STATE OF CALIFORNIA
THE RESOURCES AGENCY
DEPARTMENT OF FISH AND GAME
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NONGAME BIRD AND MAMMAL SECTION

POPULATION STUDIES OF ENDANGERED KANGAROO RATS AND BLUNT-NOSED LEOPARD LIZARDS IN THE CARRIZO PLAIN NATURAL AREA, CALIFORNIA

by

DANIEL F. WILLIAMS, DAVID J. GERMANO, AND WALTER TORDOFF III.

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Front and Back Covers: Giant Kangaroo Rat (Dipodomys *ingens)*. Photos by Daniel F. Williams.

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Population Studies of Endangered Kangaroo Rats and Blunt-Nosed Leopard Lizards in the Carrizo Plain Natural Area, California

by

Daniel F. Williams[1/], **David J. Germano**[1,2/], **and Walter Tordoff III**[1/]

Abstract

From July 1987 through December 1991, we studied interactions between cattle, the plant community, giant kangaroo rats *(Dipodomys ingens),* and blunt-nosed leopard lizards *(Gumbelia sila)* in the Carrizo Plain Natural Area, with lesser efforts on short-nosed kangaroo rats *(D. nitratoides brevinasus)* and San Joaquin antelope squirrels *(Ammospermophilus nelsoni)*. The main study sites were on the Elkhorn Plain, San Luis Obispo County, with additional sites on the Carrizo Plain, San Luis Obispo County, and along Panache Creek in Fresno County, California.

Drought prevailed during the precipitation years 1986-87, 1988-89, 1989-90, and into late March 1991, while 1987-88 had > average rainfall. Drought limited livestock grazing to a period from November 1987 to June 1989. Herbaceous plant productivity ranged from 12.8 kg/ha (11.5 lb/ac) during severest drought to 1,807 kg/ha (1,620 lb/ac) in 1991, following late spring rains. Productivity was slight in 1989 (60 kg/ha, 53.8 lb/ac) with little seed production. In 1990, the annual crop failed and there was no seed production. Cattle browsed heavily on shrubs between autumn 1988 and summer 1989. Herbaceous mulch was reduced to about 808 kg/ha (725 lb/ac) by grazing in 1989, and fell to 88.4 kg/ha (79.2 lb/ac) in 1990. Wind and rain storms in 1990 and 1991 caused considerable soil erosion in areas unprotected by plant and mulch cover. More topsoil (9.8 mm, 0.39 inch) eroded from the grazed pasture compared to the exclosure protected from grazing. Productivity of annual plants on precincts of giant kangaroo rats was 3.1 times higher than surrounding ground in 1988, and 1.9 times higher in 1991. Over the 5-year period, productivity on the Elkhorn Plain averaged 551.4 kg/ha (494 lb/ac), with a net gain of 171 kg/ha (153 lb/ac) due to the presence of giant kangaroo rats. Further, plants on precincts differed in species composition and had an average of 48.4% more protein than plants surrounding precincts. Cattle grazed mostly on precincts, consuming about 60% of the net production before drying of the annual range plants, but eating only 21% of the forage surrounding precincts. Giant kangaroo rats cached large numbers of seeds in 1988 when production was high. An average of 29 liters of seedheads were placed in piles on the surface of precincts to cure before being moved to underground larders. Cattle ate 57% of the seeds in surface caches. Caching behavior varied from year to year-despite high production in 1991, few precincts had pit caches and surface piles were not seen.

Impacts of cattle grazing on populations of kangaroo rats and blunt-nosed leopard lizards were not apparent statistically, but grazing only occurred during a 20-month period. Numbers of short-nosed kangaroo rats declined throughout the study, reaching a lowpoint in spring 1991 when none were captured An increase in density of giant kangaroo rats in 1988 and 1989 may have contributed to the decline of short-nosed kangaroo rats. No recruitment of young was seen between summers 1988 and 1991. Numbers of giant kangaroo rats increased in 1988, remained high in 1989 despite drought, probably because of large seed stores made in 1988, declined to a lowpoint in spring 1991, then began to increase in summer 1991. Estimated densities varied from about 59/ha in springs of 1988 and 1989 to < 10 in 1991. The decrease in numbers coincided with the severest drought in 1990-91, but flooding from storms in 1991 also contributed to the decline. Reproduction by giant kangaroo rats appears to be affected both by population density and food availability. The population on the Elkhorn Plain was apparently monestrous with no breeding by young-of-the-year during high densities in 1988 and 1989. During drought and seed-crop failure in 1990, few reproductive individuals were seen and no young were recruited. Yet low-density populations on the Carrizo Plain reproduced and successfully recruited young in 1990. Breaking of the drought in 1991 was accompanied by polyestry and breeding by young females. Providing food supplements during the final stages of the drought in March 1991 resulted in from 2.5 to 3.2 times more active precincts compared to nonfed controls by June. Higher numbers appeared to be due to higher survival and recruitment from surrounding areas, but the population receiving supplements continued to increase in size through October compared to the nonfed control, also suggesting higher reproduction. The mean interval between first and last capture of giant kangaroo rats present on plots > 30 days was 376 days; 15 were present for > 800 days and one marked as an adult was present 1,478 days with an estimated minimum age of 5.5 years. The greatest duration for short-nosed kangaroo rats was 766 days by an adult with an estimated minimum age of 3.4 years. For giant and short-nosed kangaroo rats, respectively, 45.4% and 47.1% were not recaptured beyond a single census session (10 days).

A translocated colony of giant kangaroo rats (15 of each sex) in a fallow grain field failed within a year. Only one progeny of the founders was captured. Predation probably was the proximate reason for failure. Standing feral grain and lack of microrelief may have interfered with predator avoidance of the kangaroo rats, but chance events also may have led to high predation. Another colony (15 of each sex) translocated to formerly occupied habitat with intact natural vegetation and microrelief grew rapidly: 18 progeny were marked in 1990 and 95 in 1991. Through September 1991, 114 active precincts were located. This translocated colony exhibited a higher rate of reproduction than the natural populations, breeding in 1990 and for a longer period in 1991 and growing when the natural populations declined. Although availability of more food cannot be ruled out, physical vigor from genetic diversity in the colony (animals came from 16, l-m^2 sections) also is a possible explanation.

Studies of blunt-nosed leopard lizards began in 1988. Numbers of lizards were about two times greater on the nongrazed plot compared to the grazed plot throughout the study, reflecting a site difference unrelated to grazing treatment. During June censuses, numbers were greatest in 1989 following a year of high plant productivity, fell to their lowpoint in 1990 during drought, then increased over twofold in 1991. The highest density estimate of adults and subadults on the nongrazed reserve was 8.2ka in June 1989; the lowest was 0.7/ha in June 1990. In 1990, adults, hatched in 1988 or earlier years, did not emerge, and no hatchlings were found. Absence of adults aboveground was the major reason for low density estimates in June. Surface activity was limited to subadults hatched in 1989 who did not breed in 1990. In 1991, adults that remained underground in 1990 emerged after about 21 months. In 1991, females produced a mean of 3.3 eggs/clutch. At least some females had more than one clutch, perhaps as many as three. Increased rainfall in 1991 was accompanied by 10-14 times more grasshoppers in June compared to 1990 and 2-4 more hatchling side-blotched lizards (Uta *stansburianu)* in August, prey for blunt-nosed leopard lizards. Adults and subadults first appeared above ground in March or April, but had the greatest surface activity from late May through mid or late June. In 1989 and 1990, almost all had disappeared from the surface by July Mating occurred in late May and June, and hatchlings appeared around the first of August in 1989 and 1991. In 1991, adults remained active on the surface in July, but only a few females and one male were aboveground by late July---eight females remained active into August.

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RECOMMENDATIONS

1. Continue long-term population studies of blunt-nosed leopard lizards and kangaroo rats on the Elkhorn Plain plots. Biannual (kangaroo rats) and triannual (leopard lizards) population censuses on grazed and nongrazed plots, measurements of seed caches, and differences in plant species composition and productivity on and around giant kangaroo rat precincts should be included. For leopard lizards, reproduction and activity should be monitored from April through October. Productivity of annual plants, shrub growth, mulch levels, soil moisture, and erosion should be measured yearly.

2. Establish a cooperative research program between the Department of Fish and Game, USDI Fish and Wildlife Service, and USDI Bureau of Land Management and other entities to assess no grazing, 3-year rest-rotation grazing, annual grazing, and controlled burns as management tools to maintain and enhance habitat for threatened and endangered species. Plots with each treatment should be replicated at three sites: Carrizo Plain Natural Area, Lokern-Elkhills, and San Joaquin Valley Floor. Sites should be selected to include several threatened and endangered plants and animals, but plots need to be established where population densities are sufficient to yield adequate data for statistical comparisons with acceptable precision. Separate plots should be established for frequent sampling of demographic data and bi- or triannual comparisons of populations in habitats with different treatments. Productivity of annual and perennial plants, amounts of grazing, soil erosion, mulch levels, soil water, and environmental variables (precipitation, temperature, wind, etc.) should be measured at each study site.

3. Small, temporary, captive colonies of listed animal species should be established to study reproduction, growth, and development.

4. Studies of methods to age live kangaroo rats and leopard lizards should be undertaken.

5. Relocate colonies of giant kangaroo rats and blunt-nosed leopard lizards. Kangaroo rats should be translocated to a fallow field where mircrorelief and plant cover are first modified to mimic conditions in natural colonies. The perimeter of the colony should be temporarily fenced to exclude terrestrial predators. Giant kangaroo rats also should be relocated to small, natural colonies in western Fresno or eastern San Benito counties and monitored demographically. Prior to moving animals, biopsy of tissue for genetic analysis should be performed on the resident and translocate individuals. Tissues from progeny of the experimental colonies and control colonies also should be biopsied and analyzed genetically. Blunt-nosed leopard lizards should be relocated to vacant natural habitat and to fallow fields. The Soda Lake relocation site for giant kangaroo rats is a good site for translocating to natural habitat. Fallow fields also should be manipulated prior to moving lizards so that habitat features mimic natural conditions.

Above: drawing of a giant kangaroo rat with its cheek pouches full of seeds. Drawing by Jody Sears based on photograph by D. F. Williams (© D. F. Williams) .

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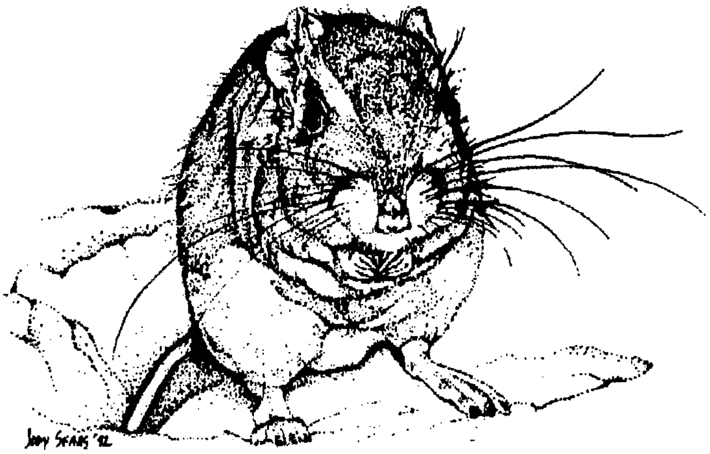

Above: drawing of a giant kangaroo rat emerging from its burrow. Drawing by Jody Sears based on photograph by Moose Peterson (drawing: © D. F. Williams) .

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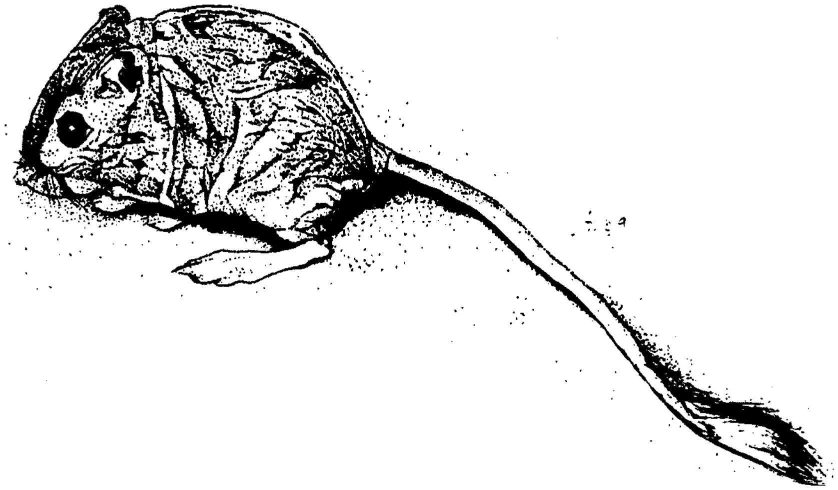

Above: drawing of a giant kangaroo rat by Jody Sears, based on photograph by D. F. Williams (© D. F. Williams).

INTRODUCTION

The Endangered Community

The desert shrub and grassland community of the San Joaquin Valley region of central California comprises one of the two faunal areas of highest endemism at the mammalian species and subspecies level in California (Williams and Kilburn in press). The area has high endemism for flowering plants, is the home of the endemic blunt-nosed leopard lizard *(Gambelia sila),* giant kangaroo rat *(Dipodomys ingens),* San Joaquin kangaroo rat (D. *nitratoides), San* Joaquin antelope squirrel *(Ammospermophilus nelsoni),* and San Joaquin kit fox *(Vulpes macrotis mutica),* provides wintering habitat for the mountain plover *(Charadrius montanus),* and represented an important foraging area for the California condor *(Gymnogyps califonianus).*

Rapid reduction in extent of natural areas in the San Joaquin Valley followed completion of the Central Valley Project (Delta Mendota Canal) and the California Water Project (California Aqueduct) in the early 1970s. Loss of habitat jeopardized those members of the unique San Joaquin Valley biotic communities that were dependent upon habitat on the valley floor and Piedmont slopes (Williams and Kilburn in press). Six resident species of vertebrates from this area dependent upon desert shrub/grassland habitats are classified as threatened (T) or endangered (E) by California (C) or Federal regulations (F): blunt-nosed leopard lizard (CE, FE), Fresno kangaroo rat *(D. nitratoides exilis,* CE, FE), Tipton kangaroo rat *D. n. nitratoides,* CE, FE), giant kangaroo rat (CE, FE), San Joaquin antelope squirrel (CT), San Joaquin kit fox (CT, FE). Others recently have been proposed for listing or are listed as U.S. Category 1 species or California Species of Special Concern. Four listed plants also are members of this association: California jewelflower *(Caulanthus californicus,* CE, FE), Hoover's woolly-star *(Eriastrum hooveri*, FT), San Joaquin woolly-threads *(Lembertia congdonii,* FE), and Kern mallow *(Eremalche kernensis,* FE).

Physical and Environmental Setting

The largest remnant block of valley aridland community with habitats for blunt-nosed leopard lizards, giant kangaroo rats, short-nosed kangaroo rats *(D. nitratoides brevina*sus), San Joaquin antelope squirrels, San Joaquin kit foxes, and several listed and candidate plant species is on the Elkhorn and Carrizo plains in eastern San Luis Obispo County. This area is separated from the San Joaquin Valley proper by the Temblor Range. The Carrizo Plain Natural Area, from approximately the north end of Soda Lake to the southern end of the Carrizo Plain, and from the crests of the Temblor Range on the east and the Caliente Range to the west, encompasses about 72,844 ha (180,000 acres). Most habitats for the endangered species are located between about 580 and 762 m in elevation (1,900-2,500 ft.) on the floor and lower slopes of the Carrizo Basin, an area of approximately

46,000 ha (113,668 ac). About 35% of this potential habitat (16,187 ha, 40,000 acres) has been cultivated for dryland grain production at sometime in the past. Most of the formerly cultivated ground has been severely degraded by soil erosion and currently does not support the endangered species characteristic of the area.

The Carrizo Plain Natural Area has a Mediterranean climate, with hot, arid summers and cool, moist winters. High temperatures are the norm during summer, typically ranging from about 29° to 35°C (85° - 95°F). In winter, nighttime temperatures occasionally drop below freezing, while daytime highs generally are from 10-21°C (50 - 70°F). Precipitation averages less than 254 mm annually, based on long-term records of the three stations on the Carrizo Plain. Most rain storms come in the winter and spring, and the period from May through September is dry.

Terrestrial communities represented in the Carrizo Plain Natural Area and providing habitat for its endangered species include: Alkali Desert Scrub (both xerophytic and halophytic associations) dominated by various subshrubs and shrubs, notably saltbushes *(Atriplex* spp.) and iodinebush *(Allenrolfea occidentalis);* Desert Grassland dominated by introduced annual grasses and forbs, principally Arabian grass *(Schismus arabicus),* red brome *(Bromus rubens),* and red-stem filaree *(Erodium cicutarium);* and High Desert Scrub, dominated by California ephedra *(Ephedra californica),* Anderson desert thorn *(Lycium andersoni),* and eastwoodia *(Eastwoodia elegans).* Higher and steeper slopes support associations dominated by elements of the High Desert Scrub community with the notable addition of chaparral yucca *(Yucca whipplei)* on dry south and westward-facing slopes; found on the more mesic northward and eastward facing slopes are a great variety of subshrubs, shrubs, and California juniper *(Juniperus califoricus),* or a complex mixture of trees and shrubs representing elements of montane hardwood and mixed chaparral communities.

Land Use and Management

Federal legislation recently provided funds for acquisition of private lands to maintain endangered species and their supporting aridland communities in the Carrizo Plain region. These funds, with money from The Nature Conservancy (TNC), California Department of Fish and Game, and California Energy Commission have resulted in the recent collective purchase of thousands of acres on the Carrizo and Elkhorn plains for inclusion in the Carrizo Plain Natural Heritage Reserve (CPNHR). The Carrizo Plain NHR (also known as the Carrizo Plain Natural Area[CPNA]) has been designated as an Area of Critical Environmental Concern (ACEC) by the U.S. Bureau of Land Management (BLM), requiring that management goals give priority to maintaining populations of the endangered species (BLM, 1988). A cooperative management plan for the Carrizo Plain Natural Area was developed in 1990, but has not undergone environmental or public review, and has not been formally approved. Yet, the grazing management scheme advanced in this plan has already been implemented.

On the Carrizo Plain NA, as elsewhere where habitats for these endangered species persist, livestock grazing and cultivated agriculture are the principal uses of land. On many parcels grazing has been intense and prolonged, and has extirpated the more palatable woody shrubs and many elements of the native herbaceous flora. Most parcels have been severely eroded and degraded by livestock grazing and cultivation, do not support most elements of the native communities, and may require revegetation and restoration of microrelief to make them suitable as habitat for the species that formerly lived there.

Before long-term land and endangered species management plans can be developed and restoration and recolonization of key species of the communities achieved, information on distribution of native species must be developed, revegetation and reintroduction processes determined, and on-going management protocols established. Research is required into each phase of these processes. To develop management protocols, the effects of livestock grazing on endangered elements of these communities must be determined because some level of grazing may be important in optimizing populations of some or all the endangered species.

Background

For the blunt-nosed leopard lizard, kangaroo rats, and antelope squirrels, available demographic data are insufficient to model population dynamics and determine viable population sizes. For these species and the San Joaquin kit fox, demographic data must be developed and cost-effective protocols devised for monitoring populations as a part of ongoing stewardship of lands dedicated to their preservation. Data from studies of *D. n. brevinasus* also will be useful for modeling and managing populations of *D. n. nitratoides* and *D. n. exilis.*

Accounts of Species Studied

Population studies reported here focused primarily on blunt-nosed leopard lizards and giant kangaroo rats. Data on short-nosed kangaroo rats were gathered incidental to investigations of giant kangaroo rats. Our initial work (Williams and Tordoff 1988a, 19883) also included population studies of San Joaquin antelope squirrels, but study of this species ceased because of insufficient funds.

Blunt-nosed Leopard Lizard *(Gambelia sila)*

Systematics. The blunt-nosed leopard lizard was first described by Stejneger (1890) as *Crotaphytus silus* from the type specimen, collected in Fresno, California. Cope (1900), however, considered this species to be conspecific with *C. wislizenii* and listed it as C. w. *silus.* Under this arrangement the leopard lizards and the collared lizards were placed in the same genus. Smith (1946) separated the collared from the leopard lizards, placing the latter in the genus *Gambelia*. The bases for separation were differences in head shape, presence or absence of regular folds, and several scutellation features. The subspecific status of G. w. *silus* was retained by Smith. This generic split was not universally agreed upon and the status, both generic and specific, of the lizards remained controversial until Montanucci (1970) presented a solid case for specific status based upon the study of hybrids between *C. wislizenii* and C. *silus.* Montanucci et al. (1975) again separated *Gambelia* from *Crotaphytus* resulting in the name, *Gambelia silus* (Jennings 1987). Germano et al. (in press) pointed out that the specific epithet, *silus,* had the wrong ending to agree in gender with the genus *Gambelia,* and that the proper spelling was *sila.*

Distribution and Habitat. The historical range of the blunt-nosed leopard lizard included much of the San Joaquin Valley and parts of the Carrizo and Elkhom plains in eastern San Luis Obispo County, and adjacent foothill and low mountain areas. It probably did not occur north of San Joaquin County because of the seasonal flooding in the Delta and the wetter and colder conditions farther north (Montanucci 1965). Agricultural development has eliminated large areas of habitat for this species and greatly reduced the range, particularly in the north. Today, little of the former range contains habitat suitable for this species, mainly along the west side of the southern San Joaquin Valley, the Carrizo Plain, Elkhorn Plain, Cuyama Valley, and adjacent foothills (Montanucci 1970).

Within their range, blunt-nosed leopard lizards inhabit sparsely vegetated flatlands and gently sloping foothills. Dry ground is important so areas that are periodically flooded, either naturally or agriculturally, are avoided. Leopard lizards rely on speed both in pursuing prey and avoiding danger, so tall grasses and thick shrubs that hamper visibility and movement are avoided. Various grasslands having combinations of the following plants are usually favored by leopard lizards: goldenbush *(Haplopappus* sp.), Arabian grass, jackass-clover *(Wislizenia californica),* pale tar-weed *(Hemizonia pallida),* saltbushes, iodinebush, and seep-weed *(Suaeda* sp.; U.S. Fish and Wildl. Service 1985).

Although adults may construct simple burrows under rocks or in loose sands, they prefer to inhabit small mammal burrows. Occupied or unoccupied kangaroo rat burrows and abandoned ground squirrel burrows are used (Montanucci 1965).

Form and Function. The blunt-nosed leopard lizard is a large (up to 128 mm snout-vent length), long-legged lizard. The tail is almost twice as long as the head-body length and the hind limbs are about twice as long as the forelimbs and much more stout. Compared with the long-nosed leopard lizard, the snout is significantly shorter and blunter and the head is significantly broader (Smith 1946). G. *sila* differs significantly from G. *wislizenii* in the relative proportions of most cranial measurements (Montanucci 1970).

The patterns and coloration of blunt-nosed leopard lizards are variable. Individuals have a series of transverse bands (7-10) that are usually broad and distinct. These extend from the lateral folds on the side to the mid-dorsal line where bands from the two sides may meet or be arranged in a staggered series. Between these bands are several moderately-sized spots arranged paravertebrally in rows (Montanucci 1970). These spots may become smaller and more numerous with age, particularly in males (Montanucci 1967, Smith 1946). The bands vary from white through cream-colored to yellow, and the dorsal ground color is light grey-brown to darker brown with the spots being dark brown Similarly colored bands or rows of transverse spots produce a banded appearance to the tail (Smith 1946). Juveniles have blood red spots on the dorsum that darken with age, becoming brown when sexual maturity is reached, although a few adults retain reddish centers to the spots (Montanucci 1967).

The undersides are uniformly white to yellow in immature lizards and prenuptial females. Nuptial females have bright red-orange markings on the sides of the head and body and the undersides of the thighs and tail. This color fades to pink or light orange by late July. Acquisition of reddish color during or after breeding may serve to advertise to potential mates that the individual is female, initiating courting and preventing attack. Males in many populations develop a nuptial color during the breeding period that spreads over the entire undersides of the body and limbs. This salmon to bright rusty-red color may be maintained indefinitely (Montanucci 1965).

The functions of these various characteristics are probably highly adaptive. Differences in substrate soil colors and textures result in the selective advantages of the particular patterns and colors observed in a given area.

These lizards are adapted for rapid running on flat areas as evidenced by the large, strong hind legs. They actively chase down their prey and avoid danger by running to shelter under bushes or in burrows. The cryptic coloration allows them to avoid detection by prey and predators alike to the advantage of the leopard lizards.

Life History. Blunt-nosed leopard lizards feed primarily on insects (mostly orthopterans) and other lizards, although some plant material is swallowed too, probably incidentally with prey. Within prey categories, they appear to be opportunistic, feeding on whatever is available. This is illustrated primarily with the insects in the diet, which tend to shift throughout the year with the peaks in insect populations (Montanucci 1965). Which lizards are eaten is largely determined by the size and behavior of the prey. Side-blotched lizards *(Uta stansburiana),* being abundant and small, are a staple in the diet throughout the year, though Tollestrup (1979) did not find any vertebrates in the stomachs of blunt-nosed leopard lizards she examined. Young of various species, including its own, spiny lizards *(Sceloporus* spp.), western whiptails *(Cnemidophorus tigris),* and coast horned lizards *(Phrynosoma coronatum)* are taken when they are in the area. As the prey size approaches the maximum size of a prey object, decision to attempt to capture it is based upon whether the prey attempts to flee (acts like prey) or continues with its activities (Montanucci 1967). Blunt-nosed leopard lizards chase their prey and even leap off the ground in attempts to capture flying insects (Smith 1946, Montanucci 1967).

Seasonal above ground activity is correlated with weather conditions, primarily temperature. Optimal activity occurs when ground temperatures are between 22° and 36°C or slightly higher (U.S. Fish and Wildl. Service 1985, Tollestrup 1976; J. Brode, California Dep. Fish and Game pers. comm.). Smaller lizards and young have a wider activity range than adults (Montanucci 1965). This results in these lizards emerging from hibernation earlier than adults, remaining active later in the year, and being active during the day earlier and later than adults (Montanucci 1965). Adults are active above ground in the spring months from the end of April through June, with the amount of activity decreasing rapidly after this time so that by the end of July almost all sightings are of immature individuals. Also, following the breeding season, the proportion of each sex changes as males tend to cease surface activity sooner than females, Thus, adults captured on the surface in August are about 70% female (Montanucci 1967).

Blunt-nosed leopard lizards seek small rodent burrows for shelter and nesting sites. Occupied or unoccupied burrows are used (Montanucci 1965). If mammal burrows are not available the lizards can construct burrows, either under rocks, loose sandy soils, or in stream banks. These burrows are simple, slanting tunnels (Montanucci 1965). Young lizards will seek shelter in brush piles or in burrows. If shrubs are present, all ages will seek to hide in or under them upon being disturbed and will usually only enter burrows if they are disturbed further (Montanucci 1965, 1967).

Eggs are laid in a chamber within the burrow, either one excavated specifically as a nest (Montanucci 1965) or one already within the burrow system suitable for that purpose (Montanucci 1967).

Breeding activity begins within a month of emergence from hibernation and lasts from the end of April through the beginning of June. During this period and for a month or more afterward, the adults are found in pairs and often occupy the same burrow systems (Montanucci 1965). In contrast to G. *wislizenii*, males of G. *sila* are highly combative in establishing and maintaining territories (Montanucci 1970). Yet, non-breeding subordinate males can remain in the area and will quickly occupy the territory should something happen to the dominant male. Male territories may overlap those of several females and a given male may mate with several females. Copulation occurs as late as June (Montanucci 1965). The male approaches the female, licks her groin area to confirm her sex, then crawls up onto her body, grasping her upper back or nape in his jaws. If the female is non-receptive, she may bite the approaching male. If that fail to dissuade him, she may attempt to throw her leg over his body. Finally, should he succeed in grasping her nape, she will arch her back and roll over to dislodge him (Montanucci 1965, 1967). Copulation occurs shortly after the male grasps the female and lasts up to 5 min (Montanucci 1965).

Two to five eggs measuring 15.6 by 25.8 mm (average) are laid in June and July and their number is correlated with the size of the female (Montanucci 1967). The incubation period is close to 2 months with the first young emerging at the beginning of August. The young are then active until mid-October by which time all leopard lizards have gone into dormancy (Montanucci 1967, U.S. Fish and Wildl. Service 1985).

Normally females produce only one clutch of eggs a year, although some may breed twice under favorable environmental conditions (Montanucci 1967, U.S. Fish and Wildl. Serv. 1985). Two or three eggs are usually produced although up to five have been found. Eggs are laid in June or earlier under warmer conditions and hatching of most eggs occurs in August (Montanucci 1965, 1967).

Sexual maturity is reached in from 9 to 21 months depending on the sex and environmental conditions (U.S. Fish and Wildl. Service 1985). Females tend to become sexually mature earlier than males, breeding for the first time after the second hibernation, while males usually do not breed until later (Montanucci 1965, 1967).

Population Ecology and Status. The relative proportions of the three age groups (adult [animals hatched 2 or more summers previously], subadult [animals hatched the previous year], hatchling [young hatched in the current year]) change through the activity season as young are added only in the late summer and differential mortality affects the age groups through the year. However, data based upon surface activity does not give an accurate estimate of these proportions since the adults cease activity above ground at about the same time as the eggs hatch. The best estimate of the relative proportions of adults and subadults may be made from data gathered in May since both groups are out and active. Data from Montanucci (1965) showed a proportion of about 85% adults and 15% subadults in May. Data gathered in August for subadults and hatchlings may yield the best estimate of their proportions since both groups are active. Figures from Montanucci (1965) indicate about 2: 1 hatchlings to subadults. Combining these figures, the population is estimated to consist of about 67% adults, 11% subadults, and 22% hatchlings. These proportions are consistent with the age structure of a population of a relatively long-lived species with only moderate recruitment each year and with adults that breed over a number of years. The numbers of the sexes are equal in most populations although some foothill populations studied by Montanucci (1965) had a 2: 1 predominance of males.

Data are lacking regarding longevity in G. *sila*. However, Parker and Pianka (1976) made estimates for G. *wislizenii* based on their data for a Utah population that are consistent with the above age structure and reproductive situation. Maximum longevity thus would be 8 to 9 years with an annual survivorship of about 50%.

Densities of blunt-nosed leopard lizards are low, even in optimal habitat. Naive estimates have been made from various studies and range from 0.25/ha (0.1 lizard/ac) to 1.2/ha (3/ac). An average “working density” for planning purposes of about l/ac of valley floor habitat and 0.5/ac for foothill and plains habitat seems to be advisable (Tollestrup 1979, Sheppard 1970, Le Fevre 1976, Chesemore 1980, U.S. Fish and Wildl. Service 1985).

Predators account for much of the leopard lizard mortality. Various mammals (spotted *skunk, Spilogale gracilis;* kit fox; coyote, *Canis latrans;* California ground squirrel, *Spermophilus beecheyi),* birds (loggerhead shrike, *Lanius ludovicianus;* roadrunner, *Geococcyx californianus;* burrowing owl, *Athene cunicularia;* American kestrel, *Falco sparverius;* and possibly other hawks), and reptiles (gopher snake, *Pituophis melanoleucus;* coach whip, *Masticophis flagellum;* California king snake, *Lampropeltis getulis;* possibly other snakes, and blunt-nosed leopard lizards themselves) feed on them.

Human activities cause leopard lizard mortality in three ways. Direct mortality is produced via road kills and off-road vehicle activities, and activities in blunt-nosed leopard lizard populations such as road building and repair, well drilling, plowing, and construction of buildings. Agricultural and urban development in leopard lizard habitat destroys the habitat and, while the lizards may not be killed directly, they are displaced and soon die of other causes. Finally, insect and rodent control programs involving the use of chemical pesticides may result in the accumulation of these poisons in lizard tissues and subsequent death or sterility of the animal and loss of food (Montanucci 1965, U.S. Fish and Wildl. Service 1985).

Giant kangaroo rat *(Dipodomys ingens)*

Systematics. *Dipodomys ingens* was described as *Perodipus ingens* by Merriam (1904). The type locality was listed as Painted Rock, 20 mi SE Simmler, Carrizo Plain, San Luis Obispo, California (the type locality was amended to 25.5 mi SE of Simmler by Williams and Kilburn 1991). The genus name *Perodipus* was used for several years to include all the kangaroo rats with five toes on the hind feet. Grinnell (1921) relegated *Perodipus* to a synonym of *Dipodomys*. This taxonomy has been sustained in the latest systematic review of the family Heteromyidae (Williams et al. in press).

Distribution and Habitat. The historical distribution of giant kangaroo rats encompassed a narrow band of gently sloping ground along the western edge of the San Joaquin Valley, California, from the base of the San Emidgio Mountains on the south, to a point about 16 km south of Los Banos, Merced Co.; the Carrizo and Elkhorn plains and San Juan Creek watershed west of the Temblor Mountains, which form the western boundary of the southern San Joaquin Valley; the upper Cuyama Valley next to and nearly contiguous with the Carrizo Plain; and scattered colonies on steeper slopes and ridge tops in the Ciervo, Kettleman, Panoche, and Tumey hills and in the Panoche Valley (Williams in press).

The habitat of giant kangaroo rats consists primarily of gently sloping Piedmont plains, largely without shrub cover (Grinnell 1932, Shaw 1934, Williams in press). Giant kangaroo rats were most numerous in arid grassland communities with about 16-22 cm or less of annual precipitation and sandy loam soils free from flooding in winter. The greatest densities known for the species were around the mouth of Laguna Seca Creek, in western Merced County. Nearly all populations examined by Grinnell (1932) and Shaw (1934) were located on sandy loam soils, and both researchers considered that giant kangaroo rats were limited to shrubless areas with such soils. An inventory of extant colonies, however, found giant kangaroo rats living on soils of widely varying textures, from fine sands to conglomerates of mixed pebbles and clay (Williams in press). B. Bolster (U.S. Bureau of Land Management in litt. 1981) found tiny colonies of giant kangaroo rats living on soils of loams, silty clay, and shale. Williams (in press) found that nearly all extant colonies were located in average to marginal conditions, based upon comparisons with descriptions of habitat and densities of expansive colonies described by Grinnell (1932) and Shaw (1934). Williams (in press) noted that presence or absence of shrubs in areas inhabited by *D. ingens* appeared to be related to the texture of soils, and that some colonies and individual burrows of giant kangaroo rats were found in areas supporting considerable numbers of shrubs.

Common plants in areas with colonies of giant kangaroo rats include: red-stem filaree, pepper-grass *(Lepidium* spp.), fiddleneck *(Amsinkia* spp.), red brome (Shaw 1934); malpais blue grass *(Poa scabrella),* snakeweed *(Gutierrezia* spp.), and California ephedra (Hawbecker 1944, 1951); desert saltbush *(Atriplex polycarpa),* golden bush *(Haplopappus acrideneus),* and Arabian grass (Williams in press).

Form and Function. *Dipodomys ingens* is among the largest kangaroo rats, having the greatest average weight and a length of head and body greater than 130 mm. The proportions of body and limbs are typical of kangaroo rats. The hind limbs are large relative to the size of the forelimbs, the neck is short, the head is large and flattened, and the eyes and ear pinnae are placed dorso-laterally. The ears are short and rounded. The tail is longer than the head and body, conspicuously thickened, and has a dorsal crest of long hairs distally, terminating in a large tuft of hairs. The claws on both the fore and hind feet are long and stout. Large, fur-lined cheek pouches open on the front of the face, on each side of the mouth. The pouches extend as deep, invaginated pockets of skin along the sides of the head (Williams and Kilburn 1991).

Dipodomys ingens does not differ notably in color from other species of kangaroo rats. The dusky-colored nose and vibrissae patches are separated, not forming a continuous dark mark, The cheeks are whitish and the eyelids are completely blackish. The lateral white stripes along the tail are only slightly narrower than the dorsal and ventral dark stripes. The tail tuft is dark in appearance due to a mix of light and dark hairs, The lateral surfaces of the body are pure white to the bases of the hairs, The buff-colored hairs of the sides and dorsum are mixed with fewer, scattered blackish and dusky hairs. The flanks have a darker appearance due to a greater number of dusky hairs. Juveniles are paler and grayer than adults, whose body color is “warm buff" (Grinnell 1922).

The muscular and skeletal structure was described by Setzer (1949). *D. ingens* exhibited extreme specialization in the cranial index (breadth across bullae/length of skull), reflecting a greatly broadened skull compared to all other species except *D. deserti* (banner-tail kangaroo rat). *D. ingens* had the second least specialized crural index (lengths of tibia/femur), suggesting a relatively poor saltatorial ability for giant kangaroo rats. Curiously, though, the tibioradial index (lengths of radius/tibia) was the second most specialized, indicating greater elongation of the hind leg relative to the fore leg than average among kangaroo rats. Other skeletal specializations of *D. ingens* were about average for the species examined.

The viscera of *D. ingens* was among the least specialized of 10 species of kangaroo rats dissected by Setzer (1949). It had a large caecum and little compaction of the visceral mass. The relatively large liver had nearly equal-sized and symmetrically-placed lobes. Variation in the degree of compaction and alignment of the viscera into a bilaterally balanced mass coincided more or less with skeletal specializations for saltation. The small intestine of *D. ingens* measured 274 mm and the large intestine was 430 mm in length. The ratio of small to large intestine lengths of *D. ingens* was the greatest for the species studied (63.7%).

