

GETTING WARMER: EFFECT OF GLOBAL CLIMATE CHANGE ON DISTRIBUTION OF RODENTS IN TEXAS

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Historically, distributions of plants and animals have shifted with changes in regional and global temperatures. Current predictions from general circulation models show changes in level and variation in temperature and rainfall over the next several decades. The magnitude and direction of such changes vary regionally. Studies are beginning to show that these changes will impact distribution of species of plants and animals, and, concomitantly, species composition of plant and animal communities. We used geographic information systems, vegetation models, and general circulation models to predict the impact of global climate change (GCC) on the distribution of vegetation at a regional scale, the state of Texas. Then we used habitat preferences for species of rodents in the state to predict how GCC would impact their geographic range and species richness. Our determination of suitable habitats for species of rodents included an average of 98% of capture points, and we found that suitable habitat averaged 62% of the geographic range of species. Size of habitat-corrected range increased an average of 2- to 3-fold under GCC, indicating that rodents were more adaptable to changes in vegetation than were other mammals we studied (e.g., lagomorphs and insectivores), whose range decreased, but similar to Chiroptera, whose ranges also increased. Geographic ranges shifted an average of 54% under a warmer, wetter climate and 61% under a warmer, drier climate, resulting in inclusion of an average of 60% new vegetation associations in the ranges under the former scenario and 64% under the latter scenario. The impact of GCC on rodents in Texas was greatest under the warmer, drier climatic scenario. Two species, *Oryzomys couesei* and *Microtus mexicanus*, were predicted to go extinct because their suitable habitats did not occur under GCC. These results demonstrated that the type of climate change (warmer, drier or warmer, wetter) and its severity would be important. GCC was predicted to have the greatest impact on rodent distributions in eastern Texas under a scenario of a warmer and wetter climate because forests expanded, whereas the impact would be greatest in western and southern Texas if climate becomes warmer and drier because desert and shrub habitats expanded. Life-history variables (e.g., habitat type or diet) were correlated with changes in size of range, location, or habitat composition, and reflected broad changes in the relative distribution of vegetation types. Granivores and herbivores used fewer new habitat associations that entered Texas after GCC than did omnivores or insectivores, as did terrestrial rodents compared with fossorial or arboreal rodents.

Key words: distribution of rodents, global climate change, Texas

Geologic records demonstrate that distribution of plants and animals have shifted

with changes in temperature no greater than those predicted for the next 100 years (Davis 1989; Davis and Zabinski 1992; Frey 1992; Overpeck 1993). One example of this

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impact of past climates on the distribution of animals comes from Graham's work (Graham 1992; Graham et al. 1996), which details how geographic ranges of individual species of mammals shifted in response to environmental fluctuations and changes in position of glacial ice sheets in the late Quaternary. Those investigators grouped species of mammals according to the geographic direction of changes in their geographic distribution. Those groupings included species that exhibited rapid northward dispersal (e.g., heather vole, *Phenacomys intermedius*; meadow jumping mouse, *Zapus hudsonius*; water shrew, *Sorex palustris*), slow northward dispersal (e.g., southern red-backed vole, *Clethrionomys gapperi*; American pika, *Ochotona princeps*; prairie vole, *Microtus ochrogaster*), eastward shifts (e.g., least shrew, *Cryptotis parva*; eastern chipmunk, *Tamias striatus*; marsh rice rat, *Oryzomys palustris*), or western retraction (e.g., montane vole, *Microtus montanus*; black-tailed prairie dog, *Cynomys ludovicianus*; plains pocket gopher, *Geomys bursarius*) of geographic ranges. Significant southward displacement of the ranges of species such as the northern pygmy mouse (*Baiomys taylori*) and eastern woodrat (*Neotoma floridana*) did not occur during cold intervals in the late Pleistocene.

General circulation models predict that doubling the concentration of preindustrial levels of CO₂ within the next 40 years will increase global mean surface air temperature 2–5°C, with increases at mid- to high latitudes reaching 8–10°C (Houghton et al. 1990; Lashof 1989; Schneider et al. 1990, 1992), and with accompanying increases or decreases in precipitation (Bradley et al. 1987). As a result, the magnitude of changes in vegetation likely will equal that achieved during the last interglacial period (10,000–14,000 years ago), but the rate of such change may be 2–5 times more rapid (Overpeck 1993). Attendant effects on consumers, such as the mammalian fauna, in

these communities are expected (Peters and Lovejoy 1992).

Global circulation models have been used to predict distribution of major, primarily forested, terrestrial ecosystems in North America that would result from global climate change (GCC). In those models, southern deciduous forests moved northward into temperate forests of the central and northeastern United States (Bonan et al. 1990; Emanuel et al. 1985; Randolph and Lee 1994; Reed and Densanker 1992; Shugart 1990; Smith et al. 1992), and temperate grasslands replaced boreal vegetation (Rizzo and Wiken 1992). Fluctuations caused by GCC in position of tree line decreased the area of alpine vegetation (Romme and Turner 1991), expanded steppe and aspen vegetation on dry sites, and replaced black spruce (*Picea mariana*) with paper birch (*Betula papyrifera*) on wet sites in Alaska (Viereck et al. 1986). Despite regional differences in rainfall patterns, relatively consistent northward shifts in geographic distributions of major world habitats have been predicted from several general circulation models, with eastern North America and eastern Europe to western Russia demonstrating the greatest sensitivity to decreases in rainfall (Cramer et al. 2001; Neilson and Marks 1994; Shaver et al. 2000). In 1 of the few nonforest studies, GCC was predicted to increase the amount of emergent cover in semipermanent wetlands in the Great Plains (Poiani and Johnson 1991).

Because not all consumers in a community will respond similarly to GCC, new community assemblages, different community structure, and altered ecosystem functions likely will result (Brown et al. 1997; Chown and Smith 1993; Graham 1992; Graham and Grimm 1990). For example, number of species of montane mammals inhabiting mountain tops in the Great Basin Desert (McDonald and Brown 1992), number of species of crayfish and freshwater amphipods in North America (France 1991), populations of stream invertebrates (Hogg et al. 1995), and number of endan-

gered Kirtland's warblers (*Dendroica kirtlandii*—Botkin et al. 1991) and polar bears (*Ursus maritimus*—Stirling and Derocher 1993) were predicted to decrease during GCC. Using field data collected over 2 decades, Holbrook et al. (1997) concluded that negative effects of climate change on benthos resulted in lower species richness and abundance, and a change in dominance of reef fishes in the Southern California Bight. In contrast, some species, particularly exotic ones (D'Antonio and Vitousek 1992), may increase in abundance after GCC (Fraser et al. 1992; Rodenhouse 1992).

Rather than focusing on particular populations, we analyzed effects of GCC at a regional scale. We predicted that distributions and richness of particular taxa of mammals in Texas would be altered and fragmented in response to shifts in preferred habitats (Cameron and Scheel 1993; Scheel et al. 1996). We focus here on the rodents because this taxon comprises nearly 50% of the mammalian fauna in Texas and includes a variety of trophic types. Accordingly, because rodents comprise vital links in food webs, impacts of GCC on individual species would reverberate differentially throughout the food web. First, we used an existing vegetation model and general circulation models to predict the impact of GCC on distribution of vegetation in Texas (Cameron and Scheel 1993). Then, using habitat preferences for each species of rodent in the state, we predicted the impact of GCC on the geographic range of each species. Finally, we compared current to predicted patterns of richness of rodents in Texas.

MATERIALS AND METHODS

Study area.—Texas is an ideal geographic area to conduct a regional analysis of the impact of climate change because of its large size, wide range of physical and environmental conditions, and diverse biota. Average annual temperature is 13°C in the north and 23°C in the south, and annual rainfall varies from 21 cm in the west to

139 cm in the east. The gradient in rainfall mirrors a gradient in plant productivity that increases from <150 g m⁻² year⁻¹ in the west to >2,000 g m⁻² year⁻¹ in the east (Owen 1990). Habitats grade from deserts in the southwest to deciduous forest in the southeast along the 1,225-km east–west axis of the state and from temperate grasslands in the north to subtropical thorn-scrub habitat near Mexico along the 1,150-km north–south axis. Largely because of these extensive environmental gradients, Texas demonstrates maximum biodiversity for non-tropical North America with nearly 5,000 species of plants (33% of species in the United States), 550 species of birds (75% of species in the United States), 139 species of mammals (37% of species in the United States), 138 reptiles (48% of species in the United States), and 61 amphibians (39% of species in the United States—Owen 1990). In addition to high biodiversity, the state has high endemism; for example, about 464 plant forms occur only in Texas (Correll and Johnston 1979).

Databases.—To uncover ecological impacts of GCC, we used a geographic information system (ARC/INFO, Environmental Systems Research Institute, Inc., Redlands, California) to model current distribution of species of rodents and vegetation throughout Texas. Distributions of plant species were assumed to be a function of climate, and actual distributions of rodents were determined by location of suitable vegetation and other habitat components. Data on current climate were obtained from historical records and future climates were predicted from general circulation models. We digitized geographic ranges for all species of rodents found in Texas (Davis and Schmidly 1994; Hall 1981; Schmidly 1977, 1983; Table 1). We excluded only exotic species (house mouse, *Mus musculus*; Norway rat, *Rattus norvegicus*; roof rat, *R. rattus*; nutria, *Myocastor coypus*), rare species (prairie vole, *M. ochrogaster*, known only from a single specimen taken in 1902 in southeastern Texas and from 8 specimens taken in 1988 in the northern Panhandle—Choate and Killebrew 1991; Jones et al. 1988), and species with primarily aquatic habits whose distributions could not be described adequately from terrestrial habitat associations (beaver, *Castor canadensis*; muskrat, *Ondatra zibethicus*). Hence, 59 species remained for our analyses.

Various life-history traits obtained from the

TABLE 1.—Species of rodents studied and their life-history characteristics. Life-history traits include taxon, body mass, food type, substrate, and type of habitat occupied. For each species, the actual number of capture points included in published geographic ranges (range) and those included in digitized maps corrected for preferred habitat vegetation, soil, and elevation, respectively, are given. Variables used to correct geographic ranges for each rodent can be determined by noting under which variable data points are included. For example, the range of *Baiomys taylori* was corrected for habitat only, whereas the range of *Ammospermophilus interpres* also was corrected for soil texture. Success of correction of range map for each habitat constituent is expressed as overall percentage of success; this metric was computed by counting the number of known capture points that were included in each map rendition and dividing by the total number of capture points. For current conditions, the area of actual habitat ($\times 10^{-3}$ km²) present in the geographic range is given (the proportion of the geographic range represented by suitable habitat is in parentheses). Using the Holdridge-modeled distribution, errors of our habitat model were computed as the proportion of the state (693,000 km²) identified as unsuitable in which the species occurred (undershoot) or as suitable in which the species did not occur (overshoot).

