An individual-based model of canid populations: modelling territoriality and social structure

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Abstract

The management of canid populations has been at the forefront of wildlife management worldwide for much of the last century. Effective management depends on the ability to integrate species biology, the environmental aspects upon which those populations depend, and the factors controlling species abundance. Further, managing canid populations requires consideration of territoriality and dominance, which may have a significant effect on population dynamics. To better understand the effect of social structure on canid populations, we developed an individual-based computer model using Swarm to mimic natural coyote population dynamics. We selected the Swarm simulation environment because it is ideally suited for creating a system of multiple interacting agents with variable schedules and hierarchies. Swarm was a software platform that allows the user to describe generic individuals and behaviours, link those behaviours in each concurrent time step, and assemble behaviours and objects in a hierarchical framework. This model stands apart from previous modelling efforts because it explicitly incorporates behavioral features, such as dominance and territoriality, as major determinates of species demography into a simple model. Individual variation, such as status within territorial social groups and age-based reproduction are incorporated, but assumptions typically associated with most demographic models are not needed. The simple population model with few parameters not only closely resembled 'real world' populations but also helped us understand population dynamics that emerged from model. The sensitivity analysis revealed that the model was largely insensitive to individual parameter estimates and could be used to guide management of territorial animal populations with social structure. The model output variables closely matched the mean and range of values reported in the literature of wild populations for population size, proportion of females breeding, offspring survival and litter size. The variation of model output was similar to the variation recorded in field studies. Further, population dynamics reported from field studies emerged from the model and may help to explain the mechanisms responsible for this variation. This type of model could also provide insights into potential management alternatives for other canid species or other species with similar social structure.
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1. Introduction

Insuring the survival of endangered canid populations or reducing the negative effects of ubiquitous

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canid species has been at the forefront of wildlife management throughout the world (Sillero-Zubiri and Gotelli, 1995; Haight and Mech, 1997; Vucetich and Creel, 1999; Bodenchuk et al., 2002). Determining the effects of management programs on wild canid populations depends upon the ability to integrate our best understandings of species biology, the environmental aspects upon which these populations depend, and the factors controlling species abundance (Gese et al., 1989; Knowlton et al., 1999; Murray et al., 1999). Previously, biologists and managers have relied upon insights provided by general analytical or computer models of animal populations. However, canid populations differ from other species because they are highly territorial, have a specific social structure, and occur at relatively low densities (Knowlton, 1972; Sillero-Zubiri and Gotelli, 1995; Vucetich et al., 1997; Knowlton et al., 1999). Analytical models are not suited to include the individual characteristics that were critical to the management of canid populations and past computer models of canid populations have not incorporated territoriality and social structure (Zarnoch and Turner, 1974; Connolly and Longhurst, 1975; Sterling et al., 1983; Haight and Mech, 1997; Jensen and Miller, 2001; Haight et al., 2002). Toward this end, we developed a model using the Swarm modelling system to provide a better understanding of canid population dynamics. We used coyotes (*Canis latrans*) to parameterise the model for this exercise because the management of coyote populations was intensely debated throughout the United States and populations have been thoroughly studied (Knowlton et al., 1999; Pitt et al., 2000, 2001b). However, the model could easily be adapted to other species with similar population structure.

The first attempts to incorporate some form of territoriality or social structure into analysis of animal distributions (Fretwell and Lucas, 1970; Fretwell, 1972) or population models (Schoener, 1973; Lomnicki, 1978, 1980; Gurney and Nisbet, 1979) were often criticised because they required unrealistic assumptions (e.g. identical individuals) about animal populations and provided only general relationships to maintain mathematical simplicity (Tregenza, 1995; Hassell and May, 1985). However, these models did provide an indication that territoriality and social structure may have significant effects on population dynamics. Since that time, analytical population models have

attempted to include more individual differences and habitat variation (Goss-Custard, 1980; Sutherland and Parker, 1985; Pulliam, 1988), but were still not suited to provide specific predictions that were needed in management and the analytical tools were not available to incorporate such detail (Lomnicki, 1992, 1999; McCauley et al., 1993; Fahse et al., 1998; Humphries et al., 2001).

