# DRAFT

# Extinction Risk Assessment for the San Joaquin Kit Fox (*Vulpes macrotis mutica*)

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# INTRODUCTION

## ***Background***

The San Joaquin kit fox (*Vulpes macrotis mutica*) is one of seven subspecies of small North American foxes that inhabit arid landscapes west of the Rocky Mountains (see Mercure *et al.* 1993 for a recent systematic review). It was once widely distributed throughout the San Joaquin Valley where it preyed primarily on rodents and lagomorphs (Grinnell *et al.* 1937). In parallel with the large-scale conversion of much of the San Joaquin Valley's natural communities to irrigated croplands, and the construction of massive water storage and delivery projects over the past sixty years, the kit fox's range contracted and its populations declined. The impact of the actual conversion of habitat to agricultural production on fox numbers was compounded by the isolation effects resulting from the fragmentation of its range. Given that more than 95% of the valley floor has been converted to croplands and kit foxes have fairly large area requirements (5-12 $km^2$ for a breeding pair), many parts of the subspecies' former range have few if any foxes remaining. Those that remain in small isolated populations are very susceptible to localized extinction.

The current range extends from Alameda and Contra Costa counties in the north to western Kern and eastern San Luis Obispo counties in the south (Figure 1). Within this area there may be several kit fox population centers, but, there are only four areas where detailed ecological studies have been carried out: the Elk Hills and Lokern region of Kern County; the Carrizo and Elkhorn plains in San Luis Obispo County; and two military bases, Camp Roberts (San Luis Obispo and Monterey counties) and Fort Hunter Liggett (Monterey County).

**Figure 1.  The current San Joaquin kit fox range**

The San Joaquin kit fox has been federally protected since 1967 under the Endangered Species Preservation Act, and, since 1973 under the Endangered Species Act. Under the California Endangered Species Act, it was listed as rare in 1971 and was reclassified as threatened in 1982. Despite the fact that the kit fox has been listed for nearly thirty years, its status throughout much of its current range is poorly known. This is partly a consequence of more than 95% of the valley floor being in private ownership. Such data limitations are common to many of the other thirty one species being addressed in the San Joaquin Valley Multi-Species Recovery Plan[4]. We view recovery[5] of the San Joaquin kit fox to be critical to recovery of many of the other listed and candidate[6] species in the San Joaquin Valley (which has more imperiled taxa than any other comparable region in the continental United States). The kit fox is our umbrella species. It occurs in the same natural communities as many other listed and candidate species and its large area requirements mean its conservation will provide an umbrella of protection for many other species with smaller area requirements. Therefore, despite the gaps in the knowledge about ecology and distribution, it was decided that an extinction risk assessment for the kit fox would benefit not only the kit fox but many other sensitive species in the San Joaquin Valley (see Shaffer 1994).

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[4] The San Joaquin Valley Multi-Species Recovery Plan is currently being developed by the San Joaquin Valley Endangered Species Recovery Planning Program for the U.S. Fish and Wildlife Service.

[5] *Recovery* means improvement in the status of listed species to the point at which listing is no longer appropriate under the criteria set out in section 4(a)(1) of the Endangered Species Act. (50 Code of Federal Regulations § 402.02)

[6] Candidates are species that are under consideration for listing as threatened or endangered by the U.S. Fish and Wildlife Service.

## ***Extinction Risk Assessment***

The ultimate goal of recovery planning, of which this risk assessment is an important part, is to recover the San Joaquin kit fox. The proximate goals of this study are to guide the development, completion, and implementation of a recovery strategy, and, to understand how to minimize the risk of extinction for the kit fox. To achieve those goals, this risk assessment needs to identify an ecological model appropriate for the kit fox and the significant deficiencies in its database (Boyce 1993, Burgman *et al.* 1993, Lindenmayer and Possingham 1994, Shaffer 1994). Placing the analysis in an extinction risk context will allow resource managers to base recovery and management decisions in a scientific framework that uses the best available biological information (Burgman *et al.*, 1993, Lindenmayer and Possingham, 1994).

A quantitative assessment of risk is important in another context: humans are poor judges of risk levels (Zeckhauser and Viscusi 1990, Burgman *et al.* 1993). We tend to overestimate the likelihood of low-probability events and underestimate the likelihood of higher risk levels, and, our perception of risk tends to be related to its visibility as well as other factors (Zeckhauser and Viscusi 1990). Clearly, a quantitative assessment of extinction risk is a necessary complement to the species experts' best guess and intuitive feel for risk.

This risk assessment is one of the first of many steps actually directed towards kit fox recovery. It synthesizes the best existing information and population models to facilitate adaptive management: "a long-term iterative process of modeling and research that can reveal more about how best to manage a species" (Boyce 1993). Through adaptive management the deficiencies in the database for the San Joaquin kit fox can be addressed.

## ***Population Viability Analysis***

This risk assessment relies to a great extent on the use of population viability analysis. Over the past decade or so, population viability analysis (PVA) has become a central theme in modern conservation biology (Shaffer 1981, 1990 and 1994, Meffe and Carroll 1994). It is a process and a tool for assessing extinction risk, identifying information critical to recovery planning, and evaluating the merits of alternative management strategies (*i.e.*, assessing *relative viability*). Recent comprehensive reviews of population viability analysis have been provided by Soulè (1987), Boyce (1992), Burgman *et al.* (1993), and Lindenmayer and Possingham (1994).

In its most simplistic sense, a PVA is a computer simulation model of a single population's persistence over time that uses the demographic parameters of reproduction and survivorship in concert with environmental variability. In its most refined sense, a PVA incorporates information on genetic variation (such as inbreeding levels) and catastrophes (*e.g.*, epidemics), and, simulates the dynamics of the metapopulation—the distribution of the species' subpopulations on the landscape—over time.

The use of population viability analysis as a tool in applied conservation biology has been growing dramatically in recent years (Boyce 1992, Burgman *et al.* 1993, Lindenmayer and Possingham 1994). The growing prevalence of PVA in conservation biology is masked to a certain extent since many viability analyses do not find their way into the published literature. Many taxa from plants (Menges 1990) and butterflies (Murphy *et al.* 1990) to elephants (Armbruster and Lande 1993) have been the foci of PVA. Some of these studies involve species, such as the red-cockaded woodpecker *Picoides borealis* (Haig *et al.* 1993), and the northern spotted owl *Strix occidentalis caurina* (Lande 1988, Thomas *et al*. 1990, Lamberson *et al*. 1992 and 1994), which are at the center of major conservation conflicts. Such conflicts are likely to become more common and viability analyses, whether published in the peer-reviewed literature or not, are likely to come under increasing scrutiny as a result in the immediate future.

If not for any other reason, this situation mandates that PVAs be carried out as quantitatively as possible so that extinction risk can be scientifically estimated.

A number of generic PVA software packages—such as RAMAS/Age (Ferson and Akçakaya 1991), VORTEX (Lacy 1993), and ALEX (Possingham *et al.* 1992 and 1993, Possingham and Davies 1995)—are available. Sometimes, however, as with recent studies on Stephens' kangaroo rats *Dipodomys stephensi* (Burke *et al*. 1991) and mountain lions *Felis concolor* (Beier 1993) in Southern California, it may be necessary to write custom PVA software to address specific demographic or geographic conditions. Unfortunately, we do not know enough of the life history details for the vast majority of species to adopt the latter approach in most cases. Even if we have the very best demographic, environmental and genetic information possible, and we do the most sophisticated PVA imaginable, we are still working in the realm of probability. We are dealing with the relationship between chance events and extinction. Chance plays important roles in determining who breeds, who survives, and what resources will be available to the population over an extended period of time, and, there is "no single model of population dynamics sophisticated enough to simultaneously incorporate all classes of chance events" (Shaffer 1994). Therefore, it is very important to understand the limitations, as well as the strengths, of the chosen model so that resource managers do not lend undue credence to the model (Boyce 1993, Lindenmayer and Possingham 1994). Further, efforts "to estimate a population's viability must be done in the context of social goals and political realities, and with an understanding that any predictions are made in a context of uncertainty." (Meffe and Carroll 1994, p. 192).

## ***Preliminary PVAs for the San Joaquin Kit Fox***

The San Joaquin kit fox has already been the subject of one PVA (Buechner 1989). A rapid decline toward extinction inside 25 years was predicted. This PVA was based on demographic data obtained from a single study at the Elk Hills Naval Petroleum Reserves, Kern County. RAMAS/Age, which models a single population, was used. This model does not incorporate the spatial structure of a metapopulation or environmental variation within different geographic areas. RAMAS/Age therefore is inappropriate as a metapopulation model—which the kit fox requires. Nevertheless, we decided to use RAMAS/Age to perform a PVA on two subsets of the kit fox metapopulation: the Carrizo Plain/Elk Hills population and the Camp Roberts population. Our analyses suggested that neither of these populations are viable by themselves (Appendix I).

We also employed the generic package VORTEX (Lacy 1993) which can model more spatially complex metapopulations. A very simplistic metapopulation consisting of only Camp Roberts, Elk Hills and the Carrizo Plain was modeled. VORTEX predicted that the San Joaquin kit fox metapopulation will go extinct in 60 years (Appendix I). However, VORTEX does not take geographic scale into account and we believe that factor is important to kit foxes considering the extensive fragmentation of their former range. VORTEX also does not model environmental variation in a realistic way (from the kit fox perspective).

## ***A Metapopulation Viability Analysis for the San Joaquin Kit Fox***

In this extinction risk assessment we conduct a viability analysis on a more comprehensive and realistic kit fox metapopulation using a modified version of the program ALEX (Possingham *et al.* 1992, Possingham and Davies 1995, also see Lindenmayer and Possingham 1994, for a comprehensive treatment of its use in extinction risk assessment). The details of the model as well as its strengths and limitations are spelled out in the next section.

To guide the development of a recovery strategy, and, to understand how to minimize the risk of extinction while that strategy is completed and implemented, we approached the kit fox model with five objectives:

1. To model a realistic metapopulation based on the best available data including environmental variation and prey dynamics,
2. To analyze the effects of deleting individual patches from the baseline metapopulation,
3. To assess the effects of incrementally adding new patches of habitat to the baseline metapopulation,
4. To investigate the importance of corridors,
5. To probe the sensitivity of the model.

## METHODS

### ***The ALEX Model***

ALEX (**A**nalysis of the **L**ikelihood of **Ex**tinction) has been used in a number of studies on a variety of species to assess extinction probabilities (Norton and Possingham 1991, Lindenmayer et al. 1993, Possingham et al. 1994, Lindenmayer and Possingham 1994). It is a Monte Carlo[7] simulation model which incorporates metapopulation spatial structure (Possingham and Davies 1995).

ALEX can assess the likelihood of extinction of a species under a wide range of scenarios. Each scenario must be run several times, and preferably many times, to gather statistics on the likelihood of extinction. The user specifies the number of runs for each scenario and the time horizon in years. All of the scenarios completed in this study were run 500 times to 500 years, and each was replicated five times to produce a smooth extinction distribution[8] for each scenario.

ALEX has strengths and weaknesses that set it apart in some significant ways from other PVA models (Possingham and Davies 1995).

*Strengths*

1. ALEX is a metapopulation model; the entire population is assumed to exist in a number of relatively isolated patches. Each patch has a unique location and may differ in habitat quality.
2. Animal movement can be modeled as either diffusion along corridors or migration.
3. ALEX allows the user to specify a wide variety of environmental processes.

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[7] The Monte Carlo method involves solving a mathematical problem by repeated sampling. This is done by constructing a model and generating samples from the model. The results are then used to assess the behavior of the model.

[8] For most of our analyses, extinction probability distributions are plotted using the mean of five simulations for each scenario. Variances were consistenly low; standard deviations were generally less than plus or minus 0.02 (2%).

4. For each patch ALEX follows a dynamic habitat variable. The habitat variable may affect the fecundity of animals in a patch. This allows the user to model any population responses to changes in habitat quality.

*Weaknesses*

1. Only females are modeled in ALEX. It is assumed that females are the limiting sex.
2. The age-structure includes only three age classes: newborn, juvenile, and adult.
3. ALEX ignores the possible effects of genetic structure on population viability.

These weaknesses are generally only associated with simulations of small populations (Lindenmayer and Possingham 1994). Problems such as demographic stochasticity and finding a mate are thought to be most important for small populations (Lindenmayer and Possingham 1994), but see also Lande (1993). In general, these factors are not important for the San Joaquin kit fox.

For our study of the San Joaquin kit fox, a modified version of ALEX, $\text{ALEX}_{\textbf{KIT}}$**,** was used. A summary of these modifications is given below. Note that each of these modifications is discussed in detail throughout the report.

- Juveniles are allowed to breed at a reduced rate. This parameter is placed in the spare catastrophe file.
- Environmental variation and habitat quality variation do not change home range size but do reduce the number of breeding females.
- The prey biomass-rainfall relationship is modeled in a similar way to the biomass/quality function. This relationship is placed in the spare catastrophe file.
- The best and worst environmental levels in the species file do nothing.
- There is no impact of drought on mortality for adults, subadults, and pups.

[HUGH: DO WE NEED A BETTER DESCRIPTION OF HOW WE MODIFIED ALEX? IF SO, WHERE SHOULD WE PUT IT? IN AN APPENDIX? PAT]

## ***Demographic Variables***

The following demographic variables are used in ALEX: number of females; age-class of animals; probability of mortality; and probability of fecundity. Each female is assigned to one of three age classes: newborn, juvenile, and adult. The user sets the number of years that individuals remain in each age class. In ALEX, newborns are defined as animals born that year; juveniles are defined as individuals that are at least one year old but cannot reproduce; and adults are at least two years of age. In $\text{ALEX}_{\textbf{KIT}}$ the following age structure: pup, subadult and adult are used. Pups are foxes that are born in that year. Zoellick et al. (1987) considered foxes to be pups until November 30 of their birth year because San Joaquin kit foxes can breed in their first year and breeding begins in December. Foxes that are at least one year old or are breeding in their first year are considered subadults. Foxes that are two years or older are adults.

For each age class there is an annual probability of death. Ralls et al. (1990) found that yearly mortality rates were 36% (transmitter-day method) and 30% (binomial method) for adults and 46% (transmitter-day method) and 42% (binomial method) for pups from 1988-1990 at the Carrizo Plain. Ralls (pers. comm.) estimated adult mortality to be 42% and pup mortality to be 79% on the Carrizo Plain from 1989 to 1991 (assuming missing animals died). No data were given for subadults. Cypher and Scrivner (1992) showed that from 1980 to 1984 adult mortality was 53.3% and pup mortality was 71.9% at Elk Hills (maximum likelihood estimation). From 1985 to 1990 adult mortality was 67.9% and pup mortality was 79.6% at Elk Hills (Cypher and Scrivner 1992). Spiegel et al. (unpubl. data) estimated the average yearly adult mortality to be 44.5% (Kaplan-Meier cumulative survival rates) from 1989 to 1993 in western Kern County. Average yearly pup mortality for the same period was estimated to be 32.7% for males and 46.8% for females (Spiegel et al. unpubl. data). Again, no information was given for subadult mortality rates. Berry et al. (1991) found that adult mortality was 47% and pup mortality was 80% at Camp Roberts. Because no estimates for subadult mortality rates are available, we are assuming that they are the same as adult mortality rates.  Taking a weighted average of the above rates, the estimated annual mortality rates at each patch are 47.0% for adults and subadults and 58% for pups.  While many of the above-mentioned studies derived mortality rates in different manners, we believe that our estimates are reasonable approximations of kit fox mortality for this analysis.

ALEX requires a probability distribution of the number of female offspring produced per litter.  Given data on the sex ratio at birth, the number of litters and the size of the litters, one can estimate that distribution using the program BIRTHS (provided with ALEX package).  The birth rate entries are the probability that any female gives birth to zero, one, two, three or more other females in a good year under ideal conditions.  To approximate these ideal conditions, we used data collected by Spiegel et al., (unpubl. data) for the Lokern Natural Area during two wet years (1992 and 1993).  The average litter size was four pups with a range from two to six, and there was a 46% probability that an offspring was a female.

Reproductive success rates must also be entered into the BIRTHS program.  Spiegel et al. (unpubl. data) recorded 44.4% of subadults and 76.9% of adults as reproductively successful at Lokern, and, 25% of subadults and 50% of adults at Midway oil fields.  Zoellick et al. (1987) noted that 25% of subadults and 51% of adults were reproductively successful.  Accordingly, we estimate that adults have a reproductive success rate twice that of subadults.  To approximate optimum conditions we assume that 100% of adult females reproduce successfully and 50% of subadult females reproduce successfully.  Kit foxes are known to be monestrous (McGrew 1979) and, therefore, only produce one litter per year.  Using the above information and the program BIRTHS, we estimate the following probabilities for female pups:  9.1% for zero, 27.2% for one, 32.0% for two, 20.7% for three, 8.7% for four, 2.2% for five, and 0.2% for six pups.

## ***Metapopulation Structure***

Any population that is modeled using ALEX is geographically distributed among a finite number of patches (Lindenmayer and Possingham 1994). Each patch has various attributes such as: position; area; prey biomass; initial fox population; environmental variability; and quality of suitable habitat. Environmental variability was modeled as annual rainfall variation. This is discussed in detail later.