Species of rodent	Life-history trait					Capture points in				Overall percent- age of success	Current		
	Taxon ^a	Body mass ^b	Food type ^c	Substrate ^d	Habitat ^e	Range	Vegetation	Soil	Elevation		Suitable habitat	Overshoot	Undershoot
<i>Ammospermophilus interpres</i>	1	3	2	1	1	4	3	3		0.75	57.6 (0.63)	0.110	0.007
<i>Baiomys taylori</i>	4	1	2	1	1, 2, 3	21	21			1.00	364.4 (0.69)	0.320	0.002
<i>Chaetodipus hispidus</i>	3	2	1	1	1, 2, 3	14	14			1.00	536.5 (0.79)	0.111	0.142
<i>Chaetodipus intermedius</i>	3	1	1	1	1	2	2	2		1.00	43.3 (0.82)	0.131	0.006
<i>Chaetodipus nelsoni</i>	3	1	1	1	1	4	4		4	1.00	66.1 (0.64)	0.101	0.010
<i>Chaetodipus penicillatus</i>	3	1	1	1	1, 3	4	4	4		1.00	44.6 (0.49)	0.116	0.003
<i>Cratogeomys castanops</i>	2	4	2	3	1, 2, 3	40	39			0.98	204.8 (0.97)	0.399	0.008
<i>Cynomys ludovicianus</i>	1	5	2	1	1, 2	11	10			0.91	276.8 (0.81)	0.028	0.134
<i>Dipodomys compactus</i>	3	3	1	1	2, 3	5	5			1.00	18.6 (0.38)	0.124	0.010
<i>Dipodomys elator</i>	3	3	1	1	1	54	54			1.00	21.2 (0.96)	0.149	0.030
<i>Dipodomys merriami</i>	3	2	1	1	1, 3	3	3		3	1.00	107.4 (0.97)	0.056	0.007
<i>Dipodomys ordii</i>	3	3	1	1	1, 2, 3	20	19	19		0.95	235.4 (0.53)	0.383	0.007
<i>Dipodomys spectabilis</i>	3	3	1	1	1	8	8			1.00	53.6 (0.81)	0.127	0.008
<i>Erethizon dorsatum</i>	6	5	2	1	1, 4	9	7			0.78	123.4 (0.26)	0.377	0.056
<i>Geomys arenarius</i>	2	4	2	3	1, 2	1	1	1		1.00	6.8 (0.47)	0.105	0.000
<i>Geomys attwateri</i>	2	3	2	3	2, 3	5	5			1.00	53.8 (0.94)	0.562	0.000
<i>Geomys breviceps</i>	2	4	2	3	2, 3, 4	13	13			1.00	117.0 (0.89)	0.037	0.032
<i>Geomys bursarius</i>	2	4	2	3	1–4	4	4	4		1.00	148.4 (0.74)	0.325	0.007
<i>Geomys knoxjonesi</i>	2	4	2	3	1	16	16	16		1.00	18.3 (0.90)	0.512	0.006
<i>Geomys personatus</i>	2	4	2	3	2, 3	114	114	112		0.98	20.1 (0.59)	0.071	0.007
<i>Geomys texensis</i>	2	4	2	3	2, 3	12	12	12		1.00	4.9 (0.81)	0.526	0.001
<i>Glaucomys volans</i>	1	3	4	2	3, 4	6	6			1.00	183.3 (0.73)	0.256	0.004
<i>Liomys irroratus</i>	3	2	1	1	1	3	3			1.00	0.8 (0.11)	0.117	0.000

TABLE 1.—Continued.

Species of rodent	Life-history trait					Capture points in			Overall percent- age of success	Current		
	Taxon ^a	Body mass ^b	Food type ^c	Sub- strate ^d	Habi- tat ^e	Range	Vege- tation	Soil		Suit- able habitat	Over- shoot	Under- shoot
<i>Microtus mexicanus</i>	5	2	2	1	4	1	1		1.00	— ^f	— ^f	— ^f
<i>Microtus pinetorum</i>	5	3	2	3	1, 3, 4	8	8		1.00	159.3 (0.91)	0.425	0.002
<i>Neotoma albigula</i>	4	4	2	1	1, 3	13	13		1.00	182.6 (0.60)	0.411	0.023
<i>Neotoma floridana</i>	4	4	4	1	3, 4	14	14		1.00	109.5 (0.46)	0.381	0.004
<i>Neotoma mexicana</i>	4	4	2	1	1, 4	3	3		1.00	2.4 (0.04)	0.016	0.002
<i>Neotoma micropus</i>	4	4	2	1	1, 3	17	17		1.00	307.1 (0.67)	0.447	0.006
<i>Ochrotomys nuttalli</i>	4	1	1, 3	1	4	3	3		1.00	29.8 (0.69)	0.129	0.003
<i>Onychomys arenicola</i>	4	1	3	1	1	3	3		1.00	87.8 (0.92)	0.088	0.007
<i>Onychomys leucogaster</i>	4	2	3	1	1, 3	17	17		1.00	209.7 (0.54)	0.481	0.027
<i>Oryzomys couesi</i>	4	3	4	1	5	2	2		1.00	2.4 (0.77)	0.000	0.003
<i>Oryzomys palustris</i>	4	3	4	1	5	8	8		1.00	107.4 (0.88)	0.098	0.016
<i>Perognathus flavescens</i>	3	1	2	1	1, 3	5	5		1.00	92.1 (0.76)	0.189	0.061
<i>Perognathus flavus</i>	3	1	4	1	1, 2	17	17		1.00	328.5 (0.03)	0.355	0.006
<i>Peromyscus attwateri</i>	4	2	4	1	1, 2, 3	10	10		1.00	152.4 (0.04)	0.375	0.034
<i>Peromyscus boylii</i>	4	2	1	1	1, 4	6	5		0.83	3.8 (0.65)	0.016	0.004
<i>Peromyscus eremicus</i>	4	2	2	1	1	2	2		1.00	84.8 (0.46)	0.135	0.007
<i>Peromyscus gossypinus</i>	4	2	4	1	3, 4	6	6		1.00	64.5 (0.65)	0.094	0.013
<i>Peromyscus leucopus</i>	4	1	2	1	1–4	26	26	26	1.00	371.6 (0.63)	0.048	0.053
<i>Peromyscus maniculatus</i>	4	2	4	1	1–4	26	26		1.00	365.3 (0.33)	0.418	0.004
<i>Peromyscus nasutus</i>	4	2	1	1	4	1	1		1.00	2.1 (0.92)	0.003	0.002
<i>Peromyscus pectoralis</i>	4	2	1	1	1, 3	16	16		1.00	135.2 (0.69)	0.430	0.019
<i>Peromyscus truei</i>	4	1	1, 3	1	1	7	7		1.00	11.6 (0.41)	0.148	0.015
<i>Reithrodontomys fulvescens</i>	4	1	3	1	1, 2, 3	19	19		1.00	284.4 (0.63)	0.504	0.024
<i>Reithrodontomys humulis</i>	4	1	1	1	2, 4	4	4		1.00	24.0 (0.28)	0.057	0.026
<i>Reithrodontomys megalotis</i>	4	1	1	1	1, 3	3	3		1.00	134.0 (0.85)	0.107	0.031
<i>Reithrodontomys montanus</i>	4	1	2	1	1–4	9	9		1.00	334.4 (0.78)	0.369	0.037
<i>Sciurus carolinensis</i>	1	5	4	2	3, 4	4	3		0.75	114.0 (0.53)	0.353	0.002
<i>Sciurus niger</i>	1	5	4	2	3, 4	18	17		0.94	288.3 (0.61)	0.204	0.071
<i>Sigmodon hispidus</i>	4	4	2	1	1, 2, 3	16	15		0.94	562.2 (0.77)	0.172	0.075
<i>Sigmodon ochrognathus</i>	4	3	2	1	1	2	2		1.00	10.9 (0.16)	0.007	0.000
<i>Spermophilus mexicanus</i>	1	4	4	1	1, 2	13	13	13	1.00	336.7 (0.91)	0.248	0.014
<i>Spermophilus spilosoma</i>	1	3	4	1	1, 2	12	12		1.00	295.1 (0.65)	0.071	0.078
<i>Spermophilus tridecemlineatus</i>	1	4	4	1	1, 2, 4	11	11		1.00	222.3 (0.91)	0.508	0.000

TABLE 1.—Continued.

Species of rodent	Life-history trait					Capture points in				Overall	Current		
	Taxon ^a	Body mass ^b	Food type ^c	Sub-strate ^d	Habitat ^e	Range	Vegetation	Soil	Elevation	percent-age of success	Suit-able habitat	Over-shoot	Under-shoot
<i>Spermophilus variegatus</i>	1	5	4	1	1, 3	9	9		9	1.00	135.5 (0.68)	0.194	0.023
<i>Tamias canipes</i>	1	3	2	1	4	2	2			1.00	0.2 (0.03)	0.004	0.000
<i>Thomomys bottae</i>	2	4	2	3	1, 2, 3	24	24		24	1.00	98.2 (0.87)	0.355	0.016
\bar{X}										98.00	(0.62)	0.218	0.020
SE										0.01	(0.036)	0.022	0.004

^a 1 = Sciuridae, 2 = Geomyidae, 3 = Heteromyidae, 4 = Muridae, Sigmodontinae, 5 = Muridae, Arvicolinae, 6 = Erethizontidae.

^b Adult body mass: 1 = <25 g; 2 = 25–50 g; 3 = 51–150 g; 4 = 151–500 g; 5 = >500 g.

^c 1 = granivore, 2 = herbivore, 3 = insectivore, 4 = omnivore.

^d 1 = terrestrial, 2 = arboreal, 3 = fossorial.

^e 1 = desert; 2 = grassland; 3 = brush; 4 = forest; 5 = swamp-marsh.

