



## Modeling Population Viability for the Desert Tortoise in the Western Mojave Desert

Daniel Doak; Peter Kareiva; Brad Klepetka

*Ecological Applications*, Vol. 4, No. 3. (Aug., 1994), pp. 446-460.

Stable URL:

<http://links.jstor.org/sici?sici=1051-0761%28199408%294%3A3%3C446%3AMPVFTD%3E2.0.CO%3B2-V>

*Ecological Applications* is currently published by Ecological Society of America.

---

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/about/terms.html>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/esa.html>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

---

The JSTOR Archive is a trusted digital repository providing for long-term preservation and access to leading academic journals and scholarly literature from around the world. The Archive is supported by libraries, scholarly societies, publishers, and foundations. It is an initiative of JSTOR, a not-for-profit organization with a mission to help the scholarly community take advantage of advances in technology. For more information regarding JSTOR, please contact [support@jstor.org](mailto:support@jstor.org).

## MODELING POPULATION VIABILITY FOR THE DESERT TORTOISE IN THE WESTERN MOJAVE DESERT<sup>1</sup>

DANIEL DOAK,<sup>2</sup> PETER KAREIVA, AND BRAD KLEPETKA<sup>3</sup>

Department of Zoology, University of Washington, Seattle, Washington 98195 USA

**Abstract.** The desert tortoise is a threatened species living in the deserts of the American Southwest. Using size-structured demographic models, we analyzed the status of the tortoise in the Western Mojave desert and evaluated the effectiveness of possible management measures. Our demographic analyses agree with the trends reported by field censuses in showing rapid population decline. Importantly, simulations that include variation and correlation in vital rates yield highly variable forecasts of population growth, indicating the uncertainties inherent in even short-term projections of tortoise population sizes. To determine where conservation efforts and data collection should be focused, we performed a series of sensitivity analyses in which the effects of changing different vital rates were quantified. We found that the rate of population growth is most sensitive to the survival of large adult females and that improving survival of this size class to reputedly "pristine" rates could reverse population declines; in contrast, large improvements in other vital rates will not, alone, reverse population decline. Thus, shooting, off-road vehicles, upper respiratory tract disease (URTD), and other major sources of adult mortality should be the primary focus of management strategies. Finally, we discuss the impact of the proposed expansion of the U.S. Army's Fort Irwin, which would reduce the Western Mojave tortoise population by  $\leq 13\%$ . We argue that the expansion could have a grave impact on the long-term population viability of the tortoise, but that this impact will be a function of the management of remaining tortoise habitat. We conclude that, although many anthropogenic impacts threaten the tortoise, the species' future could be bright, provided that research and land-use planning focus on biologically important aspects of its life history.

**Key words:** *demography; desert tortoises; Gopherus agassizii; viability analysis; Western Mojave; Xerobates.*

### INTRODUCTION

The desert tortoise, *Gopherus agassizii*, inhabits a wide range of desert environments in the American Southwest (Patterson 1982). Like many other turtle and tortoise species worldwide, its numbers are dwindling and it faces the possibility of extinction over large portions of its range (National Ecology Research Center [NERC] 1990). Indeed, the tortoise's plight prompted the U.S. Fish and Wildlife Service (USFWS) to give the species an emergency endangered-species listing in 1989, to list the species as threatened in 1990, and to issue both a draft recovery plan and a proposal for critical habitat in 1993 (USFWS 1993a, b). Although population declines are occurring over large sections of the species' range, the tortoise appears to be faring least well in the Western Mojave desert of California, where, not coincidentally, habitat destruction due to human disturbances is widespread (Chambers 1990, NERC 1990).

The desert tortoise's plight in the Western Mojave

has been widely publicized. Indeed, the tortoise has become to the Mojave what the Northern Spotted Owl is to the ancient forests of the Pacific Northwest, an environmental indicator and a legal tool widely used in efforts to preserve an ecosystem. However, ecological information on the tortoise is limited, as have been quantitative evaluations of its status (but see NERC 1990, USFWS 1993). Nonetheless, it may be possible to use population models to illuminate the most efficient strategies for tortoise preservation (for comparable examples involving other threatened species, see Crouse et al. 1987, Menges 1990, Thomas et al. 1990). We report here such an analysis, in which stage-based demographic models form the core of the study.

Our use of stage-based models for population viability analysis differs from most published stage-based models in two ways. First, when assessing the tortoise's current situation and the seriousness of different threats to its viability, we pay particular attention to the importance of temporal variability. Our incorporation of variability includes straightforward estimates of mortality and growth variation from field data, as well as a novel attempt to include correlation among demographic rates in their response to environmental variation. Second, we use our models not only to address threats to the tortoise, but also to ask how best to prioritize future data collection. Although there is an

<sup>1</sup> Manuscript received 6 January 1992; revised 9 May 1993; accepted 6 October 1993.

<sup>2</sup> Present address: Department of Environmental Studies, University of California, Santa Cruz, California 95064 USA.

<sup>3</sup> Present address: Department of Entomology, North Carolina State University, Raleigh, North Carolina 27695 USA.

abundance of demographic data on tortoises (albeit almost exclusively in unpublished government reports), major gaps in the sampling and data force one to engage in a good deal of "guessing" for even the simplest analyses. We use our models to draw conclusions about the relative benefits of further research on different life stages, and on different specific mortality sources.

#### THE DESERT TORTOISE IN THE WESTERN MOJAVE DESERT

Most plant communities of the Mojave desert are dominated by creosote bush, *Larrea tridentata* (NERC 1990) and exhibit, in comparison with the adjacent Sonoran desert, a low diversity of perennial species (Shreve 1942, Vasek and Barbour 1977). The area typically receives scattered winter rains, leading to the germination and growth of the spring annuals and grasses that form the majority of the desert tortoise's yearly food supply (Nagy and Medica 1986). Tortoise activity is centered in the spring, when tortoises' ephemeral food sources are available. Fall rains are unreliable, but when they do occur tortoises may again feed on the resulting annuals. Tortoises spend much of the remaining year in burrows, but may quickly emerge to drink and feed following chance rainstorms (Nagy and Medica 1986).

Tortoises breed during the spring growing season (Turner et al. 1986), with males actively searching within their home ranges for females (Berry 1986a). Following mating, females lay one or two clutches of 1-7 eggs each (Turner et al. 1986). Hatching times are poorly known, but the majority of hatchlings appear to emerge in late spring and early fall. Upon hatching, tortoises are  $\approx 45$  mm long (maximum carapace length, MCL). Females become reproductively active at  $\approx 90$ -105 mm MCL and commonly reach lengths  $> 220$  mm. Like most turtle species (Wilbur and Morin 1988), desert tortoises suffer high mortality rates as eggs and hatchlings and low mortality rates as adults.

Variation in growth rates between individuals (Turner et al. 1987) and the difficulty in aging individuals (Berry 1987, but see Germano 1988) make it impossible to associate a particular age with reproductive maturity or to report a maximum life-span with any confidence. Therefore, we classify individuals by size rather than age in all of our models. Our decision to build size-based models was also dictated by the fact that the largest and most comprehensive data base for tortoise growth and mortality has been indexed by size (MCL) rather than age (Berry 1984, 1990).

Prior to modern human encroachments, much of the Western Mojave was probably good tortoise habitat (Berry 1984). Importantly, desert tortoises can successfully live and reproduce in a broad array of desert habitats (NERC 1990). With the exception of soil type and topography (Wilson and Stager 1989), desert tortoises do not currently appear to be limited so much

by narrow habitat requirements as by human disturbance.

#### THREATS TO THE DESERT TORTOISE

Humans directly impact tortoises in a variety of ways (reviewed in Berry and Nicholson 1984, USFWS 1993). These include: conversion of tortoise habitat to agricultural and urban lands, degradation of habitat by off-road vehicles (ORVs), intentional killing of tortoises (which can account for up to 14% of all known mortality in some areas; Berry 1986b), and killing of tortoises on highways, roads, and ORV trails.

One major, and imminent, threat to tortoise populations is a proposed expansion of the U.S. Army's Fort Irwin (Chambers 1990). This expansion is predicted to destroy between 3 and 13% of the Western Mojave tortoise population (depending on the estimate of tortoise densities used and on which of several expansion alternatives is selected; Chambers Group 1990, 1991). The loss of such a large fraction of the total population, along with a substantial amount of tortoise habitat, is potentially of dire consequence to the population viability of the species. Indeed, the need to assess the threat posed by the Fort Irwin expansion, in the context of other dangers faced by the desert tortoise, was the original motivation for our work (Chambers 1991).

Humans can also have less blatant detrimental impacts that operate by modifying the tortoises' relationships with other species. Three such "indirect" threats to tortoises are thought to be especially important: livestock grazing, raven predation, and upper respiratory tract disease (URTD). Controlled field experiments (such as grazing exclusions matched with controls or paired contrasts between diseased and disease-free populations) testing the role of these factors have not been published. For that matter, even simple quantitative analyses establishing a statistically significant correlation between these indirect threats and rates of tortoise decline are lacking. Nonetheless, the natural history of tortoises and purely observational data suggest that grazing, raven predation, and URTD warrant serious evaluation.