The individual-based modelling approach offered an alternative that was better suited to the needs of management and allows for evaluation of specific response variables (Bart, 1995; Van Winkle et al., 1998). Several individual-oriented models have been developed that incorporate social structure or territoriality or were developed specifically for canid populations. We used the classification of individual-oriented models to include individual-based models and those models that were based on an average individual and separated only by classification (see Uchmanski and Grimm, 1996). Individual-oriented population models to date that have focused on the effects of territoriality, whereas the inclusion of individual differences has been limited. The general findings of these studies have been that territoriality limits population size, non-territorial animals may buffer populations, and intrinsic factors may effect population dynamics (Korzukhin and Porter, 1994; Carroll et al., 1995; Rohner, 1996; Matthiopoulus et al., 1998). The few individual-oriented models that have been developed for canid populations are stage-class models with no within stage-class variation other than stochastic application of parameters (Zarnoch and Turner, 1974; Haight and Mech, 1997; Vucetich et al., 1997; Haight et al., 1998; Vucetich and Creel, 1999). The models developed specifically for coyotes did not include territoriality or social structure (Connolly and Longhurst, 1975; Connolly, 1978; Sterling et al., 1983).

2. Model description

We developed an individual-based and pack-based model of a coyote population to use as a management tool. An object-based model is a logical way to construct such a model because a dual definition of coyotes or packs is possible as the fundamental unit of the simulation. The coyote population model was divided into packs and a collection of non-territorial animals.

The model functions on the premise that some aspects of coyote populations, such as the biological functions of individuals (death, feeding, etc.) are actions that are taken by individual coyotes, and other aspects, such as reproduction, are actions that are taken by packs. Our model stands apart from previous modelling efforts because it relies on field data with parameters derived from individual data sets and published papers, and explicitly incorporates behavioural features, such as dominance and territoriality, as major determinates of species demography (Connolly and Longhurst, 1975; Knowlton et al., 1999). Individual variation, such as status within territorial social groups was specified and assumptions typically associated with most demographic models were not needed (Railsback et al., 1999; Railsback, 2001). However, individual-based models were often criticised for being too complex, not easily parameterised, and so uncertain of their output that they were not useful for management (Grimm, 1994, 1999). The goal of this modelling effort was to construct a model that captured the dynamics of canid populations while maintaining a simple structure and minimal parameters.

We selected the Swarm simulation environment (Carnahan et al., 1997; Deadman, 1999; SDG, 2001) as the basis for this project as it was ideally suited to creating a system of multiple interacting agents with variable schedules and hierarchies. Swarm was a software platform that allows the user to describe individual behaviours, links those behaviours in each concurrent time step, and assembles behaviours and objects in a hierarchical framework. Hierarchies of objects and collections of objects, schedules, internal definitions of those constituent objects were specified by the user using either the Java or Objective-C programming languages (SDG, 2001).

2.1. Model structure

In the base simulation, the principle objects were the *Coyotes*, *Packs*, a *Calendar*, and the *Population model* (Fig. 1). To conform to a virtual concurrency model, we specified both objects and schedules (collections of actions to be executed at time steps), allowed Swarm's precompiled libraries to resolve scheduling of actions.

To maintain simplicity and understanding in the initial model, food supply did not vary over space and time (Grimm, 1999). Thus, each pack had the same re-
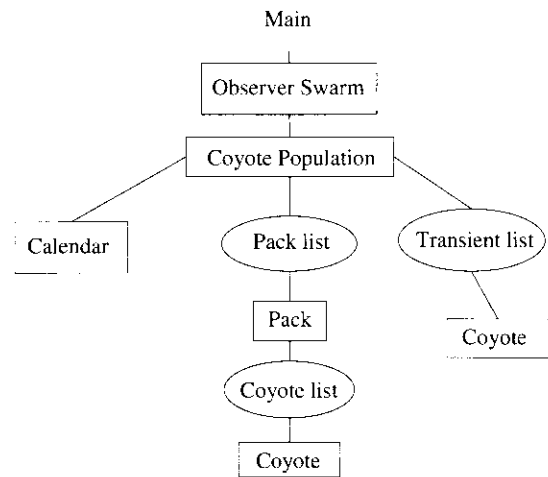

Fig. 1. Diagram of the model structure detailing the hierarchy and relationships of objects. Swarm objects are denoted by rectangles and lists are denoted by ovals.

sources available in a stable landscape. We will explicitly investigate the effect of food supply variation over time and space with future modelling efforts. Because food supply was constant over time and across packs, food supply parameters were removed from equations to avoid confusion.