^f Could not compute; see text.

literature were used as categorical variables to detect major trends among species of rodents (Table 1). Species of rodents were grouped by family (Sciuridae, Geomyidae, Heteromyidae, Muridae, and Erethizontidae) and, in the case of the Muridae, by subfamily (Sigmodontinae and Arvicolinae—Wilson and Reeder 1993), and by major habitat types in which they occurred (e.g., arid desert scrub, grassland, mesic brush, forest, or swamp-marsh). Average body mass of adults was used to separate rodent species into 5 categories: <25, 25–50, 51–150, 151–500, and >500 g. Food habits of each species were used to categorize them as granivores, herbivores, insectivores, or omnivores; for 2 species, multiple dietary types were used. Finally, species were arranged as terrestrial, arboreal, or fossorial depending on the primary type of substrate they occupied.

Published distribution maps contain the geographic limit for a species, but, because this distribution includes areas of both preferred and nonpreferred habitat, actual distribution for a species will be smaller than that reflected by published maps. We described the occupied habitats for each species of rodent by obtaining data on preferred vegetation, soil type, and elevation from the literature. Because no consistent descriptions were available in the literature of the array of habitats used by each species, those occupied habitats were standardized by using a vegetation classification adopted by Texas Parks and Wildlife (TPW) to name them (Cameron and Scheel 1993; McMahan et al. 1984). Digital maps were prepared for the distribution of these 46 vegetation (habitat) types (scale = 1:1,000,000; names provided in Scheel et al. 1996), 36 classes of soil texture (Natural Resources Conservation Service, Temple, Texas; scale = 1:250,000—Cameron and Scheel 1993), and 17 elevation categories (every 3rd data point was selected from 30-s point topography data [National Oceanographic and Atmospheric Administration; scale = 1:250,000]: 0–50, 51–100, 101–200 m, and then at intervals of 200 m to 3,000 m) in Texas. Suitable distribution (= actual distribution) for each species of rodent then was determined by using the geographic information system to overlay the geographic range of the species on the digital maps of the distribution of vegetation types and selecting only those habitats that were preferred. For some species, soil texture ($n = 11$ species) or elevation

($n = 8$ species) also were important descriptors of preferred habitat. Accordingly, sequential selections were made on preferred soil textures or elevations for those species (Table 1). A new map resulted that reflected the actual geographic distribution of suitable habitat for each species of rodent.

To assess accuracy of our determination of suitable habitat, we added the location of marginal capture records (Hall 1981) to our maps of the preferred habitat for each species of rodent (Table 1). Because those actual captures (or at least most of them) presumably occurred in occupied habitat, our digital portrayal of suitable habitat ideally should contain all of those capture points. We estimated our success at identifying actual habitat as the percentage of marginal capture records that were included in areas that we classified as suitable for each species.

Climate models.—We used general circulation models from the Geophysical Fluid Dynamics Laboratory (GFDLR30) and the Canadian Climate Centre (CCC; see Cameron and Scheel 1993 for details) to predict average temperature and rainfall in Texas under conditions of twice baseline CO_2 ($2 \times \text{CO}_2$; baseline CO_2 was 300–315 ppm; R. Jenne, pers. comm.). Those general circulation models were selected because the size of grid they used for climatic predictions was the smallest among available general circulation models, thereby providing more data points at a regional scale, such as Texas. A 40-year (1951–1990, inclusive) mean annual biotemperature (average growing season temperature—Holdridge 1967) and mean annual precipitation were calculated from 315 weather stations in Texas (National Weather Service; hereafter referred to as current climate). Current climate was adjusted according to the predictions of each general circulation model to reflect average conditions at each weather station under $2 \times \text{CO}_2$. Both models predicted that average temperature would increase by 3–4°C relative to current conditions. The GFDLR30 predicted an increase in average rainfall of about 25% throughout the state, whereas CCC predicted a slight decline of 6% in average rainfall. However, for both models, predicted temperature and rainfall varied spatially throughout the state. Greater increases in temperature occurred in the northern and western parts of the state and the smallest increases occurred in the southeastern portion. Smallest increases in precipitation oc-

curred in the northwestern, north-central, and southeastern parts of the state, with highest increases in the midportion of the state (Cameron and Scheel 1993; North et al. 1995). Thus, GFDLR30 predicted conditions that were both warmer and wetter than current climate (e.g., the wet-climate scenario), whereas CCC predicted warmer and somewhat drier conditions (e.g., the dry-climate scenario; see Cameron and Scheel [1993] and Cameron et al. [1997] for detailed predictions from those climate models).

Vegetation models.—We used the Holdridge (1947, 1967) model of climate–vegetation associations to model the type of vegetation resulting from current and $2 \times \text{CO}_2$ climatic conditions (hereafter called Holdridge-modeled habitats). The Holdridge model predicted the distribution of vegetation associations based on temperature and precipitation (Harris and Cropper 1992; Smith et al. 1992). According to that model, all warm-temperate vegetation would be lost in Texas under either $2 \times \text{CO}_2$ scenario (Cameron and Scheel 1993). Under GFDLR30 (wetter), all subtropical vegetation also would be lost and tropical forests would be added. For CCC (drier), subtropical forest, tropical dry forest, steppe, and desert scrub would be added because, compared with GFDLR30, temperature increase would be more severe and rainfall would be less (Cameron and Scheel 1993).

Species distributions under current climate conditions.—Distribution of each species of rodent under current and $2 \times \text{CO}_2$ climates was predicted with the Holdridge (1947, 1967) model of vegetation distribution. The 1st step was to translate TPW associations into Holdridge associations by using the geographic information system to overlay TPW associations and Holdridge associations. Each TPW association was identified with up to 6 Holdridge vegetation associations that overlapped it to the greatest extent under the current climate and had comparable physiognomy (Cameron and Scheel 1993; Scheel et al. 1996). Some TPW associations did not match any Holdridge association because either no comparable Holdridge type existed (e.g., crops, urban areas, or wetlands) or the association constituted <0.5% of the area of the state. Holdridge habitats for a species that used an unmatched TPW association were determined by matching them to other suitable TPW associations. Although TPW associations and their matched Holdridge life zones were not equiva-

lent plant communities, they were similar enough that vegetation suitable for rodents under the TPW classification also would be suitable in the matched Holdridge association(s).

To predict distributions of rodents using the Holdridge-modeled habitats, each species was assigned to occur in those Holdridge associations that were identified as similar to the TPW types in which the species was known to occur. Where appropriate, modeled ranges were adjusted for preferences in soil texture or elevation. We estimated our success in modeling the range of each species by comparing actual distribution (based on locations of suitable habitat) with the distribution based on Holdridge-modeled habitats under current climate conditions. We calculated the error in modeling the range of each species as the ratio of the total area within Texas incorrectly identified by the model to the total area of the state. We based the error on the total area of the state rather than on current or predicted range of a species to fix our maximum error at 1.0, and avoid results biased by size of each range. Areas incorrectly identified were either undershoots (occupied by a species but predicted to be unoccupied) or overshoots (unoccupied but predicted to be occupied). Differences in overshoot error among life-history and habitat categories were tested with analysis of variance and Fisher's least significant difference a posteriori test after transformation with $\arcsin \sqrt{p}$ (where p is a proportion—Sokal and Rohlf 1995).

Species distributions under $2 \times \text{CO}_2$ conditions.—Some Holdridge vegetation types did not occur under current climate, but did occur under $2 \times \text{CO}_2$ climates. We could not match those new types to the TPW vegetation associations based on overlap as described above. Instead, we either matched them with similar Holdridge associations that did occur under current climate (e.g., animals, using warm-temperate moist forest based on TPW–Holdridge overlap, were predicted to use subtropical moist forest, which occurred only in the $2 \times \text{CO}_2$ climate), or we designated them as suitable habitat for a species based on descriptions of the habitat of each species taken from the literature (Cameron and Scheel 1993). We assigned most rodents to ≥ 1 Holdridge vegetation type that did not occur currently in the state but was predicted to occur under $2 \times \text{CO}_2$. That was equivalent to assuming that those rodents used a broader spectrum of

habitats than currently were present within the state.

Distributions of species under $2 \times \text{CO}_2$ were modeled using the same procedure as for current conditions. We predicted that a species would become extinct in Texas when no suitable habitat occurred. From those data, we measured the ratio between suitable habitat in Holdridge-modeled current and $2 \times \text{CO}_2$ climates, the percentage of overlap between ranges predicted by $2 \times \text{CO}_2$ and the Holdridge-modeled current ranges (a measure of distance moved by habitats under $2 \times \text{CO}_2$; lower overlaps indicated longer distance moved; range = 0–100%), and the proportion of the range under $2 \times \text{CO}_2$ in which new habitat associations occurred. We used analysis of variance with Fisher's least significant difference a posteriori test to determine effect of life-history and habitat characteristics (data were transformed with $\arcsin \sqrt{p}$ —Sokal and Rohlf 1995) and a Spearman rank-correlation coefficient to test the effect of size of geographic range and size of actual range on those variables.

To assess overall impact of climate change on a species, we computed an impact index; species with high indices were most likely to be affected by climate change, whereas those with low impact indices were less likely to be affected by climate change. For each species, the impact index (range = 1–11; larger values represent most effect on species distribution) was the sum of the ratio of predicted to current range (habitat) size (-1 = ratio 0–0.49, range declined dramatically as a result of climate change; -0.5 = ratio 0.50–0.74, range declined somewhat; 0 = ratio 0.75–1.24, range remained about the same; 1 = ratio > 1.24 , range expanded), the percentage of overlap between predicted and current range (1 = overlap $\geq 81\%$, least movement; 2 = overlap 61–80%; 3 = overlap 41–60%; 4 = overlap 21–40%; and 5 = overlap $\leq 20\%$, most movement), and the proportion of the modeled range that was comprised of new habitat types (1 = 0–20%, species did not take advantage of new vegetation types; 2 = 21–40%; 3 = 41–60%; 4 = 61–80%; and 5 = $> 80\%$, species range included nearly all new vegetation types). We used a Kruskal–Wallis test to determine whether impact was affected by certain life-history traits or whether species with low or high impact occupied particular geographic parts of the state.

To produce maps of species richness for Texas, we used the geographic information system to overlay sequentially the Holdridge-modeled distributions of suitable habitat for all species of rodents, and, within each area of overlap on the final map, we tallied number of species present. That procedure produced a distribution of species richness for current, CCC, and GFDLR30 conditions. For ease of visualization, density of species was categorized as <15, 15–19, 20–24, 25–29, 30–34, 35–39, and >40 species.

