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Evaluating coyote management strategies using a spatially explicit, individual-based, socially structured population model

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ABSTRACT

Managing canid predation on livestock is the leading challenge facing canid conservation worldwide. However, removing canids, and coyotes in particular, to reduce livestock predation is environmentally and socially controversial. In addition, it can be expensive and logistically difficult to field evaluate the myriad of potential selective, spatial, and temporal canid management strategies. Here, we develop a spatially explicit, individual-based simulation model to evaluate commonly used or promoted coyote control strategies. We began with an already constructed non-spatial, individual-based stochastic coyote population model that incorporated behavioral features, such as dominance and territoriality. We added a spatial component and enhanced the social rule set to more realistically model coyote movement and territory replacement. This model merges coyote spatial, social, and population ecology into a management framework. The development, structure, and parameterization of this model are described in detail. For lethal methods, model results suggest that spatially intensive removals are more efficient and long lasting compared to random removal methods. However, sterilization appears to be the management strategy offering the largest and most lasting impact on coyote population dynamics. We recommend adding spatial prey/livestock density and environmental components to this model to further enhance its ecological reality and management usefulness. Although this model is applied to coyotes in particular, it is applicable to many canid species of conservation concern. This model provides a tool to assist in the development of more effective and socially acceptable livestock predation management strategies.

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1. Introduction

Managing canid predation on livestock is the leading challenge facing canid conservation worldwide. Coyote predation on livestock in general, and on domestic sheep in particular, has been a fundamental problem of livestock producers in North America over the past 60 years (Conover, 2002). It has been estimated that coyotes are responsible for over $40 million in damages to livestock producers in just the United States each year, with the proportionally highest losses to sheep pro-

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ducers (Mitchell et al., 2004). However, removing canids, and coyotes in particular, to reduce livestock predation is environmentally and socially controversial.

A variety of lethal and non-lethal methods are employed to reduce coyote depredation rates. Commonly used lethal methods include large-scale aerial gunning of coyotes, localized removal of all coyotes in the vicinity of an area or ranch experiencing coyote depredation, and removal of coyotes just prior to the birth pulse. A less commonly used lethal approach is selective removal of breeding adult (alpha) coyotes. Nonselective removal (e.g., aerial gunning) is based on the assumption that fewer coyotes means fewer livestock losses. Selective removal, which targets alpha coyotes, is based on the assumption that provisioning offsping is energetically costly, and one way to offset this cost is for alpha coyotes to prey on domestic livestock (Till and Knowlton, 1983). Accordingly, selective removal attempts to only remove the problem animals (alphas) in an effort to more efficiently reduce losses to livestock producers while simultaneously minimizing the impact to non-problem coyotes. Non-lethal control methods include guard animals, fencing, frightening devices, and husbandry practices (see Knowlton et al., 1999 for a thorough review). These approaches are preventative and usually focus on changing the behavior of potential problem animals rather than the manipulation of population numbers. Because we evaluate management strategies aimed at coyote populations in this paper, we restrict our analyses of non-lethal management types to the approach of sterilization (e.g., vasectomy and tubal ligation). Coyote sterilization is based on the same underlying premise as removal of alpha coyotes just prior to the birth pulse; coyotes are less likely to kill livestock if they do not need to provision for pups (Bromley and Gese, 2001). While coyote sterilization shows promise at reducing livestock depredation, it has not yet proven effective for long-term or large-scale use (Mitchell et al., 2004). Thus, for methods aimed at the coyote population, most livestock producers rely on lethal methods to reduce coyote depredation on sheep.

Coyote depredation management is controversial. Those involved in animal welfare question how well coyote removal works and whether landscape level measures, such as aerial gunning of coyotes, can be justified environmentally, economically or socially (Andelt, 1996). Mitchell et al. (2004) noted that lethal strategies may fail because alpha coyotes, which are the most likely social class to kill livestock, are the most resistant to nonselective removal techniques. Recently, there has been increased interest about selective removal, which focuses on small spatial areas, specific classes of animals (i.e., alphas), and limited timing of removal. The goal of this approach is minimize the number of coyotes removed while maximizing the reduction in depredation rates and length of the effect (Conover, 2002).

Coyote social structure and demographics have been well studied over a wide range of habitats throughout the United States and Canada. Coyote population vital rates, dynamics, and social structure vary with prey type and availability. Below we briefly discuss coyote biological and social relationships that are relevant to the construction of our model; for a thorough review of coyote biology, ecology, and management, see Knowlton et al. (1999).

Coyotes live in packs, are territorial, and have a strong social hierarchical structure in which typically only the alpha pair breeds for each pack (Camenzind, 1978; Gese et al., 1996b). Packs and territories have an exclusive relationship with one pack occupying and defending one territory (Camenzind, 1978; Bekoff and Wells, 1986; Windberg and Knowlton, 1988). Territories are typically contiguous (Windberg and Knowlton, 1988; Gese et al., 1989, 1996a,b), with each territory maintained by an alpha pair (Gese and Ruff, 1997, 1998). Packs usually also contain beta coyotes, which are typically related to the alpha pair, and pups. The larger population also contains transient coyotes (Camenzind, 1978; Bekoff and Wells, 1986) that occupy the interstitial area between several territories (Gese et al., 1988) and generally do not produce offspring (Knowlton et al., 1999). One of the biological mechanisms regulating coyote population growth rates is litter size, which decreases as population density increases (Todd et al., 1981; Todd and Keith, 1983). Two other social factors implicated in mediating population regulation are beta dispersal rates and transient mortality, which are interrelated. As population density increases, pack sizes reach a point where they no longer provide adequate resources for the entire pack. Consequently, the proportion of betas leaving territories to become transients increases (Gese et al., 1996b), which increases transient density. Increased transient density is thought to lead to increased transient mortality rates (Mills and Knowlton, 1991), which in turn decreases, and hence potentially regulates, population growth rates.

Virtually all decisions about predator management occur in the face of incomplete data, a complex, often spatially and socially structured environment, and in systems subject to temporal variation. It can be costly and difficult to evaluate the myriad of potential social, spatial, and temporal coyote removal strategies. When it comes to coyote depredation and sheep, the ultimate question is "Was the depredation rate reduced by the control strategy?" The penultimate question, which we address in this paper, is "Which strategy reduced the number of potential livestock killers for the longest time?" Modeling is a valuable heuristic tool to compare different removal strategies. For these reasons, we created a realistic, spatially explicit, individual-based, socially structured, stochastic coyote population model.

