**BioEcon: An individual-based, stochastic simulation model for wildlife population and disease management with an application to canine rabies**

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**Abstract**

We present an individual-based stochastic simulation model of wildlife population and disease dynamics under different management strategies. The model is written in R and is available for free download at www.BioEconModel.com. BioEcon can be parameterized for many different wildlife species and diseases, and it can accommodate removal, fertility control, and vaccination efforts that vary spatially, temporally, and demographically. The model allows managers to search for minimum cost strategies that achieve an abundance or disease prevalence objective. Alternatively, it can be used to search for strategies that maximize biological impact subject to some budget constraint. Other potential applications include estimating the benefits of longer-lasting contraceptives or vaccines, the benefits of more effective capture technology, or the additional funding required to substitute fertility control for lethal management. After presenting an overview of the model’s capabilities, we demonstrate application of the model by examining the impacts of alternative strategies for managing rabies in free-ranging dogs.

**1. Introduction**

Wildlife managers are often tasked with reducing the abundance of a population or the disease prevalence within a population. Abundance may be managed to mitigate a negative impact such as crop damage or livestock predation, while disease prevalence may be managed due to concerns about its impact on wildlife, domestic animals, or human health. Management might also be motivated by multiple considerations and require balancing different objectives. In many settings, the strategic options available to managers can be quite diverse. Sport hunting, professional removal, permanent sterilization, and temporary contraception might be used to control abundance. Although disease prevalence can also be managed indirectly by these same methods, in some cases it can be managed more directly with vaccination. Managers’ strategic choice problem is further complicated by the consideration of mixed strategies and strategies that vary temporally, spatially, and demographically.

In an attempt to provide guidance for managers, two types of modeling efforts are common. One approach considers the impacts of different management strategies by pairing a relatively complex model of biological dynamics (i.e. models with spatial, demographic, or social structure) with simple concepts of management (e.g. Seagle and Close 1996, Xie at al. 1999, Smith and Cheeseman 2002, Cosgrove et al. 2012). For example, a Leslie matrix model or stochastic simulation model could be used to understand dynamics under alternative levels of removal, sterilization, or contraception within the population without consideration of the effort and costs that are required to achieve those levels. For a manager seeking strategic guidance, the failure of these types of models to consider effort and costs is problematic because different strategies require different levels of effort and entail different costs. Given that managers usually face budget constraints, accounting for the links between effort, costs, and biological outcomes is critical to understanding what strategies are feasible or to what extent specific strategies can be pursued.

In contrast, a second approach, often seen in the economics literature, incorporates the concepts of effort, cost, and catch into relatively simple models of biological dynamics and pairs the resulting bioeconomic models with sophisticated optimization techniques (e.g. Rondeau 2001, Rondeau and Conrad 2003, Horan and Wolf 2005, Fenichel and Horan 2007). The relative simplicity of the biological models in these approaches is driven by the focus on identifying a globally optimal strategy and the resulting mathematical and/or computational burden imposed by the optimization method (e.g. optimal control, dynamic programming). Additionally, these models do not often assume an objective in terms of abundance or disease prevalence, but instead assume a manager attempts to maximize the net benefit of management to society. Thus, the focus is not limited to the optimal strategy to achieve a certain abundance or disease prevalence target, but also includes the optimal abundance or disease prevalence at each point in time.

In any applied setting, there is certainly value in accounting for effort and costs and identifying optimal strategies. However, in many applied settings, the focus on comprehensive optimality present in many bioeconomic models is unlikely to be useful for several reasons. First, it comes at the cost of biological and strategic sophistication. For example, a model with little (or no) demographic or spatial structure cannot effectively account for strategies that vary by age, sex, or location. Additionally, if strategies alter demographic or spatial structure of the population, such changes likely affect biological dynamics. Second, managers face not only budgetary constraints, but also political and technical constraints. Thus, the manager may be choosing among a relatively small set of strategies that are deemed intuitively, politically, and technically feasible. Furthermore, management objectives are often influenced by politics and public opinion.