Assumptions of models.—Models assumed that vegetation was linked to climate and climate change would alter distribution of vegetation; such a phenomenon has been demonstrated by numerous models (Randolph and Lee 1994; Rizzo and Wiken 1992; Shugart and Smith 1992; Smith et al. 1992). Models also assumed that distribution of rodents depended on availability of suitable habitats, which has been demonstrated for a many rodents (Barrett and Peles 1999; Lidicker 1995, 1999; Morris et al. 1989; Powell et al. 1997) and that preferences of species for habitats were fixed (except as noted above for newly arrived vegetation associations) with respect to the time scale of climate change. Our assumption that habitat specificity limited distribution of rodents did not ignore the fact that other factors (i.e., severity or frequency of abiotic variables, biogeographic features of the landscape such as mountain ranges or rivers that affect dispersal, interspecific interactions—Davis et al. 1998) also might limit distributions. However, data on the role of those factors were less available than those for habitat specificity. Biogeographic features of the landscape particularly are important because their restriction upon movement of distribution of species could lead to higher rates of extinction during GCC than we modeled. We also assumed that plant communities responded intact to climate change, an assumption shared by numerous classifications that use temperature and precipitation as primary axes along which to classify plant communities (Oriens 1993) and by mechanistic models that predict composition of plant communities under various environmental scenarios (Cramer et al. 2001; Neilson 1995; Neilson and Marks 1994; Shaver et al. 2000; Woodward 1987). All data values reported are $\bar{X} \pm SE$, and statistical significance was set at $P < 0.05$ (except that $P < 0.10$ was used in a few cases to denote trends).

RESULTS

Oryzomys cousei and *Microtus mexicanus* were the only species currently found in Texas that were not predicted to occur in the state by the current Holdridge model. Those species occupied restricted ranges at the southern and mountainous northwestern edges of the state, respectively, in habitats that were not predicted to occur by the Holdridge model. Statistics on the success of the model included those 2 species ($n = 59$), whereas statistics on effects of climate change did not ($n = 57$).

The actual distribution of rodents as indicated by distributions of suitable habitats covered 62% ($\pm 3.6\%$) of their geographic range (Table 1). No significant difference was found among taxa or body mass categories, but a significant effect was found of diet ($F = 2.32$, $d.f. = 4, 54$, $P < 0.06$) and substrate ($F = 2.45$, $d.f. = 2, 56$, $P < 0.09$). Granivores ($55.8 \pm 7.5\%$), herbivores ($59.9 \pm 6.1\%$), insectivores ($69.7 \pm 11.5\%$), and omnivores ($72.1 \pm 3.9\%$) had an increasing amount of their geographic range composed of suitable habitats. For substrate, the amount of suitable habitat in the geographic range differed significantly between fossorial ($80.9 \pm 5.2\%$) and terrestrial rodents ($58.0 \pm 4.2\%$).

The areas that we categorized as suitable encompassed an average of $98 \pm 0.01\%$ of the recorded capture points for the 59 species of rodents that we modeled with the geographic information system (Table 1). For all species of rodents, an average of 76.2% of the area of the state was identified correctly by the model as included in or excluded from the range of individual species. Overshoot errors (average = 21.8% of the area of the state) were more extensive than undershoot errors (average = 2.0%; Table 1).

Overshoot errors (proportion of the state identified as suitable in which the species did not occur) for fossorial rodents (0.33 ± 0.62) were higher than those for terrestrial (0.19 ± 0.24), but not arboreal ($0.27 \pm$

0.08), rodents ($F = 3.22$, $d.f. = 2, 56$, $P < 0.05$; Table 2). For example, highest overshoot errors were for pocket gophers (e.g., *Geomys attwateri* = 56%, *G. texensis* = 53%, and *G. knoxjonesi* = 51%), whereas lowest errors were for terrestrial species (*Peromyscus boylii* = 1.6%, *Neotoma mexicana* = 1.6%, *Sigmodon ochrognathus* = 0.7%, *Tamias canipes* = 0.4%, and *P. nasutus* = 0.3%; Table 1). Overshoot errors were lower for rodents that used swamp-marsh habitats (e.g., *O. palustris* and *O. cousei*, average = 0.05) than for rodents using other habitats (average = 0.25; $F = 2.57$, $d.f. = 4, 115$, $P < 0.05$; Table 2). Overshoot error was correlated positively with overall size of range (geographic-corrected, $r_s = 0.38$, $P < 0.01$; habitat-corrected, $r_s = 0.40$, $P < 0.002$), but did not differ among taxa ($F = 1.14$, $d.f. = 5, 53$), body mass ($F = 1.29$, $d.f. = 4, 54$), or food type ($F = 1.94$, $d.f. = 3, 57$, all $P > 0.05$; Tables 1 and 2).

Under both $2 \times \text{CO}_2$ climates, average size of Holdridge-modeled range was predicted to increase greatly relative to size of current Holdridge-modeled ranges (average ratio of $2 \times \text{CO}_2$ range size relative to current modeled range size for CCC = 2.39, and for GFDLR30 = 3.52; Table 3). Size of geographic range decreased under CCC for one-half (26 of 57) of the modeled species, remained unchanged for 4 species, and increased for 27 species (Fig. 1; Table 3). In contrast, size of the range decreased under the wetter (GFDLR30) climate for 63% (36 of 57) of species, remained unchanged for 7% (4 of 57 species), and increased for 30% (17 species). Particularly large ($>2\times$) increases for *T. canipes*, *P. boylii*, and *N. mexicana* heavily influenced the average under the CCC (drier) climate, whereas those species plus *P. nasutus* influenced the average under GFDLR30. Conversely, size of range for *Microtus pinetorum* (0.23), *Reithrodontomys montanus* (0.46), *G. texensis* (0.48), and *G. knoxjonesi* (0.48) decreased by $>50\%$ under CCC, whereas size of range for *Perognathus flavescens* (0.14),

Dipodomys elator (0.20), *G. texensis* (0.28), *G. knoxjonesi* (0.28), and *Chaetodipus hispidus* (0.29) decreased >0.7 under GFDLR30.

When categorized by habitat, the ratio of predicted to current size of range under future GCC scenarios was larger for rodents in forests (average = 4.5-fold for CCC, 8.9-fold for GFDLR30) than for those from other habitats (average = 1.4-fold for both CCC and GFDLR30; $F = 1.95$, $d.f. = 3, 113$, $P < 0.10$ for CCC; $F = 5.08$, $d.f. = 4, 113$, $P < 0.001$ for GFDLR30; Table 2). No difference was found in the ratio of predicted to current size of range under either climatic scenario when data were categorized by taxon (CCC, $F = 0.58$; GFDLR30, $F = 0.54$; both $d.f. = 5, 51$), body mass ($F = 0.76$ and 0.85 , $d.f. = 4, 52$), food type ($F = 0.39$ and 0.39 , $d.f. = 3, 54$), or substrate ($F = 0.32$ and 0.41 , $d.f. = 2, 54$, all $P > 0.05$; Table 2). Under both climate models, predicted size of range relative to current modeled size of range was correlated negatively with size of TPW suitable habitats (CCC, $r_s = -0.36$; GFDLR30, $r_s = 0.32$; $P < 0.01$) and with geographic range of a species (CCC, $r_s = 0.38$; GFDLR30, $r_s = 0.41$; $P < 0.01$).

Ranges of species moved and changed in extent. Under CCC, ranges overlapped an average of 54% and under GFDLR30 ranges overlapped an average of 61% (Table 3). Species with $<10\%$ overlap (e.g., ranges under GCC were almost totally separate from current ranges) included *T. canipes*, *P. boylii*, *P. nasutus*, and *N. mexicana*. Species with $>90\%$ overlap (e.g., little or no movement of future ranges) included *Perognathus flavus*, *C. hispidus*, *R. montanus*, *Peromyscus maniculatus*, *B. taylori*, *S. ochrognathus*, and *M. pinetorum* (Table 3).

Overlap between current Holdridge-modeled and future $2 \times \text{CO}_2$ habitats was lower for rodents in forest (0.52 for both CCC and GFDLR30) and swamp-marsh (0.21 for CCC and 0.19 for GFDLR30) habitats than for rodents in other habitats (average = 0.64 for CCC and 0.72 for GFDLR30; $F =$

TABLE 2.—Life-history traits ($\bar{X} \pm 1 SE$, in parentheses) by error (percentage of success, overshoot, undershoot; see Table 1), ratio of suitable habitats in each $2 \times \text{CO}_2$ scenario to current Holdridge-modeled conditions, proportion overlap of suitable habitat in each $2 \times \text{CO}_2$ scenario with suitable habitat under current conditions, and proportion of new vegetation associations found in both $2 \times \text{CO}_2$ scenarios relative to current conditions. Index of impact given for CCC and GFDLR30 (CCC = Canadian Climate Centre model; GFDLR30 = Geophysical Fluid Dynamics Laboratory model). Missing mean or SE could not be computed or represent $n = 1$; $SE = 0$ indicate all values were the same or $n = 1$. No significant differences were found within a particular category unless superscript letters are provided, in which case different superscript letters indicate items that were significantly different.