Using $\text{ALEX}_{\textbf{KIT}}$**,** we have modeled two distinct metapopulations of the San Joaquin kit fox: the *Baseline Metapopulation* and the *Expanded Metapopulation*. Data collected from the Carrizo Plain, Elk Hills, Camp Roberts and Fort Hunter Liggett provide the basis of the *Baseline Metapopulation* (Figure 2). Patch 1 is the Carrizo Plain (San Luis Obispo County); Patch 2 is Elk Hills (Kern County); Patch 3 is Camp Roberts (San Luis Obispo and Monterey Counties) and Patch 4 is Fort Hunter Liggett (Monterey County). The size of each patch roughly approximates the amount of suitable kit fox habitat in that area. The area of Patch 1, Carrizo Plain, is estimated to be the entire Plain minus Soda Lake (674 $km^2$). While this is undoubtedly an overestimate of kit fox habitat on the Carrizo Plain, areas of habitat outside of the Plain have been excluded and we hope that the two estimates balance each other out. The area of Patch 2, Elk Hills, is estimated to be both Naval Petroleum Reserves and the Lokern Natural Area (463 $km^2$). The area of Patch 3, Camp Roberts, we estimate to be approximately 172 $km^2$ (Reese et al. 1992). It is based on the minimum kit fox distribution polygon excluding the post boundary and the impact area. The area of patch 4, Fort Hunter Liggett, is estimated to be approximately 98 $km^2$. This estimate is based on a study done by Jones and Stokes (1992) and approximates the combined area of the main study area, the Cantonment area, Gabilan Valley, Stoney Valley and the ASP study area which serves as the ammunition storage site for Fort Hunter Liggett.

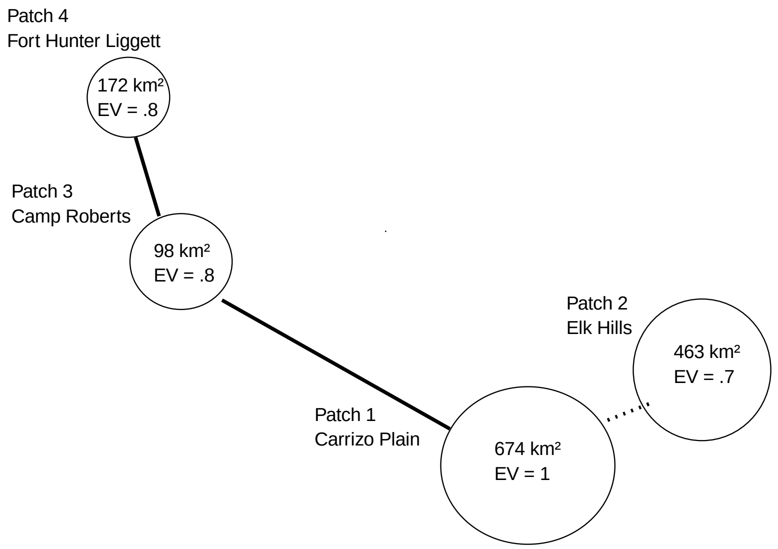

**Figure 2. Baseline Metapopulation.** Patch area and correlation of patterns in environmental variation (mean annual precipitation) with respect to Patch 1 are included. Lines indicate probable avenues of kit fox movement via corridors. Line patterns illustrate different potential avenues of movement.

To assess the importance of additional patches of habitat, six other patches are added incrementally to the baseline metapopulation. Four of the six new patches are based on spotlight surveys conducted by the California Department of Fish and Game (CDFG) on seven 30-mile survey routes ranging from Kern to Merced Counties. Because ALEX requires patch areas and we cannot provide them, the CDFG survey data are used to scale the patch sizes according to their relative kit fox abundance. Ralls and Eberhardt (1994) showed that more foxes were seen on the Elkhorn route than on any other route surveyed. In this model, we are making the naive (and erroneous!) assumption that similar densities exist throughout the kit fox's modeled range. Patch 1 is used as the baseline patch and all other patches are scaled accordingly. For example, there were ten times as many foxes seen on the Elkhorn route as on the Ortigalita route (Ralls and Eberhardt 1994). Since we estimate the rough area of the Carrizo Plain to be 674 km$^2$, we then estimate the patch size of Ortigalita to be ten times smaller, or 67.4 km$^2$. There are two other patches that are not based on CDFG spotlight surveys: the Kern and Pixley National Wildlife Refuges. Only those areas of the refuges that are owned by the US Fish and

Wildlife Service (USFWS) are used to estimate patch size. The Kern National Wildlife Refuge is estimated to be 43 km$^2$ and the Pixley National Wildlife Refuge 21 km$^2$. These six new patches are added incrementally to determine the persistence of the metapopulation as each new patch is added. Figure 3 illustrates the patch structure of this *Expanded Metapopulation* once all the patches have been added. Because there is such little information on kit fox abundance in its northern range, these areas are not included in the model.

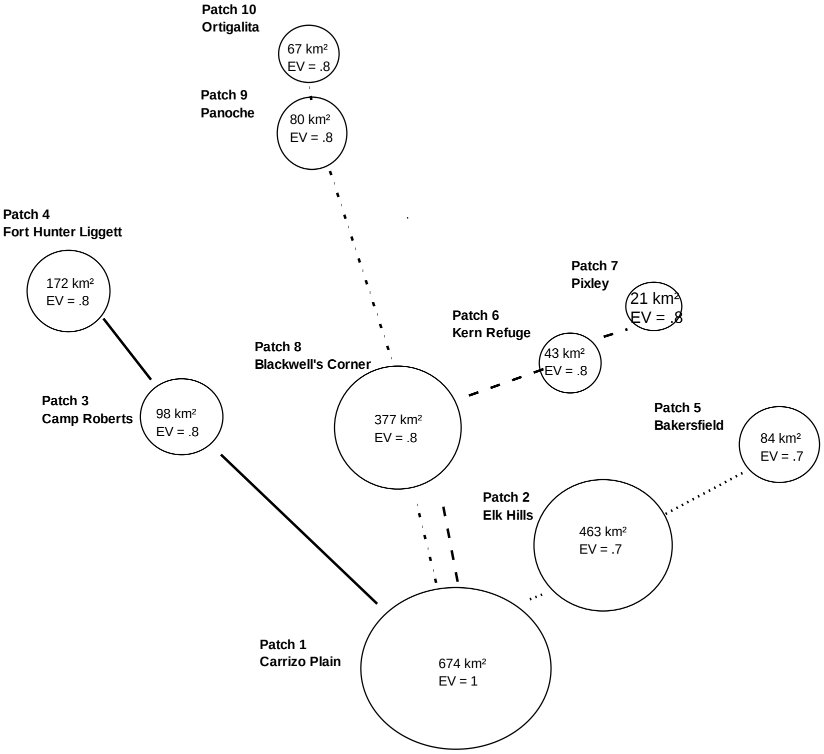

**Figure 3. Expanded Metapopulation.** Patch area and correlation of patterns in environmental variation (mean annual precipitation) with respect to Patch 1 are included. Lines indicate possible avenues of kit fox movement via corridors. Line patterns illustrate different potential avenues of movement.

## ***Movement Between Patches***

Two different forms of movement can be modeled with ALEX: diffusion and migration. Diffusion occurs only along a corridor of suitable habitat and is not associated with an increase in mortality. It is intended to reflect relatively small-scale movement. Migration is modeled as dispersal to a more distant patch which is associated with an increased risk in mortality. Migration does not occur along a corridor. The probability of reaching another patch is a function of the distance between the two patches and the size of the destination patch. If the animal does not successfully reach another patch then it dies. In this kit fox model, movement by migration is always included. When corridors are added, both diffusion and migration are modeled.

### *Diffusion*

Diffusion only occurs between patches that are connected by a corridor. The user chooses where to position the diffusion corridors and each corridor is assigned a width. The user also may set a density below which animals will not diffuse. Because of the very few accounts of kit foxes moving long distances, we believe that the density must be relatively high before long-distance movement occurs. We are estimating that the source patch must be at 70% of carrying capacity before a fox will diffuse to another patch. If the density of individuals is above this minimum population for diffusion, then each individual (of a given age class) has a constant probability of diffusing. The carrying capacity is based on area requirements for female kit foxes. This is discussed later. Following consultation with several kit fox biologists, we estimate that there is a 10% probability of pup dispersal, a 5% probability of subadult dispersal and a zero probability of adult dispersal along corridors between patches.

To assess the impact of diffusion on the persistence of the *Baseline Metapopulation*, corridors of habitat between certain patches are added. The maximum number of females in each age class that can use a corridor in any year to move between patches is the corridor width divided by the square root of the minimum area required for breeding (Lindenmayer and Possingham 1994). Since very few accounts of long distance kit fox dispersal exist, we estimate that there is a maximum of one female per age class dispersing per year from a given patch. Therefore, a maximum of two females per year disperse (adults have no probability of dispersing). The corridor width, therefore, must be 2.8 km, which is the square root of the minimum breeding area (described under area requirements). This width is used uniformly when adding corridors to the metapopulation. Corridors are added sequentially while keeping the previously added corridor in place. For example, a corridor is added between Patches 1 and 2 and the simulation results are recorded (5 replications of 500 runs to 500 years). Then a corridor is added between Patches 1 and 3 while keeping the corridor between Patch 1 and 2 in place. Finally, a corridor is added between Patches 3 and 4 while keeping the previous two in place.

Corridors are similarly added to the *Expanded Metapopulation*. These corridors are added with respect to likely avenues of kit fox movement (Figure 3). For example, one likely avenue of movement is between Fort Hunter Ligget, Camp Roberts and the Carrizo Plain. Another is between the Carrizo Plain, Elk Hills, and Bakersfield. These avenues are based on documented instances of long distance movement as well as proximity and topography.

### *Migration*

Animals will only migrate if the density of animals in the patch is above some user-defined threshold. As with diffusion, we estimate that the density of individuals in a patch has to be greater than 70% of the carrying capacity for migration to occur. If the density of individuals is above this minimum population for migration, then each individual (of a given age class) has a constant probability of migrating: 10% probability of pup migration, a 5% probability of subadult migration and a zero probability of adult migration.

Migration between patches of the *Baseline Metapopulation* is examined. We have set the mean migration distance before death at 20 km. This is based on several accounts of long-distance kit fox movement. Scrivner et al. (1987) documented one adult male who traveled 46.67 km. A subadult male kit fox was found dead near the Carrizo Plain Natural Area that had dispersed from Camp Roberts; a distance approximating 120 km (K. Ralls pers. comm.). Spiegel et al.

(1991) reported that one male pup had dispersed 16 km from a developed oilfield to an undeveloped site near Elk Hills. It was also reported that 2 male pups had dispersed 28 km (Spiegel pers. comm.). There is one account of a kit fox (sex unknown) that moved from Fort Hunter Liggett to Camp Roberts; a distance of approximately 55 km (V. Getz unpubl. data). In the northern portion of their range, one kit fox (sex unknown) was reported as moving north 37 km from Bethany Reservoir, Alameda County (H. Bell pers. comm.). Egoscue (1956) reported that one young male desert kit fox in Utah had moved about 32 km. All of these data suggest that long distance migration is occurring between patches but at a limited rate. Since ALEX only models females, the suggested male-bias in dispersal is ignored.

It is important to note that the way we have modeled movement will only be an approximation until more is known about kit fox movement.

## ***Environmental Variability***

In ALEX**,** environmental variability is modeled using a normally distributed random-variable, with patch-specific mean and variance, selected for each patch. These values can be fully correlated, partially correlated, or uncorrelated with a reference patch (Lindenmayer and Possingham 1994). The environmental variable actually reflects the annual variability in reproductive success within an entire population or patch. For our study of the San Joaquin kit fox, annual rainfall (in meters) is used as the environmental variable.

We have two relationships involving environmental variability: prey biomass dynamics and the effect of prey biomass on the number of breeding females. In ALEX, the user can specify environmental values (e.g., mean annual rainfall) below which breeding does not take place and above which breeding is no longer affected. This environmental function is related to the quality/biomass function (see Figures 2 and 3 in Possingham and Davies, 1995). In $\text{ALEX}_{\textbf{KIT}}$ we are not using this environmental function however. Instead, we have added a dynamic relationship which assumes that only rainfall affects prey biomass which, in turn, affects the quality of the patch. The patch quality determines the maximum number of females that can breed. Also, in contrast with ALEX, ALEX$_{\mathbf{KIT}}$'s environmental variability and habitat quality variation do not affect home range size of female kit foxes.

*Prey biomass and rainfall*

Each patch has an environmental variable that affects the patch quality and the prey dynamics. For both the *Baseline* and *Expanded Metapopulation* models, annual rainfall is the environmental variable. While there are rainfall data going back 60 years or more, we have only 8 years of prey data. Therefore, for each patch the 7-year average annual rainfall and standard deviations were calculated (based on data from the National Climatic Center and the U.S. Bureau of Land Management). The patterns of rainfall at each patch were correlated with Patch 1 (Figures 2 and 3). Our analysis of rainfall and kit fox prey abundance (Appendix 2) showed that March rainfall is the best predictor for the following year's kangaroo rat abundance and annual rainfall is the best predictor for the following year's lagomorph abundance. However, the variance in March rainfall is, not surprisingly, much higher than the variance in annual rainfall (Table 1). The coefficients of variation for March rainfall are, on average, more than twice those for annual rainfall. Also, even when March is dry, kangaroo rats can still breed. Therefore, annual rainfall is used to model the range-wide relationship between environmental variation and biomass.

**Table 1. Rainfall in different patches.** Variance (coefficient of variation) in both March and annual rainfall associated with each Patch. Rainfall data (mm ± SD) have been averaged from 1983 to 1993 at each patch (National Climatic Data Center and Bureau of Land Management unpubl. data).

| Patch Number | March Rainfall | CV | Annual Rainfall | CV |
|---|---|---|---|---|
| **1** | 39.32 ± 42.84 | 1.08 | 187.00 ± 071.00 | 0.38 |
| **2** | 38.97 ± 34.52 | 0.89 | 139.00 ± 049.00 | 0.35 |
| **3** | 70.32 ± 79.76 | 1.13 | 301.00 ± 127.00 | 0.42 |

| | | | | |
|---|---|---|---|---|
| **4** | 70.32 ± 79.76 | 1.13 | 301.00 ± 127.00 | 0.42 |
| **5** | 38.97 ± 34.52 | 0.89 | 139.00 ± 049.00 | 0.35 |
| **6** | 42.80 ± 48.50 | 1.13 | 165.50 ± 077.96 | 0.47 |
| **7** | 42.80 ± 48.50 | 1.13 | 165.50 ± 077.96 | 0.47 |
| **8** | 42.80 ± 48.50 | 1.13 | 165.50 ± 077.96 | 0.47 |
| **9** | 38.32 ± 37.19 | 0.97 | 223.77 ± 084.00 | 0.38 |
| **10** | 38.32 ± 37.19 | 0.97 | 223.77 ± 084.00 | 0.38 |

ALEX allows the user to model the impacts of catastrophes such as fires and droughts. We do not include any in our study of the San Joaquin kit fox. While, drought may have catastrophic effects, we do not believe it should be considered a catastrophe. It is a normal pattern of rainfall throughout the arid San Joaquin Valley. Instead, we have factored drought into the prey biomass-rainfall relationship which is explained below.

A single habitat variable, called biomass, is monitored in each patch to reflect environmental variability. We are modeling biomass as the kit fox prey base. While kit foxes have been documented to eat everything from insects to birds and small mammals (Cypher and Warrick 1993, EG&G Progress Report 1992, EG&G Annual Report 1991), sufficient data on prey abundance and environmental variability are not available to model most types of prey. Data on lagomorphs and kangaroo rats constitute the bulk of existing information. An ongoing study at the Elkhorn Plain Ecological Reserve has provided data on both giant kangaroo rat (*Dipodomys ingens*) and short-nosed kangaroo rat (*D. nitratoides brevinasus*) densities from 1987 to 1993 (D. F. Williams unpubl. data). There is also information on lagomorph (primarily *Lepus californicus*) densities from 1984 to 1993 on Naval Petroleum Reserve No.1 (EG&G Annual Report 1992, Cypher and Scrivner 1992).

In order to model prey biomass with respect to variation in yearly rainfall, both kangaroo rat and lagomorph densities should be combined. To assess the validity of combining these different prey types, prey abundance as it relates to annual rainfall is explored. The cycle of abundance for kangaroo rats and lagomorphs appears to be similar; they both appear to track annual rainfall (Figures 4 and 5). In 1991, the lowest densities of kangaroo rats were observed on the Elkhorn Plain (D. F. Williams unpubl. data). Lagomorph densities were also at their lowest in 1991 at Elk Hills (EG&G Progress Report 1992, Cypher and Scrivner 1992). In 1992, the biomass of both prey types increased markedly from the previous year. The biomass at the Carrizo Plain increased ten fold from 1991 to 1992. Similarly, at Elk Hills, the biomass increased nine fold from 1991 to 1992. This increase in biomass at both locations corresponds to increasing annual rainfall. Annual rainfall increased by 139% from 1989 to 1992 at the Carrizo and by 192% at Elk Hills for the same years. In general, it appears that the two prey species respond similarly to environmental variation and, therefore, can probably be combined and modeled as biomass.

