Modelling the challenges of managing free-ranging dog populations

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Introduction

One of the most common terrestrial carnivores in the world, the domestic dog (*Canis familiaris*) is found on every continent that humans have settled (Gompper 2014). More than 70% of the global dog population (estimated at > 700 million to ~1 billion) comprises of free-ranging dogs (FRD) (Hughes and Macdonald 2013; Gompper 2014). In many developing countries, FRD are associated with the transmission of zoonotic diseases such as rabies, zoonotic visceral leishmaniasis, canine echinococcosis, and soil-borne helminths (Jaleta et al. 2017; Deplazes et al. 2011; Ashford et al. 1998; Quinnell and Courtenay 2009; Carmena and Guillermo 2013). Rabies alone is responsible for an estimated 60,000 human deaths per year worldwide, with a majority of these deaths occurring in Asia and Africa (Hampson et al. 2015). India alone accounts for an estimated 20,000 human rabies deaths per annum (Sudarshan et al. 2007; Hampson et al. 2015).

Apart from dog-mediated rabies deaths, dog attacks also result in direct human fatalities in India (e.g. https://www.nationalheraldindia.com/india/stray-dogs-terror-in-sitapur-six-children-killed-in-one-week accessed on 19/Jun/2020). An estimated 20 million people are bitten by dogs every year in India (Gongal and Wright 2011). In addition, dogs are an important and emerging threat for livestock (Home et al. 2017) as well as biodiversity (Vanak and Gompper 2009; Doherty et al. 2017; Belsare, Vanak, and Gompper 2014; Hughes and Macdonald 2013; Gompper 2014). Furthermore, FRD also suffer from poor health, high mortality, and abuse (Jackman and Rowan 2007). There is thus a strong and urgent need to control free-roaming dog populations in India.

Efforts to control dog populations in India using a variety of lethal and non-lethal methods have been unsuccessful so far. Lethal methods were implemented haphazardly for many years, but without ancillary measures to restrict access to resources and restricting roaming behaviour, the dog populations rebounded. These methods were also criticized for being unnecessarily cruel and were subsequently outlawed in India. Since 2001, the only legal method of population control, involving capture-neuter-vaccinate-release (Animal Birth Control – ABC) was promulgated. As per the World Organisation for Animal Health (OIE), one of the main objectives of dog population control programmes like ABC is to reduce the abundance of FRD (OIE 2015). However, as several reports have shown, these measures were neither fully implemented nor evaluated (e.g. Totton et al., 2010; Uniyal & Vanak, 2016). Indeed, almost all ABC programs have only targeted urban centres. Even here, model simulations suggest that a sustained and well implemented ABC only program may result in a population reduction of ~70% over a 13-18 year period in the best case scenario of ~85% population coverage (Totton et al. 2010).

Dog population management approaches such as the ABC program which mandates surgical sterilisation, requires considerable financial, infrastructural and personnel support. Operationalising any such program therefore requires careful thought and planning for successful implementation. Often however, there is a lack of understanding of the effort required to significantly and sustainably reduce dog populations. Indeed, the general perception is that a one-time or short burst of surgical interventions will result in permanent eradication or "stray dog free" cities (https://www.royalpatiala.in/mission-patiala-to-be-first-stray-dog-free-city-bhullar/ accessed on 22/Jun/2020). Government authorities and non-government organizations (NGOs) routinely report the number of surgeries performed as a measure of success, without any mention of the baseline population size. There is thus a strong need for setting the context and realistic targets, so that the success of the ABC program can be monitored.

Population models that allow for simulation of various scenarios are often an effective planning and monitoring tool. If properly parameterised, these can be used to understand the scale of effort needed to achieve a set target reduction in population or to understand that challenges that emerge from improperly planned interventions. However, in India, such models are rarely, if ever, used by government agencies for scenario building and planning. There are several reasons behind this, including a lack of technical expertise, and the perception that such models are the domain of mathematical experts.

We have developed an agent-based model that generates a realistic *in silico* dog population, and projects it over a desired number of years. Model-generated dog populations incorporate individual attributes and characteristics (like age, sex, reproductive status, accessibility, catchability, age-specific mortality) that underpin heterogeneity observed in the real-world free-ranging dog populations. Here we apply the model to evaluate the success as well as cost-effectiveness of dog population management interventions like ABC and also if it achieves the targets necessary for rabies control. Specifically, we examine the effect of ABC interventions on dog abundance, dog recruitment in the population and population-level anti-rabies coverage.

2. Model description

The model, DogPopDy, was developed in NetLogo 6.0.4 (Wilensky 1999). NetLogo is a software platform for implementing agent-based models. Model description is provided following the ODD (Overview, Design concepts, Details) protocol for individual-based models (Grimm et al. 2006; 2010). Model code is available via website repository "Open ABM CoMSES Computational Model Library" (https://www.comses.net/codebase-release/dd1d9996-0042-4aaf-b645-8723307fe61c/).

2.1 Purpose

The purpose of this model is to provide a decision-making context for evaluating and designing dog population management and rabies control strategies.

2.2 Entities, State Variables and Scales

Entities: The model has two entities: dogs and patches. Dogs are modeled as individuals occurring on the patches in the model landscape. State variables for the two entities are described in **Table 1** .

Spatial scale : The model landscape represents a 400 square kilometer area (20 x 20 patches, each patch equals 1 square kilometer).

Temporal scale : The model has a monthly time step and is simulated for 30 years.

2.3 Process overview and scheduling

The model simulates demographic processes (birth, aging, migration and death) and ABC intervention in the model dog population (**Figure 1**). During each time step, the age and anti-rabies immunity status of agents (dogs) is updated. The age-specific probability of death during each time step is derived from annual mortality rates (See Submodels section for details).

Reproduction is seasonal; female dogs older than 8 months of age breed between September (month 9) and February (month 2). The sterilization submodel (ABC program) is implemented after the model runs for five years (burn-in period). A proportion of accessible, intact dogs are neutered and vaccinated against rabies every month for the duration of the ABC program.

2.4 Design Concepts

Emergence : The emergent effect of interest here is the percent reduction in population as a consequence of population management (ABC) efforts in an open dog population with heterogeneous accessibility (catchability). ABC effort is limited by the proportion of inaccessible dogs and immigration rate.

Stochasticity : During each time-step, individuals are selected stochastically to implement three processes: reproduction, mortality and sterilization. Number of pups in each litter is determined by randomly selecting a value between one and six.

Observation : The following observations are updated and documented during each time-step: dog population abundance (graph and monitor; Fig. S1), number of ABC surgeries per month (graph), proportion of neutered individuals in the population (monitor), total number of ABC surgeries (monitor) and percent reduction compared to population size before ABC was initiated (monitor; Fig. S1). Total cost for the entire duration of ABC program (cost per surgery * inflation * number of surgeries every year) is also reported (monitor). Results of each model run are also written as a .csv file.