Although the two common approaches discussed above are often unable to provide specific strategic prescriptions, they remain valuable because they provide general lessons. Models that do not effectively account for effort and costs still provide valuable insight into the relative effectiveness of different types of management. Conventional bioeconomic optimization models assist managers in understanding the general characteristics of optimal strategies and provide insight into what those strategies depend on. However, in light of the above discussion, we propose a bioeconomic model (BioEcon) that strikes a balance between biological sophistication and the ability to identify optimal strategies while recognizing management resource constraints.

The bioeconomic model we propose is an individual-based stochastic simulation model that explicitly accounts for the links between effort, cost, and biological outcomes. Additionally, our objective is to construct a model that (1) accounts for population *and* disease dynamics, (2) allows removal, permanent sterilization, temporary contraception, and vaccination, (3) allows strategies to vary temporally, spatially, and demographically, (4) allows mixed strategies, (5) accommodates various levels of data availability, and (5) is flexible enough to allow parameterization and functional forms for a variety of wildlife species and diseases. The manuscript proceeds with a detailed description of the model and the rationale for its various mechanisms. This is followed by a case study in which we use the model to examine alternative strategies for managing rabies in a hypothetical free-ranging dog population. We close with a discussion of the various ways BioEcon can be used and the shortcomings that users should be aware of. The model is available for free download at www.BioEconModel.com.

**2. The Model**

***2.1. General Structure***

BioEcon is written in R (R Core Team 2014). R was chosen over other languages because its use by researchers is common and growing, it is free, and the code is relatively easy to read. There are several key characteristics of the model. First, the model tracks individual animals and their traits through time. This is performed via a population matrix that contains a row for each living individual and a column for each trait associated with individuals (Table 1). Second, the model operates on a daily time step. This minimizes bias that results from discrete time steps, and enables the model to more precisely consider management efforts that vary temporally. Finally, the model contains spatial structure that consists of a grid of locations. Nine locations are available, and these may be tailored to the specific application via different carrying capacities, management strategies, immigration parameters, and any number of other parameters that govern vital rates. By default the grid is arranged with location 1 in the upper left-hand corner and location 9 in the bottom right-hand corner.

|  |  |
| --- | --- |
| **Table 1 – Columns of the population matrix** | |
| **trait** | **notes** |
| ***individual traits*** | |
| id | a number assigned to each individual that exists in an iteration |
| location | indicates current location of the individual |
| group | indicates the group number that individual belongs to |
| female | 1=female |
| day age | days since birth |
| juvenile | 1=juvenile |
| mortality probability | - |
| mating probability | - |
| pregnant | 1=pregnant |
| time pregnant | days since becoming pregnant |
| exposed probability | probability of contracting disease and entering exposed class |
| passive immunity | 1=in passively immune class |
| natural immunity | 1=in naturally immune class |
| susceptible | 1=in susceptible class |
| exposed | 1=in exposed class |
| infected | 1=in infected class |
| recovered with immunity | 1=in recovered with immunity class |
| time with passive immunity | days since acquiring passive immunity |
| time in exposed class | days since entering exposed class |
| time in infected class | days since entering infected class |
| time with immunity after recovery | days since entering recover with immunity class |
| time limit passive immunity | days that will be spent in passive immunity class |
| time limit of exposed class | days that will be spent in exposed class |
| time limit of infected class | days that will be spent in infected class |
| time limit of immunity after recovery | days that will be spent in recover with immunity class |
| sterile from disease | 1=sterile from disease |
| trapped | 1=trapped on current day |
| trapping probability | - |
| time trapped | time previously trapped |
| euthanize probability | probability if captured |
| sterilize probability | probability if captured |
| contracept probability | probability if captured |
| vaccinate probability | probability if captured |
| sterile | 1=sterile |
| contracepted | 1=contracepted |
| vaccinated | 1=vaccinated |
| believed sterile | 1=manager assumes sterile if captured |
| believed contracepted | 1=manager assumes contracepted if captured |
| believed vaccinated | 1=manager assumes vaccinated if captured |
| time contracepted | days since contraception |
| time vaccinated | days since vaccination |
| ***group-linked traits*** | |
| adult females in group | count |
| adult males in group | count |
| fertile adult females in group | count |
| fertile adult males in group | count |
| infected in group | count |
| ***location-linked traits*** | |
| abundance at location | count |
| K at location | carrying capacity at the individual’s current location |
| density at location | abundance relative to carrying capacity at location |
| adult females at location | count |
| adult males at location | count |
| juvenile females at location | count |
| juvenile males at location | count |
| fertile adult females at location | count |
| fertile adult males at location | count |
| infected at location | count |
| susceptible at location | count |
| traps at location | count |
| ***seasonality-linked traits*** | |
| day of year | [1, 365]; same for all individuals |
| 12 binary columns indicating month | 1 for current month, 0 otherwise; same for all individuals |

