Modeling Raven Predation on the Desert Tortoise: An Age and Space Structured Approach

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Abstract. As populations of the common raven expand across desert tortoise habitat, increases in predation pressure may reduce tortoise population growth. Published observations suggest that raven predation is not spatially uniform, a fact that may be important in determining its ultimate, region-wide effect on tortoise populations. To explore the potential effects of spatially structured raven predation on a dynamic tortoise population, a simple model has been developed. The modeling process points out critical deficiencies in our knowledge of raven predation strategies and tortoise dispersal patterns. However, the model shows that tortoise populations may be able to sustain substantial increases in juvenile mortality before experiencing negative growth. A 25% increase in mortality of tortoises under 5 years old is necessary to reduce a discrete population growth rate from 1.02 to below 1.0. If raven predation primarily affects this class, it may be most efficient to focus research efforts on whether ravens can significantly contribute to losses of this magnitude.

INTRODUCTION

Recent management decisions concerning the common raven (*Corvus corax*) have focused on its increasing role as a predator of desert tortoises (*Gopherus agassizii*) in California (EASCCR 1989). Raven populations in the western Mojave desert appear to be increasing, especially in developed areas, along fences, roads, transmission and power lines, and around landfills (Berry 1985). Evidence of raven predation on tortoises has been documented near nesting and perching sites (Berry 1985; Berry et al., 1986). It has been asserted that predation on juvenile tortoises has been increased over historical levels as a result of increased raven activity in desert tortoise habitat, resulting in a decrease in representation of juvenile tortoises in some current populations (EASCCR 1989).

We are interested in predicting the degree to which raven predation may decrease tortoise population growth. We believe the spatial aspect of this predation will influence its ultimate impact on tortoises. For example, a raven that takes 100% of those juvenile tortoises near its nesting site may have either more or less of an impact than one that takes 10% of juveniles throughout its entire foraging range. Depending on the dispersal rate of juvenile tortoises, more or fewer may wander into a "sink" surrounding a raven nest than would be taken by a bird that forages less efficiently across a larger area. This link between raven foraging strategies and tortoise dispersal behavior is essential to predicting the ultimate effect of raven predation on tortoise population growth. In order to explore the potential effects of spatially structured raven predation on a dynamic tortoise population, a simple model has been developed. In this paper we describe our model, present its predictions, point out some of its limitations and discuss the questions that arose out of the modeling process.

The Model

To introduce a spatial component to the dynamics of a single tortoise population, we divide the population into an array of "cells" linked by dispersal. Each cell has a distinct predation pressure that may differentiate its internal dynamics from other cells. For tractability, we have modeled a linear array of such cells, and have assumed that dispersal occurs only between nearest neighbors.

The internal dynamics of each cell are determined by stage-specificity in both growth and predation. A stage-specific growth model (see Caswell 1989) was derived from demographic data gathered on a population at Goffs, California by Turner et al. (1987), where the stages are composed of individuals that roughly represent the different rates of reproduction, survival and vulnerability to predation experienced by tortoises throughout a lifetime (adapted from Biehl 1990). Seven stages are identified and included in a population projection matrix (Fig. 1). In the absence of predation, this projection matrix results in yearly growth of about 2%.

The spatial aspect of mortality due to predation is implemented differentially across cells by specifying a symmetrical predation rate function across the one-dimensional population transect. The function decreases linearly with distance from its maximum intensity, which is focused on the most centrally located population cells (see top graph in Fig. 2). A separate predation function is defined for each stage class, so that juvenile tortoises may experience higher predation than adults, etc. However, all stages experience the same functional form, if not intensity. This predation model could represent a linear transect running perpendicular to a corridor along which ravens nest and forage, such as a road or powerline. A steeply sloped predation function with a high maximum would mimic local and intense predation, while a shallow slope and maximum would mimic less efficient predation across a larger area. We assume that raven predation pressure is independent of tortoise density; i.e., tortoises do not represent a limiting resource for ravens.

After assignment of an inter-cell dispersal rate, population growth projection is accomplished through iteration of the following: multiplying each cell's population stage vector by the population growth matrix, reducing the resulting population vectors by the stage-specific predation rates for each cell, and dispersing the given fraction of all stages between neighboring cells. Predicting the sensitivity of this model to any one parameter involves exhaustively varying the value of each parameter in turn. The sensitivity of this model has been tested for the following: the maximum (central) predation rate for any stage; the slope of the predation function; the dispersal rate between adjacent cells; and the distribution of ages included in each stage in the population projection matrix.

