabies and the Australian veterinary emergency plan for a rabies incursion (AUSVETPLAN) is triggered (Animal Health Australia, 2011).

Methods

Three populations of dogs were considered in this study; free-roaming Island community dogs, peri-urban free-roaming domestic dogs and wild dogs. Using state-transition models, each dog population was classified into four subclasses: susceptible (S), exposed (E), infectious (I) and removed or immune (R). Figure 1 describes the flow of dogs between states.

Insert Figure 1 hereabouts

For dog population i, B_i describes the annual birth rate, with births remaining constant throughout the year, σ_i denotes the inverse of the incubation period, α_i

represents the disease death rate, d_i is the natural death rate, $cull_i$ the routine culling practices (for wild dogs only) and β_i describes the transmission of rabies by interactions between infectious and susceptible dogs, where:

β_i = contact rate*P,

where P is the probability of contacts resulting in rabies virus transmission

The model was solved using a daily time step, with all populations considered to be closed (See S1 for parameter estimates).

The state-transition models were solved in R (R Core Team, 2015) using the sir function in the *Desolve* (Soetaert *et al*., 2010) and *MC2D* packages (Pouillot and Delignette-Muller, 2010). A single host model was used for scenarios one and two, while a multi-host model was also used for scenario two. For both scenarios, a single infected dog entering the population was considered the source of infection.

Model 1:

For the single host models, three ordinary differential equations were used:

$$\frac{dS_i}{dt} = (B_i - d_i) * S_i - \beta_i * \frac{I_i}{N_i} * S_i - cull_i * S_i \qquad \text{Eq. 1}$$

$$\frac{dE_i}{dt} = \beta_i * \frac{I_i}{N_i} * S_i - (\sigma_i + d_i) * E_i - cull_i * E_i \qquad \text{Eq. 2}$$

$$\frac{dI_i}{dt} = \sigma_i * \mathrm{E}_i - (\alpha_i + \mathrm{d}_i) * \mathrm{I}_i - \mathrm{cull}_i * \mathrm{I}_i \qquad \text{Eq. 3}$$

Model 2:

For the multi-host transition model used in scenario two, an additional set of parameters were included to take account of transmission between dog groups:

$$\frac{dS_1}{dt} = (B_1 - d_1) * S_1 - \beta_1 * \frac{I_1}{N_1} * S_1 - \beta_3 * \frac{I_2}{N_2} * S_1 \qquad \text{Eq. 4}$$

$$\frac{dE_1}{dt} = \beta_1 * \frac{I_1}{N_1} * S_1 + \beta_3 * \frac{I_2}{N_2} * S_1 - (\sigma_1 + d_1) * E_1 \qquad \text{Eq. 5}$$

$$\frac{dI_1}{dt} = \sigma_1 * E_1 - (\alpha_1 + d_1) * I_1 \qquad \text{Eq.6}$$

$$\frac{dS_2}{dt} = (B_2 - d_2) * S_2 - \beta_2 * \frac{I_2}{N_2} * S_2 - \beta_3 * \frac{I_1}{N_1} * S_2 - \text{cull}_2 * S_2 \qquad \text{Eq. 7}$$

$$\frac{dE_2}{dt} = \beta_2 * \frac{I_2}{N_2} * S_2 + \beta_3 * \frac{I_1}{N_1} * S_2 - (\sigma_2 + d_2) * E_2 - \text{cull}_2 * E_2 \qquad \text{Eq. 8}$$

$$\frac{dI_2}{dt} = \sigma_2 * E_2 - (\alpha_2 + d_2) * I_2 - \text{cull}_2 * I_2 \qquad \text{Eq. 9}$$

where S_1, E_1 and I_1 are susceptible, exposed and infectious free-roaming domestic dogs and S_2, E_2 and I_2 are susceptible, exposed and infectious wild dogs, and β_3 is the transmission coefficient between dog groups. Two simulations were run for this model, where the initial infected dog originated from a wild or domestic dog, respectively. In both models, an infected dog was introduced at day one, with all simulations run for 800 days.

Global and local sensitivity analyses were undertaken in R using the FME package (Soetaert and Petzoldt, 2010) for each of the three dog populations (using Model 1). The sensitivity of the model's state variables (S, E, I and N) to the parameters σ, α, contact rate and probability of transmission were examined using a global sensitivity analyses. For this analyses, all parameters were varied simultaneously over their entire feasible space (i.e. the maximum and minimum values specified; see S2), using a sampling based approach (n=100 model repetitions). For the local sensitivity analyses, parameters (σ, α, contact rate, probability of transmission, birth and death rates and, for wild dogs only, culling rate) were varied one at a time by a small amount around a fixed point (see S2).

Control strategies

After running the simulations described above, control via vaccination and dog removal, were applied to the dog populations where rabies was sustained (See S3 for model). In Scenario one, rabies was detected early and control initiated at day 14. For Scenario two, time to initial response was considered much longer due to reduced human contact with wild dogs and lower likelihood of detection, and commenced at day 200. Vaccination (Vac) and/or removal (Rem) rates of 0, 0.1, 0.3, 0.5, 0.7, 0.9 and 1 of the dog population were applied to the model over a period of 7 days in the northern Australian free-roaming dog population and for 30 days for the north-east NSW wild dog population, with control periods initiated annually. Rates were chosen based on the ability to access dogs and published data on removal (Fleming, 1996; Fleming and Ballard, 2014) and rabies vaccination success rates (World Health Organisation, 2005; Tenzin and Ward, 2012). The free-roaming northern Australian community dog control simulations were run for 300 days, while the wild dog simulations were run for 800 days.

Due to large variation reported for contact rates in wild and free-roaming dog populations, these model parameters for the control simulations were defined as either beta-pert distributions (minimum, mode, maximum), uniform distributions (minimum, maximum) or fixed values (see S1 for parameter estimates). Each simulation was repeated 1,000 times and the mean number of infected individuals per day of the simulation was calculated to compare control efficacy. Data for infected individuals per day are presented as mean (±SD). Results of vaccination-and removal-only simulations were compared using a Welch's two sample paired *t*-test (Welch, 1947).

Results

Single host, no control

For Scenario one, rabies progressed rapidly through the free-roaming community dogs, with a peak in exposed individuals at day 36 (Figure 2a). By day 127, the number of infected individuals in the population fell below one. Without intervention, rabies caused the dog population to collapse, with no dogs surviving. At the highest contact rates estimated by Sparkes *et al.* (2014), global sensitivity analysis indicated that the results were highly sensitive to contact rate (see S2). Subsequently, a narrower range of contact rates (3.0-7.0 contacts per dog per day) was used to reduce the contact rate variance and provide more realistic results from the model. Local sensitivity analysis revealed that the number of infectious (I) individuals was most sensitive to σ, contact rate and probability of transmission, followed by α and birth and death rates (See S2).

Insert Figure 2 hereabouts

In contrast to Scenario one, the free-roaming domestic dogs in Scenario two were relatively unaffected by a single rabid dog incursion (Figure 2b), likely due to limited contact between susceptible individuals. Global and local sensitivity analyses indicated that the number of infectious free-roaming domestic dogs in north-east NSW were most sensitive to α, σ, contact rates and the probability of transmission (See S2).

In the north-east NSW scenario for wild dogs (Figure 2c), the lag phase prior to an epidemic was drawn out, with the number of infected individuals peaking at day 565.

By day 781, the number of infected individuals fell below one. Without intervention, the wild dog population collapsed, with only two dogs surviving at day 800. Within the wild dog scenario modelled, α, contact rates and the probability of transmission were all equally important in rabies transmission (See S2). The number of infectious individuals was much less sensitive to σ, birth and death rates, while sensitivity to the culling rate of wild dogs was low.

Multi-host model, no control

For the multi-host model, contact between free-roaming domestic and wild dogs did not facilitate rabies transfer between reservoir dog groups. However, due to the low contact rates recorded between these dog groups, wild dogs may be an infrequent source of rabies spillover from sylvatic to urban cycles. This would be particularly important during the peak of the epidemic (in the second year of disease progression), where the risk of domestic dogs contacting an infectious wild dog would be greater compared with the early or late phase of disease dynamics (Figure 2).

Single host, with control

The results of Models 1 and 2 indicate that in free-roaming domestic dogs in north-east NSW, it is unlikely that a single infected individual will cause a rabies epizootic. As such, control simulations were carried out for northern Australian free-roaming domestic and north-east NSW wild dogs only.

Scenario 1: Free-roaming domestic dogs, northern Australia

Increasing the proportion of dogs vaccinated or removed within the community reduced the mean number of infected individuals, slowing rabies progression (Figures 3 and 4). Vaccination alone provided significantly better reductions in mean infected individuals at all vaccination and removal levels (Welch *t* test: t_5=-4.56, P = 0.006) compared with dog removal alone (Figure 3). However, the variation observed amongst simulation runs revealed vaccination alone resulted in increased uncertainty compared with dog removal (i.e. larger standard deviation was observed for vaccination versus dog removal). Despite this, vaccination of free-roaming domestic dogs remained the most effective control strategy.