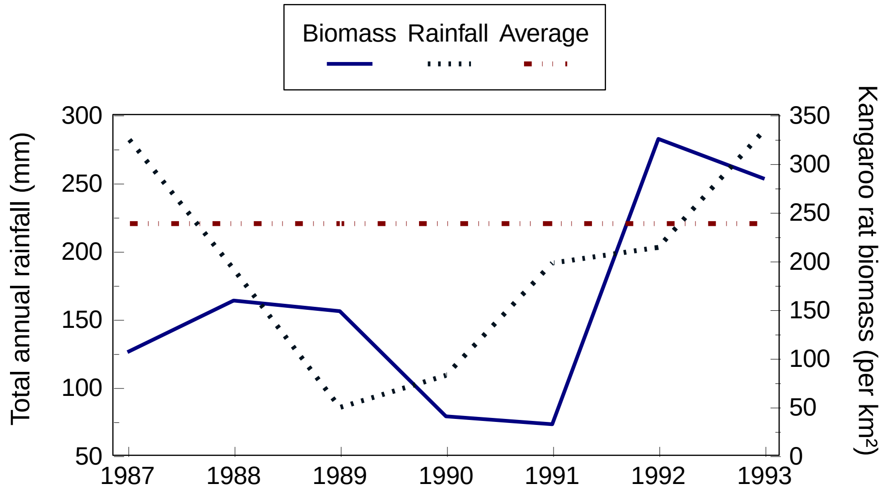

**Figure 4. Kangaroo rat biomass (converted to lagomorph equivalents) on the Elkhorn Plain** from 1987 to 1993. Data were collected by D. F. Williams (unpubl. data). Rainfall data are from the Washburn Ranch, Carrizo Plain (BLM unpubl. data). The twenty-year annual rainfall average is also shown.

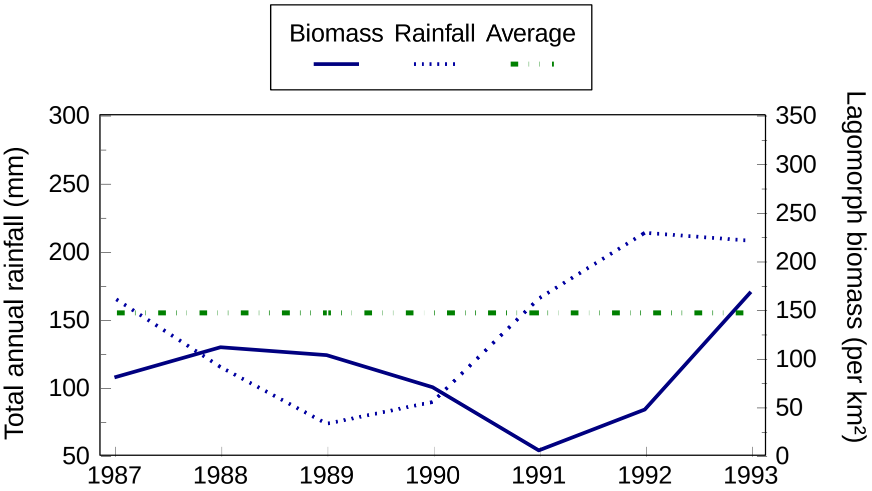

**Figure 5. Lagomorph densities on the Naval Petroleum Reserve No. 1** (EG&G unpubl. data, Cypher and Scrivner 1992) from 1987 to 1993. Rainfall data are from the Bakersfield weather station (National Climatic Data Center). The twenty-year annual rainfall average is also shown.

Since both prey species appear to respond similarly to changes in annual rainfall, they are combined to constitute prey biomass. Due to the obvious size differences of these types of prey, densities of both species of kangaroo rats are converted to lagomorph equivalents ('lag-rats'). We've assumed that the average weight of *L. californicus* is 2.5 kg, that of *D. ingens* is 100g and that of *D. n. brevinasus* is 40g. Therefore, the weight of one lagomorph is equivalent to approximately the weight of 25 giant kangaroo rats and 62 short-nosed kangaroo rats. The total biomass, in units of lag-rats, is determined for each year from 1987 to 1993 and related to variation in annual rainfall at each patch.

To approximate the rainfall in areas where biomass densities were obtained, rainfall data from the Carrizo Plain (Washburn Ranch) and Elk Hills (Bakersfield weather station) are pooled and averaged for each year from 1987 to 1993 (Table 2). Biomass multipliers are determined—the value that the previous year's biomass must be multiplied by to equal the current year—and these are compared with particular rainfall values (Table 2).

**Table 2.** The relationship between biomass (lag-rats) and the averaged annual rainfall from the Carrizo Plain and Elk Hills from 1987 to 1993. The biomass multiplier demonstrates the change in biomass from the previous year.

| **Year** | **Rainfall (mm)** | **Biomass** | **Multiplier** |
|---|---|---|---|
| **1987** | 224 | 187 | |
| **1988** | 151 | 270 | 1.44 |
| **1989** | 079 | 251 | 0.93 |
| **1990** | 099 | 110 | 0.44 |
| **1991** | 178 | 037 | 0.34 |
| **1992** | 208 | 373 | 10.0 |
| **1993** | 204 | 453 | 1.20 |

It is the pattern of rainfall, not the amount, that impacts biomass dynamics. Two years of low annual rainfall (1989 and 1990) are followed by a crash in biomass in 1991. Based on Tables 1 and 2, we estimate that biomass will be at its maximum when annual rainfall is 500 mm. This is about two standard deviations above the highest recorded mean annual rainfall at Camp Roberts and Fort Hunter Liggett (301 ± 254 mm; the wettest habitat patches used in the model). When biomass is 120 mm we estimate that biomass will stay the same. This is about one standard deviation below the twenty year average annual rainfall for the Carrizo Plain (Washburn Ranch) and Elk Hills (Bakersfield) combined (187.28 ± 46.27 mm). When annual rainfall is 100 mm we estimate that the prey biomass will drop to 40% of the previous years' value and when annual rainfall is zero the prey biomass will be zero. This relationship is incorporated in ALEX$_{\mathbf{KIT}}$ (in a spare catastrophe field) as follows :

| | | | | |
|---|---|---|---|---|
| Multiplier | 0 | 0.4 | 1 | 10 |
| Rainfall | 0 | 0.1 | 0.12 | 0.5 |

*Effect of prey biomass on the number of breeding females*

The number of females that actually breed is determined by the prey biomass. The biomass of a patch determines the number of breeding females and this is represented as patch quality. Biomass in lag-rats is compared with kit fox reproductive data collected at the Lokern Natural Area from 1990 to 1993 (Spiegel et al. unpubl. data; Table 3).

**Table 3. Biomass and reproductive success.** Biomass (lag-rats) from the Carrizo Plain and Elk Hills is compared to the proportion of females successfully reproducing at the Lokern Natural Area (Spiegel et al. unpubl. data).

| Year | Biomass | % Reproducing |
|---|---|---|
| **1990** | 110 | 50 |
| **1991** | 37 | 25 |
| **1992** | 373 | 83.3 |
| **1993** | 453 | 83.3 |

White and Ralls (1992) reported that none of their female kit foxes reproduced in 1990 and four out of seven reproduced in 1991 on the Carrizo Plain. These data were insufficient to support any particular relationship between biomass and reproductive success. They suggest, however, that kit fox reproduction may vary geographically. The relationship between reproduction and biomass is tentative at best, yet it is the best approximation we can provide at this time.

The number of female foxes reproducing is defined in terms of the quality of the habitat. The higher the quality, the more females reproduce. The quality/biomass relationship is derived similarly to the biomass/rainfall relationship described earlier:

| | | | | |
|---|---|---|---|---|
| Quality | 0 | .25 | .50 | .83 |
| Biomass | 0 | 10 | 15 | 100 |

When there are no prey, no females reproduce. When biomass is 10% of its maximum, 25% of females reproduce. When it is at 15% of its maximum, 50% reproduce. Finally, when biomass is at its maximum, 83% reproduce.

## ***Area Requirements***

The minimum living area determines the maximum number of females that can live in a patch. Because foraging is a vital activity, we assume that the foraging area is the minimum living area. Spiegel and Bradbury (1992) estimated kit fox foraging range to be 5.82 $km^2$, Spiegel et al. (1991) 6.13 $km^2$, Ralls et al. (1990) 9.09 $km^2$. However, the larger foraging range of 9.09 $km^2$ was derived from intermittent sampling periods and may be inaccurate. We are estimating the minimum living area of one female to be 6 $km^2$. The carrying capacity of any patch is its area divided by the minimum living area. We decided not to consider home range overlap due to conflicting information (Zoellick et al. 1987; Spiegel and Disney 1992; Ralls et al. 1990).

The minimum breeding area determines the maximum number of females that can breed in a patch. We assume that this is equivalent to the home range of a kit fox mated pair. Spiegel and Bradbury (1992) reported that yearly home range sizes of mated pairs averaged 7.91 $km^2$. Accordingly, we are estimating the minimum breeding area to be 8 $km^2$. The maximum number of females that can breed in a particular patch is the area of the patch divided by the minimum breeding area.

## ***Sensitivity Analysis***

Assessing the sensitivity of results to different parameters is an essential part of PVA (Possingham and Davies 1995). Estimates of population viability are sensitive to the structure and parameterization of the models used. In particular, scarcity of data for some of the baseline parameters require that their values be varied. This can result in changes in the probabilities of extinction. Large changes in some values may have little effect on viability whereas small changes in other values may have a pronounced effect. This process, termed sensitivity analysis, is important for testing model validity as well as for ranking and assessing different management options (Possingham et al. 1993). For wildlife management, the most important consideration is not determining the absolute probability of extinction—which is impossible in any case—but the extinction probability relative to those derived from other management options (Possingham et al. 1993).

ALEX has the ability to perform some sensitivity analyses automatically. Most parameters in the model can be "tagged" and the user can specify by how much the parameters should be varied for each scenario; i.e., ± 25, 50 and 75%.

Using $\text{ALEX}_{\textbf{KIT}}$, the probability of migration is varied to assess how sensitive the model output is to this parameter. Migration probabilities for both pup and subadults are varied independently for the *Baseline Metapopulation*. It is assumed that adults do not disperse. Dispersal probabilities of 10, 30, 50 and 70% are used. (Diffusion probabilities were not varied because ALEX would crash). The rate of diffusion is also varied for these two age classes for the *Baseline Metapopulation*. This is done by varying corridor width. The maximum number of individuals that can pass between two patches in each age class in each year is the corridor width divided by the square root of the minimum area required for breeding (Possingham and Davies 1995). This is performed only on the *Baseline Metapopulation*. Corridor widths of 8.48 km, 16.97 km, 25.45 km, 33.94 km, and 42.43 km are used which correspond to dispersal rates of 3, 6, 9, 12, and 15 females per age class per year.

The probability of annual mortality is varied for each age class to determine how sensitive the model output is to this parameter. Mortality probabilities of 10, 30, 47, 58, 70 and 100% are used for pups, subadults and adult kit foxes of the *Baseline Metapopulation*.

Several sensitivity analyses are performed to assess the affect of varying patch size on the model's output. Patches of the *Expanded Metapopulation* from different geographic areas of the current kit fox range (i.e. Elk Hills from the southern range, Camp Roberts from the western range and Panoche from the northern range) are varied in area: 50, 100, 200, 400, 800 and 1600 $km^2$. Patches 9 and 10 (Panoche and Ortigalita, respectively) were removed from the metapopulation and their respective areas were added to patches 6 and 7 (Kern and Pixley).

Changes in environmental mean and variance is also investigated. A series of sensitivity analyses are performed on the environmental mean and standard deviation of the Ortigalita and Camp Roberts patches.

# RESULTS

## ***Baseline Kit Fox Metapopulation***

The mean extinction probability (P(E)) of the *Baseline Metapopulation* increases steadily over time (Figure 6). This four-patch metapopulation has a 33% mean probability of extinction in 100 years, 74% in 300 years, and 91% in 500 years. The baseline scenario was extended further to 1000 years where the mean extinction probability was greater than 99%.

The populations (patches) vary in their influence on the metapopulation's viability (Table 4). The Carrizo Plain and Elk Hills (Patches 1 and 2) seem to contribute the most to metapopulation viability since both patches usually have a resident kit fox population, 83% and 85% of the time respectively. Camp Roberts (Patch 3) and Fort Hunter Liggett (Patch 4) are empty four to five times more often than Carrizo Plain and Elk Hills. These differences may be due to the relative isolation and smaller size of the Camp Roberts and Fort Hunter Liggett populations (Figures 1 and 2).

| Patch | % Time Empty |
|---|---|
| 1 Carrizo | 16.5 ± 1.1 |
| 2 Elk Hills | 15.4 ± 1.6 |
| 3 Camp Roberts | 68.7 ± 2.4 |
| 4 Fort Hunter Liggett | 74.7 ± 2.3 |

**Table 4.** The percentage of time (mean and st. dev.) that each patch in the Baseline Metapopulation does not have any kit foxes.

The contribution of Patches 1 and 2 to metapopulation viability is further explored by deleting them individually from the scenario (Figure 7). Deleting the Carrizo Plain from the metapopulation rapidly results in greatly increased mean extinction probabilities (Figure 7). Deleting Patch 1 increases the mean extinction probability: from 33 to 90% in 100 years, and 74 to 100% in 300 years. Deleting Elk Hills from the metapopulation also increases the mean probabilities of extinction but not as dramatically as with the Carrizo Plain deletion: from 33 to 44% in 100 years, 74 to 80% in 300 years, and 91 to 94% in 500 years.

### ***Patch Addition***

The incremental addition of new patches to the *Baseline Metapopulation* was expected to result in concomitant increases in metapopulation viability (i.e., reduced extinction probabilities). However, adding patches 5 (Bakersfield), 6 (Kern NWR) and 7 (Pixley NWR) to the baseline scenario had no effect on metapopulation viability (Figure 8). The addition of Patch 8 (Blackwell's Corner) had only a marginal effect and that was most pronounced at 250 to 300 years (Figure 8). Not until Patch 9 (Panoche) and Patch 10 (Ortigalita) are added to the metapopulation are there significant reductions in mean extinction probabilities from those predicted for the baseline scenario.

Compared with the baseline, the addition of Panoche decreases the mean probability of extinction in 100 years from 33 to 17%, in 300 years from 74 to 44%, and in 500 years from 91 to 63%. Addition of Ortigalita—to produce the *Expanded Metapopulation*, all ten patches (Figure 3)—results in even greater reductions in mean extinction probability: 33 to 12% in 100 years, 74 to 30% in 300, and 91 to 43% in 500 years (Figures 8 and 9). As with the baseline scenario, the expanded scenario was extended further to 1000 years where the mean extinction probability was 65%.

### ***Patch Contribution***

As with the baseline scenario, the contribution of each patch in the expanded scenario to metapopulation viability was expected to have a positive correlation with patch area. That general pattern seems to be borne out by the analyses (Figure 10). However some patches of similar size seem to have radically different population dynamics. The Bakersfield and Panoche patches (5 & 9) are about the same size, at 84 and 80 km$^2$, but they are devoid of foxes 73 and 27% of the time respectively. Even the Carrizo Plain (1), which is 8.4 times the size of Panoche (9), is empty 46% of the time, nearly twice as often as Panoche.

Also, in the *Baseline Metapopulation*, the Carrizo Plain had a resident fox population much more often than was found with the *Expanded Metapopulation*: 83 v 54% of the time respectively. Therefore, population dynamics are influenced in the model by factors other than patch area. Analysis of the simulation output for the growing metapopulation revealed that, except for Kern National Wildlife Refuge (6), intra-patch population dynamics remained remarkably stable until the last two patches, Panoche (9) and Ortigalita (10), were added to the metapopulation (Table 5). We already knew that adding those two patches had a profound effect on metapopulation viability (Figure 8) but, because of their small size and isolation, we did not expect their addition to the metapopulation to affect population dynamics in other patches. However, for nearly all patches, the mean percent time that patches were empty of kit foxes increased noticably with the addition of Panoche and Ortigalita. Interestingly, the mean percent time empty decreased for Panoche with the addition of Ortigalita but this can probably be explained by frequent movement of foxes between the two patches since they are in close proximity.

| Patch | | Area (Km$^2$) | Baseline | 5 Patch | 6 Patch | 7 Patch | 8 Patch | 9 Patch | Expanded |
|---|---|---|---|---|---|---|---|---|---|
| **1** | Carrizo | 674 | 17 | 17 | 17 | 17 | 17 | **36** | **46** |
| **2** | Elk Hills | 463 | 15 | 15 | 15 | 16 | 15 | **33** | **43** |
| **3** | Camp Roberts | 172 | 69 | 70 | 70 | 70 | 71 | **80** | **84** |
| **4** | Fort Hunter Liggett | 98 | 75 | 76 | 76 | 75 | 76 | **84** | **87** |
| **5** | Bakersfield | 84 | | 64 | 62 | 63 | 61 | **69** | **73** |
| **6** | Kern NWR | 43 | | | 82 | 83 | 73 | **79** | **84** |
| **7** | Pixley NWR | 21 | | | | 95 | 94 | **96** | **97** |
| **8** | Blackwells Corner | 377 | | | | | 37 | **52** | **60** |

|  |  |  |  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|---|---|---|
| **9** | Panoche | 80 |  |  |  |  |  | **38** | **27** |
| **10** | Ortigalita | 67 |  |  |  |  |  |  | **28** |

**Table 5:** Mean percentage of time that patches are empty in each of seven scenarios. The data for the 9 Patch and Expanded scenarios are in bold face.

If we had only investigated the influence of patch size on metapopulation viability for the eight patch scenario—excluding Panoche and Ortigalita—a strongly negative relationship between patch area and the percentage of time a patch is empty would have been indicated (Figure 11).

## ***The Importance Of Corridors***

Adding three 3 km-wide corridors to the *Baseline Metapopulation*—allowing one juvenile and one subadult female per patch per year to disperse—has little impact on extinction probabilities (Figure 12). However, adding nine corridors to the *Expanded Metapopulation* does result in lower extinction probabilities; lower by twelve percentage points at 500 years (Figure 13). However, sequential addition of diffusion corridors revealed inconsistent fluctuations in extinction probability (Figure 14). This aspect of the model needs to be investigated further.