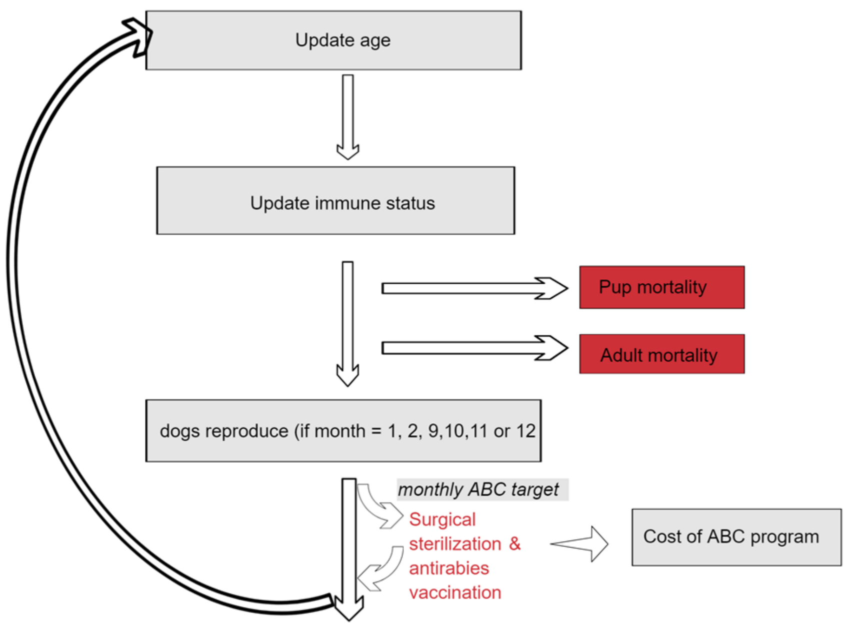

Figure 1: Sequence of events during each step of DogPopDy.

2.5 Initialization

The model dog population is created using two parameters, human population (set using slider: *human-population*) and human-dog ratio (set using slider: *human-dog-ratio;* Fig. S1). Human population is divided by the human-dog ratio to determine initial number of adult dogs in the model landscape. This is referred to as the adult dog carrying capacity for the model landscape. Adult dog carrying capacity is not explicitly enforced anytime during the model run but is used to simulate density-dependent juvenile mortality.

Mean dog density (or mean number of dogs per patch) is calculated as follows:

$$Mean\ dog\ density = \frac{\text{Initial number of adult dogs}}{\text{number of patches in the model landscape}}$$

Initial number of dogs on a patch is derived from a normal distribution around mean dog density ± 20% SD.

Age is set at 13 months or older for all dogs in the model during the setup. We therefore run the model for 5 years ("burn-in" period) before simulating ABC interventions and recording model outputs.

The cost per ABC surgery was set at a conservative INR 700 (US$ 10.5) (https://timesofindia.indiatimes.com/city/nashik/civic-body-finalizes-agency-for-stray-dog-sterilization/articleshow/71086742.cms accessed on 20/Jun/2020) with an annual inflation of 5%. However, there is an option in the model for the user to specify initial cost per ABC surgery and the annual inflation rate using the sliders provided on the Graphical User Interface (GUI; Fig. S1).

Submodels

2.6.1 update-age

Ages of all surviving dogs are updated (state variable '*aim* ' – age in months) by 1 month during each time step.

2.6.2 update-immune-status

The immune status (state variable '*imm* ') of vaccinated dogs is updated each time step to represent waning immunity. The duration of protective immunity post anti-rabies vaccination is assumed to be one year. In the developing world, a large proportion of the dog population is mostly free-roaming; these dogs are quasi-owned, never restrained nor subject to health or fertility control interventions. In such populations, there is a variation in antibody response to a single dose of anti-rabies vaccine, but most dogs do not have a protective antibody titer after a year (Pimburage et al. 2017).

2.6.3 follow-up-vaccination

A monthly probability derived from the follow-up vaccination rate (slider: *followup-vacc-rate*) determines if a neutered dog is revaccinated. Neutered dogs with duration of immunity 6 months or less ($imm < 7$, i.e. not revaccinated in the last 6 months) are revaccinated.

2.6.4 dog-mortality

Dog populations in the developing world have a high turnover rate (30-50%) (Matter 1993; Beran 1982; Kitala et al. 2001; Belsare and Gompper 2015). The annual survival estimate for adult FRD is 70% (Reece et al. 2008). Reece et al. 2008 report a low survival rate (25%) for juvenile FRD. We use these estimates to derive monthly probabilities of death for adult and juvenile dogs in the model population. Additionally, the size of the adult dog population has a density-dependent effect on juvenile mortality, such that when adult population size reaches or exceeds adult dog carrying capacity, juvenile mortality is at its maximum (75% per year) (Reece et al. 2008). As the abundance of adult dogs in the model population goes below the adult dog carrying capacity, juvenile survival increases. The effect of decreasing adult abundance on annual juvenile survival as modelled in DogPopDy is shown in **Figure 2** .

Rates are converted into monthly probabilities using the following equation:

$p = 1 - \exp\{-rt\}$

where p=probability, r= instantaneous rate, provided that it is constant over the period of interest (t) (Briggs, Claxton, and Sculpher 2006).

2.6.5 dogs-reproduce

Reproduction is simulated over a six month period every year, between month 9 (September) and month 2 (February). Intact females older than 8 months can breed once during a breeding season. Each month of the breeding season, a proportion of intact adult and subadult (> 8 months old) females produce a litter. The proportion of intact females that reproduce during a breeding season is influenced by the ratio of intact adult males to intact adult females in the model dog population. Investigations of a roaming dog population in an Indian city indicated that 47.5% (95%CI 43 -51) of adult females reproduce annually (Reece et al. 2008). The proportion of intact females that reproduce is therefore set between 0.44 and 0.51, if the intact male: intact female ratio in the model dog population is more than 0.1. If the ratio is lower than 0.1, we assume that the proportion of intact females that reproduce will decrease. In such a scenario, the number of pregnant females is calculated under the assumption that each intact male impregnates an average of 10 (range 3 – 17) females.

An average litter size of 5.6 was documented in urban, FRD, based on the number of aborted foetuses recorded during sterilization surgeries (ABC program) in Jaipur, India (Chawla and Reece 2002). In this model, we have set the average litter size at 4 ± 0.5 to adjust for embryonic and neonatal losses.