This model is a direct descendant of an individual-based stochastic coyote population model that incorporated social structure that was constructed by Pitt et al. (2003). We used parameter estimates and functional forms presented by Pitt et al. (2003) in their individual-based coyote population model, which were based mainly on estimates of coyote vital rates from the Rocky Mountain region of the United States. We consider this a 'generic population'. Pitt et al. (2003) used Swarm as their simulation environment (SDG, 2001) and modeled individuals within packs hierarchically. With relatively simple social and demographic rules, they realistically modeled the dynamics of a 100-pack coyote population. Pitt et al. (2003) adjusted model rules and calibrated parameter values so that their output matched field studies of coyote population dynamics and social structure, rather than doing a field validation. Pitt et al. (2003) model was non-spatial. However, the application of control is spatial; that is coyotes can be removed from spatially clustered locations (intensive removal over small areas) versus random removals (less intensive removal

over larger areas). Here, we began where Pitt et al. (2003) left off; we used the basic structure, rules, and model parameter values from their model, but made it spatially explicit and added additional movement rules. Then, we used this model to evaluate commonly used or promoted coyote control strategies on coyote population dynamics and social structure.

2. The model

In this paper, we follow a standard protocol for describing individual-based models (Grimm et al., 2006) because we agree that "readers are better able to absorb information if it is provided in a familiar, meaningful structure" (Gopen and Swan, 1990). The purpose of this protocol is to facilitate understanding and repeatability of individual-based simulation models written across a variety of disciplines (Grimm et al., 2006). We used the computer package IDL (Version 6.4, ITT Visual Information Solutions, Boulder Co.) to develop a stochastic, spatially explicit, socially structured (i.e., stage based), individual-based model.

2.1. *Purpose*

The overall goal of this model is to heuristically evaluate different spatially applied management actions, such as removing coyotes from spatially clustered locations versus random removals, on coyote population and social dynamics. From the wildlife-damage perspective, we hope this model will allow managers to find strategies that provide the results they require with the minimum number of coyotes removed.

2.2. *State variables and scales*

We used four hierarchical levels in the model: individual, territory (or pack), population, and management scenario. Individual coyotes were classified by the state variables: identity number, age, sex, identity of the territory where the individual lives, reproductive potential (sterile or fertile), and social status. We defined alphas as coyotes >6 months old who held a territory and reproduced. Betas were coyotes of >6 months old who were associated with a territory but did not reproduce. Transients were coyotes >6 months old who did not hold a territory and did not reproduce, and who moved among several territories. Pups were coyotes ≤6 months old and were associated with a territory. Herein, we consider pack and territory to be synonymous in this model. That is, one pack was exclusively associated with one territory, and all members of a particular pack were also members of the associated territory.

Each territory was initialized to contain one pair (male and female) of alpha coyotes and possibly betas and transients. The simulated population consisted of all packs/territories in the model. The spatial component was simulated using square grid cells, in which each cell represented a coyote territory. Because we did not use nearest neighbor statistics, movement paths per se, or connectivity, we used the more tractable square grids instead of hexagonal grids (Birch et al., 2007). Spatial structure was accounted for by associating each coyote with a territory, with their probability of moving to another territory dependent on the coyote's social status, age, pack density, and the conditions of neighboring territories (e.g., whether neighboring territories were missing one or both alphas).

2.3. *Process overview and scheduling*

We constructed the model to match the coyote biological year using discrete time intervals of 1 month; each simulation began in January. Within each month, modules are processed so that intra-territory changes are handled prior to inter-territory changes. Within each territory aging, birth (if April), mortality, change in social status (i.e., beta → alpha, beta → transient, and transient → alpha) were tracked. These actions were followed by movement actions between territories, which included betas and transients moving to new territories to become alphas, and transient simply moving between territories (Fig. 1).

2.4. *Design concepts*

2.4.1. *Emergence*

Spatial population dynamics emerge from the combined behavior of model agents (coyotes) as well as from different management perturbations. All management strategies are applied spatially (either spatially random or spatially clumped) in the form of either coyote removal or sterilization.

2.4.2. *Sensing*

Each coyote is assumed to know, without error, their age, sex, social rank, and associated territory. Furthermore, coyotes are assumed to be able to sample, without error, their neighboring territories for information such as the number of animals, and each animal's sex and social status.

2.4.3. *Functional relationships*

Within a pack, the number of offspring and probability of becoming a transient (eviction) increased with pack size. For the population, transient mortality increased with total transient density.

2.4.4. *Stochasticity*

All demographic parameters (i.e., vital rates) and social and movement rules were based on probability distributions. Stochasticity in model parameters represents demographic variation. That is, the parameters were fixed and the stochasticity is variation about the fixed parameters.

2.4.5. *Observation*

For model testing, the spatial distribution of individuals was observed process-by-process, and then summarized and output monthly. For model testing and evaluation of coyote removal strategies, population level and spatial (local) population variables were recorded during a 5-year pre-control, control, and post-control periods (for a total of 15 years).

2.5. *Initialization and input*

Because the model begins in January and coyotes are born in April, all individuals enter the population at 8, 20, 32, 44, etc. months. Alpha coyotes were required to be a minimum age of

