A New Approach to Understanding Canid Populations Using an Individual-based Computer Model: Preliminary Results

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Abstract

Ensuring the welfare of wild canid populations depends upon the ability to integrate species biology, the environmental aspects upon which those populations depend, and the factors controlling species abundance. Toward this end, we developed an individual-based computer model using Swarm to mimic natural coyote populations. Swarm is a software platform that allows the user to describe individual behaviors for all individuals, link those behaviors in each concurrent time step, and assemble behaviors and objects in a hierarchical framework. Our model stands apart from previous modeling efforts because it relies on field data and explicitly incorporates behavioral features, such as dominance and territoriality, as major determinates of species demography. Individual variation, such as status within territorial social groups and age-based reproduction are assumed, but assumptions typically associated with most demographic models are not needed. The eventual goal is to incorporate other environmental components such as prey abundance and/or competing carnivores. This type of model could also provide insights into potential management alternatives for when the gray wolf is removed from endangered status in Minnesota.

Introduction

Ensuring the welfare of wild canid populations depends upon the ability to integrate our best understandings of species biology, the environmental aspects upon which those populations depend, and the factors controlling species abundance (Gese et al 1989; Murray et al 1999). Previously, biologists and managers have relied upon insights provided by many analytical and computer models of animal populations. Canid populations, however, differ from other species because they are highly territorial and have a specific social structure, relatively low density (Knowlton 1972; Sillero-Zubiri and Gotelli 1995; Knowlton et. al 1999). Analytical models are not suited to include the individual characteristics that are critical to canid populations and past computer models have not incorporated territoriality and social structure (Connolly and Longhurst 1975). Toward this end, we developed an individual-based computer model using the Swarm modeling system to provide a better understanding of canid population dynamics. We use coyotes (*Canis latrans*) to parameterize the model for this exercise, but the model could easily be adapted to many other canid species with similar population structure. This paper is a preliminary summary of a model that will be presented in greater detail elsewhere (Pitt et al. in preparation)

The model

Swarm is a software platform that allows the user to describe individual behaviors for all individuals, link those behaviors in each concurrent time step, and assemble behaviors and objects in a hierarchical framework (Savage and Askenazi 1998; Railsback et al. 1999; SDG 2001). Our model stands apart from previous modeling efforts because it relies on field data with all population parameters derived from data sets and published papers, and explicitly incorporates behavioral features, such as dominance and territoriality, as major determinates of species demography (Connolly and Longhurst 1975; Knowlton et al. 1999; Pitt et al. 2001). Individual variation, such as status within territorial social groups and age-based reproduction are specified and assumptions typically associated with most demographic models are not needed.

The coyote population model was divided into 100 packs and a collection of non-territorial animals. Each individual is characterized by sex, age, status, and pack membership. Pack size was not limited but the likelihood of subordinates increased with the number of animals in the pack. Individuals could change status or pack membership by dispersing from natal packs, replacing a dominant animal, or by moving to a pack from non-territorial status.

As with most animals, the probability of mortality increases with age. Mortality rates are higher for non-territorial animals than pack members (Gese et al. 1989). In addition, mortality rates increase 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. Thus, density increases would either result in less food or an increase in the number of negative encounters.

Although subordinate coyotes occasionally produce offspring in natural populations, in our model only alpha females breed (Knowlton et al. 1999). The birth rate is based on a normal distribution with the mean based upon pack size. Few would disagree that the number of offspring produced is a function of the health of the animal. There has been, however, continued disagreement over what is a good indicator of health. Some evidence from captive coyote studies suggests that old (>8 years) animals will produce fewer offspring (Green et al. 2001). The most contentious argument is that litter size is a function of food supply or density (Crabtree and Sheldon 1999; Knowlton et al. 1999). Field evidence for and against this argument has been mixed (Gier 1968; Todd et al. 1981; Knowlton and Stoddart 1983; Windberg 1995; Gese et al. 1996). The most likely reason for these mixed results is that the number of offspring produced is a function of the food supply for that particular female. The food supply is a function of the food in the territory and the number of animals in the pack. Studies that have attempted to determine the relationship between offspring produced and density of food supply have looked at entire populations and large land areas (Gier 1968; Todd et al. 1981; Knowlton and Stoddart 1983; Windberg 1995; Gese et al. 1996). Thus, the relationship would only be observed if most packs were similar in size, food supply was homogenous across the landscape, and territories were identical in size. The likelihood of all of these factors being similar in one population would be low and extremely rare between populations, so this relationship would not be observed under most conditions on a population basis. For these reasons, we set the mean number of pups produced as a function of the number of pack members. In this model, territories are identical so we could ignore differences between territories.

The second part of this modeling exercise is the management model, which allows us to examine the effects of managing the population (Pitt et al. 2000). The management model combines the population model and a manipulation model so we can investigate the effect of removing individuals on population size and the resistance and resilience of the population. Herein, only random removal individuals will be considered.

Model output

We ran the population model under three management scenarios: no removal, pulse removal (a proportion of animals were removed in year five and the population then allowed to recover), or press removal (a constant proportion of animals were removed every year after year five). The populations were evaluated according to structure, the resistance to removal (proportion of animals removed required to have an effect for more than one year), and the resilience of the population (how quickly the population recovered under various removal levels).

With no removal, the population was stable and population size ranged from 350 to 700 adult animals with 15 to 35% of the population being non-territorial. The reason for this stability was animals were forced out of packs as they matured and non-territorial animals had a higher mortality rate then animals in packs. The population exhibited source-sink dynamics. Average pack size in this simulation was about four but varied from one to eight.

