

Rodents of Southwestern North America

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Habitat diversity of the Southwest

The Southwestern North America Region as defined by the IUCN/SSC Rodent Specialist Group includes the states of California, Nevada, Utah, Arizona, Colorado, New Mexico, Kansas, Oklahoma, and Texas (Fig. 3.1). Enclosing nearly 3 million km² and extending from the Pacific Coast of California to the southern Great Plains of Texas, it embraces two major mountain ranges (Sierra Nevada and southern Rocky Mountains) and seven major arid regions: California chaparral, Mojave Desert, San Joaquin Valley, Colorado Plateau, most of the Great Basin, and parts of the Sonoran and Chihuahuan deserts.

The varied biotic regions of the Southwestern Region are further fragmented west of the Great Plains into a complex mosaic of montane, desert, and riparian habitats (Crowley 1967, Küchler 1970). Three major influences together have produced this biotic diversity: 1) the extreme topographic diversity of the west; 2) its geographic position spanning mediterranean to continental climates (west-east) and boreal to subtropical climates (north-south); and 3) the shifting distributions of these major climatic regions associated with Quaternary glacial-interglacial oscillations.

The jumbled topography of the Southwestern Region west of the Rocky Mountains had its birth in Late Tertiary

plate tectonic events (Coney 1983). According to Coney, “widespread regional uplift and extensional block-faulting, and associated strike-slip faulting, which collapsed and fragmented large segments of the rising southwestern Cordillera,” produced this complex admixture of mountains, valleys, and plateaus, and “there is nothing quite like [the region] anywhere else on the planet.” This topographic diversity created a wide range of climatic regimes: adiabatic cooling with rising elevation produces cool, mesic mountaintops that in turn produce arid rainshadows on their leeward sides; rivers fed by montane glaciers above tall forests nurture lowland riparian corridors that ribbon through deserts and grasslands.

The Southwestern Region is a great meeting ground of distinct and ancient biotic associations, where east meets west and north meets south. Lush coastal forests of the Pacific Coast, extensive forests of the Sierra Nevada and Rocky Mountains, and scattered high-mountain pockets of cool, mesic habitat stand in stark contrast to the generally dry Southwestern climate. Even the arid regions are remarkably diverse, ranging from eastern grasslands and northern shrub-steppe to southern arboreal deserts and coastal chaparral.

The final ingredient in this biotic goulash is *time*. During the last 1.6 million years, the Southwestern Region



Figure 3.1. Southwestern North America Rodent Specialist Group Region. This region shares many rodent taxa with the states of northern Mexico, which are included in the Middle American Region.

has been swept repeatedly by waves of cool, mesic climate during glacial-pluvial maxima, which then retreated north and up slope during interglacial intervals. Boreal flora and fauna spread south along mountain ranges and across high-elevation plateaus and plains during cooler intervals, while southeastern grassland species spread west along with wetter climates (Harris 1985, 1989, Hafner 1993a, Hafner and Sullivan 1995). With the return of warm, dry conditions, southern species regained the northern lowlands, leaving cool- and wet-adapted species stranded on mountaintops or along rivers and isolated desert springs.

It is abundantly clear from fossil evidence that mammals currently restricted to mesic or montane habitats in the arid Southwestern Region enjoyed a far broader distribution during glacial or pluvial intervals of the Pleistocene (Harris 1985, Hafner 1993a, 1993b). However, it would be incorrect to assume that boreal and arid species simply shifted complementary ranges in response to Pleistocene climatic changes. Instead, the generally equable climate of pluvial periods resulted in mixtures of what we recognize today as two faunal elements (Graham and Mead 1987). Thus, a major component of Southwestern rodent communities during more mesic periods today persists on small, isolated patches of favorable habitat throughout the region.

Diversity of Southwestern rodents

Simpson (1964) and Wilson (1974) each identified a region of elevated mammalian species diversity in North America north of Mexico as occurring between the Rocky Mountains and the Pacific Coast, and between 30° and 40°N: essentially the Southwestern Region. The high species diversity of Southwestern mammals is expressed most dramatically among the rodents, and particularly within three families: Sciuridae (squirrels and relatives); Heteromyidae (desert rodents); and Geomyidae (pocket gophers). Of the rodents found in North America north of Mexico, the following are found within the Southwestern Region:

- 20 of the 22 species of chipmunks (*Tamias*);
- two-thirds of the ground squirrels (*Spermophilus*);
- all species of prairie dogs (*Cynomys*), antelope ground squirrels (*Ammospermophilus*), and tree squirrels (*Sciurus* and *Tamiasciurus*);
- all 37 species (and four genera) of heteromyid rodents; and
- all three genera (11 of 14 species) of pocket gophers.