The model was spatially structured because we divided the population into packs and the states and actions were dependent on local conditions (e.g. litter size was dependent on pack size). However, the model was not spatially explicit because territorial locations were not included.

2.2. Hierarchy of objects

2.2.1. Coyotes
The coyote was the primary fundamental object in the simulation. It was the coyote that actually was born, jockeyed for social position within its pack, dispersed or died. Also, coyotes could reproduce, if they occupied a breeding position.

2.2.2. Pack
The pack was the secondary fundamental unit of the simulation. It was a collection of coyotes who interact as a unit. Normally a pack had one alpha male and one alpha female, though it was possible for a pack to have neither (Knowlton et al., 1999). A pack could have

beta coyotes as members as well, with betas attempting to become alpha if there was a position open or if s/he believes that the present alpha could be killed or chased away. Transients could also become members of a pack if there was a position available. Pups were added to a pack that successfully reproduces, and these either die or grow to be adults as time progresses.

The pack implied a territory, which is relatively static in coyote terms (Kitchen et al., 2000). There were no hard-coded limits as to how many coyotes can occupy a territory, though the likelihood of being expelled from a pack increased with pack size. Litter size also decreased with pack size. Pack size was regulated by these two processes; however, rather than specify in advance what the pack size should be, it is handled as an emergent property of the system, determined by factors that affect the fundamental processes (Railsback, 2001).

2.2.3. Calendar

Because many animal activities were dependent on the time of year, a calendar object was added to count the time steps in the simulation and translate them into the month of the year for any other object. The calendar also allows additional model modules to be seamlessly added in the future.

2.2.4. Population model

The coyote population model was constructed as a collection of packs, plus a collection of non-territorial or transient coyotes that do not belong to any pack. We used 100 packs as the simulation population, which provided a large and realistic population size (Clark, 1972; Windberg and Knowlton, 1988; Knowlton et al., 1999; Stoddart et al., 2001). The model was not spatially explicit to allow the model to be applied to populations in various regions. Coyote territory size varies greatly across regions from 2 to 20 km² for a single territory (Windberg and Knowlton, 1988; Gese et al., 1996a). Although many other features may be added in the future, our initial objective was to recreate coyote population dynamics for unexploited populations using the simplest model possible (Grimm, 1994).

2.3. Actions and states

Each individual was characterised by sex, age, status, and pack membership. Pack size was not

limited but the likelihood of subordinates dispersing increased with the number of animals in the pack. Individuals could change status or pack membership by dispersing from natal packs (disperse), replacing a dominant animal (socialize) or by moving to a pack from non-territorial status. In addition, animals could die of natural causes based on their status and age or breed, depending on their status. We attempted to parameterise each relationship with data from individual animals whenever possible, but we used population averages when individual data were not available (Uchmanski and Grimm, 1996).

For all probability functions, a random number is drawn between 0 and 1 and compared to the parameterised function result. If the random number is less than the parameterised result, the action was executed.

2.3.1. Dispersal probability

The probability a coyote will disperse (leave or be driven) from the pack was determined for adult coyotes less than 2 years old. That probability was adjusted individually for each coyote at each time step, and is considered to be a function of the number of coyotes in the pack and available resources (Gese et al., 1988, 1996a; Mills and Knowlton, 1991; Patterson and Messier, 2001). The probability an animal would leave a pack (P_{leaving}) was determined with Eq. (1), where N is the number of members in the coyote's pack and D was the dispersal parameter that was set at 0.05.

$$P_{\text{leaving}} = DN_{\text{pack}}^2 \tag{1}$$

We believed, there is little likelihood of leaving when only a pair was present and D was adjusted accordingly. The dispersal function was only used for animals under 2 years. In natural populations, coyotes older than 2 years are unlikely to disperse (Gese et al., 1988, 1996a). Older animals may disperse from the pack if they were forced out under the socialize function (Eq. (6)).