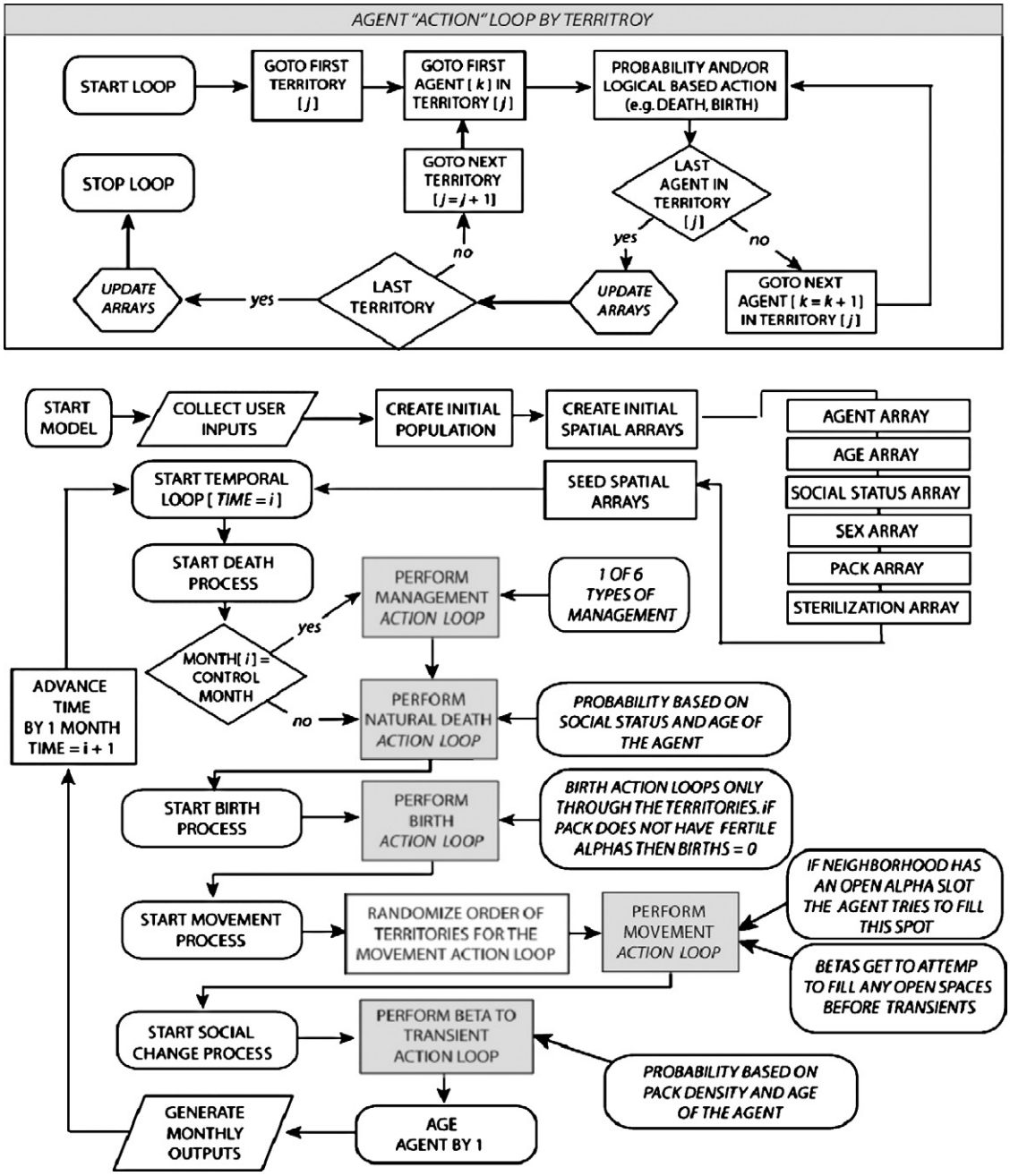

Fig. 1 – Flow diagram illustrating model processes and general scheduling of coyote population model. Initial spatial arrays are based on user inputs including number of territories, average pack size, age, sex, social status parameters, and management scenarios. Individual agents are coyotes. Packs and territories are synonymous. The box titled "agent "action" loop by territory" occurs within each shaded box in the model flowchart.

32 months to prevent an unrealistically young breeding population and a realistic age structure within packs (i.e., alphas older than betas). For this study, we used a 10 × 10 square grid to represent 100 coyote territories. Each grid cell is assumed to be the size of an average coyote home range. To mitigate edge effects on model output (i.e., animals can leave the study area but not come in), we buffered the number of territories in the simulated study area by 1 additional "ring" of territories. Thus, we tracked 144 territories (12 × 12 grid), but only summarized data on the inner 100. No control was done in the buffer.

The initial seeding parameters for the population of coyotes were the same for all model runs. Each territory was initially seeded with a pair of adult alphas, and possibly beta and transient coyotes. The maximum number of residents in initial packs was 5, and the mean number was 4. All coyote demographic and social parameters were common across all management scenarios (Table 1), but stochasticity was included to represent demographic variation. Using transient mortality as an example, an equation represents probability of transient mortality, which that is depen-

Table 1 – Overview of model input variables, parameters, functions, and stochastic processes

Parameter/variable description	Value/equation	Stochastic processes[a]
User input at simulation initialization		
Number of territories core output	100 (10 × 10)	
Number of territories including buffer	144 (12 × 12)	
Average resident pack size	4 (2 of which are always alphas)	Uniform[3,5]
Percent of population that is resident	0.75	
Sex ratio of betas	0.5	
Sex ratio of transients	0.5	
Min-max latency to fill alpha slot (months)	1–3	Uniform[1,3]
Vital rates		
Mortality probability for adults	$0.0100–0.0003A + 0.00025A^2$	Uniform[0,1]–if < equation, animal dies
Mortality probability for transients	$[0.008 + 0.089(N_{trans}/P)]–0.0003A + 0.00025A^2$	Uniform[0,1]–if < equation, animal dies
Mortality probability for pups	0.1	Uniform[0,1]–if < 0.1, animal dies
Birth rate	$6.93–0.72N_{pack}$	Normal[equation mean, 1]
Transition within territory		
Pup to beta	6 months	
Beta to transient	$0.005N_{pack}{}^2$	Uniform[0,1]–if < equation, animal dies
Beta to open alpha position	Betas get first chance before transients, depending on age and sex; see Section 2.6	Uniform[0,1]–if < 0.5, animal acquires territory
Transient to open alpha position	Transients get chance if position not filled by beta, depending on age and sex; see Section 2.6	Uniform[0,1]–if < 0.5, animal acquires territory
Transition and movement between territories		
Beta to open alpha position in different territory	Betas get first chance before transients, depending on location, age, and sex; see Section 2.6	Uniform[0,1]–if < 0.5, animal acquires territory
Transient to open alpha position in different territory	Transients get chance if position not filled by beta, depending on location, age, and sex; see Section 2.6	Uniform[0,1]–if < 0.5, animal acquires territory
Transient movement between territories	Randomly chosen transient can move within local neighborhood to territory with least transients; see Section 2.6	Uniform[0,1]–if < 0.5, transient moves

[a] The stochastic process adds demographic variation to the model. For example, the term 'Uniform[0,1]–if < equation animal dies' represents a Bernoulli trial; if the random number selected from the uniform distribution is less than the number produced by the equation, then the animal dies, otherwise it lives. If there is no distribution then the variable is not stochastic.

dent on number of transients per pack (transient density): $p_{tm} = [0.008 + 0.089(N_{trans}/P)] - 0.0003A + 0.00025A^2$, where p_{tm} is the probability of transient mortality. If a randomly selected number from a uniform distribution is less than p_{tm}, then the transient dies, which is represented as 'Uniform[0,1]–if < equation, animal dies' in Table 1. For all model parameters except birth, which is describe below, we used the Bernoulli random variables (i.e., Uniform[0,1]) as indicator variables to determine whether a coyote transitions during a particular time step, which is a month in the model (Table 1).

2.6. *Submodels*

2.6.1. *Mortality*

We do not describe the logic behind the functions used for demographic and social probabilities and rates in this paper because they were described in detail by Pitt et al. (2003). Stochasticity in mortality probabilities was added as demographic variation via Bernoulli trials (Table 1). The probability of alpha and beta mortality per month was a quadratic function of a coyote's age:

$$m_{ad} = 0.01 - 0.0003A + 0.00025A^2$$

where A is age in years.

To prevent the immediate replacement of an alpha after its death, we included a latency period in the replacement matrix for both alpha males and females. This latency period reflects the time needed to either find a replacement mate when a single alpha dies or the competition between individuals when a territory breakdown occurs (i.e., both alphas die and betas fail to take over territory). Thus, a latency period was randomly selected between 1 and 3 months based on a field study of alpha replacement (Blejwas et al., 2002). Each month the latency period was counted down until it equaled 0 and the open alpha position could be filled. In addition to being more biologically realistic, including a latency period also more realistically allows control that takes place during the mating season, a common depredation management strategy, to have an effect during the whelping period.