Insert Figures 3 and 4 hereabouts

When used in combination, medium to high vaccination and removal rates (≥50%) reduced mean infected individuals to less than 1 per day (Figure 5). However, increasing vaccination and removal rates above 0.7 did not greatly reduce the mean number of infected individuals compared with rates cf. 50-70% (Figure 5). In contrast, low vaccination rates and high removal rates resulted in an increase in mean infected individuals within the population (Figure 5).

Insert Figure 5 hereabouts

Scenario 2: Wild dogs, north-east New South Wales

Increasing the proportion of dogs vaccinated, or the proportion removed from the population reduced the mean number of infected individuals (Figures 6 and 7). However, the rate at which the mean number of infected individuals per day decreased, slowed when 70% of the population was either vaccinated or removed. In contrast to Scenario 1, there was no difference between vaccination and removal strategies when undertaken in isolation (Welch *t* test: t_9=1.26, P = 0.24; Figure 6). However, due to large variation observed around the mean number of infected individuals per simulation run (Figure 6), the outcome from wild dog rabies control strategies was less predictable compared with control strategies implemented for free-roaming community dogs.

Insert Figures 6 and 7 hereabouts

A combination of vaccination and removal provided a positive multiplicative effect on the mean number of infected individuals when removal rates exceeded vaccination rates (Figure 8). However, increasing vaccination rates above 0.7 and removal rates above 0.5 did not greatly reduce the mean number of infected individuals per day (Figures 7 and 8).

Insert Figures 7 and 8 hereabouts

Discussion

All three dog populations identified and characterised here, expressed different responses to a rabies incursion despite being the same species. By developing simple state-transition models, we found that free-roaming domestic dogs residing in the remote indigenous community were at highest risk of contracting and spreading rabies. For that group, the disease spread rapidly through the population, predominantly due to high contact rates. In reality, this occurs because of poor restraint of dogs through a lack of fencing or tethering or both. This reflected scenarios seen in developing countries, where rabies remains a serious threat to human and animal lives (World Health Organisation, 2005; Tenzin and Ward, 2012). In contrast, it appears that in the wild dog population, rabies would likely remain at low levels for an extended period of time, limiting chances for localised detection and increasing rabies infection on a larger geographic scale. Due to relatively low contact rates, free-roaming domestic dogs in north-east NSW provided the lowest risk for rabies maintenance and spread in the dog populations assessed. Although free-roaming domestic dogs in peri-urban areas of north-east NSW may be exposed intermittently to infected wild dogs, the rate at which these interactions occur are not sufficient to create an epidemic in that dog group. Similar experiences have been observed in developed countries elsewhere, where rabies exposure from wildlife reservoirs and subsequent infection in domestic dogs is minimal (Rupprecht *et al*., 1995; Holmala and Kauhala, 2006; Dyer *et al*., 2014).

To reduce the likelihood of an epidemic, response times to a rabies incursion must be rapid for some dog groups. This is particularly important for the free-roaming domestic dog population in remote northern Australia, where modelling illustrates a rabies epidemic is likely to occur within one month of an infected individual entering the community (Figure 2). High contact rates within this population (Sparkes *et al*., 2014) mean that successful control of rabies would require extensive vaccination at the onset of a rabies incursion into the population, or at the very least, confinement of dogs to the home residence. In contrast, the time to vaccinate is not as critical for low contact rate populations (i.e. wild and free-roaming domestic dogs in north-east NSW), with a longer lag phase observed prior to an epidemic and eventual population crash. However, due to the relatively long period between initial infection and an epidemic, rabies may go undetected in wild dogs for a long time.

On its own, the removal of dogs was not an effective rabies management strategy for any population modelled. Indeed, it increased the mean number of infected individuals when used in conjunction with low vaccination rates for the northern Australian free-roaming domestic dog population (Figure 4). Due to the cultural significance of dogs in indigenous communities (Constable *et al*., 2010), forced removal of dogs from communities would also likely result in mistrust of authorities, encourage undesirable behaviours such as hiding dogs or moving them between communities, thereby potentially increasing the geographical spread of rabies in Australia: this behaviour has been observed in Indonesia (Bingham, 2001; Windiyaningsih *et al*., 2004). Similar to rabies endemic regions in developing countries, high population turnover among free-roaming community dogs may limit the effectiveness of programs to vaccinate them (Hampson *et al*., 2009; Zhang *et al*., 2012; Conan *et al*., 2015). An increase in the number of annual rabies control programs and improved dog management that reduces annual birth rates and encourages confinement of pet dogs could help to ensure sufficient animals are vaccinated or removed from the susceptible state.

The control of rabies in wildlife populations is notoriously difficult (e.g. fox and raccoon rabies in the United States, Canada and Europe; Rupprecht *et al*., 1995; Smith, 1996; Freuling *et al*., 2013). Our modelling suggests that a similar scenario would be expected in Australian wild dog populations. Although reducing the wild dog population through dog removal reduced the mean number of infected individuals per day (Figure 6), it did not prevent a crash in the population at either the 70% or 90% removal rates (Figure 7), suggesting that removal alone would likely not be successful for rabies control in Australian wild dogs. Further, previous work in rabies endemic regions has found that culling was likely to disrupt dog social structures and increase contact rates between susceptible individuals, potentially increasing rate of spread (Aubert, 1992; Rupprecht *et al*., 1995; Smith, 1996; Morters *et al*., 2013).

Oral vaccination of wildlife has proven to be effective at controlling and even eliminating rabies in reservoir species such as the European Red Fox and raccoons (*Procyon lotor*) in parts of Europe, Canada and America (Sterner *et al*., 2009; Müller *et al*., 2012; Freuling *et al*., 2013). If these findings for other reservoir species correlate with effective oral vaccination campaigns in dogs, our results suggest that a similar approach could be successful here. While 100% vaccination and removal rates are modelled here (Figure 8), campaigns would be unlikely to achieve 100% coverage within wild dog populations due to limited accessibility. However, current aerial wild dog control activities can effectively remove up to 90% of wild dog populations in some regions (Fleming and Ballard, 2014). As such, if rabies were to enter Australia, target vaccination rates of up to 90% could be considered achievable.

To achieve high vaccination rates, an oral rabies vaccination program must also account for the removal of baits by non-target animals (Allen *et al*., 1989; Fleming, 1996). Wildlife including foxes, feral pigs (*Sus scrofa*) and feral cats (*Felis catus*) are numerous throughout mainland Australia (West, 2008) and will consume and cache baits, making them unavailable to dogs (Allen *et al*., 1989; Glen and Dickman, 2003; Fleming and Ballard, 2014). Bait delivery above the targeted vaccination rate may assist in maximising bait availability for wild dogs.

Despite the threat of a rabies incursion into Australia, only one parenteral rabies vaccine is approved for use in Australia, and is only approved to vaccinate animals for export (Animal Health Australia, 2011). If the vaccine was to be used in the advent of a rabies incursion, it must firstly be approved for domestic use through the Australian Pesticides and Veterinary Medicines Authority (http://apvma.gov.au/node/6). Similarly, oral rabies vaccines would need to be approved for use in Australia, with the approval process potentially taking many months or years (1 to 18 months; http://apvma.gov.au/node/1088), depending on the type of registration required. Delaying control activities and increasing the time-to-control will likely result in an increase in the geographical spread of rabies, making the disease harder to eradicate, particularly from wild dog reservoirs. To this end, it is critical that research that facilitates rapid vaccine registration (e.g. identifying non-target effects, vaccine efficacy and appropriate delivery systems for Australian environments) be initiated to enable authorities immediate access to vaccines if (or when) rabies breaches Australian borders.

Traditionally, rabies models account for a single dog category when considering rabies spread in dog populations. Our research illustrates that each dog group is associated with differing rabies disease dynamics, so should be considered as independent groups when modelling disease spread. These differences are based primarily on a dogs' ability to roam and contact other susceptible individuals. Based on the risk of disease transfer, susceptibility and potential to implement control, Australian dog communities should be disaggregated and the AUSVETPLAN for the control of rabies in Australia (Animal Health Australia, 2011), consequently revised and updated for improved rabies preparedness.

Like much previous work (e.g. Hampson *et al* 2009, Carroll *et al* 2010), the state-transition models used here assume homogenous mixing of individuals within the population. Dogs are highly social animals and their interactions are not random (Thomson, 1992; Sen Majumder *et al*., 2014; Sparkes *et al*., 2014) and the complex sociality of dogs (Morters *et al*., 2013; Sparkes *et al*., In prep) likely explains the lack of empirical support for the implicit assumption that rabies transmission is a function of dog density (i.e. density-dependency; Morters *et al*., 2013). Hence, alternative models that account for the different dog categories and heterogeneity in dog behaviours could strengthen predictive capabilities for rabies incursions and are recommended (e.g. Boehm *et al*., 2009; Cross *et al*., 2012; Reynolds *et al*., 2015).