Although less than one-fifth the size of the rest of the North America north of Mexico, the Southwestern Region has 80.1% of the total species and nearly six times the number of species per area (Table 1.1). In fact, this is an underestimate of the true diversity of Southwestern mammals, as many geographically isolated populations

Table 3.1. Comparison of number of rodent species, area, habitat types (Küchler 1970), number of separate patches of different habitat types, and average patch size for states in the Southwestern Region.

State	Species (n)	Area (10 ³ km ²)	Habitat types	Separate patches	Patch size (10 ³ km ²)
California	88	411	22	224	1.83
New Mexico	71	315	14	108	2.92
Arizona	68	295	16	128	2.30
Utah	62	220	19	106	2.07
Texas	57	692	18	50	13.84
Colorado	55	270	17	100	2.70
Nevada	55	286	12	115	2.49
Oklahoma	43	181	14	52	3.48
Kansas	34	213	8	18	11.84

are not recognized at the species level. For example, populations of various chipmunks (*Tamias*) and tree squirrels (*Sciurus* and *Tamiasciurus*) are often found on montane “islands” peppered across regional deserts, and small populations of voles (e.g., *Microtus californicus* and *M. pennsylvanicus*) persist in isolated riparian “oases” in arid regions.

The effects of habitat fragmentation and diversity on rodent species diversity can also be seen within states of the Southwestern Region (Table 3.1). Area of each state is, by itself, a poor indicator of species diversity ($r = 0.315$; $P = 0.408$). Similarly, state area is a significant predictor of neither the number of habitat types nor of patches of different habitat (as depicted by Küchler 1970) included in the state. The number of habitat types included in each state reflects the diversity of biotic influences and is a better indicator of species diversity ($r = 0.721$; $P = 0.028$). However, the best indicator of species diversity is the number of sites or patches of habitat in each state ($r = 0.913$; $P = 0.0001$). This measure incorporates all three of the factors effecting high biotic diversity of the Southwestern Region: topographic diversity, varied habitat types, and time. The average size of sites or habitat patches in each state is a measure of population diversity, and avoids bias as to whether or not an isolated population has speciated (for species-level analysis) or has been recognized as a distinct subspecies. The more homogeneous nature of habitats in states east of the Rocky Mountains (particularly Kansas and Texas) is reflected in their larger average patch size as compared to the Southwestern Region states of the Rocky Mountains and west.

Human-induced vs “natural” extinction

Although humans are certainly a natural part of the world biota, conservation agencies often make a distinction between anthropogenic and “natural” effects on

populations. Anthropogenic effects are clear in those cases where human activity directly targets species or specific regions. Examples among Southwestern rodents would include *Cynomys parvidens*, which was the specific object of poisoning campaigns, and rodents of the San Joaquin Valley desert, which were indirect victims of agricultural development of the region. However, separation of “human” and “natural” effects are more difficult for populations that represent relicts of cool, mesic pluvial intervals. Habitat loss for these populations may result from human activities such as overgrazing, deforestation, fire-suppression, and reduction of local water resources, or by natural drying trends that followed the last pluvial cycle. Realistically, the two classes of processes are probably inseparable and synergistic in effecting habitat loss for relictual populations. However, the Southwestern Region would seem to be an ideal region in which to study the relative contribution of human-induced and “natural” processes in the “desertification” (El-Baz 1983) of Southwestern grasslands, the reduction in wetlands habitat, and the loss of isolated montane populations.