2.3.2. Adult mortality

Mortality of adult coyotes (>6 months) within packs was considered to be a quadratic function of the coyote's age, based on observations of field data from unexploited populations (Davison, 1980; Knowlton,

unpublished data; Gese, unpublished data). For an adult coyote the monthly probability of dying was based on age of the coyote (Y).

$$M_{\text{pack}} = M_c Y^2 + M_b Y + M_a \qquad (2)$$

For adult coyotes in the pack, the values of these parameters were $M_a = 0.01$, $M_b = -0.0003$, and $M_c = 0.00025$.

2.3.3. Offspring mortality

For young coyotes (<6 months), a static mortality rate was used because the mechanism potentially responsible for variation in offspring mortality rate was unknown (Eq. (3)). Mortality rates for young coyotes are consistently high, often exceeding 50% in the first 4 months (Gier, 1968; Knudsen, 1976; Hallett, 1977; Crabtree, 1988; Gese et al., 1989; Windberg, 1995). Offspring mortality was likely due to variation in the amount of resources available to a particular pack (Pitt et al., 2001a; Pitt, unpublished data). In this model, food supply was constant and homogeneous across packs, so we did not vary offspring mortality across packs or years but did allow variability around the mean (Eq. (3)).

$$M_j = 0.1 \qquad (3)$$

2.3.4. Transient mortality

In most documented studies, mortality rates were higher for transient animals than for animals within packs (Andelt, 1985; Gese et al., 1989; Windberg, 1995). Thus, we modified the adult mortality rate (Eq. (2)) based on the number of transient animals. Mortality rates increased with the density of non-territorial animals because they would potentially share a common area and the probability of encountering other animals would increase with density. Transient animals had large home ranges covering 90–140 km^2 and overlap with other transients, as well as territorial animals (Gese et al., 1988). Thus, increased density would either result in less food per individual or an increase in the number of negative encounters with other transients or pack members (Gese et al., 1989). The intercept term (A in Eq. (4)) was increased based on the number of transient animals. The magnitude of the shift upward (increase in the intercept term A) was a function of the density of transients already present compared to the number of

packs in the simulation (P). The functional form was

$$A = T_b + T_a \left(\frac{N_{\text{transients}}}{P} \right) \qquad (4)$$

The parameter values were $T_b = 0.008$ and $T_a = 0.089$. The intercept was the mortality rate for transients when no other transients were present, and the slope was the rate at which mortality increases in proportion to transient density.

2.3.5. Litter size

Only alpha females had the potential to produce offspring each year, although in some wild populations subordinate coyotes occasionally produce offspring; we felt this was rare enough to be ignored in the model (Gese et al., 1996a; Knowlton et al., 1999). Female age had little effect on litter size from 2 to 8 years of age when females typically produce offspring in wild populations (Green et al., 2002). Litter size in the model was based on a normal distribution with the mean based upon pack size and food resources (Pitt et al., 2001a). The results have been mixed from field studies that attempted to determine the relationship between offspring produced and food supply over entire populations and large land areas (Gier, 1968; Todd et al., 1981; Knowlton and Stoddart, 1983; Windberg, 1995; Gese et al., 1996a). The most likely reason for mixed results was that the number of offspring produced was a function of the food supply for that particular female (Sayles, 1984). In this model, food supply was constant and homogeneous, so litter size was only dependent upon pack size (Eq. (5))

$$L_{\text{mean}} = L_b + L_a N_{\text{pack}} \qquad (5)$$

where $L_b = 8.93$ and $L_a = -0.72$. The number of pups born to a pack was drawn from a normal distribution with a mean (L_{mean}) and a variance as recorded in individual litters ($\sigma = 2.0$). The number was then cast as an integer to determine the number of pups that are born in a particular litter. Most average litter sizes reported in wild populations ranged from 3.2 to 7 (Clark, 1972; Knowlton, 1972; Andelt, 1985; Crabtree, 1988; Gese et al., 1989). The linear equation was developed based upon a pair of animals having the maximum litter size and as a pack reached the maximum size reported they would produce a small litter size of 3.2. If a breeding pair of animals was not present in the pack, no offspring were produced.

