

RECOVERY OF ENDANGERED KANGAROO RATS IN THE SAN JOAQUIN VALLEY, CALIFORNIA.

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Abstract. One candidate (*D. nitratoides brevinasus*) and three endangered kangaroo rats (*Dipodomys ingens*, *D. n. nitratoides*, *D. n. exilis*) occur in the San Joaquin Valley, California. Loss and fragmentation of their habitats because of cultivation were the main causes of endangerment. The major barriers to recovery of these and other species of the region are: the large size of the area (over 10 million acres) which renders insignificant the small amount of funds spent on range-wide population assessments; spreading scarce funds and administrative actions over many threatened and endangered species (15 species of plants and animals in the San Joaquin Valley are listed); giving land acquisition priority over habitat protection; and failure of the administrative processes dealing with endangered species to ensure funding needed for research and monitoring. There are no programs for monitoring populations. Data needed to conduct viability analyses, estimate size of habitat units required for species recovery, manage species habitat, and regulate land uses are mostly unavailable. We review the knowledge needed for management and recovery of listed and potentially jeopardized kangaroo rats in the San Joaquin Valley Region, list problems that pose major barriers to recovery, analyze research methods, and present a suggested program of research to support recovery planning.

Three species of kangaroo rats (*Dipodomys*) occur in the San Joaquin Valley Faunal Region, California (Williams and Kilburn 1992). Giant (*D. ingens*) and San Joaquin (*D. nitratoides*) kangaroo rats are endemic to its most arid portions; Heermann's kangaroo rats (*D. heermanni*) range through the valley and lower slopes of the bordering mountains, and to the coast (Williams and Kilburn 1992). The giant kangaroo rat is monotypic. The San Joaquin kangaroo rat consists of three subspecies (short-nosed, *D. n. brevinasus*; Fresno, *D. n. exilis*; and Tipton, *D. n. nitratoides*). Heermann's kangaroo rat is comprised of nine subspecies, of which six occur in the San Joaquin/Salinas valleys region, one in the hills and valleys along the east side of San Francisco Bay, and two along the Pacific Coast from Morro Bay southward to the Santa Inez River, Santa Barbara County (Williams et al. in press).

Anthropogenic changes to natural communities in the San Joaquin Valley began shortly after the gold rush of 1849. In the 1860's and 1870's irrigated and dryland cultivation spread rapidly over the northern and eastern portions of the valley, first on the alluvial fans and delta supporting oak forests, then on the deep, rich grassland soils elsewhere along the eastern edge of the valley (Griggs 1992, Werschkull et al. 1992). Agricultural developments were slowest along the western and southern parts of the valley characterized by extreme aridity and salty soils derived from marine sedimentary rocks. In the 1960's and 1970's irrigation water was delivered to most of the western, central, and southern portions of the valley by the State Water Project and the San Luis Unit of the federal, Central-Valley Project. By the late 1970's most of the valley floor was under cultivation and by

1985, only about 61,000 ha of the floor remained uncultivated (Williams 1992). When the Fresno kangaroo rat was discovered in 1891, cultivation of its habitat already was threatening the species' existence. By the early 1900's, it was believed to be extinct (Grinnell 1920), only to be rediscovered in 1933 (Culbertson 1934). Studies in Fresno County in the 1970's (Chesmore and Rhodehamel 1992) found Fresno kangaroo rats solely on several small, isolated parcels of uncultivated ground west of Fresno. The Fresno kangaroo rat was listed as rare in 1971 and endangered in 1980 by California (California Department of Fish and Game 1980), and later as federally endangered (U.S. Fish and Wildlife Service 1985). Giant kangaroo rats were jeopardized by cultivation of natural communities following completion of the irrigation projects that brought water to the western and southern portions of the valley in the late 1960's and early 1970's. By 1979, occupied habitat consisted of only about 1.6% of the area of their historic geographic range (Williams 1992). The giant kangaroo rat was listed as endangered by California in 1980 and by the U.S. Fish and Wildlife Service in 1987 (Williams and Kilburn 1991).

The agricultural developments that imperilled the Fresno and giant kangaroo rats also jeopardized Tipton kangaroo rats. By 1985, they were known to inhabit only 3.7% of their historic geographic range, and most remaining habitat was under intense development pressures or other threats. The Tipton kangaroo rat was subsequently federally- and state-listed as endangered (U.S. Fish and Wildlife Service 1988, California Department of Fish and Game 1989).

Loss and degradation of habitat also threatens the short-nosed kangaroo rat, though the level of threat is unknown because documentation of its population status is incomplete. It has yet to be proposed for state and federal listing (Williams 1986, Williams and Kilburn 1992). Another San Joaquin Valley kangaroo rat that might be threatened by habitat loss is the Merced kangaroo rat (*D.h. dixonii*).

Information on current distribution and population status, demography, competitive interactions, and effects of pesticide use, livestock grazing, oil and gas development, and vegetation control are essential to monitoring and recovery of San Joaquin Valley kangaroo rats. Yet, despite being listed as rare or endangered for up to 21 years, details of distributions, population statuses, demography, other life history traits, and effects of land-use practices and pest control are surprisingly scanty. Recovery plans have not been completed for any of the three listed taxa, and there are no coordinated plans for funding the research and monitoring needed for recovery.

In this paper we review the knowledge needed for management and recovery of listed and potentially jeopardized kangaroo rats in the San Joaquin Valley, list problems that pose major barriers to recovery, analyze research methods, and present a suggested research program. In Appendix A we discuss details of inventory and population estimation methods; and include documentation for the suggested research methods by providing data on population densities and responses to traps and trapping from our studies of giant and San Joaquin kangaroo rats.

CURRENT KNOWLEDGE

Background Literature

Papers reviewing the biology of Heermann's, San Joaquin, and giant kangaroo rats have been published recently (Kelt 1988, Best 1991, Williams and Kilburn 1991, respectively). Additional information on the Fresno kangaroo rat from contract final reports and master's theses through 1987 was reviewed by Chesemore and Rhodehamel (1992). Distribution, population status through 1987, habitat, and some aspects of the life history of the giant kangaroo rat were presented by Williams (1992). The conservation statuses of mammals endemic to the San Joaquin Faunal Region were discussed by Williams and Kilburn (1992). Results of population studies of giant kangaroo rats between 1987 and 1991 were given by Williams et al. (1992). These reports and reviews outline current knowledge and provide citations for other published and unpublished reports on the three kangaroo rats.

Data to support the following management actions are mostly nonexistent: monitoring population status,

conducting viability analyses, managing habitats, or deciding appropriate pesticide use (Table 1). There are embryo numbers for all three species, but litter size and age-specific reproductive rates are unknown. Some data on survivorship and age structure of giant and short-nosed kangaroo rat populations are available (Williams et al. 1992).

Distribution and Population Status Surveys

Distributions and population statuses have been determined for the Fresno (status through 1982, Chesemore and Rhodehamel 1992), Tipton (status through 1985, Williams 1985), and giant kangaroo rats (status through 1987, Williams 1992). But, data are not current for any of these species, and no surveys have been conducted for the other kangaroo rats.