Rodents of conservation concern in the Southwestern Region

The majority of rodents of conservation concern in this region (Table 3.2) are found in California, either in the San Joaquin Valley, in arid chaparral or desert habitats bordering the Los Angeles and San Diego metropolitan areas, or in wetlands and rainforest habitats along the northern California coast. Hall (1989) felt that this bias reflected “better communication with authorities in that state” as well as “regional differences in attitude and concern about threatened species,” and that the “relative severity of the biological circumstances [elsewhere in the Southwestern Region] is greater than we now recognize.” Comprehensive evaluation of all regional taxa of concern, however, reveals that the situation in California accurately reflects an unfortunate coincidence of intensive development in a region of high biodiversity. Not only has California, with the highest number of native mammal species among the United States, been subjected to the most extensive urban and agricultural development of all western states during the last 150 years, but that development has been focused most intensively on regions of highest biodiversity within the state. In addition, California’s native species have suffered from the onslaught of nearly 1000 species of invasive introduced species of plants (Vitousek *et al.* 1996). Elsewhere in the Southwestern Region, agricultural or grazing impacts have affected taxa with naturally restricted distributions. In Nevada, four of the taxa of concern are located in mountains or wetlands surrounding the rapidly expanding Las Vegas urban area.

A large proportion of desert rodents (family Heteromyidae) are listed as taxa of concern (Table 3.3). This reflects primarily the threatened nature of arid habitats in California (San Joaquin Valley, coastal chaparral, and northwestern Mojave Desert), but also grazing or agricultural impacts on desert rodents elsewhere in the Southwestern Region. Relative to the other North American regions, rodents of the Southwestern Region are often restricted to small patches of appropriate habitat, for example, isolated springs or mountaintops surrounded by deserts. For many of these taxa, no current threat is known, and they are listed as either Lower Risk (least concern) or Data Deficient. Onset of urban or agricultural development could drastically alter that status: for example, construction of an observatory atop Mount Graham in southern Arizona has placed at least two rodent taxa in jeopardy.

Major threats in the Southwestern Region

Urban and agricultural development

It is not surprising that over one-half of the endangered rodents of the Southwestern Region are from California (Table 3.2). By 1975, California had nearly four times the average population density of Southwestern states, and California’s population has grown faster than the rest of the United States for the past two decades. According to the 1993 census, that growth has reduced, but population growth in the western states continues to be above the national average, with Nevada now in the lead in this dubious competition. Thus, the adverse impact suffered by California rodent populations can be expected to be repeated in other states as human population growth continues, and is already being observed in areas surrounding the rapidly expanding Las Vegas urban area of Nevada.

San Joaquin Valley Desert. The San Joaquin Valley desert is rapidly disappearing in the face of agricultural development (Williams *et al.* 1992). All 15 endemic arid-adapted rodents in the valley (Williams and Kilburn 1992) could be considered as endangered on the basis of dwindling habitat; seven species are included here (*Ammospermophilus nelsoni*, *Dipodomys ingens*, *D. nitratooides*, *D. heermanni*, *Perognathus inornatus*, *Onychomys torridus*, and *Neotoma fuscipes*).

The San Joaquin Desert has been considered as a consequence of post-Wisconsin (altithermal) invasion of neighboring Mojave Desert species, followed by quantum evolution due to intense selection in extremely hot, summer-drought conditions (Axelrod 1966, 1967, Raven and Axelrod 1978, D. I. Axelrod pers. comm. 1980). Axelrod (1966) estimated that effective isolation of the San Joaquin

Table 3.2. Rodents of conservation concern in the Southwestern Region.

Species that are widespread and secure throughout most of their range, but have subspecies of conservation concern in this region, are considered to be of Lower Risk and least concern, and are listed as LR(lc). Status codes are defined in Appendix 2.