2.3.6. Alpha replacement

In addition to the dispersal function (Eq. (1)), animals could change positions within a pack or change pack affiliation by moving into a vacant position or displacing an alpha. Although the model was not spatially explicit, free alpha positions were not totally determined by the individual pack. Free alpha positions could be occupied by a beta within a pack, a beta from a neighbouring pack, or a transient animal. However, alphas were only challenged for replacement by betas within the pack due to high degree in which packs repel intruders and the high mortality rates of transient individuals (Andelt, 1985; Gese et al., 1989; Windberg, 1995; Gese, 2001). The probability that an alpha would be replaced was based on the age of the alpha (Eq. (6)).

$$P_{\text{replacement}} = 0.05(\text{age} - 5) \tag{6}$$

2.3.7. Sequence of events in simulation

We used a 1-month interval as the time step in the model. This time step allowed the model to execute actions at a realistic concurrent time-scale but does not burden the model with excessive detail that was not well documented. At each step, each coyote and each pack executed associated actions as defined by the month.

At each time step, the following sequence of events occurred:

- Every pack simultaneously
  - checked to see if both an alpha male and an alpha female were present
  - if there were suitable alphas, and it was April, attempted to produce offspring
    - created a litter of pups with a mean dependant on the number of coyotes present in the pack (see Eq. (5))
    - added pups as members of the pack
  - checked to determine if alpha would be replaced
    - both male and female alpha were compared against a replacement probability that was a function of their age
    - the oldest beta was selected as the contender. If it was December, and there was a contender, the alpha had the probability denoted in Eq. (6) of being replaced

  - if replacement occurred, the alpha became a transient and the contender became the new alpha
  - updated the death probability of each member based on status (pup or adult) of coyote
  - updated the dispersal probability of each member based on the number of coyotes in the pack (Eq. (2))
  - forced death of pups less than 2 months of age if no adults are in the pack
- For each pack member
  - each coyote completed individual tasks
    - if older than 2 months, left the den
    - if older than 6 months, graduated from pup to beta
    - calculated death probability based on age and status (Eqs. (2) and (4))
    - if coyote was beta less than 2 years old, was ejected from pack based on Eq. (1), and ejected coyote became a transient
- Model calculated summary statistics for each pack
- Every transient coyote simultaneously
  - updated intercept term of death probability (Eq. (2)) based on number of transients per number of packs (Eq. (4))
  - updated death probability based on new values for Eq. (2)
- Every pack without alphas attempted to find replacements
  - if there was an available beta in the pack, made the oldest beta of the same sex the alpha
  - if there was no beta in the pack, selected a transient of the same sex and make that coyote the alpha
  - if there were no available transients, an eligible beta from an adjacent pack was selected
- Calendar moved forward one step

3. Sensitivity analysis and calibration methods

We performed a sensitivity analysis of output variables to variation in input parameters. This was critical for any model, but especially for models used to guide management (Bart, 1995). We tested sensitivity by running the model at varying levels of the input parameters, and comparing that to selected output variables. The objective of this phase was to determine

which parameters, or combinations of parameters, had significant effects on output variables. The sensitivity analysis included testing for overall effects by both varying multiple parameters and evaluating the output using a stepwise regression, as well as testing for combined effects by varying all retained parameters in two way combinations and evaluating the output using a multiple regression (Zar, 1999). We chose to analyse the results statistically as a convenient index and not as a formal hypothesis test (Gardner et al., 1981; Swartzman and Kaluzny, 1987). We used the regression coefficient, R^2, as a measure of effect size that was absolute across multiple variables.

3.1. Selection of parameters to be tested

We selected all parameters that were based on values extracted from relevant literature for sensitivity analysis. In each case, the functional form of the model was assumed to be correct and no test was conducted for functional form.

3.2. Preparation of model output

We created a controlling model to run the population model multiple times, vary input parameters, and record conditions and model output. We specified a scheduling structure for the following actions to be repeated:

- built coyote model and load with model parameters
- a new random number seed was generated
- ran population model
- recorded values for input and output parameters
- dropped coyote model
- modified input parameter values

Each model was created and initialised anew, thus each new model had no connection to any other model run in the series.