Major problems in determining distributions and population statuses of species in the San Joaquin Valley stem from the large area to be covered and lack of detailed information on soils and current conditions of natural lands. The valley floor below the 153 m contour consists of about 3.44 million ha, and contiguous habitat for the same fauna to the west encompasses more than 1 million ha (about 11 million acres total). Until recently, no portion of the region had locations of remaining natural lands mapped, and soil surveys had never been done for most of the western and southern portions of the region. Also, the habitats of the three kangaroo rats are sufficiently broad to require inspecting nearly all natural lands (that is, never cultivated) and disturbed areas, such as oldfields, undergoing succession. In addition, parcels of natural and fallow ground as small as 4 ha and surrounded by croplands temporarily, at least, support kangaroo rats in the San Joaquin Valley. Thus, the resources required for even coarse-grained distribution and status surveys far exceed the funds provided for this purpose.

Survey methods for kangaroo rats consist of three elements: compilation of locality records from scientific specimens in museums and the literature; visual inspection of the area to locate potential habitat and determine occupancy by kangaroo rats; and identification of species by trapping or burrows and scats.

Estimating Population Size

Three methods have been used to estimate population size and density of these kangaroo rats: counts of active burrow systems in a measured area (Williams 1985, 1992); trapping on grids with uniform trap spacing (Braun 1985, Williams et al. 1992); and trapping for three days on two parallel lines with regular trap spacing, followed by trapping for three days on four parallel lines extending across the original lines at a 45° angle (assessment line method of O'Farrell et al. 1977; Clark

Table 1. Status of information in categories needed for determining endangerment status and managing habitat for endemic kangaroo rats in the San Joaquin Valley, California (0 indicates no information is available, + indicates some information is available, but is insufficient to meet current needs).

	<i>Dipodomys ingens</i>	<i>D. nitratoides nitratoides</i>	<i>D. nitratoides exilis</i>	<i>D. nitratoides brevinasus</i>	<i>D. heermanni dixonii</i>
Endangerment					
Status ¹	CE,FE	CE,FE	CE,FE	C-1	None
Status survey	1979	1978,1985	1974,1981,1988	None	None
Monitoring	0	0	0	0	0
Ecology and Demography					
Reproductive rates	+	0	+	+	0
Mating system	0 ²	0	0	0	0
Survivorship, age structure	+	0	0	+	0
Dispersal	0	0	0	0	0
Competition	+	0	0	+	0
Diet	+	0	+	+	0
Management					
Habitat	+	+	+	0	0
Transplant	+	+	0	0	0
Pesticide use	0	0	0	0	0

¹ CE = California endangered

FE = Federal endangered

C-1 = California Species of Concern and Federal Category-1 candidate

² Under study

et al. 1982, Williams 1985). Grid and assessment line methods require marking and releasing animals, and their subsequent recapture to provide data for statistical estimates of population size and density.

Burrow counts probably overestimate true population densities; but despite this and other complications elaborated in Appendix A, burrow counts are advantageous for status assessments. Populations at many sites can be evaluated using burrow counts in the time required for one trapping census at one site. And, burrow counts may be as, or more, accurate than estimates from capture-recapture methods, especially capture-recapture over short periods with naive populations.

Capture-recapture methods appear to underestimate densities in most situations (Appendix A). Yet, grid trapping and examination of captives yield data on population ecology such as home range, territoriality, and reproduction, and estimators exist for determining statistical variances of area sampled, population size and density, and other parameters. Most of the spatial parameters cannot be computed from the assessment line method; thus grid trapping is needed. Long-term periodic

trapping also yields necessary data on population recruitment, survivorship, and longevity.

For estimating population size or density by capture-recapture methods, it is not necessary to capture all animals in a population. Chosen methods should yield low variance, the most uniform trap response among individuals, and estimates that are consistent with independent estimates of numbers such as burrows or seed caches. Our data (Appendix A) show that numbers of traps and size of trapping grids need to be relatively large, requiring two or more researchers to operate traps on one plot. For management studies, experimental and control plots must be trapped simultaneously, requiring a minimum of 4 researchers. Personnel costs for obtaining scientifically credible results, even with minimal replication of studies at two or three sites, are substantial.

Population Monitoring

Population monitoring is essential for management and measuring recovery of endangered species. Yet there is no existing monitoring program for any of the

listed kangaroo rats in the San Joaquin Valley. For all but the Fresno kangaroo rat, annual monitoring of all of the numerous, scattered colonies is not cost effective. A monitoring program, stratified by habitat qualities and geographic regions, should be established to assess annually a small number of populations. A similarly stratified, but larger sample that would yield statistically acceptable samples (e.g., 30 censused areas for each rank of habitat quality or population size) should be assessed at 5-year intervals, and a range-wide assessment should be made every 10 years.

Five-year, range-wide assessments first require identifying and classifying existing colonies, then picking a statistically representative subset for assessment. The same sites should be used for each assessment. Numbers of animals should be estimated and area inhabited, habitat features, and land-use determined. Giant kangaroo rat numbers can be estimated by burrow counts on transects, with livetrapping at fewer sites than required for reliable assessment of other species. Three to six days of trapping on standardized transects are needed to measure proportions of San Joaquin and Heermann's kangaroo rats. These values can then be applied to burrow counts over the inhabited area to estimate population size.

Assessments every 10 years should be designed to locate and inventory all populations. To reduce cost, population monitoring should be combined with other objectives, such as studies of grazing, oil and gas production, pesticide application, or habitat restoration. Biannual livetrapping on experimental and control grids would track changes in population size, recruitment, turnover, and body weights on areas with different land uses. Plant production and other aspects of the ecosystem should be measured and tested for association with population changes. A range-wide system to detect in advance land-use changes that would destroy or degrade habitat also should be established.

Population Ecology

Demography.--Even elementary aspects of demography are not sufficiently known for these kangaroo rat species. Data on age-specific reproductive rates and survivorship, mating system, dispersal, and population density are necessary to estimate viable population size and minimum sizes required for conservation reserves. Viability analyses require the variances from estimates of vital rates, densities, and other demographic traits that are obtained from studying populations at different times and places, and reflect density-dependent changes in rates caused by differing habitat quality, and stochastic population and environmental events. Viability analyses can be performed without all information by making

educated guesses, but guesswork is not a desirable basis for management decisions affecting endangered species.

Estimating survivorship and reproductive parameters require frequent trapping for several years, but yields little accurate information on number of young. Numbers can be determined by digging up the burrow systems of lactating females and locating the nest, but this is expensive, may have a low rate of success (Grinnell 1932, Shaw 1934), and is not likely to be approved by regulatory agencies. Numbers also can be determined by nearly constant surveillance and trapping at the burrow systems of lactating females, but it would be prohibitively costly to monitor sufficient numbers in each age group at several sites of different habitat quality and population density for several years. Estimates of age-specific litter size based on embryo counts and age-related skeletal features, and population age structure can be obtained by examining large numbers of dead animals, but this also usually is not an option for endangered species. But, where habitat destruction is to be permitted, the resident population should be trapped and sacrificed to obtain needed data not otherwise available. All permits and habitat conservation plans should require that the applicant pay all costs for salvage, examination, and storage of specimens.