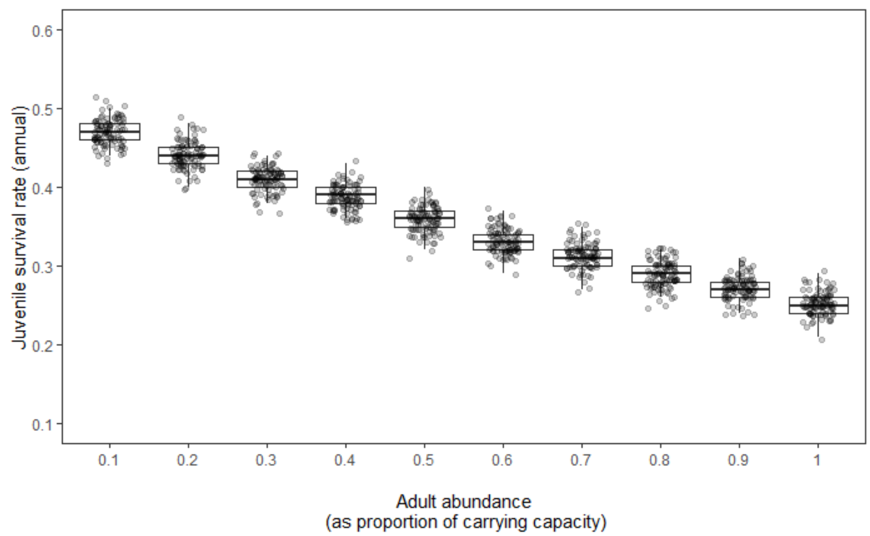

Figure 2 . Juvenile survival is modeled as a density-dependent process in DogPopDy such that only 25% juvenile dogs survive beyond the age of one year when adult dogs are at carrying capacity. Juvenile survival increases as adult abundance decreases, but the maximum rate of juvenile survival does not exceed 50%.

2.6.6 dog-sterilization

ABC is implemented by iterating over non-neutered dogs older than 6 months and changing the reproductive status of selected individuals to 'neutered'. The monthly target for ABC is limited by the number of ABC centers (user-specified, slider: *num-abc-centers*) and the maximum number of surgeries per ABC center. As per the guidelines formulated by the Animal Welfare Board of India (AWBI), the number of surgeries per month is capped at 250 per ABC facility (AWBI 2016 Revised Module for street dog population management, rabies eradication, reducing man-dog conflict).

For the best case scenario (closed population, all dogs are equally and easily catchable), stochasticity in the dog capturing process is modeled by decreasing the monthly target by up to 5%. The monthly target so derived is equally divided between males and females.

For the real-world scenario, we incorporate processes that affect dog captures, and therefore the actual number of ABC surgeries per month. Capture effort heterogeneity is an important factor influencing the number of dogs captured for the ABC program. While planning dog population management strategies, it is often assumed that all dogs are catchable. However, in the real world, the capture effort, and therefore the capture efficiency, varies between dogs. Some dogs are easy to capture (cooperative reference persons, friendly community-owned dogs accustomed to handling), while others require additional effort and time (capture using nets, cages, chemical immobilization). Based on free-ranging dog capture data from rural as well as urban sites (Belsare and Gompper, 2013; Vanak unpublished data), we estimated that 40% dogs in free-ranging dog populations are easy to capture while 60% require additional effort than what is normally deployed by the dog catching team. To incorporate capture effort heterogeneity in the model, we have included a dog state variable 'catchability'. A non-zero catchability between 1 and 100 is randomly assigned to each dog in the model population. Dogs with catchability > 60 have a capture probability of 1 (readily accessible with standard catch effort), dogs with catchability between 30 and 60 have a capture probability of 0.67 (require 50% more effort than standard catch effort), and dogs with catchability below 30 have a capture probability of 0.5 (require 100% more effort than standard catch effort). The proportion of unneutered dogs that are catchable during a time step is determined as follows:

Proportion of unneutered catchable dogs = {(Number of unneutered dogs with catchability > 60 * 1) + (Number of unneutered dogs with catchability between 30 and 60 * 0.67) + (Number of unneutered dogs with catchability < 30 * 0.5)} / Total dogs

The monthly ABC target is scaled using the proportion of unneutered catchable dogs.

For the real world scenario, it is also possible to designate a proportion of the dog population as inaccessible (using the slider '*piad* '). Owned, free-ranging dogs protected by their owners from the dog catching team or truly feral dogs fall in this category. Inaccessible dogs remain intact and unvaccinated throughout the simulation.

The desired target for the ABC program can be set using slider '*target-reduction* ' (the desired reduction expressed as percent of the initial population). A post-target ABC rate can also be specified (set using slider: *followup-abc-rate*) – this rate is implemented if the desired reduction in dog population is achieved before the ABC program duration is completed. All sterilized dogs are vaccinated against rabies, and the duration of immunity is set at 12 months.

2.6.7. dogs-immigrate

Immigration of dogs into the model dog population is simulated if the user-specified annual immigration rate is more than zero. This rate is interpreted in the context of the initial dog carrying capacity. The number of dogs immigrating during each month of the model run is determined using this rate. All immigrating dogs are sexually intact (non-neutered) and between one and two years of age. Male: female ratio in the immigrating dogs is set at 1:1.

3. Model evaluation and sensitivity analysis

The model system was populated to represent an urban area with a human population of 1,000,000 and a human: dog ratio of 33:1. The model dog population was projected over a 30 year period. An initial burn-in period of five years was followed by the intervention period (five years of ABC program, from year 6 to year 10). Three model-derived metrics were used to assess the impact of ABC interventions on the model dog population: a) dog abundance (reflecting the pre-breeding season population in the month of September), b) annual recruitment into the adult class, and c) anti-rabies vaccination coverage. Specifically, we compared population metrics before and after the intervention period (year 5/6 and years 10, 15, 20, 25, 30). To account for stochasticity in the model runs, we undertook 100 iterations for each scenario.

We evaluated the model performance by first simulating a 'business as usual' scenario (no ABC program) in a closed dog population (no immigration or emigration). Without any population control interventions, the model dog population increased over the course of 25 years from 35,183 (± 1170 SD; year 5) to 42, 879 (± 2318 SD; year 30) (**Figure 3A**). Adult dog abundance in the model landscape (enumerated in the first month of each year) reached carrying capacity in year 16 (30,186 ± 1191 SD; 95% CI 29,950 – 30,423, t(99)

= -0.97901, p = 0.33; one-sample t-test) and remained above the carrying capacity till the end of simulation at year 30 (31,956 ± 1570 SD). Annual recruitment in the adult age class increased from 9,412 (± 508 SD; year 5) to 11,090 (± 771 SD; year 30) (**Figure 3B**). There was no anti-rabies vaccination coverage in the 'business as usual' scenario.