There are three main sections of code: inputs, functions that correspond to major biological processes, and the iteration and time loops from which the various functions are called. The first section simply assigns values to the various inputs (Table 2) and can be tailored to the specific application. Biological processes executed in specific functions include mortality, mating, reproduction, dispersal, immigration, disease transmission, capture, and treatment (removal, permanent sterilization, temporary contraception, vaccination). The functions that execute the biological processes constitute the bulk of code and are discussed in detail in the next sections. The time loop exists within the iteration loop and loops through the days of the specified timeframe. Each day, it calls the functions that execute the various biological processes. These functions accept the population matrix as an argument, execute the process, and return the updated population matrix. The model was structured in this way so that it is simple to change process ordering without moving large blocks of code. Additionally, the structure makes it simple to modify or add processes without disrupting or altering other parts of the model. Finally, the iteration loop performs the specified number of iterations. Due to the stochastic nature of the model, a substantial number of iterations may be required in some applications to acquire a clear understanding of the distribution of results. Iterations are executed in parallel via the doParellel and foreach packages in R. The model should be executed on a multi-core machine so that parallel processing can be exploited.

***2.2. Mortality***

The mortality function requires two inputs. The first is a function that assigns a mortality probability to each individual on the current day. This function can be as simple as a constant, or it can use any of the columns of the population matrix as arguments. For example, density dependent mortality can be accommodated by allowing mortality probabilities to be a function of the ratio of abundance to carrying capacity at location. Sex and age-specific mortality can be accounted for by specifying a function that accepts the sex and age of the individual as arguments, and seasonal differences in mortality can be accounting for by including day of the year or the month indicators as arguments.

Mortality probabilities are updated daily. When the mortality function is called each day, a random number on [0, 1] is drawn for each individual and compared to the mortality probability. If the random draw is less than the mortality probability, the individual is removed from the population matrix. In addition to this mortality process, the population can be optionally censored to carrying capacity each day. This process occurs by randomly removing individuals from the population until carrying capacity is reached. Once these processes have been completed, the updated population matrix is returned to the time loop.

***2.3. Mating and Reproduction***

Mating and reproduction processes are executed by two separate functions. The mating function relies on mating probabilities returned from a specified function. Like the mortality probability function, the mating probability function can be as simple as a constant, or it can include many arguments. Note that mating probabilities of adult females are automatically considered zero if the individual is not fertile or there are no fertile males within the location. Random numbers on [0, 1] are drawn and compared to each fertile female’s probability of mating. If the draw is less than the probability, the female becomes pregnant.

New litters are created by the reproduction function. When a female has been pregnant for the specified gestation period, a litter size is selected based on a specified vector of probabilities. Each individual within the litter is randomly assigned a sex based on the specified fraction of offspring that are female. New individuals are added to the population matrix and the relevant columns filled (e.g. id, location, sex). The updated population matrix is then returned to the time loop.