Grazing by cattle and sheep reduces the amount of forage available for tortoises, which in turn may reduce tortoise survival, growth, and fecundity (Berry 1978, NERC 1990). Further, cattle and sheep trample tortoises and their burrows and reduce perennial plant cover, all of which may negatively impact tortoise populations (Berry 1978, NERC 1990). The combination of these effects on tortoises means that although grazing is generally quite infrequent in any one locale, it is still likely to have serious impacts on tortoise populations (USFWS 1993). However, while it is highly plausible that grazing is detrimental to tortoises, the lack of quantitative studies of grazing effects (NERC 1990, USFWS 1993) prevents us from addressing this threat in our modeling.

TABLE 1. The years in which the Bureau of Land Management's Western Mojave study sites were sampled for tortoise mark-recapture data (Berry 1990).

Fremont Valley	DTNA* Interior	DTNA* Interpretive Center	Fremont Peak	Kramer Hills	Stoddard Valley	Lucerne Valley	Johnson Valley
			1977				
1979	1979	1979	1980	1980		1980	1980
1981	1982	1985	1985	1982	1981		
1987	1988	1989	1989	1987	1987	1986	1986

\* Desert Tortoise Natural Area.

Although unable to harm larger tortoises, ravens will attack and kill individuals < 103 mm MCL (BLM 1990, USFWS 1993). Ravens are associated with human activity, particularly landfills, and their populations are believed to have increased with increasing human populations in the Mojave. Berry (1985) has hypothesized that recent increases in rates of juvenile mortality among tortoises can be attributed to increases in raven populations and hence to raven predation. However, the NERC (1990) suggests that the evidence for this pattern in the Western Mojave is equivocal.

URTD was first identified in desert tortoise populations in the mid-1980s, and its incidence is reported to have increased dramatically within the past few years (FaunaWest Wildlife Consultants 1989, NERC 1990). Both the initial introduction and its rate of spread (by release of pet tortoises) may be attributable to humans. URTD is now thought to be caused by a *Mycoplasma* species with possible confounding effects of a *Pasteurella* bacterium (Jacobson and Gaskin 1990, Jacobson et al. 1991, USFWS 1993), but otherwise very little is known of the etiology, transmission, and morbidity of URTD, or even whether the disease is capable of killing healthy individuals or only those already weakened by starvation, drought, and other factors (NERC 1990, USFWS 1993). The disease leads to nasal congestion, lethargy, and loss of appetite, eventually resulting in death. Although the incidence of URTD in infected populations is higher for larger tortoises than for small-

er ones, individuals in all size classes can be infected at high frequencies (FaunaWest Wildlife Consultants 1989).

Although desert tortoises face multiple threats, almost 25% of the remaining tortoise habitat in the Western Mojave is still undisturbed or only moderately disturbed, and the entire Western Mojave population numbers in the tens or hundreds of thousands (Chambers Group 1990). Thus, there are many possibilities for tortoise preservation, especially if the Bureau of Land Management (BLM, which controls the majority of the undisturbed land) can identify and implement appropriate management policies.

#### PRIMARY DATA SOURCES

At a minimum, realistic population modeling relies on estimates of vital rates for the species in question. Since there are almost no published demographic studies for the desert tortoise (and absolutely none for the Western Mojave region), we were forced to rely heavily on unpublished government reports and on unanalyzed mark-recapture data gathered for the BLM under the supervision of Dr. Kristin Berry at eight permanent study plots throughout the Western Mojave desert (see Table 1; descriptions of the sites can be found in Berry 1984 and 1990). Further details on our analysis of this data are presented in Chambers Group (1991).

#### MODEL FORMULATION AND ESTIMATION

We report all vital rates with respect to eight different classes of tortoises (Table 2). The first class is age-based, representing yearlings. All the remaining classes are based on size and were chosen to match those used by BLM field biologists for the last two decades. Although it would be possible to simplify the modeling by reducing the number of size classes, we felt that when developing a viability model for practical, as well as academic, insight, it was best to match the model to the standard data categories used by biologists working with the species. The demographic parameters that characterize each size class in our model are yearly

TABLE 2. Desert tortoise size classes as defined by Berry (1984) and used in our models.

Class	Name	Maximum carapace length (mm)
0	Yearling	
1	Juvenile 1	<60
2	Juvenile 2	60-99
3	Immature 1	100-139
4	Immature 2	140-179
5*	Subadult	180-207
6*	Adult 1	208-239
7*	Adult 2	>240

\* Reproductive size classes.

rates of survivorship, growth, and reproduction. Growth is defined as the probability, conditional on survival, of moving from one size class to the next largest one; of the >1400 individual transitions in the BLM data set, no tortoises either shrank or were estimated to grow more than one size class in a year. Using mark-recapture data from the eight BLM study sites, we directly calculated means and variances of growth and survivorships for size classes 2 through 7 (Table 3). Since no data are available on the demographic rates for yearlings and size class 1 tortoises, we made the optimistic assumption that they are the same as those for size class 2 individuals.

When combining mark-recapture data from several different sites, one has the option of calculating simple averages or weighting samples according to population size, within-site standard errors, and so forth. We adopted the most straightforward convention: a single sample for our estimates of means and standard deviations (reported in Table 3) was the observed growth (or survival) recorded for one site, during one time interval (thus two different censuses for growth and three for survival), standardized to a per-year rate on the assumption that the process was constant within the time interval bracketed by the censuses. Since our goal was to characterize tortoise demography across the Mojave over many different years, this definition of samples seemed logical. We did, however, experiment with alternative approaches and found that the general results were robust to the details of how samples were combined; for example, weighting samples by the number of tortoises marked and recaptured produces results very similar to those reported in Table 3. It is important to note that the standard deviation estimated for each rate includes both temporal and spatial variation, since the collection of samples combines different sites and different years. Ideally, one would like to separate temporal from spatial variation; however, the erratic sampling evident in Table 1 prevents the separation of temporal variation within sites from spatial variation between sites.

When different demographic rates vary from year to year, their variations are likely to be correlated (Tuljapurkar 1990), and this correlation can have significant impacts on population growth (Caswell 1989, Tuljapurkar 1990). To examine this effect, we estimated the population-level correlations between size-specific growth and survival rates (data were not adequate to estimate variation in reproductive rates). Although the small sample sizes available for making these calculations ( $n = 4-11$ ) warn against putting too much faith in the resulting correlation estimates, we felt that it was worthwhile to use this information in some model simulations. To include correlation effects in our model, we made the simplifying assumption that correlations between vital statistics were caused solely by a shared dependence of each demographic rate on a single environmental factor (e.g., rainfall), denoted  $E$ . Then, if

TABLE 3. Demographic rates for female desert tortoises. Growth and survival rates for size classes 2-7 are calculated for Western Mojave populations.  $n$  = the number of site-data combinations for which separate estimates were made of each growth or survival rate.

Demographic rate	Mean	SD	$n$	
Growth <sub>2</sub>	0.208	0.268	6	
Growth <sub>3</sub>	0.280	0.158	11	
Growth <sub>4</sub>	0.287	0.261	9	
Growth <sub>5</sub>	0.269	0.187	10	
Growth <sub>6</sub>	0.018	0.037	18	
Survival <sub>2</sub>	0.716	0.232	8	
Survival <sub>3</sub>	0.839	0.176	8	
Survival <sub>4</sub>	0.785	0.147	8	
Survival <sub>5</sub>	0.927	0.071	8	
Survival <sub>6</sub>	0.867	0.129	8	
Survival <sub>7</sub>	0.860	0.123	8	
Reproduction estimate				
	Low*	Med-low*	Med-high†	High†
Yearling production <sub>5</sub>	0.042	0.42	1.30	2.22
Yearling production <sub>6</sub>	0.069	0.69	1.98	3.38
Yearling production <sub>7</sub>	0.069	0.69	2.57	4.38

\* Reproductive estimates based on Western Mojave production of yearlings.

† Reproductive estimates based on Goffs, California estimates of hatchling production (Turner et al. 1986, 1987), multiplied by mean yearly survival rates estimated for the Western Mojave.

we have two demographic rates,  $X$  and  $Y$ , that are both partially composed of  $E$ , one can write

$$\text{corr}(Y, X) = \text{corr}(E, X) \cdot \text{corr}(E, Y).$$

Since we do not know how  $E$  itself varies, or the actual value of either  $\text{corr}(E, X)$  or  $\text{corr}(E, Y)$ , we arbitrarily assigned a value of 1 to  $\text{corr}(E, X)$ . Then  $\text{corr}(E, Y) = \text{corr}(Y, X)$ . Now consider a third demographic rate,  $Z$ . Since we know  $\text{corr}(Y, Z)$ , we can now estimate  $\text{corr}(E, Z)$  as

$$\text{corr}(E, Z) = \frac{\text{corr}(Y, Z)}{\text{corr}(E, Y)} = \frac{\text{corr}(Y, Z)}{\text{corr}(Y, X)}.$$

In this way, we estimated the correlation between our hypothetical  $E$  and all of the demographic rates. We arbitrarily assigned the survival of size class 2 as being completely correlated with  $E$  (the choice of which parameter is assumed to be equivalent to  $E$  has no effect on the resulting correlation structure; see Chambers [1991]). We made multiple estimates of the correlations of each of the other rates with  $E$  by substituting each in turn into the above formula as the variable  $Y$  and then calculating all of the other correlations. We then used the mean correlation for each rate as our estimate of its actual correlation with  $E$  (Table 4). The mixed negative and positive correlations with the "environment" reflect the mixture of negative and positive correlations between the estimated demographic rates themselves (Chambers Group 1991). This approach is purely phenomenological in that it simply describes

TABLE 4. Estimated correlations between  $E$ , an environmental factor (e.g., rainfall), and demographic rates of tortoise size classes 2–7 from the Western Mojave. See *Model formulation and estimation* for explanation.