Dipodomys ingens exhibited high hypothalamic and low peripheral thermosensitivities, suggesting that peripheral thermosensitivity plays a minor role in the regulation of body temperature in giant kangaroo rats. In unmanipulated animals, temperatures measured around the preoptic nuclei and hypothalamus (POH) increased with increasing ambient temperatures. Giant kangaroo rats responded to POH cooling with an increase in oxygen consumption, and huddling and shivering. Heating of POH provoked a decrease in oxygen consumption to basal levels, accompanied by general quiescence. Unmanipulated animals slept at ambient temperatures of 30°C; sleeping animals showed a profound depression or elimination of POH thermosensitivity (Glotzbach and Heller 1975).

Giant kangaroo rats have no way to cool the body when confined in ambient temperatures in excess of body temperature. During field work in 1987, several giant kangaroo rats exhibited signs of heat stress when delay in releasing captives resulted in exposure to ambient temperatures above 38°C; two of these animals died (Williams and Tordoff 1988a). Drinking water or access to succulent food is not required by *D. ingens.* In captivity, animals maintained body weight while fed only air-dried seeds (Williams and Kilburn 1991)

Life History. Giant kangaroo rats are primarily granivorous, but also eat green plants. They cut the ripening heads of grasses and forbs and cure them in small surface pits located on the precinct (Shaw 1934). They also gather individual seeds scattered over the ground surface and mixed in the upper layer of soil. Surface pits examined by Shaw (1934) were uniform in diameter and depth (about 2.5 cm), placed vertically in firm soil, and filled with seed pods. After placing seeds and seed heads in pits, the animal covered them with a layer of loose, dry dirt. Sets of pits associated with a single precinct covered 0.8, 2.6, 3.2, 5.1, 6.1, and 7.3 m^2; the 5.1 m^2 cache consisted of 875 separate pits. Numbers of pits out of 875 containing each type of seed head or pod, were: *Lepidium nitidum 873, Oenothera* sp. 179, *Erodium* sp. 169, *Gnaphalium* sp. 5, Plantago sp. 4, *Atriplex* sp. 4, and *Bromus rubens* 1 (Shaw 1934). Shaw (1934) surmised that pits were filled with the contents of the cheek pouches after a single trip to harvest seeds, and that before being moved underground the seeds were sun-dried to prevent molding. A similar behavior in some populations of *D. ingens* involves making large stacks of seed heads on the surfaces of precincts (Hawbecker 1944, Williams in press). The material is cured, then stored underground. Stacks Hawbecker (1944) measured averaged about 10 x 10 x 61 cm, although one measured 1.2 x 1.8 m and was 10 cm deep; each stack appeared to belong to one giant kangaroo rat.

In one den, 24 large, underground caches of seeds were found; 12 were apparently old, filled mostly with sand and empty seed pods, and 12 others were newer, consisting primarily of seeds of filaree and pepper grass. Measurements (averages) of the newer caches were: depth 14 cm; length, width, and height 26, 14, and 10 cm, respectively. In another den, 9 caches were located, each containing from 1.1 to 9.1 liters of seeds (Shaw 1934).

Grinnell (1932) examined three nursing females who had their cheek pouches “literally crammed with green stuff,” and speculated that green foliage might be an important part of the diet during lactation. Other individuals, including a young female and adult males were captured with foliage and fruits of pepper grass and foliage of filaree in their cheek pouches (Grinnell 1932). In captivity, giant kangaroo rats have been maintained for periods from 2 weeks to more than 2 years on a diet of air-dried seeds, consisting primarily of millet, oat, and sunflower, occasionally supplemented with green plants. Of the green plants, captives preferred forbs to annual grasses, and usually ignored the blades of perennial grasses (Williams and Kilburn 1991). Shaw (1934) found a live hymenopteran insect in the cheek pouch of a giant kangaroo rat. Eisenberg (1963) kept a giant kangaroo rat in captivity on a diet that included seeds, lettuce, and mealworm larvae *(Tenebrio* sp.).

Although primarily nocturnal, giant kangaroo rats were seen above ground in the Buena Vista Valley, Kern County in April 1987 and occasionally on the Elkhorn Plain Ecological Reserve (unpubl. data). While trapping on the Elkhorn Plain Ecological Reserve in 1987, we captured six giant kangaroo rats between the first time traps were checked at about 0630 h and the second check at about 1000 h, when traps were closed for the day, and one between 1700 and 1900 h (before sunset), after traps were reopened for the night (Williams and Tordoff 1988a).

Activity patterns were monitored by Braun (1985). The rats emerged from their burrows soon after sunset and were active for 1.8 ± 0.2 h (time of first emergence to time of last disappearance ± SD). There was no second period of activity before dawn. Animals were seen above ground only for an average of 15.2 ± 5.8 min/night. Time spent above ground (“foraging bouts”) lasted 80.7 ± 6.9 s; animals performed 3.5 ± 0.09 bouts/h. Giant kangaroo rats spent most of their time above ground near their home burrows; on average, individuals used 2.2 ± 0.35 grid squares (5 x 5 m) per bout, with a maximum distance travelled of 47.1 m by one individual during a single bout. During bouts, animals moved slowly, spending an average of 47.5 ± 3.8 s in each 5 x 5 m grid square. Activity patterns appeared to be unaffected by distance from the home burrow, snow, rain, wind, moonlight, or season (Braun 1985).

The surfaces of typical burrow systems (precincts) of giant kangaroo rats are elliptical, show little or no mounding above surrounding terrain, average about 2.3 by 2.6 m, and range in area from 8.1 to 160.6 m2 (*n* = 62; Williams in press). Precincts have one to five separate burrow openings with three being typical (Grinnell 1932, Williams in press). Burrows are probably plugged when the animals are within, although many burrow entrances lack plugs of earth visible from the entrance. Burrow openings are of two general types: a vertical shaft with a circular opening with no apron of dirt near the mouth and no well-worn trail leading from the mouth; and larger, more horizontally-opening burrows that are usually wider than high, and with a well-worn path leading from the mouth. Typically, a precinct has two slanting tunnels and one vertical shaft opening to the surface (Williams in press).

Excavations of burrows were described by Eisenberg (1963) Grinnell (1932), Shaw (1934), and Tappe (1941). Grinnell (1932) discovered that three excavated burrows were dichotomous, with no reconnecting tunnels, Tunnels were constructed in a single layer. Tappe (1941), however, dug out a burrow that had a three-layer arrangement of tunnels. Measurements based on excavated precincts were: internal tunnel diameter, 50 to 75 mm, with occasional enlargements up to 150 mm; average tunnel depth, 263 mm with greatest depth of 463 mm; greatest tunnel length, 3 m; and total lengths of three systems, including side branches, 9.1, 7.3, and 8.2 m. By February, rain water had penetrated the soil only to a depth of 220 to 230 mm, leaving most of the burrows relatively dry (Grinnell 1932). Grinnell (1932) considered that the scanty rainfall and “peculiar” consistency of the fine sandy loam soils inhabited by *D. ingens* might be factors in determining the distribution of this species, in that the water did not normally penetrate to a depth as great as the shallow burrows. Soil excavated from precincts of giant kangaroo rats had numerous seed hulls and other plant debris mixed in, suggesting that tunnels had been worked and reworked, perhaps over several decades (Grinnell 1932, Shaw 1934).

Only one nest has been found in excavated burrows (Grinnell 1932); it was located 330 mm below the surface, and consisted of sheep’s wool and tine, shredded grass stems, and 0.5 1 of seed hulls.

Scant information has been recorded on reproduction of giant kangaroo rats. Grinnell (1932) suggested that the reproductive season extended from January to May, based on capture of seven juveniles on 19 and 20 February, the largest of which weighed 103.5 g, and on other substantiating evidence from captured giant kangaroo rats. On the Elkhorn Plain Ecological Reserve, during October 1987, the testes of males had begun to enlarge, suggesting that mating might start in late November or December (Williams and Tordoff 1988a). Grinnell (1932) captured three pregnant females during February and one on 18 May. Another pregnant female was taken on 16 February (unpubl. data). During excavation of a burrow system on 3 March, Shaw (1934) discovered a lactating female and four half-grown young.

Little information is available on litter size and none exists for age-specific reproduction. The mean of known embryo counts and litter sizes (*n* = 7) is 4, probably a value higher than the number of live births (Williams and Kilburn 1991). A majority of females may have 3 or 4 young, although 2 is the modal number for many species of kangaroo rats.

The finding of a pregnant female in mid-May (Grinnell 1932) suggests that females could have two or three litters during the breeding season, or that some females born early in the season might breed during their first year of life. Based on weights of animals captured on the Elkhorn Plain Ecological Reserve during 1987 all young had attained nearly adult proportions; young animals could not be separated reliably from adults based on weight. This suggests that at least on the Elkhorn Plain during 1987, birth of young probably had ceased by March. There was no evidence that young-of-the-year bred (Williams and Tordoff 1988a). There is no information on dispersal of giant kangaroo rats.

Population Ecology and Status. There are no data on population structure or age-specific survival, and no information on longevity of wild animals. One giant kangaroo rat, captured as an adult, was kept in captivity for 2 years and 4 months (Williams in press). Of 31 animals marked on a 1-ha grid by Braun (1983) during summer 1981, 10 (35.7%) were recaptured in spring 1982.

Home range sizes for *D. ingens* ranged from 60 to 350 m2 (mean 239.3 m2). There was no significant difference in size of home range between sexes. The precinct is the most intensely-used location in the home range (Braun 1985). Grinnell (1932) suggested that giant kangaroo rats were territorial, based on the regular spacing of precincts and single occupancy of burrows. Individual precincts studied by Grinnell (1932) were never found to contain more than one adult. Shaw (1934) excavated five burrows in which he had previously placed canisters of cyanide; one of these was occupied by a male-female pair of adults; others in which animals were found were occupied by single adults. By measuring overlap between home ranges of individual animals, Braun (1985) showed that individuals exhibited strict intrasexual avoidance, with moderate levels of intersexual contact. Although each individual had a distinct home burrow, animals frequently entered burrows at some distance from their home burrows during nightly periods of activity.

Estimates of density, based on counts of precincts in high-quality habitat (Grinnell 1932), ranged from 40 to 69 per ha (mean = 52). Braun (1985), employing both trapping and counts of burrows, estimated a density of 25 adults/ha for her study site on the Carrizo Plain. This colony was typical of the larger colonies still extant in that area. Williams (in press) counted precincts on l-ha plots in the four largest remaining colonies of giant kangaroo rats in Kern and San Luis Obispo counties, recording a mean of 32/ha (range 18 to 49, *n* = 12); approximately 30% of the precincts were unoccupied, resulting in a mean estimate of density of 22 per ha during September. Counts of burrows on two l-ha plots on the Elkhorn Plain in 1987 were 64 and 76. This compared to population estimates from capture-recapture on the same plots of 31 ± 2 and 35 ± 3, respectively (Williams in press, Williams and Tordoff 19883). Other colonies of giant kangaroo rats were smaller and less dense. The largest covered about 125 ha, but most consisted of from 2 to 10 precincts, each isolated by several hundred meters or more from other colonies (Williams in press). For example, in the Panoche Hills, Fresno Co., B. Bolster (U.S. Bureau of Land Management in litt. 1981) located five separate colonies spread over about 1,500

1 hectares. Williams (in press) counted precincts and monitored these colonies from 1980 to 1985. The largest consisted of about 18 active precincts spread in three clumps over about 25 ha. The smallest consisted of five precincts in about a l-ha area. One of the five colonies declined from a high of 12 active precincts in 1980 to one or two in April, 1985, and another apparently was extirpated. A similar situation prevailed in the Ciervo and Tumey hills, sites of other colonies in the northern portion of the range of *D. ingens.*

Predators of giant kangaroo rats include: barn owls *(Tyto alba),* great horned owls *(Bubo viqinianus),* coyotes, kit foxes, and badgers *(Taxidea tamcs;* Grinnell 1932; Hawbecker 1943, 1944, 1945). Hawbecker (1944) also observed a weasel *(Mustela fenata)* being chased from a burrow system of either D. *ingens* or A. *nelsoni.* Other common, nocturnal predators seen within giant kangaroo rat colonies include short-eared owls *(Asio flammeus),* rattlesnakes *(Crotalus viridis),* gopher snakes, California king snakes, and other snakes.

Numbers of giant kangaroo rats have diminished dramatically in recent years. Grinnell (1932), Shaw (1934), and Hawbecker (1944, 1951) described colonies spread over thousands of acres of continuous habitat. Outlines of major, historical distribution areas encompassed an estimated 755,844 ha; between about 63,172 and 631,724 of this total was estimated to be historic habitat, using different assumptions. Between about 1972 and 1979, rapid conversion of natural communities to cultivated agriculture reduced available habitat and imperilled the giant kangaroo rat. Extant colonies located between 1979 and 1987 occupied approximately 11,145 ha, about 1.5% of their historic range and between about 1.6 and 17.6% of historic habitat. Several of the smaller colonies declined or disappeared after being inventoried in 1979 and 1980. Six areas totaling about 3,460 ha supported population densities approaching conditions described as typical up to the 1960’s, but with densities averaging less than one-half of those reported for high-quality habitat. The Elkhorn Plain contained the largest and densest populations of the remaining areas (Williams in press).

The decline in populations of giant kangaroo rats has been primarily due to loss of habitat by conversion of natural lands to irrigated cropland made possible by the State Water Project and the San Luis unit of the Central Valley Project. Between about 1970 and 1979, almost all land on the floor of the Tulare Basin was developed for irrigated agriculture, restricting occurrence of most species of the San Joaquin saltbush community, including *D. ingens* (Williams in press).

Use of rodenticide-treated grain to control ground squirrels and kangaroo rats may have contributed to the decline of giant kangaroo rats in some areas, as rodent control on central California rangelands has been a common practice during all of this century (Grinnell and Dixon 1918). There are broad areas in the Sunflower Valley (western corners of Kings and Kern counties), and the eastern foothills of the Panoche Hills, Fresno County, that show characteristic features of giant kangaroo rat precincts, but are unoccupied by kangaroo rats or ground squirrels. Williams (in press) believed that populations in these areas may have been extirpated by use of rodenticides.

Degradation of desert and steppe rangelands by overgrazing also might be a factor in the historic decline of giant kangaroo rats, but there is no evidence to support this hypothesis. Based on remarks by Grinnell (1932) and Shaw (1934), it is clear that giant kangaroo rats can survive in areas that have been grazed to a point where almost no plant material remains. It is not known, however, if they could survive indefinitely if those grazing intensities were sustained for several years.

Short-Nosed Kangaroo Rat *(Dipodomys nitratoides brevinasus)*

Systematics. Grinnell (1920) described *Dipodomys merriami brevinasus* from Hays Station, 19 mi SW Mendota, Fresno Co., California. Later, Grinnell (1921) elevated *nitratoides* to specific status and assigned *brevinasus* as a subspecies of *D. nitratoides.* As currently recognized, *brevinasus* is one of three subspecies of the San Joaquin kangaroo rat, the others being the Tipton *(D. n. nitratoides)* and Fresno *(D. n. exilis)* kangaroo rats. Williams (1985) discussed the boundary between the subspecies *D. n. nitratoides* and *brevinasus.* The boundary between *exilis* and *brevinasus* was a broad zone of intergradation on the valley floor between the coastal ranges and a line marked roughly by Fresno Slough and the San Joaquin River (Boolootian 1954, Hoffmann 1975, D. F. Williams unpubl. data). Ten specimens identified as *D. nitratoides* from 3 mi E Cuyama Ranch, 2,200 ft, Cuyama Valley collected in 1916 (U.S. National Museum collection) were not mentioned by Grinnell (1922) or Hall (198 1). Hoffmann (1975) examined specimens from the Cuyama Valley, but did not identify the number or museum where they were housed (presumably, they were the specimens in the U.S. National Museum). He compared them with samples of *nitratoides* from other localities and determined that they exhibited characteristics more diagnostic of Merriam's kangaroo rat, *D. merriami,* as defined by Lidicker (1960), but equivocated about their identity. Populations of similar sized *D. merriami,* however, such as *D. m. parvus,* are not geographically adjacent to populations of *D. nitratoides.* Measures of genetic similarity (Johnson and Selander 1971, Patton et al. 1976) and chromosomal data (Hoffmann 1975, Stock 1974) provide strong evidence that *D. nitratoides* is related to *D. merriami,* but is specifically distinct (also see Best and Janeck 1992).

Distribution and Habitat. Distribution of the short-nosed kangaroo rat was outlined and documented by Grinnell (1922) Hoffmann (1975), and Hafner (1979). Short-nosed kangaroo rats were found on the western side of the San Joaquin Valley, from near Los Banos, Merced Co., southward west of the San Joaquin River and a line approximately coincident with the Kettleman Hills, Lost Hills, and Elk Hills to the southern end of the valley. They also occurred in the Panoche Valley, San Benito Co., the Sunflower Valley, Kings Co., the Antelope Plain in Kern Co., the Carrizo Plain in San Luis Obispo Co., the Cuyama Valley in San Luis Obispo and Santa Barbara counties, and at the edge of the valley floor around the south end of the San Joaquin Valley from the vicinity of Maricopa on the west to northeast of Bakersfield on the east (Hall 1981, Williams 1985).

Short-nosed kangaroo rats are found mostly on flat and gently sloping terrain and on hilltops in desert-shrub associations, primarily saltbushes and California ephedra. On the western slopes of the Temblor Range, San Luis Obispo County, they also occur sparingly on steep rocky hillsides among chaparral yucca, ephedra, and other shrubs, up to about 840 m (2,750 ft; Williams and Tordoff 1988a; D. F. Williams unpubl. data). Generally, short-nosed kangaroo rats occupy grassland and desert-shrub associations on friable soils. They inhabit highly alkaline soils around Soda Lake, on the Carrizo Plains, and less saline soil elsewhere. On the valley floor, around Los Banos, Merced Co., small populations live on dikes secure from winter flooding, then move into seasonally flooded iodine bush shrublands during the summer months, where at least some individuals reproduce (Johnson and Clifton in press). Hawbecker (195 1) reported that, in the Panoche Valley, San Benito Co., short-nosed kangaroo rats were found on gentle slope and rolling, low hill-tops where some shrubs were present.

Form and Function. The San Joaquin kangaroo rat, though smaller than all other kangaroo rats except some populations of *D. merriami,* is similar in general form and appearance to other species of kangaroo rats. It is adapted for bipedal locomotion, having greatly enlarged hind limbs, a long tail, and a short neck. The head is large and dorso-ventrally flattened and with dorso-laterally placed ears and eyes. As in other members of the family Heteromyidae, it has external, fur-lined cheek pouches.

Dorsal and lateral surfaces are colored dark yellowish-buff, the underparts are white. Dark whisker patches are connected by a dark band of fur across the nose. The tail has a crest of longer hairs distally, terminating in a tuft.

Geographic variation in size occurs in the three subspecies; *D. n. brevinasus* is the largest subspecies and has pale-ochraceous dorsal and lateral coloration. *D. n. nitratoides* is smaller in size and has sayal brown pelage. *D. n. exilis* is the smallest in size (and the smallest kangaroo rat) and has snuff-brown pelage and darker facial markings. Average external and cranial measurements (mm) of 10 *D. n. brevinasus* from western Fresno Co. are: total length, 237 (221 to 252); length of tail, 135 (125 to 145); length of hind foot, 35.4 (35 to 37); length of ear from crown, 10.8 (10 to 12); greatest length of skull, 34.4 (33.8 to 35.0); breadth of skull across bullae, 22.5 (22.0 to 23.2); breadth across maxillary arches, 19.2 (18.9 to 19.7); greatest length of nasals, 12.1 (11.8 to 12.6); greatest width of rostrum near end, 3.0 (2.8 to 3.0); width of maxillary arch at middle, 4.7 (4.5 to 5.0); weight (g), 43.9 (39.6 to 52.6; Grinnell 1922).

In contrast to quadrupedal rodents, *D. nitratoides* and other ricochetors support most of the body weight on the hind limbs most of the time. To accommodate this weight, the sacro-iliac union is strengthened by extensive fusion; the innominate bone functions as part of the sacrum. The acetabulum is the fulcrum on which the body is balanced; at rest in a bipedal stance, the center of gravity is shifted posterior to the acetabula by raising the fore end of the body to a more vertical position, and the tail is used as a prop to help maintain balance. During ricochetal locomotion, the fore part of the body is lowered and the center of gravity is far anterior to the acetabula; the tail counterbalances the fore parts by being held almost horizontally. Also contributing to equilibrium while in motion, the lengthened feet of *D. nitratoides* strike the ground far forward of a vertical line intercepting the center of gravity (Hatt 1932).

Common adaptations among bipedal rodents studied by Hatt (1932) exemplified by *D. nitratoides,* were enlargement of the head and shortening of the neck, with concurrent fusion of post-atlas vertebrae. *D. nitratoides* had the normal number of seven cervical vertebrae; *Dipodomys* spp. showed differing degrees of fusion among vertebrae, depending on age. Fusion usually first occurred between vertebrae 2 and 3, and progressed posteriorly. Cervical vertebrae 6 and 7 were not fused with others. The average length of the cervical vertebrae, expressed as a percentage of the length of the thoraco-lumbar vertebrae, was 14.7.

Dipodomys nitratoides has 12 thoracic and 7 lumbar vertebrae, numbers Hatt (1932) interpreted as the primitive or ancestral condition among rodents. Because of center of gravity is farther posteriorly in *D. nitratoides* and other ricochetors, the union of head and neck (cervical flexure) is at a more acute angle than in quadrupedal rodents. To hold the neck and enlarged head in position at an increased angle, the spinalis dorsi muscles take their origins on neural spines of the anterior thoracic vertebrae that are angled more acutely posteriorly than in quadrupedal species (Hatt, 1932). The lumbar vertebrae have neural spines of increased height to accommodate the origins of the dorsal extensor and quadratus lumborum muscles. Both muscle groups are greatly enlarged in ricochetal rodents. Other modifications of the thoraco-lumbar region of *D. nitratoides,* all related to the increased strength required of the spine and associated muscles to hold the fore end of the body, include increased length and strength of the metapophyses and anapophyses, and increased ventral deflection of the lumbar diapophyses (Hatt 1932).

The sacral and pseudosacral vertebrae (i.e., those not contacting the innominate, but fused with the sacrals, which are fused to the ilium) of *D. nitratoides* do not differ markedly from those of generalized rodents. In *D. n.,* two sacral vertebrae are fused with the ilium; there are normally three pseudosacral elements; a small percentage of individuals have only two. The number of post-sacral vertebrae fused with the sacrals is somewhat age-related; the older the animal, the greater fusion among the three pseudosacral vertebrae. A relatively short sacrum is a feature of bipedal rodents with heavy, thickened tails such as springhares *(Pedetes;* Hatt 1932). Hatt (1932) grouped *D. nitratoides* and other kangaroo rats in a “thin-tailed” category. Species with thin tails are characterized by long sacra made up of several fused pseudosacral elements. The contrast in groups is due to differences in the origins of the caudal muscles. In large-tailed species, caudal muscles originate both on the diapophyses of pseudosacral and caudal vertebrae, far caudad to the pseudosacrum; in thin-tailed species, the origins of caudal muscles are confined to surfaces of the vertebrae lying within the limits of the pelvis. In many respects, however, the long and moderately thickened tails of *D. nitratoides* and other kangaroo rats are intermediate to the thin and thick tailed categories characterized by Hatt (1932).

Species of *Dipodomys* have more caudal vertebrae than other members of the Heteromyidae. The length of the tail of kangaroo rats is due both to an increase in numbers of caudal vertebrae and an increase in length of individual elements. A lengthened tail is a common feature of ricochetal rodents. Hatt (1932) remarked that, in ricochetal species, tails functions for counterpoise, maintaining lateral balance, for support while standing at rest, and perhaps for other purposes.

Dipodomys nitratoides and other bipedal rodents have forelimbs of reduced size in comparison to quadrupedal species. Reduced size and importance of the forelimbs in locomotion are reflected in a smaller pectoral girdle and its associated musculature (Hatt 1932). Magnifying the reduction in forelimbs size is the great enlargement of the hind limbs. The intermembral index (lengths of humerus and radius/femur and tibia) of *D. nitratoides* was 0.54; generalized quadrupedal mammals averaged about 0.75 (Setzer 1949). Likewise the tibioradial index of *D. nitratoides* was 0.57, compared to a value of quadrupedal species of about 0.75. In comparison to other species of *Dipodomys*, these indices in *D. nitratoides* signify greater specialization for ricochetal locomotion than some, such as Ord's kangaroo rat *(D. ordii)*, but less than others such as desert *(D. deserti)* and banner-tail kangaroo rats (Setzer 1949). Another forelimb adaptation of *D. nitratoides*, related primarily to its locomotor pattern, is a lengthened forearm relative to the upper arm, as reflected by a humeroradial index of 1.55, a value greater than average among the species studied by Setzer (1949).

The manus plays very important roles in gathering food, digging, and grooming (Eisenberg 1963). The pollex is rudimentary in *D. nitratoides*, and has a very short, blunt claw. Digit 2 is slightly shorter than digit 4, which is slightly shorter than digit 3. All three digits have long, curved claws. The palm is naked, has a slight transverse crease, and is equipped with pads and tubercles. The metacarpals are normally held at about a 45° angle to the forearm; the tips of the phalanges and claws are normally flexed, forming an angle of nearly 90° to the metacarpals (Howell 1932). Howell (1932) found that the manus of a freshly-killed kangaroo rat was highly mobile, with pronation to about 75° and supination through wrist and forearm of at least 150°.

Aside from enlargement of the hind limbs in bipedal species, Hatt (1932) and Setzer (1949) noted that the tibia is longer relative to the femur than in quadrupedal species. For San Joaquin kangaroo rats, the crural or femororadial index (lengths of tibia/femur) was 1.37, a value greater than most other kangaroo rat species studied by Setzer (1949), and in excess of an index of 1.00 expected of generalized species. Accompanying enlargement of the leg bones of the hind limb in ricochetors, such as *D. nitratoides*, is a lengthening of the hind foot. The femorotarsalmetatarsal index (lengths of tarsometatarsus /femur) of *D. nitratoides* was 0.98, reflecting slightly greater specialization for saltation than average among *Dipodomys* spp., and much greater specialization than quadrupedal species, whose average index was less than 0.50 (Setzer 1949). Howell (1932) computed a ratio of lengths of hind foot to head and body length of 0.38 for *D. nitratoides* and compared it to ratios of 0.17 to 0.20 for woodrats *(Neotoma* spp.). The elongation of the pes is primarily due to the metatarsals and phalanges, the elements of which are both lengthened in comparison to quadrupedal species. The pes is also narrower, and there is fusion of the central metatarsals (Howell 1932). The pes of *D. nitratoides* and other taxa of the *merriami* group are extremely slender compared to other species of kangaroo rats (Grinnell 1922). Digit 5 is relatively shorter than in scansorial rodents such as woodrats, and the nails of digits 2 and 4 are each turned centrad, toward digit 3 (Howell 1932). In *D. nitratoides,* the hallux (digit 1) is represented only by the rudiment of the first metatarsal; there is no evidence externally of digit 1. The sole of the foot, including all but the terminal pads of the digits, are clothed in short hairs.

The cranial index (breadth across bullae/length of skull) for *D. nitratoides,* 0.66, indicated a broader skull with more greatly inflated auditory bullae than average among *Dipodomys* spp. (Setzer 1949). Enlargement of the skull of *D. nitratoides* relative to generalized rodents is principally due to the huge, inflated auditory bullae.

The only differences that Setzer (1949) found in the musculature of *D. nitratoides* in comparison to that of *D. spectabilis,* was in the size of individual muscles. Otherwise, details of origins, insertions, and innervation were as reported in detail by Howell (1932) for *D. spectabilis.*

Life History. Little detailed information is available on the food habits of short-nosed or other populations of the San Joaquin kangaroo rat. Seeds are the staple in the diet (Culbertson 1946, Eisenberg 1963). A wide variety of seeds are probably consumed, including seeds of annual grasses, particularly wild oats *(Avena* spp.), brome grasses, wild barleys *(Hordeum* spp.), and annual fescues *(Vulpia* spp.). Seeds of annual forbs such as filaree, peppergrass, and shepard‘s purse *(Capsella buras-pastoris)* also are important foods. Seeds of woody shrubs, especially saltbushes, are diligently sought out by Tipton and short-nosed kangaroo rats (D. F. Williams unpubl. observations). Culbertson (1946) found a few seed caches in excavated burrows of Fresno kangaroo rats and remarked that they also probably ate green vegetation. Eisenberg (1963) found that short-nosed kangaroo rats ate green vegetation in captivity, and also consumed insects (mealworm larvae). Captive short-nosed kangaroo rats seem especially fond of leaves and immature seed heads of filaree and sprouts of a variety of seeds, and also eat celery stems and leaves, lettuce, apples, carrots, broccoli flowers and stems, stolons and rhizomes of perennial grasses, and several kinds of seeds, including oat, millet, and sunflower. They would not eat the leaves of perennial grasses provided in captivity, however (D. F. Williams unpubl. observations).

Most kangaroo rats gather seeds when they are available and cache them for consumption later. Typically, caches are made in small pits that hold the contents of the two cheek pouches. Caches are located on the surface of the soil, and are typically scattered over the home range of the individual. Larger caches are often made in chambers within the individual‘s burrow system, and smaller caches are made in the walls of the burrows. These small caches also hold only about the contents of two cheek pouches. The only type of caches that have been found for San Joaquin kangaroo rat are small caches in the sides of burrows. Culbertson (1946) speculated that Fresno kangaroo rats did not cache seeds in their burrows to the same extent as other species because the soil where they lived was damp much of the year. Seeds would spoil rapidly under such conditions. He further speculated that Fresno kangaroo rats, therefore, were obligated to forage on the surface year round to a greater extent than kangaroo rats that cached more food. It is not known if short-nosed kangaroo rats have similar caching and foraging behaviors; but seed spoilage would be less of a problem for populations in upland habitats. In fall and winter, after the wet season commences, sprouts of seeds and tender new growth of grasses and forbs may be essential items in the diet of short-nosed kangaroo rats. Green, developing seed heads may be important in the spring months. Seeds, and perhaps insects, are the most important items in the diet in late spring, summer, and fall.

Short-nosed kangaroo rats are nocturnal and active year round. They do not become dormant. They frequently appear above ground shortly after sunset and before dark (Tappe 1941, D. F. Williams unpubl. data). They were not captured in the morning hours after sunrise on the Elkhorn Plain, but were taken in the evening before sunset (Williams and Tordoff 1988a). In captivity, short-nosed kangaroo rats showed no difference in activity under simulated full-moon and new-moon conditions (Lockard and Owings 1974).

Individuals shelter in ground burrows that are dug by them or their predecessors. Burrows usually are found in relatively light, friable soils in raised areas. Burrows typically are placed under shrubs, rocks, or in the banks of arroyos. The surface area covered by the burrow system of individuals usually varies from about 2.1 to 3.7 m (7 to 12 ft) on a side. There are usually two or three burrow entrances that slant gently underground, and one hole that opens from a vertical shaft. Burrow entrances vary from about 25 to 70 mm in diameter. Most slanting entrances are wider than high. Entrances to vertically-opening shafts are typically circular, average about 30 mm in diameter (range, about 25 to 40 mm; Williams 1985). Tunnels are about 30 to 50 mm in diameter and extend about 30.5 to 38.1 cm (12 to 15 in) below ground. There may be several interconnecting tunnels and many dead-end side branches. No nesting material nor large food caches have been found in the few burrows excavated (Culbertson 1946).

Females may breed with more than one male during estrus, based on studies of a captive colony. Captive-bred short-nosed kangaroo rats had a gestation period of 32 days and an average litter size of 2.3 (mode = 2). Litter mass at birth averaged 7.6 g. Females showed a postpartum estrus (Eisenberg and Issac 1963). In the wild, breeding normally occurs from January through August or September. At lower elevations of the San Joaquin Valley, pregnant Fresno kangaroo rats have been taken in all months except August and September (Hoffmann 1974, Rado 1986). Culbertson (1946) captured pregnant females between February and March and June and September. Some animals may breed at any time of the year. In captivity, a young female conceived at 12 weeks of age and produced two young (Eisenberg and Issac 1963).

Population Ecology and Status. There are no data on longevity, age-specific survival, or population age structure, and no published studies of home range or territoriality of San

Joaquin kangaroo rats (Best 1991). Naive density of Fresno kangaroo rats in one study varied from 16.7 to 24.9/ha (Hoffmann 1974), and in another, estimates varied from 4.9 to 17.l/ha at different sites and in different seasons (Koos 1977). Estimated density of Tipton kangaroo rats at Pixley National Wildlife Refuge ranged from 3.0 ± 0.9 to 3.8 ± 1.6/ha using capture-recapture models and from 9.9 to 18.5/ha using counts of active burrows (Williams and Germano 1991). Williams (1985) using counts of active burrows at sites through out the geographic range, recorded a range of densities for Tipton kangaroo rats from < 1 to 50/ha, with an average of about 15/ha. These counts probably overestimated true density by 30 to 50% or more (Williams and Germano 1991, in press). Hafner (1979) provided data on counts of active burrows that averaged about 4.4/ha over the geographic range of Tipton kangaroo rats. His counts also probably overestimated true density. No information on density of short-nosed kangaroo rats were available prior to initiation of the studies presented here.

Loss of habitat has been extensive throughout the range of the short-nosed kangaroo rat, particularly on flatter lands in the Cuyama, San Joaquin and Panoche valleys, and on the Antelope and Carrizo plains. Cultivation of native communities has been the major reason for loss of habitat. Overgrazing and fire reduce habitat for short-nosed kangaroo rats where susceptible shrubs, such as saltbushes, are extirpated. Relatively small, isolated populations are found on the southern Antelope Plain west of Buttonwillow and around Taft and Maricopa, Kern Co.; on uncultivated ground in the Kettleman Hills and in and around oil fields near Coalinga, Fresno Co.; west of Interstate Highway 5 on unirrigated lands at the edge of the valley in Fresno Co.; and around Soda Lake on the Carrizo Plain, San Luis Obispo Co. The short-nosed kangaroo rat is currently listed as a California Species of Concern and a Federal Category- 1 Candidate Species (Williams and Germano in press).

History of Current Studies

Studies of the effects of livestock grazing on a community of endangered species were initiated in 1987 by the California Department of Fish and Game on the Elkhorn Plain Ecological Reserve, San Luis Obispo County (Williams and Tordoff, 1988a). The studies on the Elkhorn Plain Ecological Reserve were continued in 1988, and the project was expanded to include investigations of San Joaquin antelope squirrels at selected sites throughout their geographic range (Harris and Stearns 1991, Williams and Tordoff 1988b). The Department of Fish and Game was the sole financial supporter for the research in 1987 and 1988. Projects continued or initiated in 1988 were carried forward in 1989 through contracts with the Department of Fish and Game and The Nature Conservancy and equipment and supplies provided by the USDI Bureau of Land Management (Williams et al. 1989). In 1990 the project was funded by contracts with the Department of Fish and Game and the Bureau of Land Management (Williams et al. 1990). In 1991, funding came from the Department of Fish and Game and the Bureau of Land Management, with TNC serving as an intermediary contractor for the BLM funds. The BLM also provided logistic support, field equipment, and a vehicle for use on the project in 1989-1991. Summaries of research results for 1987 and 1988 were presented in California Dep. of Fish and Game contract final reports by Williams and Tordoff (1988a, 1988b)[a]. Although the contract endings for these field studies were 30 June 1991 (Department of Fish and Game) and 15 October 1991 (BLM/TNC), we continued field work in 1992 unsupported by these agencies, and herein report on results through December 1991, with some additional data on the translocated colony of giant kangaroo rats through the first week of February, and other observations through April 1992. Results of concurrent investigations of census methods and population numbers of San Joaquin antelope squirrels were presented by Harris and Stearns (1991).

Data gathered in 1987-1988 on trapping probabilities and response to different styles of traps were published in Williams and Germano (in press). Features of burrows and precincts, and annual weight cycles of giant kangaroo rats, gathered in 1987-1988 were included in Williams (in press). Other publications based wholly or in part on these studies are: responses of blunt-nosed leopard lizards to drought (Germano et al. in press); using PIT tags for marking leopard lizards (Germano and Williams in press); comparison of methods of marking kangaroo rats (Williams et al. submitted); and recovering blunt-nosed leopard lizards (Germano and Williams in press).

Objectives

The major objectives of the research program were: 1) determine the impact of grazing by cattle on the biotic community represented on the Elkhorn Plain Ecological Reserve; 2) obtain detailed demographic data on selected species, namely the giant kangaroo rat and blunt-nosed leopard lizard; 3) establish a procedure for and information on the effectiveness of translocating giant kangaroo rats into formerly inhabited areas; and 4) establish and evaluate a supplemental feeding program for giant kangaroo rats. Other data on life history and ecology of featured species and San Joaquin antelope squirrels and short-nosed kangaroo rats were also gathered incidental to the principal objectives.

STUDY SITES

These studies were initiated in July 1987 on the Elkhorn Plain, eastern San Luis Obispo Co., California (Figure 1). Study plots for small mammals were established on the Elkhorn Plain Ecological Reserve where cattle were excluded by a fence constructed in spring 1987, and outside the Reserve nearby, where cattle would continue to graze when conditions permitted. Two 8.1 ha (20 acre) plots for blunt-nosed leopard lizards were established in 1988. In 1989, the two small-mammal plots were expanded from 1.0 to 1.44 ha, and nine additional plots for studying small mammals were established. Details on plots are provided in the following descriptions of methods and in Table 1.

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[a] These and other unpublished reports cited herein are available through the California Endangered Species Information System, U.S. Bureau of Land Management, 2800 Cottage Way, Sacramento, CA 95825 (916-978-4725).