***2.4. Dispersal***

Dispersal refers to an individual’s dispersal from their current group or juveniles’ dispersal from their mother. Juveniles automatically disperse at a specified age, while other dispersal may occur based on defined rules governing group demographics. A number of different rules are available. The model allows no group structure, female-only groups, or groups that contain both sexes. When specified limits on group demographics are reached, individuals are randomly selected for dispersal. When an individual is selected for dispersal, the individual disperses to a new group based on a specified objective. Three options are available: (1) minimize intra-group competition from the same sex, (2) maximize intra-group abundance of the opposite sex, and (3) minimize the number of adults in the group.

Dispersal operates sequentially but randomly. That is, each day all individuals are evaluated in random order to determine if dispersal is required. If an individual must disperse because it has reached the age of dispersal or its group demographics are not within limits, the individual disperses to a new group based on the specified objective, and all group statistics are updated before the next individual is evaluated. This sequential process ensures reasonable dispersal dynamics, but it also slows execution considerably. Once all individuals have been evaluated, the updated population matrix is returned to the time loop.

***2.5. Immigration***

Unlike dispersal, immigration occurs simultaneously each day based on probabilities returned from a specified function. Similar to mortality and mating probabilities, it is straightforward to let the immigration probabilities be a function of any number of individual, group, or location characteristics (e.g. abundance relative to carrying capacity at location). If a group structure is specified, immigration takes place at the group level (i.e. groups immigrate to new locations as a whole). Individuals or groups can move to new locations with several different specified objectives. Groups (or individuals in the case of no group structure) can move randomly to a new location or they may move by choosing a location with minimum abundance relative to carrying capacity. For solo males, there is an additional option of choosing a new location based on minimum abundance of solo males. Finally, the user may specify which movements are feasible within the grid structure. For example, it may be reasonable to limit daily movements to bordering cells.

Immigration is executed similar to other processes. A random number on [0, 1] is drawn for each group or individual and compared to the immigration probability. A new location is selected randomly from the subset of feasible location, or the new location is set based on the specified objective. Once new locations are determined, the population matrix is updated and returned to the time loop.

***2.6. Disease***

BioEcon allows the following disease states: susceptible, exposed, infected, recovered with immunity, born with passive immunity, and natural immunity. By default, individuals in the exposed state are not yet capable of transmitting the disease, but they will enter the infected class with certainty assuming they live long enough. The number of days spent in each disease state is specified, and states that are not relevant for a particular disease can be ignored by ignored by entering zero for time spent in the state. Three outcomes are possible after infection: return to susceptibility, recover with immunity, and death. These outcomes are governed by three specified probabilities. Thus, if the application examines a disease with a mortality rate of one, the probability of death after infection would be set at one.

BioEcon can be used to model population dynamics in the absence of disease. To remove disease processes from the model, the day the disease is introduced is simply set beyond the time frame of the simulation. This ensures that all individuals will always be in the susceptible state. When specified this way, all other disease-related inputs are ignored by the model. If disease dynamics are to be modeled, the day the disease will be introduced and the number of individuals that will initially be exposed must be specified. Alternatively, it is possible specify an exogenous probability of exposure and the day of the iteration that this probability becomes non-zero.