Age structure of a population can be determined by examining age-specific anatomical features. Fusion of skull sutures and other ontogenetic changes in skeletal structure can be used to determine relative ages. There are annual deposits of cementum around roots of cheek teeth that might be useful for aging kangaroo rats (Nader 1966), as is true for beavers, *Castor canadensis* (Hartman 1992). However, X-raying large numbers of live animals to determine age by cementum deposition is not practical. There also may be annual deposits in bones that could be used to age individual kangaroo rats, but determining this requires amputating a toe from, or sacrificing, several known-age animals. Surrogate species could be used for preliminary study, but such a study would take 4-5 years of trapping and marking a population. Age structure of a population at the time of collection can be determined from museum specimens, but no existing sample of these species is sufficient for a one-time measure of population age structure. Captive breeding colonies provide age-specific vital rates, but using these to model wild populations is inappropriate. Thus, there is no practical substitute for frequent, long-term trapping and observations at several sites to obtain needed demographic data. Some data can be gained from studies of effects of land use and management, but the objectives of management studies could be seriously compromised by the frequency of trapping required to obtain demographic rates. Therefore, plots dedicated to this purpose are required.

Competition.—Competition between giant, San Joaquin, and Heermann's kangaroo rats is suggested from a few studies (Hawbecker 1951, Tappe 1951, Williams et al. 1992). Where giant kangaroo rats occur in shrubless areas, the other species are usually absent, but where scattered shrubs are found, short-nosed kangaroo rats coexist in small numbers with giant kangaroo rats (Williams 1992).

Competition with Heermann's kangaroo rats, coupled with stochastic events, habitat fragmentation, and changes in land use, may be a major threat to remaining populations of Fresno and Tipton kangaroo rats and some populations of short-nosed kangaroo rats. The type of widespread habitat fragmentation that recently jeopardized Tipton kangaroo rats (Williams 1985) occurred within the geographic range of the Fresno kangaroo rat decades earlier (Culbertson 1934, 1946; Boolootian 1954; Hoffmann 1974; Knapp 1975). Of the habitat remaining in 1988-1989, most parcels were too small to support cattle and too small and isolated to be grazed for short periods by sheep. Some of these had not been grazed for several years and others had been turned into feedlots and holding pens where livestock numbers exceeded carrying capacity and plants were grazed to the vanishing point. Between about 1954 and 1989, populations of Fresno kangaroo rats declined or disappeared from both grazed and nongrazed parcels (Boolootian 1954, Hoffmann 1974, Knapp 1977, Koos 1977, Chesemore and Rhodehamel 1992, D. F. Williams unpubl. data). Flooding of the Alkali Sink Ecological Reserve in Fresno County from a break in a San Joaquin River levee in 1986 may have contributed to the extirpation of Fresno kangaroo rats there. Yet Heermann's kangaroo rats are common on this and most other remaining fragments of former habitat for Fresno kangaroo rats (D. F. Williams unpubl. data), suggesting that habitat change or other factors may have been responsible.

Study of competition between Heermann's and San Joaquin kangaroo rats (preferably a population of Fresno or Tipton) should be a high research priority. Investigations should include plots with different management (for example, grazing, fire) and plots where Heermann's kangaroo rat numbers are manipulated.

Land Use and Habitat Management

Livestock Grazing.—Cattle grazing is the major land use on remaining habitat for these kangaroo rats. The effects of grazing on San Joaquin kangaroo rats are unknown and the existing reports are contradictory. Koos (1977) surmised that dense cover of grasses interfered with locomotion of Fresno kangaroo rats. Grazing decreases cover and may benefit this species. Yet Koos (1977) believed that heavy grazing reduced

their density. Her data were inadequate to demonstrate statistically significant differences in population numbers on grazed and nongrazed plots. Yet the California Department of Fish and Game ended grazing in 1977 on the Alkali Sink Ecological Reserve. By 1981 the Fresno kangaroo rat population there had declined to a few animals. None were found during trapping surveys in 1988 and 1989 (Chesemore and Rhodehamel 1992, D. F. Williams unpubl. data). Tipton kangaroo rats appear to be more common in heavily grazed areas and sites with sparse plant cover such as ground left fallow for a few months to a few years (Williams 1985). Some amount of grazing also probably enhances habitat for giant kangaroo rats.

Studies of the effects of grazing are needed for both giant and San Joaquin kangaroo rats. Sheep and cattle may have different impacts on kangaroo rats and studies should test effects of grazing by both. Grazed and nongrazed plots should include the major habitat types for kangaroo rats. To test effects of either cattle or sheep grazing would require a minimum of three paired sites for giant and four paired sites for San Joaquin kangaroo rats, without considering necessary replications. Livetrapping plots on grazed and nongrazed ground should be positioned in the center of a section or more of land with the same treatment to reduce or eliminate edge effects. Position also should be based on locations of water and travel routes of livestock to ensure that grazed plots get representative use. Change in land use (grazing or cessation of grazing) on the experimental plot should be made after the second year of population censusing. In the first year, both plots should be trapped for 20-days (four 5-day periods extending over 26 days) each in spring and summer to estimate pretreatment numbers and accustom individuals to trapping. Plots should be censused twice for 10- to 20-day periods the second year and thereafter. Studies should extend for a minimum of 5 years after change in treatment (7 years total) to encompass a range of weather and to allow time for population turnover. After pretreatment assessments, biannual censuses should take place in March-April and August-September. More frequent censuses are not advised because trapping increases kangaroo rat activity, attracts predators, probably increases mortality because of stress induced by trapping and handling, and bait augments natural food. Thus, the demographic differences between treatments could be either compounded or masked by changes caused by frequent trapping.

Other Vegetation Management.—Grazing may be impractical for vegetation management on some parcels. Fire is used at some sites, and mowing is used to control vegetation around runways at Lemoore Naval Air Station

Table 2. Kangaroo rat species included and research objectives (columns with comments or x's) for sites in the San Joaquin Valley Region: Carrizo Natural Area (NA), San Luis Obispo County; Elkhills Naval Petroleum Reserves, Kern County; Lokern, Kern County; Pixley National Wildlife Refuge (NWR), Tulare County; Tumey-Panoche region, Fresno County; Lemoore Naval Air Station (NAS), Kings County; Fresno-Madera counties.

Area	Species	Demography ¹	Vegetation Control	Oil-gas Production	Pesticide Use	Community Restoration
Carrizo NA	<i>Dipodomys ingens</i>	Complete	Cattle grazing	-	-	x
	<i>D. nitratoides brevinasus</i>	Complete	Cattle grazing	-	-	x
Elk Hills	<i>D. ingens</i>	Complete	-	x	-	x
	<i>D. nitratoides brevinasus</i>	Partial	-	x	-	x
Lokern	<i>D. ingens</i>	Partial	Sheep grazing	-	x	-
	<i>D. nitratoides brevinasus</i>	Complete	Sheep grazing	-	x	-
Pixley NWR	<i>D. nirtatoides nitratoides</i>	Complete	Cattle grazing, fire	-	x	-
Tumey-Panoche	<i>D. ingens</i>	Complete	Cattle grazing	x	-	x
	<i>D. nitratoides brevinasus</i>	Complete	Cattle grazing	x	-	x
Lemoore NAS	<i>D. nitratoides exilis</i>	Partial	Mowing, fire	-	-	x
Fresno-Madera	<i>D. nitratoides exilis</i>	Partial	Cattle grazing?	-	-	x

¹ Complete = full demographic study, partial = demographic data gathered incidental to management studies.