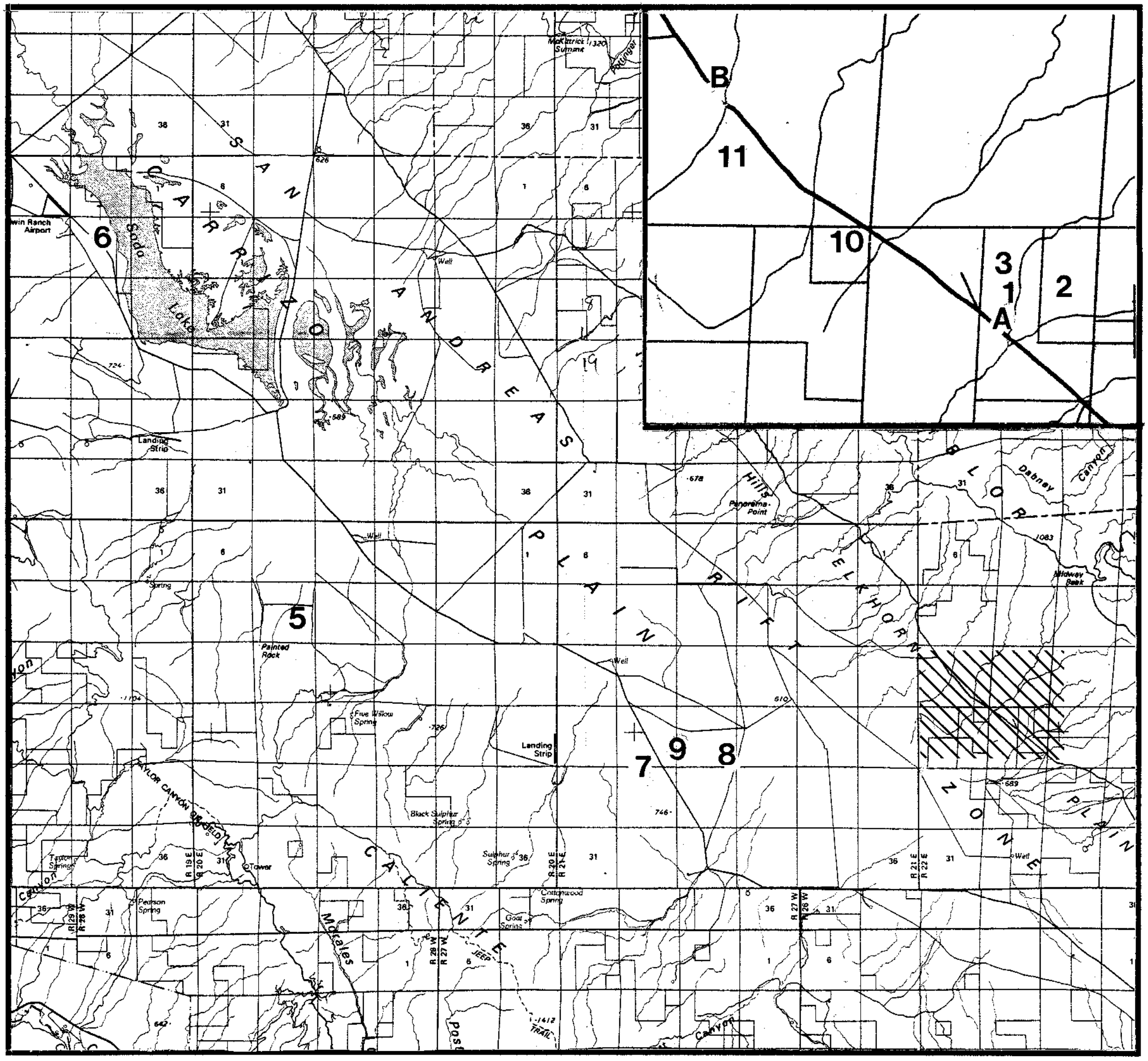

Figure 1. *Locations of study plots in the Carrizo Plain Natural Heritage Reserve, San Luis Obispo Co., California. Plot numbers are the same as those in Table 2. Shaded area shows the location of the inset in the upper left corner of the figure.*

METHODS

Community Interactions

Precipitation data were obtained from long-term records maintained by residents of the Traver and Washburn ranches on the southern Carrizo Plain, the Simmler weather station on the northern Carrizo Plain, and from rain gauges placed on the Elkhorn Plain Ecological Reserve in 1989.

Cattle were removed from the pasture where the Elkhorn Plain Ecological Reserve is located in April 1987. On their return in November 1987, they were excluded from

Table 1. *Locations and purposes of plots used in studies reported herein. Plot numbers (except plot 4) provide a key to the map of localities in the Carrizo Plain Natural Area (Figure 1).*

Plot	Location	Size	Species	Purpose	Established
1	Elkhorn Plain, NE 1/4 sec. 20, T32, R22E, 2,300 ft., San Luis Obispo Co.	1.44 ha	small mammals	experimental plot, no grazing	July 1987
2	Elkhorn Plain, NE 1/4 sec. 20, T32, R22E, 2,300 ft., San Luis Obispo Co.	1.44 ha	small mammals	control plot, grazing	July 1987
3	Elkhorn Plain, NE 1/4 sec. 20, T32, R22E, 2,300 ft., San Luis Obispo Co.	1.44 ha	small mammals	demographic studies	Juner 1988
4	Panoche Creek, NW 1/4 sec. 20, T15S, R12E, 600 ft., Fresno Co.	1.44 ha	small mammals	estimate density	June 1989
5	Painted Rock, Carrizo Plain, NE 1/4 sec. 8, T32S, R20 E, 2,160 ft., San Luis Obispo Co.	1.44 ha	small mammals	translocated colony	July 1989
6	Soda Lake, Carrizo Plain, NE 1/4 sec. 11, T31S, R19E, 1,920 ft., San Luis Obispo Co.	1.44 ha	small mammals	translocated colony	July 1989
7	Washburn Ranch, Carrizo Plain, SW 1/4 sec. 20, T32S, R21E, 2,050 ft., San Luis Obispo Co.	0.25 ha	small mammals	monitor reproduction	January 1990
8	Carrizo Plain, SE 1/4 sec. 21, T32S, R21E, 2,075 ft., San Luis Obispo Co.	8 ha	small mammals	supplemental feeding	February 1991
9	Carrizo Plain, SE 1/4 Sec 20 & SW 1/4 sec. 21, T32S, R21E, 2,075 ft., San Luis Obispo Co.	8 ha	small mammals	control, no feeding	February 1991
10	Elkhorn Plain, sec. 19 & 20, T32S, R22E, 2,275 ft., San Luis Obispo Co.	8 ha	small mammals	supplemental feeding	February 1991
11	Elkhorn Plain, SE 1/4 sec. 18, T32S, R22E, 2,250 ft., San Luis Obispo Co.	8 ha	small mammals	control, no feeding	February 1991
A	Elkhorn Plain, NE 1/4 sec. 20, T32, R22E, 2,300 ft., San Luis Obispo Co.	8.1 ha	lizards	demographics, experimental plot, no grazing	April 1988
B	Elkhorn Plain, NW 1/4 sec. 18, T32, R22E, 2,350 ft., San Luis Obispo Co.	8.1 ha	lizards	demographics, control plot, grazing	April 1988

experimental plots on the Elkhorn Plain Ecological Reserve by the newly-constructed fence. They remained in the pasture from November 1987 into June 1989. Because of drought and logistic complications no livestock grazed the pasture between June 1989 and December 1991.

Plant Productivity

Net above-ground production of herbaceous plants was measured on 0.25 m^2 plots in 1988, 1990, and 1991. Studies commenced in 1987 after the time for sampling, although photographs were coincidentally taken on 1 April when the annual plants had ripened and were drying. Herbaceous plant productivity in 1989 was so slight that we decided not to sample because it did not extend above the stubble of mulch from previous years' growth. Thus, no plots were sampled in 1987 and 1989 although productivity was estimated from photographs. In 1988 and 1991 collection of herbage was made when the seed heads had ripened and annual grasses were beginning to dry, and before antelope squirrels and kangaroo rats had began to cut significant amounts of seed heads. Plants on plots were clipped with grass shears within 3 mm of ground level. In 1990, normal sampling for productivity and species composition on grazed and nongrazed plots was not practical because of failure of the annual plants to grow. Instead, productivity was sampled on 15 randomly-chosen 0.25 m2 plots on the nongrazed Reserve. Plants had grown little beyond the cotyledon stage and had to be gathered with forceps. In 1988, 200 0.25-m^2 plots, stratified as follows, were sampled: 50 on precincts and 50 from the ground around precincts of giant kangaroo rats, both from the nongrazed Reserve and the grazed pasture. Positions of the samples on and off of each precinct were determined randomly, but each off-precinct sample came from an area in the space around its matched precinct. Twenty-five samples of each treatment came from the ephedra and annual grassland associations. In 1991, samples were taken only from the annual grassland association (to eliminate the great expense of sorting woody litter from samples, after collection, and because tests in 1988 showed no difference between the two areas in productivity), as follows: 30 randomly chosen matched pairs on and off of precincts of giant kangaroo rats both in the Reserve and pasture (120 total). Samples were placed in paper bags, labeled, and dried for storage. Before recording weights, samples were sorted to remove pebbles, dung, and woody material, then dried to uniform weight. Mass was recorded to the nearest 0.01 g. Samples on and off of the Reserve were tested for significant differences and homogeneity of variances before pooling samples from the ephedra and grassland associations. Differences were tested by ANOVA and paired t-tests for on- and off-precinct comparisons within Reserve and pasture, and independent-samples two-tailed t-tests for comparisons between Reserve and pasture.

Live shrubs on 16 50-m line transects (8 Reserve, 8 pasture) established in 1987 (Williams and Tordoff 1988a) were measured by the line intercept method (length and height) in August of 1987-1991. Data were converted to area (length*height), summed by species, and pooled by transect. Differences between years were compared using the two-tailed, independent-samples t-test. Only detailed results of pooled species measurements are presented here (see Williams and Tordoff 1988a, 1988b for statistics on individual species).

In 1987, 120 shrubs of six species were tagged (10 of each species on the Reserve and in pasture). Volumes of these individually-tagged shrubs were measured in three dimensions (two of width at right angles and height). These values were converted to volumes (maximum measures of length*width*height). Volumes measured in this way reflect above-ground space occupied by shrubs but are not an accurate measure of biomass. For *Haplopappus acradenius* and *Gutierrezia* sp., fewer than 10 were originally located on the Reserve in 1987 and some of those died subsequent to the 1988 census. Data for these two species were eliminated from statistical comparisons. Several more shrubs had died by 1989 and still more died by 1990. Though we measured survivors each year and tagged new shrubs for subsequent comparisons, results were similar to that of line transect measurements and thus are not presented here (see Williams and Tordoff 1988a, 1988b, and annual progress reports for results).

Mulch

The initial objectives in sampling mulch (plant litter) were twofold: 1) obtain a measure of the total amount of organic material on the soil surface; and 2) determine the amount of herbaceous material remaining at the end of the annual grazing season. In August of 1987 and 1988, 200 samples, stratified as follows, were obtained: 25 each from the steep rocky hillsides (hill), ephedra association (slope), grassland association (plains), and arroyo association, in grazed (pasture) and nongrazed (Reserve) areas. Williams and Tordoff (1988a) described these associations. Sample sites were chosen randomly and at each site all organic material was collected from within a 0.25 m2 sampling frame by scraping the surface of the ground with the edge of a sharp-bladed trowel. The sampling protocol for mulch collected in August 1989 through 1991 was modified from the procedures used in 1987 and 1988. No samples were taken in the shrub/subshrub community on steep slopes nor the successional community in arroyos (rational was given by Williams et al., 1989). The ephedra and plains associations were combined for sampling in 1989-1991, and the number of 0.25-m^2 samples was increased from 50 (combined) to 60 each on grazed and nongrazed plots.

In the laboratory, larger pebbles were picked from samples. Samples were placed in 100-mesh soil sieves and partly immersed in a bucket of water to float off organic material. The material was thoroughly rinsed in clean water prior to collection. This process resulted in separation of mineral soil particles from all organic material ranging in particle size from organic duff to large pieces of wood and dung. For the 1987 and 1988 samples, material was returned to labeled paper bags and dried in a 40°C drying box. When dried to uniform weight, mass was recorded to the nearest 0.01 g. Subsequently, for these samples, herbaceous mulch was separated from fine organic duff, dung, and woody material, redried and weighed to the nearest 0.01 g. For samples collected in 1989-1991, dung and woody material were rejected in the field or separated and discarded during cleaning, and only herbaceous mulch was dried and weighed. Only measurements of mulch are presented here. Samples of total organic material collected in 1987 and 1988 were presented and compared by Williams and Tordoff (19883). Samples were statistically tested for homogeneity of group variance and normality; intersample comparisons were by two-tailed, independent-samples t-tests.

Protein Content of Herbaceous Plants

The 200 herbaceous plant samples collected in 1988 for measurements of primary productivity were analyzed for nitrogen content by the Wildlife Habitat Lab, Washington State University, using the macro Kjeldahl method. Samples were dried immediately after clipping and stored for about 1 year before measuring nitrogen. Nitrogen was reported as percent crude protein (N = C.P./6.25). One sample from interspaces on the Reserve was misplaced prior to measurement so paired comparisons used 49 paired samples for that subset. Statistical comparisons were made using independent-samples two-tailed t-tests (Reserve-pasture) or two-tailed paired t-tests (precinct-interspace).

Soil Moisture

Soil samples were collected with a tube-sampler soil probe in February 1989. Sample cores were 6 cm long by 2.06 cm diameter. Randomly-chosen samples were taken at 30 sites each on and off precincts in both grazed and nongrazed areas. Samples were taken within about 20 - 50 meters on level ground on opposite sides of the fence between Reserve and grazed pasture to rule out differences in soil texture, slope, or exposure as much as possible. Samples were placed in plastic bags and weighed immediately after collection, then transferred to paper bags and oven-dried at 100°C for a minimum of 48 h, and reweighed. Statistical comparisons were made by independent-samples two-tailed t-tests.

Soil Erosion

No structures were established to measure soil erosion when the project was initiated in 1987, but severe water and wind erosion were observed in 1990 and 1991. In April 1991, it was noted that for many individual blue grass *(P. scabrella)* clumps, the crowns were on pedestals that projected several mm above the ground surface. Although this form had been noted previously, it seemed more pronounced at that time. To test if differences in pedestal height reflected different amounts of soil erosion, crown diameter and upslope pedestal height were measured for 20 grass clones each in pasture and on the Reserve. For each clone, crown diameter and pedestal height were measured to the nearest mm for 3 crowns of different diameters; size groups were < 40, 41-69, and > 70 mm diameter. We tested the association between diameter and pedestal height with least squares regression; and regression slopes were compared between pasture and Reserve samples by ANOVA. Differences in the pedestal heights of the largest and smallest crown measured for individual clones were computed, and the samples from the pasture and Reserve were compared statistically using the two-tailed independent samples t-test.

Seed Caches

Seed caches of giant kangaroo rats consist of a honeycomb-like arrangement of small pits dug in the surface of the soil, filled with individual seeds, pods, and seed heads, and covered with loose soil (pit caches). The surface of the area containing pit caches also had additional seeds, pods, and seed heads spread on most in 1988. Surface caches varied from a thin layer a few mm deep to a definite pile several centimeters high (haystacks). No such caches were seen in 1987, 1990, and 1991, probably because of drought and low (1987) or no (1990) seed production, or for other reasons (1991). In 1989, a few surface piles, consisting of a thin and discontinuous layer a few mm at the deepest, were seen, but were not measured. Only in 1988 were haystacks numerous and large enough to measure. On l-5 May 1988, seed caches made by giant kangaroo rats were measured on experimental (#l) and control plots (#2) and on 10-m wide by 1,207 m long transects along the western boundary of the Elkhorn Plain Ecological Reserve, both inside and outside the Reserve (transects were 60-m apart, 30-m each side of the fence). We did not disturb surface material to determine if stacks were always placed over clusters of pit caches, but it seemed to be the case for most of the stacks we watched grow between late March and May. On 28-29 April 1989 we counted numbers of clusters of pit caches and haystacks on the portions of plots 1 and 2 surveyed in 1988, on 10 x 1207-m transects each side of the western boundary of the Reserve, and on 10 by 1609-m transects each side of the eastern boundary of the Reserve. Because only a few caches had a thin layer of seed heads on the surface, we did not attempt to quantify area or volume of haystacks.

In 1988, the area of each haystack or cluster of pits was measured in two dimensions at right angles. Length and width were subjectively measured at an “average” position and recorded to the nearest cm. Height of surface caches were recorded to the nearest cm, being averaged from measurements of heights at different levels of the stacks. All separate seed caches were measured and recorded. For most precincts there was a single seed cache, but a few consisted of two to four smaller, separate piles of seeds in close association (i.e., within a meter of each other). The measures of area and volume of surface material for these separate but related caches were combined and treated as a single cache for statistical summary and comparison. Independent-samples, two-tailed t-tests were used for intersample statistical comparisons. Counts of caches in 1989 were summed for the pasture and Reserve and tested by the goodness-of-fit test.

Blunt-nosed Leopard Lizards

Population Ecology

Population sizes of blunt-nosed leopard lizards were estimated from 1988 through 1991. Census methods used were modified during the 4 years. Two 8.1 ha (20 acre) plots were established during April 1988 to census lizards (Table 1). Plot A was located within the fenced Reserve (not grazed) and plot B (pasture plot) was established approximately 2.4 km (1.5 mi) northwest of the Reserve (Figure 1). Each plot was 277 m (907.5 ft) by 293 m (960 R), with 16 census lines spaced 18.3 m (60 ft) apart following standard design of plots used to census this species (Tollestrup 1976). Each census line was 277 m long and was oriented in a N-S direction. The pasture plot was established in an area such that approximately the same amount of shrubs, wash, roads, soil types, etc. were contained within its boundaries as that found on the plot on the Reserve.

Each plot was walked during the morning or early afternoon during temperatures when lizards are most active (24-35°C air taken 13 mm above soil surface; 30-41°C soil taken 13 mm below soil surface; Tollestrup 1976). We tried to sample each plot simultaneously during a census period with two researchers alternating plots censused each day. However, during the course of the 4 years, plots were sometimes censused by one person, who either alternated plots each day or censused both plots each day when the temperature regime permitted.

Weather affected when plots were censused. We attempted to census each population during the entire period that blunt-nosed leopard lizards were active. We found that blunt-nosed leopard lizards may become active by late March or early April, but intermittent cool weather in the spring often limited their activity so that continuous daily activity did not occur until late May or early June. We initially planned to census adult lizards on each plot 10 days in the spring and 10 days in June, with another census of hatchlings in August. We increased the number of censuses during the 4 years so that more data could be gathered. The number and duration of censuses each year were subject to the activity of lizards (i.e., if no lizards were found in the first 3-5 days of censusing, we discontinued the census for that month).

Table 2. *Total number of days of censusing for blunt-nosed leopard lizards by month and year on the Elkhorn Plain, San Luis Obispo Co., California.*

Year	April-May	June	July	August	September	October
1988	—	10	—	3	—	—
1989	7	10	4	7	4	—
1990	8[a] - 7[b]	11[a] - 10[b]	3	5	2	—
1991	6	10	6[a] - 3[b]	13	11	6[a] - 5[b]

[a] Reserve; [b] pasture

In 1988, cool weather in the spring prevented censusing during May when researchers were at the Reserve (Table 2). The number of days censusing lizards in August and September 1990 was decreased because of the lack of lizard activity. In 1991, six censuses took place.

We did not have permission from management agencies to handle blunt-nosed leopard lizards until June 1989. Therefore, during the censuses in 1988 and the spring of 1989, we only counted the number of lizards found each day. For each lizard seen, its location was plotted on a map of the plot and its sex was determined by coloration and morphology.

Starting in June 1989, we used a pole and noose to capture lizards. Once a lizard was captured, we noted its location, determined its sex, and applied a numeral to its dorsal surface with a felt-tipped pen. Captured lizards were placed in cloth bags and held until after the daily census. Then, we took body measurements, including snout-vent length (SVL), total length (TL) in mm, and weight to the nearest g. During 1989 and 1990, we noted whether a female was gravid. During 1991, we also palpated each female to determine the number of eggs she was carrying. Starting in August 1989, we injected a Passive Integrated Transponder (PIT) tag subdermally into each blunt-nosed leopard lizard to mark permanently individuals. After lizards were processed, they were returned to their points of capture and released.

Also in June 1989, we set up an array of pitfall traps on the Reserve to increase captures of blunt-nosed leopard lizards. The array was put in north of the census grid, and consisted of 50 5-gallon buckets placed in pairs and connected by a 2-m length of sheet metal 0.66 m tall. Traps were arranged in a circular plot containing radiating lines of pairs of traps, each pair spaced 50 m apart starting from a central hub. The traps were opened for 2 days in June, 6 days in July, and 8 days in August in 1989, and for 5 days in May and 5 days in June 1990. Few blunt-nosed leopard lizards were captured in the array and its use ended in 1991.

Prey Abundance

The diet of blunt-nosed leopard lizards includes arthropods and small lizards (Montanucci 1965, Tollestrup 1979, Kato et al. 1987). We counted grasshoppers and side-blotched lizards during censuses for blunt-nosed leopard lizards in 1990 and 1991. These values were used as an estimate of food abundance on each plot.

Statistical Analyses

The size of the blunt-nosed leopard lizard population on each plot was determined for 1989, 1990, and 1991; years in which we were able to capture and mark lizards. We used two models to estimate population sizes. We made one estimate using a Monte Carlo simulation method (Minta and Mange1 1989) that estimates the population of unmarked lizards. This method is especially useful for capture-resight data of the kind gathered during lizard censuses. The simulation uses the number of marked and unmarked lizards found during censuses. We followed the recommendations of the authors of this model and ran the simulation 10,000 times. We also followed their recommendations for calculating the lower and upper stopping levels for the simulation. The total population estimate for this method is the sum of the estimate of unknown lizards from the simulation and the number of animals marked:

$$\mathrm{PE} = N_u + N_m$$

where N_U is the number of unknown animals derived from the simulation and N_m is the number marked.

We also made population estimates using the Peterson estimate with Bailey’s modification (Caughley 1977). We estimated populations using data on marked and unmarked lizards found on the last day of sampling. Peterson estimates were calculated so that comparisons could be made to past work on blunt-nosed leopard lizards, although we believe that the population estimates from the Monte Carlo simulations may be more accurate.

Densities of lizards were calculated using the population estimates and the area sampled. We estimate that adult blunt-nosed leopard lizards were not seen or flushed farther than 5 m, on average, on each side of census lines in 1989 and 1991. Using IO m, therefore, as the effective width of each census line, and including the area traversed between lines, 4.89 ha (12.07 acres) were censused on each plot. We estimate that we did not see or flush hatchling blunt-nosed leopard lizards greater than 2 m from each census line in 1989 and 1991. Most hatchlings were found directly on the path that had been worn through the ground cover. Using 4 m as the effective strip width for each line and the area traversed between lines, 1.96 ha (4.83 acres) were censused on plots in 1989 and 1991.

Because little herbaceous vegetation grew in 1990 and mulch levels were low, we were able to see lizards more than halfway between census lines; thus, the entire area of plots was censused in 1990. Each plot encompasses 8.1 ha, but lizards found while walking between lines and outside the plot on the end census lines were included. Therefore the total area censused in 1990 was 8.59 ha (21.21 acres).

We computed population estimates and densities for various months in 1989-1991 depending on when censuses were conducted and the number of lizards found. No population estimates were made for July in any year because most adults were not active and hatchlings did not emerge until August. We also did not estimate population sizes for June 1990 because few lizards were still active. Population and density estimates for August were made only for hatchlings.

We compared snout-vent lengths (SVL) between plots and sexes using the nonparametric Wilcoxon two-sample test. In 1991, numbers of eggs per female were compared between plots. Indices of food abundance in 1990 and 1991 were compared between plots using the Wilcoxon's two-sample test.

Small Mammals

Population Ecology

Population sizes and densities were estimated for small mammals based on capture/recapture data from livetrapping on experimental (#1) and control plots (#2). Trapping was simultaneous on plots established in 1987. In 1987 and 1988, plots were 10 x 10 grids with 10-m spacing between trap stations (1.0 ha). These plots were increased to 12 x 12 grids (1.44 ha) for trapping in 1989 and subsequent years. Initially, plots were trapped for longer periods and at other times of the year (Williams and Tordoff 1988a, 1988b) but starting in 1989, plots 1 and 2 were trapped only for 6-night periods in April and August. For statistical comparisons by year, we only used census sessions in late March-early April (spring or April census in discussions) and August.

Trap stations were prebaited for a 2-3 day period prior to trapping. Traps were baited with a mixture of seeds, mainly millet with about 25% oat groats, and provided with a tightly-waded paper towel for nesting material. In 1987 and 1988, traps were left open 24 h and checked two or three times between sunset and sunrise, and hourly during the day. Antelope squirrels were trapped during daytime. During subsequent sessions, traps were closed after removing animals, starting about 2 h after dark, and not reopened until near sunset the following night. Opposite ends of the grids were checked first on successive nights so that all traps were open for about the same amount of time over a census period.

In 1987, kangaroo rats were marked by tattooing a one or two-letter code on the inner surface of the left or right ear pinna. Antelope squirrels were tattooed on the postero-ventral surface of the thigh. Starting in 1988, we attached size-l, numbered, monel tags to the outer edge of cheek pouches of kangaroo rats and the ear pinnae of antelope squirrels. After the March-April census period, we attached tags only on the ear pinnae of kangaroo rats, but tags were placed on the cheek pouches of McKittrick pocket mice *(Perognathus inornatus neglectus),* whose ears were too small to hold a tag. Starting in June 1989, all subsequently marked animals were tagged with one identically-numbered ear tag in each pinnae and by subdermal injection of a PIT tag. PIT tags were injected dorsally between the middle and posterior region of the back, with the needle extending anteriorly. Antelope squirrels and San Joaquin pocket mice were not permanently marked in 1989-1991, though pocket mice were marked temporarily with a felt-tipped pen.

Between July 1987 and May 1989, each time an animal was captured, it was weighed and its age class (young, adult), reproductive condition, and capture site were recorded. Conditions recorded for females were estrus, pregnant, lactating, not reproducing; for males, we noted whether testes were swollen but of less than maximum size, scrotal and of maximum size, or not evident. Subsequently, with the use of PIT tags, marked animals were identified while still in the bag and were handled and examined only on their first capture during a session.

Data from 6- to 12-day population censuses on experimental and control plots were used to estimate population sizes and densities. Animals known to die during census periods were excluded from the data set unless their death occurred on the last day of the session. Estimates were derived from capture-recapture, closed-population models (Otis et al. 1978). Capture data for each session by species and plot were analyzed to determine the type of capture heterogeneity, capture probabilities, and the appropriate population estimation model, using the computer program Capture (White et al. 1982). Once the appropriate model was determined, population estimates were computed and densities were estimated using the nested subgrid method. For nested subgrid calculations, each plot with a 12 x 12 array of traps was partitioned into six subgrids (four subgrids for 10 x 10 arrays). Differences in estimates on experimental and control plots were compared using the two-tailed z-test (White et al. 1982).

Another plot (#4) for small mammals was established in June 1989 in western Fresno County, near the junction of Panoche and Silver creeks. This plot measured 120 by 120 m (1.44 hectare) with 144 grid points at 10-m spacing. It was trapped for 3 nights in June and 5 nights in September 1989.

Comparisons of numbers of individuals captured by species, year, and grid and overall captures by grid were compared using log-ratio goodness-of-fit tests. The goodness-of-tit values closely approximate the Chi-square distribution (x^2) and were used to determine significance (Sokal and Rohlf 1969).

Reproduction and survivorship were monitored on plots 1 and 2 by bimonthly or monthly trapping between July 1987 and April 1989 (Williams and Tordoff 1988a, 1988b). In November 1988 plot 3 (Table 1) was established on the Reserve for this purpose, and we trapped there for 2-3 nights each month or more frequently through August 1991. Most months, we only trapped on precincts on a 40 by 60-m subgrid. This portion of plot 3 was staked at 2.5-m intervals to provide better resolution for estimating movements and home ranges of captured animals. Reproduction also was monitored on plot (#7) established on the Washburn Ranch, Carrizo Plain, in January 1990. Traps were placed irregularly at active precincts for a 2-3 night period each month between January 1990 and August 1991. Density of active precincts in the area on and around plot 7 was estimated by counts on 15 transects measuring 15 by 100 m.

Translocating Giant Kangaroo Rats

In July 1989, 60 giant kangaroo rats (30 females, 30 males) were translocated from sites on the Elkhorn and Carrizo plains to two sites on the Carrizo Plain (plots 5 and 6, Table 1, Fig. 1). The animals were taken from a total of 18, l-mi^2 sections to ensure genetic diversity among translocated individuals and avoid depleting populations at any site. No more than three individuals from any section were translocated to a single site.

Animals were moved to artificial burrows previously constructed. Burrows consisted of two 1.22-m (4-foot) cardboard tubes 7.6 cm (3 inches) in diameter, sloping from opposite directions on the surface to a central nest chamber 30-46 cm (12-18) inches underground. The nest chamber was hollowed out of one wall of the trench dug to hold the tubes, walled off with pieces of corrugated cardboard, and provisioned with 2.3 kg of seeds (75% proso white millet 25% oats groats). Four to six paper towels were added for nesting material.

At the Soda Lake site (plot 6, Table l), burrows were established on adjacent raised mounds in an uncultivated, but regularly grazed pasture. The mounds showed the characteristic height and spacing of those on which precincts of giant kangaroo rats are located, although there have been no giant kangaroo rats at this site since prior to 1979 (Williams in press). During excavation of one burrow system, bones of a giant kangaroo rat were found, proving that this site was occupied sometime in the past.

The Painted Rock site (plot 5, Table 1) was a fallow field that had been under dryland grain cultivation since prior to the 1930's, based on aerial photos from that period. It probably has been fallow for the past 2 or 3 years, judging from the plant cover, which consisted of scattered wheat and weedy annual plants. The site was grazed by sheep in the past. Here no evidence of prior occupancy by giant kangaroo rats was found, although soil texture and slope are within the ranges occupied elsewhere on the Carrizo Plain by giant kangaroo rats. A tiny colony of giant kangaroo rats was extant in a small patch of uncultivated ground about 1 mile NW of the relocation site in the SE 1/4 Sec. 6, T32S, R20E, 2,040 ft. The relocation site is only about 1,300 m (0.8 mi) from Painted Rock, the type locality of the giant kangaroo rat. Slope, exposure, and soil texture do not differ materially from the area around Painted Rock.

Because cultivation over a long time had obliterated any microrelief associated with shrubs and animal burrows at the Painted Rock site, artificial burrows were arrayed in a circular pattern with 15-m spacing between burrow systems, both in concentric rings from a central burrow and between burrows within a ring. The outer ring of burrows was incomplete because only 30 animals were moved to each site. Spacing at 15 m was chosen to correspond to a moderately-high-density colony (Williams in press), but natural colonies do not exhibit uniform or regular spacing of precincts.

Giant kangaroo rats were released in small lots and monitored closely. Initially on 14 July, six animals were released at the Soda Lake site after being marked with ear and PIT tags. Animals were placed in adjacent artificial burrows on the morning of their capture. The tubes were blocked behind the animals with a wad of paper towels and small clods of dirt. They were watched closely through the afternoon.

We removed the plugs from the remainder of tubes not unplugged by the kangaroo rats at about 20:00 h. We used 450,000 and 750,000 candle-power spotlights to watch their behavior, once they emerged from tubes. After about 1 h, when we were satisfied that the animals were not fleeing and were returning to their tubes after exploring the area, we left. We moved seven more animals the next morning and inspected the burrows of the first group. Individuals in the second group were released and monitored for a few hours, but not throughout the day. In the evening, we unplugged those burrows that had not been unplugged by the newly released animals. They were observed for about 1 h. Two additional days were required to obtain an equal mix of sexes to complete the moving of 30 animals to the Soda Lake site, although some extra females were relocated to the Painted Rock site on days 3 and 4. The Soda Lake population was monitored daily in the morning and evening until translocating was completed, then daily until the Painted Rock colony was also complete. About 1 kg of additional seeds were placed on the surface of each burrow system on 7-8 August 1989.

The translocated colonies where checked and trapped monthly for 2-3 day periods starting on 7 August 1989, except for longer sessions in June 1989 (5 days) and July 1991 (6 days), and no trapping in March and June 1991. Because of lack of captures and decline of the colony, we did not trap the Painted Rock site after June 1990. During 1989, spotlights were used to locate and count animals. Sherman livetraps were set at each artificial burrow and at other sites showing evidence of use by kangaroo rats. Starting in March and ending in August 1990, Tomahawk brand wire mesh livetraps were used in place or in conjunction with Sherman traps because of our inability to recapture most founders When new burrow systems appeared, these were marked with pin flags or wooden stakes. Subsequently, established burrow systems outside the boundaries of the 12 by 12 grid were marked with numbered, wooden stakes.

Feeding Experiment - Giant Kangaroo Rats

Two experimental (supplemental feeding) and two control plots (no supplemental feeding) of 8 hectares (about 20 acres) were established at four sites on the Elkhorn and Carrizo plains (two in each region, each member of the two pairs being located about 1.6 km apart; Figure 1, Table 1). On experimental plots, a seed mix consisting of 75% millet and 25% oat groats was placed on or near giant kangaroo rat burrows. An initial application of 0.60 kg was made at every burrow system that was not clearly abandoned (i.e., no trace of entrances) on 23-24 February 1991. Seeds were placed at 231 precincts on the Carrizo plot and 243 on the Elkhorn plot. This was followed up by noting if seeds were picked up; a second application of 1.60 kg was made on 4 and 14 March at 133 and 120 active precincts on the Elkhorn and Carrizo plots, respectively. A third application of 2.2 kg was made at each of 50 active precincts on the Carrizo plot and 51 active precincts on the Elkhorn plot on 18-22 June 1991. Thus a total of 4.4 kg was applied at each precinct active between February and June, assuming the same precincts were active throughout the period. The Carrizo and Elkhorn plots received totals of 440 and 470.8 kg of seeds, respectively.

The strategy was to apply seeds over the period that would total one year's supply per animal. A year's supply was arbitrarily defined as one-tenth of the average adult body weight per day, or about 12 g x 365, equaling 4.4 kg. (9.7 lb). Twelve grams probably represents about the maximum amount that can be transported in the seed pouches of giant kangaroo rats (Morton et al. 1980 provided data on cheek pouch capacity and metabolism of *Dipodomys* spp., but had no data for giant kangaroo rats or caloric content of the seeds we used).

Numbers of giant kangaroo rats were determined at the second application on each 8-ha feeding plot by counting precincts where seeds had been picked up and burrow openings showing recent use. Other counts were made on 16 and 22 April, 19 and 23 June, and 7 and 8 August.

A 120 by 120-m plot (1.44 ha) with a 12 x 12 trap-station array spaced at 10-m was established in the center of each 8-ha plot. These trapping grids were prebaited for 2-3 days and trapped for a 6-day periods in April, June, and August. Animals captured were permanently marked with monel ear tags and PIT tags. Captives were examined for reproductive activity, aged, and weighed.

RESULTS

Lists of plants and vertebrates identified on the Elkhorn Plain Ecological Reserve are listed in the Appendix. Diversity of vertebrates was low, with no amphibians, four lizards, three snakes, 1 shrew, five rodents, three carnivores, 1 ungulate, and 23 species of birds seen on or over the Reserve. Possibly two or three other species of reptiles occur rarely in the area, and three other rodent species occur nearby on steep rocky slopes, but the area is remarkably nondiverse compared to most communities of desert vertebrates.

Community Interactions

Precipitation

The Carrizo Plain Natural Area has a desert climate, with less than 254 mm of precipitation annually, based on long-term records of the Carrizo Plain. The study site on the Elkhorn Plain receives less precipitation, on average, than the Carrizo Plain, based on the appearance of the plant community, although there are no long-term precipitation records for the Elkhorn Plain. Most rains come in the winter and spring, and May through September are hot and dry. Typically, rain falling from late May through September comes from tropical Pacific storms, and contributes little or nothing to productivity of the herbaceous community that year.