Demographic rate	Correlation with $E$	
	Mean	SD
Growth <sub>2</sub>	0.379	3.248
Growth <sub>3</sub>	0.202	0.979
Growth <sub>4</sub>	0.651	2.660
Growth <sub>5</sub>	0.548	1.516
Growth <sub>6</sub>	-0.688	2.192
Survival <sub>2</sub>	1.000	0.000
Survival <sub>3</sub>	-0.269	1.318
Survival <sub>4</sub>	-0.443	2.999
Survival <sub>5</sub>	-0.367	2.577
Survival <sub>6</sub>	0.365	2.557
Survival <sub>7</sub>	-0.135	3.278

the pattern of correlation evident in the data, but does not assume any particular mechanism underlying that correlation.

When we ran a simulation for a temporally varying environment with correlation among demographic rates in each year, we first selected a value for the survival rate of size class 2 individuals according to its mean and standard deviation, assuming that survival conforms to a Beta distribution (see Doak 1989). We then randomly drew all of the other growth and survivorship probabilities from Beta distributions, assuming that they satisfied the correlation structure summarized in Table 4 and possessed the means and standard deviations stipulated for that simulation (and based on field data). Thus, this scheme allows us to easily simulate the yearly variations in a suite of correlated demographic rates, each changing according to its own mean and variance.

Our models assume that yearly sampling occurs immediately prior to egg production; the reproductive estimates we use are therefore estimates of yearling tortoise production per female of a given size class. Only size class 5, 6, and 7 females are thought to be reproductive (Turner et al. 1986, 1987). Data regarding tortoise reproductive rates are extremely rare. For the Western Mojave, no direct observations of per-capita yearling production were available, forcing us to estimate reproduction by dividing yearling counts by the number of females censused at the time those yearlings would have been born (for details see Chambers Group 1991). This calculation was especially vulnerable to underestimation error because young tortoises are much harder to find than are large tortoises (Berry 1978, 1984, Turner et al. 1987). The reproductive rates obtained for the Western Mojave by this method are what we call our "low" rates; due to the likelihood of underestimation in this calculation, we arbitrarily multiplied them by 10 to obtain "medium-low" rates (Table 3). Because of the poor data upon which these Western Mojave estimates were based, we also used

two estimates of yearling production that are based on direct observations of egg production and survival to hatching at Goffs, California, in the extreme Eastern Mojave (Turner et al. 1986, 1987). The two different Goffs estimates assume different rates of egg survival (based on two different methods of data collection; see Chambers 1991) and are corrected for the average sizes of Western Mojave females in each reproductive size class. We multiply these hatchling production rates at Goffs by our Western Mojave estimates of hatchling survival to obtain two estimates of yearling production rates that we refer to as "medium-high" and "high" reproduction (Table 3). It is important to note that the Goffs site is climatically and vegetatively different from the Western Mojave and that tortoise populations there are extremely healthy (Turner et al. 1986, NERC 1990). Hence, vital rate estimates from this area may differ substantially from those in the Western Mojave. We have found no data sufficient to estimate yearly variation in reproductive rates or their correlation with other demographic rates.

All of our analyses and simulations were of size-structured projection matrix models for female tortoises only. We do not include density dependence in any rates, due to the lack of data supporting its importance for tortoises at their current population levels. For example, there is no evidence of male limitation of female reproductive rates or of any density dependence in survival and growth rates in the BLM's Western Mojave data set (Chambers Group 1991). Neither have we found documentation of density dependence in vital rates for desert tortoises from other areas (USFWS 1993). The incidence of URTD also reveals no relationship with tortoise density (FaunaWest Wildlife Consultants 1989). This does not mean that density plays no role in tortoise demography; at high densities, we would expect density to be a factor. Even at low densities such as those now typical of the Western Mojave, variations in density may influence demography, but too weakly for our tests to detect it. In the absence of estimable density effects, we decided to omit them from our models, especially since their omission will probably lead to conservative estimates of population risks (Ginsberg et al. 1990). Similarly, we do not include between-individual differences in demography (other than differences based on size) in our analyses, as there were insufficient data available to usefully do so (Chambers 1991).

The models we present here also ignore spatial structure, because existing demographic and movement data are not extensive enough to support metapopulation or other spatial analyses. However, it is unlikely that metapopulation dynamics, in particular, are important in the Western Mojave now or will be in the near future. While tortoise populations are clearly subdivided in the Western Mojave, many of the barriers creating these subpopulations are essentially uncrossable (e.g., freeways and towns). Further, throughout the 1980s all

TABLE 5. Average population projection matrices for the Western Mojave.\*

Size class	Size class							
	0	1	2	3	4	5	6	7
0	0	0	0	0	0	0.042† 0.42‡ 1.30§ 2.22	0.069† 0.69‡ 1.98§ 3.38	0.069† 0.69‡ 2.57§ 4.38
1	0.716	0.567	0	0	0	0	0	0
2	0	0.149	0.567	0	0	0	0	0
3	0	0	0.149	0.604	0	0	0	0
4	0	0	0	0.235	0.560	0	0	0
5	0	0	0	0	0.225	0.678	0	0
6	0	0	0	0	0	0.249	0.851	0
7	0	0	0	0	0	0	0.016	0.860

\* We show, in condensed form, the four matrices that are constructed with average growth and survival probabilities shown in Table 3. The matrices differ only in their reproductive rates (see Table 3), as shown on the first row of the table: † = low reproduction, ‡ = medium-low, § = medium-high, || = high.

tortoise subpopulations surveyed in the Western Mojave suffered rapid, simultaneous declines (Berry 1990, Berry and Avery 1990). Average annual rates of decline in the most recent estimated population densities ranged from 3 to 18% at seven of the eight BLM sites (Berry 1990; the eighth site showed a 3% increase between 1979 and 1986; however, Berry attributes this result to sampling problems and cites evidence indicating that this population is also declining). In the absence of frequent dispersal between subpopulations and without independent increases and decreases in local densities, extinction/colonization processes or rescue effects can, at best, be of only secondary importance in determining population dynamics. In this situation there is little point in pursuing spatial modeling.

#### MODELING TORTOISE VIABILITY IN A CONSTANT ENVIRONMENT

##### *Theoretical "long-term" population growth rates*

The simplest information to obtain from a population projection matrix description of a population is its intrinsic annual multiplication rate,  $\lambda$ , which is equivalent to the dominant eigenvalue of the matrix (Caswell 1989). This rate of population increase (or decrease) is defined for populations whose size distribution has stabilized (which occurs only after several years of population change in a constant environment). The annual multiplication rate is a powerful summary of the viability of a population.

We constructed four "average" projection matrices that were meant to span the range of gloomy to optimistic assumptions by combining the mean rates of survival and growth (averaged over all BLM Western Mojave sites) with our four different estimates of reproduction (low, medium-low, medium-high, and high; Table 5). These matrices contain only three kinds of elements: yearling production rates; the probabilities of surviving and growing from one size class into the next largest one, which are equal to (survival proba-

bility)(growth probability); and the probabilities of surviving but remaining the same size, which are equal to (survival probability)(1 - growth probability). Throughout our presentation "growth" and "survival" will refer to the measurable vital rates in Table 3, rather than to the matrix elements, which are combinations of these rates. Because we had reasonably complete growth and survival data from a few sites and time intervals, we also constructed matrices by combining these suites of site- and time-specific growth and survival probabilities with our four different reproductive rates.

The multiplication rates (or dominant eigenvalues) associated with the different site- and time-specific matrices vary considerably (Table 6), with approximately half of the matrices predicting increasing populations ( $\lambda > 1$ ), and the remaining half predicting a continuing decline in tortoises. It is important to note that of the 14 matrices predicting population growth, 7 include one or more survivorship estimates equal to one (a result of small sample sizes) and 6 others are based on survivorship data obtained from 1973 to 1979, when tortoise populations are believed to have been much healthier than they are currently (Berry and Avery 1990, USFWS 1993). Notably, all four "average" matrices, even the one using the most optimistic estimate of reproductive rates, predict population decline (Table 6). Due to the severe problems of small sample sizes used in estimating the survival probabilities, we believe that these "average" matrices, which are based on the most data, provide the best summary of tortoise demography. In addition to their use of all the available data, their prediction of a general decline in tortoises is in agreement with the widespread population declines in the Western Mojave that BLM censuses have suggested (Berry 1990, Berry and Avery 1990). Therefore, we use these "average matrices" in all further analyses.