The probability of transient mortality followed the same function as resident adults, but was additively higher, depending on the average transient density per pack over the simulated population:

$$m_{trans} = \left[0.008 + 0.089\left(\frac{N_{trans}}{P}\right)\right] - 0.0003A + 0.00025A^2$$

where N_{trans} is total number of transients in the population, P is the total number of packs in the population, and A is the

age in years. The probability of pup mortality was constant:

$$m_{pup} = 0.10$$

2.6.2. Birth

The number of offspring produced by a given pack was a linear function of pack size:

$$b = 6.93 - 0.72N_{pack}$$

where N_{pack} was number of adults in the pack. Stochasticity in the number of offspring produced was added differently than for other vital rates. We used a normal distribution in which the final number of offspring produced was drawn from a normal distribution, with a mean (b) from the equation above and a standard deviation of 1.0, that is, $\sim N(b,1)$. We rounded the number of offspring so that only whole numbers were used in the model, and truncated so that any negative values were set equal to zero.

2.6.3. Dispersal

We did not include long-distance dispersal explicitly. Rather, we allowed betas to transition to transients (ejection) and transients to move among a neighborhood of territories at each time step as described below. This way, a transient could make its way around all territories in a population, which is a form of quasi-dispersal restricted to staying within the simulated area. The absence of long-distance dispersal is meant to emulate the observed dynamics of coyote social structure in which alpha individuals do not leave their territories once they become "owners" and by which open territories are taken by coyotes in neighboring territories.

2.6.4. Stage (social status) changes

There were four stage transition probabilities in the model. Alphas could not change stage, but could be replaced by a beta or transient of the same sex when they died. Thus, the 4 transition probabilities were pup to beta, beta to alpha, transient to alpha, and beta to transient. There were 2 levels of stage changes; within and between territories. Within territory changes occurred before changes that involved movement (i.e., before between territory changes).

2.6.5. Alpha replacement from within territory

When there was an open alpha position, animals of the appropriate sex associated with the territory filled it in the order of oldest to youngest beta, followed by oldest to youngest transient associated with the territory at that time step. Each individual at its turn had a probability of 0.5 of filling the open alpha position.

2.6.6. Alpha replacement from outside its territory and canonical movement

These transitions included a probability of movement between territories. We used a random order to move through all territories for each time step in the simulation to prevent particular territories from always having first access to open positions. We chose to model movement as movements "out" of a territory, which we refer to as the focal territory, and into an adjacent territory. We used a Moore neighborhood (i.e., 8 neighbors), which we refer to as the focal neighborhood, for all local movement rules.

For each randomly chosen focal territory, the focal neighborhood was checked for any open alpha positions that were not filled by coyotes associated with the focal territory. If there was no open alpha position, or if open alpha positions had an associated latency value > 0, then there was no social status change or movement. However, if there was an open alpha position and a latency value of zero in the focal neighborhood, then the opportunity to fill this position by animals in the focal neighborhood was in the order of oldest to youngest beta, followed by oldest to youngest transient. Each individual at its turn had a probability of 0.5 of filling the open alpha position.

2.6.7. Transition of beta to transient (eviction)

The probability of betas being forced out of their territory, and thus transitioning to transient status, was dependent on adult (alphas and betas) pack density in the focal territory (N^2_{pack}):

$$t_{evict} = 0.005N^2_{pack}$$

Although betas transition to transient status, movement from their natal territory was handled in a separate step (see transient movement below).

2.6.8. Transient movement without social change

For each focal territory we randomly ordered the associated transients to determine the order for movement processing. Once ordered, for each transient animal, we queried the focal neighborhood for the number of transients. The first randomly chosen transient moved to the territory (cell) with the least number of transients. If there were >1 territories tied for lowest numbers of transients, then the transient was randomly assigned to one of the tied territories. Each transient made ≤1 move per time step. We repeated this process for transients in the neighborhood according to their randomly assigned order. Transient movement occurred regardless of whether there was an open alpha position in the neighborhood. Transient coyotes had a probability of 0.5 of moving from one territory to a neighboring territory during a given time step.

3. Simulation experiments

This study evaluated the response of spatial coyote population dynamics to 6 different coyote control strategies. We ran the model for 5 years pre-control, 5 years of control, and 5 years post-control. We used a 5-year window because wildlife management plans and agency management plans often operate on a 5-year time frame. In addition, 5 years was long enough for model properties to emerge. We ran 100 simulations of each strategy.

3.1. Management control strategies (input scenarios)

All management control strategies except no control and sterilization were removals, which emulate lethal methods.

1. No control.

2. Spatially random (nonselective): We removed 50% of the pre-control population randomly across space over a 5-month period (February–June). The total number of animals removed was divided evenly across the 5 months. This represents an area wide nonselective control technique such as aerial gunning, trapping/snaring, or randomly distributed M-44 cyanide devices.
3. Selective spatially random: We removed 50% of the pre-control alpha coyotes randomly across space over a 5-month period. The total number of alphas removed was divided evenly across the 5 months. This represents area wide selective lethal control such as livestock protection collars, calling and shooting, and "denning" (i.e., a control method whereby coyotes are called and shot during the period when they have pups) strategies.
4. Sterilization spatially random: We sterilized 50% of the pre-control population randomly across space over a 5-month period. The total number of animals sterilized was divided evenly across the 5 months. Because operational examples of sterilization do not exist, we followed the experimental protocol of sterilizing all animals regardless of sex and social status (Bromley and Gese, 2001). Sterilization is assumed to only directly impact reproduction (i.e., not territoriality, mortality, dispersal, etc.).
5. Spatially clumped (nonselective): We removed 50% of the pre-control population from a spatially clustered area. We divided the spatial grid into quadrants and randomly placed the "control cluster" into one of the randomly selected quadrants to prevent the grid being in the same place each simulation. This control cluster consisted of a contiguous block of 50% of the territories in the population. That is, all removals were from a cluster comprised of 50% of the territories. The total number of animals removed was divided evenly across the 5 months. Stochastic behavior of the model may result in the "control cluster" containing slightly less than 50% of the population. In cases where this occurred, 50% of the pre-control population could not be removed and all animals in the "control area" were eradicated. This represents more intense nonselective control methods intended to eradicate all coyotes from a particular area.
6. Selective spatially clumped: We removed 50% of the pre-control alpha coyotes from a spatially clustered area. We divided the spatial grid into quadrants and randomly placed the "control cluster" into one of the randomly selected quadrants to prevent the grid being in the same place each simulation. This control cluster consisted of a contiguous block of 50% of the territories in the population. That is, all removals were from a cluster comprised of 50% of the territories. The total number of alpha coyotes removed was divided evenly across the 5 months. This represents intense selective control methods such as calling and shooting and denning that are intended to eradicate all alpha coyotes from an area.
7. Sterilization spatially clumped: We sterilized 50% of the pre-control population from a spatially clustered area. We divided the spatial grid into quadrants and randomly placed the "control cluster" into one of the randomly selected quadrants to prevent the grid being in the same place each simulation. This control cluster consisted of a contiguous block of 50% of the territories in the population. That is, all removals were from a cluster comprised of 50% of the territories. Because operational examples of sterilization do not exist, we followed the experimental protocol of sterilizing all animals regardless of sex and social status (Bromley and Gese, 2001). Sterilization is assumed to only directly impact reproduction (i.e., not territoriality, mortality, dispersal, etc.). Similar to the spatial lethal control, stochastic behavior of the model may result in the "control cluster" containing slightly less than 50% of the population. In cases where this occurred, complete sterilization occurred inside the control cluster area.