Drought prevailed during this study, with 3 of the 5 years having less than 70% of average precipitation. Between July 1986 and June 1991, annual precipitation averaged only 155 mm. Effects of drought were compounded in the 1986-87 and 1989-90 seasons by having from one-quarter to one-third of the rainfall outside the October-April period

Table 3. *Yearly precipitation in the study area, San Luis Obispo County, California, for the 1987-1991 seasons (July to June). Data from July 1987 to February 1990 are the means for precipitation at Traver and Washburn ranches on the Carrizo Plain; subsequent data are from the Elkhorn Plain Ecological Reserve. Percent of Normal is the percentage of the long-term annual mean (22.2 cm), based on data from the Traver and Washburn ranches, received during that precipitation year.*

Year	Annual Total July to June	% of Normal (Annual Mean)	Winter October to April	Winter % of Total
1986-1987	138.0	62.0%	90.9	66.5%
1987-1988	258.5	116.2%	257.6	99.7%
1988-1989	107.1	48.2%	100.6	94.0%
1989-1990	85.6	38.6%	63.2	73.8%
1990-1991	185.9	83.7%	160.6	86.3%

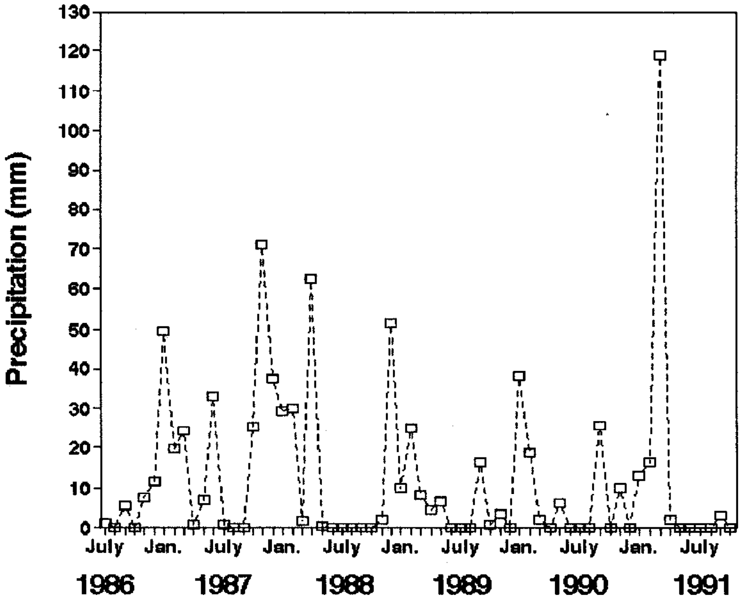

Figure 2. *Monthly precipitation on the Carrizo Plain, based on mean values for Simmler, Traver Ranch, and Washburn Ranch (through 1989-1990); and precipitation for 1990-91 at the Elkhorn Plain Ecological Reserve, San Luis Obispo County, California.*

when temperatures are favorable for germination and growth of annual plants (Table 3). The winter of 1987-88 was wetter than average, but was preceded by 1 and followed by 2 drought years (Figure 2). Only 38.6% of the annual mean fell in 1989-90, and of that, only 73.8% fell during the winter months. Precipitation increased in 1990-91, although 74% of the winter total fell in March, and most of that came during a storm between 17 and 19 March (Figure 3). This late precipitation turned what had been a poor year for plant growth into a year of high annual productivity and promoted the germination and establishment of plants, notably perennial saltbushes, that had not been seen in some areas for more than a decade.

Annual Plants

The effects of rainfall on herbaceous production during the 5-year study period are illustrated in Figure 4. Plant growth was sparse in 1987 and few plants produced seeds. Likewise, little growth or seed production occurred in 1989, and annuals that managed to germinate grew little beyond the cotyledon stage before dying of desiccation in 1990. In 1987 and 1989 there were no noticeable differences in productivity on and around precincts of giant kangaroo rats. Plant growth in 1990 also was sparse, and differences on and between precincts were not apparent. Thus, these values were used for both precincts and interspaces those years (Table 4).

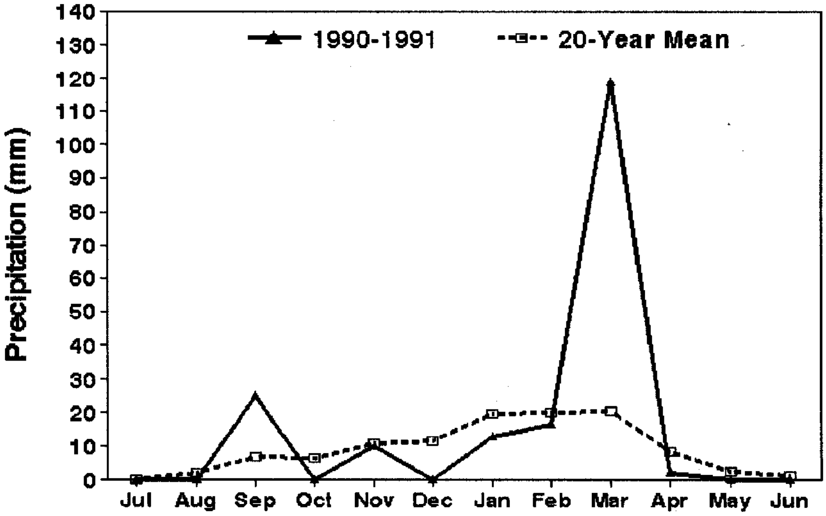

Figure 3. *Monthly mean precipitation on the southern Carrizo Plain and monthly rainfall for 1990-91 at the Elkhorn Plain Ecological Reserve, San Luis Obispo Co., California.*

Annual net above-ground primary productivity in nongrazed annual desert grassland, between 1987 and 1991, averaged about 9.5 g/0.25 m^2, or 380 kg/ha (341 lb/acre) in areas between giant kangaroo rat precincts. This compares with the 5-year average on giant kangaroo rat precincts of 19.4 g/0.25 m^2, or 777.6 kg/ha (697 lb/acre). Precincts occupied 43% of the surface area within the Elkhorn Plain colony (Williams in press); therefore, annual productivity for the Elkhorn Plain study area averaged about 551.4 kg/ha (494 lb/acre) for the period, or a gain of about 171 kg/ha (153 lb/acre) due to the presence of

Table 4. *Net above-ground primary productivity of herbaceous plants on the Elkhorn Plain, San Luis Obispo Co., California. Values are mean ± SD g/0.25 m^2 from plots (*n *= 50 each in 1988, 30 each in 1991, 15 in 1990) except for 1987 and 1989, which are estimates based on photographs. Samples were collected from precincts of giant kangaroo rats and the spaces around precincts (interspace). Pasture was grazed in the 1986-87, 1987-88 and 1988-89 seasons, but not 1989-90 and 1990-91.*

	Reserve		**Pasture**	
Year	**Precinct**	**Interspace**	**Precinct**	**Interspace**
1987	3.50	3.50	1.50	1.50
1988	32.63 ± 15.40 (13.65-93.03)	10.43 ± 6.78 (1.59-35.56)	13.00 ± 8.85 (2.23-38.31)	8.19 ± 4.34 (1.15-19.52)
1989	1.50	1.50	1.50	1.50
1990	0.32 ± 0.29 (0.07-1.10)	—	—	—
1991	59.24 ± 26.09 (16.40-143.72)	32.00 ± 14.35 (12.61-71.55)	56.78 ± 25.21 (22.89-125.43)	32.71 ± 14.35 (12.61-71.55)

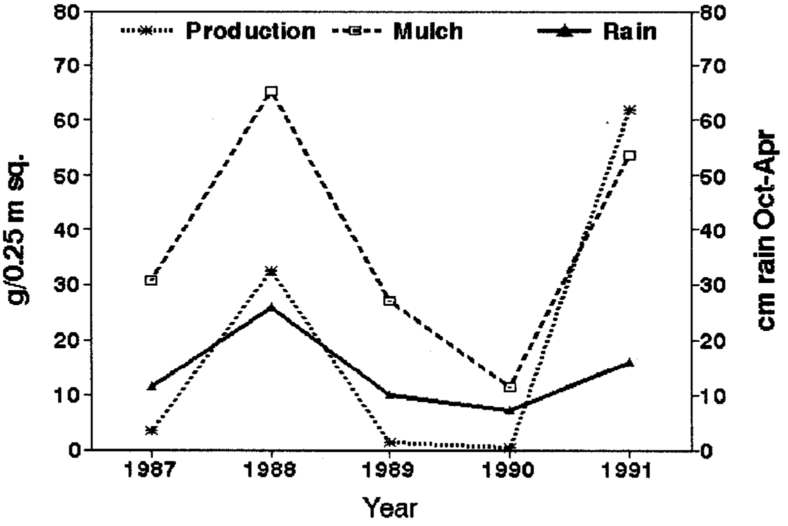

Figure 4. *Mean annual precipitation (cm) and its relationship to annual herbaceous productivity (net above-ground production) and mulch levels on the Elkhorn Plain, San Luis Obispo Co., California. Values of the latter two measures are in g/0.25 m^2. Productivity values are for giant kangaroo rat precincts on the nongrazed Reserve. Mulch values are also for the nongrazed Reserve.*

giant kangaroo rat precincts.

The effects of giant kangaroo rats on production of annual plants are demonstrated best by values in 1988 and 1991 for the Reserve (Figure 5). Precincts produced 3.13 times as much growth as intervening spaces in 1988 and 1.85 times more growth in 1991 (Table 4). Similar differences were found for plots in the pasture in 1991 (no cattle had grazed there since July 1989). Differences between precincts and interspaces on the Reserve were highly significant both years ($t = 9.737$, d.f. = 49, $P < 0.0001$ and $t = 5.772$, d.f. = 29, $P < 0.0001$ for 1988 and 1991, respectively). On the Reserve, except for a few centimeters around exit holes, there was little evidence of grazing by rodents before the vegetation dried. Values for plots in the pasture in 1988 represent material remaining after grazing by cattle. In 1988 cattle had consumed about 60% of the production on precincts, but only about 21% of the plants between precincts by 1 May (Table 4). Differences in plant biomass on precincts in the Reserve and pasture were highly significant in 1988 ($t = 7.814$, d.f. = 98, $P < 0.0001$), but not in 1991 when cattle were absent ($t = -0.725$, d.f. = 58, $P = 0.471$). In contrast, differences in biomass between precincts for the Reserve and grazed pasture were barely significant in 1988 ($t = 1.971$, d.f. = 98, $P = 0.052$) and not significant in 1991 ($t = 0.461$, d.f. = 58, $P = 0.647$). The lesser biomass in pasture showed some grazing effects in 1988. By 1 May 1988, cattle had almost denuded precincts, but only had grazed lightly on grasses in the intervening areas.

One of the 200 samples in 1988 was dominated by red brome; all others consisted mostly of Arabian grass, with smaller amounts of red-stem filaree, and, infrequently, still lesser quantities of *Vulpia microstachys*, *V. myuros*, *Hordeum leporinum*, or other species.

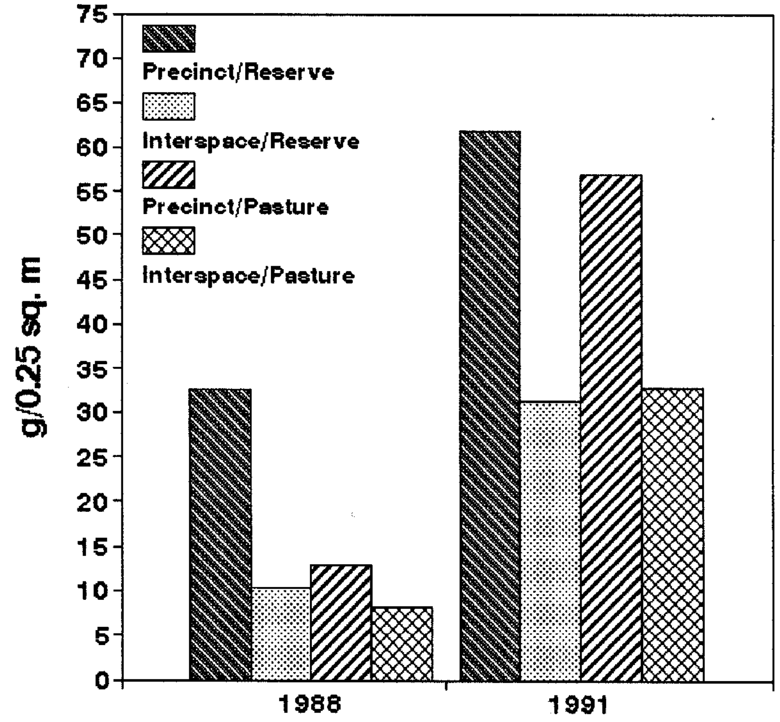

Figure 5. *Mean annual herbaceous productivity (net above-ground) on and between giant kangaroo rat precincts on the nongrazed Reserve and grazed pasture. Cattle were not present on the pasture plot in the 1990-91 growing season.*

For 1991, red-stem filaree dominated in a majority of samples (for the Reserve and pasture, respectively, 15 and 28 on precincts, and 12 and 24 on interspaces). *E. cicutarium and S. arabicus* were equally abundant in 5 samples each on precincts and interspaces on the Reserve. *S. arabicus* was dominant on the Reserve in 10 and 13 samples for precincts and interspaces, respectively, whereas in pasture it was dominant only on 2 precincts and 3 interspaces and was not codominant on any plot. In 1991, only a few samples included *Vulpia* spp. or *H. leporinum*, but *Eriogonum roseum* was a minor component of most samples and dominated only three samples from interspaces in pasture. Species diversity was lower in 1991 than 1988.

Shrubs

Measurements of area (m^2) for live shrubs on line transects and differences between years are given in Table 5. Shrubs increased in size both in grazed and nongrazed areas in 1988 compared to 1987, but the increases were not significantly different, measured on line transects. The impacts of drought in 1989 and 1990 are shown by shrub growth on the Reserve: area increased only 2.1% in 1989 and then decreased 10% in 1990 due to death of limbs or whole plants. The 13.1% loss of shrub area in pasture in 1989 reflects browsing by cattle between August 1988 and June 1989. In contrast, cattle browsed

Table 5. *Total shrub area (m^2) measured on 16, 50-m line transects (8 each on grazed and nongrazed plots), and changes (differences) from year to year and between the start and end of the study (1991-1987). Probability values are for changes in pasture compared to the nongrazed Reserve, using log-liklihood tests and the x^2 distribution.*

Place	Year	Area m^2	Differences				
			1988-1987	**1989-1988**	**1990-1989**	**1991-1990**	**1991-1987**
Difference: Reserve			10.47	1.16	-5.65	16.66	22.65
Reserve	1987	43.87					
	1988	54.34					
	1989	55.51					
	1990	49.86					
	1991	66.52					
Probability			0.59	0.02	0.07	0.81	0.42
Pasture	1987	46.80					
	1988	54.93					
	1989	47.72					
	1990	49.02					
	1991	64.34					
Difference: Pasture			8.13	-7.22	1.30	15.32	17.54

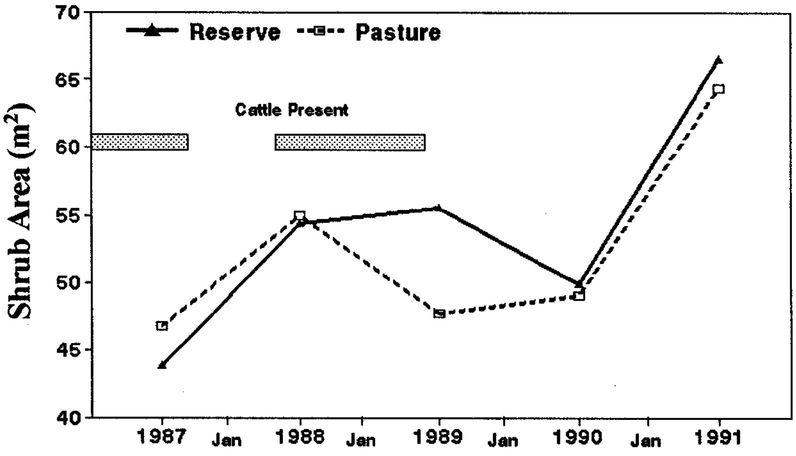

Figure 6. *Total shrub area (m^2) on 8 line transects each on the nongrazed Reserve and grazed pasture, Elkhorn Plain, San Luis Obispo Co., California. The shaded box indicates the period when cattle were on the pasture.*

Table 6. *Mass (g) of herbaceous plant mulch gathered on 0.25 m^2 plots on the Elkhorn Plain, San Luis Obispo Co., California. Mulch is all herbaceous material that did not pass through a 100 mesh (per inch) screen, and represents plant remains from several years. Cattle were present in pasture in the 1986-87, 1987-88, and 1988-89 growing seasons, but not subsequently. Cattle were present on the Reserve only in the 1986-87 growing season. Significant differences shown are for Reserve-Pasture comparisons within years.*

	Reserve		**Pasture**	
Year	***n***	**mean ± SD (range)**	***n***	**mean ± SD (range)**
1987	50	30.65 ± 13.15 (5.48-61.32)*	50	42.59 ± 28.20 (1.41-112-57)
1988	50	66.29 ± 36.04 (20.45-155.22)*	50	47.68 ± 36.32 (8.61-166.75)
1989	60	26.99 ± 12.69 (5.10-56.40)*	60	20.22 ± 9.82 (1.72-49.63)
1990	60	11.40 ± 8.55 (0.50-36.47)*	60	2.21 ± 4.77 (0.01-28.39)
1991	60	53.63 ± 34.02 (22.27-245.85)	60	48.95 ± 29.63 (7.65-160.42)

*$P < 0.05$

significantly less on shrubs between November 1987 and August 1988 (Figure 6). The increase in shrub area was only 6.5% less in pasture than the Reserve between 1987 and 1988, but 15.2% less in 1989. In 1987, cattle were not present between April and November. The most dramatic changes in shrub amounts occurred between the 1990 and 1991 seasons, when late spring rains in 1991 promoted a rapid growth in shrubs.

Herbaceous Mulch

Mulch collected in 1990 was mostly the remains of herbaceous growth in 1988, as there was little productivity in 1989 and almost none in 1990 (Table 6). Differences between Reserve and pasture samples were significant ($P < 0.01$) for 1987-1990, but not 1991 ($t = 0.797$, d.f. - 118, $P = 0.427$). Year-to-year differences in mulch biomass in Reserve and pasture samples all were highly significant ($P < 0.0001$) except for comparisons of pasture samples in 1987 and 1988 ($t = -0.783$, d.f. = 98, $P = 0.436$).

The effects of drought (Figure 4) and livestock grazing are reflected in changes in mulch biomass over the 5-year period of this study. On the Reserve, there was 2.3 times more mulch in the wet year, 1988, compared to 1987, a year of drought. The low point in mulch levels was reached in 1990 after successive drought years, when only 4.6% of the amount in pasture in 1988 was found. Most of this was from production in the 1987-88 growing season. Changes in mulch levels between 1987 and 1989 between Reserve and pasture show that cattle consumed all of the annual plant productivity in the 1987-88 and 1988-89 growing seasons, plus some of the residual mulch from previous seasons (Figure 7). By 1990, ground in the grazed pasture was essentially denuded, with a mean of 88.4 kg/ha (79.2 lb/acre) of mulch. In the absence of cattle, mulch levels increased dramatically

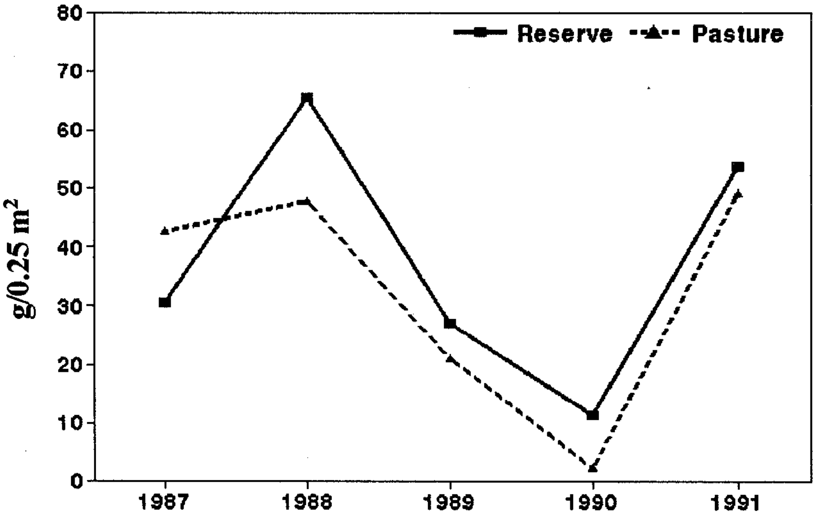

Figure 7. *Mean mass (g) of herbaceous mulch by year for grazed pasture (between 1987 and 1989) and nongrazed Reserve, Elkhorn Plain, San Luis Obispo Co., California. The Reserve also was grazed in the 1986-1987 growing season.*

in 1991 in both grazed and nongrazed areas. Mulch values in Table 6 can be converted from g/0.25m^2 to lb/acre by multiplying by 35.85.

Nitrogen Content of Herbaceous Plants

Nitrogen content of annual herbaceous plants, collected when seeds were ripe and the plants were drying, is reported as percent crude protein (N = crude protein/6.25) in Table 7. Differences in nitrogen content of plants from interspaces on the Reserve and in pasture

Table 7. *Crude protein content of samples of herbaceous plants collected on 0.25 m^2 plots on and around (interspaces) giant kangaroo rat precincts on grazed pasture and nongrazed Reserve, Elkhorn Plain, San Luis Obispo Co., California. Sample size was 50 each except for nongrazed interspaces (49). Significant differences shown are for Reserve-Pasture comparisons; values for precincts and interspaces also differed significantly for both Reserve and pasture, but differences for interspaces between Reserve and pasture did not differ significantly at the 5% probability level.*

	Precincts		Interspaces	
Treatment	**Mean ± SD**	**Range**	**Mean ± SD**	**Range**
Nongrazed (Reserve)	12.873 ± 2.107*	8.27-17.3	8.675 ± 1.246	6.6-11.86
Grazed (Pasture)	11.159 ± 1.956*	6.99-15.58	8.213 ± 1.245	6.132-11.32

* $P = < 0.05$

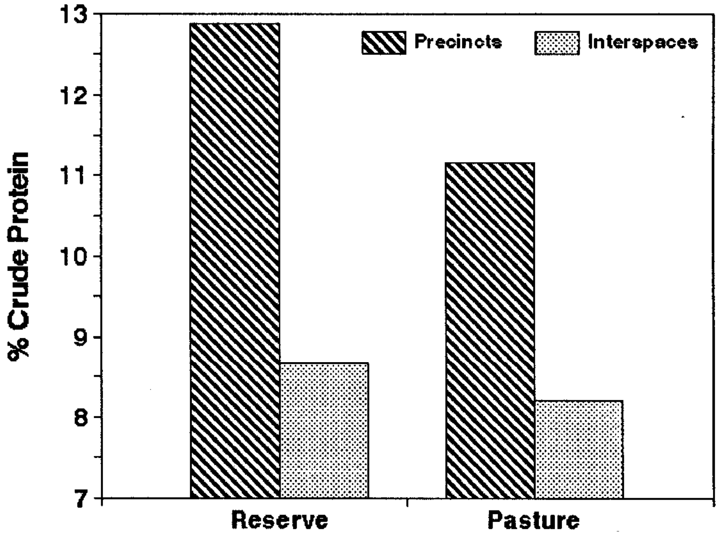

Figure 8. *Mean percent crude protein for herbaceous plants collected on and between giant kangaroo rat precincts on grazed pasture and nongrazed Reserve, Elkhorn Plain, San Luis Obispo Co., California. Samples were drawn from plants clipped on 0.25 m^2 plots when ripe but still green.*

were not significant (t = 0.1.845, d.f. = 97, P = 0.068). Significantly lower amounts (13.3% less) of nitrogen in precinct samples from pasture compared to the nongrazed Reserve (t = 4.216, d.f. = 98, P = 0.00013) show the impact of cattle on the plants on precincts by the beginning of April (Figure 8), since the two areas had different treatments only during the 1987-88 growing season. More nitrogen (48.4% more on the Reserve) in plants on precincts compared to those in the interspaces was highly significant for both treatments (t = 11.58, d.f. = 48, $P < 0.0001$, and t = 9.589, d.f. = 49, $P < 0.0001$, for Reserve and pasture samples, respectively).

Soil Moisture

More soil water was found in the areas around precincts than on precincts and in samples from pasture compared to the Reserve (Table 8). Although differences in these values seem slight, they represent substantial differences in the absolute amounts of water. Mass of soil water between precincts in pasture was 9.9% of dry soil mass; mass of soil water from precincts in pasture was 9.2% of dry soil mass (these values were not significant: t = 1.944, d.f. = 29, P = 0.062). On the Reserve, mass of soil water from interspaces and precincts, respectively, were 9.0% and 8.7% of dry soil mass, a significant difference (t = 2.186, d.f. = 29, P = 0.037). Comparisons of soil water between the Reserve and pasture for interspaces and precincts, respectively, were significant (t = 2.614, d.f. = 58, P = 0.011; t = 2.317, d.f. = 58, P = 0.024). Generally, differences in soil water in February 1989 were the mirror image of differences in plant productivity in 1988 (Tables 4 and 7).

Table 8. *Mean (± SD, with range in parentheses) dry weight as percentage of wet weight of soil samples collected in February 1989 on and between gaint kangaroo rat precincts in pasture and nongrazed Reserve, Elkhorn Plain, San Luis Obispo Co., California (*n *= 30 for each sample). Significance is indicated for comparison between precincts and interspaces.*

Reserve		**Pasture**	
Precinct	**Interspace**	**Precinct**	**Interspace**
0.913 ± 0.007* (0.899-0.931)	0.910 ± 0.008 (0.891-0.927)	0.908 ± 0.009 (0.893-0.933)	0.901 ± 0.016 (0.826-0.920)

* $P = < 0.05$

Erosion

Measurements (mm) of malpais blue grass crowns show that pedestal height above the soil surface averaged 2.2 times greater in grazed pasture than the nongrazed Reserve (Table 9), a highly significant difference ($t = -9.459$, d.f. = 118, $P < 0.0001$). Differences between pedestal height of the largest and smallest crowns measured for each clone are not significant between the pasture and Reserve ($t = -0.039$, d.f. 118, $P = 0.969$); yet, the regression slopes (model: height = constant + diameter) each are significant (Figure 9). Regression values for pasture are height = 4.141 + 0.065 diameter ($r^2 = 0.103$, $n = 60$, *F*-

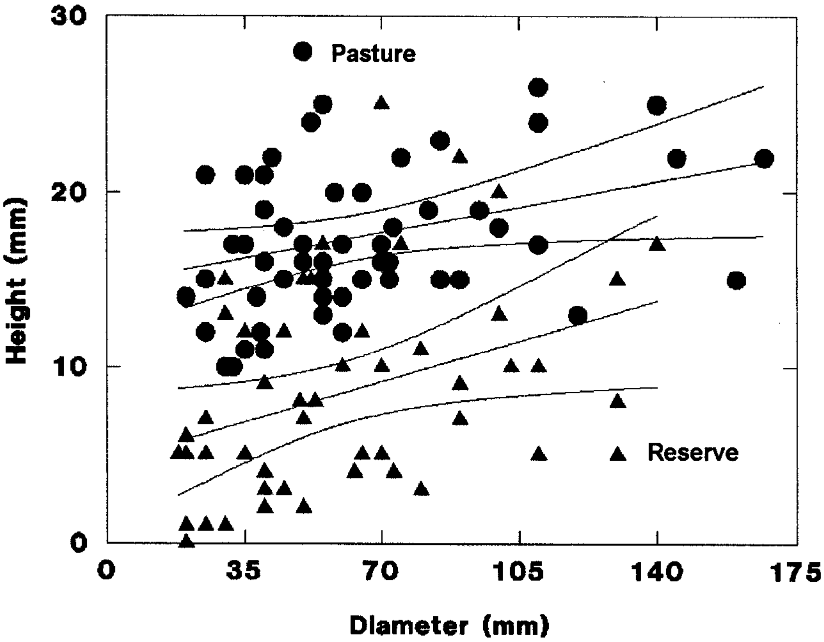

Figure 9. *Bivariate plots of relationship between diameter and height above ground level of malpais blue grass (*Poa scabrella*) crowns on the Elkhorn Plain, San Luis Obispo Co., California. Regression slopes and their 95% confidence intervals are shown for measurements of crowns in grazed pasture and the nongrazed Reserve, respectively.*

Table 9. *Statistical summaries of measurements (mm) of diameter and height above ground level of malpais blue grass (*Poa scabrella*) crowns on the Elkhorn Plain, San Luis Obispo Co., California. Difference is the difference in crown height between the largest and smallest crowns measured in individual clones (n = 60)*

Reserve			**Pasture**		
Diameter	**Height**	**Difference**	**Diameter**	**Height**	**Difference**
60.6 ±30.97 (18-140)	8.1 ± 6.29 (0-25)	2.9 ± 5.65 (-12-20)	66.9 ± 38.95 (20-210)	17.8 ± 4.85 (10-32)	2.8 ± 3.56 (-5-10)

ratio = 6.689, $P = 0.012$); values for the Reserve are height = 14.463 + 0.050 diameter ($r^2 = 0.161$, $n = 60$, F-ratio = 11.134, $P = 0.001$). The relationships between diameter and height of crowns differ significantly between pasture and nongrazed Reserve -- the ANOVA test for a place effect yields an F-ratio of 58.93 (d.f. = 1, $P < 0.0001$).

Seed Caches of Giant Kangaroo Rats

Numbers of seed caches in 1988 were remarkably similar on the four plots measured in 1988 (1.0 and 1.2 ha plots both on pasture and Reserve): 31 on plot 1 (Reserve), 32 on plot 2 (pasture), 33 for the 1.2 ha transect on the Reserve, and 30 for the transect in the grazed pasture. Measurements of surface area covered and volume of surface seed caches (haystacks) of giant kangaroo rats, measured in spring 1988, show significant differences

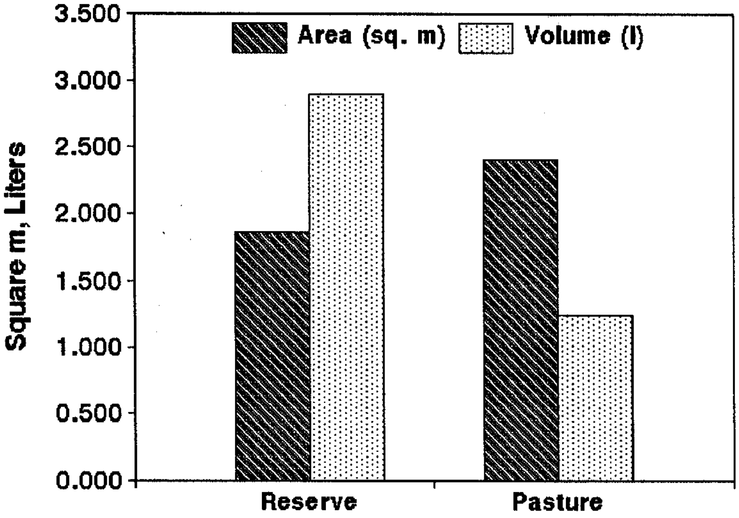

Figure 10. *Mean surface area and volume of surface seed caches (haystacks) of giant kangaroo rats in spring 1988 on the Elkhorn Plain, San Luis Obispo Co., California. Cattle were present in the pasture during caching and measurement of haystacks.*

Table 10. *Measurements of volume (cm^3) and surface area (cm^2) of surface seed caches (haystacks) of giant kangaroo rats in grazed pasture and nongrazed Reserve. Values represent pooled measurements from 1.0 and 1.2 ha plots each in pasture and Reserve. Significant differences shown are for Reserve-Pasture comparisons.*

Treatment	Area (cm^2)	Range	Volume (cm^3)	Range	*n*
Not Grazed	18,570.8 ± 10,773.9*	2,400-53,200	29,012.3 ± 39,171.8*	0-153,000	64
Grazed	23,953.1 ± 18,018.6	1,500-81,000	12,402.3 ± 18,047.7	0-72,000	62

* $P < 0.05$

in mean volume ($t = 3.085$, d.f. = 124, $P = 0.002$) and surface area ($t = 2.063$, d.f. = 124, $P = 0.041$; Table 10). Volume was greater on the Reserve, but surface area was greater in pasture (Figure 10).

The volume of haystacks on the Reserve averaged 57% greater than those in pasture. A few haystacks (not included in these measurements) were found that extended on each side of the fence separating grazed and nongrazed ground. The portions on the grazed side had only a sparse scattering of material on the soil surface, while those on the Reserve side were several cm high. Surface area covered by haystacks averaged 34% greater in pasture compared to the Reserve (Table 10).

In 1990, only 3.2% (14 of 437) of the caches had a layer of seed heads exposed on the surface. All others consisted of small clusters of pit caches. Counts for plot 1 (1 ha) and the 1.2 ha and 1.61-ha transects on the Reserve were, respectively, 49, 79, and 100. Counts in pasture for the same sequence of plot and transects were 57, 56, and 96. The *G*-test statistics for the Reserve and pasture totals (228 and 209, respectively) were: $G = 0.826$, d.f. = 1, $P = 0.726$. Estimated densities of caches for Reserve and pasture, respectively, were 59.8 and 54.9/ha.

Population Ecology of Blunt-Nosed Leopard Lizards

1988 Census

There was no cenus in April, and early May was cool and blunt-nosed leopard lizards were seldom active. When censuses resumed at the beginning of June, adult blunt-nosed leopard lizards were active aboveground (Figure 11). More sightings were made on the Reserve compared to the pasture plot. More than twice as many males than females were seen on the Reserve, but more females than males were observed on the pasture plot. By August, hatchling blunt-nosed leopard lizards had emerged, and one adult female was seen. Four times more hatchlings were seen on the Reserve compared to the pasture plot. No censuses were conducted in September, but one day was spent on the Reserve in early October. No blunt-nosed leopard lizards were found during this census, but several individuals were seen at other sites on the Elkhorn Plain.

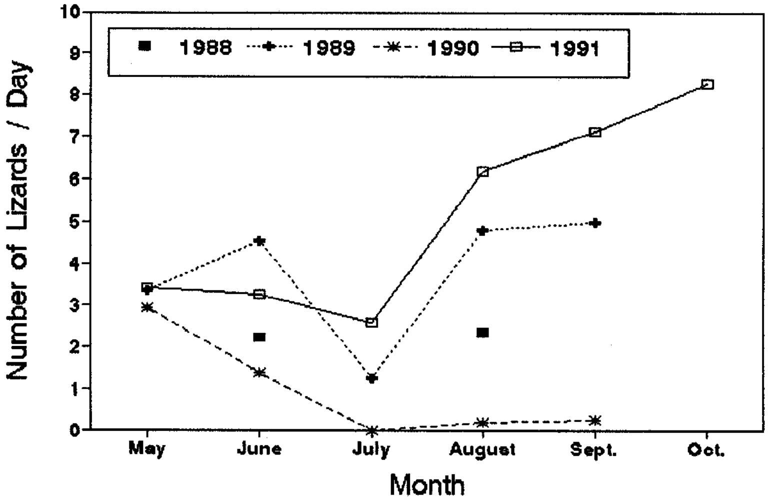

Figure 11. *Monthly level of activity of blunt-nosed leopard lizards on the Elkhorn Plain, San Luis Obispo Co., California, expressed as the mean number of lizards seen per day. Each value is the combined mean for both the Reserve plot and pasture plot except July and September 1989 when censuses were conducted only on the Reserve plot.*

1989 Censuses

Activity. Cold weather at the end of April shortened the spring census. Only adults and subadults were seen at this time (27 April - 3 May). Males and females already were in breeding colors although no females appeared gravid. We continued to find only subadult and adult lizards in June. Adults were in breeding colors, and eight of 21 (38%)

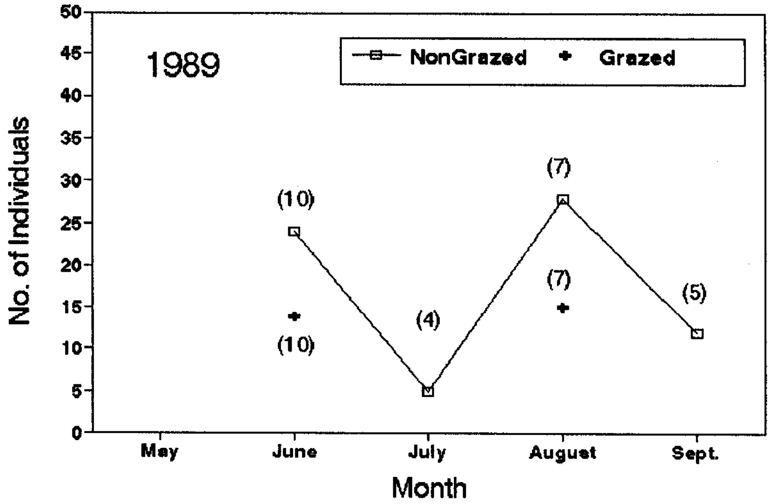

Figure 12. *Numbers of individual blunt-nosed leopard lizards found on the Reserve (nongrazed) and pasture (grazed) plots on the Elkhorn Plain, San Luis Obispo Co., California, during 1989. Number of census days are given in parentheses for each month.*

females were gravid. By early July, the activity of adults was greatly reduced (Figure 11). Breeding colors of adults were visible but faded. Neither of the two females that were caught were gravid. No young were found.

Hatchling blunt-nosed leopard lizards were abundant during the 7-day census in mid August. Three adults also were seen during the August census, although none were caught. Hatchling lizards continued to be active in early September (Figure 12).

Population Estimates. During the late spring census (April/May), more than twice as many lizards were seen on the Reserve as on the pasture plot, although mean numbers of sightings were not significantly different (Table 11). Sex ratios were not significantly different than one. In June, no significant differences were seen between sites in the mean number of lizards seen per day, total numbers marked, or sex ratios (Table 11).

Table 11. *Relative abundance and demographic data listed by census month during 1988 and 1989 for blunt-nosed leopard lizards on nongrazed (Reserve) and grazed (pasture) plots on the Elkhorn Plain, San Luis Obispo Co., California. Days are the number of days of census; Mean Seen is the mean number of lizards seen per day; No. Marked is the total number of lizards marked with PIT tags during the census; Prev. Marked is the total number of newly marked lizards during the census; Ad is the total number of adults and subadults; Yg is the total number of young hatched during the year.*

Census	Plot	Days	Mean Seen	No. Marked	Prev. Marked	Sex			Age	
						M	F	Ratio	Ad	Yg
				1988						
June	Reserve	10	2.6	—	—	15	6	2.50:1	21	0
	Pasture	10	1.9	—	—	6	9	0.67:1	15	0
August	Reserve	3	4.0	—	—				0	12
	Pasture	3	0.7	—	—				1	3
				1989						
April/May	Reserve	7	4.7	—	—	18	10	1.80:1	28	0
	Pasture	7	2.0	—	—	9	4	2.25:1	13	0
June	Reserve	10	7.0	24	0	12	12	1:1	24	0
	Pasture	10	2.1	14	0	5	9	0.56:1	14	0
July	Reserve	4	1.3	3	0	1	4	0.25:1	5	0
August	Reserve	7	7.0	27	0	14[a]	11[a]	1.27:1[a]	1	27
	Pasture	7	2.6	13	0	9[a]	4[a]	2.25:1[a]	2	13
Sept.[b]	Reserve	5	5.0	9	3	6	6	1:1	0	12

[a] Values are for hatchlings; [b] all values are for hatchlings.