## ***Sensitivity Analyses***

The model does not appear to be sensitive to variation in migration probability for either pups or subadults in the *Baseline Metapopulation* (Figure 15). Increasing pup and subadult migration probabilities, if anything, increase extinction probabilities slightly, by a few percentage points at both 250 and 500 years.

The model output is also insensitive to variation in the rate of pup and subadult dispersal via corridors per year in the baseline scenario (Figure 16). As the number of dispersing females per age class increases from 3 to 15 (by varying the corridor width), extinction probabilities at 250 and 500 years do not appear to change at all.

The baseline scenario is sensitive to variation in annual mortality probabilities for pups and adults, but not for subadults (Figure 17). Variation in adult mortality results in the most substantial change in extinction probability at 250 years. (A very similar pattern is found for extinction probabilities at 500 years but that is not presented.) Increasing the probability of adult mortality from 25% to 75% practically triples the extinction probability; it increases from 34 to 94%. Similarly increasing pup mortality rates nearly doubles the extinction probability (51–99%). By contrast, increasing subadult mortality rates seems to have no effect on extinction probability.

We decided to vary the size of three patches which approximate the geographic extremes of the *Expanded Metapopulation*: Panoche in the north, Camp Roberts in the west, and Elk Hills in the southeast. The results of varying the areas of these patches from 50 to 1600 $km^2$ are shown in Figure 18. Increasing patch area only results in significantly lower extinction probabilities (250–year) for Panoche. (Although not shown here, the pattern for 500-year extinction probabilities is similar.) The mean metapopulation extinction rate drops from 36 to 10% when Panoche increases from 50 to 1600 $km^2$. Camp Roberts and Elk Hills change very little; producing a metapopulation extinction probability of about 25% regardless of patch size.

Clearly, there is something about patches 9 and 10, Panoche and Ortigalita, that set them apart from all other patches in the *Expanded Metapopulation*. To try to understand this distinction, we performed a series of simulations and sensitivity analyses modifying scenarios and various of the model parameters.

Initially we suspected that perhaps Panoche and Ortigalita were so close together, within the average kit fox migration distance apart, that there was a reciprocal rescue effect operating. When one patch dropped to low population levels it could be rescued by higher population levels in its nearby neighbour. To address this question we moved the center of the Panoche patch 25 km to the south and redid the simulations. If such a rescue effect was operating, the extinction probability for the *Expanded Metapopulation* should have risen considerably but this was not the case (Figure 19).

To further investigate the effect of area, we eliminated Panoche and Ortigalita from the metapopulation and added their respective areas (80 & 67 $km^2$) to the Kern and Pixley patches (6 and 7). This eight patch metapopulation had an extinction probability only slightly lower than the *Baseline Metapopulation* (Figure 20). The addition of 147 $km^2$ by itself did not significantly reduce extinction probability. Also, we found that as long as Panoche and Ortigalita were present in the metapopulation, extinction probabilities were low. Elimination of Bakersfield, Kern, and Pixley (7 Patch), or those three patches along with Blackwell's Corner (6 Patch) did not result in higher metapopulation extinction probabilities (Figure 21).

Clearly there are some characteristics intrinsic to the Panoche and Ortigalita patches, other than size and location, that result in lower extinction probabilities. We felt that environmental variation (rainfall mean and variance) in those patches might be responsible for the difference in extinction probability. Panoche and Ortigalita have the same environmental mean and standard deviation values: 0.22 and 0.084 (meters) respectively. Similarly, Kern and Pixley are both 0.165 and 0.078. Changing the environmental parameters for Panoche and Ortigalita to those of Kern and Pixley increased the *Expanded Metapopulation* extinction probability dramatically, to the extent that it is barely distinguishable from that of the *Baseline Metapopulation* (A in Figure 22). By contrast, changing the environmental parameters of Kern and Pixley to those of Panoche and Ortigalita had little effect on the extinction probability for the

*Expanded Metapopulation* (B in Figure 22). This result suggests that the model is very sensitive to the Panoche/Ortigalita value for the environmental mean, the environmental standard deviation, or both. However, if we merely exchange the environmental parameter values between Panoche/Ortigalita and Kern/Pixley, the extinction probability is only marginally lower than for the *Baseline Metapopulation* (C in Figure 22). This suggests that some other factor is operating in the case of the Kern and Pixley refuges; perhaps their small size, 43 and 21 km$^2$, respectively. This is supported by the patch area sensitivity analysis (Figure 18).

To investigate the influence of environmental variation in more detail, we performed a series of sensitivity analyses on the environmental mean and standard deviation of the Ortigalita and Camp Roberts patches for the expanded and baseline metapopulations respectively. Camp Roberts was chosen because it—along with Fort Hunter Liggett—has the highest average annual rainfall (envir. mean = 0.301 m) and the highest variance in rainfall (envir. st. dev. = 0.127 m). The 500- and 250-year extinction probabilities for those analyses are depicted in Figures 23 to 27.

Extinction probabilities were lowest when the environmental mean was in the range of 0.24 to 0.30 for the *Expanded Metapopulation* (Figure 23), but no sensitivity was found for any environmental mean value between 0.06 and 0.42 in the *Baseline Metapopulation* (Figure 24). Further analysis actually revealed that the model is most sensitive to an environmental mean of 0.27 although this result is not shown in Figure 24.

The different outcomes of those two sensitivity analyses is possibly explained by the high variance in annual rainfall at Camp Roberts. Analyses of the environmental standard deviation for both Ortigalita and Camp Roberts both revealed that the model is very sensitive to environmental variance. Lowest extinction probabilities occur when that parameter value is 0.075 or less (Figures 25 and 26). If Camp Roberts is provided with lower environmental variance, say 0.07 (= envir. st. dev. for the Carrizo Plain), and an environmental mean in the range of 0.20 to 0.30 (which includes Panoche and Ortigalita), the extinction probability for the *Baseline Metapopulation* drops considerably (Figure 27), from 91 to 13% at 500 years.

It seems clear that the contribution of the Panoche and Ortigalita patches, which is disproportional relative to their patch size and degree of isolation from the rest of the metapopulation, is primarily a consequence of their coincidentally having environmental parameter values in the range most suitable for low extinction probabilities.

In conclusion, we can say that the model is insensitive to changes in the probability of subadult or pup migration and dispersal (Figures 15 and 16), but, is isensitive to changes in the probability of adult and pup mortality (Figure 17), changes in area for some patches under certain conditions (Figure 18), and to changes in the environmental mean and standard deviation (Figures 22 to 27).

## DISCUSSION

To be added at a later date.

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# APPENDIX I--A Population Viability Analysis for the San Joaquin Kit Fox using RAMAS/Age and VORTEX

## *Introduction*

Two computer models, **RAMAS/Age** (Ferson and Akçakaya 1989) and **VORTEX** (Lacy 1993), have been widely used to analyze the viability of populations (Buechner 1989; Ferson et al. 1990; Lacy et al. 1989; Seal and Foose 1989; Lacy and Clark 1990; Maguire et al. 1990). Both of these computer programs utilize Monte Carlo computer simulation techniques. From random sampling of defined probability distributions, these models can predict population trends. Age-specific survival and fecundity rates and the year to year variance in those rates (coefficients of variations) are used. Example populations are generated and exposed to vital rates chosen at random from the distributions provided by the user. Both programs output the probability of extinction at specified intervals, mean population trends, and expected future population fluctuations.

**Ramas/age** is designed to model a single population of a single species. A modified Leslie matrix approach is used to determine the age distribution of the population. It is assumed that all age classes have the same width i.e. each class represents one year. The year-to-year variance in survival and fecundity for a population is assumed to be the result of environmental variation in the habitat of the species. This variance is entered in the program as the coefficient of variation (CV) of the parameter value. It is also assumed that there are no trends in vital rates of the population over time.

Fecundity is entered as the mean number of female offspring produced per female for each age class. Mortality is entered as the mean survival rate through each age class. Age classes are broken down as follows: age class 0 are juveniles < 1 year old and are not reproductively active; age class 1 are yearlings < 2 years old and are reproductively active but not yet mature; age class 2 are mature adults age 2 years and older.  A listing of the terms used, and their definitions, throughout this paper is given in Appendix 1.

The estimated population trends usually are sensitive to changing parameters.  It is important to locate which parameters most heavily influence the predicted population patterns.  This process of varying parameters and determining the impact on extinction predictability is termed sensitivity analysis. It is extremely important for assessing and ranking management options (Possingham et al. 1993).  For each model, I varied a given parameter (pup survival, adult/yearling survival, fecundity, coefficient of variation for mortality or fecundity, carrying capacity or initital population size) while holding the other parameters constant at their initial values.

**VORTEX** (Lacy 1993) can model both single populations and up to 20 populations with distinct population parameters.  Migration and managed supplementation, catastrophes, and genetic drift can be factored into the model. Genetic drift is modeled by simulation of the transmission of alleles at a hypothetical locus.  Therefore, inbreeding depression can be analyzed, which is increasingly important in small populations.  Assumptions made by this model are:  1) survival probabilities are density independent when population size is less than carrying capacity, 2) all animals of reproductive age have an equal probability of breeding, 3) the probabilities of reproduction and mortality are constant from the age of first breeding until an animal reaches the maximum longevity, 4) a simulated catastrophe will have an effect on a population only in the year that the event occurs,and 5) migration rates among populations are independent of age and sex..

### ***Model A***

This is a replication of Buechner's model of the entire San Joaqun kit fox population.  The parameter values (Table 1) are based on data collected by EG&G at Elk Hills from 1980 to 1985 (Berry et al. 1987, Zoellick et al. 1987). EG&G estimated annual survival rates using maximum-likelihood estimation and were averaged over six years.

**Table 1. Model A.** Data obtained at Elk Hills from 1980 to 1986 (Berry et al. 1987; Zoellick et al. 1987).

| Age Class | Survivorship | Fecundity |
|---|---|---|
| 0 | 0.26 | 0.0 |
| 1 | 0.48 | 0.32 |
| 2 | 0.48 | 1.22 |
| 3 | 0.48 | 1.22 |
| 4 | 0.48 | 1.22 |
| 5 | 0.48 | 1.22 |
| 6 | 0.48 | 1.22 |
| 7 | 0.48 | 1.22 |
| 8 | 0.48 | 1.22 |
| 9 | 0.48 | 1.22 |
| 10 | 0.48 | 1.22 |

$R_0 = 0.358$

cv survival age 0 = 0.46

cv survival ages 1-10 = 0.33

cv fecundity = 0.26

The parameter values shown in Model A may be innacurate for several reasons: they are summaries of annual averages of only one population, are several years old and do not include data from the drought years. Also, the pup survival rates in Table 1 are much lower than survival rates calculated by other researchers at Elk Hills. Disney and Spiegel (1992) estimated pup survival rates from 1989 through 1991 ranging from .50 to .80 and averaging .0.593 at Midway oil fields and 0.56 at Lokern . This is a 24% and a 16% increase in pup survival at Midway and Lokern, respectively. This disparity may be attributed to the different types of radiocollars used. Radiocollars weighing approximately 50 g were used for the study at Midway and Lokern (Spiegel and Bradbury 1992). From 1980 to 1983, 113 g ( 4 oz) Model L2B5 radiocollars were used at the Naval Petroleum Reserves (Berry et al. 1987). Beginning in 1984, pups were fitted with 57 g (2 oz) Model MOD 095 transmitters. There were significantly more juvenile deaths from 1980 to 1983 than from 1984 to 1986 ($U_{4,3} = 12$, $p = 0.05$) at the Petroleum Reserves. It seems likely that the heavy radiocollars were contributing to pup mortality and therefore negatively biasing pup survival rates.

Using the parameters shown in Table 1, extinction is predicted, as it was in Buechner's study, inside 25 years (Figure 2). However the predicted abundance of females is higher in this analysis than in Buechner's. Her study predicted that in six years there would be approximately 1000 adult females left in the population. Figure 2 shows that in six years a predicted population of 3930 adult females is expected to remain. This disparity may be due to environmental variance. The vital rates for this population are shown in Table 2. The net reproductive rate ($R_0$ = 0.376) is the same as that obtained by Buechner, which predicts a rapidly declining population.

**Table 2.** Vital rates for the predicted total kit fox population as modeled by Buechner.

| | |
|---|---|
| Finite rate of increase ($\lambda$) | 0.7746 |
| Instantaneous rate of increase (r) | -0.2554 |
| Net reproductive rate ($R_0$) | 0.3760 |
| Mean generation time (T) | 3.829 |
| Life expectancy at birth ($e_0$) | 1.5 |

### *Changing survival and fecundity rates*

This model is most sensitive to changes in adult survival (Figure 3). Increasing adult survival from 20% to 90% results in a 425% rise in the reproductive growth rate ($R_0$). Changes in pup survival result in a linear increase in $R_0$ whereas similar increases in adult survival result in an accelerated increase in $R_0$. This is consistent with Buechner's findings. Changing yearling survival rates has very little effect on the growth rate of the population.

This model is also sensitive to changing fecundity rates (Figure 4). Increasing fecundity rates for both yearlings and adults results in a linear increase in the net reproductive rate. The rate of increase in both yearling and adult $R_0$ is nearly equal: 0.26 and 0.24, respectively.

## ***Model B***

This model represents the current Elk Hills/Carrizo Plain kit fox population. The parameter values (Table 3) are based on data collected from 1989 to 1991 at Lokern and Midway Oil Fields (Spiegel et al. unpl. data; Spiegel et al. 1991), from 1985 to 1990 at the Naval Petroleum Reserves (Zoellick et al. 1987; Berry et al. 1987; O'Farrell et al. 1987; Cypher and Scrivner 1992) and from 1989 to 1991 at the Carrizo Plain (White and Ralls 1993; Ralls and White 1994). These are averages based on data obtained from both developed and undeveloped areas during both dry and wet years. Note that only 4 age classes are listed. Since kit foxes in general do not live longer than three years in the wild (Spiegel pers. comm.), 4 age classes are sufficient. Also, since the survival rate of of 3 year old foxes is greater than zero (Table 3) it is implied that some foxes will continue to live past age 3. While there were no age-specific fecundity rates determined at Midway or Lokern (due to lack of data), the rates for all foxes are lower than adult fecundity rates shown in Table 1. From 1990 to 1993, fecundity at Midway was 0.81 and at Lokern was 1.18. The effects of this disparity on the population trend is addressed during the sensitivity analysis.

**Table 3. Model B.** Survival and fecundity rates used for the model.

| Age Class | Survivorship | Fecundity |
|---|---|---|
| 0 | 0.416 | 0.00 |
| 1 | 0.53 | 0.848 |
| 2 | 0.53 | 1.02 |
| 3 | 0.53 | 1.02 |

cv survival age 0 =0.468
cv survival ages 1 to 3 = 0.155
cv fecundity = 0.441

Initial population size for the Elk Hills/Carrizo Plain is based on the following data: as of the summer of 1986, the minimum population at NPR-1 was 33 adult foxes (Harris et al. 1987) and at NPR-2 was 142 adult foxes (O'Farrell et al. 1987); as of 1993, the minimum number known alive at Lokern and Midway Oil Fields was 19 and 11 adult foxes (Spiegel et al. unpubl.data), respectively and at the Carrizo Plain, in 1991 the fox density was 0.12/km$^2$ (Ralls and White 1994). Extrapolating out from this density estimate, and excluding Soda Lake, the estimated adult kit fox population is 81 adult foxes at the Carrizo Plain. Since the average sex ratio is not statistically different than 1:1 for each of these areas, the estimated total adult female population is 143 foxes.

Ramas/a predicted a steadily declining kit fox population with a lot of variation around the mean (Figure 5). There is a 30% probability quasi-extinction (falling below 1 female) within the next 50 years (Figure 6). While the net reproductive rate ($R_0$) is 121% greater than $R_0$ in Model A, the finite rate of increase ($\lambda$) is only 22% higher but is still < 1 (Table 4).

**Table 4. Vital rates** for the current Elk Hills/ Carrizo Plain kit fox population as predicted by Ramas/age.

| | |
|---|---|
| Finite rate of increase ($\lambda$) | 0.9458 |
| Instantaneous rate of increase (r) | -0.115 |
| Net reproductive rate ($R_0$) | 0.8321 |
| Mean generation time (T) | 3.29 |
| Life expectancy at birth ($e_0$) | 1.885 |

*Changing survival and fecundity rates*

This model is sensitive to increasing juvenile, yearling and adult survival rate. Increasing survival rates have a greater impact on $R_0$ than on $\lambda$ (Figures 7 and 8). For example, an adult survival rate of 90% results in a net reproductive rate that is more than twice that of the finite rate of increase. This accelarated increase in $R_0$ was also observed in Model A. In order to have a stable or growing Elk Hills/Carrizo Plain population, juvenile survival needs to be at least 50%, yearling survival at least 71.6% and adult survival at least 65.2% (Figures 7 and 8).

Model B is also sensitive to varying fecundity rates (Figure 9). Increases in both yearling and adult fecundity rates result in a linear and nearly identical increase in the net reproductive rate. Increasing both the yearling and adult fecundity rate from 1 to 4 more than doubles $R_0$.

Initial population size is also closely associated with the quasi-extinction rate (Figure 10). There is a significant negative correlation between these two variables ($r = -0.925$, $p < 0.05$). Even when the initial population is more than 3 times (480 adult females) that of the current population (143 adult females), there is still a 28% chance of extinction within the next 50 years.

Variance in adult survival appears to have a greater influence on the quasi-extinction rate than does variance in juvenile survival or fecundity (Figure 11). However, adult and juvenile survival, and fecundity are all significantly positively correlated with the quasi-extinction rate ($r = 0.946$, $p < .01$; $r = 0.918$, $p < .01$; $r = 0.961$, $p < .01$, respectively).