(NAS). San Joaquin kangaroo rats were found there in the early 1980's, but apparently disappeared after mowing began and ground cover increased. The site also burned during this period and some people think the fire caused the extirpation of the kangaroo rats (D. F. Williams unpubl. data), but we do not believe that this is likely. Determining techniques appropriate for control of vegetation at the air station to enhance habitat for endangered species and meet safety and operational needs will have wider applicability. Fire and mowing require study.

Without replication, three plots are needed: no vegetation management, mowing, and controlled burning. Combining these studies with livestock grazing would be most economical because the plot with no vegetation management could serve as the control for all experimental treatments. There is too little extant habitat at Lemoore NAS for these experiments, but attempts to convert unoccupied land there to habitat should not await the outcome of long-term management studies elsewhere.

Oil and Gas Development.—Oil and gas production are major activities in habitats for giant and San Joaquin kangaroo rats. The effects of exploration and extraction,

efficacious mitigation, and methods of habitat restoration in depleted petroleum fields require study. The Elk Hills Naval Petroleum Reserves (NPR) in the southwestern San Joaquin Valley represent a substantial block of extant habitat for giant and short-nosed kangaroo rats, and are logical sites for studies. Experimental and control plots for studying impacts of exploration, production, or restoration would use the same trapping program as grazing studies.

Pesticide Use.—Habitats for these endangered kangaroo rats are treated with insecticides to control beet leafhoppers (*Circulifer tenellus*), the vector for the curly-top virus that affects sugarbeets. There are no data on the effects of this program on kangaroo rats. Studies to measure population effects should incorporate the same procedures as those for grazing. Trapping before and after treatment to check for direct effects should be on plots separate from those for biannual censuses to avoid complications from frequent trapping. Other studies on surrogate kangaroo rat species are needed to measure direct effects of pesticide exposure.

To control California ground squirrels (*Spermophilus beecheyi*), rodenticides are applied regularly on or around

the edges of extant parcels of kangaroo rat habitat, most frequently on habitat next to crops. New state and federal regulations on rodenticide use within the geographic ranges of these species probably will eliminate mortality to endangered kangaroo rats at many sites. Banning their use within these species historic geographic ranges might be an economic hardship on farmers and is unnecessary. Needed are revised regulations on pretreatment assessments, application methods, and types of baits, and stronger enforcement of regulations. Development of rodenticide bait stations that are inaccessible to kangaroo rats or bait attractive only to California ground squirrels would best resolve this issue.

Summary of Research Needs

Research could be done most economically by coordinating ongoing efforts and combining many projects at a few sites. An outline of some aspects of an integrated plan is presented in Table 2. Although not shown, studies of the endangered blunt-nosed leopard lizard (*Gambelia sila*), San Joaquin antelope squirrel, San Joaquin kit fox (*Vulpes macrotis mutica*), and most of the listed endangered plants should be included at all sites except Lemoore NAS, where none of these species currently are known to occur. Demographic and management studies also would serve for annual population monitoring without additional efforts, but other sites would be needed for monitoring.

Sites listed are regional instead of specific. The Lokern and Elk Hills areas are close together and have similar biotic communities, but their land use and management needs differ. Sites for complete demographic studies would have plots where frequent trapping occurred. Plots for management experiments would yield some demographic data, but would not be trapped often enough to obtain most information needed. Studies of short-nosed kangaroo rats could provide much of the information used in recovery planning for Tipton and Fresno kangaroo rats if population parameters and responses to changing weather are similar, but significant habitat differences mandate complete studies of Tipton kangaroo rats. There is no known population of Fresno kangaroo rats that can be used for large-scale studies, but their population ecology probably differs little, if any, from that of Tipton kangaroo rats. Restoration and management of habitat for Fresno kangaroo rats are needed and could form the bases of smaller studies, if populations of adequate size can be located.

DISCUSSION

Recovering these endangered kangaroo rats requires habitat protection and restoration, information on population ecology, and range-wide population monitoring. The major barriers to recovery of all listed

plant and animal species in the San Joaquin Valley are: the inadequately small amount of funds appropriated for inventory of potential habitat that is fragmented and distributed over a vast area; the scarcity of dollars for research and administration that must be spread over 15 threatened and endangered species and a larger number of candidate species; past and existing practices of giving land acquisition priority over habitat protection; lack of population monitoring programs for listed species; and failure of recovery plans, permitting processes, and habitat conservation plans to ensure that all recovery needs are met.

Habitat protection must have highest priority for species endangered primarily by habitat loss. Land acquisition and conservation easements on land alone do not achieve habitat protection. Fencing and restriction of land uses also do not necessarily protect habitat for these species. Available data are insufficient to know the types and amounts of compatible land uses or appropriate forms of habitat restoration and management, or to predict with any acceptable probability future trends in population numbers or sizes of habitat parcels required.

Populations are dynamic in time and space, a basic principle too often ignored in making management decisions. Our collective experiences with a given species are too limited to form the basis for decisions affecting species range-wide for decades into the future. Yet uninformed decisions will be made unless those involved in land and endangered species protection and management resolve to develop a different approach; one that gives monitoring programs and acquisition of adequate information on population ecology and habitat management the same priority as land acquisition.

Developing needed information for recovering threatened and endangered species will take time and be costly. To date, no entity has been able or willing to provide more than a small fraction of the funds needed for research. Ironically, a project applicant's budget for a typical endangered species assessment on a few sections of land exceeds all funds expended to date for range-wide distribution/status surveys for the endangered kangaroo rats, San Joaquin antelope squirrel, San Joaquin kit fox, and blunt-nosed leopard lizard. The budget for a single city or county habitat conservation plan exceeds all research dollars spent on San Joaquin Valley endangered species except the San Joaquin kit fox. Most project assessments and habitat conservation plans have added little or no new information on distribution and population status, and none on demography. Yet several million dollars have been spent on these activities, while only a few hundred thousand dollars have been spent on range-wide status surveys and population ecology. Priorities must be changed if endangered species and their natural communities are to be preserved and recovered. Research

and monitoring are essential for protecting habitat and their support must be included along with acquisition of title or conservation easements for habitat. Currently, funds for research come primarily from: federal appropriations; California Endangered Species Tax Check-Off; California Tobacco Tax; and nonprofit foundations and conservation organizations.

We believe that a valley-wide conservation plan involving the entire biota must be developed. It should include mechanisms to protect lands needed to maintain viable populations of endangered species and ensure that other species are not endangered in the process. Assessment of modest development fees valley-wide for endangered species recovery should be a provision of this conservation plan. Funds now spent by project applicants for habitat conservation plans could be expended on research and population monitoring programs. Another provision should be a cooperative agreement between all levels of government whose actions affect habitat for listed species.