Table 12. *Snout-vent lengths (mean ±* SD *in mm) of blunt-nosed leopard lizards captured on nongrazed (Reserve) and grazed (pasture) plots on the Elkhorn Plain, San Luis Obispo Co., California, in 1989, 1990, and 1991. Pooled samples of males and females are labeled "Combined." Significance between means was determined using the Wilcoxon two-sample test. Significant differences shown are for Reserve-Pasture comparisons.*

		Male		Female		Combined	
Census	**Plot**	**Mean**	**n**	**Mean**	**n**	**Mean**	**n**
				1989			
June	Reserve	112.5 ± 5.84*	11	101.8 ± 8.20*	12	107.0 ± 8.95	23
	Pasture	109.8 ± 7.73	5	97.7 ± 5.81	9	102.0 ± 8.77	14
July	Reserve	110.0	1	111.0 ± 4.24	2	110.7 ± 3.06	3
August	Reserve	54.9 ± 4.08	14	56.6 ± 3.02*	11	55.7 ± 3.75	25
	Pasture	55.8 ± 3.05	9	60.5 ± 2.29*	4	57.2 ± 3.58	13
September	Reserve	62.0 ± 6.19	6	63.0 ± 6.28	6	62.5 ± 6.46	12
				1990			
April/May	Reserve	88.9 ± 5.15	7	87.4 ± 5.26	8	88.1 ± 5.08	15
	Pasture	91.5 ± 1.29	4	85.3 ± 5.13	3	88.9 ± 4.53	7
June	Reserve	94.7 ± 2.08	3	87.5 ± 2.12	2	91.8 ± 4.32	5
	Pasture	92.5 ± 2.12	2	88.8 ± 5.62	4	90.0 ± 4.85	6
July	Reserve	—	0	—	0	—	0
	Pasture	—	0	—	0	—	0
August	Reserve	—	0	90.0	1	—	0
	Pasture	91.0	1	—	0	—	0
September	Reserve	—	0	—	0	—	0
	Pasture	—	0	96.0	1	—	0
				1991			
April/May	Reserve	110.0 ± 6.69	11	103.7 ± 5.24	6	107.8 ± 6.81	17
	Pasture	105.3 ± 3.40	4	101.4 ± 5.94	5	103.1 ± 5.11	9
June	Reserve	108.0 ± 5.68	8	104.4 ± 6.13	9	106.1 ± 6.02	17
	Pasture	102.8 ± 5.34	6	101.8 ± 4.71	6	102.3 ± 4.83	12
July	Reserve	112.0 ± 4.64	5	106.9 ± 6.96	7	109.0 ± 6.42	12
	Pasture	—	1	106.3 ± 4.19	4	107.0 ± 4.00	5
August[1]	Reserve	54.3 ± 3.90	28	53.9 ± 3.51	11	54.2 ± 3.75	39
	Pasture	54.5 ± 4.44	12	56.4 ± 3.57	9	55.3 ± 4.12	21
September[1]	Reserve	68.8 ± 7.42	19	68.4 ± 8.18	14	68.7 ± 8.12	33
	Pasture	65.3 ± 8.39	16	68.2 ± 7.28	9	66.4 ± 8.13	25
October[1]	Reserve	86.1 ± 7.30	20	82.8 ± 7.98	13	84.8 ± 7.74	33
	Pasture	81.3 ± 5.63	8	84.3 ± 8.37	12	83.1 ± 7.54	20

* $P < 0.05$; [1] hatchlings only

Table 13. *Estimated population sizes and densities of blunt-nosed leopard lizards by month for nongrazed (Reserve) and grazed (pasture) plots on the Elkhorn Plain, San Luis Obispo Co., California, in 1989, 1990, and 1991. For the Monte Carlo estimates, 95% likelihood intervals are given in parentheses. For the Peterson estimates, 95% confidence intervals are given in parentheses. Significant differences shown are for Reserve-Pasture comparisons.*

		Population Estimates		Density - Monte Carlo		Density -Peterson	
Census	**Plot**	**Monte Carlo**	**Peterson**	**Hectares**	**Acres**	**Hectares**	**Acres**
1989							
June	Reserve	40	32	8.2	3.3	6.5	2.7
		(33-53)	(21-43)	(6.7-10.8)	(2.7-4.4)	(4.3-8.8)	(1.7-3.6)
	Pasture	24	14	4.9	2.0	2.9	1.2
		(17-36)	—	(3.5-7.4)	(1.4-3.0)	—	—
August	Reserve	61	54	31.1	12.6	27.6	11.2
		(48-85)	(20-88)	(24.5-43.4)	(9.9-17.6)	(10.2-44.9)	(4.1-18.2)
	Pasture	28	28	14.3	5.8	14.3	5.8
		(17-52)	(7-49)	(8.7-26.5)	(3.5-10.8)	(3.6-25.0)	(1.4-10.1)
1990							
April/May	Reserve	20	14	2.3	0.9	1.6	0.7
		(17-26)	—	(2.0-3.0)	(0.8-1.2)	—	—
	Pasture	19	21	2.2	0.9	2.4	1.0
		(12-32)	(5-37)	(1.3-3.7)	(0.6-1.5)	(0.6-4.3)	(0.2-1.7)
1991							
April/May	Reserve	48	35	9.8	4.0	7.2	2.9
		(36-73)	(9-61)	(7.4-14.9)	(3.0-6.0)	(1.8-12.5)	(0.8-5.0)
	Pasture	32	24	6.5	2.7	4.9	3.6
		(15-80)	(-3-51)	(3.1-16.4)	(1.2-6.6)	(0-10.4)	(0-4.2)
June	Reserve	26	30	5.3	2.2	6.1	2.5
		(20-39)	(9-51)	(4.1-8.0)	(1.7-3.2)	(1.8-10.4)	(0.8-4.2)
	Pasture	28	17	5.7	2.3	3.5	1.4
		(16-55)	(6-27)	(3.3-11.2)	(1.3-4.6)	(1.2-5.5)	(0.5-2.2)
August	Reserve	50*	58*	25.5	10.4	29.6	12.0
		(43-57)	(29-86)	(21.9-29.1)	(8.9-11.8)	(14.8-43.9)	(6.0-17.8)
	Pasture	27*	20*	13.8	5.6	10.2	4.1
		(20-38)	(12-28)	(10.2-19.4)	(4.1-7.9)	(6.1-14.3)	(2.5-5.8)
September	Reserve	38	44	19.4	7.9	22.4	9.1
		(34-47)	(22-66)	(17.3-24.0)	(7.0-9.7)	(11.2-33.7)	(4.6-13.7)
	Pasture	31	34	15.8	6.4	17.3	7.0
		(27-39)	(20-48)	(13.8-19.9)	(5.6-8.1)	(10.2-24.5)	(4.1-9.9)
October	Reserve	46*	46	23.5	9.5	23.5	9.5
		(38-59)	(27-65)	(19.4-30.1)	(7.9-12.2)	(13.8-33.2)	(5.6-13.5)
	Pasture	24*	26	12.2	5.0	13.3	5.4
		(22-29)	(15-37)	(11.2-14.8)	(4.6-6.0)	(7.7-18.9)	(3.1-7.7)

*$P < 0.05$

More than twice as many hatchlings were marked in August on the Reserve as on the pasture plot (Figure 12), although numbers were not significantly different (Table 11). Sex ratios of young were not significantly different than one for either plot. Twelve hatchlings were caught on the Reserve during 5 days of censusing in early September. Of these 12, 3 had been tagged in August.

Males on the Reserve in June had a significantly larger mean SVL than females, but the difference between the sexes on the pasture plot was not significant (Table 12). There were no significant differences between plots for the same sex or when sexes were combined. In August, hatchling females on the pasture plot had a significantly larger mean SVL than females on the Reserve, but no significant differences existed between males, between sexes within a plot, or between plots when sexes were combined.

No significant differences were found in estimates of population size between plots in June or August, based on either the Monte Carlo or Peterson estimate (Table 13). Both methods estimated nearly twice as many adults and hatchlings on the Reserve plot compared to the pasture plot, and produced similar estimates, particularly for hatchlings, in August.

Mean density of adults in June ranged from 2.9/ha on the pasture plot based on the Peterson estimate to 8.2/ha on the Reserve, based on the Monte Carlo estimate (Table 13). In August, mean density of hatchlings ranged from 14.3/ha on the pasture plot based on either model, to 31.1/ha on the Reserve based on the Monte Carlo estimate.

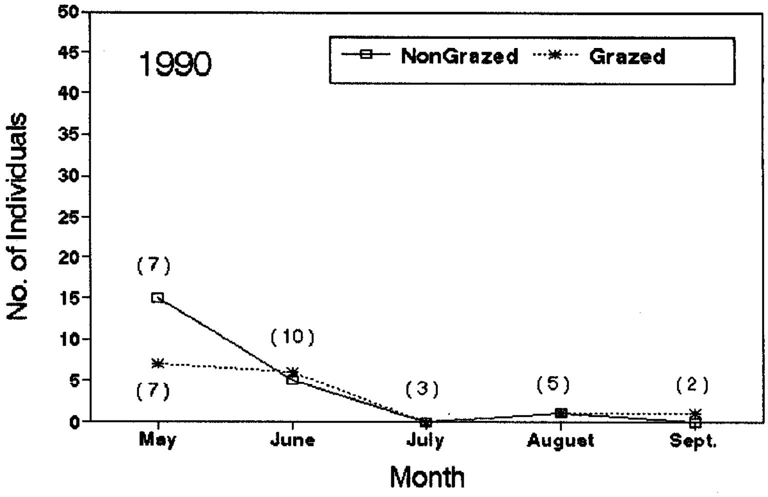

Figure 13. *Numbers of individual blunt-nosed leopard lizards found on the Reserve (non-grazed) and pasture (grazed) plots on the Elkhorn Plain, San Luis Obispo Co., California, during 1990. Number of census days are given in parentheses for each month.*

Table 14. *Relative abundance and demographic data listed by census month during 1990 and 1991 for blunt-nosed leopard lizards on nongrazed (Reserve) and grazed (pasture) plots on the Elkhorn Plain, San Luis Obispo Co., California. Days are the number of days of census; Mean Seen is the mean number of lizards seen per day; No. Marked is the total number of lizards marked with PIT tags during the census; Prev. Marked is the total number of lizards marked previously that were caught during the census; Ad is the total number of adults and subadults; Yg is the total number of young hatched during the year.*

Census	Plot	Days	Mean Seen	No. Marked	Prev. Marked	Sex			Age	
						M	F	Ratio	Ad	Yg
				1990						
April/May	Reserve	7	4.0	14	1	7	8	0.88:1	15	0
May	Pasture	7	2.0	5	2	4	3	1.33:1	7	0
June	Reserve	11	1.5	0	5	3	2	1.50:1	5	0
	Pasture	10	1.3	2	4	2	4	0.50:1	6	0
July	Reserve	3	0	0	0	0	0	—	0	0
	Pasture	3	0	0	0	0	0	—	0	0
August	Reserve	5	0.2	1	0	0	1	—	1	0
	Pasture	5	0.2	1	0	1	0	—	1	0
Sept.	Reserve	2	0	0	0	0	0	—	0	0
	Pasture	2	0.5	1	0	0	1	—	0	0
				1991						
April/May	Reserve	6	4.8	10	7	11	6	1.83:1	17	0
	Pasture	6	2.0	7	2	4	5	0.80:1	9	0
June	Reserve	10	4.1	10	7	8	9	0.89:1	17	0
	Pasture	10	2.4	8	4	6	6	1:1	12	0
July	Reserve	6	3.7	3	9	5	7	0.71:1	12	0
	Pasture	3	3.0	2	3	1	4	0.25:1	5	0
August	Reserve	13	7.4	40	6	28[a]	11[a]	2.55:1[a]	7	39
	Pasture	13	5.0	21	5	11[a]	9[a]	1.33:1[a]	6	20
Sept.	Reserve	11	7.6	16	19	19[a]	14[a]	1.36:1[a]	2	34
	Pasture	11	6.6	16	11	16[a]	9[a]	1.78:1[a]	2	24
October[b]	Reserve	6	10.2	11	22	20	13	1.54:1	0	33
	Pasture	5	6.4	6	14	8	12	0.67:1	0	20

[a] Values are for hatchlings; [b] all values are for hatchlings.

1990 Censuses

Activity. Censusing during April and May was difficult because of fluctuating temperatures from one day to the next. Brief periods of warm weather were punctuated by cool days throughout the spring resulting in only 7 days of censusing for this period (Table 14). Even though no sustained periods of warm weather occurred during April and May, the greatest level of lizard activity and the highest number of lizards caught occurred during the warm days at this time (Figures 11 and 13). However, no adults were seen during the spring census on either plot. All captures were of subadult lizards that hatched the preceding year.

By June, temperatures were increasing during the day, but lizard activity was decreasing (Figure 11). As in the spring, all lizards found on both plots in June were subadults, most of which were captured during the spring census (Table 14). No blunt-nosed leopard lizards were seen during the July census. During 5 days of censusing in August, only one subadult was found on each plot. One subadult lizard was seen in September. No hatchlings were seen in 1990. In general, activity of blunt-nosed leopard lizards in 1990 steadily decreased from a high in spring to almost no activity after June (Figures 11 and 13).

Population Estimates. Of the 15 individual lizards caught during April and May on the Reserve, 1 had been marked in August 1989 (Table 14) and 14 had not been PIT-tagged previously. On the pasture plot, two of seven lizards had been previously tagged. No lizards were greater than 100 mm SVL, with overall means of 88.1 mm SVL for the nongrazed plot and 88.9 mm SVL for the pasture plot (Table 12).

The five lizards that were active on the Reserve in June had been marked in May, while four of the six lizards caught on the pasture plot were marked in May. All were also subadults. Growth had occurred during the period between captures, and several males on both plots were developing salmon coloring typical of breeding individuals.

No significant differences in SVL were found between sexes or plots in April/May or June (Table 12). All means were near 90 mm SVL. Mean SVL increased slightly on both plots from April/May to June. In August, a female with a SVL of 90 mm was caught on the Reserve and a male with a SVL of 91 mm was caught on the pasture plot. In September, a female measuring 96 mm SVL was found on the pasture plot.

A population estimate only could be made for the spring census because of the low level of activity by leopard lizards through the season. The estimates for each plot, based on the Monte Carlo model, were almost identical (Table 13). Additionally, the Monte Carlo estimate for the Reserve was significantly smaller than the Monte Carlo estimate for the June 1989 and the April/May 1991 censuses on the same plot. Mean densities of lizards in spring 1990 were much lower than in 1989, ranging from 1.6/ha on the Reserve, based on the Peterson estimate, to 2.3/ha on the Reserve based on the Monte Carlo estimate (Table 13). The lower estimates of densities, compared to other years, are due mostly to the lack of aboveground activity by adults.

1991 Censuses

Activity. Weather during April was cool; no leopard lizards were found on either plot until the 29th, when temperatures finally warmed enough for blunt-nosed leopard lizards to be active. A series of dry but cool storms in May limited activity of lizards then. All lizards found in the spring were adults, hatched no later than 1989 (Table 14).

June temperatures in 1991 averaged lower than in June 1990, but days were warm and adult lizards were active throughout the month. Adults continued to be active in July; however, only a few adults remained active during the 3-day census at the end of the month (22-25 July). Also by the end of the month, females were predominately seen. Only one male was seen at the end of July, whereas eight females remained active. In general, activity of adults was highest in the spring and slowly decreased into July in 1991 (Figure 11). This pattern was mirrored by the actual number of lizards caught on the Reserve, but the greatest number of adults on the pasture plot were caught in June (Figure 14).

The first hatchlings were seen on 1 August while setting traps for rodents. The first captures of hatchlings were made the next day. Several adults, mostly females, remained active in August (Table 14). September and October were unusually warm, and length of activity of hatchlings increased in both months (Figure 11). However, actual number of hatchlings caught on both plots decreased each month (Figure 14). Hatchlings were last found on 24 October. Two censuses were conducted during sunny days after this date but no lizards were seen.

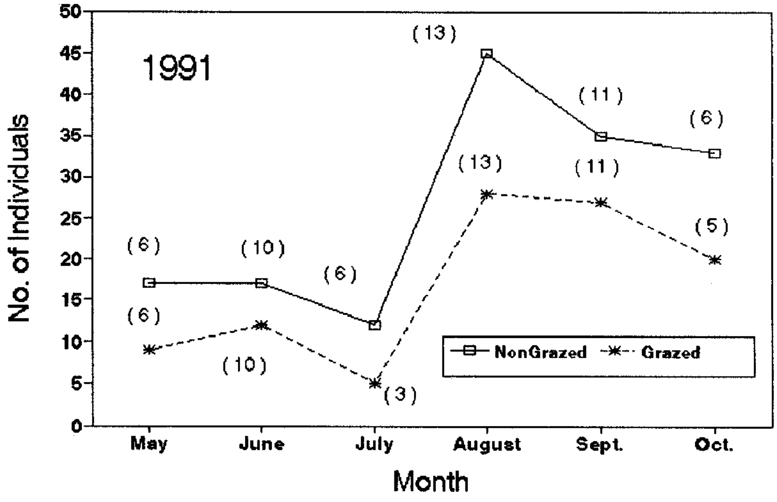

Figure 14. *Numbers of individual blunt-nosed leopard lizards found on the Reserve (non-grazed) and pasture (grazed) plots on the Elkhorn Plain, San Luis Obispo Co., California, during 1991. Number of census days are given in parentheses for each month.*

Population Estimates. Seven of the 17 lizards captured on the Reserve in the spring were previously marked, including 1 that was marked as an adult in July 1989. Two of the nine lizards captured on the pasture plot were already marked (Table 14). Except for the one marked adult, all other previously marked lizards on both plots were subadults in 1990.

In spring, more than twice as many lizards were seen each day on the Reserve compared to the pasture plot (Table 14). Males and females averaged larger on the Reserve than on the pasture plot in the April/May census (Table 12), but the differences were not significant. Lizards ranged in SVL from 96 to 121 mm on the Reserve, and from 93 to 110 mm on the pasture plot.

Ten of the 17 lizards caught on the Reserve in June had not been previously marked, as were 8 of 12 lizards caught on the pasture plot (Table 14). Nearly twice as many lizards were seen per day on the Reserve compared to the pasture. The mean SVL of male and female lizards on the Reserve in June averaged larger than the means for the pasture plot (Table 12), but they were not significantly different. On the Reserve, SVL ranged from 96 mm to 117 mm, whereas they ranged from 93 mm to 109 mm on the pasture plot.

In July, most captures were of previously marked adults (Table 14). The mean SVL of lizards were similar between plots, and ranged from 98 mm to 117 mm on the Reserve and 100 mm to 109 mm on the pasture plot (Table 12). In August, 39 and 20 hatchlings were caught on the Reserve and pasture plots, respectively. Seven adults also were caught on the Reserve; one was not previously marked. Six adults, one also not previously marked, were found on the pasture plot. Five of the seven adults found on the Reserve were females, and four of the six adults found on the pasture plot were females (Table 14).

The mean SVL of hatchlings was nearly identical between plots, between sexes within a plot, and for the same sex across plots for August, September, and October (Table 12). The mean SVL of each sex on each plot progressively increased from August to October (Table 12). In August, hatchlings ranged from 49 mm to 62 mm SVL on the Reserve and from 45 mm to 63 mm on the pasture plot. In September, they ranged from 53 mm to 81 mm SVL on the Reserve and from 50 mm to 80 mm on the pasture plot. By October, lizards hatched in August ranged from 64 to 99 mm SVL on the Reserve and from 68 mm to 96 mm on the pasture plot. Many young-of-the-year were greater than 80 mm by October, lengths characteristic of subadults.

Estimates of population size for adults were greater for the April/May census than for the June census for both plots; however, the 95% confidence intervals (likelihood interval for Monte Carlo estimates) were also larger in the spring census (Table 13). The population estimates were larger for the Reserve in the spring than those of the pasture plot, but the estimates are not significantly different. Monte Carlo estimates of adult population sizes in June were nearly identical between plots. The Peterson estimate for June was considerably larger for the Reserve than for the pasture plot, but the values overlapped. For adults, mean densities of lizards ranged from 5.3/ha to 9.8/ha using the Monte Carlo

Table 15. *Numbers of eggs found in blunt-nosed leopard lizards on the nongrazed (Reserve) and grazed (pasture) plots on the Elkhorn Plain, San Luis Obispo Co., California in 1991. Females identified by letters were not found on the plots but were within the Reserve or pasture.*

Reserve				Pasture			
ID No.	**Date**	**SVL (mm)**	**No. Eggs**	**ID No.**	**Date**	**SVL (mm)**	**No. Eggs**
2	17 June	100	3	6	10 June	102	1
7	9 June	96	0	11	21 June	101	4
	19 June	96	2	12	23 June	105	3
10	9 June	110	4	E	22 June	101	5
	19 June	110	0	F	22 June	106	5
11	19 June	117	4	3	9 July	98	2
14	21 June	101	3				
12	22 May	104	2				Mean = 3.33
	21 June	104	3				SE = 1.633
13	21 June	104	4				n = 6
16	23 June	102	2				
C	18 June	109	3				
D	20 June	119	5				Combined Samples
3	22 July	98	3				Mean = 3.29
			Mean = 3.27				SE = 1.160
			SE = 0.905				n = 17
			n = 11				

simulation method. Density estimates based on the Peterson method were slightly lower.

In August, there were significantly more hatchlings on the Reserve than on the pasture plot irrespective of the estimation method used (Table 13). No significant difference in population estimates between plots for September exists, but the estimate for the Reserve in October is significantly larger than the pasture plot, based on the Monte Carlo method. The population of hatchlings on the Reserve was estimated to be nearly twice as large as the one on the pasture plot in both months based on the Monte Carlo method, and was almost three times as large for the Reserve in August based on the Peterson method. The Monte Carlo estimate is similar to the Peterson estimate each month. Densities of hatchlings ranged from 10.2/ha for the pasture plot in August to 29.6/ha for the Reserve in August, both based on the Peterson estimate.

Reproduction. Eleven female blunt-nosed leopard lizards were found carrying eggs within the Reserve, nine on the plot. Six females were found with eggs off the Reserve, four on the pasture plot (Table 15). Means between plots were not significantly different. The earliest and latest dates when gravid females were found were 22 May and 22 July, respectively. Most females were gravid from mid to late June (Table 16). The number of eggs per clutch ranged from 1 to 5 (Table 15). The smallest female with eggs was 96 mm SVL. The number of eggs per clutch was not well correlated to SVL ($r^2 = 0.281$). One female on the Reserve (# 4) was found with a clutch of two eggs on 22 May and a clutch of three eggs 21 June (Table 15). The female on the pasture plot that had a clutch of two eggs on 9 July was not carrying eggs 29 April or 8 June.

Table 16. *Reproductive condition of female blunt-nosed leopard lizards captured on the Elkhorn Plain, San Luis Obispo Co., California in 1991.*

Dates	No. of Females Captured	No. of Gravid Females	% of Females Gravid
29 April-10 May	2	0	0%
16 - 25 May	11	1	9%
8 - 10 June	7	3	43%
17 - 23 June	13	11	85%
5 - 9 July	5	1	20%
22 - 25 July	8	1	13%
3 - 5 August	3	0	0%
14 - 23 August	7	0	0%

Prey Abundance

The abundance of grasshoppers and side-blotched lizards differed substantially between 1990 and 1991 (Figure 15). Abundance of grasshoppers was highest in the spring on both plots in 1990, and steadily decreased throughout the year (Table 17). In 1991, the abundance of grasshoppers generally increased throughout the year. Mean numbers of grasshoppers found on plots were only slightly greater in the spring 1991 compared to 1990, but reached 10-60 times greater abundance in later months. Significantly more grasshoppers were counted on the Reserve than on the pasture plot in spring 1990, in June 1991, and October 1991.

Table 17. *Indices of prey abundance (mean ± SD) of blunt-nosed leopard lizards on nongrazed (Reserve) and grazed (pasture) on the Elkhorn Plain, San Luis Obispo Co., California, in 1990 and 1991. Numbers listed are the mean counts of prey during a census. Sample size (n) is the number of days of censusing prey. Significant differences shown are for Reserve-Pasture comparisons .*

		Grasshoppers		**Side-blotched Lizards**	
Census	**Plot**	**Mean**	***n***	**Mean**	***n***
		1990			
April/May	Reserve	32.2 ± 7.19*	6	3.1 ± 2.1	7
	Pasture	15.7 ± 4.59*	6	2.3 ± 2.4	7
June	Reserve	16.4 ± 9.11	11	3.4 ± 2.5	11
	Pasture	10.1 ± 5.08	7	2.3 ± 2.1	10
July	Reserve	12.0 ± 6.24	3	2.7 ± 1.5	3
	Pasture	9.0 ± 1.0	3	3.7 ± 6.4	3
August	Reserve	10.3 ± 4.43	5	6.6 ± 4.4	5
	Pasture	7.80 ± 5.59	5	3.8 ± 2.3	5
		1991			
April/May	Reserve	52.0 ± 28.8	6	1.7 ± 0.8	6
	Pasture	39.5 ± 21.5	6	2.8 ± 2.1	6
June	Reserve	224.6 ± 51.7*	7	4.2 ± 2.6	9
	Pasture	104.6 ± 16.0*	9	3.1 ± 2.3	10
July	Reserve	159.3 ± 43.3	4	4.5 ± 3.1	4
	Pasture	134.7 ± 5.7	3	11.7 ± 7.4	3
August	Reserve	194.9 ± 30.7	10	13.7 ± 4.8	13
	Pasture	196.3 ± 22.2	10	15.0 ± 4.3	13
September	Pasture	488.0 ± 166.6	11	26.3 ± 9.1	11
	Reserve	361.3 ± 69.0	11	29.5 ± 13.4	11
October	Pasture	647.3 ± 123.5*	6	18.7 ± 7.8	6
	Reserve	336.6 ± 56.3 *	5	30.8 ± 10.6	5

* $P < 0.05$

A similar pattern between years was seen in counts of side-blotched lizards (Figure 15). Although not significant between plots in either year, counts were two to four times larger in 1991 than 1990 by August (Table 17). In both years, the increases in daily counts of side-blotched lizards in August were due to the appearance of young lizards.

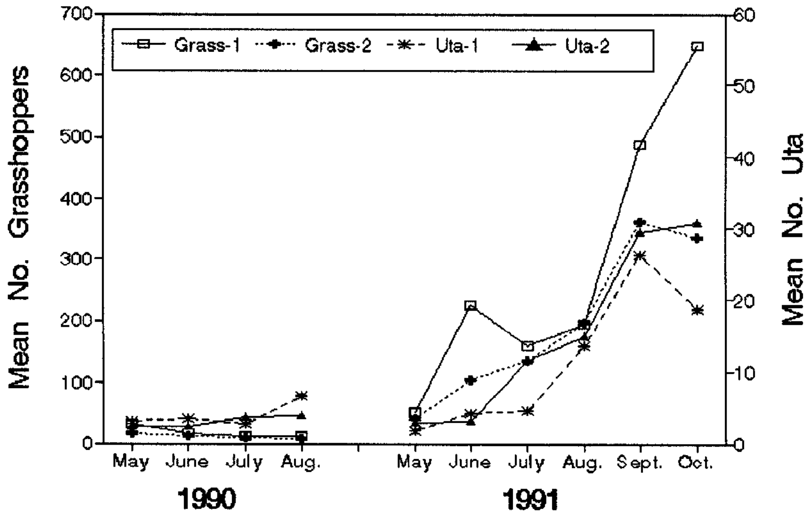

Figure 15. *Mean numbers of grasshoppers and side-blotched lizards (*Uta stansburiana*) counted per day each month in 1990 and 1991 during surveys for blunt-nosed leopard lizards on the Elkhorn Plain, San Luis Obispo Co., California. Means are shown for the Reserve plot (Grass-1, Uta-1) and the pasture plot (Grass-2, Uta-2).*

Population Ecology of Small Mammals

Diversity and Numbers

Total numbers of small mammals captured on plots 1 and 2, Elkhorn Plain, are listed in Table 18. We did not trap during the day for antelope squirrels after 1988, and those captured were released without being marked. These values represent extremely low diversity. For example, using the combined captures on both plots for 1988 (5 species,

Table 18. *Numbers of small mammals captured on grazed (# 2) and nongrazed (# 1) plots annually on the Elkhorn Plain, San Luis Obispo Co., California. Trapping effort was not equal between years, and there was no daytime trapping for antelope squirrels in 1989 through 1991. Those inadvertently captured are not included in these totals. Values reported by Williams and Tordoff (1988*a*) for 1988 differ because they did not include captures in the November session nor animals that died on first capture.*

	Plot 1 - Reserve					Plot 2 - Pasture				
Species	**1987**	**1988**	**1989**	**1990**	**1991**	**1987**	**1988**	**1989**	**1990**	**1991**
Ammospermophilus nelsoni	13	29	—	—	—	19	32	—	—	—
Dipodomys ingens	48	88	61	24	12	48	82	58	30	19
Dipodomys nitratoides	25	19	11	4	2	26	14	15	9	1
Perognathus inornatus	0	2	0	2	5	0	0	0	1	7
Onychomys torridus	0	0	0	0	0	1	1	0	0	0

267 individuals), the Simpson Diversity Index is 0.529, Simpson Dominance Index is 0.471, and the Shannon indices, using natural logarithms, are: Diversity (H') = 0.939, H_{max}' = 1.607, and Evenness (H'/H_{max}') = 0.585. Overall, numbers were highest in 1988, and declined to their low points in 1991. Kangaroo rats, mostly giants, provided the greatest percentage of the annual captures. Numbers of kangaroo rats captured annually did not differ significantly between grazed and nongrazed plots.

McKittrick pocket mice became more numerous as numbers of kangaroo rats declined during drought; about 70% of the pocket mice were captured in 1991 (12 of 17). Numbers of giant kangaroo rats increased in 1988 compared to 1987, but numbers of short-nosed kangaroo rats declined. At the low point in 1991, short-nosed kangaroo rats captured were 5.8% of the highest number taken in 1987 (3 and 51, respectively, Table 18).

Table 19. *Mean densities and numbers captured (*n*) of giant and short-nosed kangaroo rats captured on plots 1 (Reserve) and 2 (pasture), Elkhorn Plain, San Luis Obispo Co., California, between July 1987 and August 1991. Statistical significance (*) is indicated for comparisons between plots by census. Significant differences shown are for Reserve-Pasture comparisons .*

	Reserve		Pasture	
Census	***n***	**Density ± SD**	***n***	**Density ± SD**
		Dipodomys ingens		
7/1987	45	40.5 ± 1.1	40	30.3 ± 3.1
8/1987	31	31.9 ± 4.0	29	30.3 ± 0.1
4/1988	67	58.2 ± 5.7	79	57.1 ± 7.1
8/1988	61	56.9 ± 7.6	51	49.6 ± 7.6
4/1989	65	62.1 ± 5.6	59	56.0 ± 5.5
8/1989	47	50.7 ± 2.3	47	51.9 ± 1.1
4/1990	41	45.7 ± 2.1*	35	22.5 ± 1.7
8/1990	18	12.2 ± 0.3*	24	15.8 ± 0.4
4/1991	2	—	1	—
8/1991	13	9.7 ± 7.9	18	12.2 ± 1.5
		Dipodomys nitratoides		
7/1987	18	22.6 ± 7.7*	21	22.0 ± 4.6
8/1987	13	15.9 ± 2.3*	20	20.2 ± 16.3
4/1988	14	17.8 ± 5.7	3	—
8/1988	13	10.9 ± 2.9	11	9.5 ± 6.6
4/1989	17	14.2 ± 1.39	10	8.7 ± 5.8
8/1989	7	—	6	—
4/1990	9	—	7	—
8/1990	0	—	5	—
4/1991	0	—	0	—
8/1991	2	—	1	—

* $P < 0.05$

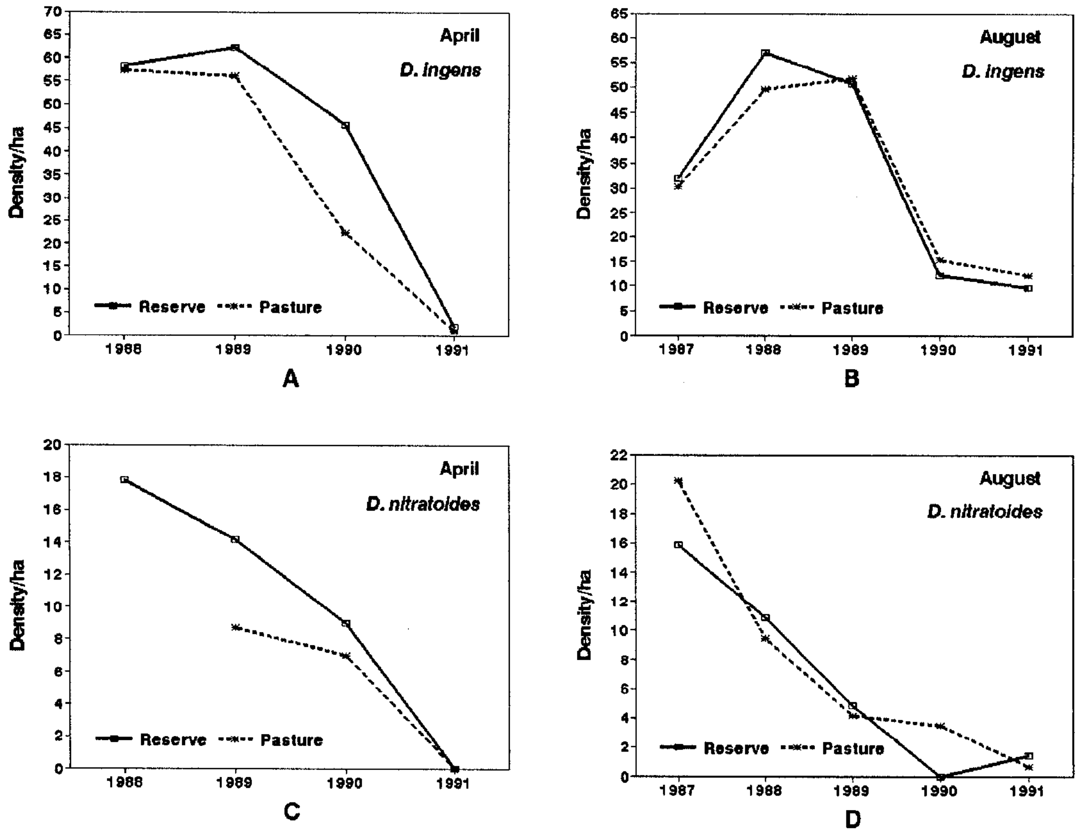

Figure 16. *Mean densities of kangaroo rats per hectare by year for plots 1 (Reserve) and 2 (pasture), Elkhorn Plain, San Luis Obispo Co., California. Values for* D. ingens *for April 1991 (A) are numbers captured per ha; and those for* D. nitratoides *for August 1989 and both censuses in 1990 and 1991 also are numbers captured per ha (Table 19).*

Their decline was about three times greater than that of giant kangaroo rats, whose lowest number in 1991 was 18.2% of their highest number in 1988 (31 and 170, respectively).

Only four giant kangaroo rats were captured on plot 4 along Panoche Creek in Fresno Co. Two adults (one male, one female) were captured in June, and two young-of-the-year (one male, one female) were captured, along with the adults, in September 1989. One McKittrick pocket mouse was also captured in September. Because of the low number of animals taken, we decided not to continue studies at that site.

Density of Kangaroo Rats

Densities for giant and short-nosed kangaroo rats, estimated using capture-recapture models and the nested subgrid model for estimating effective sampling area from trapping on plots 1 and 2, are listed in Table 19. Although the July 1987 trapping session had higher estimated densities of both species than the August 1987 session, the August census was used for comparison with other years because a portion of the populations captured that session had prior experience with being trapped and handled, as was the case for subsequent biannual population censuses.

For giant kangaroo rats, densities for both spring and summer censuses differed significantly between 1987- 1988 and 1989- 1990, and for springs 1990- 1991, but did not differ significantly between plots within census periods except in 1990. Values for two-tailed z-tests for comparisons between plots for the April and August 1990 censuses, respectively, are: $z = 8.587$, $P < 0.00001$; $z = -6.4$, $P < 0.00001$

The August censuses provide a more reliable picture of year-to-year changes because unsettled weather during the late-March - early-April censuses probably had a negative effect on trap response some years. This was especially true in the April 1991 census (Table 19), when cold weather and rain kept animals underground. Generally, densities of giant kangaroo rats increased from moderate levels in 1987, peaking between summer 1988 and spring 1989, then declining to their low point in 1991 (Figure 16a, 16b; Table 19).

Densities of short-nosed kangaroo rats were significantly higher on plot 1 than plot 2 at the start of the study in 1987 (values for the 7/1987 and 8/1987 estimates are, respectively: $z = 2.46$, $P = 0.014$; $z = 8.96$, $P < 0.00001$). The apparent decrease in density between the July and August 1987 censuses may have been partly or wholly due to negative trap response of previously captured individuals. Only three short-nosed kangaroo rats were captured during the April 1988 census on plot 2, so density could not be estimated (Table 19, Figure 16c). Too few individuals were captured in censuses between August 1989 and 1991 to estimate density, so values plotted in Figure 16c for 1990 and 1991 and Figure 16d for 1989 through 1991 represent numbers of individuals captured. Unlike giant kangaroo rats, densities of short-nosed kangaroo rats declined steadily between 1987 and 1991.