	Historical distribution	Red List Category	Species account (p.)
APLODONTIDAE			
<i>Aplodontia rufa</i>	USA: CA,NV,OR,WA Canada: BC	LR(nt)	30
<i>A. r. nigra</i>	USA: CA	VU:B1;B2d;B2e	
<i>A. r. phaea</i>	USA: CA	VU:B1;B2e	
SCIURIDAE			
<i>Ammospermophilus nelsoni</i>	USA: CA	EN:A1a;B1;B2c	33
<i>Cynomys ludovicianus</i>	USA, Canada, Mexico	LR(nt)	35
<i>Cynomys parvidens</i>	USA: UT	LR(cd)	36
<i>Glaucomys sabrinus</i>	USA, Canada	LR(lc)	37
<i>G. s. californicus</i>	USA: CA	DD	
<i>Spermophilus elegans</i>	USA	LR(lc)	45
<i>S. e. nevadensis</i>	USA: ID,NV,OR	DD	
<i>Spermophilus lateralis</i>	USA, Canada	LR(lc)	46
<i>S. l. wortmanni</i>	USA: CO,WY	DD	
<i>Spermophilus mohavensis</i>	USA: CA	VU:B1;B3d	47
<i>Spermophilus tereticaudus</i>	USA, Mexico	LR(lc)	50
<i>S. t. chlorus</i>	USA: CA	DD	
<i>Tamias canipes</i>	USA: NM,TX	LR(nt)	54
<i>Tamias minimus</i>	USA, Canada	LR(lc)	54
<i>T. m. atristriatus</i>	USA: NM	CR:A1a;B1;D	
<i>Tamias palmeri</i>	USA: NV	VU:A2c	55
<i>Tamias quadrivittatus</i>	USA: AZ,CO,NM,UT	LR(lc)	56
<i>T. q. australis</i>	USA: NM	VU:C2a;D2	
<i>Tamias umbrinus</i>	USA	LR(lc)	57
<i>T. u. nevadensis</i>	USA: NV	CR:A1a	
<i>T. u. sedulus</i>	USA: UT	DD	
<i>Tamiasciurus hudsonicus</i>	USA, Canada	LR(lc)	58
<i>T. h. grahamensis</i>	USA: AZ	CR:B1;C2b	
GEOMYIDAE			
<i>Geomys arenarius</i>	USA: NM	LR(nt)	60
<i>Geomys personatus</i>	USA: TX Mexico	LR(nt)	61
<i>G. p. fuscus</i>	USA: TX	LR(nt)	
<i>G. p. maritimus</i>	USA: TX	VU:D2	
<i>G. p. streckeri</i>	USA: TX	VU:D2	
<i>Geomys texensis</i>	USA: TX	LR(nt)	62
<i>G. t. bakeri</i>	USA: TX	LR(nt)	
<i>Thomomys mazama</i>	USA: CA,OR,WA	LR(nt)	63
<i>Thomomys umbrinus</i>	USA: AZ,NM Mexico	LR(lc)	67
<i>T. u. emotus</i>	USA: NM	LR(nt)	
HETEROMYIDAE			
<i>Chaetodipus californicus</i>	USA: CA Mexico	LR(lc)	68
<i>C. c. femoralis</i>	USA: CA Mexico	DD	
<i>Chaetodipus fallax</i>	USA: CA Mexico	LR(lc)	69
<i>C. f. fallax</i>	USA: CA Mexico	DD	
<i>C. f. pallidus</i>	USA: CA	DD	
<i>Dipodomys elator</i>	USA: OK,TX	VU:B1;B2c	69
<i>Dipodomys heermanni</i>	USA: CA	LR(lc)	70
<i>D. h. berkeleyensis</i>	USA: CA	VU:B1;B2c	
<i>D. h. dixonii</i>	USA: CA	LR(nt)	
<i>D. h. morroensis</i>	USA: CA	CR:B1;B2c;D	