Model performance was further evaluated by implementing a 5-year ABC program with 1 ABC center (~250 ABC surgeries per month) in the closed model population where all dogs were equally and easily catchable ('best case' scenario). This resulted in an average of 14,687 ABC surgeries per model iteration, incurring a cost of US$170,426. Model dog population decreased over a 9 year period from 35,121 (± 1329 SD; year 5) to 31,254 (± 1512 SD; year 14), but by year 20 the dog population was at pre-intervention levels and continued to increase thereafter (40,686 ± 1614 SD; year 30) (**Figure 4A**). The adult proportion of the model dog population also decreased over a 10-year period from 26,656 (± 948 SD; year 6) to 23,830 (± 1095 SD; year 15), and increased thereafter until it reached carrying capacity by year 29 (30,145 ± 1137 SD; 95% CI 29,919 – 30,371, t(99) = -1.389, p = 0.168; one-sample t-test). Annual recruitment in the adult age class decreased from 9,359 (± 634 SD; year 5) to 8,439 (± 589 SD; year 15) over a 10 year period; and increased thereafter over the course of model run (10,689 ± 679 SD; year 30) (**Figure 4B**). This best case, low-intensity ABC scenario resulted in a maximum anti-rabies vaccination coverage of 8% during the intervention period. The vaccination coverage waned rapidly within a year after the intervention period.

Sensitivity analysis

We performed a local sensitivity analysis of dog abundance (mean pre-breeding season abundance) during assessment interval 1 (years 11 to 15). Sensitivity values were generated for select parameters following steps outlined in Railsback and Grimm (2012). We examined sensitivity of parameters that were related to mortality rates (adult mortality and juvenile mortality), reproduction (mean litter size), and carrying capacity (human: dog ratio). A range was constructed for each parameter analyzed such that the lower (R^-) and upper (R^+) endpoints were within 5-15% of the reference value (R). One hundred iterations of DogPopDy without ABC were undertaken for each parameter value to generate sensitivity values. The sensitivities were calculated as follows:

$S^+ = ((C^+ - C) / C) / ((R^+ - R) / R)$

$S^- = ((C^- - C) /C) / ((R - R^-) / R)$

where C^-, C and C^+ are average dog abundance values when a parameter is valued at R^-, R and R^+, respectively.

The sensitivity analysis indicated that dog abundance values were particularly sensitive to juvenile mortality and mean litter size, and to a lesser extent on adult mortality (**Table 2**).

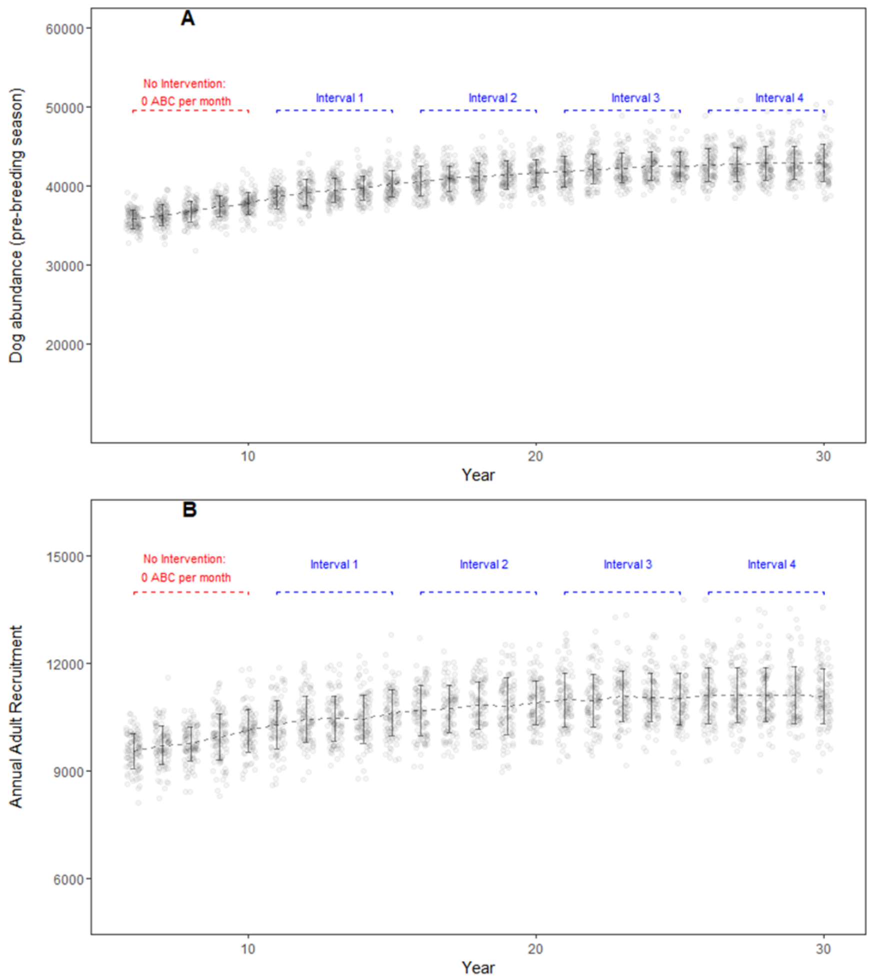

Figure 3 . DogPopDy evaluation using a 'business as usual' scenario (no population control intervention). Model dog population was projected over a 30 year period. **A** . Dog abundance (pre-breeding season, month = September), and **B** . Annual recruitment of juveniles into the adult age class, summarized for 100 DogPopDy iterations. The four assessment intervals are indicated by dashed lines (blue).