There was a total of 96 active precincts in April 1990 on 15, 15-m x 100-m transects on and around plot 7 on the Carrizo Plain, for a mean of 6.4 ± 4.16 precincts/transect. Estimated density was 42.7 ± 27.73 active precincts/ha. Counts of active precincts were 64 and 76/ha on plots 1 and 2, Elkhorn Plain in August 1987, using the same criteria. Such counts were consistently higher than estimated density from capture-recapture and counts of haystacks and clusters of pit caches.

Recruitment of Kangaroo Rats

Newly marked (newly recruited) kangaroo rats by age category (young-of-the-year and adults about a year or more older) when they appeared on plots 1 and 2 are listed in Table 20 and shown in Figure 17. “No. Captured” are the total individuals captured that session: new recruits and animals previously trapped. Numbers of young giant kangaroo rats on plot 1 (Reserve) in the August censuses of 1987-1989 were significantly greater

Table 20. *Newly marked kangaroo rats (recruits) by age category, trapping session, and year captured on nongrazed (Reserve) and grazed (pasture) plots, Elkhorn Plain, San Luis Obispo Co., California. "No. Captured" is the total of recruits and previously-marked individuals captured that session. Yng is the total number of young-of-the-year. Ad are adults about 1 year or more old (but see discussion for caveats).*

	Plot 1 - Reserve								**Plot 2 - Pasture**							
	D. ingens				***D. nitratoides***				***D. ingens***				***D. nitratoides***			
	Recruits			**No. Captured**	**Recruits**			**No. Captured**	**Recruits**			**No. Captured**	**Recruits**			**No. Captured**
Date	**Ad**	**Yng**	**Total**		**Ad**	**Yng**	**Tot.**		**Ad**	**Yng**	**Total**		**Ad**	**Yng**	**Total**	
1987																
8/8-19	23	22	45	45	20	0	20	20	29	11	40	40	14	6	20	20
8/27-9/2	0	2	2	31	3	0	3	13	4	2	6	29	4	0	4	20
10/10-11	0	1	1	15	2	0	2	11	1	1	2	16	2	0	2	15
Total	23	25	48		25	0	25		34	14	48		20	6	26	
1988																
2/13-14	3	2	5	17	6	0	6	11	—	—	—	—	—	—	—	—
3/25-4/5	17	32	49	67	4	4	8	14	37	25	62	79	1	0	1	3
5/1-2	3	6	9	40	0	0	0	1	3	1	4	47	1	0	1	3
5/31-6/3	9	8	17	65	2	0	2	2	7	3	10	67	0	0	0	1
8/8-15	4	3	7	61	1	1	2	13	4	2	6	51	6	1	7	11
10/7-9	0	0	0	36	0	1	1	15	0	0	0	26	1	4	5	14
11/25-26	0	1	1	17	0	0	0	9	—	—	—	—	—	—	—	—
Total	36	52	88		13	6	19		51	31	82		9	5	14	
1989																
1/7-8	1	0	1	17	0	0	0	5	—	—	—	—	—	—	—	—
2/5-7	2	0	2	28	3	0	3	18	2	0	2	24	8	0	8	13
3/19-24	28	14	42	94	5	0	5	17	26	10	36	85	2	0	2	10
8/10-15	8	8	16	67	3	0	3	7	16	4	20	70	5	0	5	6
Total	39	22	61		11	0	11		44	14	58		15	0	15	
1990																
4/7-12	19	0	19	59	2	0	2	9	27	0	27	50	5	0	5	7
8/6-12	5	0	5	18	0	0	0	0	3	0	3	24	2	0	2	0
10/12-13	0	0	0	7	2	0	2	2	0	0	0	10	2	0	2	4
Total	24	0	24		4	0	4		30	0	30		9	0	9	
1991																
3/23-28	1	0	1	1	1	0	1	1	0	0	0	1	0	0	0	0
8/1-6	5	6	11	13	1	0	1	2	7	12	19	19	1	0	1	1
Total	6	6	12		2	0	2		7	12	19		1	0	1	

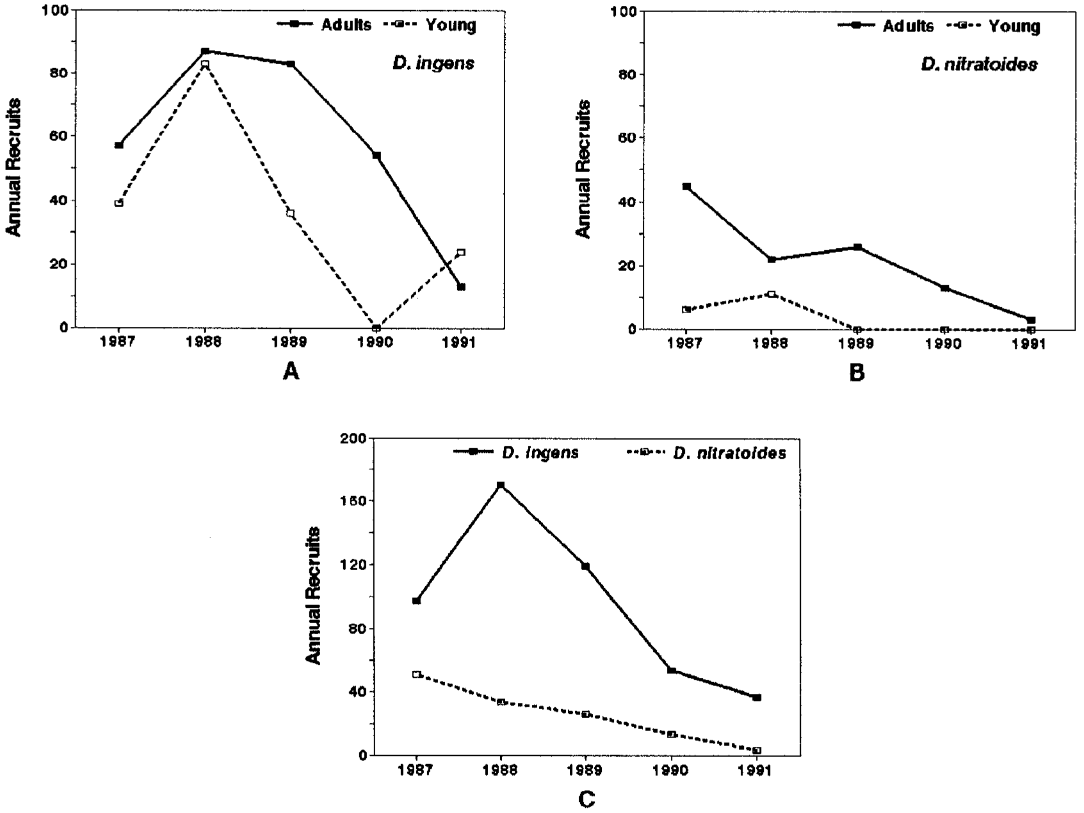

Figure 17. *Numbers of giant (A) and short-nosed (B) kangaroo rats recruited by species, age, and year on plots 1 and 2 (combined), Elkhorn Plain, San Luis Obispo Co., California; C shows totals of adults and young. All animals were "recruits" (newly marked) in 1987.*

than expected, compared to numbers on the pasture plot, although when age categories are combined, the differences were not significant (Tables 18 and 19). The total number of young giant kangaroo rats seen in April 1989 census (3/19-24) was only 42.1% of the number in 1988 (3/25-4/5; 24 versus 57). Production and recruitment of young in 1988 was largely responsible for the increase in density in 1988 and 1989. Failure of recruitment of young giant kangaroo rats on the Elkhorn Plain in 1990 contributed significantly to the steep decline in density that year (Figure 16a, 16b). No young were taken on plots 1 and 2 in 1990, and only two tiny individuals were caught once that year on plot 3. They weighed about half (35 and 43 g) of most newly captured young. We believe that they may have been on the surface because of the mother's death. No young were captured on plots 1 and 2 in 1990 or in the April census of 1991. For the 5-year period, giant kangaroo rats that were young when first captured represented 37.4% of all newly-captured individuals (176 of 470) on plots 1 and 2. Young animals ranged from 0 (1990) to 58.1% (1991) of the numbers of giant kangaroo rats marked by year. Productivity of young was highest in 1988, when 83 were recruited (Figure 17a). This compares with a total of 93 for the other 4 years (Table 20).

Few young short-nosed kangaroo rats were captured during the 5 years on plots 1 and 2 (Table 20). Only 6 young were taken on plot 2 in 1987, 11 in 1988 on plots 1 and 2, and

2 in June 1989 on plot 3. Young that may have been born in February or March of 1987 probably were indistinguishable from older adults by the time we first trapped in July, so the amount of recruitment in 1987 is unknown. The few young captured in 1988 were despite a trapping effort of 5,910 trap nights. Young represented only 13.5% (17 of 126) of the short-nosed kangaroo rats marked during the 5-year period. By year, the proportion of young among new recruits varied from 0 (1989 through 1991) to 33.3% (11 of 33), with 1988 being the most productive (Figure 17b).

The downward trend in recruitment through the drought, regardless of age, for both species of kangaroo rats is shown in Figure 17c and mirrors the declines in densities over the 5-year period. The decline was much steeper for giant kangaroo rats, but the number of short-nosed kangaroo rats at their high point was small in comparison.

Reproduction of Small Mammals.

Giant Kangaroo Rats. No evidence of reproduction was seen for giant kangaroo rats between July and December 1987 on the Elkhorn Plain. Estrus, pregnant, and lactating females and young > 12 weeks (95 and 105 g) were captured on 12-14 February 1988; presumably, breeding started in December 1987. Lactating females also were found in March and April, and young less than about 90 g were trapped from March to early May 1988 (Figure 18). All reproductive females examined in 1988 were probably about 1 year old or older. We found no evidence that females produced more than one litter or that young-of-the-year reproduced. The breeding season in 1989 appeared to start somewhat later and finish sooner than in 1988 (Figure 18). Pregnancies were observed only in February, and young giant kangaroo rats less than about 90 g were found only in March and early April. Again, there was no evidence of multiple litters by single females nor breeding by young-of-the-year,

Few giant kangaroo rats on the Elkhorn Plain showed evidence of reproductive activity in 1990. On the nongrazed Reserve (Plot l), one female was in estrus and one showed evidence of recent lactation during the April population census. Three females on the grazed plot (2) showed evidence of lactation. No young animals were taken on either plot in the April or August censuses, suggesting that there was no successful reproduction in those populations during 1990. On Plot 3 on the nongrazed Reserve, two females were captured while in estrus, one was pregnant and later lactating, and another showed evidence of lactation (Figure 18). Two young giant kangaroo rats weighing 35 and 43 g were captured on Plot 3 on 6 April; they were never recaptured. No other young giant kangaroo rat weighing less than 55 g had been captured at any site during our studies. These and other data (Table 20) suggest that the great majority of the females did not reproduce and those that did failed to raise young to independence in 1990 on the Elkhorn Plain.

On Plot 7 (Washburn Ranch, Carrizo Plain), 11 adult females were captured in 1990; nine showed evidence of reproduction. Additionally, six young were captured through 13 October 1990. The population on plot 7 had an estimated density in 1990 about 40%

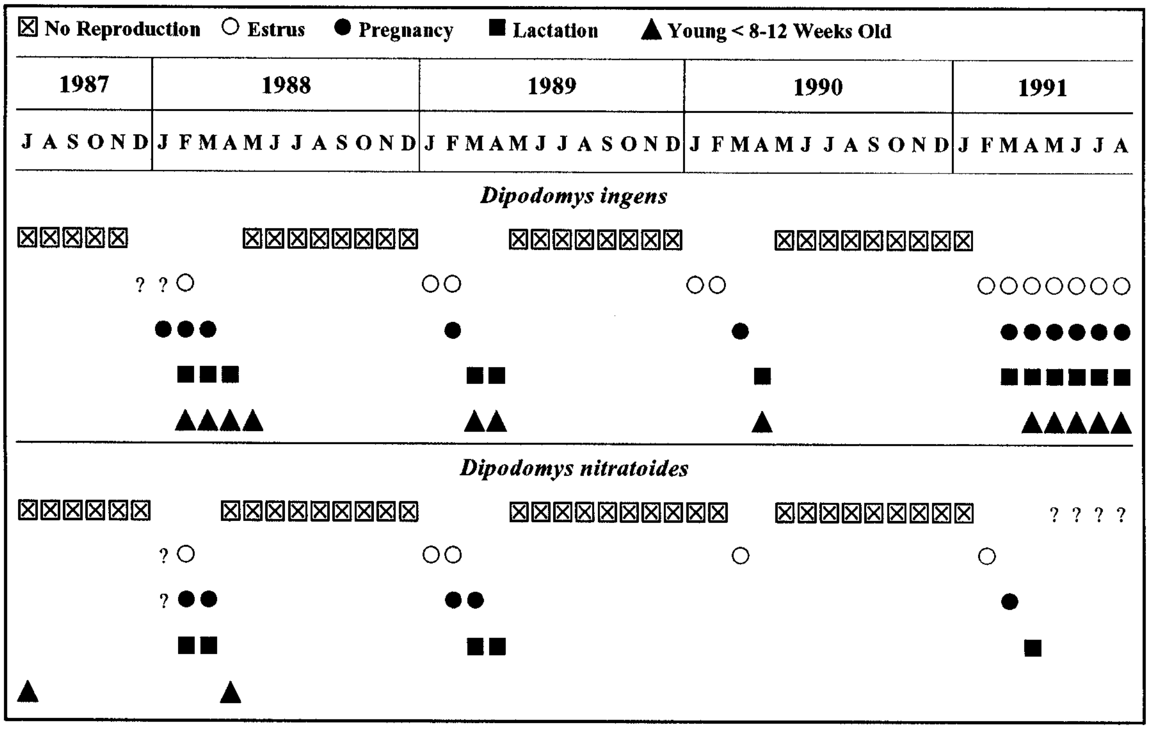

Figure 18. *Composite reproductive activity of female kangaroo rats by month on the Elkhorn Plain between July 1987 and August 1991. Question marks indicate probable activity based on indirect evidence rather than observation. Young giant kangaroo rats, < 8-12 weeks old, were those weighing < about 90 g. Heavier animals may have been near or within this age category, but weights > 90 g are unreliable for aging giant kangaroo rats. Young short-nosed kangaroo rats were those weighing < 33 g.*

lower than the density of the Elkhorn Plain population in 1987-1989, based on number of active precincts. Plants were similar in the two areas (about 4 miles apart), and green herbaceous plants were not available in 1990 during the dry season at either site after about March. At the relocation site at Soda Lake (Plot 6), one female was in estrus on 12 October 1989 (she was young when first captured in July 1989) and was lactating in March 1990. She was not captured between those dates so it is not known if she had two pregnancies. Four other females on Plot 6 were active reproductively in 1990 (Figure 19); one of these was an animal born after the colony was established in July 1989. She was first captured on 6 March 1990, weighed 123 g, and was in estrus. Six of the original 15 females translocated to Plot 6 were captured in 1990. Two of these showed no evidence of reproduction, but they may have reproduced sometime between autumn 1989 and March 1990. Eighteen young (nine of each sex) were captured at the site through October 1990.

In 1991, one female was in estrus in February, another in March, and estrus was presumed for April-August on the Elkhorn Plain because young < 90 g were caught in those months, and in September and October on plot 6. Four pregnant females were caught during the August census (Figure 18). Most females on the Elkhorn Plain ap-

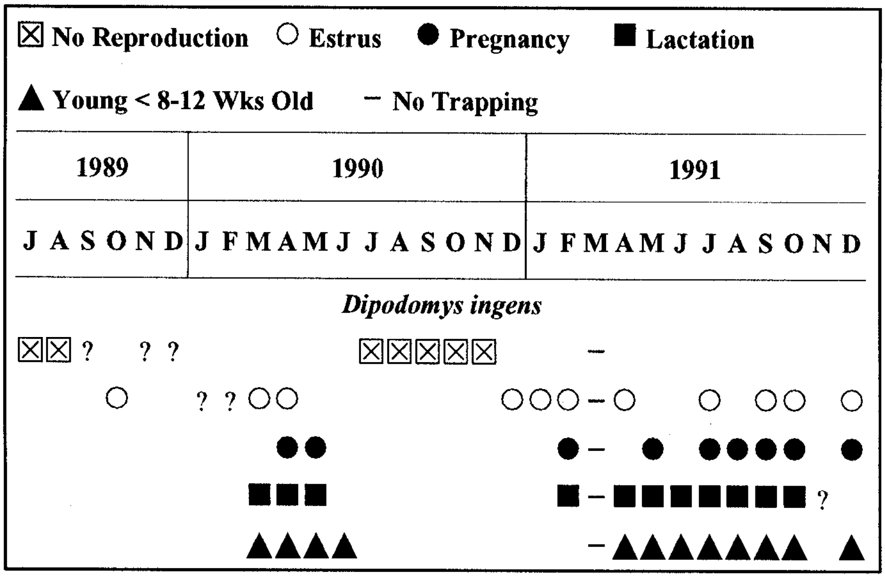

Figure 19. *Composite reproductive activity of female giant kangaroo rats by month on the Carrizo Plain (plots 6 and 7, mostly 6) between July 1989 and December 1991. Plot 7 was not trapped after August 1991. Question marks indicate probable activity based on indirect evidence rather than observation because of lack of trapping of females or for other reasons. Young < 8-12 weeks old were those weighing < about 90 g. Heavier animals may have been near or within this age category, but weights > 90 g are unreliable for aging giant kangaroo rats.*

peared to reproduce sometime after late March rains in 1991. We stopped monitoring reproduction on the Elkhorn Plain and on plot 7 on the Carrizo Plain after August 1991, but continued monitoring the population at Soda Lake on the Carrizo Plain. On the Carrizo Plain, young < 90 g first appeared in April 1991 in the translocated colony (plot 6) and July on plot 7. Females continued to breed through September on plot 6, although only three were in estrus in September and early October. No pregnant or estrus females were found in late October through early December 1991, but one estrus and one pregnant female were seen in late December.

In summary, female giant kangaroo rats on the Elkhorn Plain appeared to be monestrous in 1988 and 1989, and young born during the brief reproductive season did not breed that year. The breeding season was shorter during the 1989 drought year compared to 1988. In 1990, most females appeared to be anestrous; the few that breed apparently failed to raise young to successful recruitment. In 1991, there were few reproductive females seen until late April, and this was the first year that estrous females were seen after February. Most adult-sized females were reproductive (estrus, pregnant, or lactating) during August. In contrast, on the Carrizo Plain some females were reproductive in July 1989 when we were trapping for animals to translocate to plots 5 and 6, and at least one of the young translocated animals was reproductive in October 1989 (estrus). The reproductive season in 1990 extended longer for the translocated population at Soda Lake than the Elkhorn Plain population, and started earlier in winter of 1991 (Figures 18 and 19).

In 1991 in the Soda Lake colony (plot 6) a 90 g female (probably about 12 weeks old), first captured on 21 July, had a vaginal plug on 8 September, indicating copulation. She did not appear to be pregnant or lactating when next captured on 9 October. A juvenile female weighing 59 g when first captured on 18 August, had a vaginal plug when next captured on 8 September. She weighed 94 g and was estimated to be about 10- 11 weeks old. It is not known if she became pregnant because she was not captured again until January 1992. Other apparently young females in the Soda Lake colony of indeterminable age showed evidence of reproduction in 1991. One female, captured as an adult of unknown age (134 g) was in estrus when first seen on 11 February 1991. She had a vaginal plug on 23 July, and another plug on 8 September. She was not captured in August, so it is not known if the mating in July resulted in pregnancy. Five females on plot 6 were pregnant at least twice during 1991, either in January or February and again in August, September, or October; another was thought to be pregnant on 18 August and again on 1 October.

Short-Nosed Kangaroo Rats. Reproduction started later in winter 1988 for short-nosed than giant kangaroo rats. The testes of males were scrotal on 12 February and two females were in estrus; one had a vaginal plug. Another female may have been pregnant, but there was no evidence of lactation. Four adult females captured elsewhere on the Elkhorn Plain Ecological Reserve on 12 March and held in captivity for 2 months were not pregnant when captured. By the 25 March - 5 April trapping session, two females were in estrus, two were pregnant, and one was lactating. The testes of all males were scrotal and of maximum size. No young animals were captured until the April census. The testes of males had begun to regress in size by 1 June and no females evidenced pregnancy or lactation after early April. A few subadults of indeterminate age were captured in the 8-15 August period. Two adult males still had scrotal testes in August. By 9 October, testes were no longer apparent, except for one individual. By 26 November, the testes of males were enlarging again, but they were only about half of their maximum size. Females showed no evidence of reproduction between May and November.

Our data do not suggest more than a single pregnancy nor reproduction by young-of-the-year for short-nosed kangaroo rats between 1988 and 1990. In 1989, as in 1988, the population peak for reproduction of short-nosed kangaroo rats seemed several weeks behind that of giant kangaroo rats, and some adult males were found with full-sized testes through June. One female in estrus was captured on 7 January, and males had full-sized testes then. Another female in estrus was captured on 5 February and several females appeared to be pregnant then, although young were not captured prior to 1 June. The lack of capture of young prior to around the first of June also was the case in 1988. Some animals bred in late spring or summer, judging by the capture ofjuveniles in August 1988 and the enlarged testes of adult males. We have no explanations for the small number of young found and their apparent tardy appearance in traps.

No evidence was found suggesting that short-nosed kangaroo rats bred successfully on the Elkhorn Plain during 1990 (Figure 18). Only one was seen in estrus in March. No pregnancies were seen and no young animals were captured.

Too few animals were captured in 1991 to determine the duration of the breeding season, but it may have been protracted, similar to that of giant kangaroo rats. In 1991 on plot 3, one estrous female was seen in January and she was pregnant when caught in February. Another female, captured in March was lactating. Two lactating females were captured in August 1991, one each on plots 1 and 2. No individuals of this species were captured on plots on the Carrizo Plain, precluding observations on reproduction there.

San Joaquin Antelope Squirrels. Male San Joaquin antelope squirrels had fully enlarged testes on 13 February 1988, and females showed evidence of lactation by the first week in April. Juveniles weighing between 50 and 65 g were first trapped on 1 May. By 1 June, most animals caught were subadults weighing between 95 and 115 grams; none lighter than 95 g were captured in June. By the August census period (8-15 August) the lightest individuals weighed more than 100 g. There was no evidence of an extended reproductive season or more than a single litter of young produced by a female. We did not purposefully trap for antelope squirrels in 1989-1991. Observations of free ranging animals and a few animals captured while trapping for kangaroo rats suggest that the reproductive cycle those years was similar to 1988. Young were seen all 3 years.

Survival of Small Mammals

Giant Kangaroo Rats. Longevity on plots (time between first and last capture) do not correspond to demographic longevity because times of birth and death are unknown. Giant kangaroo rats first captured plots 1 and 2, Elkhorn Plain, and having been recaptured > 30 days later, had a mean duration between first and last capture of 376 days (Table 21). Those first captured when young had a mean duration of 401 days and adults had an average interval of 363 days. Maximum possible longevity on plots 1 and 2, from first day of trapping on 7 July 1987 to the last day of trapping on 6 August 1991 was 1,490 days. One male, captured as an adult was last trapped 1,478 days later. His minimum age, assuming he was born on 15 February 1986, was 1,996 days (5.47 years). Another adult had an interval between first and last capture of 1,124 days, and a minimum age, using the same assumption, was 1,634 days (4.48 years). Four captured as young had durations of greater than 1,100 days.

The time between the first and last trapping session on plot 3 was 983 days. The longest interval for a giant kangaroo rat was 833 days for a female first captured when young. Two males, first captured when adults, had intervals of 699 and 609 days, with estimated minimum ages of 1,095 (3.0 years) and 1,006 (2.76 years), assuming births the previous year on 15 February. The longest-lasting adult female had a duration of 566 days and a minimum estimated age of 1,005 days (2.76 years). The longest interval for a short-nosed kangaroo rat on plot 3 was 862 days for a male first captured as an adult on plot 1 in February 1988. His minimum age, assuming birth on 15 March 1987, was 1,007 days (2.76 years).

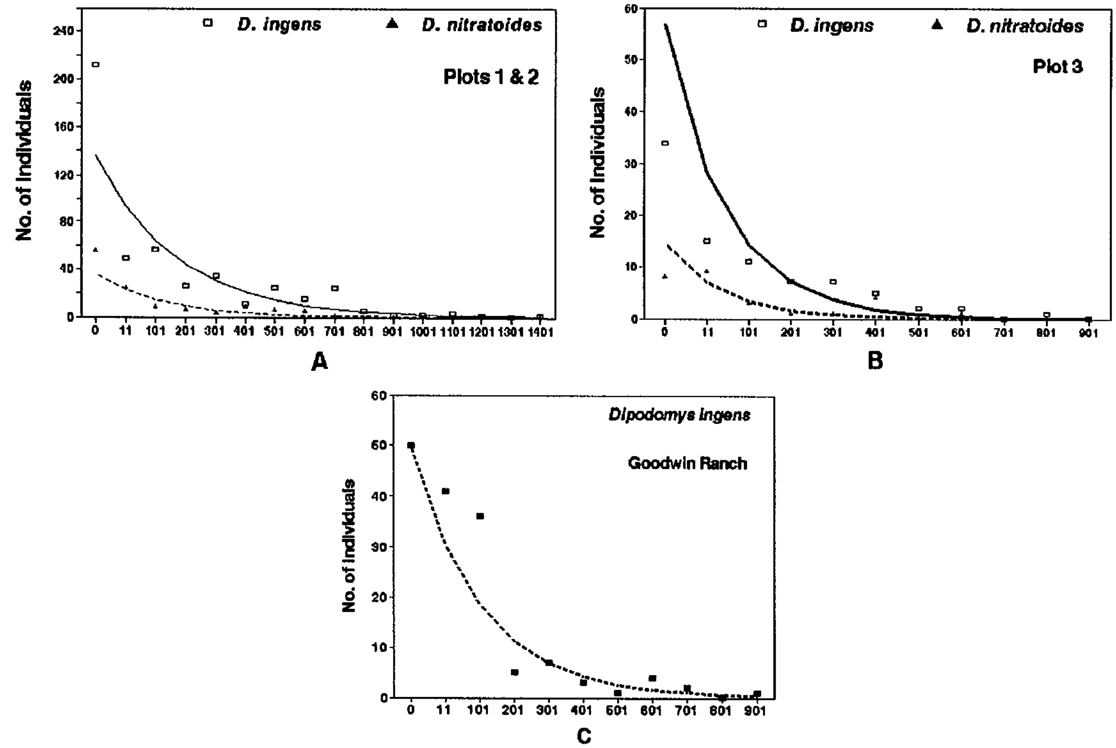

Figure 20. *Survival (days between first and last capture) of two species of kangaroo rats on four plots on the Carrizo Plain Natural Area, San Luis Obispo Co., California. Plotted values are the numbers in each period. Curves are exponential curves fitted to the data.*

In the Soda Lake colony of giant kangaroo rats, only founders that were adult when first captured in July 1989 were considered "adult" for these purposes. The maximum possible interval between first and last capture extended from 8 July 1989 to 2 February 1992, a period of 932 days. Only data for animals recaptured beyond 30 days of first capture (progeny) or release (founders) were included. Adult founders had a mean duration of 493 days, compared to a mean of 195 days for founders translocated as young and progeny of the colony. The maximum period between first and last capture was 932 days for a female founder (the maximum possible), first captured as a young animal weighing 119 g. A young of this weight probably would be about 120 days old (see Growth), giving an estimated age at last capture of 1,052 days (2.88 years).

More than 82% of the giant kangaroo rats on the Elkhorn Plain plots were recaptured, but a majority disappeared before 100 days elapsed since first capture (Figure 20, Table 22). For plots 1 and 2 combined, 17.3% (81 of 467) were never recaptured and 45.4% were not captured beyond 10 days after first capture (1 trapping session). Six giant kangaroo rats (2.1%) were last captured after 901 or more days. For plot 3, 15.5% were never recaptured and 40.5% were not captured after 10 days. Animals still present about 3 months after their first capture had higher probabilities of being present for a year or more: 44.1% of the individuals on plots 1 and 2 were last trapped greater than 100 days since first capture. For plots 3 and 6, these values are 42.9% and 39.4%, respectively.

Table 21. *Mean ± SD days (range in parentheses) between first and last capture of two species of kangaroo rats on the Carrizo Plain Natural Area, San Luis Obispo Co., California. Animals with < 11 days between first and last capture were excluded from the computations. Maximum possible intervals are: plots 1 and 2 - 1,490 days; plot 3 - 983 days; plot 6 - 932 days (through 2/2/1992). Plot 1 was not grazed whereas plot 2 was grazed some years.*

Plot	*Dipodomys ingens*						*Dipodomys nitratoides*					
	n	Adult	*n*	Young	*n*	Pooled	*n*	Adult	*n*	Young	*n*	Pooled
Elkhorn Plot 1	72	372 ± 254.7 (32-1006)	53	390 ± 287.3 (38-1222)	125	380 ± 269.1 (32-1222)	30	365 ± 214.5 (36-766)	0	—	30	365 ± 214.5 (36-766)
Elkhorn Plot 2	91	357 ± 269.2 (31-1478)	25	424 ± 337.0 (31-1161)	116	371 ± 286.5 (31-1478)	23	228 ± 191.0 (35-727)	7	247 ± 180.9 (89-578)	30	232 ± 188.9 (35-727)
Elkhorn Pooled	163	363 ± 263.0 (31-1478)	78	401 ± 304.5 (31-1222)	241	376 ± 277.7 (31-1478)	53	305 ± 215.6 (35-766)	7	247 ± 180.9 (89-578)	60	298 ± 212.7 (35-766)
Elkhorn Plot 3	46	240 ± 173.0 (36-699)	2	537.5 (242-833)	48	252 ± 189.4 (36-833)	18	206 ± 194.9 (31-682)	2	158 (37-279)	20	201 ± 198.4 (31-682)
Soda Lake Plot 6	3	493 ± 104.0 (386-634)	80	195 ± 185.7 (33-932)	83	206 ± 191.6 (33-932)	0	—	0	—	0	—

Short-Nosed Kangaroo Rats. The maximum durations between first and last capture of short-nosed kangaroo rats on plots 1 and 2 were an adult male (766 days) and adult female (727 days; Table 21). The male, first captured in July 1987, was a minimum age of 1,246 days (3.4 years), assuming his birth on 15 March 1986. The female was first captured in August 1988; assuming her birth on 15 March 1987, she was a minimum of 1,240 days old. The maximum duration for those captured when young was 766 days.

Short-nosed kangaroo rats had lower mean persistance, and presumably survival, but the percentage of animals disappearing before 11 days was similar to giant kangaroo rats (smaller numbers of short-nosed kangaroo rats make the exponential curves in Figure 20 appear to be less steep for short-nosed than giant kangaroo rats). On plots 1 and 2, 29.1% were never recaptured and 47.1% were not recaptured after 10 days (Table 22, Figure 20). Only 32.8% were still present after 100 days, and none lasted more than 800 days since first capture.

San Joaquin Antelope Squirrels. Data for antelope squirrels was gathered only from July 1987 to November 1988. Fifteen of 25 (60%) antelope squirrels first captured as adults were never recaptured. The mean duration on plots from first capture of adults was 46.4 ± 117.8 days for all individuals, including those never recaptured. Excluding animals that were not recaptured, the mean duration between first and last capture of adults was 115.9 ± 158.9 days. The longest time between first and last capture was 458 days.

For antelope squirrels first captured as young, 39 of 67 (58.2%) were never recaptured. Mean duration from first capture was 24.4 ± 68.0 days; the mean duration exclud-

Table 22. *Numbers of kangaroo rats by interval (days) between first and last capture on plots 1-3, Elkhorn Plain, San Luis Obispo Co., California. The zero interval indicates those not recaptured.*

	Dipodomys ingens					***Dipodomys nitratoides***			
Interval (days)	**Plot 1**	**Plot 2**	**Plots 1 & 2**	**Plot 3**	**Plot 6**	**Plot 1**	**Plot 2**	**Plots 1 & 2**	**Plot 3**
0	44	37	81	13	38	15	20	35	6
1-10	55	76	131	21	12	9	12	21	2
11-100	22	27	49	15	41	8	16	24	9
101-200	30	27	57	11	36	3	6	9	3
201-300	18	8	26	7	5	4	2	6	1
301-400	19	15	34	7	7	3	1	4	1
401-500	7	4	11	5	3	3	5	8	4
501-600	7	17	24	2	1	5	2	6	1
601-700	9	6	15	2	4	5	0	5	0
701-800	13	11	24	0	2	1	1	1	0
801-900	2	3	5	1	0	0	0	0	0
901-1,000	2	0	2	—	1	0	0	0	—
1,001-1,100	2	0	2	—	—	0	0	0	—
1,101-1,200	1	3	4	—	—	0	0	0	—
1,201-1,300	1	0	1	—	—	0	0	0	—
1,301-1,400	0	0	0	—	—	0	0	0	—
1,401-1,500	0	1	1	—	—	0	0	0	—

ing animals never recaptured was 58.3 ± 94.5 days. The longest time between first and last capture was 398 days. The greatest proportion of both adult and young antelope squirrels become trap shy after their initial capture, complicating the acquisition of data on population structure.

Weights of Giant Kangaroo Rats

Between July 1987 and October 1988, weights of adult males averaged significantly greater than adult female giant kangaroo rats during winter and spring, but did not differ significantly between sexes in August-October (Table 23). The only period when females had a greater mean weights than males was August 1991, but numbers were too low at that time to determine significance of the difference. Over the period from August 1987 to August 1991, weights of adult males fluctuated on an annual cycle, but peaks in weights shifted from year to year (Figure 21). In 1989 and 1990, weights peaked in April and did not decline to the low values seen in 1987 and 1988. In 1991, weights of males remained steady during winter and spring, then declined in summer. Their weights through August 1991 were lower than anytime since February 1990.

Changes in weights of adult female giant kangaroo rats corresponded to those of males, except in 1991. Female weights peaked in February 1988, April 1989, April 1990, and August 1991. For the first time, female adults averaged heavier than males in August 1991 (Figure 21). Mass of females reached a low point over the 5-year period in February 1991, following 2 years of severe drought. Likewise, for 1990, they had the lowest average weights in February. Although mass peaked at a relatively high level in April 1990, at greater average weight than any time in 1989, these females were nearly all nonreproductive, and remained so through 1990 and into 1991.

Mass of juvenile kangaroo rats when first captured ranged from about 55 to 90 g, with the exception of two caught a single time on plot 3, weighing 35 and 43 g (see Recruitment of Kangaroo Rats for more information on these two young). Juveniles weighing between 55 and 68 g were estimated to be 47-60 days old, using the formula: *age in days*

Table 23. *Statistical summaries of weights (g) of adult giant kangaroo rats by season on plots 1-3, Elkhorn Plain, San Luis Obispo Co., California. Values for April and August are all weights of adults captured during the spring and summer censuses respectively. Values for February and October are all weights of adults captured during January-February, and September-October, respectively.*

		Males			**Females**		
Year	**Season**	**Mean ± SD**	**Range**	***n***	**Mean ± SD**	**Range**	***n***
1987	August	122.6 ± 9.5	93-151	93	121.1 ± 4.6	102-132	78
	October	127.4 ± 4.8	118-136	18	120.5 ± 3.8	116-126	8
1988	February	143.0 ± 9.9	134-162	11	135.8 ± 8.2	117-151	30
	April	133.7 ± 10.2	106-158	281	126.7 ± 10.1	104-156	312
	August	123.0 ± 10.3	101-150	190	122.3 ± 10.5	101-146	218
	October	121.0 ± 12.2	102-144	52	120.3 ± 8.7	102-143	79
1989	February	128.9 ±11.0	108-148	52	123.9 ± 10.9	105-150	59
	April	136.8 ± 10.3	111-166	531	128.4 ± 10.6	109-156	428
	August	133.6 ± 8.5	113-150	29	127.5 ± 8.0	110-149	36
	October	127.7 ± 10.1	108-155	22	122.2 ± 10.3	104-141	21
1990	February	123.4 ± 10.4	103-144	32	120.0 ± 9.2	101-131	21
	April	138.0 ± 11.2	108-164	111	132.9 ± 11.2	106-158	79
	August	124.9 ± 11.5	103-145	19	131.3 ± 10.5	105-147	28
	October	130.1 ± 8.9	112-144	16	121.7 ± 7.6	110-140	14
1991	February	127.7 ± 7.7	120-141	6	116 ± 3.0	113-119	2
	April	127.7 ± 1.2	126-129	3	124.8 ± 6.9	115-133	4
	August	125.6 ± 9.9	110-142	17	135.6 ± 13.6	111-164	16

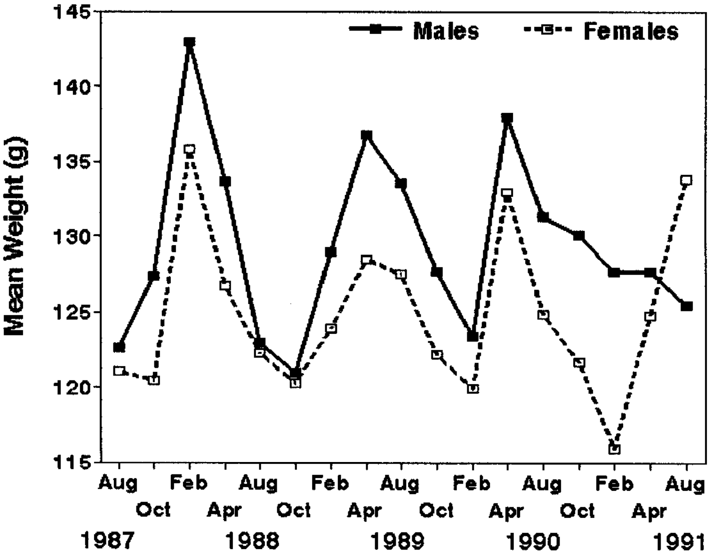

Figure 21. *Fluctuations in mean weights of adult male and female giant kangaroo rats on plots 1-3, Elkhorn Plain, San Luis Obispo Co., California, between August 1987 and August 1991. Seasons indicated as months on the x-axis are defined in Table 23.*

= *mass in g - 8*, based on values for banner-tail kangaroo rats (newborns averaged about 8 g, and gained about 1.0 g/day their first 4-5 weeks; Holdenried 1957). Data for 5 juveniles, captured 3 or more times within 65 days of first capture and weighing between 55 and 68 g at first capture, were used to plot a quadratic growth curve for the first 120 days of life (Figure 22).