Table 3.2 ... continued

	Historical distribution	Red List Category	Species Account (p.)
<i>Dipodomys ingens</i>	USA: CA	CR:A1a;B2c	72
<i>Dipodomys merriami</i>	USA, Mexico	LR(lc)	74
<i>D. m. collinus</i>	USA: CA	DD	
<i>D. m. parvus</i>	USA: CA	DD	
<i>Dipodomys microps</i>	USA	LR(lc)	74
<i>D. m. alfredi</i>	USA: UT	DD	
<i>D. m. leucotis</i>	USA: AZ	VU:B1;B2c	
<i>Dipodomys nitratooides</i>	USA: CA	LR(nt)	76
<i>D. n. brevinasus</i>	USA: CA	LR(nt)	
<i>D. n. exilis</i>	USA: CA	CR:B1;B2c	
<i>D. n. nitratooides</i>	USA: CA	CR:A1c	
<i>Dipodomys stephensi</i>	USA: CA	LR(cdd)	78
<i>Microdipodops megacephalus</i>	USA: CA, ID, NV, OR, UT	LR(lc)	79
<i>M. m. nexus</i>	USA: NV	DD	
<i>Microdipodops pallidus</i>	USA: CA, NV	LR(lc)	80
<i>M. p. restrictus</i>	USA: NV	VU:D2	
<i>Perognathus alticola</i>	USA: CA	LR(nt)	81
<i>P. a. alticola</i>	USA: CA	CR:B1;B2b	
<i>P. a. inexpectatus</i>	USA: CA	LR(nt)	
<i>Perognathus flavus</i>	USA, Mexico	LR(lc)	82
<i>P. f. goodpasteri</i>	USA: AZ	LR(nt)	
<i>Perognathus inornatus</i>	USA: CA	LR(lc)	82
<i>P. i. neglectus</i>	USA: CA	LR(nt)	
<i>P. i. psammophilus</i>	USA: CA	LR(nt)	
<i>Perognathus longimembris</i>	USA, Mexico	LR(lc)	83
<i>P. l. bangsi</i>	USA: CA	DD	
<i>P. l. brevinasus</i>	USA: CA	VU:B1;B2c	
<i>P. l. internationalis</i>	USA: CA	DD	
<i>P. l. pacificus</i>	Mexico USA: CA	CR:B1;B2c;C1;C2a;C2b	
MURIDAE			
<i>Arborimus albipes</i>	USA: CA, OR	DD	86
<i>Arborimus pomo</i> (=longicaudus)	USA: CA	DD	86
<i>Microtus californicus</i>	USA: CA, OR Mexico	LR(lc)	90
<i>M. c. mohavensis</i>	USA: CA	VU:A1d;A2d;D2	
<i>M. c. scirpensis</i>	USA: CA	VU:B1;B3c;B3d	
<i>M. c. stephensi</i>	USA: CA	DD	
<i>M. c. vallicola</i>	USA: CA	LR(nt)	
<i>Microtus longicaudus</i>	USA, Canada	LR(lc)	93
<i>M. l. bernardinus</i>	USA: CA	DD	
<i>M. l. leucophaeus</i>	USA: AZ	DD	
<i>Microtus mogollonensis</i>	USA: AZ, CO, NM, TX, UT	LR(lc)	95
<i>M. m. hualpaiensis</i>	USA: AZ	VU:B1;B2c;D2	
<i>Microtus montanus</i>	USA, Canada	LR(lc)	96
<i>M. m. arizonensis</i>	USA: AZ, NM	LR(nt)	
<i>M. m. fucosus</i>	USA: NV	VU:D2	
<i>M. m. nevadensis</i>	USA: NV	VU:D2	
<i>M. m. rivularis</i>	USA: UT	LR(nt)	
<i>Neotoma fuscipes</i>	USA: CA, OR Mexico	LR(lc)	103
<i>N. f. annectens</i>	USA: CA	DD	
<i>N. f. luciana</i>	USA: CA	DD	
<i>N. f. riparia</i>	USA: CA	CR:B1;B2c	
<i>Neotoma lepida</i>	USA, Mexico	LR(lc)	104
<i>N. l. intermedia</i>	USA: CA Mexico	DD	
<i>Ondatra zibethicus</i>	USA, Canada, Mexico	LR(lc)	106
<i>O. z. ripensis</i>	USA: NM, TX Mexico	DD	