3.3. Output parameters

The output variables tested were selected because they are typically measured in real population studies (Clark, 1972; Knowlton, 1972; Windberg et al., 1985; Andelt, 1985; Gese et al., 1989). We chose a variety of output variables, so the overall pattern of outputs from the model could be analysed (Grimm et al., 1996;

Railsback, 2001). The output variables were recorded at the end of the year or when it was biologically appropriate as follows:

- Total population (December)
- Proportion of transients (December)
- Offspring survival (September)
- Average litter size (March)
- Proportion of breeding females (March)

3.4. Parameter effects

3.4.1. Analysis methods

We tested effects of varying multiple parameters on model output by varying each of the nine input parameters and determining the effects on output variables. In this step, each input parameter was adjusted in turn to values 5% above and below the published values (10% range), while all other values were held constant. We ran the model 18 times (each run equals 6 years) for each varied parameter plus one run for baseline information (all nine parameters at the recorded level). The complete set of runs was repeated six times, giving a total of 114 model runs. Each model was run with 100 coyote packs (400 animals for the initial population) for a total of 72 months, or 6 simulated years of coyote time; the number of runs required for the model to reach equilibrium population size and within range of the published values. The nine input parameters were then regressed using the high, medium, and low values as factors against the five output variables (population size, proportion of transients, proportion of females breeding, offspring survival, litter size) using multiple linear regression to test for significant effects (Zar, 1999). We used an automated stepwise regression procedure, which minimises the Akaike Information Criterion to reduce the number of terms in the regression (Venables and Ripley, 1997; Anderson et al., 2001). This analysis provided an effect size and a simple method to compare the importance of parameter variation (Gardner et al., 1980, 1981).

3.4.2. Calibration procedure

We tested the model output using a pattern analysis approach to ensure that the model would be a reliable tool to guide management (Bart, 1995; Grimm et al., 1996). We compared five output variables to literature values obtained in field studies. These output variables

are typically measured in many population studies, were not hard-coded in the model, and were developed with data from individual animals (Grimm et al., 1996; Uchmanski and Grimm, 1996). We gathered literature values from several published sources to minimize the effects of any one study. We ran the model holding the input parameters constant and sampled the five output variables. A total of 4642 runs of the model were conducted with the same nine input parameters as in the previous section. The parameters were either directly extracted from field studies or modified slightly to conform to similar reporting times. The population estimates were calculated from literature values of pack size and proportion transient. The reported pack size was multiplied by 100 (number of packs in the model) and then the respective proportion of transient animals was added. This was necessary to have data that were comparable to the model and across habitat types.

4. Sensitivity analysis and calibration results

4.1. Analysis results

The total population over the 114 runs was normally distributed, with a mean size of 535.3 ± 18.5. Multiple regression sensitivity analysis indicated that the model was robust to variation in the parameter values (Table 1). Litter size L_b significantly affected four of the five output variables but the effect size was small. Dispersal probability significantly effected litter size and proportion of females breeding. The

dispersal probability parameter was the only parameter that had an effect on population size. The input parameters accounted for up to 23% of the variation in the output variables.

4.2. Calibration results

The model output variables closely matched the values reported in the literature of wild populations (Table 2). None of the output variables varied from the literature values by more than 10%. The model output of litter size deviated more than any other output variable compared to the literature values. Field studies often use intrauterine placental scars to estimate litter size. This technique likely overestimates the number of young actually produced (Knowlton, 1972). We would also expect to see a similar deviation in the proportion of females reproducing because this was often based on the same technique, however the close agreement between the model and the literature values suggest that this technique may be adequate for these purposes. We did not alter the model as a result of the calibration because the output variables closely matched literature values.

4.3. Emergent dynamics

In addition to the close agreement between the mean literature values (as detailed in the calibration results) and the model output, the behaviour of the model matched literature descriptions of the variations observed in real populations. The proportion of females breeding often varies widely across population and

Table 1

Sensitivity analysis results of multiple regression between multiple nine input parameters (dispersal probability (D), litter size (L_a, L_b), juvenile mortality (M_j), adult mortality (M_a, M_b, M_c), and transient mortality (T_a, T_b)) and five output variables

Output variables	Input parameters									
	Multiple R^2	D	Litter size		Mortality					
			L_a	L_b	M_j	M_a	M_b	M_c	T_a	T_b
Population size	0.21			***	*					
Proportion of population transient	0.09			*						
Offspring survival	0.11			***			*			
Litter size	0.23	*	*	***						
Proportion females breeding	0.11	***							*	

Regression coefficients (R^2) presented for the combined effect of parameters on output variables. The symbols (*), (**), and (***) denote significant effects of the input parameters at $P < 0.05$, $P < 0.01$, and $P < 0.001$, respectively.