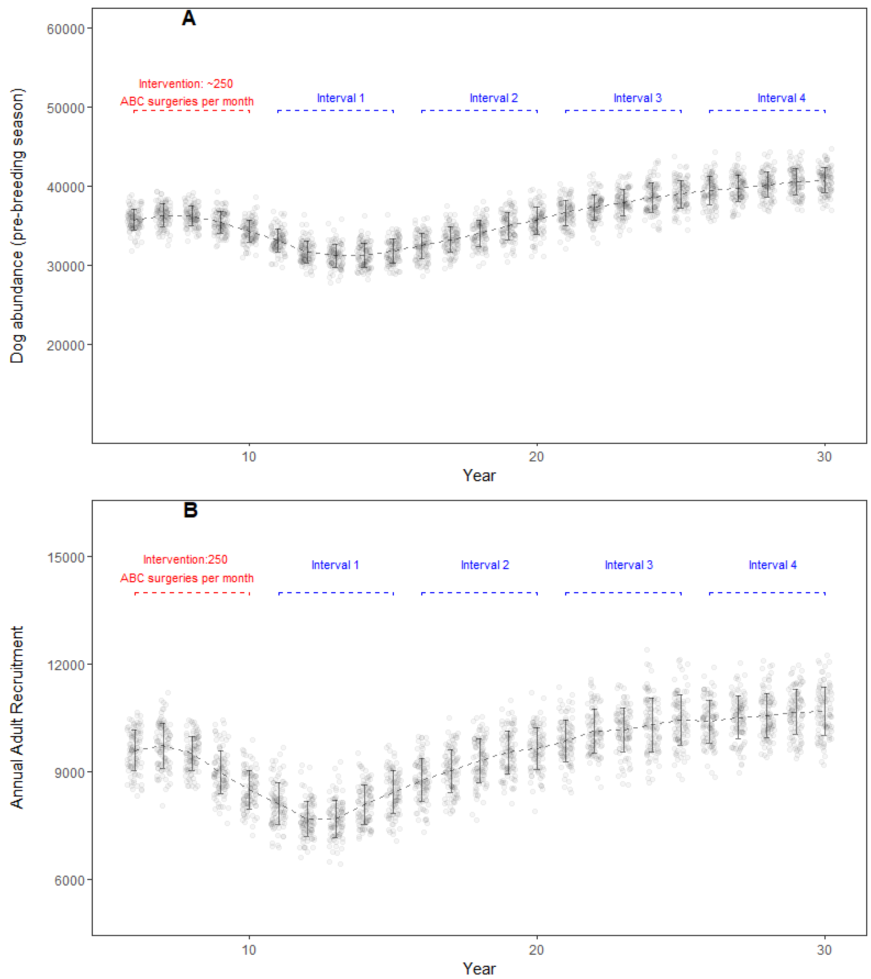

Figure 4 . DogPopDy evaluation using a 'best case' scenario (closed population, all dogs in the population are equally and easily catchable) with a 5 year ABC program (1 ABC center = ˜ 250 ABC surgeries per month).**A** . Dog abundance (pre-breeding season, month = September), and**B** . Annual recruitment of juveniles into the adult age class, summarized for 100 DogPopDy iterations. The four assessment intervals are indicated by dashed lines (blue).

4. Model application

We used DogPopDy to assess the impact of ABC effort intensity (number of ABC surgeries per month) on the efficacy of dog population management programs. The model was set up as described under *Model evaluation and sensitivity analysis* (Section 3). Using the best case scenario, two levels of ABC efforts were assessed: moderate intensity (2 ABC centers ˜ 500 ABC surgeries per month for 5 years) and high intensity (3 ABC centers ˜ 750 ABC surgeries per month for 5 years), We further evaluated high intensity ABC effort in a real-world context. Specifically, we incorporated capture heterogeneity (see 2.6.6 *dog sterilization*) in the model simulation, designated 5% dogs in the model population as inaccessible for ABC intervention, and set the net annual immigration of dogs into the model population at 1%. The results of all scenarios are summarised in Table 3.

Moderate intensity ABC effort (Best case scenario)

An average of 29,380 ABC surgeries per iteration of the moderate intensity 5-year ABC effort incurred a cost of US$340,918. Model dog population decreased from 34,980 (± 1,178 SD; year 5) to 20,306 (± 1,657 SD; year 15) over a 10 year period, but by year 26 the dog abundance had increased to pre-intervention level (34,447 ± 1660 SD), and continued to increase thereafter (37,650 ± 1,588 SD; year 30) (**Figure 5A**). The adult proportion of the model dog population initially decreased over a 10-year period from 26,629 (± 908 SD; year 6) to 15,561 (± 1227 SD; year 15,), but increased thereafter until it reached pre-intervention level by year 27 (26,310 ± 1,219 SD). The adult dog abundance remained below the carrying capacity throughout the model run. Annual recruitment in the adult age class decreased from 9,297 (± 576 SD; year 5) to 5,105 (± 565 SD; 15) over a 10 year period; and increased thereafter over the course of model run (10,111 ± 621 SD; year 30) (**Figure 5B**). The maximum anti-rabies vaccination coverage achieved with a moderate-intensity ABC scenario was 18%, but the coverage rapidly waned within a year after the intervention period.

High intensity ABC effort (Best case scenario)

High intensity ABC effort resulted in an average of 42,608 ABC surgeries per iteration and incurred a cost of US$492,682. Model dog population decreased from pre-intervention abundance of 34,647 (± 1,084 SD; year 5) to 1,447 (± 1,359 SD; year 20), and a gradual increase thereafter until year 30 (3,032 ± 5,532 SD; year 30) (**Figure 6A**). After the second assessment interval, mean dog abundance values were generally low (< 3,000) but overdispersed as indicated by the standard deviations. Nine out of 100 iterations had > 10,000 dogs (with a maximum value of 28,136) in the 30th year. The adult dog abundance mirrored this decreasing trend (from 26,394 ± 863 SD in year 6 to 1,161 ± 2,140 SD in year 25) but increased to 2,248 ± 4,102 SD by the 30thyear. Only six iterations out of 100 had adult dog abundance above 10,000 in the 4th assessment interval. High intensity ABC effort was able to keep the adult dog abundance below the carrying capacity throughout the model run. Annual recruitment in the adult age class decreased from 9,247 (± 540 SD; year 5) to 87 (± 195 SD; year 15) over a 10 year period; and gradually increased thereafter over the course of the model run (1,019 ± 1,811 SD; year 30) (**Figure 6B**). The maximum anti-rabies vaccination coverage achieved with a high-intensity ABC scenario was 35%, but the coverage rapidly waned within a year after the intervention period.