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| **Table 2 – List of user inputs** | | |
| **input** | **structure** | **notes** |
| ***initial conditions inputs*** | | |
| iterations | single integer | - |
| simulation end time | single integer; units=days | number of days that will be modelled |
| K | 9-element vector; units=individuals | elements correspond to locations |
| max age | single integer; units=days | set arbitrarily high if not wanted |
| max juvenile age | single integer; units=days | day age of sexual maturity |
| initial abundance | 9-element vector; units=individuals | elements correspond to locations |
| initial females | 9-element vector; units=individuals | same as above |
| initial groups | 9-element vector; units=individuals | elements correspond to locations; only relevant if groups structure is specified |
| ***mortality inputs*** | | |
| mortality probability | a function | function must return a vector of probabilities that correspond to each individual in the population; can be a constant or any function of any column(s) in the population matrix |
| hard limit at K | 0=no; 1=yes | if=1, population will be randomly censored at carrying capacity |
| ***mating and reproduction inputs*** | | |
| mating probability | a function | function must return a vector of probabilities that correspond to each individual in the population; can be constant or any function of any column(s) in the population matrix; any non-zero probabilities will be ignored except in the case of fertile, sexually mature females |
| gestation days | single integer; units=days | - |
| litter size probabilities | a 15-element vector | probabilities associated with litter size=1, 2,…, 15 |
| fraction female offspring | [0,1] | - |
| ***dispersal inputs*** | | |
| mutli-sex group structure | 0=no; 1=yes | if=1, then groups containing both sexes will form |
| female-only group structure | 0=no; 1=yes | if=1, then groups containing only females (and juvenile males) will form |
| max adults per group | single integer; units=individuals | individuals will disperse from group when this limit it reached |
| max adult males per group | single integer; units=individuals | individuals will disperse from group when this limit it reached |
| max adult females per group | single integer; units=individuals | individuals will disperse from group when this limit it reached |
| age male dispersal | single integer; units=days | juvenile males will leave mother or group at this age |
| age female dispersal | single integer; units=days | juvenile females will leave mother or group at this age |
| male dispersal goal | 1, 2, or 3 | disperse to new group based on this; 1=min inter-group same-sex competition, 1=max intra-group opposite sex abundance, 3=min number of adults in groups |
| female dispersal goal | 1, 2, or 3 | disperse to new group based on this; 1=min inter-group same-sex competition, 1=max intra-group opposite sex abundance, 3=min number of adults in groups |
| ***immigration inputs*** | | |
| immigration probability | function | function must return a vector of probabilities that correspond to each group (or individual if no groups) in the population; can be constant or any function of any column(s) in the group matrix |
| immigration goal for groups | 1 or 2 | immigrate to new location based on this; 1=random, 2=minimize abundance relative to K; also applies to individual in case of no groups |
| immigration goal for solo males | 1 or 2 | immigrate to new location based on this; 1=random, 2=minimize same sex competition |
| feasible movements | a 9x9 matrix of 0’s and 1’s | a 1 in cell *i*, *j* implies it is possible for an individual in location *i* to move to location *j*; default setting limit single day movement to bordering locations |
| ***disease inputs*** | | |
| probability natural immunity | 0=no; 1=yes | fraction of individuals in the population that are immune through unmodeled vaccination or by nature |
| day disease begins | single integer; unit=days | the disease will be introduced on this day |
| disease start location 1 | 0=no; 1=yes | if=1 disease is introduced only to location 1; otherwise it can be introduced in any location |
| constant disease threat | 0=no; 1=yes | if=1 individuals in outside cells are under constant threat of exposure; this option overrides previous option |
| exogenous exposure probability | [0, 1]; per year | this is the probability an individual in an outside cell is exposed assuming constant disease threat |
| initial diseased population | single integer; unit=individuals | this number of individuals will be randomly selected for exposure |
| mate while infected | 0=no; 1=yes | - |
| abortion if infected | 0=no; 1=yes | - |
| offspring infected if mother infected | 0=no; 1=yes | - |
| offspring immune if mother immune | 0=no; 1=yes | - |
| probability recovered=susceptible | [0, 1] | probability that an individual will return to the susceptible class after infection |
| probability recovered=immune | [0, 1] | probability that an individual will recover with immunity |
| probability recovered=dead | [0, 1] | probability of death after infection |
| time limit passive immunity | single integer; units=days | individual born with passive immunity will remain immune for this many days |
| time limit exposed | single integer; units=days | individuals will remain in the exposed class for this many days |
| time limit infected | single integer; units=days | individuals will be infected for this many days |
| time limit immune after recovered | single integer; units=days | individuals will remain immune after infection for this many days |
| ***trapping or capture inputs*** | | |
| trapping probability | a function | function must return a vector of probabilities that correspond to each individual in the population; can be constant or any function of any column(s) in the population matrix |
| trap numbers | a 9-column matrix | element *i*, *j* defines the number of traps set on day *i* and location *j*; alternatively measured in units of effort |
| trap cost | monetary units | cost per day per trap; alternatively cost per day per unit effort |
| ***policy or treatment inputs*** | | |
| contracepted marked | 0=no; 1=yes | if=1, previously contracepted individual can be identified as such |
| sterilized females marked | 0=no; 1=yes | if=1, previously sterilized individual can be identified as such |
| sterilized males marked | 0=no; 1=yes | same as above |
| vaccinated marked | 0=no; 1=yes | if=1, previously vaccinated individual can be identified as such |
| contraceptive assumed days effective | single integer; units=days | If captured again, animal will not be re-contracepted before this time |
| vaccine assumed days effective | single integer; units=days | If captured again, animal will not be re-vaccinated before this time |
| contraceptive decay | 20 element vector | probabilities that effectives is lost after years 1, 2,…, 20 |
| vaccine decay | 20 element vector | probabilities that effectives is lost after years 1, 2,…, 20 |
| juvenile male policy | 3-d array | fraction of captured animals that receive each treatment option; array has a row for each day, a column for each location, and a sheet for each treatment (sheet 1=euthanize, sheet2=sterilize, sheet3=contracept, sheet 4=vaccinate |
| juvenile female policy | 3-d array | same as above |
| adult male policy | 3-d array | same as above |
| adult female policy | 3-d array | same as above |
| vaccine override | 0=no; 1=yes | if=1, a captured animal that is recognized as effectively vaccinated will be euthanized if the policy at the time of capture call for euthanize; if=0, the same animal would be released without further treatment |
| euthanasia cost | monetary units | per animal; excludes capture cost |
| female sterilization cost | monetary units | per animal; excludes capture cost |
| male sterilization cost | monetary units | per animal; excludes capture cost |
| contraception cost | monetary units | per animal; excludes capture cost |
| vaccination cost | monetary units | per animal; excludes capture cost |