To determine the effect of pulse removal on the population, we let the population run for five years and then randomly removed 10 to 90% of the adult population in one year and then examined the response of the population. All populations recovered within one year when less than 60% of the population was removed (Figure 1). Basically, the population was reduced until new offspring were produced. The number of transients decreased as animals moved into packs and fewer animals moved out of packs. Populations subject to removal had younger age structures. When more than 60% of the population was removed, the population required more than one year to return to the population size prior to removal.

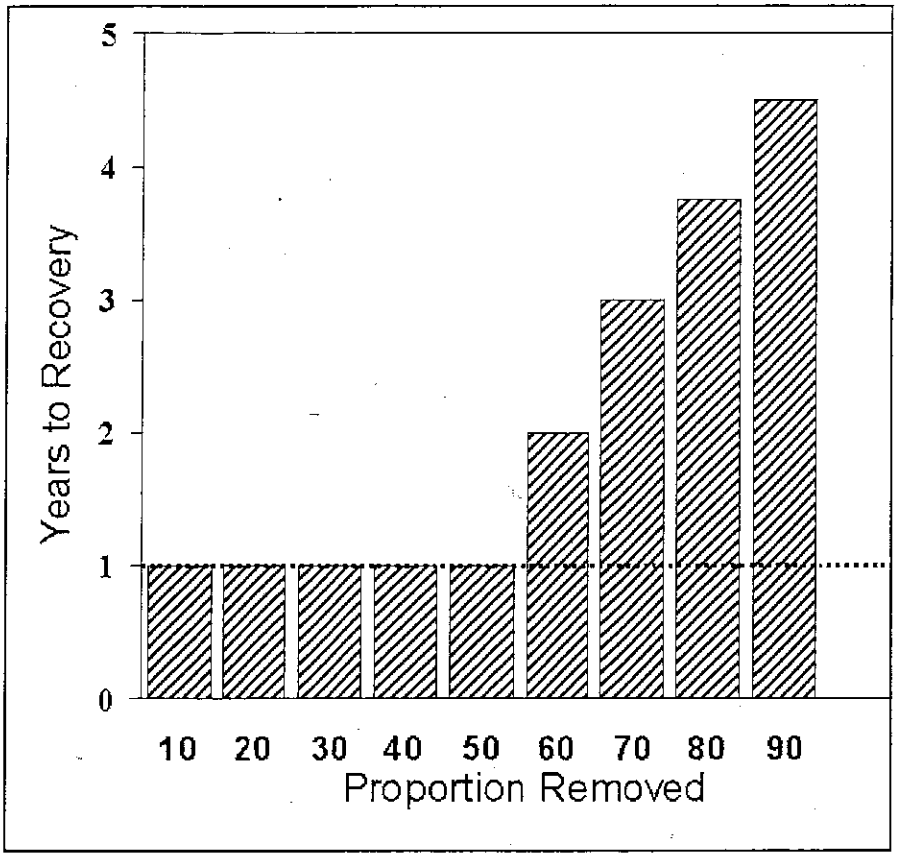

Figure 1. Number of years required for a population to return to pre-removal size after a certain proportion of animals are randomly removed from the population in one year. The horizontal line indicates the threshold where annual reproduction compensates for animals removed.

This removal proportion is lower than reported in previous computer models (Connolly and Longhurst 1975). The population recovered within five years, however, even with 90% removal in one year. When a large (>70%) proportion of the population was removed, the number of non-territorial animals decreased. In natural populations less time would be required to recover than what was depicted in the model because in the model, territories remained even at low densities, animals were not allowed to move out of their territories to mate, and animals were not allowed to move in from surrounding areas. Furthermore, we did not reduce natural mortality rates at low densities.

To determine the effect of sustained or press removal on the population, we let the population run for five years and then randomly removed 10 to 90% of the adult population each year and examined the response of the population. When removal was less than 60% of the population, population size was the same as an unexploited population, and it did not decline, even after 50 years of simulation. The population structure, however, differed from an unexploited population. The population with press removal at 50% had fewer transient animals (10 to 25%), a younger age structure, and higher reproduction than an unexploited population. High removal rates (>70% per year) resulted in an initial loss of non-territorial animals and after seven years the entire population was removed. In natural populations, a population decline could take several more years because territories remained in the model and animals did not move to mate, natural mortality rates were not reduced at low densities, and animals did not move in from surrounding areas. Removing more than 70% of the population annually would become logistically difficult at low densities. Territoriality would likely dissolve at low densities, animals would move to mate, natural mortality may be reduced, animals would immigrate into the population, and the high removal rates could not be achieved.

Implications for management

These simulations suggest that coyotes and other canid populations are very resistant and resilient to change. A population decrease was not observed until more than 60% of the population was removed annually. The populations are buffered against change by the high reproductive capacity and the non-breeding animals in the population, subordinates and non-territorial animals. Non-breeders would replace breeding individuals lost from the population so the reproductive capacity of the population is not reduced. Coyote and other canid populations are resilient because they have a high reproductive capacity. These conclusions may provide insight into the potential effects of disease on Ethiopian wolves (*Canis simensis*) or the potential management of timber wolves (*Canis lupus*). These species would also have similar population characteristics as was displayed in this model.

In the future, the model analysis will be expanded to investigate various types of removal, e.g. selective versus random removal. The management model allows the user to remove animals of a specific status, litters of offspring, during a particular month, and/or animals in a specific area. In addition, we can also investigate the effects of reproductive control or the effects of disease on populations. To determine the effects of unequal resource distribution, we can also vary resources among packs and over time as part of the foraging and predation models. Other components we contemplate adding are competing carnivores, predator-prey interaction, as well as, management cost-benefit programs to the model.

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