## ***Model C***

The current Camp Roberts kit fox population is represented in Model C. The survival and fecundity values used are based on data collected from 1989 to 1991 at Camp Roberts (Spencer et al. 1992; Standley et al. 1992) and are shown in Table 5. There were not enough data to obtain age-specific fecundity rates. Using the minimum population size determined by Berry and Standley (1992), the initial population size used is 45 adult foxes (23 adult females).

**Table 5. Model C.** Camp Roberts population parameters based on data collected from 1989 to 1991 (Spencer et al. 1992; Standley 1992).

| Age Class | Survivorship | Fecundity |
|---|---|---|
| 0 | 0.20 | 0 |
| 1 | 0.53 | 0.41 |
| 2 | 0.53 | 0.41 |
| 3 | 0.53 | 0.41 |

cv survival age 0 = 0.53

cv survival ages 1 to 3 = 0.11

cv fecundity = 0.15

Assuming that the current population trend does not reverse itself in the near future, the prediction from Ramas/a is a rapid decline toward extinction within the next 15 years at Camp Roberts (Figure 12). The vital rates for this population are shown in Table 6. Note that the net reproductive rate is extremely low. The drought may have contributed to this low rate by reducing prey abundance. Ralls and White (1993) reported that the primary effect of drought on kit foxes on the Carrizo Plain was to decrease reproductive success due to a reduction in the number of prey.

**Table 6. Vital rates** for the current Camp Roberts population as predicted by Ramas/age.

| | |
|---|---|
| Finite rate of increase ($\lambda$) | 0.6552 |
| Instantaneous rate of increase (r) | -0.4229 |
| Net reproductive rate ($R_0$) | 0.1745 |
| Mean generation time | 4.1289 |
| Life expectancy at birth $e_0$ | 1.4255 |

*Changing survival and fecundity rates*

This model is most sensitive to changing juvenile survival rates and least sensitive to changing yearling survival rates (Figure 13). Increasing the juvenile survival rate from 20% to 40% results in a 99% increase in the net reproductive rate ($R_0$). A similar increase in both yearling and adult survival rates increases $R_0$ by 29% and 13%, respectively. Increasing adult survival rates results in an accelerated increase in $R_0$ whereas increases in juvenile rates are more linear. However, even with a 90% survival rate for any given age class $R_0$ is still less than one.

Increasing survival rates also results in increases in the finite rate of increase (Figure 14). The rate of change in $\lambda$ is greatest when changing adult survival (0.673) than when changing yearling or juvenile survival, 0.165 and 0.389, respecitvely. However, a stable population growth rate ($\lambda = 1$) was not attained at any survival rate.

Model C is also sensitive to changing fecundity rates. Changing yearling and adult fecundity rates have a similar effect on the net reproductive rate of the population (Figure 15). As fecundity rates for both age classes increase so does $R_0$. However, an adult fecundity rate of 4 female pups per year results in a population with a net reproductive rate of 1 ($R_0 = 1$) but a similar yearling fecundity rate results in a declining population ($R_0 < 1$).

Because the population decline is so steep for this model, the probability of quasi-extinction is 100% at every coefficient of variation (0.1-0.9) for age 0 survival, adult survival, and fecundity. Similarly, the terminal population is 0 for every initial population size chosen (Table 7). Even an initial population three times the original size (1800 adult females) is predicted to go extinct in the next 50 years!

**Table 7. Effect of varying initial population size** on both the quasi-extinction rate and the terminal population for current Camp Roberts population.

| Initial Population Size | Quasi-Extinction Rate | Terminal Population |
|---|---|---|
| 60 | 100% | 0 |
| 120 | 100% | 0 |
| 240 | 100% | 0 |
| 480 | 100% | 0 |
| 960 | 100% | 0 |
| 1800 | 100% | 0 |

## ***Model D***

Model D is a simplistic representation of a kit fox metapopulation consisting of the Elk Hills/ Carrizo Plain (Population 1) and Camp Roberts (Population 2) with very simplistic assumptions. The input values were derived from the same sources used in the Ramas/a analysis. There are a few new parameters required for the VORTEX program. The rationale for these estimates are outlined below. Table 8 summarizes the parameters used in the basic model.

### *Sex Ratio*

Sex ratio at birth and in adults is 1:1 for each population (Spencer et al. 1992; Zoellick et al. 1987; O'Farrell et al. 1987; Spiegel et al. unpl. data;Spiegel et al. 1991; White and Ralls 1993). For the purposes of our analyses, we assumed that all adult males have the potential to reproduce.

### *Fecundity*

Age-specific fecundity is based on annual data collected from the Camp Roberts population (Spencer et al. 1992). For population 1, only age-specific averages are available in the literature. Therefore, these values had to be estimated.

**Table 8. Parameter values for metapopulation study using VORTEX** (Spencer et al. 1992; Zoellick et al. 1987; O'Farrell et al. 1987; Spiegel et al. unpl. data; Spiegel et al. 1991; White and Ralls 1993).

| Parameters | Elk Hills/ Carrizo Plain Population | Camp Roberts Population |
|---|---|---|
| **Inbreeding depression** | none | none |
| **Breeding system** | monogamous | monogamous |
| **Adult males in breeding pool** | 100% | 100% |
| **Breeding age of females** | 1 year | 1 year |
| **Breeding age of males** | 1 year | 1 year |
| **Maximum no. of young per year (one litter per year)** | 6 | 6 |
| **Adult females producing 0 young** | 40.67% | 68.40% |
| **1 young** | 4.51% | 2.70% |
| **2 young** | 4.51 | 7.52% |
| **3 young** | 19.78% | 13.54% |
| **4 young** | 19.78% | 2.70% |
| **5 young** | 6.25% | 2.70% |
| **6 young** | 4.5% | 1.50% |
| **Mortality of females** | | |
| **0 to 1 year olds** | 53.62% | 75% |
| **1 to 4 year olds** | 40.70% | 47% |
| **Mortality of males** | | |
| **0 to 1 year olds** | 57.80% | 84% |
| **1 to 4 year olds** | 41.15% | 46% |
| **Population carrying capacity (K)** | 546 | 71 |
| **Migration rate** | 1% | 1% |
| **Environmental stochasticity** | | |
| **Binomial variance for breeding success** | 1-10% | 1-10% |
| **Binomial variance for mortality rates** | 1-30% | 1-35% |
| **Poisson variance for carrying capacity** | 25.84% | 36.10% |
| **Probability of catastrophe** | 0 | 0 |
| **Initial population size** | 286 | 45 |
| **Females 1 year old** | 76 | 7 |
| **Adult females > 2 years old** | 74 | 18 |
| **Males 1 year old** | 74 | 18 |
| **Adult males > 2 years old** | 69 | 13 |

All of the available literature on kit fox reproduction for these two populations state that both sexes become reproductively active at 1 year of age (Spencer et al. 1992; Zoellick et al. 1987; O’Farrell et al. 1987; Spiegel et al. unpl. data; Spiegel et al. 1991; White and Ralls 1993). Unfortunately, VORTEX only distinguishes between young and adults; yearlings are not specified. Adult breeding females are assumed to produce an average of 4 young per year at Elk Hills/ Carrizo and 3 young per year at Camp Roberts until death (Spencer et al. 1992; Zoellick et al. 1987; O’Farrell et al. 1987).

### *Mortality and Lifespan*

While kit foxes have been known to live up to 12 years in captivity (Mann 1930; Crandall 1964), telemetry studies have shown that very few foxes survived to be more than 4 years old (Berry et al. 1987; Spiegel et al. unpl. data; Spiegel et al. 1991). For modelling purposes, the maximum age of death is 4 years. Age-specific mortality rates are given in several studies (Berry et al. 1987; Standley et al. 1992; Cyhper and Scrivner 1992; Ralls and White 1994; Spiegel unpl. data; Spiegel et al. 1991). These data were averaged across studies for each population.

### *Population Size and Carrying Capacity*

Carrying capacity is defined as the number of San Joaquin kit foxes that can be supported by the amount of suitable habitat based on current density estimates. These estimates were obtained from capture-recapture studies at Camp Roberts, Elk Hills and the Carrizo Plain (Berry et al. 1992; O’Farrell et al. 1987; Harris et al. 1987; Spiegel et al. unpl. data; Spiegel et al. 1991; Ralls and White 1994). The amount of suitable habitat was crudely estimated as follows: at Camp Roberts it is based on the previously derived minimum distribution polygon (EG&G Progress Report 1992); at Elk Hills it is the Lokern and Midway Oil Fields plus both Naval Petroleum Reserves, and at the Carrizo Plain it is the entire natural area minus the area of Soda Lake.

### *Simulations*

All simulations were run for 100 years, and were replicated 100 times. At ten year intervals, the probability of extinction, the population size, and the standard deviation of population size are reported. The probability of extinction is the number of populations, out of 100 that went extinct within 100 years. Both deterministic and stochastic measures of the intrinsic rate of increase (r) are reported.

### *Environmental variability*

The impacts of environmental variation were examined using a range of values to model the year to year variance reproductive success and mortality (Lacy 1993). Demographic stochasticity was not included . Environmental variation was calculated from the same equation used to determine coefficients of variation in Ramas/age (see glossary).

The predicted course of the metapopulation is inevitable extinction within 60 years (Figure 16). Even though the estimated population size increases to nearly 330 adult foxes, the population crashes. Figures 17 and 18 illustrate the vulnerability to extinction of both the Elk Hills/Carrizo and Camp Roberts populations. Note that within 10 years the Elk Hills/Carrizo population has a 66% probability of extinction and the Camp Roberts population has an 83% probability of extinction. The mean time to extinction for the metapopulation is 11.21 years (± 0.98 year). However, in contrast to the predictions made by Ramas/age, Vortex predicts that the Elk Hills/ Carrizo population is growing annually by 2.6% (Table 9).

The disparity between the net reproductive rates of the two populations is noteworthy. Population 1 has an $R_0$ that is 4.5 times the $R_0$ of the population 2. In other words, the average number of female offspring produced per female at Elk Hills/Carrizo is 4.5 times the average produced at Camp Roberts. This is most likely contributing to the very low deterministic growth rate (r) for population 2

**Table 9. Vital rates** for two kit fox populations as predicted by Vortex.

| | Elk Hills/ Carrizo | Camp Roberts |
|---|---|---|
| Finite rate of increase ($\lambda$) | 1.026 | 0.505 |
| Deterministic growth rate (r) | 0.026 | -0.684 |
| Net reproductive rate ($R_0$) | 1.05 | 0.230 |
| Mean generation time | | |
| females | 1.88 years | 1.87 years |
| males | 2.15 years | 2.17 years |

*Changing initial population size*

The results of PVA suggest that there is substantial loss of genetic variation from populations of 100 to 570 animals (Table 10). There is a 100% probability of extinction for each population analyzed. Increasing the initial population size does result in a linear increase in the time to extinction. However, since the carrying capacity for the metapopulation is 617 adult foxes, the initial population sizes cannot be increased enough so that there is no threat of extinction within the next 100 years given the current parameters.

*Environmental variability*

The results showed that with increasing levels of annual environmental variation on reproduction, pup mortality, and adult mortality there was a decrease in the mean time to extinction (Figure 19a, b, c). For population 1, adult mortality is the most sensitive variable to environmental variation (Figure 19a). Increasing the environmental variation acting on adult survival from 10 to 20 % resulted in a decrease in the mean time to extinction of 10 years. In contrast, pup mortality was the most sensitive variable to environmental variation in population 2 (Figure 19b). For the metapopulation, both pup and adult mortality were similarly sensitive to environmental variation except when variation was low i.e. 10% (Figure 19c). Note that increasing environmental variation in reproduction had little effect on the mean time to extinction for both populations and the metapopulation. Further analysis showed that increasing the environmental variation acting on reproduction from 1 to 20% had little effect on the population size, heterozygosity, and probability of extinction of the metapopulation (Figure 20a,b,c).

*Changing mortality and fecundity rates*

Both populations 1 and 2 are sensitive to changing juvenile and adult mortality rates but are more sensitive to changing juvenile mortality rates (Figure 21a and b). Increasing the juvenile mortality rate from 20 to 60% results in a 90% decrease in $R_0$ for population 1 and a 100% decrease for population 2. Even when juvenile mortality is only 20%, population 2 is still predicted to decline ($R_0 < 1$). For population 1, however, population growth is predicted when juvenile mortality is less than 60%.

## DISCUSSION

Both computer simulation programs predict that neither the Elk Hills/Carrizo Plain nor the Camp Roberts populations are viable on their own and extinction will occur within the next 100 years if the current population trends persist. The metapopulation is predicted to go extinct within 60 years.

Environmental variation, population size, genetic factors and changes in habitat suitability all influence the viability of these populations. Changes in juvenile survival rates have the greatest impact on population trends at both Camp Roberts and Elk Hills/Carrizo Plain. Since coyote predation has a more pronounced effect on pup mortality than on any other age class (Berry et al. 1987), management efforts should focus on effective predator control as a means of minimizing pup mortality. While coyotes are the most ubiquitous predators, red foxes may pose an equal or greater threat to kit fox survival. More information needs to be collected regarding kit fox-red fox interactions.

More information is also needed regarding the amount of suitable kit fox habitat remaining. Since variations in the carrying capacity have been shown to influence population size and genetic diversity, a comprehensive effort is needed to map the suitable habitat left in the San Joaquin Valley. Special attention needs to be given to the northern and eastern kit fox range. The contribution of these areas in terms of wildlife corridors needs to be studied as well.

There are limitations on both of the computer simulation programs used. Ramas/a does not allow for metapopulation analysis and therefore can only be used to model single populations. While this is valuable for determining the viability of an individual population, it provides little information for management of the species as a whole. Also, Ramas/a does not consider habitat quality or genetic diversity. Since habitat fragmentation and degradation are key factors in the demise of this species, it is important that they should be included in predicting population trends and the genetic stability of isolated populations. Another limitation is that only one sex is modeled; females are considered to be the limiting sex.

While VORTEX does allow assessment, genetic diversity and delineation of both sexes, only two age classes can be modeled: juvenile and adult. Yearlings cannot be included in the analysis. This is unfortunate since kit foxes begin breeding at one year of age. Habitat quality and carrying capacity can be specified but often times this variable proves more of a hindrance than a help. There is no way of turning off the carrying capacity so that when performing a sensitivity analysis on changing population sizes, you are limited by the carrying capacity.

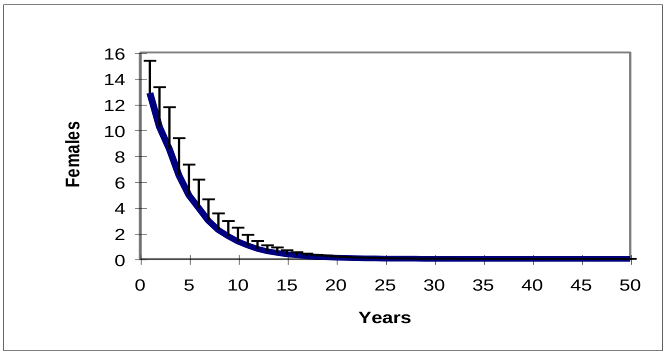


**Figure 2. The results (mean and standard deviation) of 250 runs of Ramas/age for a population of 7,000 kit foxes using the parameters shown in Table 1. The y axis is the # of adult females measured in thousands**

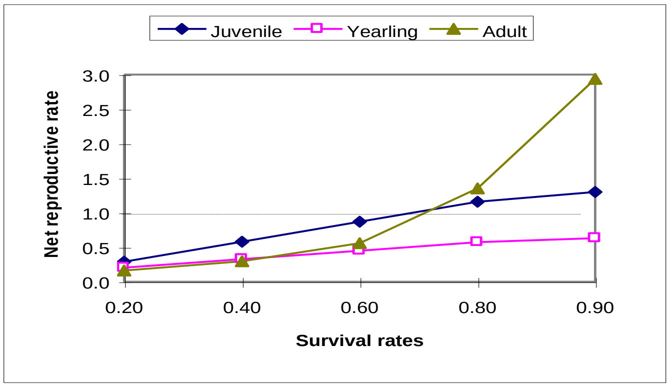


**Figure 3. The effect of varying survival rates of three age classes on $R_0$, Model A.**

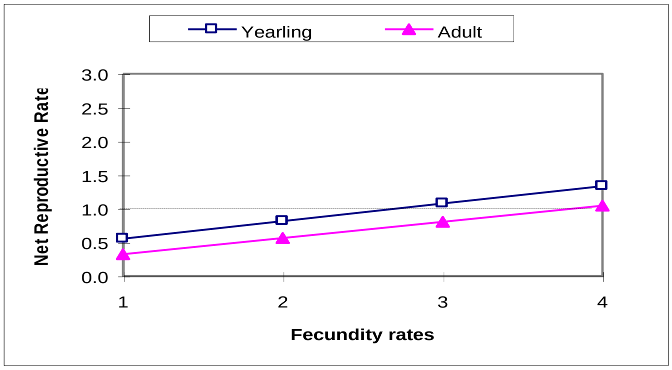


**Figure 4. The effect of varying fecundity rates of two age classes on $R_0$, Model A**

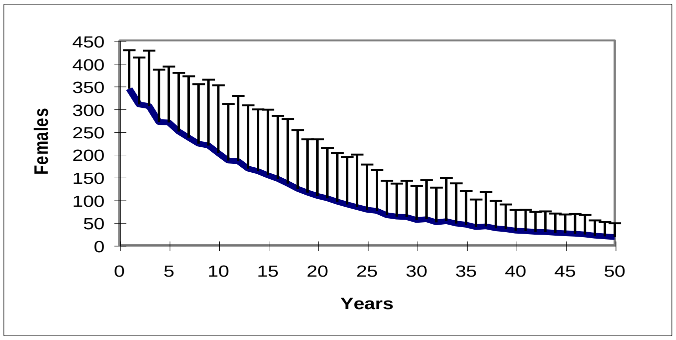


**Figure 5. Model B: the results (mean and standard error) of 250 runs of Ramas/age for a population of 143 adult kit foxes using the parameters shown in Table 2. Y axis is the # of adult females**