Category of life-history trait	<i>n</i>	Percent- age of success	Over- shoot	Under- shoot	Ratio of suitable habitat to current		Percentage of overlap		Percentage of new vegetation		Impact index	
					CCC	GFDLR30	CCC	GFDLR30	CCC	GFDLR30	CCC	GFDLR30
Body mass (g)												
<25	14	1.00 (0.00)	0.19 (0.04)	0.02 (0.01)	1.21 (0.14)	0.90 (0.16)	0.60 (0.09)	0.64 (0.08)	0.62 (0.07)	0.66 (0.09)	6.78 (0.42)	6.53 (0.51)
25–50	12	0.99 (0.01)	0.19 (0.05)	0.02 (0.01)	2.74 (1.12)	6.98 (4.40)	0.45 (0.10)	0.51 (0.10)	0.51 (0.10)	0.51 (0.10)	6.82 (0.35)	5.86 (0.44)
51–150	13	0.98 (0.02)	0.18 (0.05)	0.01 (0.01)	5.01 (3.62)	6.86 (5.52)	0.44 (0.10)	0.55 (0.10)	0.65 (0.08)	0.72 (0.10)	5.01 (0.67)	4.63 (0.69)
151–500	15	0.99 (0.00)	0.30 (0.05)	0.01 (0.00)	1.62 (0.51)	1.64 (0.83)	0.59 (0.07)	0.69 (0.08)	0.63 (0.05)	0.70 (0.07)	6.97 (0.83)	6.77 (0.69)
>500	5	0.88 (0.05)	0.23 (0.06)	0.06 (0.02)	0.96 (0.09)	0.84 (0.14)	0.65 (0.05)	0.72 (0.07)	0.52 (0.11)	0.52 (0.18)	5.30 (1.43)	5.00 (1.41)
Taxon												
Sciuridae	10	0.94 (0.03)	0.20 (0.05)	0.03 (0.01)	5.68 (4.53)	7.82 (6.91)	0.58 (0.08)	0.68 (0.09)	0.58 (0.07)	0.61 (0.11)	3.40 ^A (0.19)	3.95 ^A (0.54)
Geomyidae	9	1.00 (0.00)	0.32 (0.07)	0.01 (0.00)	1.35 (0.37)	0.97 (0.32)	0.53 (0.07)	0.62 (0.09)	0.66 (0.07)	0.76 (0.09)	5.61 ^B (0.84)	5.28 ^B (0.77)
Heteromyidae	12	1.00 (0.00)	0.16 (0.03)	0.02 (0.01)	1.51 (0.32)	0.77 (0.23)	0.44 (0.09)	0.63 (0.07)	0.56 (0.08)	0.62 (0.10)	5.33 ^B (0.32)	5.79 ^B (0.48)
Sigmodontinae	25	0.99 (0.01)	0.21 (0.04)	0.02 (0.00)	2.01 (0.59)	4.29 (2.13)	0.57 (0.07)	0.58 (0.07)	0.61 (0.06)	0.65 (0.07)	7.89 ^C (0.32)	6.71 ^B (0.46)
Arvicolinae	2	1.00 (0.00)	0.21 (0.21)	0.00 (0.00)	0.23 (0.00)	0.63 (0.00)	0.45 (0.45)	0.48 (0.48)	0.50 (0.50)	0.50 (0.50)	11.00 ^D (0.00)	10.00 ^C (0.00)
Erethizonidae	1	0.78	0.38	0.06	0.73	0.65	0.46	0.52	0.66	0.35	11.00 ^D	10.00 ^C
Food type												
Granivore	17	1.00 (0.00)	0.27 (0.09)	0.02 (0.00)	2.32 (0.77)	4.90 (3.01)	0.40 (0.08)	0.58 (0.08)	0.46 (0.07)	0.56 ^A (0.09)	6.22 ^A (0.29)	5.50 (0.37)

TABLE 2.—Continued.

Category of life-history trait	<i>n</i>	Percent- age of success	Over- shoot	Under- shoot	Ratio of suitable habitat to current		Percentage of overlap		Percentage of new vegetation		Impact index	
					CCC	GFDLR30	CCC	GFDLR30	CCC	GFDLR30	CCC	GFDLR30
Herbivore	25	0.97 (0.01)	0.24 (0.04)	0.02 (0.01)	3.27 (1.87)	4.21 (2.85)	0.56 (0.06)	0.66 (0.07)	0.61 (0.05)	0.59 ^A (0.07)	6.98 ^A (0.63)	6.65 (0.59)
Insectivore	5	1.00 (0.00)	0.27 (0.09)	0.02 (0.00)	1.29 (0.30)	1.06 (0.35)	0.62 (0.19)	0.56 (0.14)	0.73 (0.11)	0.81 ^B (0.09)	8.25 ^B (0.75)	7.00 (1.37)
Omnivore	14	0.98 (0.02)	0.25 (0.04)	0.02 (0.01)	1.09 (0.09)	1.07 (0.19)	0.63 (0.07)	0.68 (0.07)	0.60 (0.07)	0.84 ^B (0.06)	4.85 ^C (0.45)	4.96 (0.51)
Substrate												
Terrestrial	46	0.98 (0.01)	0.19 ^A (0.02)	0.02 (0.00)	2.75 (1.05)	4.27 (1.90)	0.52 (0.05)	0.59 (0.05)	0.57 (0.04)	0.59 ^A (0.05)	6.57 (0.34)	6.21 ^A (0.34)
Arboreal	3	0.90 (0.08)	0.27 ^A (0.04)	0.03 (0.02)	0.93 (0.14)	1.06 (0.07)	0.65 (0.05)	0.75 (0.03)	0.73 (0.00)	0.95 ^B (0.00)	4.00 (0.00)	2.67 ^B (0.33)
Fossorial	10	1.00 (0.00)	0.33 ^B (0.06)	0.01 (0.00)	1.24 (0.35)	0.93 (0.28)	0.57 (0.08)	0.66 (0.09)	0.70 (0.07)	0.78 ^B (0.08)	6.15 (0.93)	5.75 ^A (0.83)
Habitat												
Desert	42	— ^a	0.24 ^A (0.03)	0.02 (0.01)	1.56 ^A (0.63)	1.37 ^A (0.49)	0.58 ^A (0.05)	0.70 ^A (0.04)	0.56 (0.04)	0.57 ^A (0.05)	6.01 (0.36)	5.05 ^A (0.30)
Grassland	24	— ^a	0.27 ^A (0.04)	0.03 (0.01)	1.21 ^A (0.17)	0.89 ^A (0.15)	0.66 ^A (0.06)	0.73 ^A (0.06)	0.62 (0.04)	0.76 ^B (0.05)	6.04 (0.51)	5.86 ^A (0.50)
Brush	32	— ^a	0.29 ^A (0.03)	0.02 (0.01)	1.09 ^A (0.13)	0.90 ^A (0.12)	0.67 ^A (0.04)	0.74 ^A (0.04)	0.62 (0.04)	0.72 ^B (0.05)	5.73 (0.37)	5.67 ^A (0.39)
Forest	20	— ^a	0.20 ^A (0.04)	0.02 (0.01)	4.52 ^B (2.45)	8.91 ^B (4.34)	0.52 ^B (0.08)	0.52 ^B (0.08)	0.72 (0.07)	0.70 ^B (0.08)	6.68 (0.54)	6.98 ^B (0.43)
Swamp-marsh	2	— ^a	0.05 (0.05)	0.01 (0.01)	1.65 ^A	2.32 ^A	0.21 ^C (0.21)	0.19 ^C (0.19)	0.41 (0.41)	1.00 ^C	7.00 (2.00)	9.50 ^B (0.50)

^a Success could not be computed because collection localities were not identified by habitat within geographic range.

TABLE 3.—Area of suitable habitat ($\times 10^{-3}$ km²; corrected for habitat preferences) predicted by the Holdridge model for each species of rodent for current, Canadian Climate Centre (CCC), and Geophysical Fluid Dynamics Laboratory (GFDLR30) climatic models. Ratio of suitable habitat under each climatic scenario relative to that under the current climate is given in parentheses. Overlap represents the area of suitable habitat under each climatic scenario that overlapped the extent of the Holdridge-modeled range under the current climate. The overlap area relative to the amount of suitable habitat in that climatic scenario is given in parentheses. The geographic area of suitable habitats under CCC and GFDLR30 models predicted to be comprised of vegetation associations not currently found in Texas (e.g., new associations) is given. The proportion of new vegetation associations relative to the area of suitable habitat under CCC and GFDLR30 models is given in parentheses.

Species	Suitable habitat					Overlap				New associations			
	Current	CCC		GFDLR30		CCC		GFDLR30		CCC		GFDLR30	
<i>Ammospermophilus interpres</i>	129.0	282.8	(2.19)	238.9	(1.85)	84.5	(0.30)	73.6	(0.31)	149.9	(0.53)	67.3	(0.28)
<i>Baiomys taylori</i>	584.9	528.0	(0.90)	496.8	(0.85)	501.9	(0.95)	481.7	(0.97)	389.4	(0.74)	475.9	(0.96)
<i>Chaetodipus hispidus</i>	515.3	374.1	(0.73)	150.0	(0.29)	353.6	(0.95)	144.6	(0.96)	142.6	(0.38)	65.8	(0.44)
<i>Chaetodipus intermedius</i>	130.1	187.6	(1.44)	76.3	(0.59)	88.9	(0.47)	48.9	(0.64)	51.0	(0.27)	15.5	(0.20)
<i>Chaetodipus nelsoni</i>	129.2	191.6	(1.48)	88.5	(0.68)	86.8	(0.45)	52.7	(0.60)	50.2	(0.26)	25.8	(0.29)
<i>Chaetodipus penicillatus</i>	123.3	214.3	(1.74)	58.3	(0.47)	77.7	(0.36)	27.9	(0.48)	87.1	(0.41)	19.8	(0.34)
<i>Cratogeomys castanops</i>	476.3	336.3	(0.71)	140.7	(0.30)	244.9	(0.73)	102.0	(0.73)	175.7	(0.52)	77.4	(0.55)
<i>Cynomys ludovicianus</i>	203.6	200.5	(0.98)	83.8	(0.41)	147.6	(0.74)	77.3	(0.92)	56.8	(0.28)	20.5	(0.24)
<i>Dipodomys compactus</i>	97.7	302.9	(3.10)	234.2	(2.40)	32.6	(0.11)	34.9	(0.15)	250.5	(0.83)	234.2	(1.00)
<i>Dipodomys elator</i>	103.4	53.3	(0.52)	20.5	(0.20)	1.8	(0.03)	9.9	(0.48)	53.3	(1.00)	20.5	(1.00)
<i>Dipodomys merriami</i>	141.3	215.2	(1.52)	88.5	(0.63)	105.0	(0.49)	58.0	(0.66)	59.9	(0.28)	25.8	(0.29)
<i>Dipodomys ordii</i>	495.8	334.8	(0.68)	176.4	(0.36)	270.8	(0.81)	169.8	(0.96)	200.5	(0.60)	137.4	(0.78)
<i>Dipodomys spectabilis</i>	135.9	159.8	(1.18)	86.0	(0.63)	45.5	(0.28)	47.1	(0.55)	60.9	(0.38)	25.8	(0.30)
<i>Erethizon dorsatum</i>	346.1	253.3	(0.73)	226.1	(0.65)	115.7	(0.46)	118.2	(0.52)	168.1	(0.66)	78.3	(0.35)
<i>Geomys arenarius</i>	79.7	173.0	(2.17)	81.8	(1.03)	30.1	(0.17)	18.8	(0.23)	84.5	(0.49)	44.1	(0.54)
<i>Geomys attwateri</i>	443.0	471.0	(1.06)	452.5	(1.02)	412.6	(0.88)	369.8	(0.82)	338.4	(0.72)	431.6	(0.95)
<i>Geomys breviceps</i>	120.7	208.3	(1.73)	336.8	(2.79)	98.9	(0.47)	117.2	(0.35)	208.3	(1.00)	336.8	(1.00)
<i>Geomys bursarius</i>	368.7	262.6	(0.71)	151.7	(0.41)	121.3	(0.46)	99.0	(0.65)	208.7	(0.79)	135.7	(0.89)
<i>Geomys knoxjonesi</i>	368.7	177.5	(0.48)	102.6	(0.28)	99.1	(0.56)	95.6	(0.93)	123.6	(0.70)	86.6	(0.84)
<i>Geomys personatus</i>	64.2	252.1	(3.92)	146.0	(2.27)	64.2	(0.25)	41.2	(0.28)	206.9	(0.82)	144.1	(0.99)
<i>Geomys texensis</i>	368.7	177.5	(0.48)	102.6	(0.28)	99.1	(0.56)	95.6	(0.93)	123.6	(0.70)	86.6	(0.84)
<i>Glaucomys volans</i>	357.4	281.8	(0.79)	352.4	(0.99)	170.9	(0.61)	277.7	(0.79)	204.2	(0.72)	331.5	(0.94)
<i>Liomys irroratus</i>	81.8	344.2	(4.21)	197.8	(2.42)	66.1	(0.19)	74.7	(0.38)	287.5	(0.84)	197.8	(1.00)
<i>Microtus mexicanus</i>	— ^a												
<i>Microtus pinetorum</i>	452.4	101.9	(0.23)	284.3	(0.63)	91.3	(0.90)	275.3	(0.97)	101.9	(1.00)	284.3	(1.00)
<i>Neotoma albigula</i>	451.7	377.8	(0.84)	270.8	(0.60)	285.4	(0.76)	229.7	(0.85)	136.3	(0.36)	59.8	(0.22)
<i>Neotoma floridana</i>	371.1	343.5	(0.93)	401.8	(1.08)	300.5	(0.87)	314.2	(0.78)	219.5	(0.64)	380.9	(0.95)
<i>Neotoma mexicana</i>	11.9	95.7	(8.03)	154.6	(12.97)	0.0	(0.00)	11.9	(0.08)	88.0	(0.92)	27.7	(0.18)
<i>Neotoma micropus</i>	612.9	600.4	(0.98)	358.7	(0.59)	527.7	(0.88)	355.9	(0.99)	383.1	(0.64)	295.5	(0.82)