Table 2
Comparison of model results of five output variables with values taken from published studies

Output variables	Model results	Literature values		
		Mean	Range	Sources
Population size	525	500	420–560	1, 2, 4
Proportion of population transient	0.26	0.26	0.13–0.58	1, 2
Offspring survival	0.41	0.41	0.32–0.73	1, 2, 5, 6, 8, 12
Litter size	4.10	4.6	3.2–7.0	1, 2, 4, 6, 7, 11, 12
Proportion females breeding	0.43	0.44	0.33–0.7	2, 3, 5, 7, 9

Population size estimate was calculated by multiplying pack sizes by 100 and adding in the corresponding proportion of transient animals. Literature sources correspond to (1) Camenzind (1978), Gese et al. (1988, 1989), Windberg (1995); (2) Andelt (1985), Crabtree (1988); (3) Jean and Bergeron (1984); (4) Gese et al. (1996a,b); (5) Gier (1968); (6) Hallett (1977); (7) Knowlton (1972); (8) Knudsen (1976); (9) Moore (1981); (10) Nellis and Keith (1976); (11) Pyrah (1984); (12) Till (1982).

time. This variation is often attributed to changes in the number of females breeding, but our model suggests another mechanism (Connolly and Longhurst, 1975; Sterling et al., 1983; Miller et al., 2002). The number of females breeding in the model varied little (98–100), but the proportion of females breeding varied from 43 to 61%. This variation was entirely due to changes in the number of transient and subordinate females and not due to changes in the number of females breeding as suggested by others (Connolly and Longhurst, 1975; Sterling et al., 1983).

Mean pack size of the model (4.0) was similar to the mean pack sizes reported (3.8) in many studies (Camenzind, 1978; Andelt, 1985; Gese et al., 1988, 1996b). Although close agreement between the model variables and field study results does not validate the model, the similarity between model and field study results increases the confidence in model results. In addition to comparing the means of field studies and the model results, we evaluated the variability of model results over time. The model variability in individual parameters was very comparable to field results. The model variation in pack size of individual packs (1–7), the proportion of transient animals in the model (15–35%), and litter size (1–8) mirrored the variability reported in field studies. Thus, we feel the population model closely resembled natural population dynamics.

The model age structures were similar to those reported in field studies of unexploited or lightly exploited coyote populations (Andelt, 1985; Crabtree, 1988; Gese et al., 1996a,b, 1988). As in these field studies, less than 30% of the population was less than 1 year of age and some coyotes lived as long as 12 years.

5. Discussion

5.1. Comparison to other models

This model was designed to capture the dynamics of canid populations while maintaining a simple structure and using minimal parameters. Many individual-based models that have been developed are complex and required a large number of parameters (Grimm, 1994, 1999). In addition, the parameters required were not easily obtained and often required intensive study. This model appeared to mimic many of the attributes of canid populations and the parameters were easily obtainable from the literature.

The other canid models developed did not include important behavioural features, and thus did not mimic the dynamics of natural populations. Most of the other canid models were analytical models and were not suited to include the individual characteristics that were critical to the management of canid populations (Zarnoch and Turner, 1974; Connolly and Longhurst, 1975; Sterling et al., 1983; Haight and Mech, 1997; Jensen and Miller, 2001). Our model results suggest that these aspects are critical to canid populations because territoriality limited population size and social structure limited reproduction. Miller et al. (2002) and Haight et al. (2002) developed similar stage-class models for gray wolf (*C. lupus*) management. Both models emphasised many of the same aspects that were included in our model, such as high juvenile mortality, territoriality, and high reproductive capacity. Miller et al. (2002) did not include territoriality in their model, and our model results suggest