Inspection of data on weights over time of all juveniles first captured when weighing less than about 85 grams, show that young animals weighing more than about 90 grams cannot be reliably distinguished from adults based on mass. Juvenile kangaroo rats have shorter tails with shorter, blacker distal crests, but these differences are apparent only when young are less than about 3 months old. Mass of many adults falls to around 100 g at the low point in their annual cycle, and a few adults known to be a year or more old have been captured when weighing between 93 and 100 g. Mass of some animals captured as juveniles in 1988 peaked between about 90 and 105 g and remained in that range into 1990. During winter and early spring, nonreproductive animals weighing between about 95 and 120 g were presumed to be young-of-the-year if other evidence was consistent with being young. These criteria were applied in 1987-1989, but were not used in 1990 because most of the population of known adults were nonreproductive. In 1991 these criteria also could not be used because we presumed that young-of-the-year, born in spring, were reproducing by August. Generally, animals a year or more old have torn or scarred ears, and other evidence of their struggles with life, but adult-sized animals appearing in the populations in the nonreproductive season, and those reproductive individuals appearing in 1991, had to be assigned to the "adult" age category.

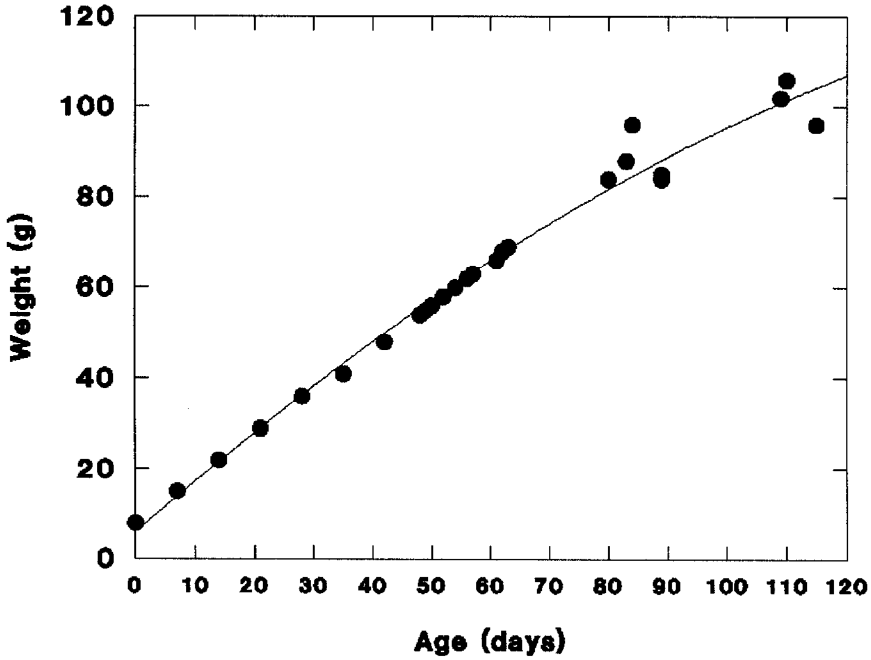

Figure 22. *Quadratic growth curve for juvenile giant kangaroo rats between 0-120 days of age. Plotted values from 0 to 42 days of age were estimated from data on banner-tail kangaroo rats (Holdenried 1957). The other values are based on weights of five juvenile giant kangaroo rats weighing between 55 and 68 g when first captured.*

Translocating Giant Kangaroo Rats

Observations on Released Animals

The following describes observations made on the first group of six animals released at the Soda Lake site on 14 July 1989. Around sunset, while still light, animals began to appear at the entrances of their tubes. Soon after that they made short excursions around their mounds. Within about 30 min of emergence some animals were exploring for 30 to 50 m or more from their burrows, then returning quickly. We stopped watching the first group about 1 h after they first emerged, when it seemed that they were not going to leave the area where they were released. The next morning we inspected their burrows and all appeared to be occupied, judging by evidence of digging on the mounds or plugged tubes (giant kangaroo rats typically plug their burrow entrances during the daytime, although the plug may not be visible from the opening of the burrow).

That evening, we watched both the newly released animals and the six released the previous day. During that time, all six of the first group were confirmed to be present and most of the newly released seven had been seen on the surface. Similar observations were made for the additional releases at both Soda Lake and Painted Rock. Some animals were reluctant to enter the tubes when first released and three pulled a plug out within a few minutes and emerged. Two were captured by hand and returned to their burrows, which were then sealed more tightly. One at Soda Lake escaped into an open gopher tunnel on the same mound as its artificial burrow. Its burrows were left unplugged so that it could retreat there if it decided to leave the gopher burrow during the day. That evening it was seen around its artificial burrow, although it was not clear if that burrow was being used. The next morning, tracks at the openings to the tubes suggested that it had at least explored the artificial burrow by entering and exiting several times. By the next day, the animal had plugged a large tunnel made by a California ground squirrel, near the artificial burrow, and opened two new holes to the gopher burrow system. When we finished monitoring in July, it still was not clear if it was residing in the artificial burrow, but it was living in the mound. It was still present when checked in August 1989.

When both colonies were next checked, from 7 to 9 August, most animals had dug additional tunnels outside the trench made for the artificial burrows. It was not determined if these connected to the artificial burrows, or represented new burrow systems. Judging from external evidence, some appeared to represent new systems and others appeared to be connected to artificial burrows.

Dirt had settled and in places the artificial burrow systems had collapsed due to the extensive digging by the occupants. Dirt over the burrow systems was repacked and more dirt added and tamped down.

Barn owls were seen foraging near both colonies while we were watching translocated animals, and coyotes and kit foxes were seen near the Painted Rock colony during the time we were translocating animals. A coyote was seen foraging about 100 m east of the plot and tracks of a kit fox were found on the plot during the August observation period. A coyote had dug into several artificial burrow systems at the Painted Rock site sometime before 7 August. One system was extensively damaged; the cardboard tubes had been exposed for about half their length but the tubes apparently interfered with digging and the central nest chamber was not exposed. Coyote scats were found on top of one artificial burrow system.

Remains of three giant kangaroo rats were found on and near the translocated colony at the Painted Rock site on 9 August, They consisted of skins (turned inside out) with some leg and jaw bones attached or found nearby. The metal ear tags were attached to remains of two, but PIT tags could not be located. The animal responsible for killing and eating the kangaroo rats was not determined. We have not found similar remains at any site over 10 years of studying giant kangaroo rats, but their condition was similar to remains left by small raptors such as burrowing owls.

Population Trends

1989. A livetrap set at each artificial burrow (30 total) in August only captured one giant kangaroo rat at the Soda Lake site. Numbers of animals alive in August 1989 at each site were estimated, based observations and sign of activity (picking up the seeds scattered around traps and piled near entrances; reopening burrow entrances that were closed when we repaired burrow systems). Assessments based on sign were made within 2 h after dark immediately after the colony had been under observation by spotlights. These values probably underestimate the actual numbers alive at each site because some animals probably did not emerge on the nights or during the times when we were present.

In August 1989, at the Painted Rock site we confirmed that at least 12 animals were present on the plot and that 2 others had moved to a California ground squirrel burrow system about 40 m west of the plot. One additional animal probably was living in another ground squirrel burrow just off the plot, based on sign, but the animal was not seen. Thus, 15 animals appeared to be present approximately 1 month after the release of 30 animals at the site. It is possible that other animals moved off the plot to more distant sites and therefore were not detected.

By September 1989, only six of the burrows showed evidence of use at the Painted Rock site. No animals were seen or captured between September and December. By October, only three or four burrow systems appeared to be occupied, and by December, only two or three burrow systems evidenced recent activity.

At the Soda Lake site, evidence of predation was not found, but a kit fox was seen foraging on the edge of the plot on 7 August, and a coyote was seen nearby on 9 August. At least 19 animals were present on the plot (11 were seen simultaneously on 9 August), and another moved to a gopher burrow system on an old precinct about 30 m SW of the plot in August.

Four individuals were captured at the Soda Lake site in September, and 20 burrows showed evidence of activity. California ground squirrels were seen entering or exiting burrows within the translocated colony and some giant kangaroo rats probably visited neighboring artificial burrows, resulting in some burrow systems evidencing activity than were not inhabited. One animal was captured in October at Soda Lake, and none were captured at either site in November and December, but most burrow systems continued to show evidence of activity. On 10 November 1989, at the Soda Lake site, 23 of the 30 artificial burrow systems were active, 2 were possibly active, and 5 were inactive.

1990. One animal was seen in the Painted Rock colony during trapping and spotlighting in January 1990, and one young male giant kangaroo rat was captured in April 1990. By June 1990, only two or three of the artificial burrow systems appeared to be in use, but there was no conclusive evidence that they were used by giant kangaroo rats. We caught five McKittrick pocket mice during 4 days of trapping in June. No animals were seen while spotlighting between February and June. We decided to suspend monitoring of the colony after June 1990.

The colony at Soda Lake expanded beyond the boundaries of the artificial burrows, Some of both the founders and progeny had established burrow systems outside the

Table 24. *Captures of founders and progeny of translocated giant kangaroo rats at the Soda Lake relocation site, Carrizo Plain, San Luis Obispo Co., California, between March 1990 and December 1991. Values by month are numbers of individual founders or progeny caught that session. Totals are total number of founders released at the site and number of progeny captured since establishment in July 1989.*

1990										1991												Total
Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	
Founders																						
3	9	5	12	2	9	5	3	5	3	2	2	—	3	1	—	3	3	2	2	1	0	30
Progeny																						
2	3	6	8	3	8	6	5	10	6	6	10	—	9	3	—	33	34	51	58	22	54	113

confines of the original colony. Numbers of captures of giant kangaroo rats between March 1990 and December 1991 in the Soda Lake colony are given in Table 24. One Heermann's kangaroo rat (*D. heermanni)* was captured once on the plot in May 1990. No other small mammals except a few California ground squirrels were trapped or seen at the study site in 1990. Thirteen of the 30 founders translocated to the site were captured between May and August 1990. Six were females. Eighteen progeny were marked through December 1990. Based on numbers of apparently active burrow systems (51), we believe the colony numbered more than 50 in June 1990, but only 20 individuals were captured during that trapping session. A total of 31 individuals were captured in 1990.

1991. In 1991, two of the founders were trapped regularly, and a third was trapped occasionally. Numbers of progeny increased rapidly, with 95 progeny being marked in 1991, for a total of 113 since founding the colony. In July 1991, 61 precincts were located and mapped off the grid placed over the area containing the original artificial burrows; 36 burrow systems, most associated with the original translocation burrows, were active on the grid, for a total of 97 active precincts. Because both juveniles and adults were caught at some precincts, we estimated the population to number > 100 individuals then, although only 36 individuals were captured during a 6-day session. Fifteen additional new precincts were located in August, and 3 more were located in September, for a total of 78 off of the original plot, and a grand total of 114 precincts in 1991.

Data on reproduction in the Soda Lake colony were presented in the section on reproduction (Figure 19). Survival and longevity also were treated in the section on survival (Table 21, Figure 20c).

Associated Small Mammals.

One Heermann's kangaroo rat was captured a single time in 1990 and a California pocket mouse (*Chaetodipus californicus*) was captured once in August 1991 in the translocated giant kangaroo rat colony at Soda Lake. The only other species seen and occasionally

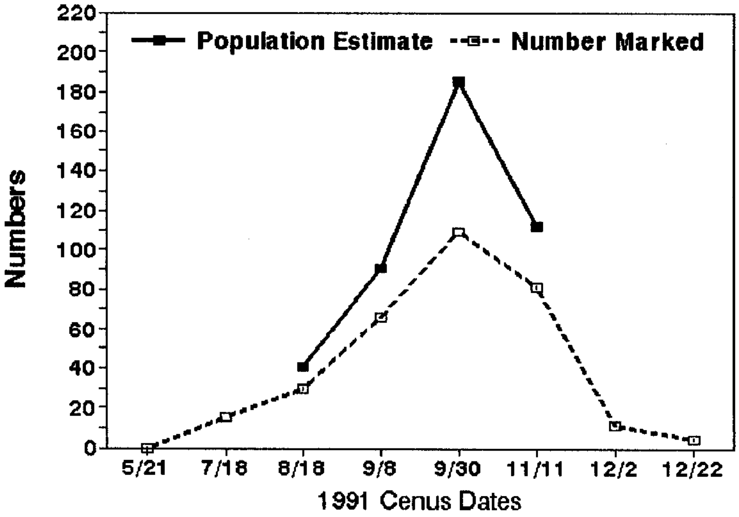

Figure 23. *Numbers marked and estimated population size (Schnabel model) for McKittrick pocket mice (*Perognathus inornatus neglectus*) at the relocation site, Soda Lake, Carrizo Plain, San Luis Obispo, California. The decrease in numbers in December probably was due to reduced activity and presumed dormancy during cold weather.*

captured (when we used Tomahawk wire-mesh traps) in 1990 was the California ground squirrel. In 1991, only giant kangaroo rats were captured in monthly sessions between January and June at Soda Lake. In July 1991, 15 McKittrick pocket mice were captured in a 6-day session; captures of pocket mice increased in subsequent sessions until cold weather in December reduced their activity. Captures and population estimates of McKittrick pocket mice for sessions in June-December (3 days in June, 6 days in July, 5-day periods for August-November, two 3-day periods for December) are shown in Figure 23. Values for populations estimates (numbers marked in parentheses) are: 5 June (0); 18 July (15); 18 August - 41 ± 25 (30); 8 September - 91 ± 33 (66); 30 September - 185 ± 69 (109); 11 November - 112 ± 29 (81); 2 December (11); 22 December (4).

Feeding Studies on Giant Kangaroo Rats

Trapping on the four plots used for feeding studies were affected by severe dust storms, interference by kit foxes who learned to open both Sherman and Tomahawk live traps, and apparent trap shyness. Captures most sessions were too few to reliably estimate population size. Data on counts of giant kangaroo rat precincts, although probably overestimating numbers, are comparable from period to period, and provide a better index to population size and changes than captures (Table 25, Figure 24). Counts in February (Table 25) differ from the subsequent counts in that all precincts that showed any evidence of burrows were counted (counts were made during a period of severe, daily sand storms, so the usual criteria of recent digging or other fresh signs could not be applied). March counts represent more conservative criteria for "active" burrow systems. The experimental plots (fed) did not differ significantly from the control (not fed) plots at that time. By

April, however, the control plot on the Carrizo Plain had only 26.4% of the number of active precincts found on the experimental plot, while active precincts on the experimental plot increased 29% compared to March. On the Elkhorn Plain control plot, active precincts had decreased to 17.6% of the number found on the experimental plot, but both the experimental and control plots had significantly fewer active precincts than in March. The April numbers for the experimental and control plots, respectively, represented 38.3% and 7.4% of the March values (Table 25). Numbers increased slightly on the control plot on the Elkhorn Plain in June, but declined on the control plot on the Carrizo Plain. Because of the end of funding, we ceased monitoring on the Elkhorn Plain, but continued periodic assessments on the Carrizo Plain. Numbers on both plots increased in August and October, but percentage gains were greater on the plot receiving seeds (Figure 24).

Plots on the Carrizo Plain were located in an area subject to severe wind erosion in 1990 and 1991. There was no ground cover on the Carrizo plots in February-April. Plants first started growing in April following rainstorms in late March, but plants were few, ground cover sparse, and few seeds were produced prior to September. Most plants that grew were early secondary-succession weeds such as Russian thistle (*Salsola kali*)

Table 25. *Numbers of active precincts (burrows) of giant kangaroo rats by month (1991) on experimental (fed = provided with seeds at active precincts) and control (not fed = no seeds provided) plots of 8.0 ha each on the Carrizo and Elkhorn plains. Counts in February were more liberal than subsequent counts because severe sand storms during that period obscured sign of recent activity. Those counts are not included in row-wise statistical tests. Statistics (*G *and* P*) are for log-ratio goodness-of-fit tests: column-wise comparisons of experimental and control plots by month; and row-wise comparisons of experimental and control plots across months.* G *and* P *in the Feb. column are for comparison of fed plots on the Carrizo and Elkhorn plains.*

	Active Precincts by Month						
Treatment	**Feb**	**Mar**	**Apr**	**Jun**	**Aug**	**Oct**	**R x C Test**
				Carrizo Plain			
Fed	231	120	155	50	70	150	$G =$ 39.513 (d.f. = 4)
Not Fed	↑	111	41	20	24	72	$P =$ < 0.00001
G	0.17188	0.35059	70.66736	13.28284	23.50818	27.99902	
P	0.67845	0.55378	< 0.00001	0.00027	< 0.00001	< 0.00001	
	↓			**Elkhorn Plain**			
Fed	243	133	51	51	—	—	$G =$ 31.694 (d.f. = 2)
Not Fed		122	9	16	—	—	$P =$ < 0.00001
G		0.47461	32.45258	19.22195	—	—	
P		0.49087	< 0.00001	0.00001			

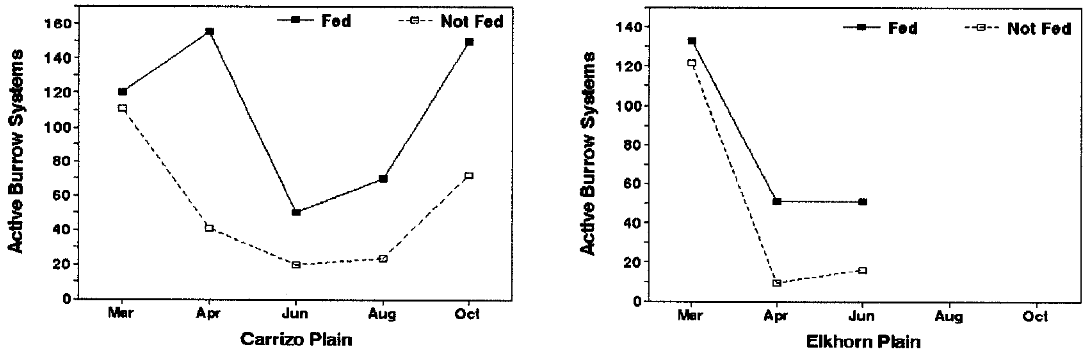

Figure 24. *Numbers of active giant kangaroo rat precincts from monthly counts on experimental (fed) and control (not fed) plots on the Carrizo (left) and Elkhorn (right) plains, San Luis Obispo Co., California, during 1991. Seeds were provided in February, March, and June. High rainfall occurred in late March.*

and turkey mullein or dove weed (*Eremocarpus setigerus*)—species that did not mature until autumn (Table 26). At the end of the growing season, estimated ground cover on plot 8 (fed plot) was 6.2% and on plot 9 (not fed) 7.3%. In areas not subject to severe erosion, ground cover was > 90% in autumn 1991.

Table 26. *Mean (*± SD*) number of individual plants per grid cell of cells in which they occurred, number of 10 x 10-m grid cells in which each plant species occurred (*n *= 144), and estimated percent cover of plants on experimental feeding and control plots (8 ha size) on the Carrizo Plain during 1991.*

	Experimental (Fed)		**Control (Not Fed)**	
Species	**Mean ± SD**	**n (cells)**	**Mean ± SD**	**n (cells)**
Astragalus	(1)	1	(1)	1
Avena sativa	4.2 ± 3.90	15		
Compositae, Chichorieae			(1)	1
Cucurbita			(1)	1
Eremocarpus setigerus	23.7 ± 20.33	117	16.9 ± 17.08	115
Euphorbia	1.9 ± 1.03	32	11.8 ±10.32	97
Marubrium vulgare			(1)	1
Salsola kali	1.0 ± 0	5	1.1 ± 0.36	14
Schismus arabicus			12.4 ± 13.85	61
Trichostema lanceolatum			1.1 ± 0.36	21
Total Number of Plants	2,906		3,890	
Total Cover	6.2%		7.3%	

DISCUSSION

Low rainfall, received mainly in the cool, winter season, combined with a long, hot dry season during summer make the San Joaquin desert, including the Carrizo Plain Natural Area, unique among hot deserts in North America. Values for herbaceous plant productivity on the Elkhorn Plain for the 5-year period averaged (13.8 g/m^2) considerably below means for drier sites in the Chihuahua and Sonoran deserts, which ranged from about 52-190 g/m2, and a mean of 29 g/m^2 for one normal and one drought year in the Mojave Desert (Ludwig 1986). The lack of xeric-adapted succulents, except chaparral yucca, which is confined to steep, rocky slopes at elevations generally above 610 m, signifies a longer, harsher, dry season than typical among North American deserts. Low diversity of shrub species and lack of shrubs over vast areas of the southwestern San Joaquin Valley and Carrizo Natural Area also may result from the hot, xeric environment.

Drought was the overriding factor influencing changes in the biotic community of the Elkhorn Plain during this study. Only the 1987-88 precipitation year exceeded the long-term mean. Precipitation in 1986-87, 1988-89, and 1989-90 were all < 70% of the long-term mean of the southern Carrizo Plain. The most severe episode of drought was from 1988-89 through 1989-90, when 48.2 and 38.6% of normal rain fell, respectively, and when much of the total came too early or late in the season to promote herbaceous growth (Table 3). Drought forced the suspension of livestock grazing after the 1988-89 grazing season, making the time that experimental and control plots were exposed to different grazing treatments too brief to measure responses by plant and animal species. Thus, the following discussions will focus on plant and animal responses to drought, although some effects of cattle are noted.

Community Interactions

Plant Productivity and Plant/Animal Interactions

Herbaceous Productivity. Plant production was affected, as expected, by drought, but both productivity and species composition of annual plants also were significantly influenced by giant kangaroo rats. Hawbecker (1944) measured 560% more plant biomass on precincts in the Panoche area, but he did not report sufficient data to make statistical comparisons. Hawbecker (1944) ascribed greater plant productivity seen on precincts of giant kangaroo rats to greater amounts of water in the soil. He and Grinnell (1932) attributed this to the better infiltration of rainwater on the loose dirt of precincts, resulting from the seed caching and burrowing of the kangaroo rats. Although this hypothesis is appealing, it does not account for the higher nitrogen content of plants on precincts, which alone could be responsible for greater production of biomass. Williams (in litt. 1985) reported similar results in a preliminary study involving the fencing of individual precincts to exclude sheep. Productivity on precincts averaged 1.8 times greater than in intervening areas. Williams (in litt. 1985) believed that in other areas or years with lower rainfall, the productivity on precincts would be greater in comparison to interprecinct spaces if soil water alone was responsible for differences in production.

In unfenced areas in the Panoche Mountains, sheep focused grazing on giant kangaroo rat precincts and left the growth of grasses in intervening spaces largely untouched (Williams in litt. 1985). Our data show that cattle behave similarly. Activities of giant kangaroo rats benefit livestock production by increasing the productivity of grasses and forbs on their precincts. The net gain in forage averaged 31%, when growth on and around precincts are combined for the two years with sufficient rainfall for plant growth (Table 4). Additionally, the 43% of the rangeland forage found on giant kangaroo rat precincts had an average of 4.2% more protein than areas surrounding precincts (Table 7). Cattle were the primary beneficiaries of this increased productivity and nutritional quality, focusing their grazing in the greener, lusher-appearing growth on precincts, and consuming about 60% of the production on precincts before the plants had died and dried (Table 4). They grazed the nitrogen-rich tops more then the nitrogen-poor lower stems, Cattle ate only about 21% of the plant biomass surrounding precincts-evidence of their favoring the growth on precincts.

Greater quantities of soil nitrogen probably accumulate on precincts over several years through the activities of the giant kangaroo rats. They harvest and move nutrient-rich seeds to their burrow systems, where they are consumed. Most of their time is spent on the precincts (Braun 1985) and fecal and urinary wastes are deposited mostly there. These activities, coupled with constant burrowing and incorporating seed hulls, chaff and other plant litter and animal wastes into the soil, result in greater nitrogen content. This soil microenvironment probably is more favorable for plant growth, and may promote greater numbers and activity of nitrogen-fixing organisms. If these hypotheses are correct, then in areas newly colonized by giant kangaroo rats, nitrogen levels in the root zone of soil and plant productivity on precincts would not be significantly different from values for surrounding ground.

Differences in soil water (Table 8), measured only a single time during drought in February 1989, were not as expected from the infiltration hypothesis of Grinnell (1932) and Hawbecker (1944). Yet, apparently insufficient rain fell by February to mask differences in soil moisture resulting from the previous year’s plant growth. Heavy grazing by cattle in pasture and their preference for grazing on precincts reduced the surface area of plant leaves and lowered transpiration of water during the growing season in comparison to the nongrazed Reserve. That the soil on precincts on the Reserve held less water is probably due to the greater transpiration from the larger volume of herbage on precincts in 1988. Water may infiltrate loose soil on precincts more readily than on the harder-packed ground between precincts, but the latter areas are often lower and probably accumulate runoff from the edges of mounded precincts and other higher ground during heavy rains. Water probably also evaporates more readily from the bare, loose dirt on precincts, negating some potential gain from greater infiltration rates. The net balance in 1989 appeared to favor transpiration and evaporation from the soil surface, resulting in lower water content of the upper 15 cm (6 inches) of soil on precincts (Table 8). In years with greater rainfall, when effects of the previous season's transpiration are overcome, the relative amounts of soil water may be greater on precincts where water may infiltrate faster

Our observations convince us that the kangaroo rats and antelope squirrels eat an insignificant amount of green herbaceous material and do not adversely impact livestock by competing for green forage. If livestock were removed from the range at about the time annual grasses ripened and dried, their grazing probably would have little impact on small mammals because of the abundance of seeds remaining. Removal of livestock upon ripening of the annual grasses and forbs is also good animal husbandry because once plants of California annual rangelands dry out, their nitrogen content drops precipitously and cattle do poorly, often loosing weight when kept on this range. Cows held on dry annual rangelands are thin, producing fewer and smaller calves that weigh less at weaning and bring a lower price per pound than calves from cows fed supplements or pastured elsewhere (Wagnon et al. 1959).

Shrubs. Cattle also exhibited a significant impact on woody shrubs on the Elkhorn Plain (Table 5, Figure 6). All species, including unpalatable desert thorn and ephedra, were browsed heavily by cattle between summers of 1988 and 1989, when there was no green herbaceous forage and mulch largely had been consumed, but not in winter and spring of 1988 when herbaceous production was high. California buckwheat *(Eriogonum fasciculatum),* winter-fat *(Eurotia lanata),* and eastwoodia apparently were not browsed significantly by cattle in the 1987-1988 season (Williams and Tordoff 19883). Buckwheat and winterfat are relished by cattle, but eastwoodia is not a plant that they normally eat (Sampson and Jespersen 1963). Buckwheat and winterfat grew almost exclusively on the steep slopes and narrow ridges uphill from the watering trough. Cattle rarely grazed in these areas compared to the flat and gently sloping ground downhill from the watering tank, sites where Anderson desert thorn and ephedra were common. Cheeseweed *(Hymenoclea salsola)* grew mainly in the gravel soils along the bottoms of arroyos where slopes are gentle. The latter three species were most heavily browsed by cattle, but only ephedra was considered by Sampson and Jespersen (1963) to be palatable to livestock; they ranked it fair to poor for cattle.

Dramatic changes in shrub cover in pasture occurred during the 1988-89 season when several shrubs were killed by cattle browsing. Growth in the 1988-89 season was mostly eaten by livestock, and additional shrubs died (Table 5, Figure 6). Release from browsing in the 1989-90 season resulted in a modest shrub growth in pasture. Few shrubs died on the Reserve in 1987-88 and 1988-89. Yet, some less hardy shrubs on the Reserve, which survived in the absence of browsing in 1988 and 1989, succumbed to drought in 1990. This caused a decrease in shrub area on the Reserve, while shrubs in pasture registered a slight gain. Shrubs on the Reserve lost area in 1990 because some shrubs or branches died before measuring. All species of shrubs decreased in size on the Reserve in 1990. When the changes from the start of the study (1987) through 1991 are compared (Table 5), however, the total area of shrubs on transects was greater on the Reserve than in pasture.

Another factor affecting shrub response to drought was a greater Reserve of soil water in the pasture compared to the Reserve. Grazing livestock in 1988 and 1989 reduced the extent of herbaceous and woody vegetation, reducing the transpirational surface area and conserving soil water in pasture compared to the Reserve (Table 8). The differences in soil water seems to have been sufficient to promote modest growth of shrubs in pasture, especially since there was little competition with herbaceous plants for water in 1990. High amounts of rainfall late in the wet season in 1991 may have been largely responsible for the great gain in shrub area on both sites,

Mulch. Differences in mulch levels measured in 1987 and 1988 were smallest on the steep hillsides with slopes between 5 and 10° and in the arroyos where total productivity was low and litter was widely scattered in clumps (Williams and Tordoff 19883). In the 1987-88 grazing season, when herbaceous material was available, cattle rarely went upslope from water tanks on the steep hillsides supporting the shrub/subshrub association. The nearly continuous presence of cattle in the area in 1988 and to June 1989, coupled with the late rains and drought, however, eliminated accessible forage in preferred sites on the plains and gentle slopes. Cattle were forced to graze and browse on herbs and woody shrubs on steep slopes. Cattle were routinely seen on steep hillsides from November 1988 through June 1989.

Data in Tables 4 and 6 suggest that mulch does not decompose readily in this environment -- mulch values for the Reserve were substantially greater than productivity values the same year, except 1991. Mulch collected in 1990 was mostly the remains of herbaceous growth in 1988, as there was low productivity in 1989 and almost none in 1990; little mulch remained in August 1990 (Figures 4 and 7). Cattle consumed most of the herbaceous mulch produced in the 1987-88 and 1988-89 growing seasons in the pasture. Wind storms between summers 1990 and 1991 caused noticeable erosion and probably accelerated loss of mulch. Rain storms in September 1990 and March 1991 washed away additional organic material,

Using our method, mulch levels were about 725 lb/acre in 1989 at the end of an intense period of grazing. By 1990, mulch had decreased to 79 lb/acre. Mulch from previous years was so slight that mulch levels in 1991 were mostly the remains of production that year (Figure 4). Our method of measuring mulch does not distinguish residual herbaceous material for previous years from the current years' growth. There is, however, no cost-effective way to separate the two groups of plant litter.

Areas not grazed in successive wet years may have a large buildup of mulch and become highly prone to wildfire, interfere with locomotion of animals requiring large patches of bare ground, and change the species composition of the plant community. Yet, grazing at the intensity seen on the Elkhorn Plain in 1988-89 also threatens the community from soil erosion.

Erosion

We have no direct measure of the severity of soil erosion, but small dunes appeared on the southern Elkhorn Plain in August and September 1990. Previously, we had seen no evidence of dune formation. Soil on the Reserve was not much better protected from erosion because only in 1988 was primary production sufficient for plant litter to accumulate. Water erosion in September 1990 was extensive both on the Reserve and in pasture.

We believe that differences in pedestal heights of malpais blue grass crowns on the Reserve and pasture were due to soil erosion. These data suggest that the pasture lost about 9.8 mm (0.39 inch) more soil to erosion than the Reserve, a 65% difference resulting from a single episode of cattle grazing between November 1987 and June 1989. Measurements of crowns and pedestals show that crowns of smaller diameter have shorter pedestals, suggesting younger age. The lower pedestal height and steeper regression slope of crowns on the Reserve compared to pasture can be explained as lesser overall erosion and a more constant rate of erosion over time, assuming there is a positive relationship between crown diameter and age of crowns, and that projecting crowns in this perennial bunch grass at least are partly due to erosion of soil at their bases. The greater pedestal height and flatter regression slope of crowns in the grazed pasture suggest a much greater rate of erosion recently, in that there was less difference in height between large and small crowns, based on regression, but a significantly greater absolute height of pedestals compared to those on the Reserve.

Our informal observations suggest that soil erosion was greatest between July 1990 and April 1991. A tropical storm in September 1990 dropped about 2.5 cm of rain in a few hours, which led to sheet flow, flash floods, and noticeable soil erosion. Severe dust storms started in July 1990 and continued into winter on the Elkhorn Plain and summer 1991 on the Carrizo Plain. Other torrential rain storms occurred in March 1991. Leaving cattle in the pasture from autumn 1987 though the 1988-89 precipitation season, when herbaceous production was slight, reduced mulch and left soils highly vulnerable to erosion. Erosion was noticeable on both the Reserve and pasture, but differences in grazing treatment only was for that one period.

Seed Caches of Giant Kangaroo Rats

Aspects of seed caching behavior of giant kangaroo rats was first reported by Shaw (1934), who described in detail the small, thimble-sized pit caches on the surface of precincts. Shaw (1934) measured underground larders, and described the sequence of cutting and curing seed heads in surface pits, then moving the caches underground. Later, Hawbecker (1944) described seed head caches placed in large piles on the surface of precincts to dry in the sun. Surface piles that Hawbecker measured averaged about 5 x 10 x 61 cm, considerably smaller than the surface caches found in this study (Table 10).

There appears to be considerable individual and geographic variation in seed-caching behavior of giant kangaroo rats. On the Elkhorn Plain, pit caches of giant kangaroo rats typically were closely spaced and were covered with a layer of loose dirt. Some caches consisted of a mixture of several liters of loose dirt and seed heads piled on the surface and others contained only seed heads. These caches were not disturbed so it is not known if pit caches were always located under the pile, but sometimes traces of pit caches could be seen under haystacks. Some caches, consisting primarily of pits, had scattered seed heads on the surface; others had piles of seed heads from 0.1 to several cm deep covering portions of the pit caches. In 1988, in any area of about a hectare could be found caches consisting wholly of closely spaced pits, mixtures of dirt and seed heads piled on the surface, and large haystacks. Other years and in some parts of their geographic range, haystacks were seldom or never observed. This may have been due to depredation by livestock in some cases, but also probably reflects differences in caching behavior (Williams in press).

Caching of seed heads in large surface piles or haystacks by giant kangaroo rats was seen only in 1988 in the Carrizo Natural Area. In 1989, few seeds were produced and only a few, small haystacks were noted. Small clusters of pit caches were found, however, on most precincts in 1989. We did not attempt to measure size of clusters because to do so would have required sweeping away dirt covering the pits and otherwise disturbing caches. Density of clusters of caches in grazed pasture were greater on the east side (58.6/ha) than the west side (46.7/ha) of the Reserve, the latter being close to the water trough where cattle were concentrated. Density on the transect on the Reserve, next to the western boundary, was 29% greater (65.8/ha) than the adjacent grazed transect.

In 1990 there was no seed production by annual plants and no caches were seen. Antelope squirrels consumed many of the ephedra flowers, the only ones produced, shortly after pollination while the ovaries were swollen and moist. In 1991, we saw no haystacks and found few pit caches despite an abundance of seeds. Absence of surface caches in 1991 might have been due to the later, hotter season when seeds ripened, negating the need for drying on the surface in pits or piles before being moved underground. The kangaroo rats may have gathered and taken seeds directly underground. Lack of caching also may have been due to an overlap between seed ripening and reproduction of the kangaroo rats. In 1988, seed ripening and caching occurred at the close of the reproductive season-few females were still pregnant or lactating at that time and the testes of males had shrunk in size. In 1989 reproduction was over for the year before caching was noted. In 1991, reproduction continued through summer and animals may not have had sufficient time to devote portions both to social interactions related to reproduction and caching large stores of seeds.

Consumption by cattle explains the significantly greater volume (57%) for caches on the Reserve compared to those in the pasture in 1988 (Table 10, Figure 10). The significantly greater area covered by caches (36%) in the pasture might have been due to scattering of seed heads as cattle ate the haystacks or it might represent greater numbers of pit caches with traces of seed heads on the surface, or both. Direct evidence that loss of haystacks to cattle reduced survivorship of owners is lacking. Higher density of caches in 1989 on the nongrazed side of the fence compared to the grazed side probably reflects lower density of giant kangaroo rats where cattle concentrated near the water trough. Caching and curing seed heads in pits covered with loose dirt, and mixing seed heads with loose dirt on the surface of the precinct probably do not result in loss to cattle. These observations suggest that giant kangaroo rats experiencing loss of haystacks may have responded by increasing the amount of seed heads cached in pits. This hypothesis can be tested by sweeping the surface of precincts clear of loose dirt after caches have been moved to larders in burrows and counting numbers of seed pits in Reserve and pasture.

Individuals that experience significant losses to depredating livestock also may be able to compensate by continued seed gathering during summer and fall. This likely takes much greater effort per unit of seeds gathered because seed heads have shattered and dispersed their seeds, and fewer seeds are available, having been consumed by ants, birds, other granivores, and cattle. Clearly, though, giant kangaroo rats continue to gather seeds throughout the year, even after their main harvest has been stored and their larders filled.