Disease transmission is governed by probabilities returned by a specified function. Thus, the model can easily be tailored to density-dependent transmission, frequency-dependent transmission, or more exotic forms of transmission. Each day, random numbers on [0, 1] are compared to transmission probabilities. Individuals that are exposed are moved into the exposed state and a timer is started. Additionally, each day all individuals in the exposed, infected, recovered with immunity, and passively immune states are evaluated. If an individual has been in a particular state for the specified maximum time, the individual transitions to the next state. For individuals moving out of the infected state, an additional random number draw determines their fate.

***2.7. Capture***

The number of units of effort (e.g. traps, labor hours) used each day at each location must be specified. An effort unit cost is also specified so that the total cost of capture effort on each day at each location can be calculated. Another specified function returns capture probabilities for each individual on each day. Typically, this function will take the units of effort at location as an argument so that the probability of being captured is zero if no effort is expended and the probability increases as effort increases. Other possible arguments include abundance at location, age, sex, and the number of times the animal has been trapped or captured previously. If a random number draw on [0, 1] is less than the individual’s probability of being trapped, the individual is marked as captured.

***2.8. Policy or Treatment***

Once an individual is marked as captured, a number of different policies or treatments are possible. The elements of an array define the fraction of captured animals that receive each treatment. The policy array has a row for each day of the iteration, a column for each location, and a sheet for each policy (i.e. removal, sterilization, contraception, and vaccination). A separate policy array must be specified for each of four classes of individual: juvenile female, juvenile male, adult female, and adult male. All elements of the first three sheets of these arrays must be on the [0, 1] interval and are interpreted by the model as the fraction of animals of that class captured on a particular day that receive a particular treatment. A given row and column of the array must sum to one across the first three sheets; otherwise the implication is that some animals receive both contraception and sterilization or receive fertility treatment at the time they are removed from the population. The fourth sheet of all arrays represents vaccination and is restricted to zero or one. If the element equals one, then all animals of that particular class and at that location that are captured on that day will be vaccinated if they are released (not removed). A zero implies they will be released without vaccination.