##### *Sensitivity analyses*

We present here only the sensitivity results for two matrices: the average growth-and-survival matrix for

TABLE 6. Annual multiplication rates of transition matrices constructed from different sites and dates.

Plot	Years of growth data	Years of survival data	Hatchling production rates			
			Low	Med-low	Med-high	High
2	All	1976-1978-1979	0.969	1.001	1.031	1.053
	All	1978-1979-1981	1.009*	1.053*	1.121*	1.152*
	All	1979-1981-1987	0.839*	0.907*	0.951*	0.978*
3	All	1973-1978-1979	0.940	1.027	1.114	1.158
	All	1978-1979-1988	0.887*	1.014*	1.126*	1.176*
4	1979	1979-1985-1989	0.863	0.933	0.990	1.024
7	All	1980-1982-1987	0.915	0.916	0.916	0.918
Average	All	All	0.875	0.918	0.958	0.982

\* Matrices for which survival estimates for one or more size classes were  $> 1$ , and hence were set equal to one for the calculation of multiplication rates.

all of the Western Mojave combined with the medium-low estimates of reproduction, and the average matrix combined with the medium-high estimates of reproduction (Table 5). We feel these two matrices represent our best summaries of tortoise demography, since they include survival and growth rates averaged over all sites, and the two intermediate estimates for yearling production. Use of the "high" or the "low" reproductive rates does not alter the qualitative results of our sensitivity analyses.

We determined sensitivity to small changes in annual survival, growth, and reproductive rates by calculating elasticity values (Caswell 1989) for these "medium-low" and "medium-high" matrices. Note that we calculated the elasticities of the measurable vital rates (Table 3), not the combinations of these rates that comprise the actual elements of the projection matrices (Table 5). Elasticities measure the proportional change in the multiplication rate of the population, given a proportional change in a single demographic rate, when all other demographic rates used to construct the matrix are held constant. The elasticities we obtained indicate that tortoise population growth is far more sensitive to changes in survival rates than to either growth or reproduction rates (Figs. 1 and 2). The relative lack of sensitivity to changes in growth rates or yearling production rates and the large sensitivity to survival rates emphasize the need to better quantify survival rates, particularly given Berry and Avery's (1990) evidence of rapidly decreasing survivorships. The other striking result from these calculations is the extent to which the elasticity of survival rates for size class 6 stands out as especially high when compared to all other demographic entries (Figs. 1 and 2); this result suggests that any management policy having a substantial impact on the survival of size class 6 females is likely to produce the most dramatic change in population trends. Finally, the sensitivities shown by the two matrices are quite similar (compare Fig. 1 to Fig. 2), indicating that the results are robust to large shifts in estimated reproductive rates.

Although elasticities aptly summarize the relative effects of small modifications in different demographic

rates, they do not necessarily reflect the outcome of modifying demographic rates by a large amount (Crouse et al. 1987, Caswell 1989), such as would occur due to management for tortoise recovery. To assess the effects of large increases or decreases in selected demographic rates resulting from changes in management, we computed the population multiplication rate for systematically modified versions of the average "medium-low" and "medium-high" matrices described above. In particular, we created new matrices by either increasing or decreasing each survival, growth, and reproductive rate (Table 3) by 20% of its original value. For the survival rates of classes 3, 5, 6, and 7, a 20% increase yields survival rates  $> 1$  (which we then set equal to one). We increased or decreased each parameter separately for each size class, except for reproductive rates; for these, we simultaneously either increased or decreased the per-capita yearling production values for all three of the reproductive size classes by 20%. The most striking result of these 20% perturbations was the difficulty of reversing the population decline predicted by our average matrices. Of the 30 "improved" matrices we examined (15 for each "average" matrix), only those with increased survival of size class 6 or 7 females yielded positive population growth, and the positive growth associated with a boosted survival of size class 7 individuals was quite marginal (Figs. 3 and 4). Similarly, a 20% decrease in size class 6 survival had a much greater impact on population growth than did a decrease in any other parameter. Thus, the results of these large-scale matrix perturbations agree well with the elasticity calculations; changes in the survival of size class 6 tortoises is clearly of premier importance to the tortoise's viability, while improvements in all other vital rates are of only secondary importance.

#### *Simulating the consequences of specific management options*

In addition to the systematic sensitivity analyses summarized above, we examined the consequences of two management scenarios that are currently being discussed or implemented: reducing human disturbance and removing ravens (BLM 1990, USFWS 1993).



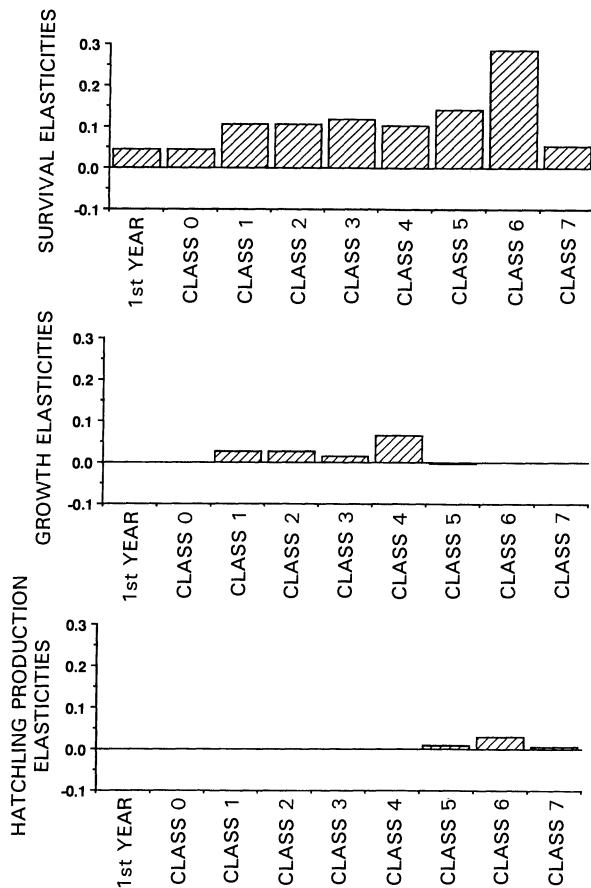


FIG. 1. Elasticities for all entries into the average projection matrix, using "medium-high" reproductive rates (see *Model formulation and estimation*). Note that for hatchling production, elasticities are reported only for size classes 5, 6, and 7, since those are the only reproductive classes in tortoises.

The tortoise populations from which our demographic estimates were obtained all suffer at least some human-related disturbance (Berry 1990), and one way of improving the tortoise's prospects would be the exclusion of human-associated mortality. To analyze the effectiveness of reducing different mortality sources (e.g., shooting, crushing, URTD), we created two matrices, using the medium-low and medium-high reproductive rates, that had survivorships increased to 98% for the three largest size classes. We focused on the three largest size classes because they are typically most vulnerable to human activities and chose an annual survivorship of 98% because this represents an optimistic estimate of tortoise survival in undisturbed areas (Berry 1978, NERC 1990, USFWS 1993). The matrices incorporating these changes yield population growth rates of  $\lambda = 1.00$  and 1.02 for the medium-low and medium-high reproductive rates, respectively. Thus, it appears that eliminating human-associated mortality in large tortoises might, alone, be enough to reverse population declines.

The BLM has advocated a policy of raven control as a means of promoting tortoise population growth (BLM 1990). To simulate such a policy, we had to guess at the effect raven control might have on tortoise demography (since the amount of juvenile mortality that can be attributed to raven predation is not well documented; NERC 1990). Because larger tortoises are safe from ravens, we restricted the reduced mortality that might result from raven control to yearlings and size classes 1 and 2. In particular, we constructed matrices with a one-third decrease in mortality among these smallest tortoises and a one-third increase in the medium-low or medium-high reproductive rates (because reproduction includes survival of hatchlings, which are especially vulnerable to ravens). The choice of a one-third reduction in mortality due to raven control is probably far more than could be expected in the real world (Chambers 1991). But even with this optimistic scenario, the benefits realized were not impressive: populations enjoying a 33% cut in mortality among smaller tortoises would still decline (with  $\lambda = 0.95$  for medium-low reproduction and 0.99 for medium-high reproduction).