Table 3.2 ... continued			
	Historical distribution	Red List Category	Species Account (p.)
<i>Onychomys torridus</i>	USA, Mexico	LR(lc)	107
<i>O. t. ramona</i>	USA: CA Mexico	DD	
<i>O. t. tularensis</i>	USA: CA	DD	
<i>Peromyscus maniculatus</i>	USA, Canada, Mexico	LR(lc)	110
<i>P. m. anacapae</i>	USA: CA	LR(nt)	
<i>P. m. clementis</i>	USA: CA	LR(nt)	
<i>Peromyscus truei</i>	USA, Mexico	LR(lc)	113
<i>P. t. comanche</i>	USA: TX	LR(nt)	
<i>Reithrodontomys raviventris</i>	USA: CA	VU:A1c;A2c;B2c	114
<i>R. r. halicoetes</i>	USA: CA	LR(cd)	
<i>R. r. raviventris</i>	USA: CA	EN:A2c;B1;B2c	
<i>Sigmodon arizonae</i>	USA: AZ,CA Mexico	LR(lc)	116
<i>S. a. arizonae</i>	USA: AZ	EX	
<i>S. a. plenus</i>	USA: AZ,CA	LR(nt)	
<i>Sigmodon fulviventris</i>	USA: AZ,NM Mexico	LR(lc)	117
<i>S. f. goldmani</i>	USA: NM	EX	
<i>Sigmodon hispidus</i>	USA, Mexico	LR(lc)	118
<i>S. h. eremicus</i>	USA: AZ,CA Mexico	LR(nt)	
<i>Synaptomys cooperi</i>	USA, Canada	LR(lc)	120
<i>S. c. paludis</i>	USA: KS	EX	
DIPODIDAE			
<i>Zapus hudsonius</i>	USA, Canada	LR(lc)	120
<i>Z. h. luteus</i>	USA: AZ,NM	LR(nt)	
<i>Z. h. preblei</i>	USA: CO,WY	EN:B1;B2c	
<i>Zapus trinotatus</i>	USA: CA,OR,WA Canada: BC	LR(nt)	123
<i>Z. t. orarius</i>	USA: CA	LR(cd)	

Table 3.3. Rodent taxa of concern in the South-western Region.								
"Species of concern" include only those that are of concern at the global level, and do not include those that are LR(lc). Numbers of taxa listed at the species level are indicated in boldface. Families are listed in order of their contribution to the North American rodent fauna.								
Family	Total species (n)	IUCN Red List Category						
		EX	CR	EN	VU	LR(cd)	LR(nt)	DD
Muridae	57	3	1	1	1 5	1	8	2 9
Sciuridae	54		3	1	2 1	1	2	5
Heteromyidae	37		1 5		1 4	1	2 6	9
Geomyidae	11				2		4 3	
Dipodidae	3			1		1	1	1
Castoridae	1							
Erethizontidae	1							
Aplodontidae	1						1	
Totals	165	3	1 9	1 2	4 14	2 2	10 18	2 23

flora from that of the Mojave occurred as recently as 3,000 years ago. Documented introgressive hybridization between San Joaquin and Mojave forms of leopard lizards (*Gambelia*; Montanucci 1970, 1978) is consistent with this interpretation. However, at least some San Joaquin taxa may be far older: Friesen's (1979) Vicariant Model postulates entry of ancestral desert taxa into the San Joaquin Valley prior to the middle Pleistocene uplift of the Tehachapi Mountains, which then isolated San Joaquin and Mojave taxa.

Most of the San Joaquin Valley floor has been converted for agricultural or urban use. Remaining patches of desert habitat, mostly nestled against the hills lining the western edge of the valley, are subjected to livestock grazing, invasion of weedy exotic plants, and pesticide overdrift from neighboring agricultural fields (Williams *et al.* 1992). The San Joaquin Valley desert is a clear example of human impact. While the current natural climatic cycle would favor expansion and success of desert biota, agricultural and urban development is rapidly destroying this desert habitat.

Southern California Coastal Chaparral. Like the San Joaquin Valley desert, the narrow coastal belt of chaparral

habitat and pockets of desert vegetation in intervening valleys are suffering rapid habitat loss despite favorable climatic conditions. Urban development is the primary culprit, resulting in direct habitat loss and the more insidious invasion of introduced exotic species, including weedy plants and an extremely successful predatory species, the feral house cat. Areas not directly subjected to urban development suffer grazing pressures and agricultural development, particularly in arid valleys, while suppression of natural fire cycles in chaparral undoubtedly alters the vegetative community. Eleven species of coastal chaparral and desert rodents are included in this report: *Spermophilus tereticaudus*, *Chaetodipus californicus*, *C. fallax*, *Dipodomys heermanni*, *D. merriami*, *D. stephensi*, *Perognathus longimembris*, *Microtus californicus*, *Neotoma fuscipes*, *N. lepida*, and *Onychomys torridus*. Loss of the coastal chaparral and associated arid habitat is not limited to southern California: further south, in northern Baja California, Mexico, another coastal species of rodent, *Dipodomys gravipes*, may be near extinction due to loss of the same coastal desert habitat (Best and Lackey 1985).