3.2. *Outputs*

We wanted to provide a useful "fingerprint" (Grimm and Railsback, 2005) of coyote population dynamics that summarized data by territory and for the whole population. For territory statistics, we reported the mean of pack size, number of alphas per territory, and number of transients per territory summarized by month and year. We primarily reported results output from December following Pitt et al. (2003). December was chosen as a month that represented the population without the fluctuation caused by pups because pups were already graduated to adults (i.e., recruited into the population).

For the whole population (i.e., all territories summed), we reported total population size and percent alphas and transients. We also reported population recovery time, which we defined as the point when the coyote population size rose to $\geq$90% of the maximum population size in the pre-control period, based on December population sizes. To evaluate management effectiveness, we calculated the average outputs across the 5 years of pre-control, control, and post-control time periods, which were then averaged across the realizations of the 100 simulations.

It is redundant to calculate mean pack size, which could be estimated from total population size and number of packs, which was always 100. However, were interested in the spatial variation in pack size for the random versus clumped control strategies. We did not present litter size because it is somewhat misleading during control. That is, average litter size appears to increase partly due to a reduction in density, but partly as an artifact of reducing the denominator during control in the equation (average litter size = number of pups/number of coyotes).

3.3. *Simulation results*

Because our spatial model was based on Pitt et al. (2003) model, we compared our outputs, for the no control scenario, to ensure our spatial base model was equivalent with their field-result matched non-spatial model. Our model outputs matched those of Pitt et al. (2003); specifically, we had similar mean pack size (4.0), proportion transients (0.27), litter size (4.4), and proportion of females breeding (0.43).

For the no control scenario, and during pre-control for all scenarios, the monthly mean pack size fluctuated widely within a year due to the birth of pups in April and their subsequent high mortality rate (Fig. 2). However, when any single

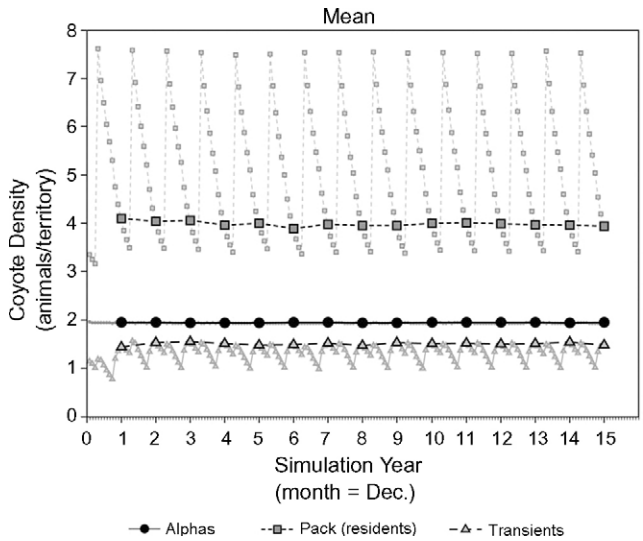

Fig. 2 – Comparison of mean monthly outputs to mean yearly outputs from December for the non-control scenario. Means were calculated for 100 core territories in a 10 × 10 grid, and averaged across 100 simulations.

month is compared from year-to-year, mean pack size (and hence total population size), as well as the mean number of each social class per territory, was stable (Figs. 2 and 3).

All control strategies resulted in a reduction in coyote density during the control period (Fig. 3). For lethal removals (not sterilization), spatially clumped strategies resulted in greater reductions in coyote density relative to randomly applied strategies, but selective removals performed similarly to their nonselective counterparts (Fig. 3). For all lethal strategies, reductions in coyote density were temporary with coyote population responding to pre-control levels during the post-control period (Fig. 3). In contrast, sterilization resulted in the lasting reductions that lasted throughout the post-control period; that is the coyote population did not rebound during the 5-year post-control period (Fig. 3). In contrast to lethal removal, random sterilization preformed better than spatially clumped sterilization. Random sterilization resulted in the largest reduction in coyote numbers and the longest effect (Fig. 3).

We used averages across the 5-year windows and recovery times to quantify differences between control strategies. During the control period, spatially clumped lethal control was more efficient than its random counterpart, as the mean number of coyotes removed was 21–33% less (Table 2), while delivering somewhat better results. That is, spatially clumped lethal strategies had recovery times that were 1.5–2.6 years longer and reduced the total population size 5–16% lower during the control period than their random counterparts (Tables 2 and 3). In addition, spatially clumped lethal strategies reduced the number of alphas (calculated as total population size × percent alphas) by 28–39% more during the control period, compared to their analogous random strategies (Table 2).

There was little difference in coyote population results between the nonselective and selective strategies (Tables 2 and 3). During the control period, the total population size was larger for selective lethal control, but the number of alphas was lower compared to its random counterpart (Tables 2 and 3). However, removal of alphas was more efficient; for similar effects on coyote population outputs, the number of coyotes removed was 10–25% less for selective strategies compared to their random counterparts.

Sterilization strategies had comparable results to lethal strategies during the control period, but had the largest impact on coyote population numbers post-control (Table 2). The recovery time for random sterilization was >5 years (end of simulation time frame), which was >4 years longer than its random lethal counterpart (Table 3), and total population size was 79% less in the post-control period (Table 2). Most importantly, only sterilization strategies had a lasting effect to year 15 (Table 3). For the random sterilization scenario, both total population size and percent (and hence number) of alphas were still dramatically reduced (84 and 63%, respectively) 5 years after the end of the control period (Table 3). This was in contrast to all other lethal scenarios that showed no effect (≤3% reduction) by year 15 (Table 3). In contrast to lethal removals, spatially clumped sterilization did not perform as well as spatially random sterilization. The total population size was reduced by 18%, which was greater than any lethal strategy, but substantially less than the reduction for random sterilization (Table 3). Moreover, similar to lethal strategies, there was no decrease in the percentage of alphas in the 5 years after the end of the control period (Table 3).