Numbers of active precincts as evidenced by seed caches, may provide the best measure of the number of resident animals, and may be the most efficacious method of estimating populations without the need for trapping. In 1988, densities of seed caches for the Reserve and pasture were, respectively, 29.1 and 28.2/ha. This compares to estimated densities of giant kangaroo rats from capture-recapture of 58.2 and 57.l/ha. Captures included many young that had not dispersed. In 1989, estimated densities/ha of seed caches and of giant kangaroo rats from capture-recapture, respectively, were: Reserve - 59.8, 62.1; and pasture - 54.8, 56.0. In 1988 through May, there were 66 young marked on plots 1 and 2, compared to 24 in 1989. Young were 51% of all recruits in 1988 but only 23.8% of the 1989 recruits (Table 20, Figure 17). Counts of caches both years were made about 4 weeks after the spring population census. Given the lower number of young and the earlier cessation of reproduction in 1989, numbers of caches in 1989 probably reflect a greater number of resident kangaroo rats compared to 1988. Whether or not young still living in the same natal den as their mother contribute to a single seed cache on the precinct, make their own cache, or do not engage in this caching behavior is unknown.

Clusters of pit caches are more difficult to locate than haystacks, especially if there is much loose dirt on a precinct, which is often the case from May through autumn. Unfortunately, haystacks are made less frequently and apparently are not universal geographically or individually. Yet, in all but one case out of 126 precincts examined in a 4.4-h area in 1988, there was only a single area on precincts devoted to seed caches. In that one case, two large surface piles were separated by about 2 m. On many precincts, haystacks started out from two or more small, independent piles located less than 1 m apart, but eventually merged as they grew.

Although not reported in the literature, some populations of Heermann's kangaroo rat also cut and cache seed heads in haystacks. This has been seen in the southern San Joaquin Valley around the Elk Hills (R. Anderson and L. Spiegel pers. comm.), and in western and central Merced and Madera counties (D, F. Williams unpubl. data). Surveys and population censuses for giant kangaroo rats that depend solely or mainly on the presence of haystacks to identify giant kangaroo rats are unreliable.

Blunt-Nosed Leopard Lizards

Population Dynamics

The overriding factor affecting blunt-nosed leopard lizards on the Elkhorn Plain from 1989 to 1991 was drought. The lack of rain meant that cattle did not graze the Plain for most of this period. Cattle were last on the Plain in June 1989. Therefore, both plots were affected about the same since.

Yearly total rainfall can be deceptive, however, for predicting affects on these lizards. The 1989-90 precipitation period produced only 38.6% of the long-term mean (85.6 and 222 mm, respectively) and little annual plant production occurred (Figure 4). Rainfall in the winter of 1988-89 was not especially high, with only 48.2% of normal precipitation, but there was more annual plant production. The rainfall in the winter of 1987-88 (116.2% of normal) led to high amounts of annual plant production. The rainfall total on the Reserve in the 1990-91 season was about 83.7% of average, but it led to a high amount of annual plant productivity, primarily because of timing of the rains (Table 3). Blunt-nosed leopard lizards were affected by these changes in precipitation and plant production.

Comparisons of the number and sizes of lizards found during the June and August censuses on the plots in 1989-1991 show how blunt-nosed leopard lizards responded to differences in precipitation. In 1989, many adults and subadults were found. In 1990, following a dry winter, no adults were found on either plot. We have no evidence that adult blunt-nosed leopard lizards came aboveground in 1990, a year of low abundance of prey. Only subadults, hatched in 1989, were seen. Subadult leopard lizards probably do not have sufficient energy reserves to remain underground, and must forage on the surface to grow sufficiently to breed and store fat reserves, even if the gains are low and the risks are high. Adults can stay underground at least 1 year beyond the normal period of inactivity of about 9 months (21 months total). On average, the chances that the next year would provide enough food to recover from any extra energy loss and allow for breeding probably outweigh the risks of predation and energy depletion from being active during severe drought. Observations during April-June 1991 support this hypothesis. We found that older adults were active on both plots, as were individuals that were subadult in 1990.

Density estimates of blunt-nosed leopard lizards during this time decreased from 8.2/ha on the Reserve and 4.9/ha on the pasture plot, in June 1989 (Table 13), to 0.7/ha (no range) on the Reserve and 1.1 per ha (0.9 - 1.3) on the pasture plot in June 1990. However, by June 1991, the estimated densities of lizards increased to 5.3/ha on the Reserve and 5.7/ha on the pasture plot. This fluctuation in densities among years can most easily be explained by the absence of adults aboveground in 1990. Some adults probably died while underground in 1990, but many survived this period of inactivity.

An even more dramatic change occurred in the censuses of blunt-nosed leopard lizards in August. In 1989, we found a large number of hatchlings on the Reserve and about half as many on the pasture plot. However, no hatchlings were found in 1990. Only one subadult blunt-nosed leopard lizard was found on either plot during 5 days of censusing. The lack of reproductively-mature lizards aboveground in 1990 meant that no young were produced. We again found many hatchling blunt-nosed leopard lizards on both plots in 1991, a year when older adults were again found aboveground. Densities of hatchlings were similar in 1989 and 1991.

Another major difference between 1989 and 1991 was the duration of activity of hatchlings. Cool weather in the fall of 1989 caused cessation of activity by hatchlings beyond about mid September, for a total of about 1.5 months above ground. In 1991, warm weather continued until the end of October and hatchlings remained active for about 3 months. Numbers of grasshoppers and side-blotched lizards also continued to increase throughout this period.

Predators also may have been fewer in 1991 than previous years. Loggerhead shrikes were absent from the Elkhorn Plain in 1991. A check of the barbed wire fence that surrounds the Reserve in September confirmed this as no prey of shrikes were found impaled on barbs. In 1988 and 1989, we found many grasshoppers, crickets, and young-of-the-year leopard lizards impaled on the fence. The fewer predators, greater abundance of prey for lizards, and the extended period of warm weather combined to allow high survivorship and rapid growth of blunt-nosed leopard lizards hatched in 1991.

We saw more than one or two adult blunt-nosed leopard lizards active into August, 1991 on the Elkhorn Plain for the first time since 1987. Only a few adults were active in early July 1989, and only one adult was seen on each plot in August. No lizards were found in July 1990, but we did see one subadult on each plot in August and September. In 1991, however, we found seven adults on the Reserve and six adults on the pasture plot. The extended period of adult activity in 1991 may have been due to the abundant food supply and the need for adults to regain fat deposits depleted during 21 months underground, and the prolonged breeding season, or both. Yet not all adults remained active aboveground into August. Many were not seen after the June census.

There are differences in numbers of leopard lizards between the Reserve and the pasture plot that first were seen in 1988 and continued into 1991. Although most differences were not significant, the Reserve consistently maintained about a 1.5 to 2 times as many lizards as the pasture plot. These differences appear not to have been related to grazing by livestock because they were seen immediately during the study and remained throughout the drought.

There also appears to be a behavioral difference in the response of blunt-nosed leopard lizards to intruders based on the amount of available cover. Generally, these lizards prefer open habitat and run to bushes or down rodent burrows when approached. We saw this during 1989 and 1990. However, in 1991, most of the adults we found during censusing held still in the herbaceous vegetation and only flushed when we were within a few meters. Remaining stationary probably is a behavioral response to the thick vegetation, which greatly impedes their ability to run. We caught a few adults by hand in 1991, and many of the hatchlings were caught by hand in August as they hid under dry herbaceous plants. The disadvantage of dense ground cover, which impedes the movement of blunt-nosed leopard lizards, may be overcome by the concealment that the vegetation affords individuals that do not flush readily.

Reproduction

Our estimate of 3.29 eggs/female is similar to other averages for this species. During the 1970s, blunt-nosed leopard lizards from the San Joaquin Valley floor had an overall clutch size of 2.90 (*n* = 61), with a range of values for different sites from 2.64 to 3.33 (Tollestrup 1982). We found an average of 2.67 eggs per female in June on the Pixley National Wildlife Refuge (Williams and Germano 1991), on the valley floor.

There are indications that female blunt-nosed leopard lizards on the Elkhorn Plain produced multiple clutches in 1991. One female on the Reserve was carrying different numbers of eggs one month apart. Newly-hatched blunt-nosed leopard lizards (45-50 mm SVL) were found three times in August and September. Also, SVLs of young found on the Reserve in September 1991 are clustered in three groups (Figure 25), suggesting that

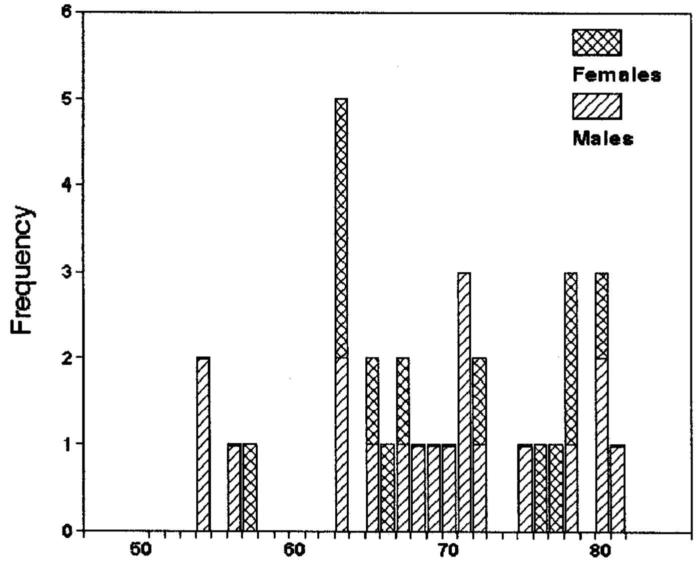

Figure 25. *Snout-vent lengths (SVL) of hatchling blunt-nosed leopard lizards captured on the Reserve plot, Elkhorn Plain, San Luis Obispo Co., during September 1991. Three fairly distinct groups are evident: hatchlings 54 - 57 mm SVL, 63 - 72 mm SVL, and 75 - 81 mm SVL.*

some females laid as many as three clutches in 1991. Yet differential growth rates of individuals and asynchronous egg-laying by females could account for this wide range of hatchling SVL. More work is needed to determine if multiple clutches occur in blunt-nosed leopard lizards. Determination of the mean number of clutches is an important life-history parameter that bears on viability of populations.

Prey Abundance

Grasses and forbs provide food and cover for grasshoppers. Soil moisture is a critical factor in reproduction in that eggs are laid in the soil. Drought and the lack of herbaceous ground cover in 1990 appeared to have adversely impacted grasshoppers. Numbers were low in 1990 and high in 1991. The differences in successive years suggest that grasshopper populations can quickly increase to great abundance when food and moisture conductions are favorable.

The high abundance of grasshoppers on the Elkhorn Plain in 1991 was not found at two other sites within the range of the blunt-nosed leopard lizard where we worked. We found 90% fewer grasshoppers during censusing for blunt-nosed leopard lizards in June at Pixley National Wildlife Refuge (Williams and Germano 1991). Few grasshoppers were found in August during surveys for blunt-nosed leopard lizards on the Tule Elk State Reserve (Germano 1992). A major difference between these sites and the Elkhorn Plain is that Pixley and the Elk Reserve are surrounded by irrigated agriculture and the Elkhorn Plain is not. It is possible that the general use of insecticides in irrigated croplands reduced grasshopper populations at those sites.

In both 1990 and 1991, the numbers of side-blotched lizards increased throughout the yearly activity period (Table 17). In 1991 high numbers of side-blotched lizards were counted from August through October. Although adult side-blotched lizards may be too large for hatchling blunt-nosed leopard lizards to eat, young-of-the-year side-blotched lizards are abundant when blunt-nosed leopard lizards are small. In September 1991, we saw a juvenile (80 mm SVL) leopard lizard eat a hatchling side-blotched lizard. Side-blotched lizards were found to comprise a small portion of the diet of blunt-nosed leopard lizards by Montanucci (1965) and Kato et al. (1987), although vertebrates in their diet were not recorded in one study on the valley floor (Tollestrup 1979).

Small Mammals

Population Dynamics of Kangaroo Rats

Impacts of cattle grazing on populations of kangaroo rats were not apparent in this study, which is expected from the lack of grazing most years and the overriding influence of drought (Figure 16, Table 19). Generally, population sizes on the pasture plot were lower than the Reserve plot in 1989 and 1990 for both kangaroo rat species, although differences were not significant at the 5% probability level. Density estimates, however, were significantly different between plots in April and August 1990 for giant kangaroo rats. The reserve plot had higher density in April, but lower density than the pasture plot in August. The two species showed different population changes over the 5-year period.

Giant Kangaroo Rats. Giant kangaroo rats increased in numbers in 1988 during a year of high plant production, sustained high densities in 1989 despite drought, probably with the help of large seed stores made in 1988, then decreased markedly in 1990, and 1991. The populations reached their low points in August 1991. Although mortality from the effects of the extended drought were a factor in the decline, we believe that flooding and hypothermia from high rainfall in late March 1991 contributed to mortality that year, even though the rains promoted high plant productivity. This productivity created conditions for a rapid population increase starting in summer 1991, We found evidence of this in the Soda Lake population, the only one trapped monthly after August,

Recruitment of giant kangaroo rats was highest in 1988 during high plant production-young and adults of unknown age contributed equally to the population of new recruits on plots (Figure 17a, 17c). Recruitment of young was much lower in 1989, but recruitment of adults ofunknown age was nearly as high as 1988, showing that the drought in 1988-89 affected reproduction much more than survival of adults. Recruitment of young fell to zero in 1990 after two years of drought, and fewer adults showed up on plots. Recruitment of adults continued to decline in 1991, while that of young increased. This is as expected if adults new to plots were mostly born 2 or more years earlier and probability of survival was decreasing with increasing age.

Appearance of adult recruits in high numbers in 1988 through 1990 suggests that at the highpoint, population densities may have exceeded saturation of available habitat, and that many animals were forced to remain in portions of their natal dens until opportunity to inherit or disperse arose. We believe this was the case in 1988 and 1989 when we saw one or more fully-grown young remain in their natal precincts with the adult female into at least October. Another factor that could have contributed to recruitment of adults was the use of seeds as bait while trapping. However, plots 1 and 2 were trapped only in the April and August censuses after February 1989, so attraction to the plots from use of bait was probably minimal.

All plots had a small core of long-lived residents, with a rapid turnover in higher proportion of the populations. Animals first captured as young had a higher, though not significant, duration on plots (Table 21). Exponential curves based on times between first and last capture have forms similar to expected survivorship curves, with a high proportion (55-58%) disappearing within about 100 days on different plots (Figure 20). Developing life tables and survivorship curves was complicated by lack of reproduction and recruitment of young during drought and the relatively high proportions of new recruits that were adult-sized and of unknown age. Monthly or more frequent trapping on plots is necessary to develop more precise information on birth and disappearance, and a relatively large, trappable population is required to obtain data on sufficient individuals from birth to disappearance and presumed death. Plots devoted to studies of grazing provided the longest interval of trapping, but monthly trapping would have compromised the study by masking or enhancing effects of grazing. Little successful reproduction occurred in the Elkhorn Plain populations after plot 3 was established and trapped monthly to measure reproduction, recruitment, and survival. The Soda Lake colony was too small at the outset, and the animals too trap shy to yield necessary data, but its size now exceeds that needed.

Giant kangaroo rats have an adaptable reproductive pattern that appears to be affected by both population density and availability of food. During times of relatively high density on the Elkhorn Plain, between 1987 and 1989, females had a short, winter reproductive season with no evidence of polyestry nor breeding by young-of-the-year. This was true both in years of high plant productivity and drought. Yet simultaneously a few miles away on the Carrizo Plain, where population density was lower and there were many vacant precincts, animals were breeding in summer during drought (presumably a continuation of breeding started in winter). Availability of food did not appear to differ, but we have no measure of seeds. Neither site had green grasses or forbs that might account for continuation of reproduction where green herbs were present (Rowsemitt and O'Connor 1989). Most females in the population on the Carrizo Plain also reproduced in 1990, whereas only a few females in the Elkhorn Plain showed evidence of reproduction and no young were recruited. Rainfall and plant growth were essentially the same at both sites in 1990. Few plants grew beyond the cotyledon stage before dying and no seeds were produced. With the decline in population density and the late growth of plants in 1991, for the first time giant kangaroo rats on the Elkhorn Plain bred in summer, some females had more than one litter, and young-of-the-year bred (Figure 18). This pattern was repeated at sites on the Carrizo Plain. Breeding there in 1991 extended from February to October, with a short quiescent period in November, then breeding resumed in December (Figure 19).

Annual weight cycles of adult giant kangaroo rats occurred even in the absence of reproduction. In 1989, mean mass was greatest in April when all but one or two of the population were nonreproductive and green vegetation was not available (Figure 21). The failure of females to gain weight in late autumn and winter of 1989 and 1990 was probably due to drought and lack of green grasses and forbs, and presaged the steep decline in population numbers in 1990 and 1991.

Short-Nosed Kangaroo Rats. Numbers of short-nosed kangaroo rats declined throughout the 5-year period. The decrease in density in 1988 and 1989 compared to 1987 may have been partly due to the increased numbers of giant kangaroo rats (Figure 16). Numbers became too small to calculate population estimates with acceptable precision in 1989 through 1991, but there was a clear trend of population decline on both plots, as well as on plot 3, over the 5-year period. The population of short-nosed kangaroo rats was affected more quickly and dramatically by drought than that of giant kangaroo rats, perhaps because short-nosed kangaroo rats do not cache large quantities of seeds in their burrows. Animals that must rely on frequent foraging on the surface for scarce seeds probably have higher predation rates and also may be more vulnerable to other forms of mortality. Short-nosed kangaroo rats also may be affected more by flooding and hypothermia from water in their burrows on the Elkhorn Plain. There, and elsewhere where they coexist with giant kangaroo rats, their burrows are concentrated in sandy arroyos, an area avoided by giant kangaroo rats (Williams and Tordoff 1988a). Also, short-nosed kangaroo rats coexisted with giant kangaroo rats on the Elkhorn Plain only where there were shrubs, suggesting that absence of the former species from shrubless areas was by competetive exclusion. Our informal observations of animals around camp were that giant kangaroo rats chased short-nosed kangaroo rats on sight. Shrubs may provide visual and escape cover, allowing coexistance. A large increase in density of giant kangaroo rats would be expected to cause a decrease in density of short-nosed kangaroo rats under these circumstances.

Lack of successful reproduction, shown by absence of young recruits, appears to have been a major factor in the population decline, especially in 1989 through 1991 when no young recruits were seen (Figure 17b). The small number of captures on the Elkhorn Plain in 1991, and the failure to catch young before August prevented determination of the breeding pattern then. Yet, evidence of reproduction in March and April on plot 3 and the appearance of young recruits in the August census prove successful reproduction, and suggest a longer reproductive season in 1991.

Longevity of short-nosed kangaroo rats appears lower than giant kangaroo rats, based on duration between first and last capture. Short-nosed kangaroo rats averaged about 60 to 130 days shorter duration than giant kangaroo rats (Table 21). Young had a shorter mean duration than adults, the reverse of the situation with giant kangaroo rats, but numbers of young short-nosed kangaroo rats (7) were low and these findings may not reflect population trends. No short-nosed kangaroo rats had durations longer than about 800 days, whereas 2% of the giant kangaroo rats had intervals longer than 800 days (Table 22, Figure 20). Again, because of lower numbers of short-nosed kangaroo rats, these apparent differences may be due to chance. Only 119 short nosed kangaroo rats were captured on plots 1 and 2 in the 5-year period. If about 2%, on average, live longer than 800 days, the expected number would be between 2 or 3 animals (2.38) a value too low to have a high probability of occurring on our plots and being trapped at appropriate times.

Feeding Experiment

Providing seeds to giant kangaroo rats had a significant effect on subsequent population sizes on both experimental plots compared to their controls (Figure 24). By June 1991, both experimental plots, where seeds were provided, had from 2.5 to 3.2 times as many active burrow systems as their nonfed controls (Table 25). Because of difficulties with trapping animals we were unable to determine if differences in numbers were due to greater survival, recruitment of animals from surrounding areas, or reproduction. Greater reproduction does not appear to account for the differences into June, because little reproduction was apparent in any of the populations prior to April or May. If gestation takes about 1 month (27 days), as determined for banner-tail kangaroo rats (Holdenried 1957), weaning occurs about at 3.5 weeks, and independence occurs at about 8 weeks of age, then young conceived on 15 April would not begin dispersing to vacant precincts before about 24 June. Yet differences in numbers were greatest on the four plots by April.

We think that the initial increase in numbers seen on the experimental plot on the Carrizo Plain, between March and April, was due both to recruitment of animals to the plot from surrounding ground and higher survival on the plot. During the time the number of active burrows increased on the experimental plot by 29%, they declined on the control plot by 63%. This decline was apparently due to death of residents, probably from predation, starvation, or other factors related to food scarcity. On the Elkhorn Plain, numbers decreased in April compared to March on both plots, but the decrease was significantly greater on the control plot (93% and 62% declines, respectively).

Changes in population sizes of giant kangaroo rats on plots between March and April coincided with torrential rain storms over a few days in late March (Figures 3 and 24) complicating interpretation of results. Plots on the Elkhorn Plain were located on alluvial fans and much of both plots had water running over the surface during these storms. Flooding, with consequent drowning or death from hypothermia, probably contributed significantly to the declines in numbers on both plots between the March and April censuses. Plots on the Carrizo Plain were located on leveler ground and nothing seen suggested wide-spread flooding. Yet, we believe that the high amount of rainfall affected the population in a less direct way. Rainwater probably penetrated deep enough into the soil to spoil seed stores (Grinnell 1932). Significant declines in numbers between April and June on both Carrizo Plain plots could have been caused by loss of food stores to spoilage and ensuing mortality. More seeds were provided in June, and the experimental plot subsequently increased in numbers at a greater rate than the control plot, despite greater plant cover and consequent seed production on the control plot (Tables 25 and 26, Figure 24).

Translocated Giant Kangaroo Ruts

The artificial burrows were sufficiently acceptable to induce most translocated animals to remain in place, but the microhabitat at the Painted Rock site apparently was wrong. Low vegetation height and varied microrelief probably are important in avoiding predation, as predation appeared to be responsible for the loss of most individuals in the Painted Rock colony where tall, feral wheat and lack of microrelief probably reduced visibility of predators by kangaroo rats. Unknown to us at the time we selected sites for establishing colonies, the Painted Rock site was within the 95% utilization contour of a pair of San Joaquin kit foxes (P. J. White in litt. 1991). Although most sign of predators were of coyotes, and remains of animals found suggested predation by a small raptor, kit foxes probably also contributed to predation on the colony.

Presence of pocket gophers *(Thomomys bottae)* and an abundance of their holes may enhance successful establishment of translocated colonies. Pocket gophers were present at both sites, and translocated giant kangaroo rats opened and explored many old gopher tunnels in and near both colonies. They appeared to have moved to such burrow systems or incorporated them into their precincts in several instances, Burrows of California ground squirrels also were occupied by translocated animals. Some had moved several meters to ground-squirrel burrows. Yet, we saw California ground squirrels raid seed stores of giant kangaroo rats on the Elkhorn Plain and have indirect evidence that at least one of the kangaroo rats was killed or evicted when a ground squirrel took over his burrow system. Competition probably favors the ground squirrels because of their much greater size. For these reasons translocating animals to sites with moderate or high densities of California ground squirrels is not advisable.

In the Soda Lake colony, one founder was located about 275 m straight-line distance from his release site, and one progeny marked at an artificial burrow was found in the same area, having dispersed a similar distance. However, most animals located off of the plot covering the artificial burrows were unmarked progeny. Spread of animals in the Soda Lake colony was in all compass directions, but where softer soils were encountered, subsequent establishment of new burrows was in a line following the contour where these more friable soils were encountered. By winter 1991, few animals had spread into an area protected from grazing since about 1984. Instead, burrows were spread along the fence line separating grazed from nongrazed ground, but on the grazed side. When softer soils were encountered at lower elevations near the saltbush community around Soda Lake, they spread southwestward in the grazed pasture, but not in the opposite direction in the area that had not been grazed. By April 1992, we had located only 5 or 6 precincts in the nongrazed area, although there were more than 25 precincts on the formerly grazed side within 15 m of the fence, both along its north-south size parallel to the contour and east-west with the slope.

The Soda Lake translocated colony exhibited a high level of reproduction not seen in the natural populations on the Elkhorn and Carrizo Plains. This population increased through the 1989-91 drought period when all natural populations declined substantially. Giant kangaroo rats there had a longer reproductive season than on Carrizo Plain plot 7 in 1990 and produced young while the population on the Elkhorn Plain did not (Figures 18 and 19). In 1991, reproduction appeared to be greater than on the Elkhorn Plain, especially in winter and spring before the late spring rains. Translocated animals were provided with a total of about 3 kg of seeds (2 when moved and 1 a month later) in 1989, but received no other supplements except bait from trapping. Because no small mammals other than a few California ground squirrels occupied the site prior to the introduction of the 30 kangaroo rats, seed reserves may have been higher than in areas occupied by natural populations, and may account for differences in reproduction. The founders came from 16 different localities in different l-m^2 sections and probably represented greater genetic diversity than a natural deme of similar size, and perhaps of populations several times larger. Greater genetic diversity may have contributed to physical and reproductive vigor that were responsible for the higher reproductive performance in this colony.

Background for Recommendations

Studies summarized in this report represent substantial efforts by personnel in the sponsoring agencies to overcome the lack of knowledge on endangered species biology and management. Contributing to recovery of endangered species, by providing information needed to formulate management plans for lands providing habitat for these and other listed and candidate species, was the goal of our studies, which represent only a beginning. The Nature Conservancy and California and Federal resource-management agencies have given high priority to acquiring land for endangered species habitat; but insufficient support has been provided for research and monitoring of endangered species on these lands. Land acquisition does not protect habitat. Interim land management plans have been developed and implemented without prior quantitative assessments of endangered species populations, and without establishment of mechanisms to ensure support for future research and monitoring. Further, these plans are apparently based on assumptions of livestock/endangered species interactions that are not supported by available observations and scientific studies, namely that the interactions are detrimental to endangered plants and animals. We do not know how land should be managed for each species or collectively for the community, and consider lack of knowledge on the population biology of endangered species, compatible land uses, and appropriate management of endangered species habitat to be major barriers to their recovery.

Our results make clear the need for long-term, replicated studies. Yet, they do not provide sufficient understanding of interactions between cattle and the community of endangered species, partly because of drought and lack of grazing during most of the study period, but also because information needed requires greater efforts over longer periods at several sites (Williams and Germano in press, Germano and Williams in press).

The data gathered over 5 years and reported here, together with that of the sixth year now under study, provide information on population dynamics and plant/animal interactions during a severe episode of drought that may not be repeated for many decades. Understanding population responses to rare, stochastic environmental events is important in developing and implementing recovery plans, Continuation of biannual population censuses of kangaroo rats, population studies of blunt-nosed leopard lizards, and annual measures of plant growth and impacts of cattle on herbaceous and woody plants on the Elkhorn Plain plots will increase this understanding much faster than could be achieved by new studies elsewhere.

Yet, the Elkhorn Plain Ecological Reserve is too small (64.8 ha, 160 ac) and incorrectly shaped (L-shaped) to be a good study site for grazing studies. The featured endangered animals are not sufficiently insulated there from the influences of grazing in the surrounding pasture. Further, the topography and location of the water trough result in uneven grazing by cattle on different sides of the Reserve. For experimental studies, better control is needed over stocking and foraging rates than can be achieved in the existing pasture.

Rest-rotation and non-grazed pastures currently are the sole options for land management in the Carrizo NA. Their effects on listed species must be measured. Some pastures also should receive grazing annually at stocking rates common in the geographic ranges of these endangered species. Studying this level of grazing is necessary because annual grazing will continue to be the prevailing land use on private and public lands elsewhere, and because populations of all endangered species of the San Joaquin desert communities are most abundant and widespread on lands that have been heavily grazed for nearly 2 centuries. Understanding how different levels of livestock use affect the community is essential to making good decisions on endangered species management. We do not suggest that heavy annual grazing is necessary or desirable for the recovery of these endangered species. We would be remiss, however, not to point out these relationships and uncertainties. We think that there may be jeopardy to endangered species from either too little or too much grazing.

Cessation of grazing on large portions of the Carrizo NA, and the 3-year, rest-rotation grazing elsewhere, implemented for interim management, may adversely affect some species by buildup of high levels of mulch, and others by wildfire. Native perennial bunchgrasses are reduced in abundance or eliminated by high mulch levels resulting from long-term suppression of wildfire and absence of grazing (Edwards 1992). San Joaquin kangaroo rats are absent from or found in lower densities in areas protected from grazing (Williams 1985, Williams and Germano 1992), but effects on the other endangered animal species still are unknown. Most native annual plants are absent or less abundant in California annual rangelands protected from both grazing and fire (Edwards 1992). Many perennial shrubs, whose establishment is one goal of the current low- and no-grazing prescriptions, are also vulnerable to fires (Sampson and Jesperson 1963), the frequency and intensity of which are enhanced by lack of grazing and fire suppression. Fire as a management tool to maintain habitats for endangered plants and animals and adverse effects of wildfire on habitats require evaluation.

Replicated population studies of endangered species in pastures receiving the four treatments (no grazing, annual grazing, 3-year rest-rotation grazing, and controlled burns) should start with 2-year pretreatment population assessments, and proceed for 5 additional years, or longer, until a range of annual weather patterns has been included. Studies of endangered plants and animals and their interactions with each other and livestock should be combined where and when feasible. Suggested protocols for population studies of blunt-nosed leopard lizards and kangaroo rats were presented by Germano and Williams (in press) and Williams and Germano (in press).

New plots should be established for these land management studies. Plots should be located near the middle of a section (259 ha, 640 ac) or more of land with a given management protocol (e.g., annual grazing, no grazing, fire). All plots should receive identical treatment for a 2-year period prior to a change in treatment on experimental plots. During that time, featured species on plots should be inventoried, individuals permanently marked, and population estimates made at least two times per year. This will result in pretreatment population data against which future changes can be measured and associated with one or another management protocol. Plots for management studies should not be trapped or inventoried more frequently than necessary to monitor population dynamics; two or three censuses per year are sufficient. Replicates should be placed in different plant communities representing the range of habitats of the endangered species.

Separate plots receiving different management treatments should be established where reproduction, recruitment, and survival can be studied by monthly or more frequent sampling. For kangaroo rats, females should be monitored almost continuously from beginning to end of the reproductive season, Young should be monitored frequently to gather data on growth rates, reproduction, and dispersal times and distances. Reliable information is needed on numbers of young produced, especially for giant kangaroo rats, that can be most easily obtained by bringing several pregnant females into captivity and maintaining them until they give birth and raise their young to weaning. The offspring also would provide needed information on growth rates for this species. Female blunt-nosed leopard lizards need to be monitored almost continuously between when they are first gravid in spring and disappearance underground in June or July. Frequent inventories from when hatchlings start emerging until only older young are found aboveground also is necessary. Ten-day population censuses for blunt-nosed leopard lizards, using procedures described by Germano and Williams (in press), should be made at least three times, in April-May, June, and late August or early September. These methods will increase the number of lizards detected, balance detectability on plots with different amounts of ground cover, lower variance in population estimates, help overcome other problems of small sample sizes, and provide additional data on home range, movements, and territoriality. The methods, however, require increasing the length and number of lines and two people walking together on adjacent lines on a plot. Four people will be needed to census a grazed and nongrazed plot concurrently, which must be done to negate day-to-day influences of weather on lizard activity.

Ages of adult-sized leopard lizards and kangaroo rats appearing on plots are needed for determining survivorship and age-specific reproduction. Permission and support should be provided for research on methods for aging animals.

Translocating giant kangaroo rats provided valuable information on reproduction, dispersal, and population growth and contributed to development of efficacious relocation methods. Additional relocations should be supported. Establishment of populations in fallow fields is one desired goal. There are thousands of acres of recently fallowed agricultural land in the Carrizo NA that must be restored and repopulated by endangered species as part of their recovery from endangerment. Translocating giant kangaroo rats populations may be a cost-effective way to speed restoration of other elements of the community. Another goal is to discover if inbreeding contributes to the lack of productivity of small, isolated colonies of giant kangaroo rats in the northern part of their range (Williams in press), and if translocating animals from widely scattered sites into these colonies will increase their productivity and population size. Animals held temporarily in captivity to provide data on litter size and growth of young could be one source of animals for relocation. Translocation studies for blunt-nosed leopard lizards and other endangered animals are also needed. Proper support for development and implementation of translocating methods and detailed monitoring for a 3-year post-relocation period is needed.

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APPENDIX

List of Plants on the Elkhorn Plain Ecological Reserve

Amaryllidaceae
- *Brodiaea pulchella*

Boraginaceae
- *Amsinckia vernicosa* (var. *furcata)*
- *Amsinckia tessellata*
- *Pectocarya penicillata*
- *Plagiobothrys* sp.

Compositae
- *Achyrachaena mollis*
- *Anisocoma acaulis*
- *Chaenactis stevioides*
- *Coreopsis calliopsidea*
- *Eastwoodia elegans*
- *Gutierrezia bracteata*
- *Haplopappus acradenius*
- *Hymenoclea salsola*
- *Lasthenia coronaria*
- *Lembertia congdonii*
- *Microseris sp.*
- *Monolopia lanceolata*
- *Monolopia stricta*
- *Rafinesquia neomexicana*
- *Senecio vulgaris*

Cruciferae
- *Brassica geniculata*
- *Caulanthus inflatus*
- *Caulanthus* sp.? (possibly *californicus* or uninflated *inflatus)*
- *Erysimum capitatum*
- *Lepidium nitidum*
- *Sisymbrium* sp.
- *Thelypodium lasiophyllum*
- *Tropidocarpum gracile*

Ephedraceae
- *Ephedra californica*

Euphorbiaceae
    Euphorbia sp.

Fabaceae
    Astragalus didymocarpus
    Astragalus lentiginosus var: *nigricalycis*
    Lotus humistratus
    Lupinus ruber
    Lupinus horizontalis
    Trifolium depauperatum

Geraniaceae
    Erodium cicutarium

Gramineae
    Avena sp.
    Bromus rubens
    Hordeum leporinum
    Poa scabrella
    Schismus arabicus
    Stipa speciosa
    Vulpia microstachys
    Vulpia myuros

Hydrophyllaceae
    Pholistoma membranaceum
    Phacelia tanacetifolia

Labiatae
    Salvia carduacea

Malvaceae
    Eremalche cf. *parryi*

Onagraceae
    Camissonia boothii decorticans
    Camissonia campestris campestris

Papaveraceae
    Eschscholzia lemmonii
    Platystemon californicus
    Stylomecon heterophylla

Plantaginaceae
    Plantago erecta

Polemoniaceae
    Eriastrum plurtflorum
    Gilia clivorum
    Gilia minor
    Linanthus bigelovii
    Linanthus liniflorus
    Microsteris sp.

Polygonaceae
    Atriplex polycarpa
    Eriogonum angulosum
    Eriogonum fasciculatum var. *polifolium*
    Eriogonum roseum
    Eurotia lanata
    Oxytheca luteola
    Rumex sp.
    Salsoa kali

Portulacaceae
    Calandrinia ciliata
    Montia perfoliata

Scrophulariaceae
    Cordylanthus sp.
    Orthocarpus densiforus

Solanaceae
    Lycium andersonii
    Solanum sp.

Ranunculaceae
    Delphinium gypsophilum
    Delphinium Parryi
    Paeonia californica

Umbelliferae
    Lomatium utriculatum

List of Vertebrates on the Elkhorn Plain Ecological Reserve

Reptiles

Cnemidophorus tigris - western whiptail
Gambelia sila - blunt-nosed leopard lizard
Phrynosoma coronatum - coast horned lizard
Uta stansburiana - side-blotched lizard
Crotalis viridis - Pacific rattlesnake
Masticophis flagellum - coachwhip
Pituophis melanoleucus - gopher snake

Birds

Cathartes aura - turkey vulture
Circus cyaneus - northern harrier
Buteo jamaicensis - red-tailed hawk
Falco sparverius - American kestrel
Falco mexicanus - prairie falcon
Callipepla californica - California quail
Geococcyx californianus - greater roadrunner
Tyto alba - barn owl
Asio flammeus - short-eared owl
Zenaida macroura - mourning dove
Calypte anna - Anna's hummingbird
Selasphorus sp. - hummingbird
Aeronautes saxatalis - white-throated swift
Tyrannus vociferans - Cassin's kingbird
Sayornis saya - Say's phoebe
Eremophila alpestris - horned lark
Corvus corvax - common raven
Toxostoma lecontei - Leconte's thrasher
Lanius ludovicianus - loggerhead shrike
Sturnella neglecta - western meadowlark
Euphagus cyanocephalus - Brewer's blackbird
Amphispiza bilineata - black-throated sparrow
Amphispiza belli - sage sparrow
Chondestes grammacus - lark sparrow

Mammals

Sorex ornatus - ornate shrew
Lepus californicus - black-tailed hare

Sylvilagus audubonii - desert cottontail
Ammospermophilus nelsoni - San Joaquin antelope squirrel
Spermophilus beecheyi - California ground squirrel
Dipodomys ingens - giant kangaroo rat
Dipodomys nitratoides - San Joaquin kangaroo rat
Dipodomys heermanni - Heermann's kangaroo rat
Perognathus inornatus neglectus - McKittrick pocket mouse
Onychomys torridus - southern grasshopper mouse
Vulpes macrotis - kit fox
Canis latrans - coyote
Taxidea taxus - American badger
Mustela frenata - long-tailed weasel
Antilocapra americana - pronghorn