Other funds for recovery probably will be required. Potential sources are the users of public lands and resources whose activities contribute significantly to the jeopardy of the San Joaquin Valley biota. Beneficiaries of government subsidies include agricultural, industrial, and municipal recipients of water from state and federal facilities, farmers growing supported crops, and farmers growing crops protected by state pest control programs. Businesses using public land and resources include: agribusinesses that trespass farm on state- and federally-owned lands along water-conveyance facilities; farmers leasing lands on military bases and other public-owned lands; and ranching, oil, gas, and mining companies operating on public lands. Requiring that trespass farming cease by either selling or leasing the land at fair market value could provide dollars for recovery of listed species. Reducing subsidies for water delivery or growing supported crops in the valley and spending the savings on endangered species research and habitat protection also could partly fund needs. Small additional fees, assessed for grazing and petroleum and mineral extraction on public lands within the range of these species, could provide other needed funds.

All people living in and using the valley have contributed directly or indirectly to habitat loss and other adverse effects on its native biota and will continue to do so unless habitat can be protected. People nationwide also benefit from the valley's agricultural and industrial developments. Therefore, state and federal governmental appropriations should provide the additional funds needed for recovery of listed species.

Raising funds from all these sources would spread the costs of endangered species recovery and natural community preservation among the segments of society

that benefit from developments in the valley. It would also place greater costs on those benefiting most from those uses of public resources that adversely affect the native biota of the valley, yet minimize economic impacts to any single segment.

LITERATURE CITED

- Best, T. 1991. *Dipodomys nitratoides*. Mammal. Species 381:1-7.
- Booolootian, R.A. 1954. An analysis of subspecific variations in *Dipodomys nitratoides*. J. Mammal. 35:570-577.
- Braun, S.E. 1985. Home range and activity patterns of the giant kangaroo rat, *Dipodomys ingens*. J. Mammal. 66:1-12.
- Braun-Hill, S.E., and D.F. Williams. A method for determining optimum distance between traps on line transects. Acta Theriol. 26:353-358.
- Chao, A., Lee, S.M., and S.L. Jeng. 1992. Estimating population size for capture-recapture data when capture probabilities vary by time and individual animal. Biometrics 48:201-216.
- California Dept. Fish and Game. 1980. At the crossroads: a report on the status of California's endangered and rare fish and wildlife. Calif. Dept. Fish and Game, Sacramento. 149pp.
- _____. 1989. 1988 annual report on the status of California's state listed threatened and endangered plants and animals. Calif. Dept. Fish and Game, Sacramento, 129pp.
- Chesemore, D.L., and W.M. Rhodehamel. 1992. Ecology of a vanishing subspecies: the Fresno kangaroo rat (*Dipodomys nitratoides exilis*). In press in D. F. Williams, S. Byrne, and T. A. Rado, eds. Endangered and Sensitive Species of the San Joaquin Valley, California. The Calif. Energy Comm., Sacramento.
- Clark, W.A., S.J. Juarez, and D.L. Chesemore. 1982. Nature conservancy small mammal inventory of Paine Wildflower Preserve and the Voice of America in Kern County, California. Unpubl. Report, The Nature Conservancy, 47pp.
- Culbertson, A.E. 1934. Rediscovery of *Dipodomys nitratoides exilis*. J. Mammal. 15:161-162.
- _____. 1946. Observations on the natural history of the Fresno kangaroo rat. J. Mammal. 27:189-203.
- Eisenberg, J.F. 1963. The behavior of heteromyid rodents. Univ. Calif. Publ. Zool. 69:1-100.
- Griggs, F.T. 1992. The remaining biological diversity of the San Joaquin Valley, California. In press in D. F. Williams, S. Byrne, and T. A. Rado, eds. Endangered and Sensitive Species of the San Joaquin Valley, California. The Calif. Energy Comm., Sacramento.

- Grinnell, J. 1920. A new kangaroo rat from the San Joaquin Valley, California. *J. Mammal.* 1:178-179.
- _____. 1932. Habitat relations of the giant kangaroo rat. *J. Mammal.* 13:305-320.
- Hartman, G. 1992. Age determination of live beaver by dental X-ray. *Wildl. Soc. Bull.* 20:216-220.
- Hawbecker, A.C. 1951. Small mammal relationships in an ephedra community. *J. Mammal.* 32:50-60.
- Hoffmann, W.M. 1974. The Fresno kangaroo rat study. Calif. Dept. Fish and Game, Spec. Wildl. Invest., Proj. Final Rep., W-54-4, Job II-5.4 23pp.
- Kelt, D. 1988. *Dipodomys heermanni*. *Mammal. Species* 323:1-7.
- Knapp, D.K. 1975. The Fresno kangaroo rat study. Calif. Dept. Fish and Game, Wildl. Invest., Final Rep., Proj. W-54-R-7, Job I-1.8 21pp.
- Koos, K.A. 1977. The Fresno kangaroo rat population survey, 1977. Calif. Dept. Fish and Game, Wildl. Invest., Final Rep., Proj. E-1-1, Job IV-1.1 10pp.
- Lockard, R.D., and D.H. Owings. 1974. Moon-related surface activity of bannertail (*Dipodomys spectabilis*) and Fresno (*D. nitratoides*) kangaroo rats. *Anim. Behav.* 22:262-273.
- Nader, I.A. 1966. Roots of teeth as a generic character in the kangaroo rats, *Dipodomys*. *Bull. Biol. Res. Centre, Baghdad* 2:62-69.
- O'Farrell, M.J., D.W. Kaufman, and D.W. Lundahl. 1977. Use of live-trapping with the assessment line method for density estimation. *J. Mammal.* 58:575-582.
- Otis, D.L., K.P. Burnham, G.C. White, and D.R. Anderson. 1978. Statistical inference from capture data on closed animal populations. *Wildl. Monogr.* 62:1-135.
- Pollock, K.H., J.D. Nichols, C. Brownie, and J.E. Hines. 1990. Statistical inference from capture-recapture experiments. *Wildl. Monogr.* 107:1-97.
- Shaw, W.T. 1934. The ability of the giant kangaroo rat as a harvester and storer of seeds. *J. Mammal.* 15:275-286.
- Smith, M.H., R.H. Gardner, J.B. Gentry, D.W. Kaufman, and M.J. O'Farrell. 1975. Density estimation of small animal populations. Pages 25-53 in F.B. Golley, K. Petruszewicz, and L. Ruzkowski, eds. *Small mammals: their production and population dynamics*. Cambridge Univ. Press, London. 451pp.
- Tappe, D.T. 1941. Natural history of the Tulare kangaroo rat. *J. Mammal.* 22:117-148.
- U.S. Fish and Wildlife Service. 1985. Endangered and threatened wildlife and plants; determination of endangered status and critical habitat for the Fresno kangaroo rat. *Fed. Register* 50:4222-4226.
- _____. 1988. Endangered and threatened wildlife and plants; determination of endangered status for the Tipton kangaroo rat. *Fed. Register* 53:25608-25611.
- Werschkuhl, G.D., F.T. Griggs, and J.M. Zaninovich. 1992. Tulare Basin protection plan. In press in D.F. Williams, S. Byrne, and T.A. Rado, eds. *Endangered and Sensitive Species of the San Joaquin Valley, California*. The Calif. Energy Comm., Sacramento.
- White, G.C., D.R. Anderson, K.P. Burnham, and D.L. Otis. 1982. Capture-recapture and removal methods for sampling closed populations. U.S. Dept. Energy, Los Alamos Natl. Lab., Los Alamos, N.M., LA-8787-NERP, UC-11 235pp.
- Williams, D.F. 1985. A review of the population status of the Tipton kangaroo rat, *Dipodomys nitratoides nitratoides*. Final Rep., USDI, Fish and Wildl. Serv., Endangered Species Office, Sacramento, Calif., 44pp.
- _____. 1986. Mammalian species of special concern in California. Calif. Dept. Fish and Game, Wildl. Manage. Div. Admin. Rep. 86-1:1-112.
- _____. 1992. Geographic distribution and population status of the giant kangaroo rat, *Dipodomys ingens* (Rodentia, Heteromyidae). In press in D. F. Williams, S. Byrne, and T. A. Rado, eds. *Endangered and Sensitive Species of the San Joaquin Valley, California*. The Calif. Energy Comm., Sacramento.
- _____, and S.E. Braun. 1982. Comparison of pitfall and conventional traps for sampling small mammal populations. *J. Wildl. Manage.* 47:841-845.
- _____, H.H. Genoways, and J.K. Braun. In press. Taxonomy. In H.H. Genoways and J.H. Brown, eds. *Biology of the family Heteromyidae*. *Am. Soc. Mammal. Spec. Publ.* 10.
- _____, D.J. Germano, and W. Tordoff III. 1992. Population studies of endangered kangaroo rats and blunt-nosed leopard lizards in the Carrizo Plain Natural Area, California. Calif. Dept. Fish and Game, Nongame Bird and Mammal Sec. Rep. in press.
- _____, and K.S. Kilburn. 1991. *Dipodomys ingens*. *Mammal. Species* 377:1-7.
- _____, and _____. 1992. The conservation status of the endemic mammals of the San Joaquin Faunal Region, California. In press in D.F. Williams, S. Byrne, and T. Rado, eds. *Endangered and Sensitive Species of the San Joaquin Valley, California*. The Calif. Energy Comm., Sacramento.