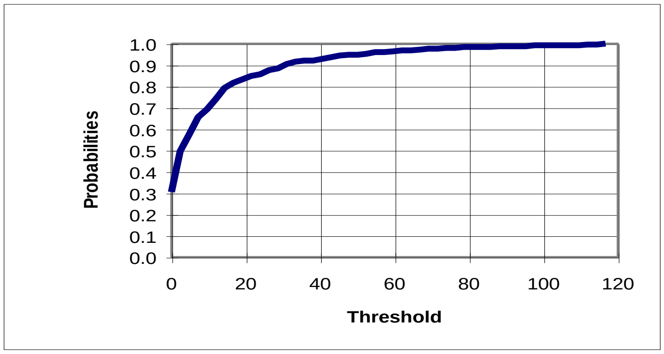


**Figure 6. Model B. The probability that a population of 143 adult kit foxes will the paramters shown in Table 2 will drop below various threshold population sizes in fifty years. Based on 250 runs of Ramas/age.**

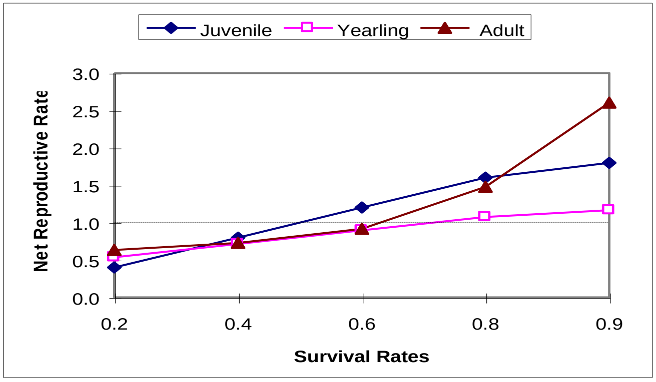


**Figure 7. Model B. The effect of varying survival rates on $R_0$**

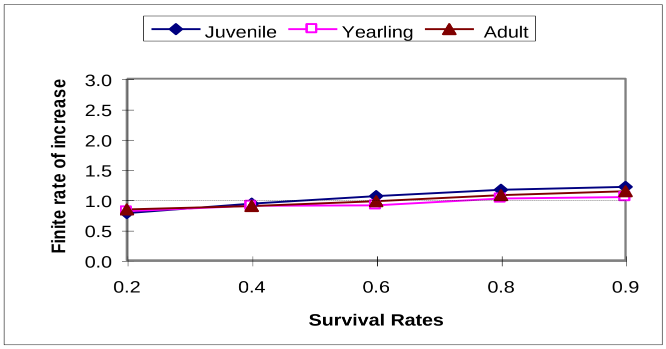


**Figure 8. Model B. The effect of varying survival rates of three age classes on lambda**

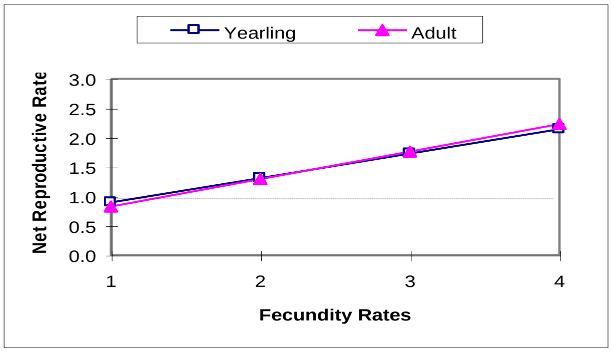


**Figure 9. The effect of varying fecundity rates of two age classes on $R_0$, Model B.**

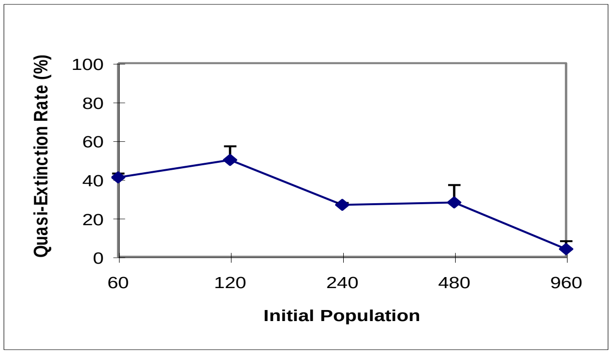


**Figure 10. Model B: Effect of varying initial population size on quasi-extinction rate (mean and standard error of five runs based on 50 replicates each).**

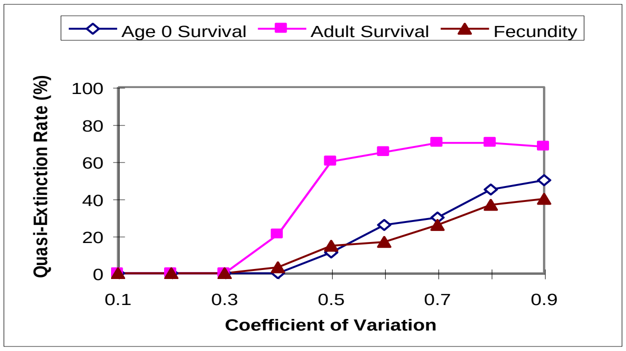


**Figure 11. Model B: The quasi-extinction rates (%) as a function of the variation in survival and fecundity rates (based on 250 replications using Ramas/a).**

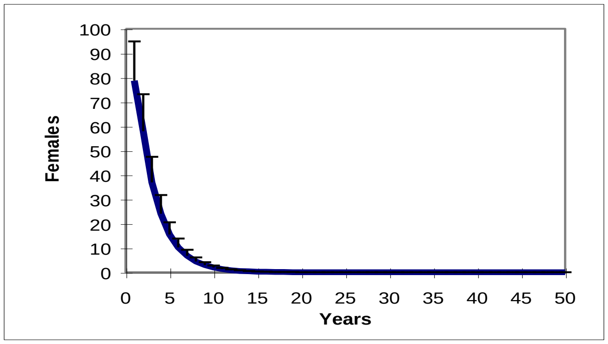


**Figure 12. Model C. The results (mean and standard error) of 250 runs of Ramas/a of a population of 23 adult females using the parameters shown in Table 5.**

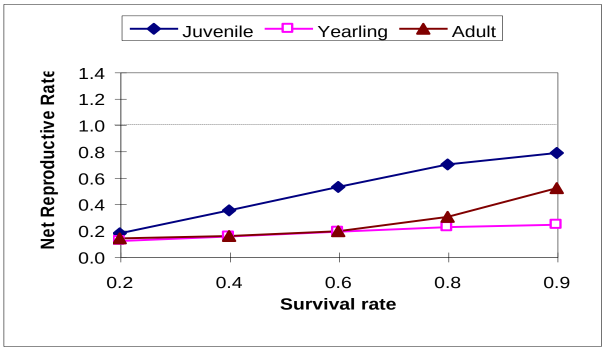


**Figure 13. Model C. The effect of varying survival rates of three age classes on $R_0$.**

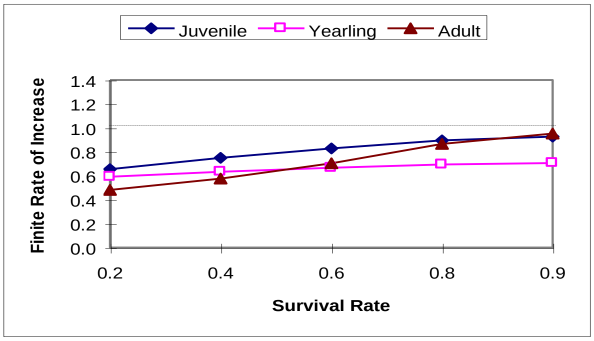


Figure 14. Model C. The effect of varying survival rates of three age classes

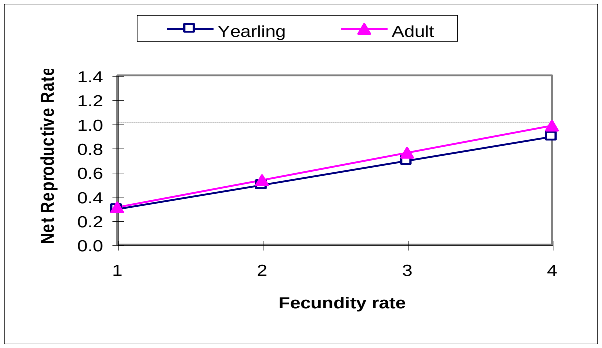


Figure 15. Model C. The effect of varying fecundity rates of two age classes on $R_0$

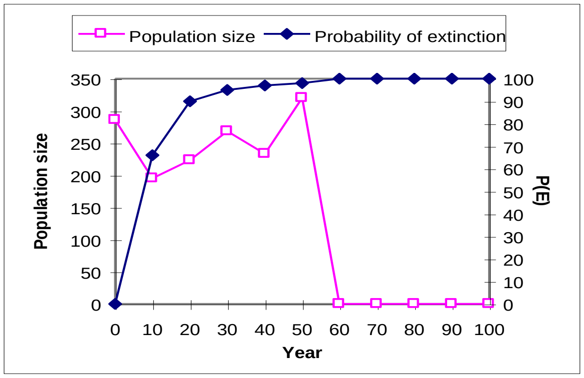


Figure 16. Model D. The estimated population size and extinction probabilities of the metapopulation over the course of 100 years. Based on parameters shown in Table 8.

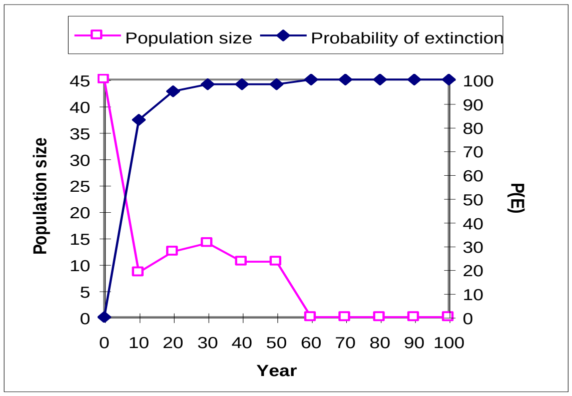


Figure 17. Model D. The estimated population size and extinction probabilities of population 1 over the course of 100 years. Based on parameters shown in Table 8.

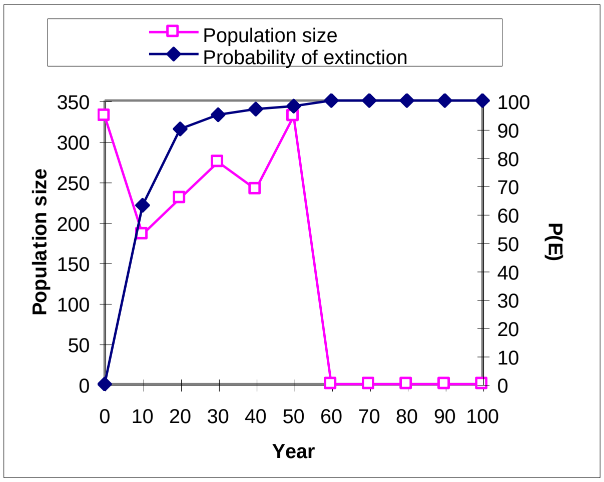


**Figure 18. Model D. The estimated population size and extinction probabilities of population 2. over the course of 100 years. Based on parameters shown in Table 8.**

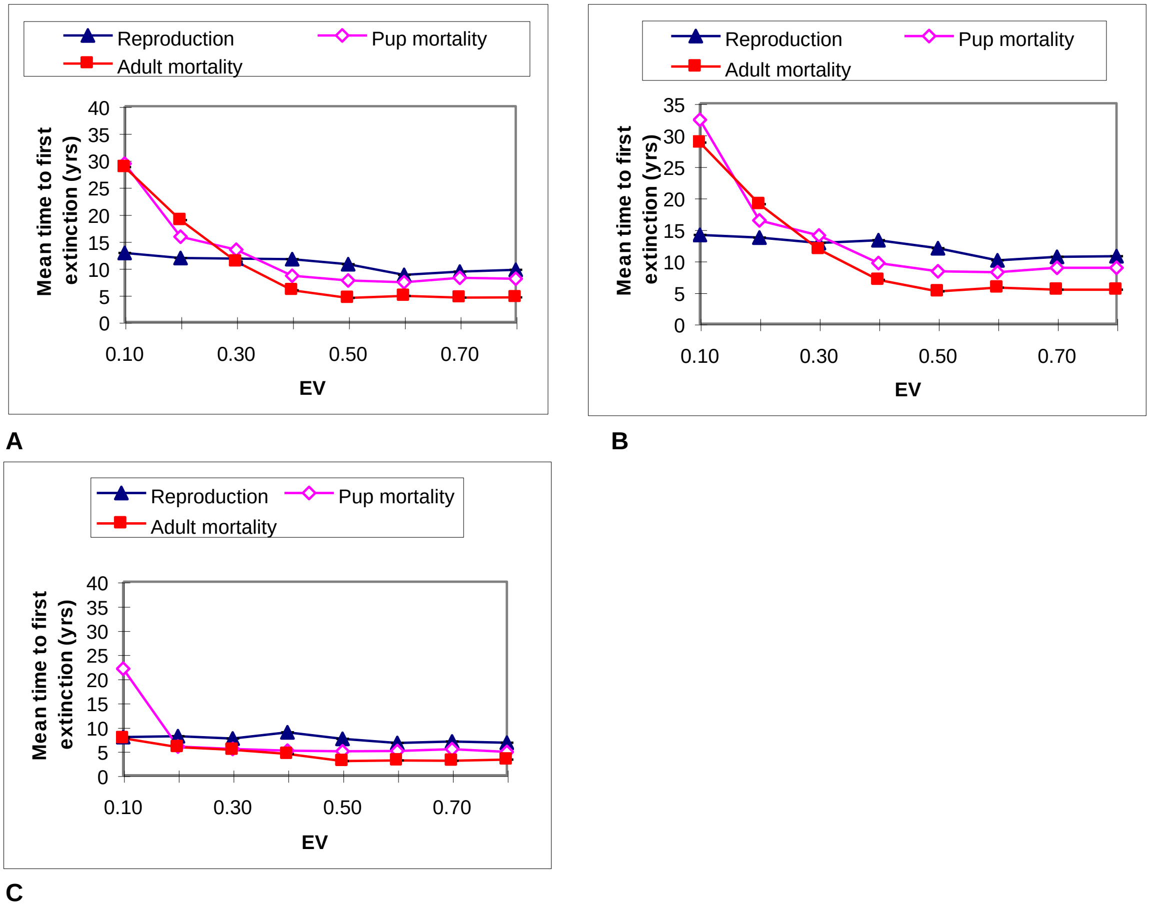
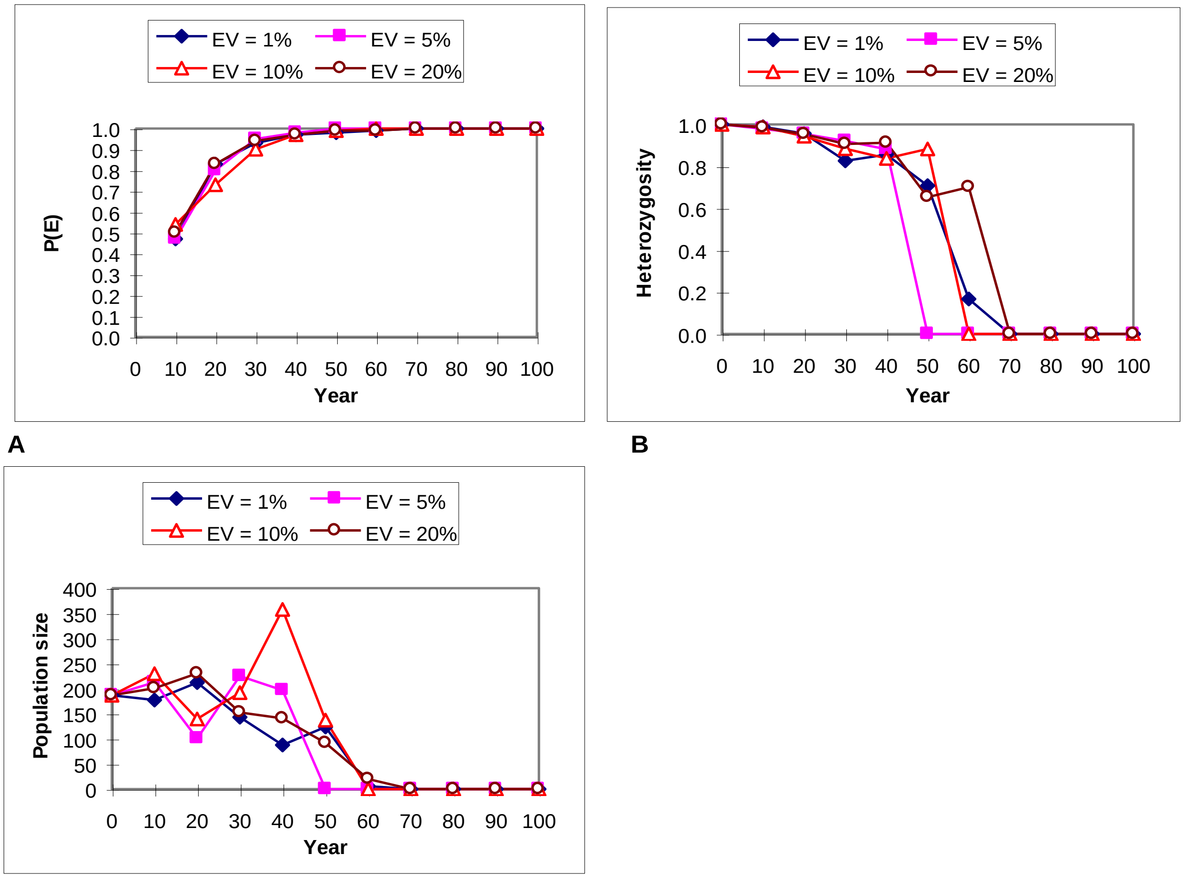