***2.9. Management Costs***

Two types of management costs are specified: the cost of a unit of effort (e.g. the per day cost associated with a single capture team) and the cost of each policy of treatment on a per animal basis. Sterilization and contraception costs are sex-specific, but removal and vaccination costs apply to both sexes. The model calculates total trapping costs each day based on the units of effort, and it calculates daily treatment costs separately for the four classes of individuals based on the number of individuals captured and the treatments they receive.

***2.10. Benefits***

Calculating the benefits of a management strategy requires two steps. We assume that benefits arise from a strategy through a reduction in some negative impact or an increase in some positive impact. Thus, the impact must be measured under some baseline scenario (e.g. no management or current strategy) and under the proposed strategy. To enable this, up to five ‘impact’ functions can be specified. These functions can accept any of the columns of the population matrix as arguments, and their output may represent an impact measured in monetary terms (e.g. crop damage) or a non-monetary impact (e.g. potential human exposures to a disease).

**3. Parameterization for Case Study**

***3.1. Case Study Overview***

The objective of this case study is not to provide a detailed examination of alternative strategies for managing rabies in a free-ranging dog population. Given the scope of this paper, it is not feasible to fully examine the multitude of strategic possibilities and alternative parameter values that exist. Rather, our intention is to illustrate 1) parameterization of the model, 2) a variety of results provided by the model, and 3) a functioning model that can serve as starting point for a more comprehensive assessment.

< insert more information here about the case study – i.e. background on the region, dog ownership, rabies prevalence, etc. >

***3.2. Population Model***

We assume each of the nine cells is 100 km2 and that carrying capacity is 10 dogs/km2 based on Hampson et al. 2007. Kitala et al. 2002, Hampson et al. 2007, and Hampson et al. 2009 assume free-ranging dog populations in sub-Saharan Africa grow according to

(1) .

The assumption of logistic growth can be decomposed into a density-independent recruitment rate and a density-dependent mortality rate as

(2)

where is the per capita recruitment rate, is per capita mortality rate at low densities, and . Following Kitala et al. 2002 and Hampson et al. 2007, we assume year-1 (note that these rates reflect changes in density rather than abundance). For use in BioEcon, the annual rate must be converted to daily probabilities. An annual per capita mortality rate of implies a daily mortality probability of

(3) .

Hampson et al. 2007 assumed an annual birth rate of 0.42. The yields an annual probability of . However, the model that relied on the rate of 0.42 year-1 did not distinguish between males and females or juveniles and adults. Thus, the expected number of births per day is simply . BioEcon requires a daily probability of successful mating for each adult female that is fertile. We assume a mean litter size of 4.7 and a disease-free population that is 40% female (Kitala et al. 2001), Furthermore, trial simulations imply that about 67% of the population is sexually mature. Then we can assign a daily probability for mating by writing

(4) ,

where 0.93 reflects the probability that a females survives the gestation period. Solving equation 4 yields a daily probability of successful mating by a sexually mature female of 0.00094.

Gestation duration is set at 63 days (Pal 2005), dispersal of puppies from mothers at 13 weeks (Pal 2005), and puberty at 10 months (Concannon 2011). Finally we assume that 40% of puppies are female (Kitala et al. 2001).[[1]](#footnote-1)

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| **Table 3 – Inputs and sources for the population model** | | | | |
|  | **BioEcon parameter** | **reported parameter** | | **source** |
| ***initial population and carrying capacity inputs*** | | | | |
| initial focal population | 600 dogs | - | | - |
| initial population in each of eight surrounding locations | 600 dogs | - | | - |
| K (rural) | - | 10 dogs km-2 | | Hampson et al. 2007 |
| K (focal 100 km2 location) | 1000 dogs | - | | - |
| K (per eight 100 km2 surrounding rural locations) | 1000 dogs | - | | - |
| ***mortality, mating, and reproduction inputs*** | | | | |
| annual per capita mortality rate | - |  | | Kitala et al. 2002 |
| daily mortality probability |  | - | | - |
| annual birth rate | - | 0.42 | |  |
| daily probability of becoming pregnant |  | - | | - |
| litter size | 4 (prob = 0.3), 5 (prob = 0.7) | 4.7 (mean) | | Kitala et al. 2001 |
| gestation duration | 63 days | 63 days | | Pal 2005 |
| proportion of puppies that are female | 0.40 | 0.40 | | Kitala et al. 2001 |
| age of puberty | 10 months | 6 – 14 months | | Concannon 2011 |
| ***dispersal and immigration inputs*** | | | | |
| group structure | none | - | - | |
| dispersal of puppies from mothers | 13 weeks | 13 weeks | Pal 2005 | |
| immigration probability | 0.5 year-1 | - | - | |
| immigration goal | random | - | - | |