TABLE 3.—Continued.

Species	Suitable habitat					Overlap				New associations			
	Current	CCC	GFDLR30			CCC	GFDLR30			CCC	GFDLR30		
<i>Ochrotomys nuttalli</i>	117.2	89.4	(0.76)	279.9	(2.39)	89.4	(1.00)	117.2	(0.42)	89.4	(1.00)	279.9	(1.00)
<i>Onychomys arenicola</i>	144.3	332.0	(2.30)	140.7	(0.98)	107.9	(0.33)	60.5	(0.43)	175.7	(0.53)	77.4	(0.55)
<i>Onychomys leucogaster</i>	524.0	380.7	(0.73)	180.6	(0.34)	330.9	(0.87)	163.2	(0.90)	214.2	(0.56)	117.4	(0.65)
<i>Oryzomys couesi</i>	— ^a			6.2								6.2	(1.00)
<i>Oryzomys palustris</i>	164.0	270.3	(1.65)	380.9	(2.32)	110.7	(0.41)	141.9	(0.37)	219.5	(0.81)	380.9	(1.00)
<i>Perognathus flavescens</i>	180.6	116.6	(0.65)	25.8	(0.14)	28.1	(0.24)	19.4	(0.75)	104.0	(0.89)	25.8	(1.00)
<i>Perognathus flavus</i>	570.8	518.5	(0.91)	265.4	(0.47)	485.6	(0.94)	263.0	(0.99)	301.2	(0.58)	202.2	(0.76)
<i>Peromyscus attwateri</i>	389.0	331.7	(0.85)	197.9	(0.51)	140.2	(0.42)	126.8	(0.64)	254.1	(0.77)	177.0	(0.89)
<i>Peromyscus boylii</i>	11.9	167.4	(14.04)	206.2	(17.30)	0.0	(0.00)	11.9	(0.06)	159.7	(0.95)	79.3	(0.38)
<i>Peromyscus eremicus</i>	173.9	264.6	(1.52)	89.1	(0.51)	123.2	(0.47)	58.6	(0.66)	104.0	(0.39)	25.8	(0.29)
<i>Peromyscus gossypinus</i>	120.7	208.3	(1.73)	336.8	(2.79)	98.9	(0.47)	117.2	(0.35)	208.3	(1.00)	336.8	(1.00)
<i>Peromyscus leucopus</i>	368.1	357.5	(0.97)	280.4	(0.76)	254.2	(0.71)	239.4	(0.85)	190.3	(0.53)	118.7	(0.42)
<i>Peromyscus maniculatus</i>	652.0	641.0	(0.98)	526.3	(0.81)	599.9	(0.94)	487.8	(0.93)	352.1	(0.55)	442.2	(0.84)
<i>Peromyscus nasutus</i>	2.6	7.7	(2.91)	133.1	(50.46)	0.0	(0.00)	2.6	(0.02)	0.0	(0.00)	6.2	(0.05)
<i>Peromyscus pectoralis</i>	420.6	409.0	(0.97)	294.7	(0.70)	251.8	(0.62)	168.4	(0.57)	175.7	(0.43)	83.7	(0.28)
<i>Peromyscus truei</i>	103.4	172.2	(1.67)	77.4	(0.75)	4.8	(0.03)	11.8	(0.15)	172.2	(1.00)	77.4	(1.00)
<i>Reithrodontomys fulvescens</i>	617.0	624.1	(1.01)	526.3	(0.85)	552.7	(0.89)	460.0	(0.87)	352.1	(0.56)	442.2	(0.84)
<i>Reithrodontomys humulis</i>	45.5	81.9	(1.80)	93.3	(2.05)	21.6	(0.26)	11.2	(0.12)	81.9	(1.00)	93.3	(1.00)
<i>Reithrodontomys megalotis</i>	186.9	146.3	(0.78)	183.1	(0.98)	108.8	(0.74)	129.3	(0.71)	43.7	(0.30)	20.5	(0.11)
<i>Reithrodontomys montanus</i>	564.3	257.7	(0.46)	354.3	(0.63)	247.9	(0.96)	349.7	(0.99)	146.2	(0.57)	294.2	(0.83)
<i>Sciurus carolinensis</i>	357.4	285.9	(0.80)	357.8	(1.00)	170.9	(0.60)	277.7	(0.78)	208.3	(0.73)	336.8	(0.94)
<i>Sciurus niger</i>	380.4	458.3	(1.20)	453.4	(1.19)	347.0	(0.76)	317.2	(0.70)	334.3	(0.73)	432.5	(0.95)
<i>Sigmodon hispidus</i>	629.5	447.3	(0.71)	472.1	(0.75)	388.9	(0.87)	454.3	(0.96)	260.6	(0.58)	391.0	(0.83)
<i>Sigmodon ochrognathus</i>	15.6	10.9	(0.70)	15.0	(0.96)	9.9	(0.91)	13.8	(0.92)	3.6	(0.33)	1.3	(0.09)
<i>Spermophilus mexicanus</i>	498.8	506.5	(1.02)	232.5	(0.47)	418.6	(0.83)	200.1	(0.86)	227.8	(0.45)	148.7	(0.64)
<i>Spermophilus spilosoma</i>	290.7	466.9	(1.61)	260.1	(0.89)	233.0	(0.50)	196.7	(0.76)	254.0	(0.54)	196.8	(0.76)
<i>Spermophilus tridecemlineatus</i>	574.4	401.6	(0.70)	259.5	(0.45)	320.9	(0.80)	252.2	(0.97)	263.0	(0.66)	238.5	(0.92)
<i>Spermophilus variegatus</i>	253.8	273.0	(1.08)	233.6	(0.92)	185.8	(0.68)	156.1	(0.67)	59.9	(0.22)	26.2	(0.11)
<i>Tamias canipes</i>	2.6	122.5	(47.21)	184.7	(71.04)	0.0	(0.00)	2.6	(0.01)	114.8	(0.94)	57.8	(0.31)
<i>Thomomys bottae</i>	333.1	293.9	(0.88)	110.0	(0.33)	202.3	(0.69)	77.6	(0.70)	70.5	(0.24)	25.8	(0.23)
\bar{X}			2.39		3.52		0.54		0.61		0.60		0.642
SE			0.83		1.51		0.04		0.04		0.04		0.044

^a Could not compute; see text.

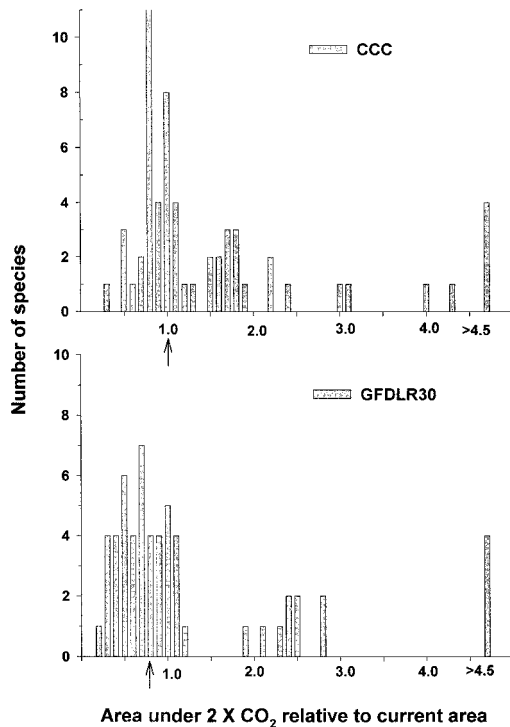


FIG. 1.—Area of suitable habitat for species of rodents ($n = 57$) under $2 \times \text{CO}_2$ scenarios (Canadian Climate Centre [CCC] and Geophysical Fluid Dynamics Laboratory [GFDLR30] models) relative to area of suitable habitat under current conditions. Values <1.0 indicate range shrinkages, and values >1.0 indicate range expansion after global climate change. Median is indicated by arrow.

2.61, $d.f. = 4$, 115, $P < 0.05$ for CCC and $F = 4.33$, $d.f. = 4$, 115, $P < 0.001$ for GFDLR30; Table 2). Overlap was not affected under either climatic scenario for taxa (CCC, $F = 0.35$; GFDLR30, $F = 0.21$; both $d.f. = 5$, 53), body mass ($F = 0.91$ and 0.83 , $d.f. = 4$, 54), food type ($F = 1.24$ and 1.3 , $d.f. = 3$, 56), or substrate ($F = 0.31$ and 0.53 , $d.f. = 2$, 56, all $P > 0.05$; Table 2). For both climatic models, overlap was affected by extent of geographic (CCC, $r_s = 0.62$; GFDLR30, $r_s = 0.69$; $P < 0.001$) and habitat-corrected ($r_s = 0.43$ and $r_s = 0.48$; $P < 0.001$) ranges.