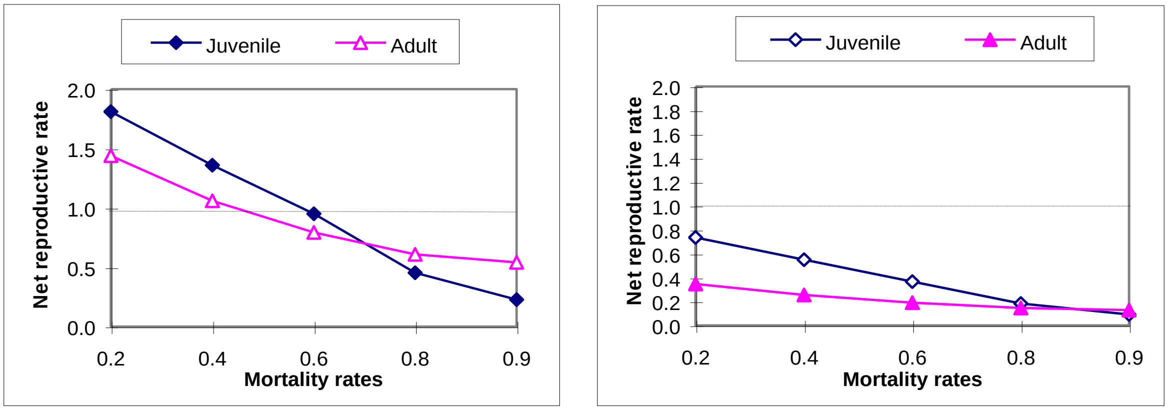
**Figure 19. Mean time to extinction as a function of environmental variation in reproduction, pup mortality and adult mortality for A) population1, B) population 2, and C) metapopulation.**



**A** **B**

**C**

**Figure 20. Envrionmental variation acting on reproduction and how this affects A) the probabilitiy of extinction B) expected heterozygosity, and C) the population size of the metapopulation.**



**A** **B**

**Figure 21. The net reproductive rate (Ro) as a function of variation in juvenile and adult mortality rates for A) population 1 and B) population 2.**

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## GLOSSARY OF TERMS USED

**Carrying capacity, K:** The maximum number of organisms that can be supported in a given unit of habitat.

**Coefficient of variation, CV:** Is a measure of the year to year variance of a given parameter value and is defined as the standard deviation of a sample relative to the mean of the sample:

$$\frac{\dfrac{\text{max Y - min Y}}{\text{mean normal range}}}{\bar{\text{Y}}}$$

**Environmental variation, EV:** Is also a measure of the year to year variance of a given paramter value and is assumed to follow a binomial distribution for birth and death rates and a normal distribution for carrying capacity.

**Fecundity:** The average number of female offspring produced per female per year. This is calculated by multiplying the average litter size, sex ratio, and percent successfully reproducing females in a population.

**Finite rate of increase, λ**: The proportion by which the population increases with each time step. It is calculated as the dominant eigenvalue of the Leslie matrix and therefore ignores the effects of density dependence, stochasticity and migration.

**Generation time, T**: The average time between the birth of parents and birth of offspring. Also the average time it takes for the population to increase by the net reproductive rate.

**Instantaneous rate of increase, r**: The (infinitesimal) rate of increase for a population which is in a stable age distribution; simply the rate of population growth that the population would experience at stable age distribution, ignoring the effects of stochasticity, migration and density dependence. If $r < 1$, the population abundance is expected to decrease and, if $r > 1$, it is expected to increase. If it is exactly zero, the population will be stationary.

**Life expectancy, $e_0$**: An estimate of how much longer individuals at age 0 will live.

**Mortality rate**: 1 - survival rate.

**Net reproductive rate, $R_0$**: The average number of female offspring per female over her entire lifetime. If $R_0 < 1$ the population is decreasing, if $R_0 > 1$, the population is increasing. If it is exactly zero, the population will be stationary. Net reproductive rate is the proportion by which the population changes with each generation.

**Quasi-extinction**: A decrease in population abundance or density to some level. If the level is zero then quasi-extinction is equivalent to true local extinction of the population. For this study falling below 1 adult female is termed quasi-extinction.

**Sex ratio**: The proportion of females in the population.

**Survival rate**: The proportion of age-specific individuals alive per year.

**Vital rates**: The parameters in a demographic model. They include the fecundity and survival rates. These values are also known as demographic rates.

**Table 10. Basic model summarizing metapopulation.** Mean population size and heterozygosity (± SE) are provided for each 10-year interval of the 100-year simulation. Mean time to extinction of those populations that went extinct, and probability of extinction for each founding population size are also given.

| Year | Mean population size | Mean observed heterozygosity (%) | Mean population size | Mean observed heterozygosity (%) | Mean population size | Mean observed heterozygosity (%) | Mean population size | Mean observed heterozygosity (%) | Mean population size | Mean observed heterozygosity (%) |
|---:|---:|---:|---:|---:|---:|---:|---:|---:|---:|---:|
| 0 | 100.00 | 100.00 | 115.00 | 100.00 | 230.00 | 100.00 | 470.00 | 1.00 | 570.00 | 1.00 |
| 10 | 95.00 | 93.00 | 125.00 | 97.00 | 175.00 | 97.00 | 241.00 | 98.00 | 228.27 | 0.98 |
| 20 | 49.00 | 86.00 | 212.00 | 90.00 | 137.00 | 91.00 | 195.00 | 96.00 | 121.9 | 0.96 |
| 30 | 82.00 | 78.00 | 271.00 | 93.00 | 192.00 | 87.00 | 110.00 | 93.00 | 151.71 | 0.75 |
| 40 | 62.00 | 44.00 | 128.00 | 93.00 | 311.00 | 80.00 | 45.00 | 89.00 | 69.5 | 0.91 |
| 50 | 497.00 | 31.00 | 236.00 | 187.00 | 0.00 | 0.00 | 367.00 | 94.00 | 0.00 | 0.00 |
| 60 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 149.00 | 91.00 | 0.00 | 0.00 |
| 70 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 80 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 90 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 100 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| Mean time to extinction ± SE (in years) | 12.00 |  | 11.00 |  | 13.00 |  | 13.00 |  | 13.55 |  |
| Mean probability of extinction (%) | 100.00 |  | 100.00 |  | 100.00 |  | 100.00 |  | 100.00 |  |

## APPENDIX 2--RAINFALL AND KIT FOX PREY ABUNDANCE

Rainfall data are correlated with kit fox prey abundance as a basis for modeling the relationship between biomass and environmental variability. This section shows how monthly rainfall data can be used as a predictor of the San Joaquin kit fox prey abundance, specifically lagomorphs (*Lepus californicus*), giant (*Dipodomys ingens*) and short-nosed kangaroo rats *(Dipodomys nitratoides brevinasus*). First, rainfall data and prey abundance are correlated. Second, rainfall data over the entire geographic range of the San Joaquin kit fox are analyzed to quantify the amount of environmental heterogeneity.

### *Statistical Methods*

Monthly rainfall data are compared with the August census counts of two heteromyid rodents, *D. ingens* and *D. nitratoides brevinasus* using forward stepwise regression with alpha-add = 0.1 and alpha-delete = 0.15 (Neter et al. 1985, BIOSTAT program Sreg). Monthly rainfall records from October through April, 1985 to 1993, for the Washburn Ranch (on the Carrizo Plain) are correlated with abundance as measured by annual trapping data in August, for the years 1987 to 1994 (D. F. Williams unpubl. data).

Annual rainfall data from Bakersfield for the years 1982 to 1992 are compared with lagomorph counts from 1983 to 1993 at Elk Hills Naval Petroleum Reserve #1( Cypher and Scrivner 1992, EG&G Annual Report 1992). A Pearson product-moment correlation is performed as is a linear regression. Again, rainfall data are the independent variable and lagomorph densities the dependent variable.

The covariation of precipitation at 9 weather stations approximating the geographic range of the kit fox (Figure 1) is also evaluated using 40 years of annual rainfall data (National Climatic Data Center 1933-1993). Since the total annual rainfall data from the 9 weather stations are not normally distributed, the data are normalized by transformation to natural logarithms. The relationship between each pair of weather stations is then analyzed using Pearson product-moment correlation coefficients with significance at the 95% confidence level

(SYSTAT statistical package). A one-way ANOVA at the 95% confidence interval is also performed to test the level of difference between each site (Neter et al. 1985).

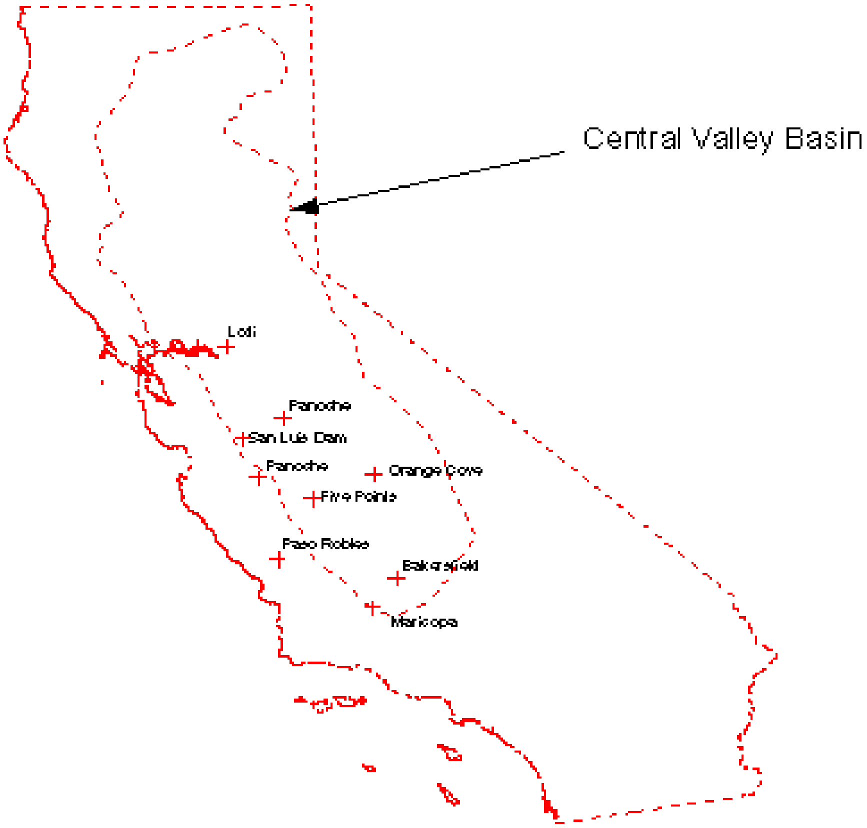

**Figure 1. The nine weather stations used which approximate the current San Joaquin kit fox range.**

*Correlation of Rodent Abundance and Rainfall*

The results of the stepwise regression of population density against monthly rainfall show that March rainfall of the previous year is the best predictor of August kangaroo rat abundance at the Elkhorn Plain, Carrizo Natural Area. There is a significant positive linear relationship (Figures 2*a*, *b*) for *D. nitratoides brevinasus* abundance ($n = 8$, $R^2$ adj = 0.646, $P < 0.05$) and rainfall in March of the previous year. However, there is no such linear relationship between *D. ingens* and March rainfall ( $n = 8$, $R^2$ adj = 0.333, $P > 0.05$). When density estimates for both heteromyid species are combined (Figure 3), a positive linear relationship is suggested but is not significant ($n = 8$, $R^2$ adj = 0.476, $P < 0.1$) between total kangaroo rat abundance and March rainfall of the previous year. The Pearson product-moment correlation coefficients are shown in Table 1. Again, note that only *D. n. brevinasus* density is significantly correlated with March rainfall of the previous year.

March rainfall of the same year is not significantly correlated with August kangaroo rat abundance at the Elkhorn Plain ($n = 8$, $R^2$ adj = 0; $P > 0.05$). There appears to be a lag effect in which kangaroo rat density does not drop or increase until the year following a drop or rise in March rainfall (Figure 4). This may be due to the seed caching behavior of giant kangaroo rats. During a year of lower than normal rainfall, these kangaroo rats may still have plenty of seeds which they have stored. They may, therefore, continue to breed even during years of low rainfall. However, several years in a row of low rainfall will result in a drop in kangaroo rat density.

**Table 1.** The Pearson correlation matrix of kangaroo rat density and March rainfall of the previous year at the Carrizo Plain from 1987 to 1993.

| | **March rain** | ***D. ingens density*** | ***D. n. brevinasus* density** | **Total kangaroo rat density** |
|---|---|---|---|---|
| **March rain** | 1.000 | | | |
| **D. ingens density** | 0.655 | 1.00 | | |
| **D. n. brevinasus density** | 0.834 | 0.588 | 1. 00 | |
| **Total kangaroo rat density** | 0.742 | 0.988 | 0.696 | 1.00 |

To illustrate this "lag effect", kangaroo rat densities are compared with the previous year's March rainfall, as a percentage of the 20 year mean (Figure 5). In terms of predicting kangaroo rat population trends, we need to look at the preceding year's March rainfall. Once March rainfall levels drop below 40% of average, kangaroo rat densities fall the next year. There also appears to be a cumulative effect such that two or more subsequent years of low rainfall (below 20%) results in total density estimates of less than 15 individuals per 1.44 ha, only 19% of the 7 year average.

There is also an apparent lag effect when comparing lagomorph densities with total annual rainfall (Figure 6). As shown in Figure 7, there is a significantly positive relationship between the previous years' total rainfall and lagomorph density ( $n = 10$, $R^2$ adj = .410, $P < 0.05$). In 1983 there were 403 lagomorphs counted per $km^2$, the highest density over the course of the study. By 1991, only 1% of this maximum were counted. This low followed a year where annual rainfall was 58% of normal.

## Geographic Covariation

Annual variation is correlated at the 95% confidence level between all pairs of the 9 sites analyzed (Table 2).

**Table 2.** The Pearson product moment correlation matrix of annual rainfall (mm) from seven geographic locations from 1974 to 1992. These rainfall data have been normalized by log transformation.

| | **Carrizo** | **Bakersfield** | **Panoche** | **Paso Robles** | **Visalia** | **Coalinga** | **Delano** |
|---|---|---|---|---|---|---|---|
| **Carrizo** | 1.000 | * | * | * | * | * | * |
| **Bakersfield** | 0.900 | 1.000 | * | * | * | * | * |
| **Panoche** | 0.838 | 0.875 | 1.000 | * | * | * | * |
| **Paso Robles** | 0.927 | 0.959 | 0.901 | 1.000 | * | * | * |
| **Visalia** | 0.880 | 0.912 | 0.836 | 0.931 | 1.00 | * | * |
| **Coalinga** | 0.834 | 0.916 | 0.827 | 0.911 | 0.877 | 1.000 | * |
| **Delano** | 0.944 | 0.916 | 0.868 | 0.938 | 0.941 | 0.883 | 1.000 |

This relationship implies that variation in rainfall is homogenous throughout the range of the San Joaquin kit fox (Figure 8). Population fluctuations and viability of the San Joaquin kit fox may be correlated throughout most of this range.

The apparent homogeneity suggests that the distance between patches within the current kit fox range does not lessen the impacts of drought. In other words, a drought may affect all patches somewhat equally. However, the kit fox response to drought may vary between patches. For example, in 1991 no captured female foxes reproduced at the Carrizo Plain (White and Ralls 1993). In contrast, 25% of females reproduced successfully at the Lokern Natural Area during this same year (Spiegel et al. unpubl. data). It is unclear whether this difference is the result of small sample sizes or differing reproductive strategies in these two areas. The Lokern Natural Area is closer to urbanized areas than the Carrizo Plain. It is possible that the higher reproductive rates may, in part, be the result of anthropogenic food sources.

### *Regional Rainfall Amounts*

A one-way ANOVA of differences in log annual rainfall among weather stations shows that there is a significant difference in the mean annual rainfall (mm) at each weather station (Table 3). Note that Orange Cove and Maricopa were excluded due to lack of several years worth of data. Mean log annual rainfall amounts are shown for seven weather stations in Figure 9. The Lodi weather station, which is the northernmost station, receives significantly more annual precipitation than the other stations. The Bakersfield and Maricopa weather stations, which are the southernmost stations, receive significantly less annual precipitation than the other stations. In general, the southern stations receive less rainfall than the northern ones. Paso Robles, the westernmost station, is the exception do to its close proximity to the coast.