4. Discussion

Recent coyote depredation models have become more complex as the understanding of the coyote biological, ecological, and social systems has matured and computing speed has increased. Originally, simple analytic and stochastic population models were used to illuminate coyote dynamics and evaluate management strategies (Connolly and Longhurst, 1975; Windberg and Knowlton, 1988; Stoddart et al., 2001). More recently (Pitt et al., 2003), constructed an individual-based stochastic coyote population model that incorporated social structure via pack rules. Although not externally validated, the good match of that model with field results indicate that the model is viable for addressing management actions (Grimm and Railsback, 2005). Because our model outputs matched those of Pitt et al. (2003), we conclude that it too is useful for addressing management actions.

4.1. *Simulation results: management scenarios*

There are three main coyote control comparisons illuminated by the simulation output: random versus spatially clumped strategies, nonselective versus selective strategies, and lethal versus contraceptive strategies. We begin by comparing random to spatially clumped strategies.

Model results suggest that the spatial strategy of intensively removing coyotes from a reduced area is more efficient than random removal and produces better results, especially considering that it resulted in a greater reduction in the number of alphas, the putative primary livestock killers. In

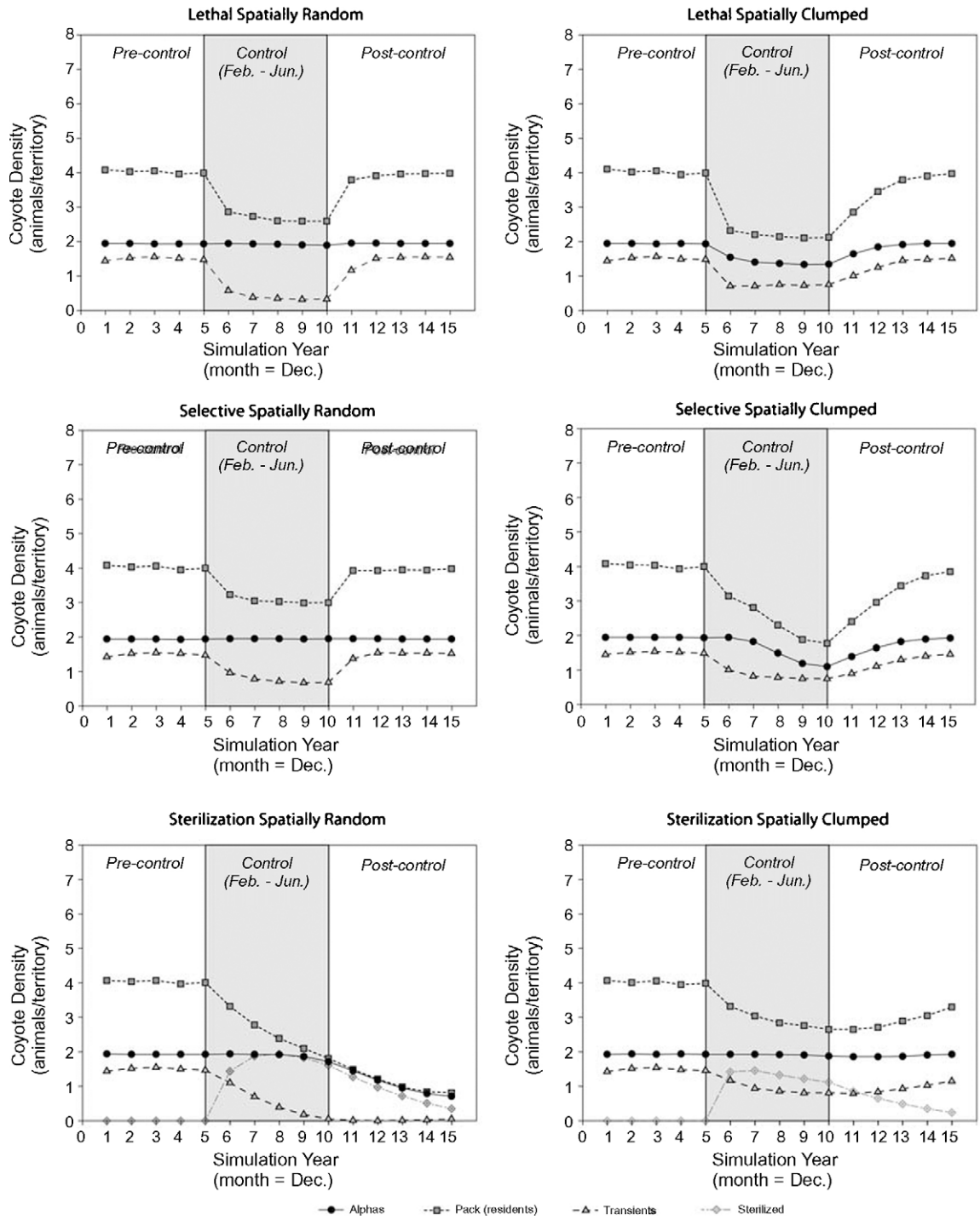

Fig. 3 – Territory means from December of each year for coyote management scenarios. Means were calculated for 100 core territories in a 10 × 10 grid, and averaged across 100 simulations.

addition, the reduction in coyote numbers lasted longer, which is important to reducing control cost. These results were somewhat unexpected; consequently, we took a closer look at our results to understand why spatially clumped lethal control had more dramatic effects. The relatively more intensive, spatially clumped removal resulted in more pack sizes near 0 during the control period (Fig. 4 top, points B and C) compared to random removal (Fig. 4 bottom, points B and C). More packs with sizes near 0 resulted in more packs without alphas, which explained the effect on alphas. Because of the movement rules, the territories, especially those near the control corner, took longer to fill for spatially clumped removal (Fig. 4 top, between points C and D on graph) than for random removal (Fig. 4 bottom, between points C and D on graph). This temporal effect is likely due to our movement rules which do not allow instantaneous movement into non-neighborhood