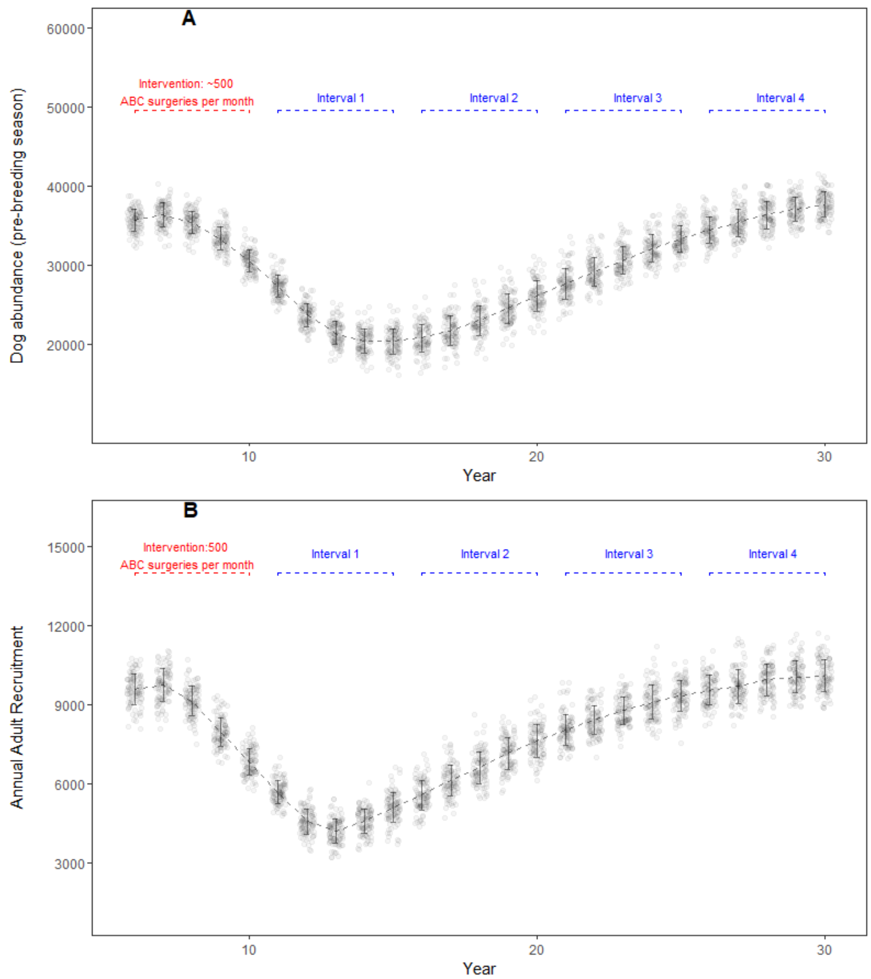

Figure 5 . DogPopDy assessment of a moderate intensity ABC effort using a 'best case' scenario (closed population, all dogs in the population are equally and easily catchable). Two ABC centers (~500 ABC surgeries per month) represented moderate intensity ABC effort. **A** . Dog abundance (pre-breeding season, month = September), and **B** . Annual recruitment of juveniles into the adult age class, summarized for 100 DogPopDy iterations. The four assessment intervals are indicated by dashed lines (blue).

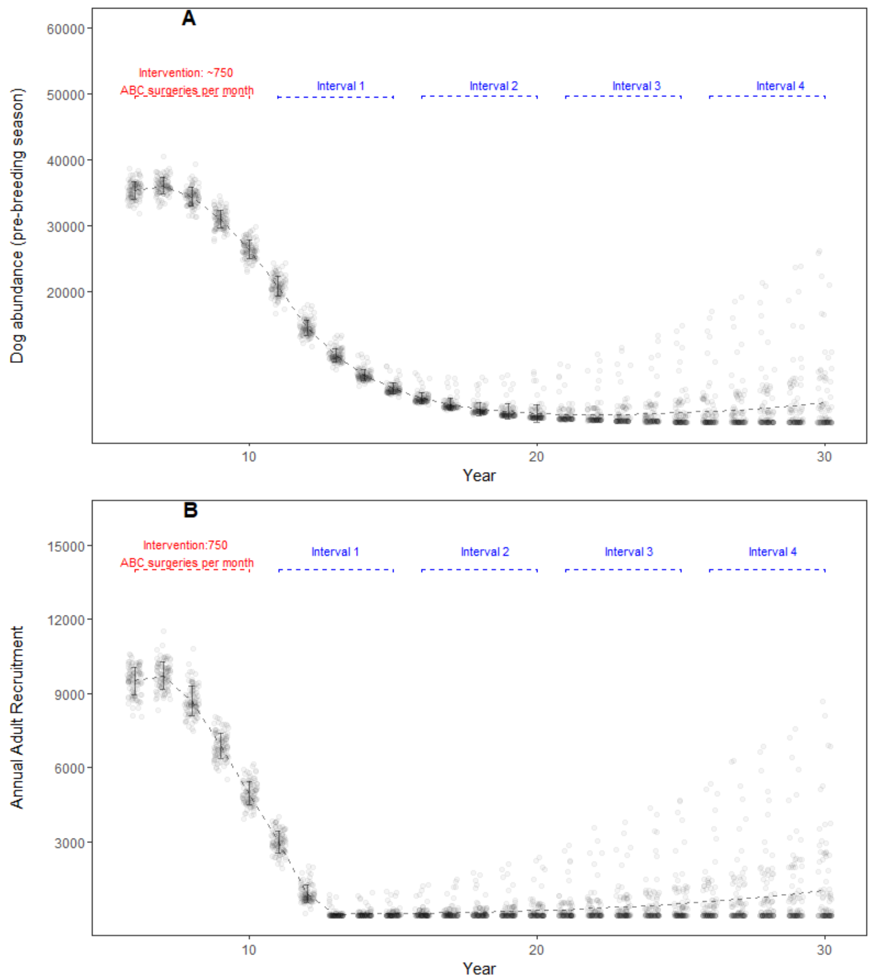

Figure 6 . DogPopDy assessment of a high intensity ABC effort using a 'best case' scenario (closed population, all dogs in the population are equally and easily catchable). Three ABC centers (˜750 ABC surgeries per month) represented high intensity ABC effort. **A** . Dog abundance (pre-breeding season, month = September), and **B** . Annual recruitment of juveniles into the adult age class, summarized for 100 DogPopDy iterations. The four assessment intervals are indicated by dashed lines (blue).

High intensity ABC effort (real world scenario)

The high intensity ABC effort was not effective when real world processes were incorporated in the model simulation. An average of 21,099 ABC surgeries per iteration incurred a cost of US$ 243,393. Model dog population decreased from pre-intervention abundance of 35,829 (± 1,154 SD; year 5) to 29,150 (± 1,439 SD; year 15), increased thereafter surpassing the pre-intervention abundance, and was 42,095 (± 2,038 SD) in year 30 (**Figure 7A**). The adult dog abundance decreased initially from 27,442 ± 850 SD in year 6 to 21,945 ± 975 SD in year 14, and increased thereafter, eventually surpassing the carrying capacity in year 28 (30,874 ± 1,339 SD) and reached 31,444 ± 1437 SD in year 30. Annual recruitment in the adult age class decreased from 9,386 (± 556 SD; year 5) to 7,556 (± 526 SD; year 15), then increased over the course of the model run (10,878 ± 744 SD; year 30) (**Figure 7B**). The maximum anti-rabies vaccination coverage achieved with a high intensity ABC scenario with real world processes was only 9%, and the coverage rapidly waned within a year after the intervention period.