We assumed that rodents under $2 \times \text{CO}_2$ climates would use new vegetation types

that did not occur within Texas under the current climate. If rodents were not as flexible in using those new habitats, those species largely using new vegetation types under $2 \times \text{CO}_2$ climates may be at risk of decline or extinction. The effect of that assumption was indicated by the proportion of the range for each species that was composed of new vegetation types under each $2 \times \text{CO}_2$ climate (Table 3). On average, about 60% of $2 \times \text{CO}_2$ ranges were composed of new habitat types (CCC = 0.60; GFDLR30 = 0.64). Seven species under CCC and 11 species under GFDLR30 occupied all new habitats. The only species that did not occupy any new habitats under CCC was *P. nasutus*, whereas several species occupied $<30\%$ new habitats (*Spermophilus variegatus*, *Thomomys bottae*, *Chaetodipus nelsoni*, *C. intermedius*, and *Dipodomys merriami*). Under GFDLR30, all species occupied some new vegetation associations, but the range of several species contained only a small proportion ($\sim 10\%$) of new vegetation types (*P. nasutus*, *S. ochrognathus*, *Reithrodontomys megalotis*, and *S. variegatus*).

Amount of new habitats in ranges of taxa with granivorous and herbivorous food habits was less than the amount of new habitats for taxa with insectivorous or omnivorous food habits under GFDLR30 ($F = 2.5$, $d.f. = 3$, 56, $P < 0.05$), but no difference was found under CCC ($F = 0.36$, $d.f. = 3$, 57, $P > 0.05$). No difference was found in the proportion of new habitats in Holdridge-modeled ranges of species occupying different substrates under the CCC model ($F = 1.3$, $d.f. = 2$, 56, $P > 0.05$), but a strong relationship was found between substrate occupied and amount of new habitat in ranges of species under GFDLR30 ($F = 2.8$, $d.f. = 2$, 56, $P < 0.07$; Table 2). Terrestrial species occupied significantly fewer new vegetation associations than either arboreal or fossorial rodents. The amount of new vegetation associations under CCC did not differ significantly for rodents in different habitats, but under GFDLR30, rodents

TABLE 4.—Predicted impact of global climate change on species of rodent under 2 climatic scenarios, that of Canadian Climate Centre (CCC) and Geophysical Fluid Dynamics Laboratory (GFDLR30). Impact index is computed by summing ranks of percentage suitable habitat, overlap, and new associations (see Table 3 and text). Index ranges from 1 (minimum impact) to 11 (maximum impact).

Species of rodent	CCC	GFDLR30
<i>Ammospermophilus interpres</i>	8.0	8.0
<i>Baiomys taylori</i>	5.0	6.0
<i>Chaetodipus hispidus</i>	2.5	3.0
<i>Chaetodipus intermedius</i>	6.0	2.5
<i>Chaetodipus nelsoni</i>	6.0	4.5
<i>Chaetodipus penicillatus</i>	8.0	4.0
<i>Cratogeomys castanops</i>	4.5	4.0
<i>Cynomys ludovicianus</i>	4.0	2.0
<i>Dipodomys compactus</i>	11.0	11.0
<i>Dipodomys elator</i>	9.5	7.0
<i>Dipodomys merriami</i>	6.0	3.5
<i>Dipodomys ordii</i>	4.5	4.0
<i>Dipodomys spectabilis</i>	6.0	4.5
<i>Erethizon dorsatum</i>	6.5	4.5
<i>Geomys arenarius</i>	9.0	7.0
<i>Geomys attwateri</i>	5.0	6.0
<i>Geomys breviceps</i>	9.0	10.0
<i>Geomys bursarius</i>	6.5	6.0
<i>Geomys knoxjonesi</i>	6.0	5.0
<i>Geomys personatus</i>	10.0	10.0
<i>Geomys texensis</i>	6.0	5.0
<i>Glaucomys volans</i>	6.0	7.0
<i>Liomys irroratus</i>	11.0	10.0
<i>Microtus mexicanus</i>	— ^a	— ^a
<i>Microtus pinetorum</i>	5.0	5.5
<i>Neotoma albigula</i>	4.0	2.5
<i>Neotoma floridana</i>	5.0	7.0
<i>Neotoma mexicana</i>	11.0	7.0
<i>Neotoma micropus</i>	5.0	5.5
<i>Ochrotomys nuttalli</i>	6.0	9.0
<i>Onychomys arenicola</i>	8.0	6.0
<i>Onychomys leucogaster</i>	3.5	4.0
<i>Oryzomys couesi</i>	— ^a	— ^a
<i>Oryzomys palustris</i>	9.0	10.0
<i>Perognathus flavescens</i>	7.5	6.0
<i>Perognathus flavus</i>	8.0	4.0
<i>Peromyscus attwateri</i>	9.0	6.5
<i>Peromyscus boylii</i>	9.0	8.0
<i>Peromyscus eremicus</i>	6.0	3.5
<i>Peromyscus gossypinus</i>	9.0	10.0
<i>Peromyscus leucopus</i>	6.0	4.0
<i>Peromyscus maniculatus</i>	5.0	6.0
<i>Peromyscus nasutus</i>	3.0	7.0
<i>Peromyscus pectoralis</i>	5.0	4.5
<i>Peromyscus truei</i>	11.0	10.0

TABLE 4.—Continued.

Species of rodent	CCC	GFDLR30
<i>Reithrodontomys fulvescens</i>	4.0	6.0
<i>Reithrodontomys humulis</i>	10.0	11.0
<i>Reithrodontomys megalotis</i>	4.0	3.0
<i>Reithrodontomys montanus</i>	3.0	5.5
<i>Sciurus carolinensis</i>	7.0	7.0
<i>Sciurus niger</i>	6.0	7.0
<i>Sigmodon hispidus</i>	3.5	6.0
<i>Sigmodon ochrognathus</i>	2.5	2.0
<i>Spermophilus mexicanus</i>	4.0	4.0
<i>Spermophilus pilosoma</i>	7.0	6.0
<i>Spermophilus tridecemlineatus</i>	4.5	5.0
<i>Spermophilus variegatus</i>	4.0	3.0
<i>Tamias canipes</i>	11.0	8.0
<i>Thomomys bottae</i>	4.0	3.0
\bar{X}	6.4	5.9

^a Could not be computed; see text.

in desert and swamp-marsh habitats had lower and higher, respectively, amounts of new habitat in their ranges than did rodents in other habitats (average = 0.72, $F = 2.61$, $d.f. = 4, 115$, $P < 0.05$). No difference was found in the proportion of new habitats in the Holdridge-modeled range of species grouped by taxa (CCC, $F = 0.22$; GFDLR30, $F = 0.45$; both $d.f. = 5, 53$) or body mass ($F = 0.57$ and 0.95 ; $d.f. = 4, 54$, $P < 0.05$; Table 2). Finally, the amount of new habitats in geographic ranges of rodents after GCC was not affected by size of the geographic (CCC, $r_s = -0.17$; GFDLR30, $r_s = -0.16$) or habitat-corrected ($r_s = 0.06$ and $r_s = 0.11$) range of a species.

The average impact was greater under CCC (6.4 ± 0.32) than under GFDLR30 (5.9 ± 0.32 ; $t = -2.14$, $d.f. = 56$, $P < 0.05$; Table 4). Species impacted the most by GCC (impact index ≥ 10), included *Dipodomys compactus*, *Geomys personatus*, *Liomys irroratus*, *Peromyscus truei*, and *Reithrodontomys humulis* under both CCC and GFDLR30; *N. mexicana* and *T. canipes* under CCC; and *Geomys breviceps*, *O. palustris*, and *Peromyscus gossypinus* under GFDLR30 (Table 4). The species most affected under CCC alone and under both CCC and GFDLR30 occurred in western and southern Texas, except *R. humulis* that

occupied eastern Texas; species most affected under GFDLR30 occurred in eastern Texas. Species impacted the least (impact index ≤ 3 for CCC and ≤ 2.5 for GFDLR30) included *S. ochrognathus* under both CCC and GFDLR30; *C. hispidus*, *R. montanus*, and *P. nasutus* under CCC; and *C. intermedius*, *C. ludovicianus*, and *Neotoma albigula* under GFDLR30 (Table 4). All of the species affected the least occurred in western Texas, although the range of *N. albigula* also extended into central Texas.

Impact was higher under CCC on insectivores than on granivores and herbivores, and was least on omnivores ($F = 3.0$, $d.f. = 3$, 55 , $P < 0.05$; Table 2). Impact was affected for taxa under both climatic scenarios (CCC, $F = 17.6$; GFDLR30, $F = 4.1$; both $d.f. = 5$, 53 , $P < 0.001$; Table 2). For CCC, impact was least on Sciuridae, intermediate for Geomyidae and Heteromyidae, and greatest on Arvicolinae and Erthizontidae. Impact on Sigmontinae under CCC was significantly less than on Arvicolinae but significantly more than on Heteromyidae. For GFDLR30, impact was least on Sciuridae; intermediate on Heteromyidae, Geomyidae, and Sigmontinae; and highest for Arvicolinae and Erthizontidae (Table 2). Impact was greater on terrestrial and fossorial rodents than on arboreal rodents under the GFDLR30 climate ($F = 3.4$, $d.f. = 2$, 56 , $P < 0.05$; Table 2) but did not differ among taxa under CCC. Impact was not affected by body mass (CCC, $F = 1.6$; GFDLR30, $F = 1.9$; both $d.f. = 4$, 54 , $P > 0.05$), food type under GFDLR30 ($F = 1.9$, $d.f. = 3$, 57 , $P > 0.05$), or substrate under CCC ($F = 1.7$, $d.f. = 2$, 56 , $P > 0.05$; Table 2). Impact did not differ among habitats under CCC (Kruskal-Wallis $H = 2.9$, $d.f. = 4$, $P > 0.05$; Table 2), but impact under GFDLR30 was greater for rodents in swamp-marsh and forest habitats than for rodents in the other habitats ($H = 15.7$, $d.f. = 4$, $P < 0.001$; Table 2).

Four species of rodents illustrated the range of effects of climate change on distributions of individual species (Figs. 2–5).