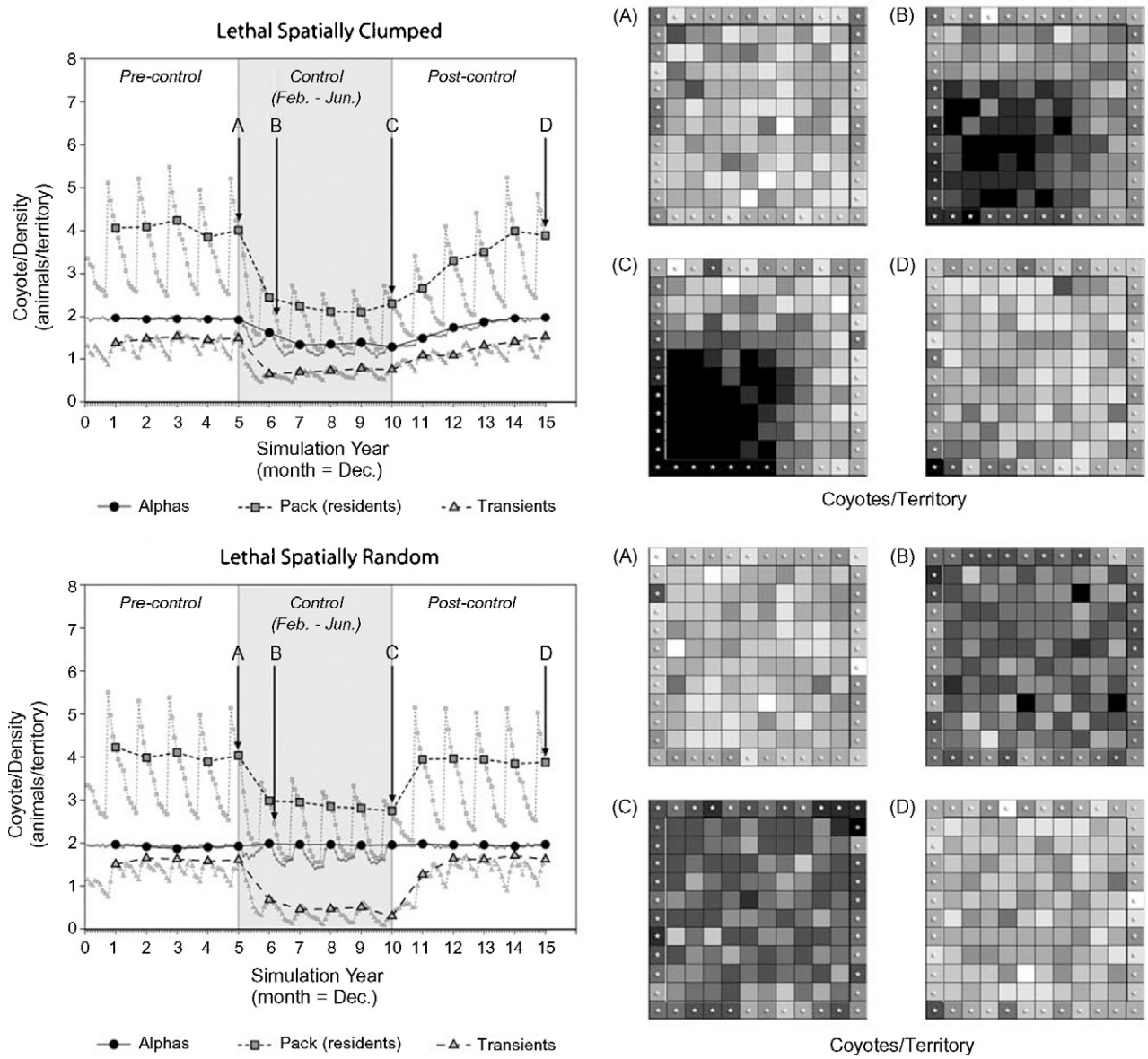

Fig. 4 – Spatial and temporal depiction of coyote management effects for lethal spatially clumped and lethal random control. Output at (A) is for December just prior to the start of control, (B) is for the second year of control in the month before births (i.e., 14 months after start of first control event), (C) is for December in the last year of control, and (D) is for the last December of the simulation. Black squares represent 0 coyotes/territory and white represent 8 coyotes/territory, with >0 and <8 coyotes/territory classified into 6 bins and shown as graduations of gray. Buffer territories are shown with a dot, along the periphery of the 100 core territories.

territories; that is, it takes a couple time steps or more before a transient coyote can move to an open territory that is not in its direct neighborhood.

These results are generally concordant with Windberg and Knowlton's (1988) simulation model. Based on their model results, Windberg and Knowlton (1988) concluded that removal from a specific area would influence coyote abundance over a much larger area. However, they still promoted applying removal efforts over a broader area based on the assumption that transient animals almost immediately occupy vacant territories, which results in small scale removals being effective for only short time periods (Windberg and Knowlton, 1988). Future simulations could evaluate the length of time to recovery for various sizes of spatially clumped removal strategies to more thoroughly evaluate the relative effectiveness of spatially clumped strategies and timing of the filling of distant open territories.

In contrast to lethal methods, spatially clumped sterilization was not as effective as random sterilization. For sterilization to work, only 1 of the alpha pair needs to be sterilized. Because spatially clumped sterilization concentrated the number sterilized into a focused area, both alphas were sterilized most of the time. Consequently, random sterilization, which spread the impact of control over the entire area, left

Table 2 – Average number of coyotes treated (i.e., removed or sterilized) and annual coyote population values

Control scenario	Total treated	Pre-control period			Control period			Post-control period		
		Tot. pop.	Alpha (%)	Transient (%)	Tot. pop.	Alpha (%)	Transient (%)	Tot. pop.	Alpha (%)	Transient (%)
No control	0	553	35	27	546	36	28	549	36	28
Spatially random (nonselective)	869	553	35	27	307	63	13	539	36	27
Selective spatially random	772	554	35	27	384	51	20	547	36	28
Sterilization spatially random	889/473	555	35	27	298	69	14	111	93	2
Spatially clumped (nonselective)	691	553	35	27	291	48	25	494	38	27
Selective spatially clumped	514	553	35	27	321	37	26	452	39	27
Sterilization spatially clumped	1044/395	552	35	27	386	50	24	389	49	25

Pre-treatment period was years 1–5, control period was years 6–10, and post-control period was years 11–15. Total treated was the sum of coyotes treated for all 5-control years. All values are means across the 5-year periods for December of each year, calculated from totals across 100 core territories, which were then averaged across 100 simulations. The two numbers for sterilization scenarios show first the number of attempts and second the number actually sterilized. Because choice of coyote for treatment was random, some coyotes captured were already sterilized.

Table 3 – Long-term effects of control strategies (control was enacted for 5 years; year 6–10) on coyote population numbers

Control scenario	Recovery time		Year 5			Year 15			Difference (Years 15 to 5)		
	Mean (month)	Std	Total pop.	Total alpha	Total transient	Total pop.	Total alpha	Total transient	Total pop. % change	Total alpha % change	Total trans. % change
No control	0	0	548	194	148	542	195	148	−1.1	0.5	0.0
Spatially random (nonselective)	9	6	547	194	147	552	195	154	0.9	0.5	4.8
Selective spatially random	3	5	549	195	148	551	195	153	0.4	0.0	3.4
Sterilization spatially random	>60	0	550	194	148	87	72	6	−84.2	−62.9	−95.9
Spatially clumped (nonselective)	27	8	549	194	148	549	195	151	0.0	0.5	2.0
Selective spatially clumped	34	16	549	194	149	532	193	146	−3.1	−0.5	−2.0
Sterilization spatially clumped	>60	0	546	194	147	447	194	116	−18.1	0.0	−21.1

Recovery time is defined as the return to 90% of the maximum of pre-treatment total population size. Totals were across 100 core territories, which were averaged across 100 simulations.

more "non-breeding" territories because at least 1 of the alpha pair was sterilized. Clumped sterilization had less impact simply because fewer territories were "non-breeding".