Contact rates used within these models are based on best available data for Australian scenarios and include contacts where individuals are in close proximity; not only those instances where one dog has bitten another. This could overestimate contact rates within each population. However, not all individuals within a population can be monitored at once (e.g. due to logistic constraints), particularly the crepuscular and cryptic wild dogs. Indeed, many direct physical contacts would likely go undetected with the currently available observation technology, leading to an underestimation of contacts. Once more research has been undertaken and parameter estimates improved, these models could be updated to improve accuracy and predictive capabilities for a rabies incursion in Australia.

Although simple models have been used here to demonstrate differences amongst dog groups, it would be beneficial to develop additional stochastic models to further explore how rabies could spread in Australia, especially considering the complexities that exist within and between different dog communities. The interactive application of the stochastic, spatially explicit model of Dürr and Ward (2015) to the three dog groups identified here also holds potential.

Future research should also focus on understanding inter- and intra-specific interactions of other susceptible species, including foxes, feral cats and native animals and their interactions with the disaggregated dog groups. This will improve our understanding of how they could contribute to the spread and maintenance of rabies in Australia.

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Figure Captions

Figure 1 Transition model diagram of rabies within and between dog populations. S_i, E_i, I_i, R_i represent susceptible, exposed, infectious and removed or immune dogs, respectively. The dashed lines indicate movement of individuals between states only when control is implemented.

Figure 2 Rabies progression in a single dog category without intervention for a) free-roaming community dogs, remote northern Australia, b) peri-urban north-east New South Wales free-roaming domestic dogs and c) peri-urban north-east New South Wales wild dogs. Lines represent total population (grey), susceptible (black), exposed (red) and infectious (green) individuals. Time is in days.

Figure 3 Mean infected individuals per day (±SD) with 0, 0.1, 0.3, 0.5, 0.7 and 0.9 of the free-roaming remote northern Australian community dog population vaccinated (dark) or subject to removal (light), based on 1,000 simulation runs per control option.

Figure 4 Example simulation runs for 0.7 (left column) and 0.9 (right column) of the Tiwi Islands free-roaming domestic dog population vaccinated (a), (d), removed (b) (e) and combined vaccinated and removed (c), (f), with a contact rate of 5.24 contacts per dog per day. Lines represent total population (light blue longdash), susceptible (black solid), removed (immune) (blue dotdash), exposed (red dashed) and infectious (green dotted) individuals and time is in days.

Figure 5 Response surface showing the interaction between vaccination and removal rates expressed as mean infected free-roaming community dog individuals per day, northern Australia, based on 1,000 simulation runs per control combination. Light to dark shading depicts fewer to greater numbers of infected individuals.

Figure 1 Mean infected individuals (±SD) per day with 0, 0.1, 0.3, 0.5, 0.7 and 0.9 of the peri-urban north-east New South Wales wild dog population vaccinated (dark) or subject to removal (light), based on 1,000 simulation runs per control option.

Figure 7 Example simulation runs for 0.7 (left column) and 0.9 (right column) of the wild dog population vaccinated (a), (d), removed (b) (e) and combined vaccinated and removed (c), (f), with a contact rate of 0.71 contacts per dog per day. Control strategy was implemented annually. Lines represent total population (light blue longdash), susceptible (black solid), removed (immune) (blue dotdash), exposed (red dashed) and infected (green dotted) individuals. Time is in days.

Figure 8 Response surface showing the interaction between vaccination and removal rates expressed as mean infected wild dog individuals per day, based on 1,000 simulation runs per control combination. Light to dark shading depicts fewer to greater numbers of infected individuals.

S2: Global and Local sensitivity analysis parameters, code and results for free-roaming domestic dogs residing within with a remote Indigenous community (Tiwi Islands) and free-roaming domestic and wild dogs in north-east New South Wales

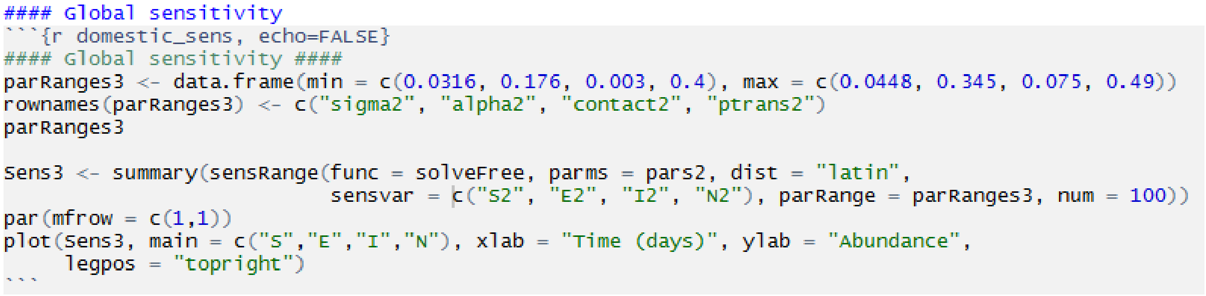
Table 1 Minimum and maximum values for parameters used for the Global sensitivity analyses*

Parameter	**Min**	**Max**
Free-roaming domestic dogs, Tiwi Islands		
σ	0.0316	0.0448
α	0.1760	0.3450
Contact rate^	0.0010	24.0000
ptrans	0.4000	0.4900
Free-roaming domestic dogs, north-east New South Wales		
σ	0.0316	0.0448
α	0.1760	0.3450
Contact rate^	0.0030	0.0750
ptrans	0.4000	0.4900
Wild dogs, north-east New South Wales		
σ	0.0316	0.045
α	0.1760	0.345
Contact rate^	0.0700	1.990
ptrans	0.4000	0.490

* Values are based on ranges provided in S1

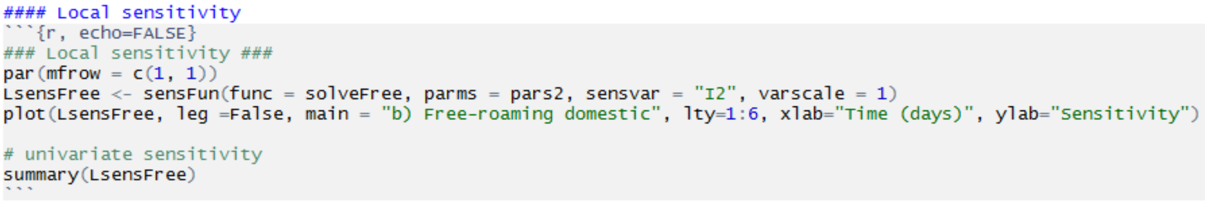
^ Due to contact rates overwhelming the Global Sensitivity analyses at these Min and Max values, the analyses were subsequently run with contacts = Min: 3.0, Max: 7.0

R code for Global and Local Sensitivity Analyses for one dog population, free-roaming domestic dogs, north-east New South Wales



~~~
#### Global sensitivity
```{r domestic_sens, echo=FALSE}
#### Global sensitivity ####
parRanges3 <- data.frame(min = c(0.0316, 0.176, 0.003, 0.4), max = c(0.0448, 0.345, 0.075, 0.49))
rownames(parRanges3) <- c("sigma2", "alpha2", "contact2", "ptrans2")
parRanges3

Sens3 <- summary(sensRange(func = solveFree, parms = pars2, dist = "latin",
                           sensvar = c("S2", "E2", "I2", "N2"), parRange = parRanges3, num = 100))
par(mfrow = c(1,1))
plot(Sens3, main = c("S","E","I","N"), xlab = "Time (days)", ylab = "Abundance",
     legpos = "topright")
```
~~~



~~~
#### Local sensitivity
```{r, echo=FALSE}
### Local sensitivity ###
par(mfrow = c(1, 1))
LsensFree <- sensFun(func = solveFree, parms = pars2, sensvar = "I2", varscale = 1)
plot(LsensFree, leg =False, main = "b) Free-roaming domestic", lty=1:6, xlab="Time (days)", ylab="Sensitivity")