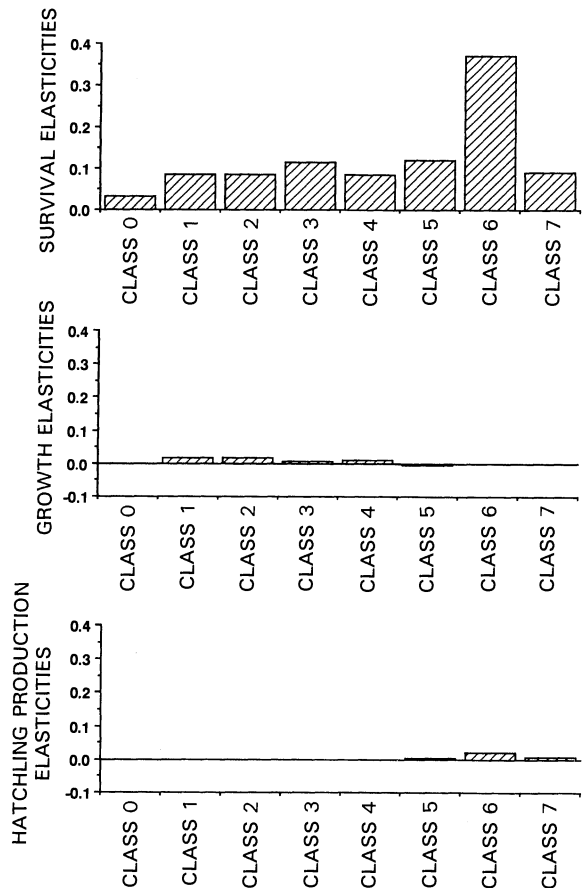


FIG. 2. Elasticities for all entries into the average projection matrix, using "medium-low" reproductive rates.

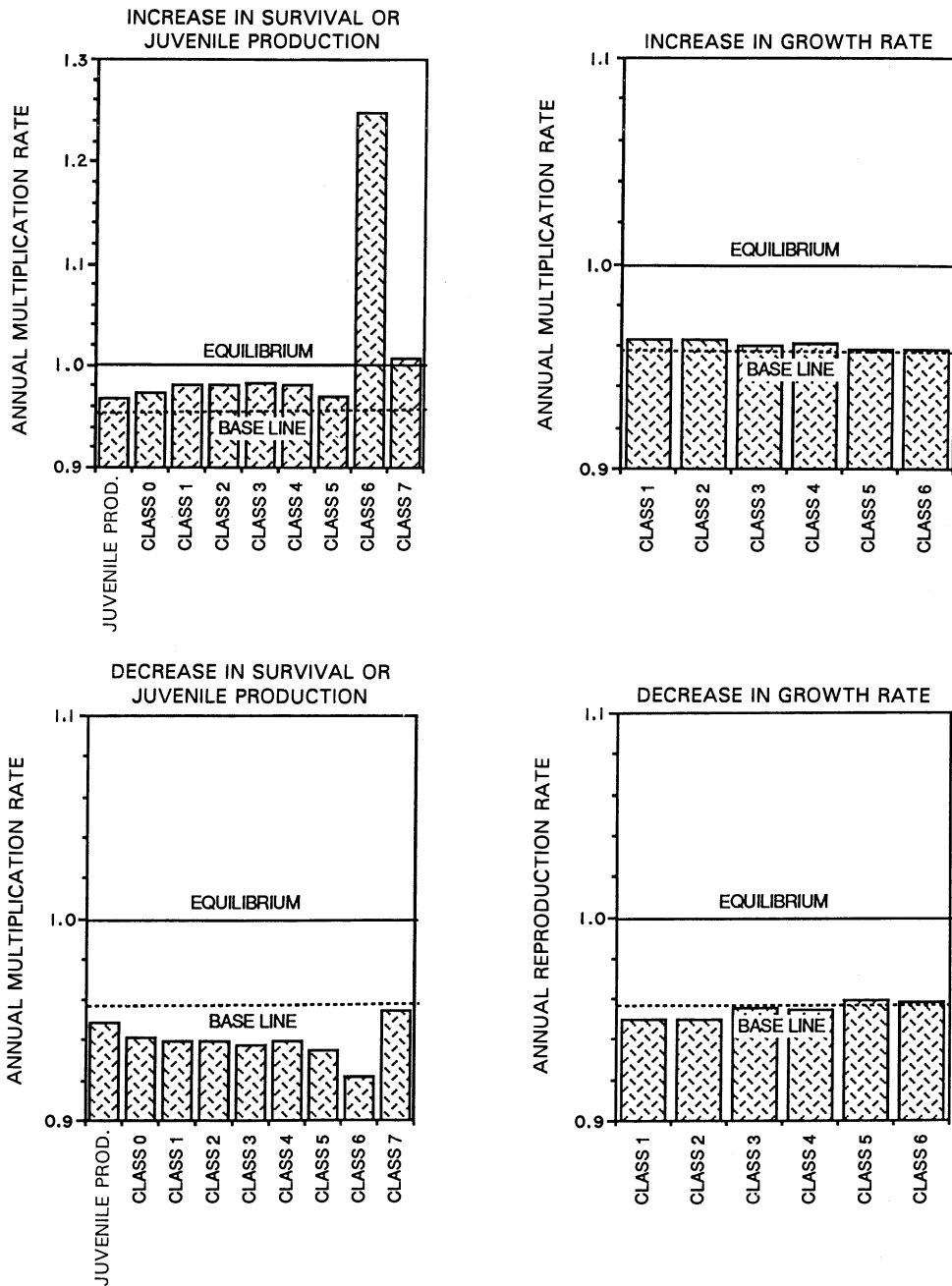


FIG. 3. The long-term population growth rate (dominant eigenvalue) produced by 20% perturbations (increases or decreases) of entries in the average projection matrix, using "medium-high" reproductive rates; --- indicates the growth rate of the baseline "unperturbed" matrix, and — separates the region of a shrinking population from the region of a growing population.

MODELING TORTOISE VIABILITY IN A  
VARIABLE ENVIRONMENT

*Methods for treating temporal variation  
in demographic rates*

Most previous efforts to evaluate the effects of temporal variation on the population dynamics of stage- or age-structured models have simulated variation by randomly drawing from two or more projection ma-

trices, each containing transition probabilities estimated over a separate time step (e.g., Bierzychudek 1982, Silva et al. 1991; but see Burgman and Gerard 1990 and Menges 1992). There are two difficulties with this approach. First, some data sets, such as the BLM data for desert tortoises, do not allow the estimation of every entry in the projection matrix for every time step or location. This can be due to experimental design problems or simply to sample sizes that are too small

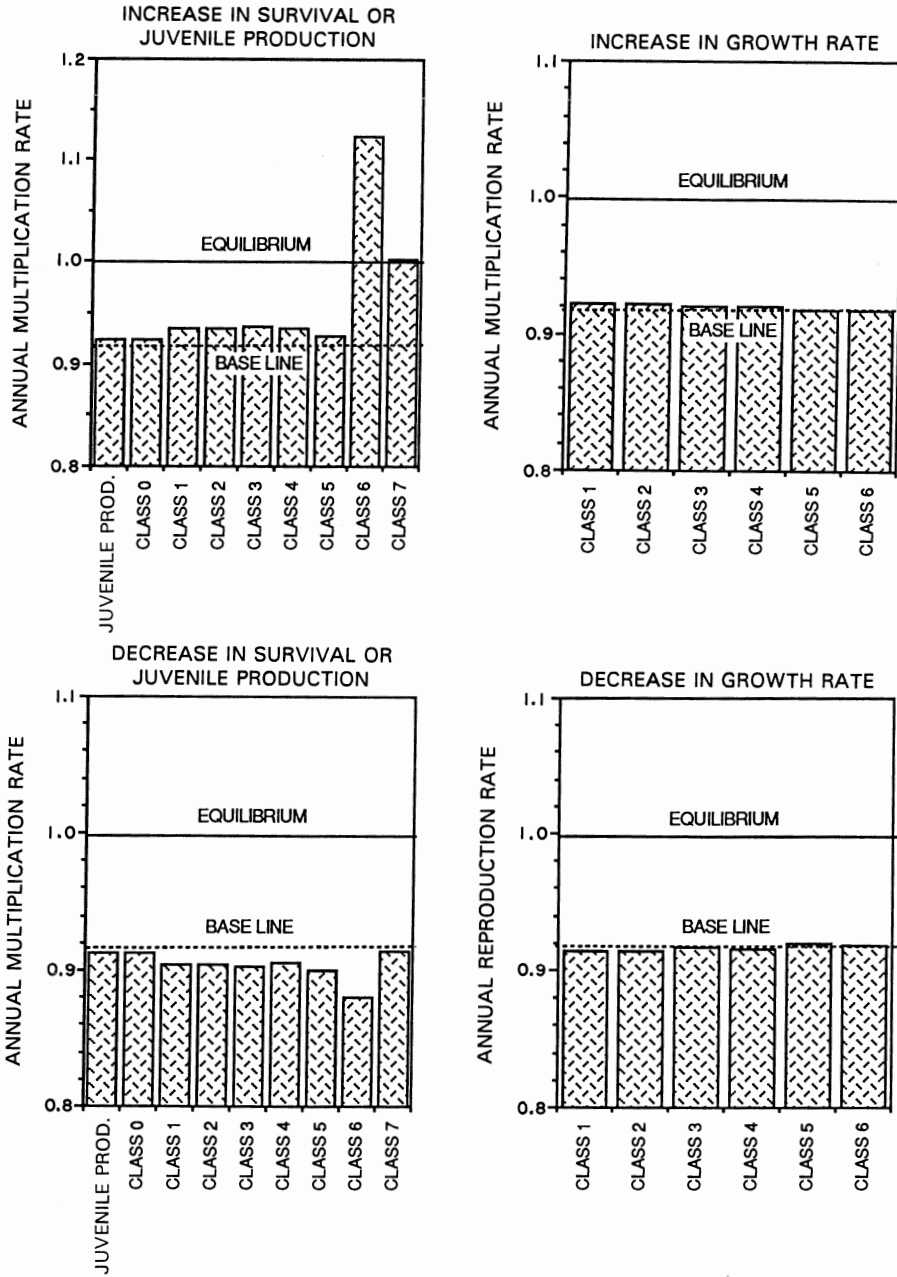


FIG. 4. The long-term population growth rate produced by 20% perturbations (increases or decreases) of entries in the average projection matrix, using "medium-low" reproductive rates. Presentation as in Fig. 3.