Northwestern Mojave Desert. Although urban developers undoubtedly consider this region to be the edge of a far larger Mojave Desert, and perhaps less in need of protection, that does not appear to be the case at least for some species. Instead, desert taxa paradoxically may represent relicts of cool, mesic pluvial intervals. Hafner (1992) has postulated that this corner of the Mojave Desert served as a cold-desert refugium for at least one species, the Mohave ground squirrel, (*Spermophilus mohavensis*) during pluvial intervals. The current zone of contact between this species and its sister-taxon, *S. tereticaudus* (Hafner and Yates 1983) has shifted no more than 30km beyond the full-pluvial system of lakes and rivers that isolated the two forms and disappeared at least 6,000 years ago. It is reasonable to assume that the same area served as a refugium for the white-eared pocket mouse, *Perognathus alticola*, which is related to the northern, cold-desert *P. parvus*. Unlike *S. mohavensis*, which occupies the Mojave Desert floor, *P. alticola* is restricted to patchy desert habitat in the adjacent Tehachapi and Transverse ranges. It is certainly possible that other cryptic species shared a full-pluvial refugium here, and persist in the northwestern Mojave Desert and bordering ranges. Adequate survey, however, must race with explosive urban development of this region from the Los Angeles Basin, the most populous area of California. Both species (*S. mohavensis* and *P. alticola*) are included in this report.

Pacific Coast Wetlands and Rainforest. Five species included in this report appear to have had limited ranges prior to human development of coastal habitats, and it is not clear when they became restricted to these areas. Saltmarsh habitat surrounding San Francisco Bay had suffered tremendous loss (about 80%) from human development of the bay's margin before measures were

taken to conserve remaining saltmarsh to which the saltmarsh harvest mouse, *Reithrodontomys raviventris*, is restricted. It is unknown whether other rodent species shared a similar restriction, and disappeared before they ever were detected.

Habitat loss along the narrow strip of rainforest along the northern California coast has been less severe, but populations of mountain beaver (*Aplodontia rufa nigra* and *A. r. phaea*), red tree mice (*Arborimus pomo*), and jumping mice (*Zapus trinotatus orarius*) are restricted to this mesic area. All of these species undoubtedly enjoyed a somewhat broader distribution during wetter pluvial times. The two subspecies of mountain beaver are particularly isolated and vulnerable to increased urban development of the coast. Habitat restriction also renders these populations vulnerable to natural catastrophes: the effects of a 1995 wildfire on populations of *Zapus* and *Aplodontia* in Point Reyes National Seashore is not yet known.

Grazing impacts

In less populous areas of the Southwestern Region, adverse human impacts are often less obvious, and more difficult to separate from climatic change. The prolonged and widespread practice of livestock grazing on open range has certainly modified grasslands, particularly those that were already marginal and suffering from reduced annual precipitation. However, most arid grassland rodents have broad geographic ranges, and the gradual degradation of grasslands has probably resulted in an overall reduction in densities rather than reduced distribution. This more subtle effect is more obvious in taxa with small geographic distributions. In central New Mexico, for example, the hispid pocket mouse, *Chaetodipus hispidus*, persists in patches of grassland along railroads and at the base of the Sandia Mountains in the Rio Grande Valley, but has been eliminated from most of the valley by a combination of overgrazing and reduced precipitation. Two taxa with limited distributions that appear to suffer from, or are vulnerable to, grazing pressures are included in this report, *Dipodomys elator* and *D. microps leucotis*, the Texas kangaroo rat and the House Rock Valley kangaroo rat.

Post-glacial warming

Desert Oases and Sky Islands. Full-glacial relicts abound in arid regions of the Southwestern Region, either in riparian zones associated with rivers and springs, or on isolated mountaintops. At least 53 species (nearly one-third of all Southwestern Region rodents) have one or more isolated, relictual populations in the region that date from pluvial intervals; 23 of these species are included in

this Action Plan. Populations of nine species are (or were) restricted to low-elevation riparian or remnant grassland sites (*Geomys arenarius*, *G. personatus*, *G. texensis*, *Microtus californicus*, *Ondatra zibethicus*, *Sigmodon arizonae*, *S. fulviventer*, *S. hispidus*, and *Synaptomys cooperi*), and isolated populations of 13 others persist in mesic montane areas (*Sciurus arizonensis*, *S. nayaritensis*, *Tamias canipes*, *T. minimus*, *T. palmeri*, *T. quadrivittatus*, *T. speciosus*, *T. umbrinus*, *Tamiasciurus hudsonicus*, *Thomomys umbrinus*, *Microtus mexicanus*, *M. montanus*, and *Peromyscus truei*). Relictual populations of an additional species, *Zapus hudsonius*, survive in both montane strongholds and patchy marshlands in Colorado, Arizona, and New Mexico.