***3.3. Disease Model***

We follow Coleman and Dye 1996, Kitali et al. 2002, Hampson et al. 2007, and Zinsstag et al. 2009 and assume density-dependent transmission of the form . Hampson et al. estimates a transmission coefficient of 13.2. This coefficient and the assumption of density-dependent transmission imply a daily probability of transmission of approximately

(6) .

Time spent in and are based on estimates by Hampson et al. 2007 and are set at 25 days and 6 days respectively.

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| --- | --- | --- | --- |
| **Table 4 – Inputs and sources for the disease model** | | | |
|  | **BioEcon parameter** | **reported parameter** | **source** |
| ***disease inputs*** |  |  |  |
| transmission coefficient | - | 13.2 km2/(dog·week) | Hampson et al. 2007 |
| daily exposure probability |  | - | - |
| time of exposed stage | 25 days | 25.5 days | Hampson et al. 2007 |
| time of infected stage | 6 days | 5.7 days | Hampson et al. 2007 |
| exogenous exposure probability | 0.01 | - | - |
| day disease threat begins | 1 | - | - |

***3.4. Management***

|  |  |  |  |
| --- | --- | --- | --- |
| **Table 5 - Management inputs and sources** | | | |
|  | **BioEcon parameter** | **reported parameter** | **source** |
| ***capture inputs*** |  |  |  |
| number of capture teams | ? | - | - |
| daily cost per capture team | ? | ? | ? |
| capture function | ? | ? | ? |
| ***policy or treatment inputs*** |  |  |  |
| juvenile female policy | various | - | - |
| juvenile male policy | various | - | - |
| adult female policy | various | - | - |
| adult male policy | various | - | - |
| vaccine effective time | 2.5 years | 2.5 years | Hampson et al. 2007 |
| contraception effective time | ? | ? | ? |
| euthanasia unit cost | ? | ? | ? |
| vaccination unit cost | ? | ? | ? |
| contraception unit cost | ? | ? | ? |
| female sterilization cost | ? | ? | ? |
| male sterilization cost | ? | ? | ? |

***3.5. Simulation***

**4. Results**

***4.1. Dynamics without Disease***

We begin by examining population dynamics without disease. To illustrate growth at different levels of abundance we allow the population to grow from an initial abundance of 100 to near carrying capacity (Figure 1). Results are based on a single iteration so that the amount of randomness in the dynamics is clearly shown.

**Figure 1 – Population growth from relatively low abundance over 50 years without disease**

**Figure 2 – Random immigration from location 1 to all other location over 50 years**

***4.2. Disease Dynamics without Management***

**Figure 3 – Disease spread starting with 10 infected individuals in location 1**

**Figure 4 – Dynamics under exogenous probability of exposure (0.05% annual probability)**

**Figure 5 – Dynamics under exogenous probability of exposure (1% annual probability)**

**Figure 6 – Dynamics under exogenous probability of exposure (2% annual probability)**

***4.3. Costs of Management and Resulting Dynamics***

**5. Discussion and Conclusion**

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1. The sex ratio of living dogs reported by Kitala et al. 2001 may not be representative of the sex ratio of living dogs at birth, but we assume 40% of births are female because we do not specify sex-specific mortality probabilities. Pal 2005 reports 37% of births are female, which lends further support to our assumption. [↑](#footnote-ref-1)