for the estimation of particular growth and mortality rates. If one uses only the demographic data that correspond to a complete projection matrix, a great deal of information is lost (i.e., all those data from sites or years that did not yield complete projection matrices, but that may represent good information on selected vital statistics). Second, the use of fixed matrices, each corresponding to an actual year of observations, enforces a rigid and very specific set of correlations in the variation of the demographic rates. Although these

correlations will exactly reflect the observed data, the use of fixed matrices prevents the exploration of alternative correlation structures or of the importance of correlation structure itself, separate from the means and variance of individual demographic rates.

To more flexibly model variation and correlation in demographic rates, we represented growth and survival as realizations of a Beta distribution (Doak 1989), with means and variations estimated from the BLM data sets (sample means and variances allow the estimation

of the parameters for a Beta distribution, Hastings and Peacock 1974). For some simulations we also forced the variations in different rates to be correlated with one another by assuming that the correlations arise through independent correlations with a single environmental factor that itself varies each year (for our estimation protocol see the discussion of Table 3 in *Model formulation and estimation*). Mean reproductive rates are also certain to show annual variation, but we were unable to find any data sets that allowed reasonable estimation of this variance. Consequently, we did not vary reproductive values in the simulations.

For the reasons given when discussing our analysis of constant environments, the mean survival and growth rates that we used in our variable environment models were the mean rates over all of the Western Mojave sites, which were then combined with either medium-low or medium-high reproductive rates. We performed simulations using these mean rates in combination with four different suites of variability and correlation values for each rate: (1) the variation as estimated from the entire Mojave data set (Table 3), but without any correlation among parameters; (2) the full variations and correlations as estimated in Table 4; (3) half the variation estimated from the data (since the estimates include spatial as well as temporal variation) and no correlation among parameters; and (4) half the variation and the full estimated correlation among parameters.

To account for demographic stochasticity at low population sizes, we used Monte-Carlo simulation to determine the fate of each tortoise in the population separately if the number of tortoises in any size category fell below 20 (our choice of this cutoff is based on the results of Goodman 1987). For each set of conditions, we performed 100 replicate runs, having found that simulations of  $\geq 50$  replicates were sufficient to yield stable mean results (Harris et al. 1987).

The simulations we report here were all started with a total of 444 842 females distributed among size classes to conform to the stable size distribution for the "medium-high" matrix (i.e., the matrix constructed by combining average growth and survival rates with the medium-high reproduction estimate). Our results are not dependent on the starting size distribution or precise starting number, but would of course be different if we assumed some astonishingly low total population size (since in that case the effects of demographic stochasticity might predominate). Our initial total population of 444 842 was derived from a high (in order to be as optimistic as possible) estimate of the total number of tortoises in the Western Mojave (based on the results of Chambers 1990; see Chambers 1991), adjusted for the bias toward observing larger individuals (Berry 1990, Chambers 1991). Although our simulations were initiated with what is believed to be the current tortoise population size in the Western Mojave, we do not feel that our model should be used to predict

future populations. Instead, we advocate using the model to indicate general trends in tortoise populations (i.e., increasing or decreasing) and the magnitude of uncertainty about these trends.

*Including environmental variability strongly  
influences the uncertainty of tortoise  
population projections*

Two metrics are commonly used to summarize the behavior of stochastic population growth: (1) the rate of growth of the mean population size through time, with the size at each time averaged over many replicate simulations (commonly denoted  $\log \mu$ ; see Caswell 1989), and (2) the average of the growth rates of many replicate simulations (commonly denoted  $\log \lambda$ ; Caswell 1989). For a simulation model such as ours,  $\log \mu$  is, by proof, unaffected by environmental variation in vital rates (Caswell 1989, Tuljapurkar 1990). In contrast,  $\log \lambda$  is affected by variations in vital rates and is an appropriate measure of mean population behavior. However,  $\log \lambda$ , as an average over time and simulations, still does not capture the aspect of stochastic population growth that is most important for conservation planning: the uncertainty that variable vital rates introduce into projected population sizes and growth rates, especially over the short term.

We believe that it is more commensurate with the needs and interests of population viability assessment to neglect mean population behavior, and we instead emphasize the range of outcomes possible with each set of parameter assumptions. In particular, we report 95% confidence intervals of population size for our simulation results (Fig. 5), calculated by assuming a lognormal distribution of population sizes (Caswell 1989, Tuljapurkar 1990). We calculated confidence intervals for population size, rather than mean population size, because our concern in viability analysis is with the possibility of extinction or near-extinction in any one realization of the future (i.e., any one simulated population). It is clear that both greater variation and the addition of correlation among demographic rates tend to broaden the 95% confidence intervals of population size (Fig. 5). Although the confidence limits around population size ultimately shrink as a result of the convergence on zero produced by extinctions, over the time horizon of 10–20 yr remarkable uncertainty is evident. For example, during the first decade of simulated demography, the 95% confidence intervals for the medium-high matrix with full variation and correlation include both substantial growth and precipitous decline as reasonably likely outcomes.

In addition to examining population sizes through time, it is useful to observe the range of realized population growth rates for stochastic population simulations. In particular, we show the distributions of realized average annual growth rates (realized  $\lambda$ 's) for years 25–50 for simulations using the medium-high matrix and each of our four suites of variation and