APPENDIX A.

Here we discuss methods for distribution and population status surveys and estimating population size and density of kangaroo rats. We report unpublished results of studies on the Elkhorn Plain Ecological Reserve and elsewhere in the Carrizo Plain Natural Area of eastern San Luis Obispo County, and at Pixley National Wildlife Refuge, Tulare County. Data are presented to document densities and trapping responses: information that is needed to develop sampling protocols for population studies. Further details of methods and results can be obtained from unpublished project progress and final reports cited by Williams et al. (1992).

Burrow Counts

Counts of active burrows have been used to estimate densities of giant and Tipton kangaroo rats because large areas can be surveyed inexpensively compared to trapping methods (Williams 1985, 1992). The area covered can be precisely measured for estimating density. Major assumptions of this method are: 1) burrows are correctly identified with a species; 2) a burrow system assigned to a species is occupied by that species; 3) each burrow system is occupied by 1 animal; and 4) separate burrow systems are distinguished.

Burrows are correctly identified.--Distinctive burrows and scats of giant kangaroo rats can allow identification of colonies by experienced persons. However, geographic and seasonal variation in burrow construction and surface features can cause errors in identification by inexperienced workers (Williams 1992). Geographic variation in body size and size of burrow openings of San Joaquin and Heermann's kangaroo rats, erosion of tunnel entrances, and overlap in size of fecal pellets cause too many errors in identification for this method to be useful for estimating population size where these species occur together (Williams 1985, unpubl. data).

The burrow is currently occupied by the identified species.--This assumption leads to an unknown number of errors because many species use kangaroo rat burrows. Lizards, San Joaquin antelope squirrels (*Ammospermophilus nelsoni*), and the smaller species of kangaroo rats regularly use burrows of 1 or more of the larger kangaroo rats, leading to unknown levels of overestimation of population size.

A single animal occupies the burrow.--Giant kangaroo rats are typical of the genus, exhibiting strong territoriality (Braun 1985). Therefore, this assumption probably is reasonable for measuring their relative abundance; but, giant kangaroo rats do not always disperse after weaning. In high-density populations, two

or more young animals may live in different portions of their natal burrow systems, though they and their mother are intolerant of each other (Williams et al. 1992). An adult pair of San Joaquin kangaroo rats and their progeny were kept in a single cage for 10 months (Eisenberg 1963); whether this is due solely to captivity or suggests that San Joaquin kangaroo rats are less territorial is unknown.

Separate burrow systems are distinguished.--This assumption creates the greatest source of error. Individuals of the three species often place burrows in proximity to their conspecifics. Burrows are frequently remodeled as new entrances are made and old ones are plugged and abandoned. Trails connect neighbors' burrows and entrances of the same burrow system. This makes determination of the number of closely-clustered systems inaccurate. Also, individuals apparently regularly visit unoccupied burrows nearby (Williams et al. 1992). Digging and fresh signs from these visits cause errors in determining occupancy.

Our estimates from trapping and concurrent counts of burrows or surface seed caches (haystacks) differed greatly, ranging from 1:0.18 for burrows:individuals of Tipton kangaroo rats trapped at Pixley NWR to 1:2.0 for haystacks:individual giant kangaroo rats trapped on the Elkhorn Plain (Table A-1). Burrow counts overestimated density while counts of haystacks underestimated density compared to capture-recapture estimates. Giant kangaroo rats do not make haystacks every year or throughout their geographic range. Heermann's kangaroo rats make haystacks in some parts of their range, but San Joaquin kangaroo rats do not (D.F. Williams, unpubl. observ.). Therefore, presence or absence of haystacks on burrow systems alone is not useful for determining presence or population size.

When burrow counts are to be used to compare relative densities by sites or seasons, they should be made by an experienced person or team using well-defined criteria and procedures. Where both San Joaquin and Heermann's kangaroo rats occur, trapping on lines with standard numbers and spacing of traps for 3-6 days will establish proportions of the two species that can be applied to burrow counts.

Sites to be inventoried should be selected randomly, stratified by habitat features. Burrow counts on randomly selected belt transects probably are most efficacious for population status surveys over large areas. Yet additional studies are needed on: the number of animals living in a single burrow system; most accurate methods for distinguishing burrows of San Joaquin and Heermann's kangaroo rats; and time of year when this method yields acceptable accuracy.

Table A-1. Numbers of kangaroo rats and their burrows and seed caches on plots, densities (numbers/ha \pm SD), and capture probabilities at Pixley National Wildlife Refuge (NWR), Tulare County, and Elkhorn Plain Ecological Reserve (EHP), San Luis Obispo County, California. Plots at Pixley NWR were 3.24 ha; those at EHP were 1 ha in 1987-1988 and 1.44 ha in 1989-1991 (Williams et al. 1992). For EHP, values are means for two plots and two censuses. Caches consisted of seed heads of grasses in large surface piles (haystacks).