that territoriality limited reproduction and population size. Haight et al. (2002) included territoriality but the actions were not locally determined beyond two landscape categories of wild and farm range and the propensity to kill livestock. For example, all wolves had the same mortality rate based on two age classes and this only occurred once per year and the behavioural dynamics were simplified. The effect of these actions was unclear because the model was not calibrated (Bart, 1995; Grimm et al., 1996). Both models did not include non-territorial animals, although Haight et al. (2002) did include non-persistent dispersers. Our model suggests that transient animals, although experiencing high mortality rates, were critical for filling vacant positions within packs and buffering the reproductive capacity of the population. Overall our model depended greatly on individual variability, local conditions, and social structure which were not accounted in Haight et al. (2002) and Miller et al. (2002) models, and would likely lead to divergent predictions as others have found (Stephens et al., 2002).

Several individual-based models have been developed for other species that have similar structure to the model presented here (Korzukhin and Porter, 1994; Carroll et al., 1995; Rohner, 1996; Hendry et al., 1997; Artois et al., 1997; Matthiopoulus et al., 1998; Stephens et al., 2002). Our model agrees with the collective findings of these studies on the importance of including territoriality, the buffering capacity of non-territorial, and the local factors may effect populations. The major difference in these models and our model was that our model had fewer parameters, easily measured parameters, and a simple structure even though we included territoriality and social structure. Most of the other models did not include both territoriality and social structure except Stephens et al. (2002). Hendry et al. (1997) model of territorial behaviour produced varied population dynamics that we did not see in our model, but the authors attributed these dynamics to the spatial nature of their model. Nonetheless, these individual-based models had different goals and were designed for other animals that may have required additional complexity beyond our model, so a direct comparison should not be made. Our model results suggest that a fairly sophisticated model does not have to be overly complex or include numerous parameters.

5.2. Management implications

The impetus for developing our model was to build a management tool for wild canid populations. The primary management implications from this model were that territoriality and social structure produce vastly different results than a model without such structure. Often these attributes are not included in analytical models. The number and quality of territories would limit an expanding canid population more than the number of available females in a population as is often modelled (Zarnoch and Turner, 1974; Connolly and Longhurst, 1975; Sterling et al., 1983; Jensen and Miller, 2001; Miller et al., 2002). From our model results, the proportion of females breeding was likely an artefact of the social structure and did not reflect changes in reproductive capacity. The proportion of transients in the population had key effects on the population dynamics. We initially had considered not including non-territorial animals because they have such a high mortality rate and we had assumed they would not effect the population dynamics (Haight et al., 2002; Miller et al., 2002). However, our model results suggest that transients and non-breeders alter dynamics by slowing the growth rate of populations and also buffering a population's reproductive capacity from a loss of breeding individuals. We plan to add additional components to the model to fully evaluate the effects of management on canid populations. We will evaluate the effects of removal, reproductive control, and other options in future publications.

5.3. Conclusion

Overall, we feel that this simple model of a coyote population accurately captures the dynamics of real coyote population dynamics. The sensitivity analysis revealed that the model was largely insensitive to individual parameter estimates and could be used to guide management of territorial animal populations with social structure (Bart, 1995). The calibration results suggest that the model structure and parameters accurately portray a real population.

This modelling exercise highlighted the importance of litter size and juvenile mortality on population dynamics in canids. The litter size parameters in the model had a significant influence on most of the output variables (Table 1). Further efforts to refine the

model should be focused on these parameters. In addition, little research has focused on mechanisms that effect litter size and offspring mortality (Sayles, 1984; Green et al., 2002). Knowledge of the mechanisms that effect litter size in canid populations has arisen from casual observations or broad correlations of field data (Gier, 1968; Todd et al., 1981; Knowlton and Stoddart, 1983; Windberg, 1995; Gese et al., 1996a). In this model, we did not include any mechanisms that could influence offspring mortality, although food resources would likely have some effect (Pitt, unpublished data). The influence of food resources on litter size and mortality deserves further study.

The calibration results and the dynamics were very similar to field data of unexploited coyote populations. This suggests that the model was an adequate representation of an average population. This model was not tied to a specific geographic area and does not account for regional differences among populations (e.g. litter size, pack size or territory size). Additional model development may account for this variation with changes in resources among regions.

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