In general, there was little difference on coyote population dynamics between the effects of nonselectively removing coyotes or selectively removing alpha coyotes. The theory behind selective removal is based on coyote social behavior. First, research has confirmed that not all coyotes with access to livestock kill livestock (Conner, 1995); most depredations can be attributed to territorial, dominant coyotes (Till and Knowlton, 1983; Sacks et al., 1999). Second, selective removal of suspected livestock killers has been found to be more efficient at reducing lamb predation rates than nonselective removals (Blejwas et al., 2002). Thus, although there may be minimal differences between nonselective and selective removals on coyote population outputs, targeting alphas may be more effective at reducing livestock depredations, an output not included in our model. Finally, because selective removal of alphas was more efficient, in that it required fewer animals killed compared to their random counterparts, it may have less ecological impacts and be more socially acceptable. We caution that, at present, the logistical difficulty and expense of identifying alpha coyotes to target for removal may outweigh ecological and social factors.

Our simulation model highlighted the large impact fertility control could have on population dynamics. In all metrics, sterilization had the greatest impact of any management scenario we evaluated, especially in the post-control period. However, coyote sterilization has not been widely used to reduce livestock depredation, due to cost and difficulty of application (Bromley and Gese, 2001), although several studies have indicated it may be a highly effective strategy. For example, Till and Knowlton (1983) found removal of pups stopped depredation on lambs, the main component of livestock loss. Based on this finding, they hypothesized that sterilizing alpha coyotes in the vicinity of depredation areas would be highly effective because, in addition to abstaining from lamb killing, sterilized coyotes may exclude other coyotes from killing in their territories and could have a multi-year effect. Another computer model on canids has also illustrated dramatic population declines with periodic (every 5 years), but not intensive (20% population treated) fertility control for wolves (Haight and Mech, 1997). In one of the few field studies on fertility control, Bromley and Gese (2001) found a dramatic 91% reduction in the lamb kill rate between packs that had been sterilized and control packs of intact coyotes, and this effect lasted through the following year (80% reduction). Bromley and Gese (2001) concluded that coyotes changed their predatory behavior when pups were present, by increasing predation on lambs, a non-native prey. From a management standpoint, our simulations suggest sterilization can have a lasting effect on coyote population and social dynamics. When considered in light of the Bromley and Gese (2001) and if we assume that sterilization only impacts reproduction (i.e., territoriality does not breakdown), which has not been shown over the time scale of our modeling exercise, we conclude sterilization could be an effective method for reducing livestock depredation.

Based on our simulations, sterilization appears the management strategy offering the largest and most lasting impact on coyote population dynamics. If it is true that more coyotes lead to more depredations, sterilization is most effective coyote management strategy. However, the cost issues associated with coyote sterilization, given, at present, coyotes need to be captured and surgically sterilized, may be prohibitive. In general, fertility control will not be an option until inexpensive and coyote-specific delivery methods become available. And, contraception or sterilization, delivered inexpensively through baits or vectors is in its infancy as a technology (Barlow, 2000). Thus, for the present, lethal control will predominate. Within the realm of lethal removal, simulation results suggest a spatial strategy of intensively removing coyotes from a reduced area requires fewer removals and produces a larger impact than random removal over a larger area. Most importantly, the spatial strategy reduced a greater number of alphas, the putative primary livestock killers compared to the random strategy. Therefore we conclude that sterilization, when it becomes practical, will be the most efficient coyote management strategy for reducing coyote population numbers. But, until sterilization becomes practical, we recommend the strategy of spatially clustered removal of coyotes in small areas, particularly in the areas where depredation occurs.

4.2. *Model behavior*

There were a couple unexpected results associated with having a buffer in the model. For example, new transients from the buffer territories occasionally moved into the 100-territory core study population via the movement rules. Also, some coyotes were "lost" from the core study area and then later "reappeared" from the buffer area. This is unlike most models in which animals are lost through dispersal, or are reflected back into the simulation area at the boundary. The buffer was logistically easy to incorporate and seems a realistic feature of spatial models that should be included. However, the downside is that it takes geometrically more time to run a simulation for each ring of territories added. For relative comparison, the lethal random scenario on our system took 13 min to run 1 simulation (180 time steps) for 100 (core) territories and 43 min (3.3× longer) for 144 (core plus buffer) territories. The jump in time mostly reflects the number of spatial queries (e.g., assessing the focal neighborhood) and array updates required for each individual and/or territory.

5. Conclusions

Because modeling is constrained by complexity limitations, "the essence of successful modeling is valid simplification" or reducing the complexity of the system while still ensuring the model is valid within its objectives (Aumann, 2007). Adding a spatial component to an already constructed socially structured population model added a layer that allowed realistic evaluation of typical coyote management strategies. Namely, we could compare, given similar numbers of coyotes removed, the spatial strategy of intensive removal over a small area with random removal over a large area. Similar simulation studies have found space a necessary component of their models. For example, spatially explicit models have been used to describe the spread of scabies through a coyote population (Leung and

Grenfell, 2003) and to evaluate different aphid control strategies (Parry et al., 2006). In addition, the spatial component will facilitate additions of future spatial components such as landscape factors or livestock and prey density. In particular, a spatial component paves the way for comparison of different livestock management techniques (e.g., rotated grazing regimes versus stationary grazing regimes, different densities, etc.) on coyote predation rates. The addition of space, in general, greatly increases the ability to evaluate typically used coyote and livestock management strategies.

On the down side, the improvement in model realism added many layers of rules, some of which would be difficult to test empirically. Much of the complexity in our model came from movement rules. In particular, the rules describing alpha replacement, especially in distant neighborhoods, are a good example of the model's additional complexity beyond its non-spatial progenitor (Pitt et al., 2003). Moreover, because we have worked on field studies of coyotes that included trapping and radio- or GPS-collaring, we understand the expense and difficulty acquiring empirical data for validation of movement rules. That is, it would take years of daily observations on perhaps 40–60 animals, coupled with frequently recorded location data (e.g., from GPS collars), to determine the age and status of every coyote in a neighborhood of territories, as well as determining who, how, and when open alpha positions are filled.

We view this model as a starting point, like Pitt et al. (2003) model was for this model, to which prey and/or livestock, environmental, and economic components could be added as one step in the continuing evaluation and development of useful coyote strategies. In addition, there are many other coyote management strategies that could be evaluated using this model to identify further efficiencies. For example, future work could evaluate effects of reducing the length of the removal period, shifting the removal period, and reducing the area of spatially clumped control strategies. We hope this model will assist in the development of management strategies that minimize the number of coyotes removed while maximizing the reduction in depredation rates and length of the effect.

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