# univariate sensitivity
summary(LsensFree)
```
~~~

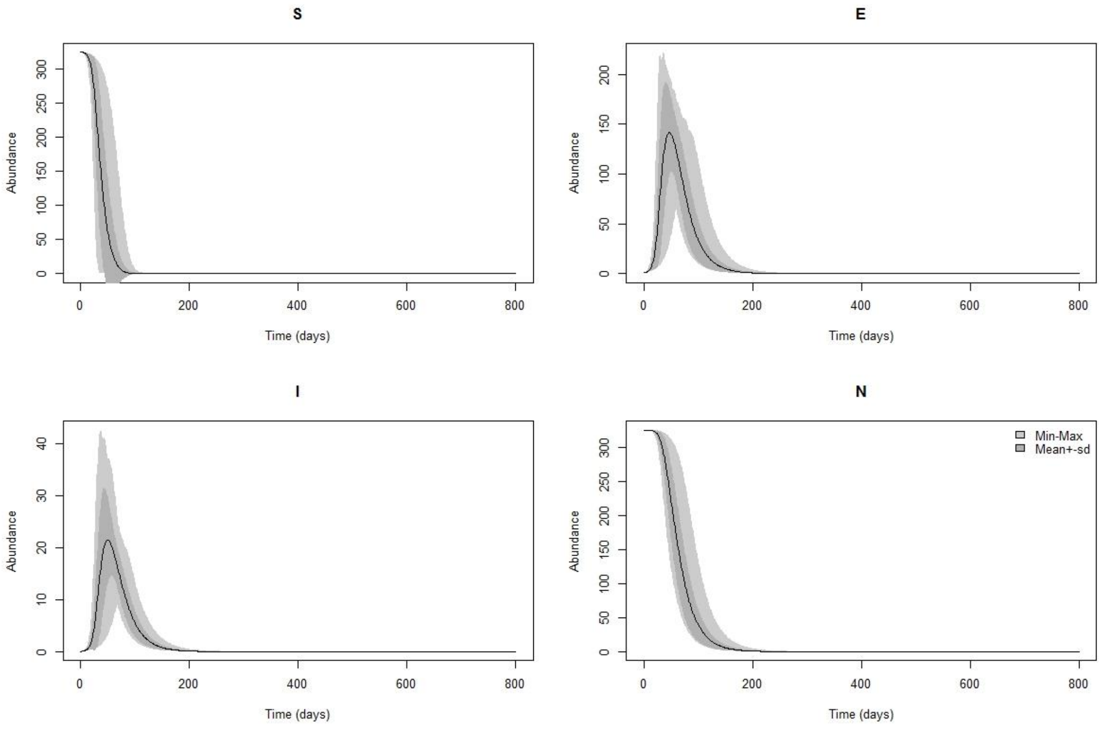


Figure S1: Global sensitivity analyses results for free-roaming dogs within a remote indigenous community, northern Australia, for each state variable S, E, I and N

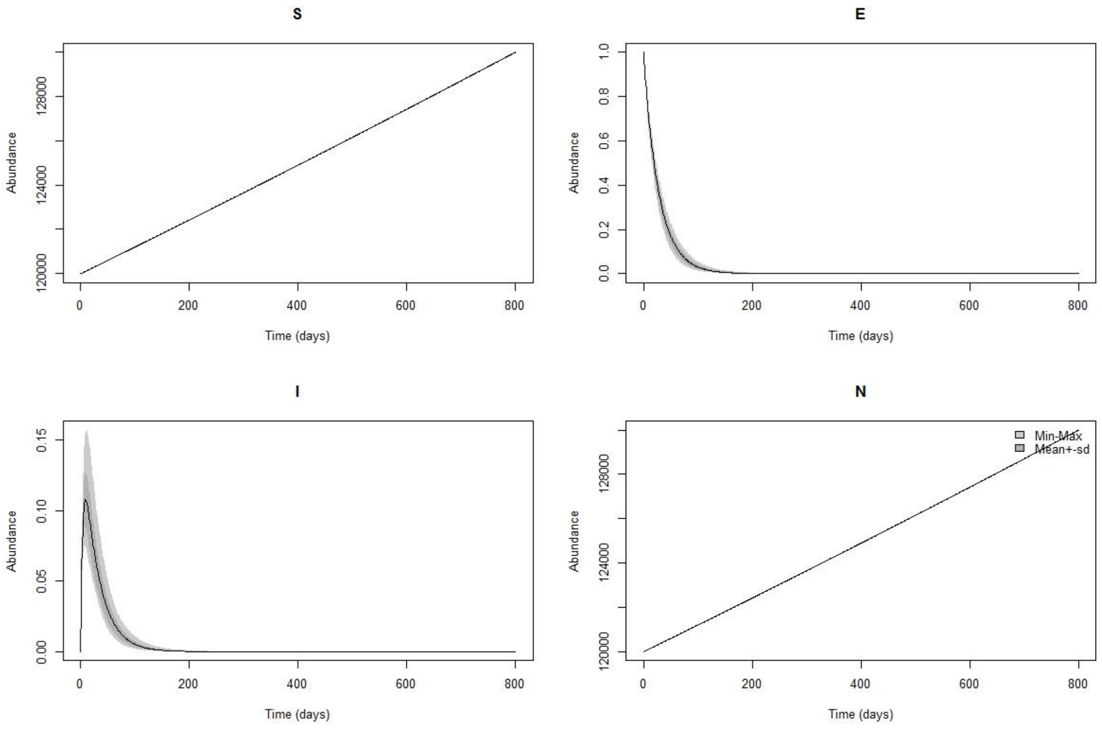


Figure S2: Global sensitivity analyses results for free-roaming dogs in peri-urban north-east New South Wales, Australia, for each state variable S, E, I and N

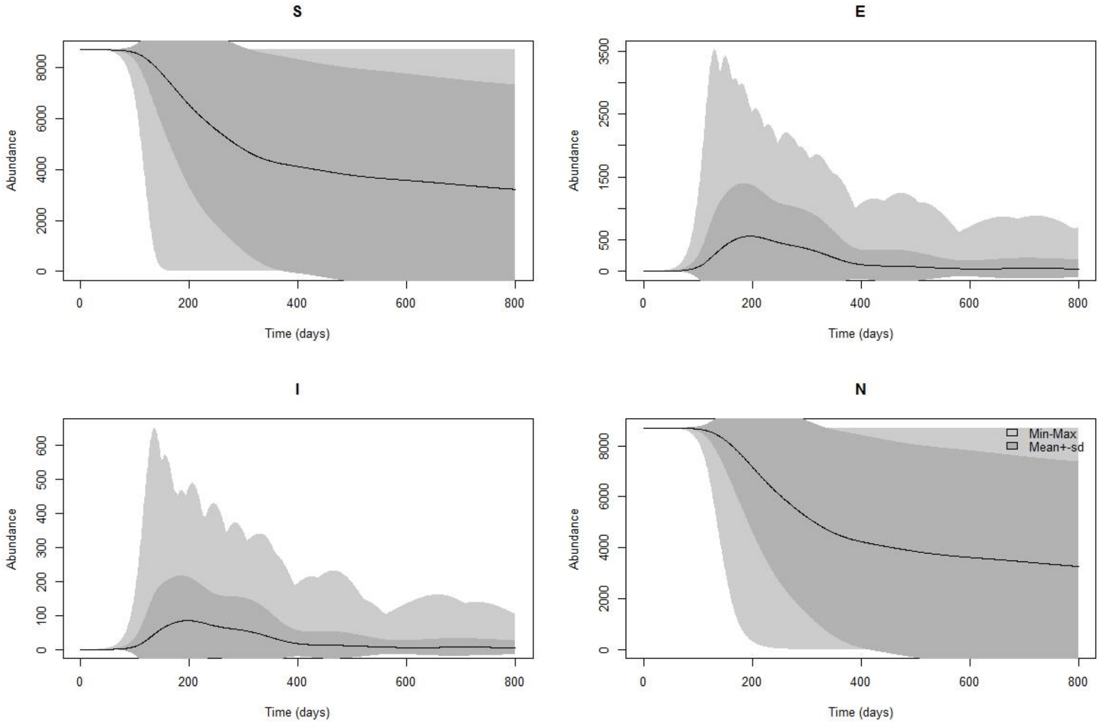


Figure S3: Global sensitivity analyses results for wild dogs in peri-urban north-east New South Wales, Australia, for each state variable S, E, I and N