It is highly probable that more of these isolated populations will be discovered as the result of increased survey efforts, particularly in remote areas of the Southwestern Region. During the last decade, previously unreported relict populations of various rodents have been discovered on mountaintops and at isolated riparian areas in the Southwestern Region: e.g., *Microtus mexicanus hualpaiensis* (Kime *et al.* 1992), *M. pennsylvanicus* (R. A. Smartt pers. comm. 1993), *Zapus hudsonius luteus* (Morrison 1992), and *Spermophilus tridecemlineatus* (T. L. Best pers. comm. 1991).

Although less than half of the 53 species with relict populations have attracted the attention of conservation biologists, all relictual populations should be considered as vulnerable to both increasing drying or warming trends and human-induced effects that would reduce these restricted habitats. It is axiomatic that species with small geographic distributions and low ecological tolerances are most vulnerable to habitat loss. Due to its high topographic diversity and dynamic climatic history, the Southwestern Region has numerous rodent taxa with patchy distributions. From the perspective of agricultural and urban developers, these small, often cryptic populations are unmarked landmines, and endangered species lists largely document contact between development and vulnerable populations. In the future, conservationists and developers will have to choose which patches of habitat can be protected from development, which must be sacrificed because of economic demands, and which should be studied to determine the effects of climatic trends on relictual populations. Such choices are not often palatable, particularly where a habitat patch and its relictual populations may be sacrificed. However, this would seem preferable to the current system (or lack thereof) in which vulnerable populations await accidental

discovery by uninformed developers, who then enter into a confrontation with conservationists who attempt to halt the planned development. Where a necessary choice must be made between these habitat patches, factors should include the “Alamo” issue (is this the “last stand” for any of the involved species?) and cost-efficiency (how many isolated populations are affected?).

Extermination programs

Rodents have seldom been the target of the trapping or poisoning campaigns that have endangered a number of carnivore species. However, prairie dogs (*Cynomys* spp.) were a major exception in the West, where they were considered a competitor for food with domestic livestock (Bailey 1931). Fagerstone and Biggins (1986) reported a reduction of prairie dog (*C. ludovicianus* and *C. leucurus*) geographic range from 283 million ha in the late 1800s (Merriam 1902) to 0.6 million ha by 1971 (Cain *et al.* 1971). Findley *et al.* (1975) and Cockrum (1960) describe the extirpation of blacktail prairie dogs (*C. ludovicianus*) from Arizona and southwestern New Mexico as a result of widespread poisoning by the United States Bureau of Biological Survey, beginning in 1915 (Day and Nelson 1929). Prairie dog populations in Kansas, Oklahoma, and Texas had already declined prior to poisoning campaigns as a result of cultivation and livestock grazing, as indicated by the earlier disappearance of black-footed ferrets from these areas (Anderson *et al.* 1986). Populations of black-footed ferrets (*Mustela nigripes*) declined precipitously as a result of the systematic eradication of *Cynomys*, their principal prey (Anderson *et al.* 1986, Henderson *et al.* 1969). Simultaneously, prairie dogs repeatedly suffer catastrophic population losses due to sylvatic plague (Hubbard and Schmitt 1984), and increasing aridity which has decreased the productivity of peripheral grasslands.

The Utah prairie dog (*Cynomys parvidens*) was particularly vulnerable to all of these effects (poisoning, cultivation, overgrazing, disease, and increasing aridity) due to its smaller geographic range, and it is now the target of recovery efforts (United States Fish and Wildlife Service 1991a). Although the other prairie dog species have suffered extreme habitat loss, it is unlikely that any protective measures would have been considered for these species except for their importance to black-footed ferrets. For example, prairie dogs are considered “infestations” on North and South Dakota Indian lands (Martin 1973).