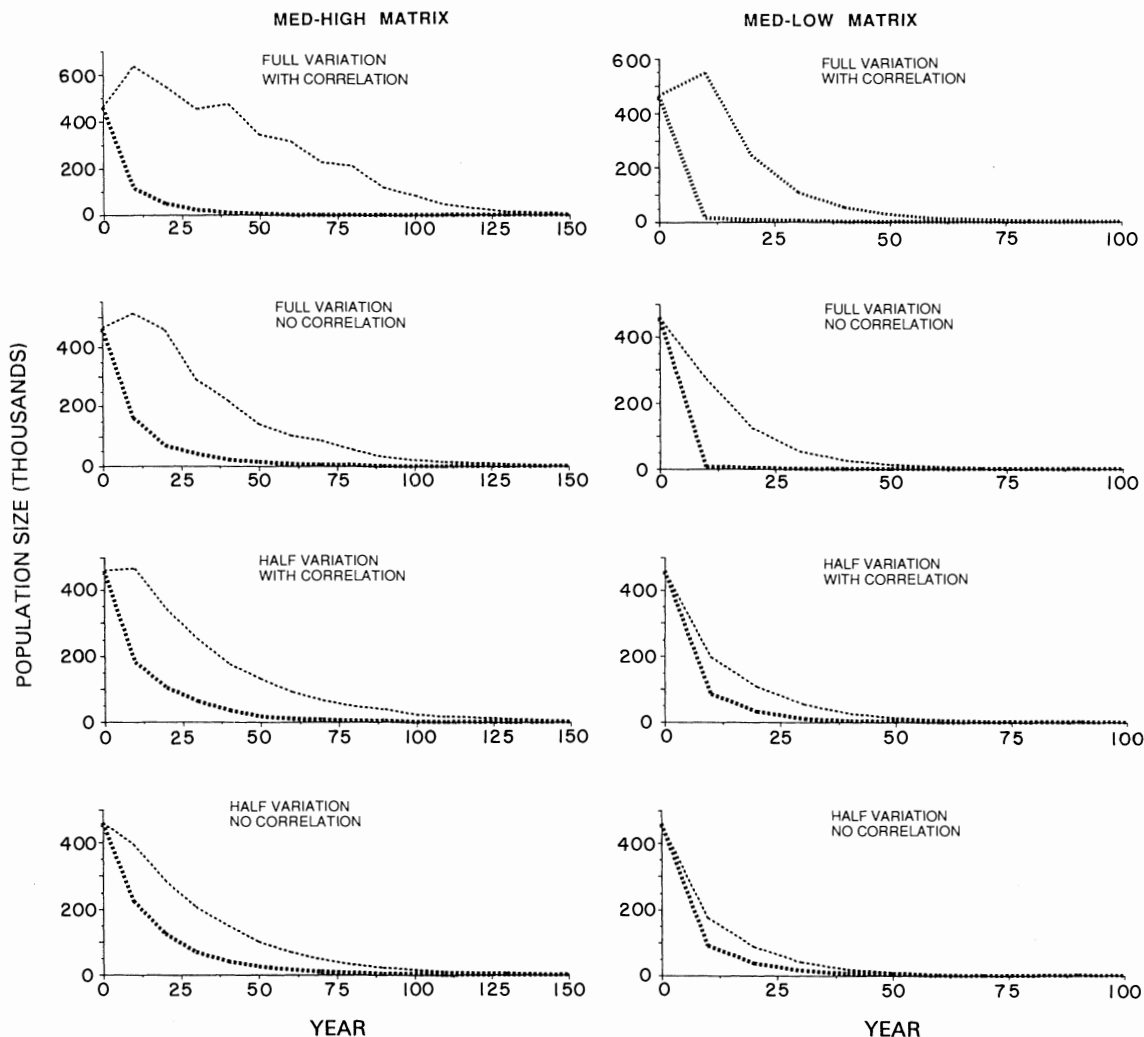


FIG. 5. The 95% confidence limits obtained from 100 simulations for each of four different types of variation, using as baseline matrices the average matrix using "medium-high" reproductive rates and the average matrix using "medium-low" reproductive rates. See *Methods for treating temporal variation in demographic rates*.

correlation values (Fig. 6). While the average growth rates are relatively unaffected by differences in the variation and correlation of vital rates (varying between 0.948 and 0.958 for the four sets of assumptions) these differences have dramatic effects on distribution of growth rates. Both increased variation and the addition of correlation between the variations lead to much wider distributions of realized population growth rates, even though we have calculated these rates as averages over 25 yr for each simulation run. If our estimates of temporal variation in demographic rates are roughly correct, then this short-term uncertainty poses serious challenges: such uncertainty means that we might observe tortoise populations increasing over the next 10 yr even when the long-term risk of extinction is high.

#### DISCUSSION

Our most obvious conclusion is that populations of the desert tortoise in the Western Mojave desert are in

grave danger. Our demographic analyses concur with field data that show tortoise populations rapidly declining (Berry and Avery 1990). More interesting than this obvious conclusion is the way in which variation and correlation in demographic rates affect the tortoise's prognosis. When environmental variation at levels estimated directly from field data is included in the simulations, one obtains extremely broad 95% confidence limits for population sizes over the next two decades. Correlation among demographic parameters in their response to this variation adds further width to these confidence bands (Fig. 5), illustrating that such correlation can markedly elevate the uncertainty of population projections, particularly the possibility of extinction. Clearly, we are in no position to predict with any confidence what will happen to the tortoises over the next few years, even whether populations will increase or decrease. Whereas population projections based solely on mean rates would predict substantial

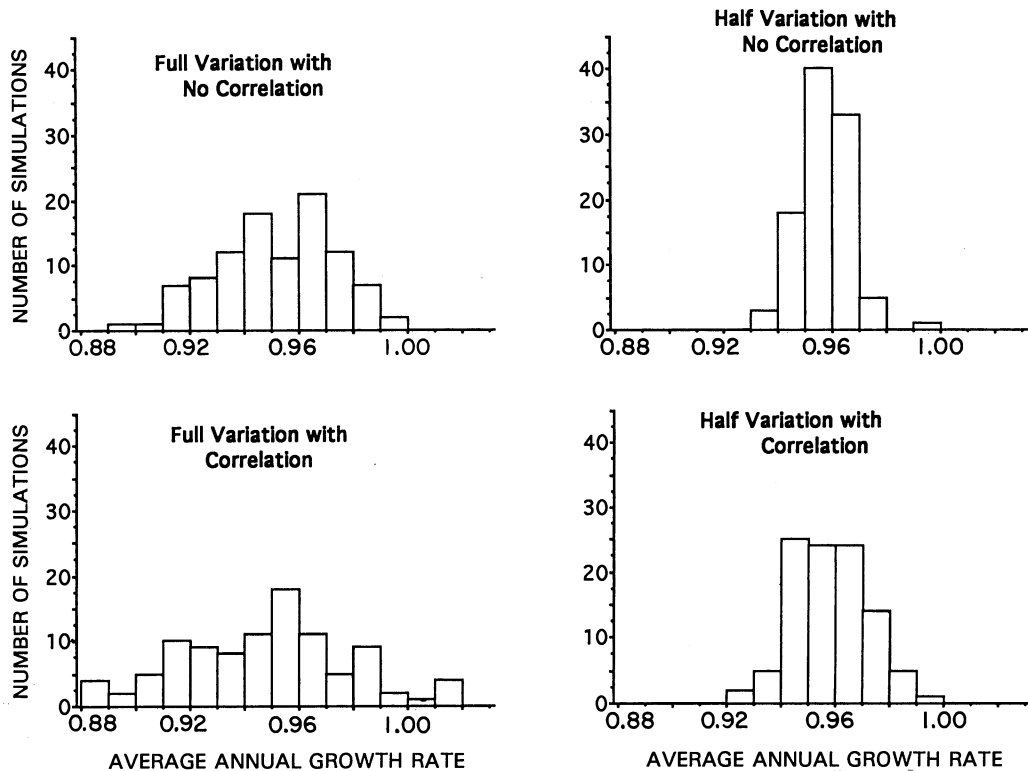


FIG. 6. Distributions of realized mean annual growth rates for stochastic population simulations of the average matrix using "medium-high" reproductive rates with differing amounts of variation and correlation in vital rates. Each plot shows the distribution of annual growth rates for 100 simulations. The growth rates plotted are the average annual growth rates between years 25 and 50 for each simulation.

numbers of tortoises 100 yr into the future, the same mean rates combined with their estimated variation and correlation indicate a striking risk of population extinctions within decades. Thus, for the desert tortoise in particular, and, we suspect, for most other endangered species as well (Menges 1992), population viability models that lack variability may mislead us into thinking there is ample time to act before a population approaches zero, when in fact extinction could be imminent, due simply to the vagaries of the environment.

A variety of factors threatens desert tortoises. Our sensitivity analysis indicates that efforts to help tortoise populations will be most effective if they concentrate on decreasing the mortality rates of large, rather than juvenile, individuals. For example, reducing mortality from shooting, which kills primarily large individuals, would be particularly effective in reducing population declines. In contrast, programs to reduce raven predation of small tortoises (BLM 1990) are unlikely to significantly change the current population trends unless combined with other, more effective, measures.

Neither the existing data nor our modeling allow us to reliably gauge the impact of the proposed Fort Irwin expansion on the viability of the Western Mojave desert tortoise population. While destroying  $\leq 13\%$  of all remaining individuals is undeniably a major blow to the tortoise population, the effect of the expansion on long-

term population viability clearly depends on the management of the remaining habitat. If the current rapid population declines due to anthropogenic impacts (Table 6; Berry and Avery 1990) are not reversed, the expansion represents just another source of tortoise mortality; the tortoises in the expansion area will be doomed whether or not the expansion occurs. However, if a substantial amount of desert land were to be effectively managed for the health of desert tortoises in the future (as is planned, USFWS 1993a, b), and if some of this land were to be in the expansion area (as is proposed, USFWS 1993b), then the Fort Irwin expansion could be a major setback for the future size and viability of the Western Mojave population. Thus, the Fort Irwin expansion must be gauged in light of management plans for tortoises throughout the Mojave, especially management by the BLM, which controls the majority of the lands that the Army wishes to acquire (Chambers 1990), as well as the majority of all other remaining tortoise habitat.

Although the current demographic rates for the desert tortoise paint a gloomy picture of continued decline, our results suggest that preventable anthropogenic impacts may play a large role in that decline. Indeed, management to decrease the direct human harassment and killing of adult tortoises, along with the cessation of livestock grazing on desert lands, might alone re-

verse current declines. However, our modeling also emphasizes that some well-meaning management strategies, in particular the control of raven populations, are unlikely to be either cost-effective or biologically sound. These results parallel those of Crouse et al. (1987), who found that the ongoing efforts to help loggerhead sea turtle populations by the protection of eggs and nests would not alone significantly improve the species' chances for recovery.

As we have emphasized, our results and their implications must be viewed in light of the often uncertain ecological data that are available for the tortoise. Models as management tools can be no better than the data upon which they are based, and we have repeatedly drawn attention to uncertainties in the desert tortoise data base. However, our modeling also provides information needed to prioritize research efforts for the tortoise. Further information on the spatial and temporal variation in adult female survival rates is especially important to obtain, given the low sample sizes currently available to calculate these rates and given their importance in determining population growth. Investigating the mechanisms and epidemiology of a potentially important mortality source, URTD, should also be a research priority, as should the role of grazing pressure in influencing tortoise survival and reproduction.