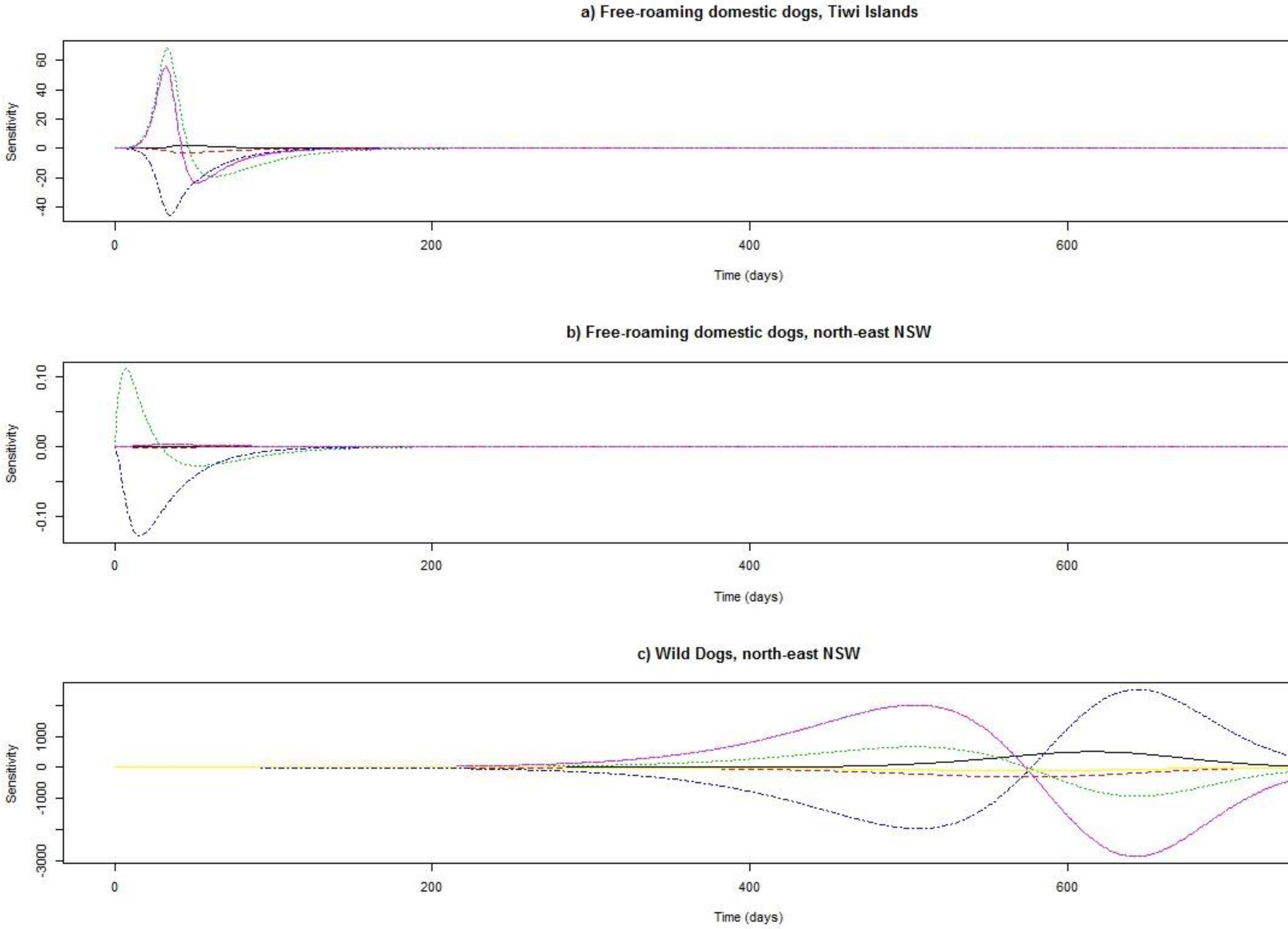


Figure S4: Local sensitivity analyses for a) Free-roaming domestic dogs residing with a remote indigenous community, b) Free-roaming domestic dos in peri-urban north-east New South Wales and c) Wild dogs in peri-urban north-east New South Wales. Colours and line styles denote: Birth ▬; Death ---; σ ….; α ._._; contact – – –; ptrans - – - –; cull ▬

S2: Ordinary differential equations used to simulate control strategies for northern Australian free-roaming domestic and north-east New South Wales wild dog populations

Prior to control:

Eq. S1 $$\frac{dS}{dt} = (\mathrm{B} - \mathrm{d}) * \mathrm{S} - \beta * \frac{\mathrm{I}}{\mathrm{N}} * \mathrm{S} - \mathrm{cull} * \mathrm{S}$$

Eq. S2 $$\frac{dE}{dt} = \beta * \frac{\mathrm{I}}{\mathrm{N}} * \mathrm{S} - (\sigma + \mathrm{d}) * \mathrm{E} - \mathrm{cull} * \mathrm{E}$$

Eq. S3 $$\frac{dI}{dt} = \sigma * \mathrm{E} - (\alpha + \mathrm{d}) * \mathrm{I} - \mathrm{cull} * \mathrm{I}$$

Eq. S4 $$\frac{dR}{dt} = 0$$

During control:

Eq. S5 $$\frac{dS}{dt} = (\mathrm{B} - \mathrm{d}) * \mathrm{S} - \beta * \frac{\mathrm{I}}{\mathrm{N}} * \mathrm{S} - \mathrm{cull} * \mathrm{S} - (\mathrm{vac} * \mathrm{vacef}) * \mathrm{S} + \mathrm{vacloss} * \mathrm{R} - \mathrm{rem} * \mathrm{S}$$

Eq. S6 $$\frac{dE}{dt} = \beta * \frac{\mathrm{I}}{\mathrm{N}} * \mathrm{S} - (\sigma + \mathrm{d}) * \mathrm{E} - \mathrm{cull} * \mathrm{E} - (\mathrm{vac} * \mathrm{vacef}) * \mathrm{E} - \mathrm{rem} * \mathrm{E}$$

Eq. S7 $$\frac{dI}{dt} = \sigma * \mathrm{E} - (\alpha + \mathrm{d}) * \mathrm{I} - \mathrm{cull} * \mathrm{I} - \mathrm{rem} * \mathrm{I}$$

Eq. S8 $$\frac{dR}{dt} = (\mathrm{vac} * \mathrm{vacef}) * \mathrm{S} + (\mathrm{vac} * \mathrm{vacef}) * \mathrm{E} - (\mathrm{d} + \mathrm{vacloss} - \mathrm{B}) * \mathrm{R} - \mathrm{cull} * \mathrm{R} - \mathrm{rem} * \mathrm{R}$$

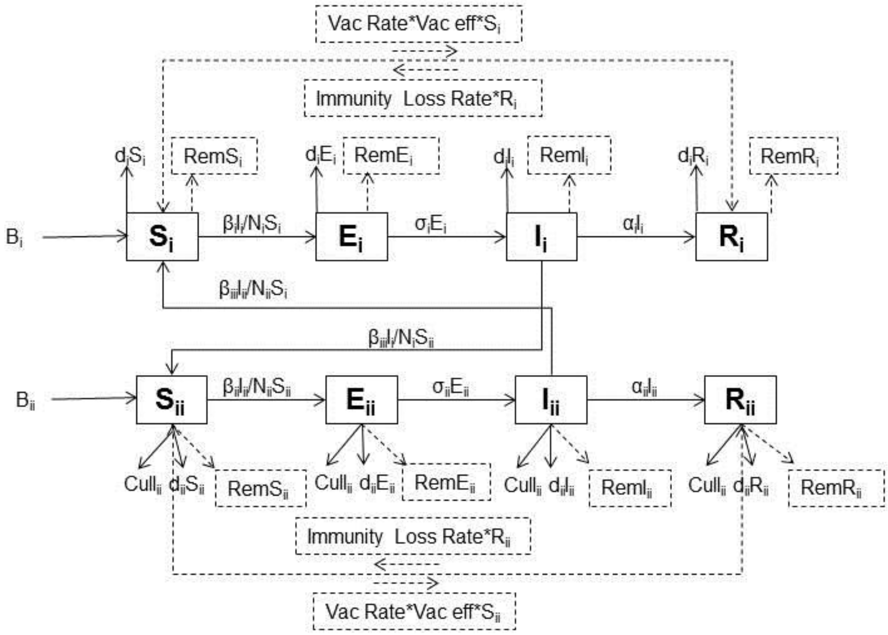
Post control:

Eq. S9 $$\frac{dS}{dt} = (\mathrm{B} - \mathrm{d}) * \mathrm{S} - \beta * \frac{\mathrm{I}}{\mathrm{N}} * \mathrm{S} - \mathrm{cull} * \mathrm{S} + \mathrm{vacloss} * \mathrm{R}$$

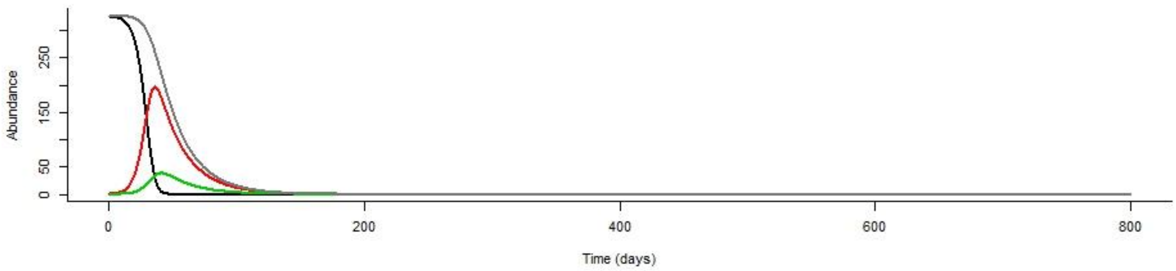
Eq. S10 $$\frac{dE}{dt} = \beta * \frac{\mathrm{I}}{\mathrm{N}} * \mathrm{S} - (\sigma + \mathrm{d}) * \mathrm{E} - \mathrm{cull} * \mathrm{E}$$

Eq. S11 $$\frac{dI}{dt} = \sigma * \mathrm{E} - (\alpha + \mathrm{d}) * \mathrm{I} - \mathrm{cull} * \mathrm{I}$$

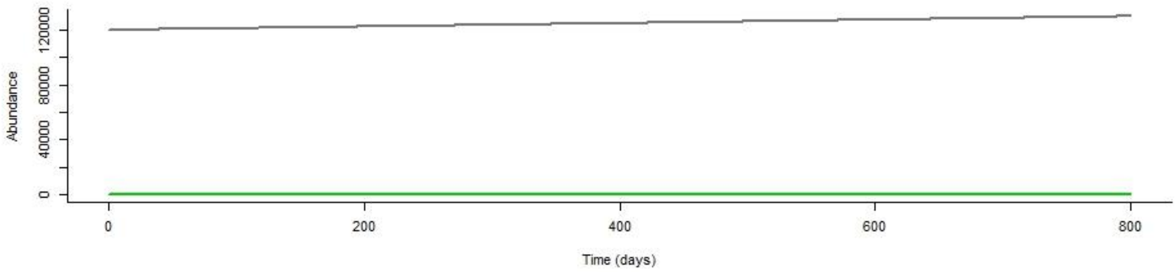
Eq. S12 $$\frac{dR}{dt} = -(\mathrm{d} + \mathrm{vacloss} - \mathrm{B}) * \mathrm{R} - \mathrm{cull} * \mathrm{R}$$