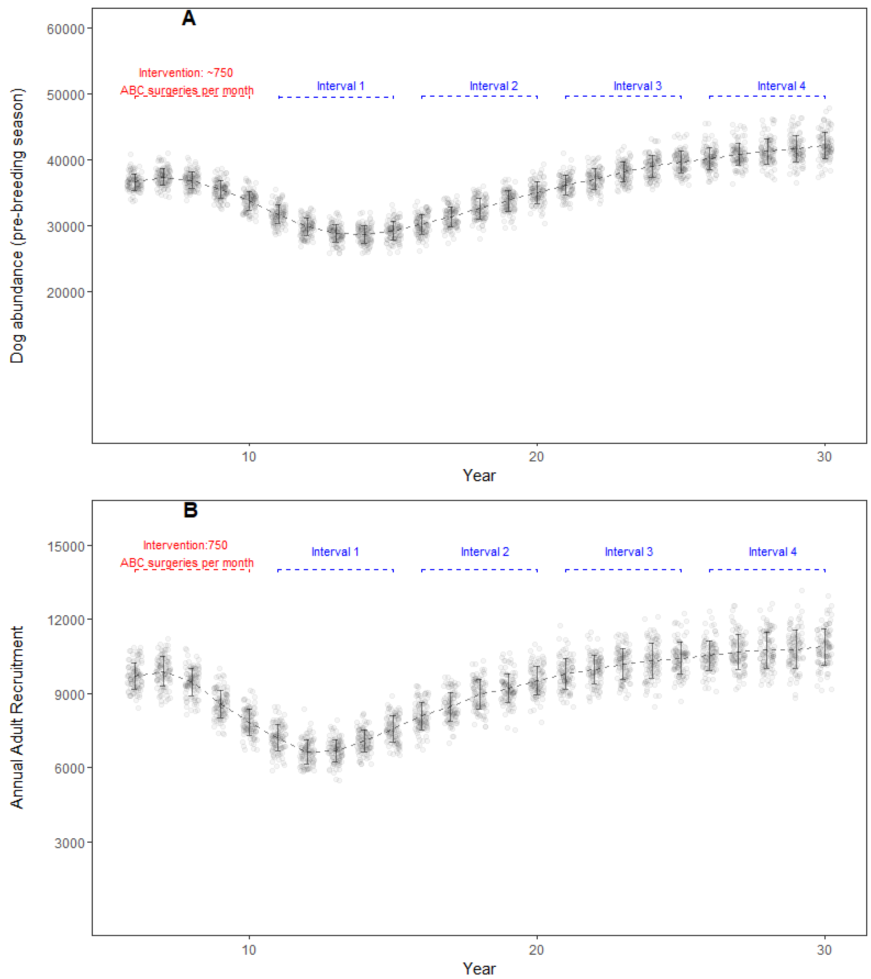

Figure 7 . DogPopDy assessment of a high intensity ABC effort using a 'real world' scenario (open population, capture heterogeneity, 5% dogs inaccessible for population management interventions). The actual number of ABC surgeries performed in a month is influenced by the catchability of the intact dogs in the population. Furthermore, inaccessible dogs and immigration also influence the population dynamics. **A** . Dog abundance (pre-breeding season, month = September), and **B** . Annual recruitment of juveniles into the adult age class, summarized for 100 DogPopDy iterations. The four assessment intervals are indicated by dashed lines (blue).

4. Discussion

The presence of a large, FRD population has double negative consequences - high public health problems as well as poor animal welfare outcomes. There is thus a strong need for effective management of dog populations in developing countries. According to WHO (2004), the goal of ABC programs is to "reduce dog population turnover as well as the number of dogs susceptible to rabies and limit aspects of male dog behaviour (such as dispersal and fighting) that facilitate the spread of rabies"(WHO 2004). Clearly, it would seem that reducing the population of FRD would result in considerable savings as well as a more sustainable program for elimination of rabies. The successful elimination of rabies in many countries in the early 1900s involved not just mass vaccination, but also strong pet ownership laws, and the removal of unowned free-ranging dogs. For example, in Japan, between 1925-1928 (both years inclusive), 935,771 dogs were vaccinated, and 856,328 "stray" dogs were captured and removed from the population. This, combined with strict rules regarding vaccination, ownership and regulation of pet dogs ensured a reduction in both free-ranging dogs as well as the elimination of canine rabies (Kurosawa et al. 2017). Indeed, in the Osaka prefecture, the first epidemic between 1914 to 1921 was controlled wholly through the leashing of pet dogs and the removal of unowned dogs (Kurosawa et al. 2017).

Lethal methods for population control have rarely been successful, mainly due to societal barriers, as well as ineffective and incomplete implementation. The use of alternate strategies, such as fertility control, are instead seen as more "humane" and socially acceptable (Yoak et al. 2014). However, in the absence of a systematic planning and monitoring protocol, well intentioned, but poorly planned programs may likely do little good. Our population modelling tool highlights the importance of understanding the dynamics of dog populations, the effort needed to achieve a particular target goal, and the associated costs over a long-period of time. Our simulations show that, even under a limited set of ideal conditions, the target of "zero" reproducing dogs is not achievable within a reasonable timeframe, given the current methods, and more importantly, this method will fail to achieve the goal of eliminating dog-mediated rabies (ZeroBy2030). In our simulations, only the high intensity ABC best case scenario achieved the stated goal of substantially reducing the number of adult dogs in the population (Table 3). However, this required substantial investment of close to half a million US dollars and more than 42,600 surgeries (for an initial dog population of only ~34,650) over the five year intervention period. Despite such a high rate of intervention, the maximum vaccination coverage achieved did not exceed 35%, which is half the recommended rate by WHO.

We further showed that even if there was a small proportion of the population being inaccessible for capture (5% of the initial adult carrying capacity) and very low levels of immigration (1% net immigration per annum), population control was not achieved, even with very high effort. The peak anti-rabies vaccination coverage remained below 10% even though the cost associated with this program was close to a quarter of a million US dollars. It is important to point out here that the scenarios mentioned above are highly conservative, and that in actuality both the proportion of inaccessible dogs, as well as immigration rates are likely to be much higher. This is because, unlike the situation in countries from the African continent (and other parts of the world), where most dogs are either wholly or partially owned by individuals or communities (Lembo et al. 2010), in India, a significant proportion of dogs may be unowned (as much as 30% in rural areas – Vanak, A. T. unpubl. and higher in urban). Interventions like ABC or mass vaccination require capture and handling of such dogs. Some dogs are readily accessible, but some require considerably greater effort than regular central point mass vaccination campaigns (Belsare and Gompper 2013). An assumption of equal catchability implies that monthly ABC targets from a particular region will be readily met. However, if a certain proportion of dogs require additional efforts for catching, then, given the human resources and time available, it is likely to result in shortfalls in the number of dogs captured and sterilised. The infusion of even highly conservative "real world" parameters in our models, renders the ABC exercise futile, both in terms of reducing population size, as well as in achieving sufficient anti-rabies vaccination coverage levels.

The parameters, and results from our model simulations, are not far from reality. For example, the amount of financial resources allocated by cities is typically half of what was required in our "real-world" scenario. For example, the city of Nashik in western India, allocated a budget of ~US$ 141,000 (1 crore INR, https://timesofindia.indiatimes.com/city/nashik/civic-body-finalizes-agency-for-stray-dog-sterilization/articleshow/71086742.cms accessed on 22/Jun/2020)

for a city with a human population of 1.5 million, and a derived dog population of 45,000 (based on human:dog ratios). There was no mention of estimating the actual population size, which is a common lacuna in most such exercises (Tiwari et al. 2018), and thus no target reduction in dog population size. The assumption from the city planners is that this operation will yield results similar to that achieved by the "high intensity best-case scenario" (**Figure 6**), but given the realities on the ground, the result is more likely to be similar to **Figure 7**. Furthermore, breaks in or discontinuation of, the ABC program can result in even lower coverage levels and reduce the effectivity of the program (e.g. https://timesofindia.indiatimes.com/city/guwahati/birth-control-scheme-for-stray-dogs-hits-roadblock-due-to-limited-funds/articleshow/69081059.cms accessed on 22/Jun/2020).

Thus, a lot of effort, resources and time will have been spent, without any significant impact in either reducing dog populations or in achieving sufficient vaccination coverage.