Model Predictions

Figure 2 is an example of model output. The graphs illustrate the relationship (at time t = 15) between three independent variables (tortoise dispersal, predation slopes and maximums) and two dependent variables (population cell stage distribution and growth rate), for an arbitrary choice of independent variable values. At t = 0, each population cell contained 100 individuals in the stable stage distribution that would have resulted if raven predation were absent (resembling the outer cells in Fig. 2). With no dispersal, the entire population growth rate would have remained 1.02 (it would be slightly depressed in the presence of dispersal because this model allows dispersal off the "ends" of the transect).

Several general conclusions can be drawn from this model. First, predation on the younger stages is not as effective as predation on the older stages in lowering the population

Stage class transition matrix

	1	2	3	4	5	6	7
1	.696	.000	.000	.908	1.988	2.310	2.642
2	.093	.665	.000	.000	.000	.000	.000
3	.000	.143	.606	.000	.000	.000	.000
4	.000	.000	.232	.748	.000	.000	.000
5	.000	.000	.000	.137	.841	.000	.000
6	.000	.000	.000	.000	.089	.915	.000
7	.000	.000	.000	.000	.000	.032	.947

Figure 1. This seven-stage matrix for tortoise population projection was based on data from a tortoise population at Goffs, California (Turner et al. 1987). The dominant eigenvalue of the matrix (population growth rate) is 1.024.
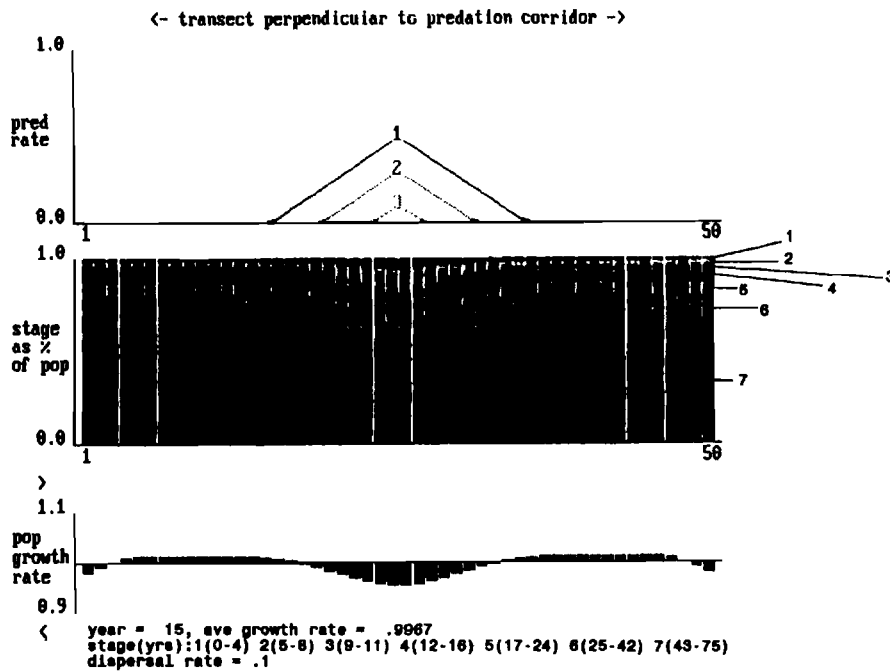

Figure 2. In this example of the predation model output, predation functions for the first 3 tortoise stage classes can be observed in the top graph. Predation on the first class is highest, with a maximum of 50% of these hatchlings taken in the middle of the population transect. The middle graph represents the stage distribution of each population cell. These distributions are not significantly different than they will be at stable stage distribution. The current growth rates of each cell are indicated in the lower graph. The population will eventually relax to a growth rate of 1.01.