Vac Rate*Vac eff*S_i
Immunity Loss Rate*R_i
d_iS_i
$RemS_i$
d_iE_i
$RemE_i$
d_iI_i
$RemI_i$
d_iR_i
$RemR_i$
B_i
S_i
$\beta_i I_i/N_i S_i$
E_i
$\sigma_i E_i$
I_i
$\alpha_i I_i$
R_i
$\beta_{iii} I_{ii}/N_{ii} S_i$
$\beta_{iii} I_i/N_i S_{ii}$
B_{ii}
S_{ii}
$\beta_{ii} I_{ii}/N_{ii} S_{ii}$
E_{ii}
$\sigma_{ii} E_{ii}$
I_{ii}
$\alpha_{ii} I_{ii}$
R_{ii}
$Cull_{ii}$
$d_{ii}S_{ii}$
$RemS_{ii}$
$Cull_{ii}$
$d_{ii}E_{ii}$
$RemE_{ii}$
$Cull_{ii}$
$d_{ii}I_{ii}$
$RemI_{ii}$
$Cull_{ii}$
$d_{ii}R_{ii}$
$RemR_{ii}$
Immunity Loss Rate*R_{ii}
Vac Rate*Vac eff*S_{ii}

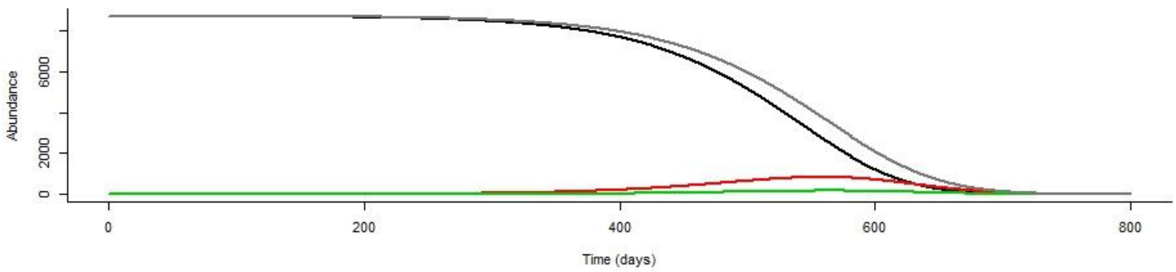
a) Tiwi Islands

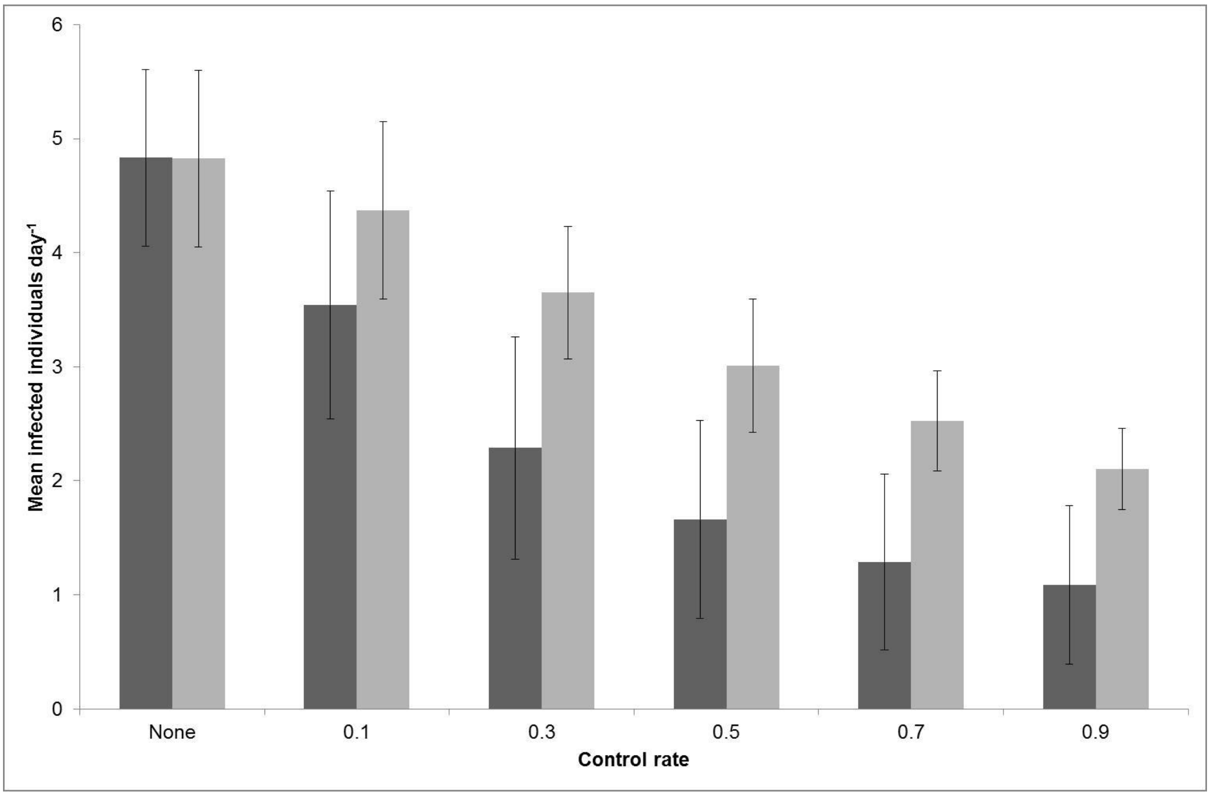