Efforts to combat rabies mainly focus on mass dog vaccination campaigns (Cleaveland et al. 2014; Lankester et al. 2014). The World Health Organisation and other leading international agencies have advocated annually vaccinating 70% of the dog population to break transmission cycles. With this strategy, the WHO and other organisations aim to eliminate dog-mediated human rabies deaths by 2030 (Abela-Ridder et al. 2016). Several pilot and scale projects have shown promising results using this strategy, giving hope that achieving "Zero by 2030" may not be such an ambitious target (Cleaveland and Hampson 2017). However, as we have shown, if this strategy is combined with an ABC program to simultaneously reduce dog populations, it is logistically unfeasible to achieve the necessary coverage levels.

Mass vaccination without ABC is advocated as an alternate mechanism to achieve 70% coverage levels (Gibson et al. 2015; 2018). The sensitivity analysis on our model shows that dog population is sensitive to both litter size and juvenile mortality. Anti-rabies vaccination has been shown to also reduce all-cause mortality in a cohort of dogs in South Africa (Knobel et al. 2017). Thus, it is likely that in the absence of an effective population control measure, only vaccination campaigns may end up in increasing dog populations. This is problematic for several reasons, including, in hampering the success of future anti-rabies vaccination programs. At current levels of vaccine production and the financial resources committed, Wallace et al. (2017) estimate a vaccine shortfall of 7.5 billion doses and a resource gap of US$ 3.9 billion to achieve global dog rabies elimination by 2030 (Wallace et al. 2017). This analysis also does not take in to account that a substantial proportion of unowned dogs may fail to sero-convert to the required protective antibody levels with a single dose of vaccine (Pimburage et al. 2017). It therefore becomes imperative to not lose focus on effective and long-term solutions to dog population management.

Our model simulation tool allows for relatively easy manipulation of all key parameter settings to test for capacity to effectively reduce populations within a reasonable period of time. The tool, developed as a customizable agent-based model (DogPopDy), can incorporate real-world processes like density-dependent survival, capture heterogeneity and immigration. The model program has a user-friendly Graphical User Interface (GUI), and the interface sliders and choices allow users (even non-modelers) to update model assumptions and perform virtual experiments. Practitioners and civic agencies can employ model-based explorations to estimate the amount of effort needed to achieve a particular target objective, as well as the time and effort needed to maintain the population at the target levels. It allows public authorities to incorporate defensible decisions while planning and implementing dog population management programs. Potentially the tool can also be modified and developed to model the impact of vaccination strategies under different population density scenarios, as well serve as a decision support system for strategic intervention planning. Here, we've simulated relatively simple scenarios, with highly conservative parameter estimates. However, our model tool allows for more complex scenario building with better estimates of population vital rates, breaks in ABC programs (due to funding cuts or other reasons), spatial heterogeneity in ABC programs or in planning long-term programs with set population targets, re-vaccination strategies, and the reduction of carrying capacity.

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Author contributions

AVB and ATV conceptualised and designed the study. AVB developed the model, conducted the simulations and produced the results. AVB and ATV wrote the paper.

Additional Information

The authors declare no competing interests.

Table 1. State variables of agents included in DogPopDy.

Agent	State variable	Meaning/Value
Patches	*patch_dog_density*	Sets the initial number of dogs on a patch; derived from a normal distribution around average number of dogs per patch ± 20% SD. Average number of dogs per patch is calculated using the carrying capacity (human population / human-dog ratio) and total number of patches.
Dogs	*aim sex bred? bc? ia imm*	age in months male = 1, female = 0 TRUE for females bred in current year (birth control) TRUE if neutered, FALSE if intact 0 if readily accessible, 1 if inaccessible protective immunity as a result of rabies vaccination; 0: no protective immunity, 1 – 12: duration of protective immunity (months)

Table 2 . Sensitivity analysis results for mean pre-breeding season abundance during assessment interval 1 (years 11-15). DogPopDy was simulated without ABC intervention and 100 model iterations were analyzed to derive the sensitivities.

Parameter	Range	Assessment interval 1	Assessment interval 1
		S^{+}	S^{-}
adult-mortality-probability	[0.027, 0.029, 0.031]	1.33	-1.08
juvenile-mortality-probability	[0.091, 0.101, 0.112]	3.13	-1.64
mean litter size	[3.5, 4, 4.5]	-1.7	2.61
human: dog ratio	[32, 33, 34]	1.27	-0.44

Table 3 . Model dog population parameters (pre-breeding season abundance and annual recruitment in the adult class) compared for five ABC scenarios. Business as usual scenario is simulated in a closed dog population without any ABC intervention. For all other scenarios, ABC program is implemented over a 5-year period (year 6 to year 10). Best case scenario assumes a closed population and homogeneous capture probability. Real world scenario simulates 1% net annual immigration into the model dog population and heterogenous capture probability. Shaded cells indicate values exceeding pre-intervention level.

ABC target (per month)	Scenario	Model population parameter (±SD)	Pre-ABC	Year 10	Year 15	Year 20	Year 25	Year 30
No ABC	Business as usual	Abundance	35183 (±1170)	37756 (±1343)	40178 (±1661)	41573 (±1766)	42420 (±1843)	42879 (±2318
		Annual adult recruitment	9412 (±508)	10131 (±593)	10622 (±648)	10913 (±616)	11011 (±710)	11090 (±771)

ABC target (per month)	Scenario	Model population parameter (±SD)	Pre-ABC	Year 10	Year 15	Year 20	Year 25	Year 30
˜250	Best case	Abundance	35121 (±1329)	34271 (±1395)	31781 (±1529)	35584 (±1785)	38944 (±1762)	40686 (1614)
		Annual adult recruitment	9539 (±634)	8512 (±531)	8439 (±589)	9647 (±592)	10,441 (705)	10,689 (±679)
˜500	Best case	Abundance	34980 (±1178)	30507 (±1366)	20306 (±1657)	26069 (±1934)	33265 (±1650)	37650 (±1588
		Annual adult recruitment	9297 (±576)	6831 (±501)	5105 (±565)	7634 (±620)	9244 (±572)	10,111 (±621)
˜750	Best case	Abundance	34647 (±1084)	26333 (±1381)	5217 (±833)	1447 (±1359)	1540 (±2886)	3032 (±5532
		Annual adult recruitment	9247 (±540)	4952 (±476)	87 (±195)	211 (±462)	481 (±968)	1019 (±1811
˜750	Real world	Abundance	35829 (±1154)	33726 (±1416)	29150 (±1439)	34976 (±1608)	39577 (±1636)	42095 (±2038
		Annual adult recruitment	9386 (±556)	7835 (±522)	7556 (±526)	9514 (±580)	10422 (±639)	10878 (±744)

Supplementary Information

Figure S1. A screenshot of the model dashboard of DogPopDy in NetLogo with the various parameter adjustments and project simulation tools available, as well as the visual outputs of the simulation results.