growth rate. This will be true as long as desert tortoise demographic parameters are at all similar to those found by Turner et al. (1987). The low survival rate of juveniles to reproductive stages increases the value of reproductive-staged individuals; reproductive values of individuals in the first stage class are less than 5, while those in the fifth class range between 50 and 60 (Biehl 1990). Similar results were obtained by Crouse et al. (1987) for loggerhead sea turtles, which have only qualitatively similar demographic parameters. Second, predation on the youngest stage class decreases the representation of the middle stage classes in the stable stage distribution, while increasing representation of the mature (and sometimes the younger) classes. This effect is created by reduced recruitment to the middle stages and the relatively assured survival of the mature stage class(es). The relatively small decrease in representation of the youngest stage class that can be seen in Fig. 2 is due to the larger percentage of 0-year-olds born to the fractionally larger mature stage class. Third, if predation is applied uniformly across all cells and impacts only the youngest stage class (under 5 years old), it requires a predation rate of almost 25% to push the ultimate growth rate of the population below 1.0, at which point the population declines. Alternatively, predation losses of 15% of the first two stages (under 9 years old) can push the growth rate below 1.0. If the elements of the population projection matrix are uniformly decreased until the yearly population growth is only 1% (to test for sensitivity to errors in the demographic data), a predation rate of almost 15% of the youngest stage class is required to push the growth rate below 1.0.

Model Limitations

This model is bound to misrepresent the potential for raven predation to lower tortoise population growth due to the unavoidable omission of several factors for which we have no data. Two of the most important omissions are those of density dependence in both tortoise population growth and dispersal. Without knowledge of these factors, we cannot make meaningful predictions based on analyses of model sensitivity to the combined effects of non-uniform predation functions and non-zero inter-cell dispersal rates.

Omitting density dependence in tortoise population growth, while allowing dispersal, prevents spatially patchy predation from affecting the population growth rate. If predation reduces growth in every cell, then the average growth of the population is also reduced. If only the ends of the population transect are complete "sinks", then average population growth is reduced by the amount of dispersal into those sinks (if a percent d is dispersed to either side of each cell, then 2d is eventually lost off the ends of the transect, and the population growth rate is depressed by 2d percent). If predation creates additional complete sinks in the midst of the population, those contiguous cells that include at least one growing cell will eventually grow at the rate of the cell with the highest growth rate (minus 2d percent). However, if tortoise growth were density dependent, all cells would eventually reach a carrying capacity, after which the amount of individuals they disperse would be fixed. Cells with pre-immigration growth rates of less than 1.0 would not continually benefit from the exponentially increasing dispersal that drives their growth rates to the maximum in the current model.

It would be straightforward to make cell growth density dependent in this model. However, the form of density dependence, about which we have no knowledge, would so drastically affect predictions of tortoise sensitivity to the predation function that the exercise would be nearly futile. For example, tortoise density dependence could result from reduced female egg production when the number of adults feeding within a cell exceeds some limit.

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Alternatively, the growth-limiting factor could be the number of "hiding places" where a hatchling can successfully take refuge from predation. Tortoise population growth would respond very differently to raven predation on hatchlings depending on which of these mechanisms was operating. If the latter mechanism operates, ravens may be simply displacing other predators as a constant mortality factor that depends more on the physical qualities of tortoise habitat than on the biological composition of the community.

The predictive capacity of our model may be further limited by the omission of density dependence in tortoise dispersal. The potential importance of this factor can be visualized using the diagrams in Fig. 3. If tortoises move toward areas of lower density, individuals in the clear region, who would not normally be impacted by predation in the shaded region, will be lost. Raven predation strategy A creates a precipitous decline in tortoise densities across a relatively narrow region, whereas strategy B creates a shallowly sloping tortoise density gradient across a wider region. The degree to which tortoise dispersal is (hypothetically) an inverse function of density gradient determines how effectively each strategy can lower overall population growth. The stronger this relationship, the higher the rate of loss will be from the population cells on either side of predation strategy A relative to those on either side of strategy B. There are of course many strategy variations on this theme, but the general problem remains: we cannot predict overall population decline given spatially differential predation without knowledge of tortoise reaction to spatial population variation.