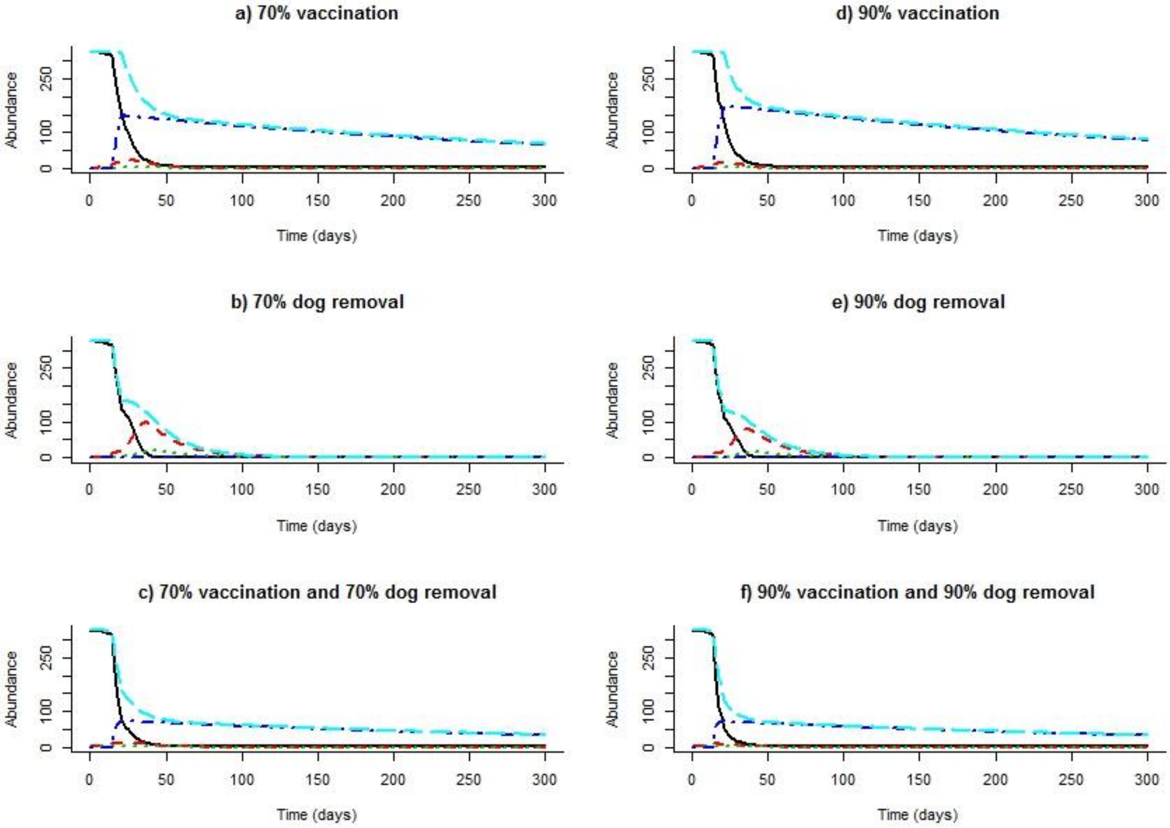
b) Free roaming domestic

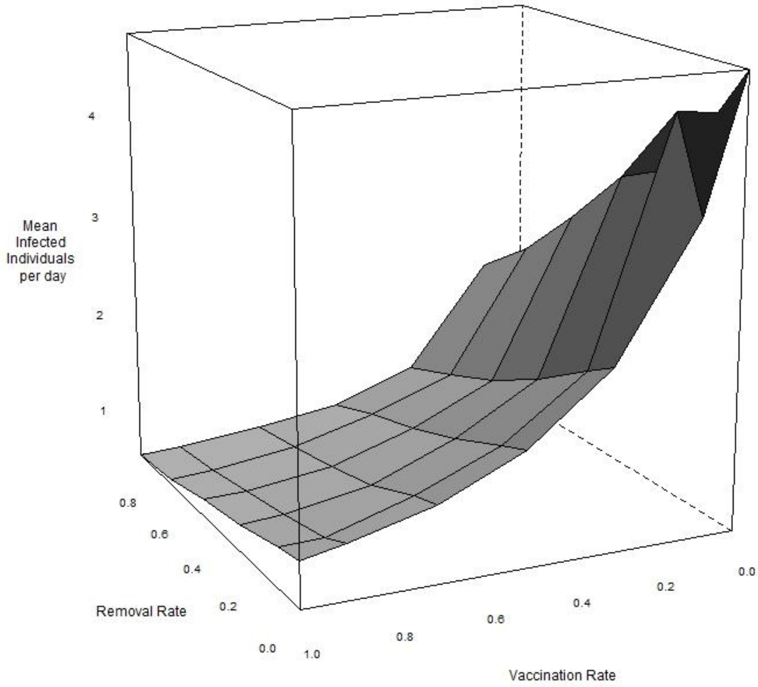


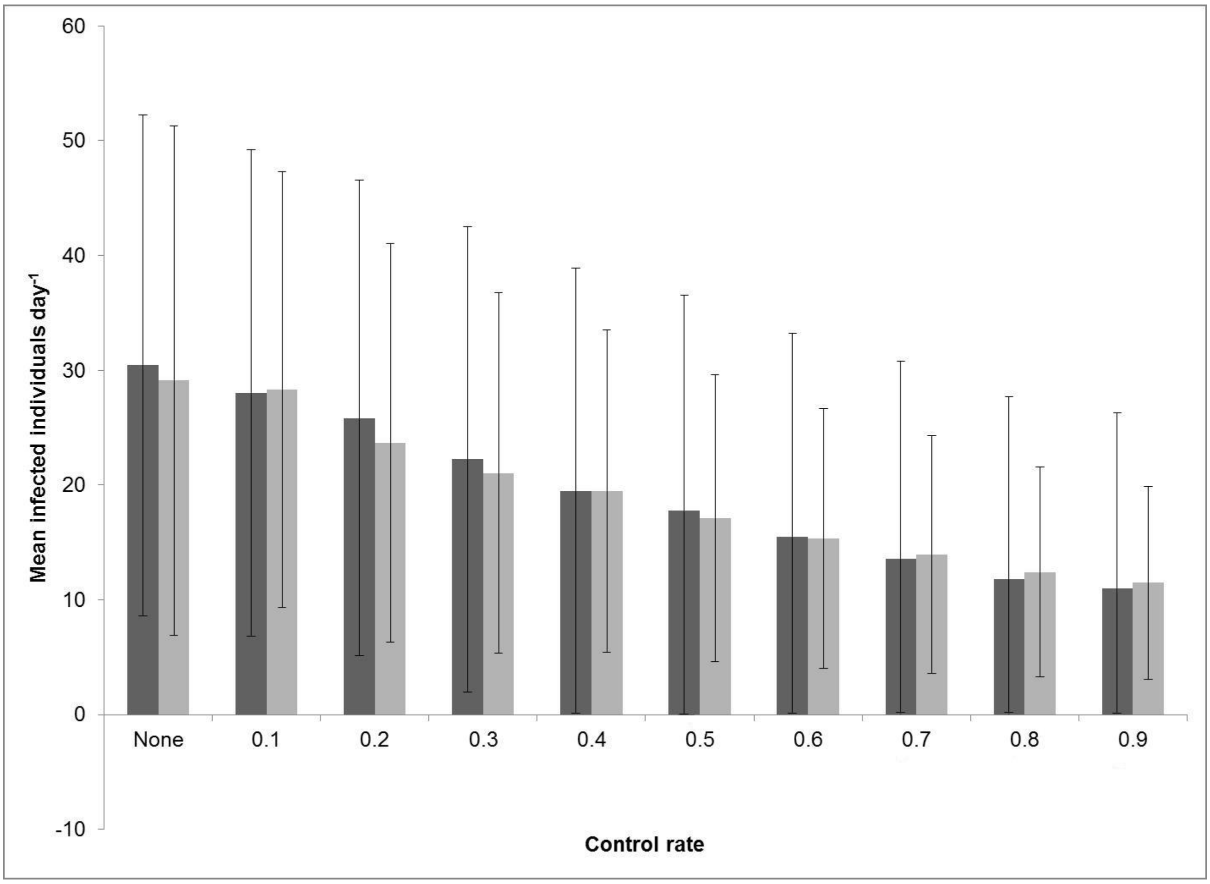
c) Wild

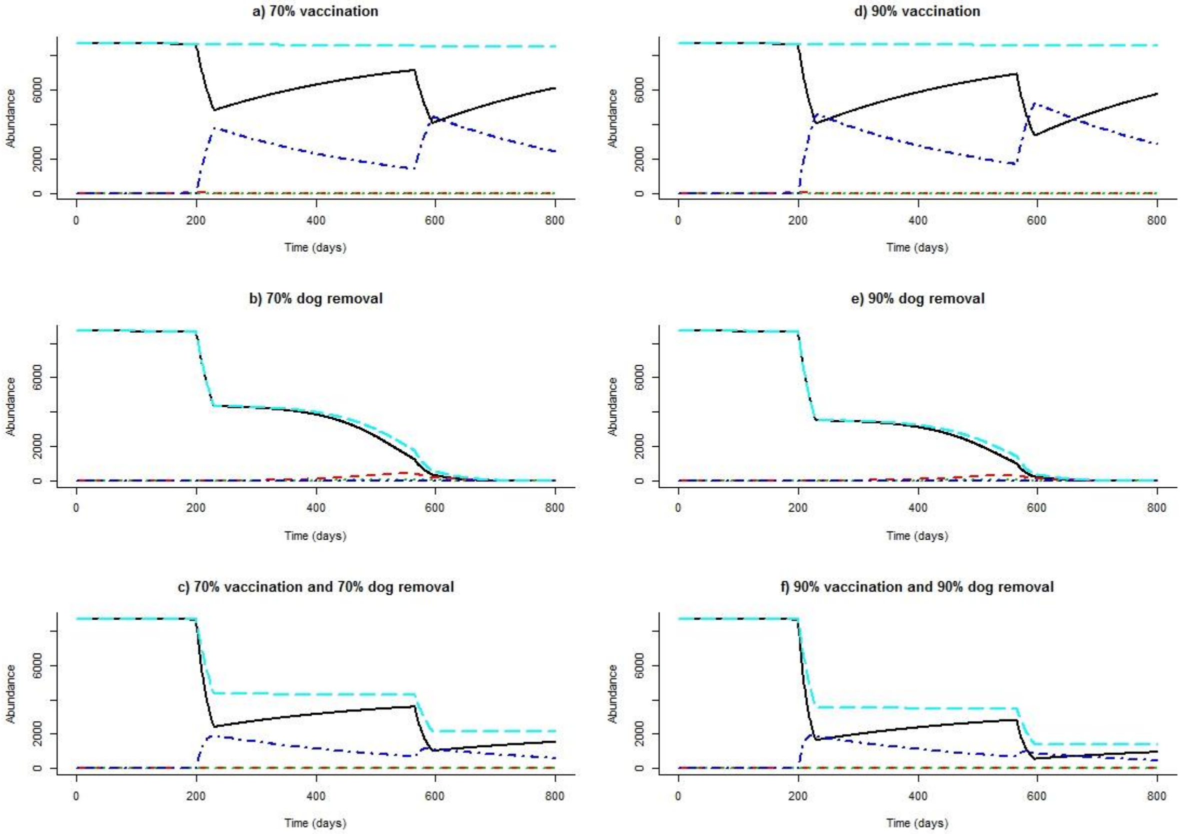



6
5
4
3
2
1
0
Mean infected individuals day⁻¹
None
0.1
0.3
0.5
0.7
0.9
Control rate


a) 70% vaccination
d) 90% vaccination
b) 70% dog removal
e) 90% dog removal
c) 70% vaccination and 70% dog removal
f) 90% vaccination and 90% dog removal
Abundance
0
100
250
0
50
100
150
200
250
300
Time (days)


4
3
2
1
Mean
Infected
Individuals
per day
0.8
0.6
0.4
Removal Rate
0.2
0.0
1.0
0.8
0.6
0.4
0.2
0.0
Vaccination Rate