Species, Site	Year	n	Burrows or Caches	Density \pm SD	Capture Probability
<i>Dipodomys nitratoides</i>					
Pixley NWR (non-grazed)	1991	18	28	3.8 + 1.6	0.189
Pixley NWR (grazed pasture)	1991	11	60	3.0 + 0.9	0.278
EHP	1987	18	-	20.2 + 7.7	0.229
EHP	1988	10	-	10.3 + 5.1	0.103
EHP	1989	10	-	11.4 + 3.6	0.135
EHP	1990	5	-	-	-
EHP	1991	1	-	-	-
					Mean = 0.187
<i>Dipodomys ingens</i>					
EHP	1987	36	70	33.2 + 2.1	0.277
EHP	1988	65	32	55.4 + 4.1	0.480
EHP	1989	66	-	55.2 + 3.6	0.661
EHP	1990	26	-	23.7 + 3.3	0.494
EHP	1991	9	15	10.9 + 4.7	0.306
					Mean = 0.444

Livetrapping

Trapping data have many potential biases that can make estimates of size and density inaccurate. The statistical models for estimating population size are sensitive to bias, and the heterogeneity in trap response by individuals often renders inappropriate the use of any population estimator (Otis et al. 1978). One set of biases are associated with trapping protocol: type, size, and operation of traps, type of bait, and cleanliness of traps (Williams and Braun, 1983). Other biases in trapping data may result from changing activity patterns with changes in weather, moonlight, and season. Where populations are compared between areas or experimental treatments, censuses should be simultaneous. Year-to-year comparisons should be made under similar conditions of season and weather. Moon phase may also affect activity, but we have no evidence of a negative trap response by these species on moonlit nights (Williams et al. 1992). Nor did captive San Joaquin kangaroo rats exhibit differences in activity during artificial moonlight (Lockard and Owings 1974).

On the Elkhorn Plain Ecological Reserve, we set different sized traps on opposite grid rows (1-ha grids with 10 by 10 trap stations) and switched them every 7 days of trapping during 1987 and 1988. Extra-long, folding Sherman traps (ELFA, 7.62 x 9.53 x 30.48 cm) captured significantly more giant and San Joaquin kangaroo rats than the standard, large, folding traps (LFA; 7.62 x 7.62 x 22.86 cm). Total captures, mean captures/day \pm SD (66 days), and range, followed by significance values were: LFA 1,238, 18.8 \pm 9.4, 4-47; ELFA 1,644, 24.9 \pm 14.9, 3-56; $t = 4.54$, paired t -test, $P < 0.0001$. We also caught more trap-shy giant kangaroo rats with Tomahawk brand, wire-mesh traps than Sherman traps. Trap shyness was ascribed to animals with lowered capture probability after first capture and those residents trapped in wire-mesh but not in Sherman traps (Williams et al. 1992). We have not routinely used wire-mesh traps because they are more than twice as expensive, much bulkier to transport, more cumbersome to set, and removing animals is more difficult. These factors either increase costs substantially or reduce the number of traps that can be used simultaneously.

Capture-Recapture Studies

For capture-recapture studies many individuals must be captured and recaptured to provide satisfactory estimates of population size. Captures are determined primarily by: 1) population size; 2) capture probabilities; 3) number of traps used and area covered; and 4) duration of trapping session. Using the crude guidelines of White et al. (1982), a population with a mean capture probability of 0.2 must number about 200 to obtain sufficient captures and recaptures. For a mean capture probability of 0.4 to 0.5, the population sampled should have at least 50 individuals.

The mean capture rate during 6-12 day trapping sessions for San Joaquin kangaroo rats is 19% (Table A-1). For naive populations on the Elkhorn Plain, 49% of the animals taken in 11-12 day sessions were first captured on days 4-6 and 18% on days 7-12. At Pixley NWR, 66% were first captured on days 4-6 and 17% on days 7 to 9. Only about 34% of the animals first captured on days 1-3 were recaptured on days 4-6 (Fig. A-1). Plots for habitat management studies of San Joaquin kangaroo rats would have to contain about 200 individuals. Mean capture probability and recapture rate for naive giant kangaroo rats are 44% and 82%, respectively. Plots for giant kangaroo rats should contain a minimum of about 50 individuals.

Assessment Lines.—This method requires recapture of animals on 4 assessment lines (running across the census lines at a 45° angle) that were previously marked on two parallel census lines. Success depends on pattern and spacing of lines and traps that are species and habitat specific, requiring information that is often unknown. It also requires a high recapture rate, and many statistics that are derived from grid trapping (White et al. 1982) cannot be computed. It can produce good results, but often fails because of insufficient initial captures and recaptures.

Our experience with the assessment line method for estimating density of kangaroo rats is limited (Williams 1985), but data on densities and capture-recapture rates from grid trapping confirm that this method usually would yield unacceptable results for San Joaquin kangaroo rats because of too few recaptures on assessment lines to statistically determine size of the area sampled (Table A-1). Mean capture probability and recapture rate for naive giant kangaroo rats suggests that the assessment line technique could provide satisfactory results for this species when densities were high (Table A-1, Fig. A-1).

Grid Trapping.—Several statistical estimators can be used to estimate density from grid-trapping data (Otis et al. 1978, Pollock et al. 1990, Chao et al. 1992). These and related estimators and the nested subgrid model for estimating effective sampling area yield statistical

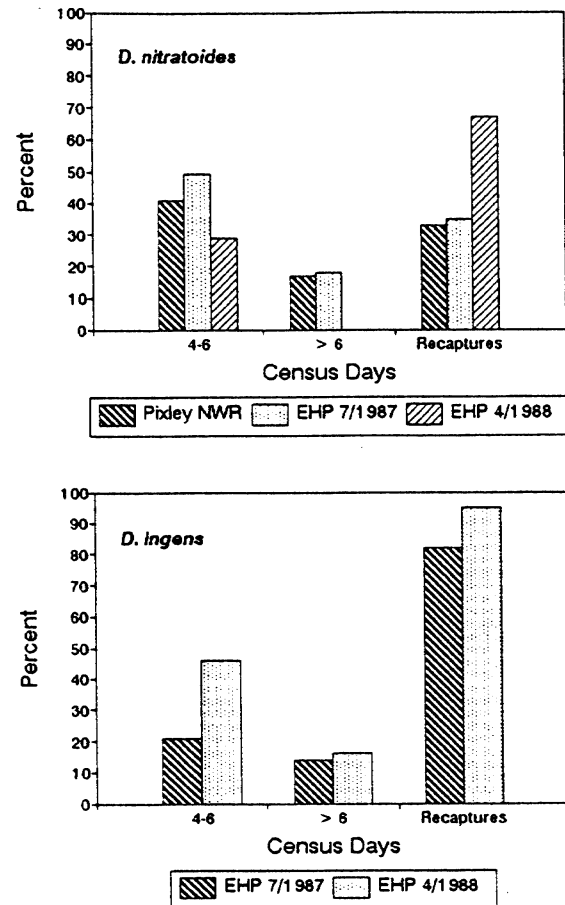


Fig. A-1. Percentages of total captures of kangaroo rats (*Dipodomys*) on days 4-6 and > 6 on grids during nine (Pixley NWR), 12 (EHP 7/1987), and 11 (EHP 4/1988) days of trapping. Recaptures are the percentages of animals recaptured on days 4-6 that were first captured on days 1-3. Animals taken at Pixley NWR and during the 7/1987 census at EHP had no prior experience with traps, whereas a majority taken in the 4/1988 census had been trapped previously. EHP - Elkhorn Plain Ecological Reserve, San Luis Obispo County; Pixley NWR - Pixley National Wildlife Refuge, Tulare County, California.

measures of the models' applicability and precision. The nested subgrid procedure requires equal numbers of columns and rows of trap stations with equal spacing between stations. Grids more completely cover a measured area than assessment lines, and data from trapping on grids can be tested for closure and uniform density.