Our model has also ignored the possibilities of temporal variation in raven predation and of different dispersal capacities of tortoise stage classes. Again, these factors can strongly influence the effectiveness of raven predation. If ravens were using tortoises as a major food source, we would expect them to track tortoise density both spatially and temporally, reducing the impact of tortoise dispersal behavior on the effect of predation. However, if raven activity is concentrated at sites that offer sustained food resources, such as roads and landfills, we would expect tortoise dispersal to remain important. Of course, this importance also depends on the existence of a positive relationship between the dispersal capacity of a stage class and the predation it experiences. If hatchlings are the predominant prey, then considering the dispersal behavior of hatchlings is of major importance. There may still be a need to consider the dispersal behavior of adults, however, as these would be capable of dispersing across corridors of high raven density in order to colonize, recolonize or rescue populations cut off by such corridors.

CONCLUSION

It appears that much research will be necessary to establish the effect of spatially structured raven predation on desert tortoise populations. Even such fundamental variables as the functional form of raven predation over space, the mechanism(s) limiting tortoise density, and tortoise dispersal behavior are relatively unknown. However, the necessity of determining these factors is brought into question by the predictions of a simple model that incorporates only uniform predation across a tortoise population. In order to lower a population growth rate from 1.02 to just below 1.0, a decrease of almost 25% in the survival of tortoises under 5 years old is necessary. Given that over 70% of a tortoise population can be comprised of such hatchlings (Biehl 1990), raven predation would have to account for an extremely large number of tortoise deaths in order to be the sole force behind the decline of
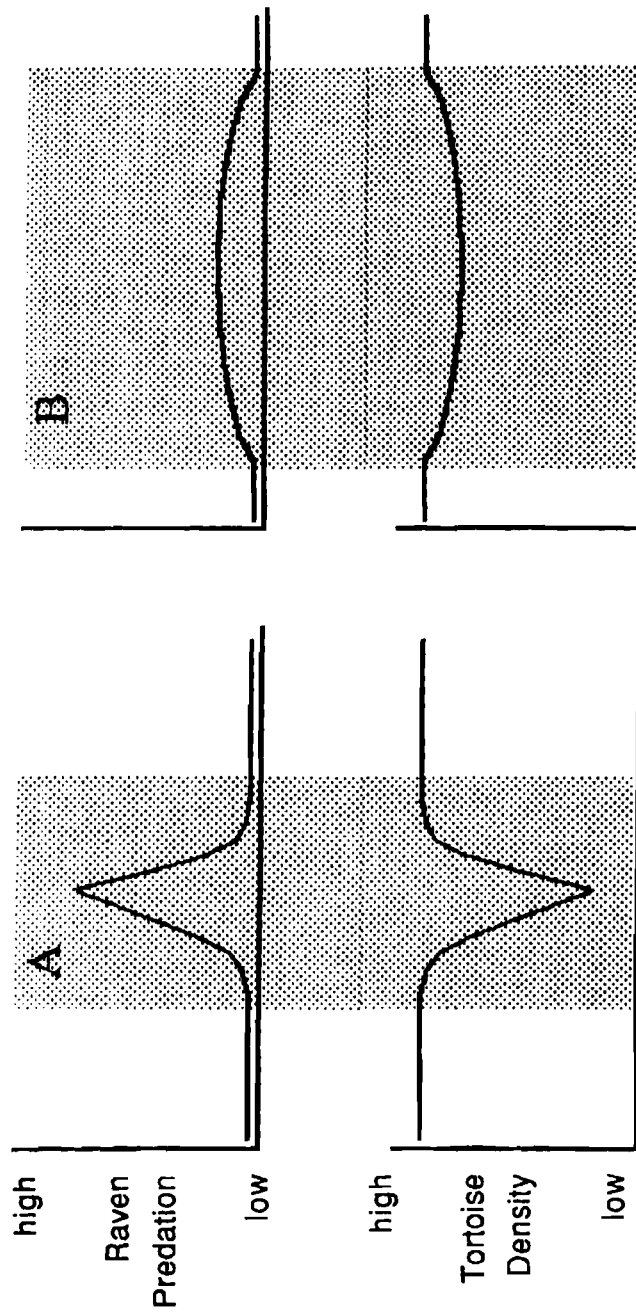
Transect across tortoise-raven habitat

Figure 3. If tortoise dispersal rates are inversely related to the tortoise density gradient, populations under raven predation strategy A will suffer higher losses due to dispersal into the predation zone than will populations under predation strategy B.

a population. It may be most efficient to focus research efforts first on whether or not ravens are capable of approaching this magnitude of predation on desert tortoises.

ACKNOWLEDGEMENTS

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