60
50
40
30
20
10
0
-10
Mean infected individuals day-1
None
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
Control rate


a) 70% vaccination
d) 90% vaccination
b) 70% dog removal
e) 90% dog removal
c) 70% vaccination and 70% dog removal
f) 90% vaccination and 90% dog removal
Abundance
0
2000
6000
Time (days)
0
200
400
600
800

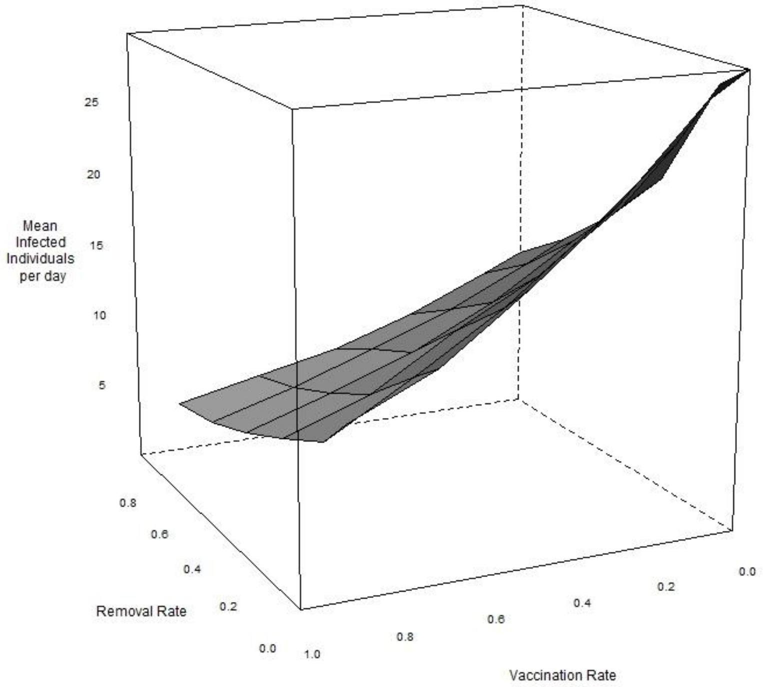

Mean
Infected
Individuals
per day
25
20
15
10
5
0.8
0.6
0.4
Removal Rate
0.2
0.0
1.0
0.8
0.6
0.4
0.2
0.0
Vaccination Rate

Table S1: Model parameters. Parameter, description, value^ and source of parameters used in the rabies simulation models; stochastic values follow either a Uniform distribution (Unif(Min, Max)) or a beta-pert distribution (Pert(Min, Mode, Max)).

Parameter	Description	Value^	Source
Disease parameters			
ptrans	Probability of transmission	**0.45**	Hampson et al., 2009; Zhang et al., 2011
σ	1/Incubation period	**0.045**	
	Incubation period	22.3 days (20.0-25.0 at 95% CI)	Hampson et al., 2009
α	Disease death rate	**0.208**	1/Infectious period
	Infectious period	4.8 days (Range: 2.9-5.7 days)	Hampson et al., 2009; Zinsstag et al., 2009; Carroll et al., 2010
vacef	Vaccine efficiency	**0.89%**	Sage et al., 1993; Kennedy et al., 2007; Minke et al., 2009; Berndtsson et al., 2011
vacloss	Loss of immunity from vaccine (1/365 days)	**0.003**	Assumption; vaccine provides 1 year immunity

Scenario 1 – Free-roaming dogs residing within a remote Australian Indigenous Island community			
N[#]	Initial start population	**326 dogs**	Sparkes et al., 2014
B	Natural birth rate	**0.002**	(Annual births/365/Initial start population)
	Annual births	237 pups	(Initial start population*% female and entire*Litters per entire female*Pups per litter)
	% female and entire	26.32%	J. Sparkes unpub. data, N = 95
	Litters per entire female	0.52 litters	Reece et al., 2008; Acosta-Jamett et al., 2010; Gsell et al., 2012
	Pups per litter	5.31 pups	Reece et al., 2008; Acosta-Jamett et al., 2010; Gsell et al., 2012; Morters et al., 2014
d	Natural death rate	**0.0019**	(Annual deaths/365/Initial start population)
	Annual deaths	230	(Initial start population*P of mortality for adults + Annual births*P of mortality for <1yr old)
	P of mortality for <1yr old	0.48	Reece et al., 2008; Morters et al., 2014
	P of mortality for adults	0.36	Reece et al., 2008; Morters et al., 2014
Contact	Contact rate per dog per day	**Unif(0, 23.8)**	Sparkes et al., 2014

Scenario 2 – Wild dogs			
N$^{\#}$	Initial start population	**8701** dogs	(Wild dog density*State Forest and National Park area)
	Wild dog density	0.31±0.53 dogs km^{-2}	McIlroy et al., 1986; Thomson, 1992; Corbett, 2001; Fleming et al., 2001; Sparkes, Ballard, Fleming *et al*. In press.
	NE-NSW State Forest and National Parks area	28,259km^{2}	National Park and State Forest area within 3 LLS boundaries: Hunter, North Coast and Northern Tablelands
B	Natural birth rate	**0.004**	(Annual births/365/Initial start population)
	Annual births	11,281 pups	(Initial start population*%female*prop females sexually mature*litters per female*pups per litter)
	% female	46%	J. Sparkes unpub. camera data, N = 44
	Proportion of females sexually mature (across all ages)	0.70	Jones and Stevens, 1988
	Litters per female	0.79 litters	Thomson et al., 1992
	Pups per litter	5.1 pups	Thomson et al., 1992; Corbett, 2001; Fleming et al., 2001

d	Natural death rate	**0.003**	(Annual deaths/365/Initial start population)
	Annual Deaths	11,038	(Initial start population* P of mortality for adults + Annual births*P of mortality for <1yr old)
	P of mortality for <1yr old	0.67±0.02	J. Sparkes unpub. camera data, N = 11; Corbett, 2001
	P of mortality for adults	0.40±0.34	J. Sparkes unpub. collar data, N = 11; McIlroy et al., 1986; Thomson et al., 1992
Contact	Contact rate	**Pert(0.07, 0.71, 1.99)**	(Contacts km^{-2}*Daily activity range)
	Contacts km^{-2}	0.2 ±0.2 Range: 0.02-0.56	Sparkes, Ballard, Fleming *et al*. In press.
	Daily activity range	3.56 ± 4.98km^{2}	Ballard, Sparkes, Meek *et al.* unpub. data, N = 4041 days, 23 dogs
Cull	Routine culling	**0.001 dogs day^{-1}**	Assumption

Scenario 3 – Free-roaming domestic dogs			
N$^{\#}$	Initial start population	**120,000** dogs	(Prop dogs free-to-roam*NE-NSW domestic dog population)
	North-east NSW domestic dog population	0.46 million dogs	Office of Local Government, 2015
	% domestic dogs free-to-roam	26%	Sparkes, Ballard and Brown. In. Prep.
B	Natural birth rate	**0.0005**	(Annual births/365/Initial start population)
	Annual births	19,809 pups	(Initial start population*Prop female and entire*Litters per entire female*Pups per litter)
	% female and entire	10.84%	Sparkes, Ballard and Brown. In. Press.
	Litters per entire female	0.51 litters	Di Nardo et al., 2007
	Pups per litter	3 pups	Di Nardo et al., 2007
d	Natural death rate	**0.0004**	(Annual deaths/365/Initial start population)
	Annual deaths	19,531 dogs	(Initial start population*P of mortality for adults + Annual births*P of mortality for <1yr old)

	P of mortality for each age class	varied Range: 0.02-1	Di Nardo et al., 2007
	Mean age at death	11 years	Michell, 1999
	% dogs in each age class	varied	Sparkes, Ballard and Brown. In. Prep.
Contact	Contact rate	**0.02**	(Contacts km^{-2}*Daily activity range)
	Contacts km^{-2}	0.016 ±0.025 Range: 0.003-0.075	Sparkes, Ballard, Fleming *et al*. In press.
	Daily activity range	0.26 ± 1.88km^{2}	Sparkes, Körtner, Ballard *et al.* unpub. data, N = 892 days, 21 dogs

Between-group transmission: Free-roaming domestic dogs and wild dogs, north-east NSW			
Contact		**0.00012** contacts/dog/day	
	(Prop dogs free-to-roam*NE-NSW domestic dog population*(Attacks per year/Free-roaming dog population)+Non-violent dog contacts)		
	Non-violent contact	0.000115 contacts/dog/day~	Sparkes, Ballard, Fleming *et al*. In press.
	Attacks on domestic dogs	19.35 attacks yr^{-1}	Local Land Services domestic dog reported attacks, north-east NSW
	North-east NSW domestic dog population	0.46 million dogs	Office of Local Government, 2015
	% domestic dogs free-to-roam	26%	Sparkes, Ballard, Fleming *et al*. In. Prep.

^ Bolded parameter values are presented as daily increments per dog

[#] For all scenarios, S = Initial start population – 1, E = 1, I = 0 and R = 0