Despite the method's desirable attributes, trapping on grids also often yields unacceptable population estimates. A common cause is inappropriate trap spacing

and grid size. Spacing must be uniform to make comparisons between treatments and seasons. The de facto trap-spacing standard for studies of small mammals is 15 m (Smith et al. 1975). Spacing should be based upon the average home range size and recognition distance of traps by the target species (Smith et al. 1975); however, these recommendations often are not useful because values are unknown (Braun-Hill and Williams 1985). Giant kangaroo rats have a mean home range size of about 0.04 ha, or a 20- by 20-m area (Braun 1985). Ten-m spacing of traps on grids worked well on the Elkhorn Plain Ecological Reserve for giant kangaroo rats because it yielded a high ratio of captures per trap (Table A-1).

Mean maximum distance between capture points for individual giant kangaroo rats was 15.3 m for 8, 6- to 11-day censuses on the Elkhorn Plain Ecological Reserve in 1987 and 1988. The mean value was calculated from means of individual sessions. Means \pm SD for these sessions are: 18.0 ± 4.5 , 17.6 ± 5.8 , 14.1 ± 2.9 , 15.1 ± 4.0 , 17.3 ± 4.8 , 14.2 ± 5.6 , 15.6 ± 3.4 , 11.4 ± 2.9 . Mean distance moved by 96 animals from trap-station release-point to entry into a burrow was 4.5 ± 0.3 m.

Mean home range sizes of Heermann's and San Joaquin kangaroo rats are not well known, but are substantially larger than the mean for giant kangaroo rats. Trap spacing at 10 m with 100 or 144 traps typically provided too few captures of individual San Joaquin kangaroo rats for statistical comparison at the 95% confidence level. Maximum mean distance between capture points for San Joaquin kangaroo rats averaged 19.8 m for 7 sessions in 1987 and 1988 on the Elkhorn Plain Ecological Reserve. Mean values \pm SD for individual sessions were: 20.7 ± 11.1 , 21.3 ± 11.8 , 19.1 ± 10.4 , 23.3 ± 17.0 , 18.1 ± 8.5 , 27.1 ± 12.4 , and 9.0 ± 6.6 . Mean distance from trap release point to entry into a burrow by 44 San Joaquin kangaroo rats was 6.0 ± 0.5 m.

Captures and recaptures of giant kangaroo rats were sufficient for statistical comparisons, but were inadequate for San Joaquin kangaroo rats. We increased the grid size to 1.44 ha, with a 12 x 12 grid (144 traps) for trapping in 1989-1991, but declining numbers of both species kept total captures too low. Trapping on 12 by 12 grids with 15-m spacing (144 traps, 3.24 ha) for a 9-day period at Pixley National Wildlife Refuge (NWR) in 1991 yielded insufficient numbers of captures and recaptures of naive Tipton kangaroo rats for satisfactory comparison of plots (Table A-1).

Giant and San Joaquin kangaroo rats respond differently to trapping and differ in average density among sites with different habitat qualities (Williams et al. 1992, Table A-1). The size and number of trap stations required for sufficient captures and recaptures

thus also differ. A 12- by 12-point grid with 10-m spacing (1.44 ha) is about the minimum size for estimating density of giant kangaroo rats with acceptable precision. For San Joaquin kangaroo rats, a minimum grid size is about 4.4 ha (14- by 14-points with 15-m spacing). A 16 by 16 grid spaced at 15 m (256 traps, 5.76 ha) may be required for acceptable population estimates of San Joaquin kangaroo rats in habitats supporting densities of about 35 animals/ha, based on an average capture probability of 0.20; but this grid would be too small for most occupied habitat unless the capture rates were increased by longer trapping sessions, different traps, or both.

Duration of Trapping.—Trapping for population estimates of small mammals is commonly conducted for a 6-day period (Smith et al. 1975, O'Farrell et al. 1977). Duration, however, should be adjusted to meet specific circumstances, especially individual and population responses to traps and trapping, and study objectives. In 1987 on the Elkhorn Plain, we trapped on the two 1-ha plots for a 12-day period followed by a 7-day period 8 days later to accustom animals to traps. For the next census in March-April 1988, we trapped for 11 days. Recaptures in these sessions showed considerable heterogeneity due to behavior, time, and unidentified causes (White et al. 1982). In response, we shortened sessions to six days in August 1988 through 1991. The effects were reduction in variances of density estimates and increases in recapture probabilities of giant kangaroo rats compared to 1988. Smaller numbers in 1990-1991 due to drought decreased precision of estimates or prevented calculation of densities (Table A-1).

About half or more of the individuals captured in 1988-1991 were accustomed to trapping (Williams et al. 1992). Naive populations require longer trapping sessions to overcome trap shyness by a majority. About 18% of the San Joaquin kangaroo rats and 15% of the giant kangaroo rats captured in 11-12 day sessions in July 1987 and April 1988 were first captured after day 6. On day 19 of trapping in 1987 (day 7 of the second session) seven giant and two San Joaquin kangaroo rats were captured for the first time. In April 1988 no San Joaquin kangaroo rats were first captured after six days, but all had been captured in previous sessions. None of the 24 giant kangaroo rats first captured after day 6 in April 1988 had been captured in prior sessions (Fig. A-1). After nine days of trapping San Joaquin kangaroo rats on two 3.24-ha grids at Pixley NWR, the estimated proportions of the populations captured at least once, based on burrow counts, were 64.3% in a nongrazed enclosure and only 18.3% in grazed pasture (Table A-1).

The effects of trap shyness also are shown by capture probabilities of giant kangaroo rats by year. Naive

populations in 1987 had lower capture probabilities than populations containing half or more experienced animals in 1988 and 1989. High population turnover and higher proportions of naive individuals are reflected by lower capture probabilities in 1990-91 (Table A-1).

For one-time comparisons and the first session of long-term studies, trapping should be for 20 days or more. Twenty days also may be needed for population censuses conducted one or two times per year because of population turnover. This duration of trapping may introduce unwanted heterogeneity in capture data, but methods exist to accommodate some common sources of

heterogeneity (e.g., Chao et al. 1992, Pollock et al. 1990). Although most population estimators assume closed populations, we believe that breaking sessions into 5-day periods with 2 days between sessions is more practical than continuous trapping. This reduces personnel problems inherent in long, continuous trapping periods while increasing the proportion of trappable animals in the population. The results of each 5-day session can be analyzed separately or pooled. Also, open population estimators are available should closed models prove inappropriate (Pollock et al. 1990).