**Table 3.** Results of one-way ANOVA to test for differences among average annual rainfall at seven stations ($n = 105$). Orange Cove and Maricopa are excluded due to insufficient numbers of years with rainfall data.

| Source of variation | Sum of squares | df | Mean square | F-ratio | *P* |
|---|---|---|---|---|---|
| Site | 12.048 | 6 | 2.008 | 16.201 | < 0.05 |

| | | | |
|---|---|---|---|
| Error | 12.146 | 98 | 0.124 |

### *Summary*

- **March rainfall of the previous year is the best predictor of August kangaroo rat densities**
- **There is a significantly positive linear relationship between kangaroo rat densities and March rainfall of the previous year.**
- **There is a cumulative effect of two or more years of low rainfall**
- **There is a significantly positive linear relationship between the previous years' annual rainfall and lagomorph densities**
- **Annual variation in rainfall is significantly correlated between all pairs of the nine weather stations across the kit fox range**
- **Weather stations in the northern and western portions of the kit fox range receive significantly more rainfall than stations in the southern portion of the range.**

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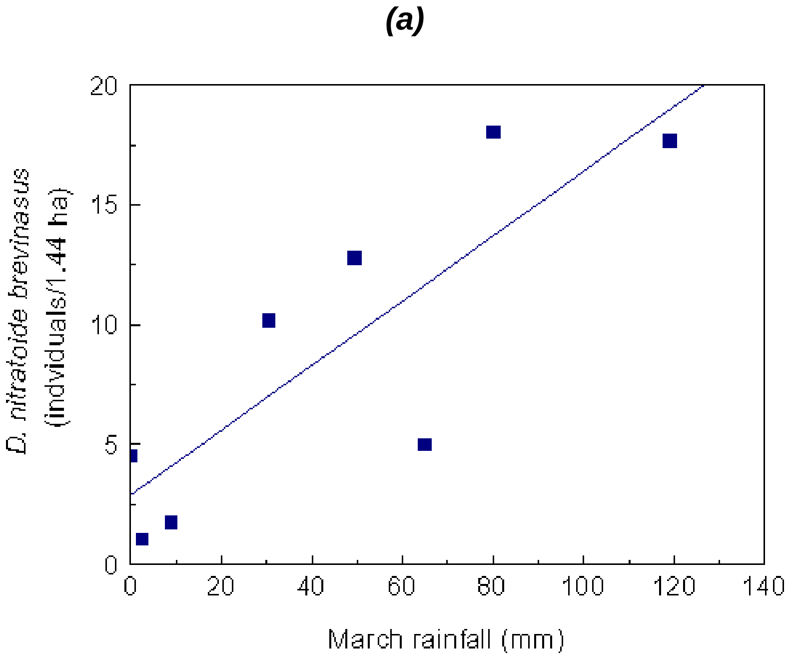
## FIGURES



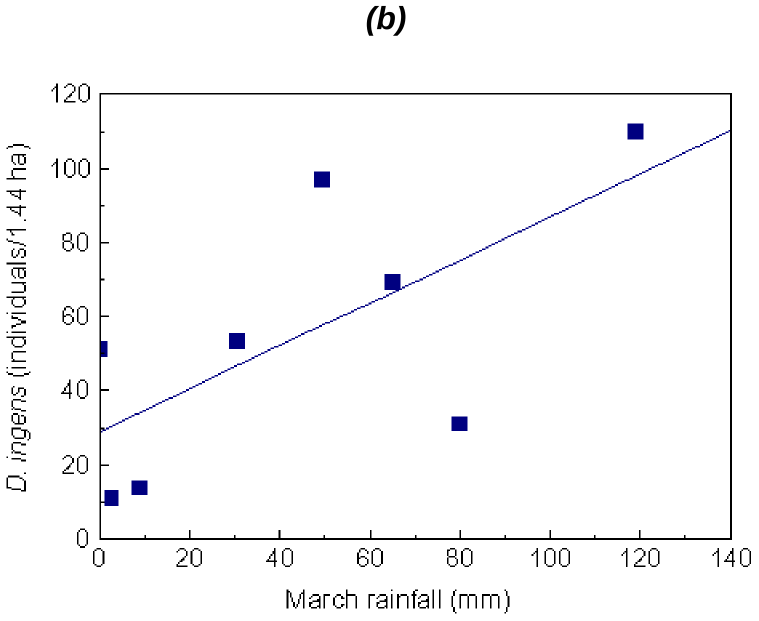


**Figure 2.** Relationship between March rainfall and fall abundance for a) *D. nitratoides brevinasus and* b)*. D. ingens*. Rodent data, from D. F. Williams unpubl. data, represent total number of individuals per 1.44 ha. Rainfall data from Washburn Ranch, 1987 to 1994.

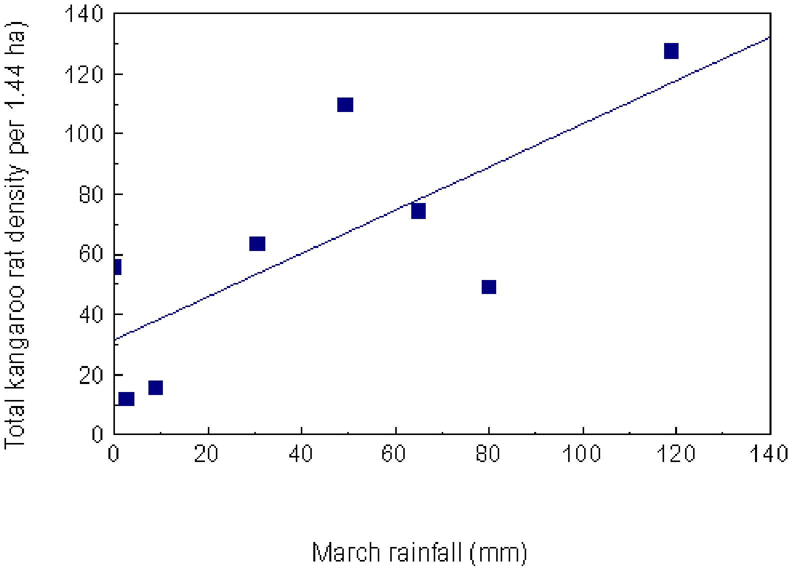


**Figure 3.** Relationship between March rainfall and fall abundance for *D. ingens* and *D. nitratoides brevinasus* combined. Rodent data, from D. F. Williams unpubl. data, represent total number of individuals per 1.44 ha. Rainfall data from Washburn Ranch, 1987 to 1994.

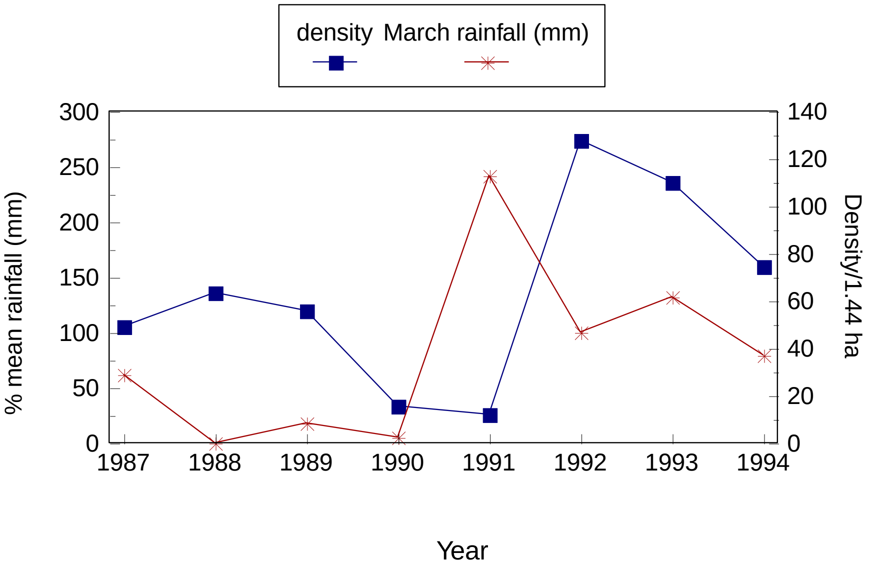


**Figure 4.** Relationship between total kangaroo rat density and March rainfall as a percent of the 20 year mean (1973 to 1993). Rodent data, from D.F. Williams unpubl. data, represent total number of individuals per 1.44 ha. Rainfall data from Washburn Ranch, 1987 to 1994.

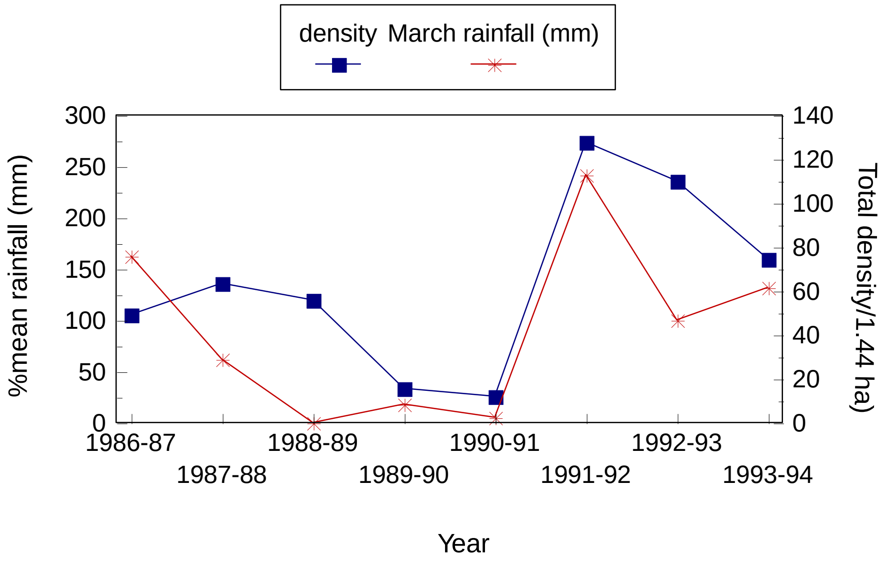


**Figure 5.** Relationship between kangaroo rat density and the previous year's March rainfall, as a percent of the 20 year mean (1973 to 1993). Rodent data, from D. F. Wiliiams unpubl. data, represent total number of individuals per 1.44 ha. Rainfall data from Washburn Ranch, 1986 to 1993.

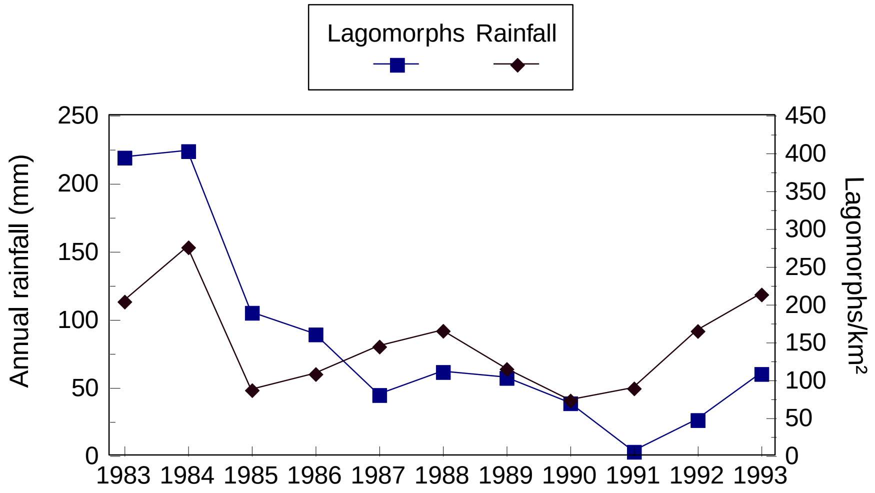


**Figure 6.** Relationship between lagomorph density and total annual rainfall. Lagomorph data (Cypher and Scrivner 1992, EG&G unpubl. data) represent total number of individuals per km$^2$. Rainfall data from Bakersfield weather station.

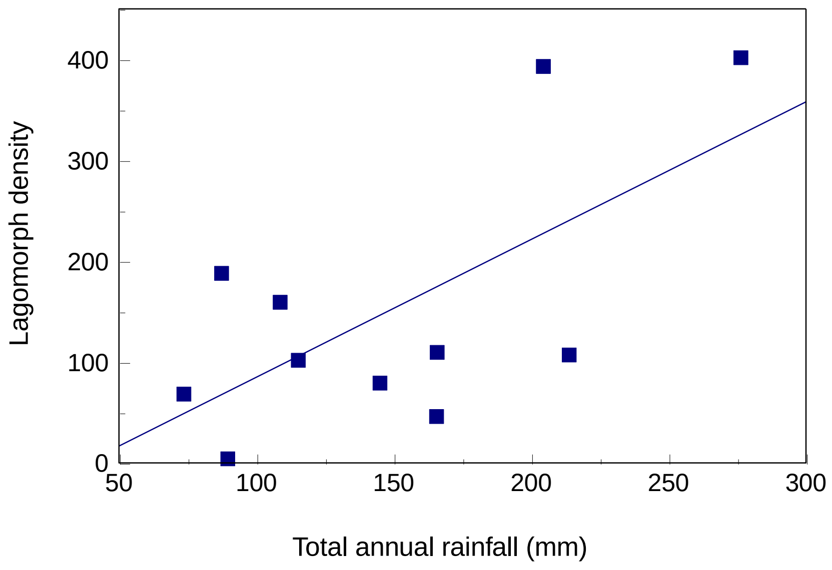


**Figure 7.** Relationship between lagomorph density at NPR #1 and total annual rainfall at NPR #2. Lagomorph data (Cypher and Scrivner 1992, EG&G unpubl. data) represent total number of individuals per km$^2$. Rainfall data from the Bakersfield weather station, 1983 to 1993.

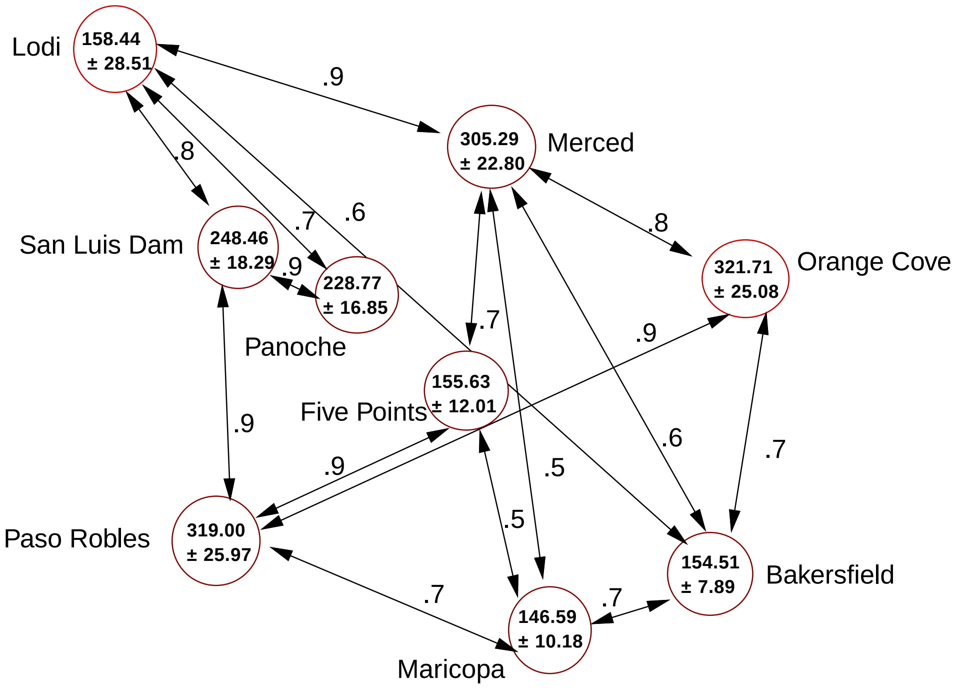


**Figure 8.** The correlation structure of environmental variation over the San Joaquin kit fox range (average annual rainfall (mm) and S.D.).

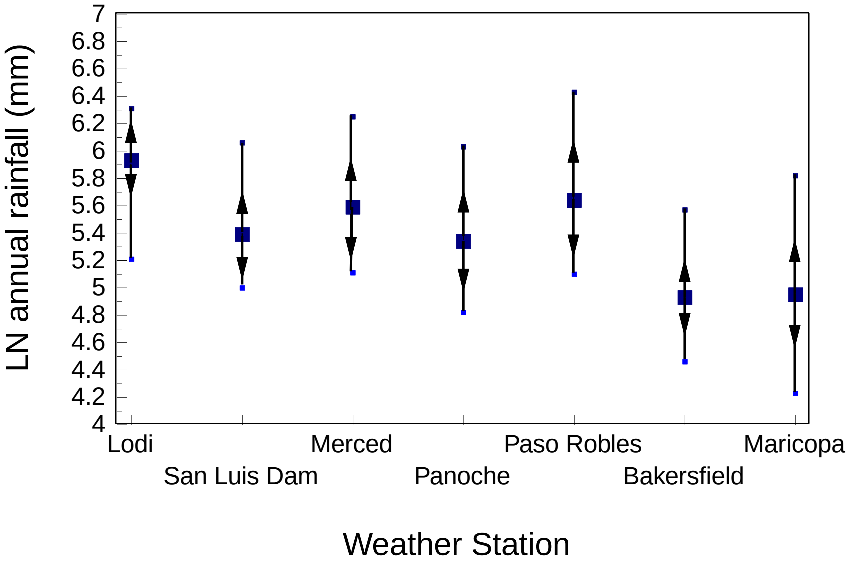


**Figure 9.** Comparison of total annual rainfall (1965 to 1990) from seven weather stations within the San Joaquin kit fox range. Closed, large box is mean, arrow is standard deviation from mean, and vertical line is range.