In summary, we believe that the case of the desert tortoise is a hopeful one. The tortoise has received federal protection and scientific attention while population sizes are still relatively large, and the data necessary to evaluate the viability of tortoise populations is vastly better than that available for most endangered vertebrates. Further, the control of several human disturbances could have major positive effects for the tortoise. However, our stochastic simulation results also illustrate that complacency is unwarranted; decisive action to quickly improve the tortoise's situation in the Western Mojave is needed, given the uncertainty inherent in our predictions of future population trends.

#### ACKNOWLEDGMENTS

This work was supported by a subcontract from Chambers Group Inc., under the aegis of a contract awarded by the U.S. Army Corps of Engineers for desert tortoise studies. The authors were also supported by an NSF grant to P. Kareiva and a start-up grant to D. Doak from the University of California while preparing the results for publication. We thank Hal Caswell, Martha Groom, Ellen Gryj, Lloyd Goldwasser, Ingrid Parker, Jennifer Ruesink, Scott Mills, and two anonymous reviewers for commenting on the manuscript, and Marc Mangel for suggestions on the presentation of stochastic simulation results. Jeff Kaufman provided logistical help, biological insight, and much-needed humor during the course of our work.

#### LITERATURE CITED

- Berry, K. H. 1978. Livestock grazing and the desert tortoise. *North American Wildlife and Natural Resources Conference Transactions* 43:505-519.
- , editor. 1984. The status of the desert tortoise (*Gopherus agassizii*) in the United States. Desert Tortoise Council Report to the U.S. Fish and Wildlife Service, Sacramento, California, USA.
- . 1985. Avian predation on the desert tortoise (*Gopherus agassizii*) in California. Report to Southern California Edison, Rosemead, California, USA.
- . 1986a. Desert tortoise (*Gopherus agassizii*) relocation: implications of social behavior and movements. *Herpetologica* 42:113-125.
- . 1986b. Incidence of gunshot deaths in desert tortoises in California. *Wildlife Society Bulletin* 14:127-132.
- . 1987. Using growth ring counts to age wild juvenile desert tortoises (*Gopherus agassizii*). Draft report. U.S. Department of Interior, Bureau of Land Management, Riverside, California, USA.
- . 1990. The status of the desert tortoise in California in 1989. Draft. U.S. Fish and Wildlife Service, Portland, Oregon, USA.
- Berry, K. H., and H. Avery. 1990. A summary of the 1990 data on status of desert tortoise populations in the Western Mojave Desert. Draft 1. U.S. Department of Interior, Bureau of Land Management, Riverside, California, USA.
- Berry, K. H., and L. L. Nicholson. 1984. The distribution and density of tortoise populations in California in the 1970's. Chapter 2 in K. H. Berry, editor. The status of the desert tortoise (*Gopherus agassizii*) in the United States. Desert Tortoise Council Report to U.S. Fish and Wildlife Service, Sacramento, California, USA.
- Bierzuchudek, P. 1982. The demography of jack-in-the-pulpit, a forest perennial that changes sex. *Ecological Monographs* 52:335-351.
- BLM (Bureau of Land Management). 1990. Environmental impact statement for the management of the Common Raven in the California Desert Conservation Area. Draft. U.S. Department of Interior, Bureau of Land Management, Riverside, California, USA.
- Burgman, M. A., and V. A. Gerard. 1990. A stage-structured, stochastic population model for the giant kelp *Macrocystis pyrifera*. *Marine Biology* 105:15-23.
- Caswell, H. 1989. Matrix population models. Sinauer, Sunderland, Massachusetts, USA.
- Chambers Group. 1990. Cumulative impacts study on the desert tortoise in the Western Mojave desert. Draft. Prepared for U.S. Army Corps of Engineers, Los Angeles District, Los Angeles, California, USA. Chambers Group, Santa Ana, California, USA.
- . 1991. Population viability models and analysis of the desert tortoise (*Gopherus agassizii*) in the Western Mojave desert. Prepared for U.S. Army Corps of Engineers, Los Angeles District, Los Angeles, California, USA. Chambers Group, Santa Ana, California, USA.
- Crouse, D., L. Crowder, and H. Caswell. 1987. A stage-based population model for loggerhead sea turtles and implications for conservation. *Ecology* 68:1412-1423.
- Doak, D. 1989. Spotted owls and old growth logging in the Pacific Northwest. *Conservation Biology* 3:389-395.
- FaunaWest Wildlife Consultants. 1989. A survey for diseased desert tortoises in and near the Desert Tortoise Natural Area, spring, 1989. U.S. Department of Interior, Bureau of Land Management, Riverside, California, USA.
- Germano, D. 1988. Age and growth histories of tortoises using scute annuli. *Copeia* 4:914-920.
- Ginzburg, L. R., S. Ferson, and H. R. Akcakaya. 1990. Reconstructibility of density dependence and the conservative assessment of extinction risks. *Conservation Biology* 4:63-70.
- Goodman, D. 1987. The demography of chance extinction. Pages 11-34 in M. Soule, editor. *Viable populations for conservation*. Cambridge University Press, Cambridge, England.

- Harris, R., L. Maguire, and M. Shaffer. 1987. Sample sizes for minimum viable population estimation. *Conservation Biology* 1:72-75.
- Hastings, N., and J. Peacock. 1974. *Statistical distributions*. Butterworths, London, England.
- Jacobson, E., and J. Gaskin. 1990. Clinicopathologic investigations on an upper respiratory disease of free-ranging desert tortoises, *Xerobates agassizii*. Abstract, the Desert Tortoise Council, 15th annual meeting and symposium. The Desert Tortoise Council, Palm Desert, California, USA.
- Jacobson, E. R., J. M. Gaskin, M. B. Brown, R. K. Harris, C. H. Gardiner, J. L. LaPointe, H. P. Adams, and C. Reggiardo. 1991. Chronic upper respiratory tract disease of free-ranging desert tortoises (*Xerobates agassizii*). *Journal of Wildlife Diseases* 27:296-316.
- Menges, E. S. 1990. Population viability analysis for an endangered plant. *Conservation Biology* 4:52-62.
- . 1992. Stochastic modeling of extinction in plant populations. Pages 253-276 in P. L. Fiedler and S. K. Jain, editors. *Conservation biology: the theory and practice of nature conservation preservation and management*. Chapman and Hall, New York, New York, USA.
- Nagy, K., and P. Medica. 1986. Physiological ecology of desert tortoises in southern Nevada. *Herpetologica* 42:73-92.
- NERC (National Ecology Research Center). 1990. Assessment of biological information for listing the desert tortoise as an endangered species in the Mojave desert. U.S. Fish and Wildlife Service, Portland, Oregon, USA.
- Patterson, R. 1982. The distribution of the desert tortoise (*Gopherus agassizii*). Pages 51-55 in R. Bury, editor. *North American tortoises: conservation and ecology*. Wildlife Research Report 12. U.S. Fish and Wildlife Service, Portland, Oregon, USA.
- Shreve, F. 1942. The desert vegetation of North America. *Botanical Review* 7:195-246.
- Silva, J. F., J. Raventos, H. Caswell, and M. C. Trevisan. 1991. Population responses to fire in a tropical savanna grass, *Andropogon semiberbis*: a matrix model approach. *Journal of Ecology* 79:345-356.
- Thomas, J. W., E. D. Forsman, J. B. Lint, E. C. Menslow, B. R. Noon, and J. Verner. 1990. A conservation strategy for the northern spotted owl. The report of the interagency scientific committee to address the conservation of the northern spotted owl. U.S. Department of Agriculture, Portland, Oregon, USA.
- Tuljapurkar, S. 1990. *Population dynamics in variable environments*. Springer-Verlag, New York, New York, USA.
- Turner, F., K. Berry, D. Randall, and G. White. 1987. Population ecology of the desert tortoise at Goffs, California, 1983-1986. Draft report for Southern California Edison, Rosemead, California, USA.
- Turner, F., P. Hayden, B. Burge, and J. Roberson. 1986. Egg production by the desert tortoise (*Gopherus agassizii*) in California. *Herpetologica* 42:93-104.
- USFWS (U.S. Fish and Wildlife Service). 1993a. Draft recovery plan for the desert tortoise (Mojave population). U.S. Fish and Wildlife Service, Portland, Oregon, USA.
- . 1993b. Endangered and threatened wildlife and plants; proposed determination of critical habitat for the Mojave population of the desert tortoise; proposed rule. 50 CFR, part 17. *Federal Register* 58:45748-45768.
- Vasek, F. C., and M. G. Barbour. 1977. Mojave desert shrub vegetation. Pages 835-867 in M. G. Barbour and J. Major, editors. *Terrestrial vegetation of California*. John Wiley and Sons, New York, New York, USA.
- Wilbur, H. M., and P. J. Morin. 1988. Life history evolution in turtles. Pages 387-439 in C. Gans and R. B. Huey, editors. *Biology of the Reptilia*. Alan R. Liss, New York, New York, USA.
- Wilson, R. W., and R. D. Stager. 1989. Association between soils and desert tortoise population densities and distribution, Piute Valley Nevada. U.S. Department of Interior, Bureau of Land Management, Las Vegas, Nevada, USA.