The differences between geographic and suitable-habitat ranges are given in the upper left panels of Figs. 2–5 (note the fragmentation of the range indicated as clear holes). *R. megalotis* and *C. hispidus* were among the species least impacted by modeled climate change (Table 4). The Holdridge-modeled range for *R. megalotis* included western Texas and the eastern parts of the Panhandle (Fig. 2). The distribution of *R. megalotis* remained similar under both CCC and GFDLR30, with expansion into the rest of the Panhandle. New (hatched) habitats replaced some current habitats but did not account for much of the range expansion. *C. hispidus* occupied nearly the entire state except eastern Texas and scattered areas in southern, western, and central Texas under Holdridge-modeled current conditions (Fig. 3). The overall range was slightly compressed toward the west under CCC, but occupancy of original habitats was restricted to the Trans-Pecos region and the western Panhandle, whereas the rest of the distribution resulted from occupation of new habitats. The impact under GFDLR30 was much greater, with the entire range restricted to western Texas and the far northern Panhandle, although the range contained fewer new vegetation types than under CCC.

Geomys personatus and *O. palustris* were among the species most affected by GCC (Table 4). The current Holdridge-modeled distribution of *G. personatus*, a fossorial species, was restricted to far southern Texas and a narrow portion in eastern Texas (Fig. 4). Under CCC, the range expanded to include large areas in southern, eastern, and western Texas, with penetration into the Panhandle. Under GFDLR30 a similar, but less extensive, distribution resulted. The majority of those range expansions were into new vegetation associations. *O. palustris* occurred predominantly in low-lying areas in eastern Texas, coastal areas, and scattered areas toward the west under Holdridge-modeled current conditions (Fig. 5). Under CCC, the range ex-

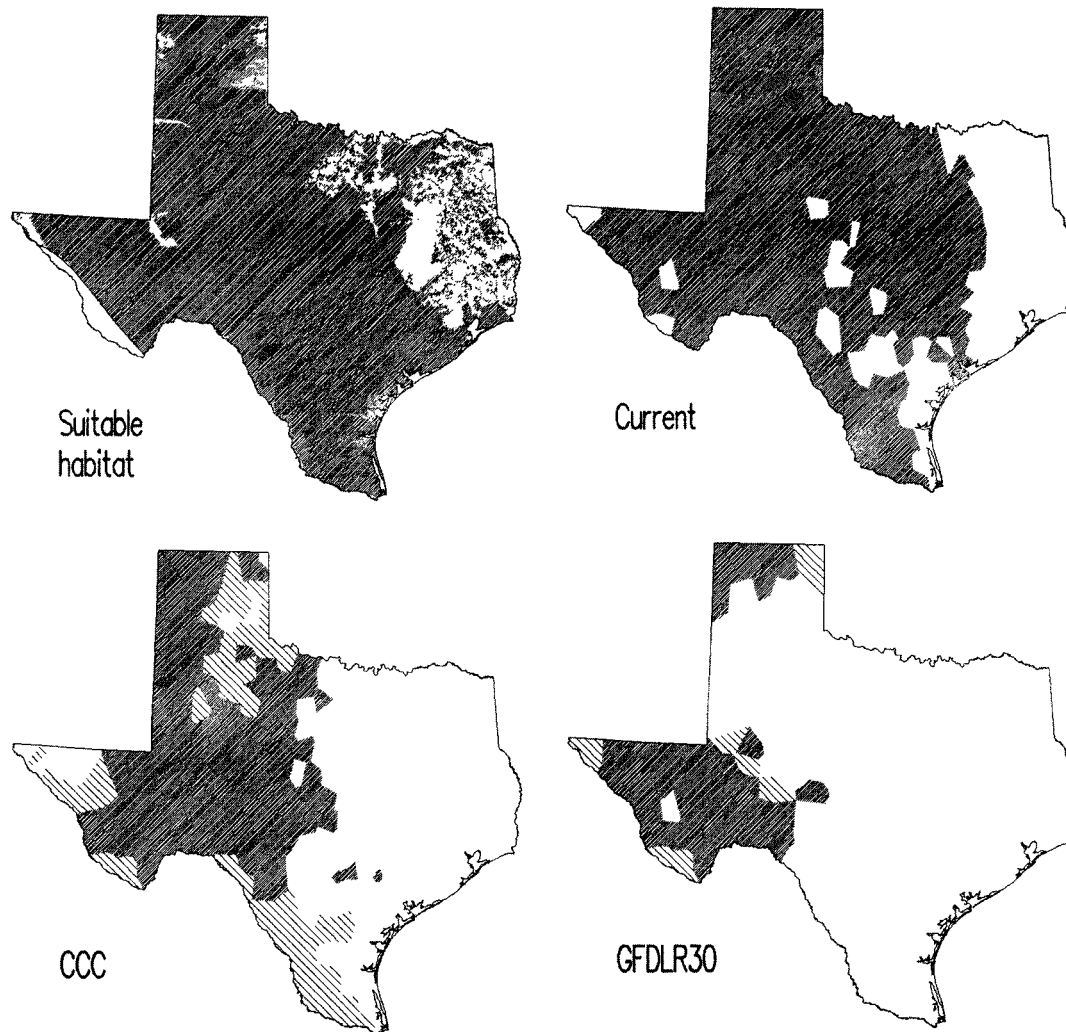


FIG. 2.—Geographic distribution of *Reithrodontomys montanus*. Distinction between suitable habitat (filled areas) and geographic range (solid line limiting the distribution) shown in upper-left pane (note: white areas within range represent unoccupied habitats and illustrate the extent of habitat fragmentation), whereas Holdridge-modeled ranges under current, Canadian Climate Centre (CCC)-modeled, and Geophysical Fluid Dynamics Laboratory (GFDLR30)-modeled climates are shown in upper-right, lower-left, and lower-right panels, respectively. Dark shading in lower panels represents vegetation types currently found in Texas and light hatching represents new vegetation types predicted to occur as a result of global climate change.

panded, largely because of occupancy of new habitats, into central Texas and the Panhandle, whereas distribution along the lower coast was noticeably missing. Under GFDLR30, all habitats occupied were new, and a further westward expansion of that species occurred.

Under the Holdridge-modeled current climate, richness of species of rodents in Texas was highest on the edge of the Edwards Plateau and extended into the Trans-Pecos area, where richness ranged from 30 to >40 species (Fig. 6A). Modest richness of 25–29 species was present in patches in eastern

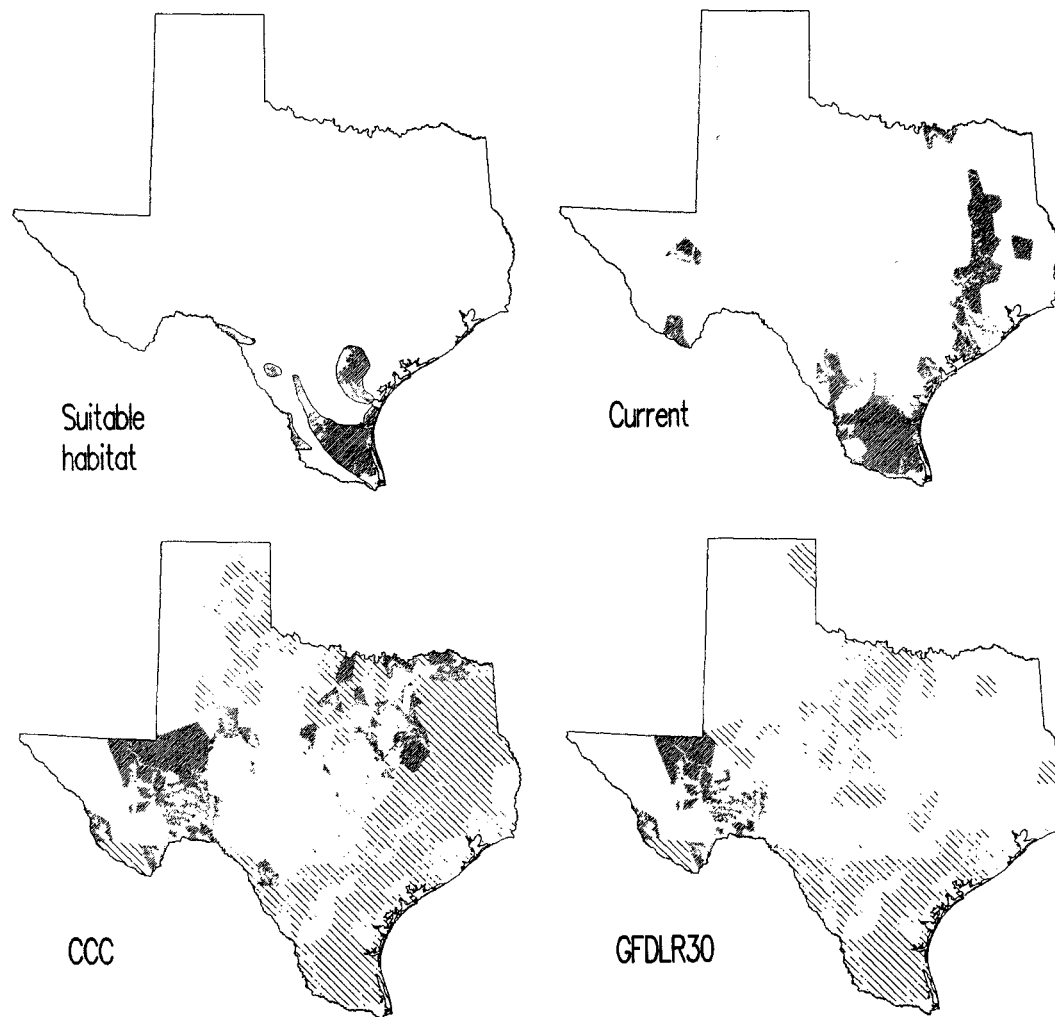


FIG. 3.—Geographic distribution of *Chaetodipus hispidus*. See Fig. 1 for description.

Texas and throughout the north-central part of the state. Lowest richness, from 15 to 24 species, occurred along the coast and in the Panhandle. Under CCC, highest richness shifted to the eastern part of the Panhandle, where >40 species occurred (Fig. 6B). Other foci of richness occurred along the border with Mexico, where areas containing 30–40 species were in the mountainous areas of western Texas, in the area around Big Bend National Park, and along the Rio Grande River into southern Texas. Intermediate richness of 25–30 species occurred in eastern Texas, along the Gulf coast, and from central

and western Texas into the western part of the Panhandle. Lowest densities of 15–20 species occurred in southeastern and central Texas. Under GFDLR30, richness generally was lower than under either current or CCC conditions (Fig. 6C). A small pocket of high richness (>40 species) occurred in west-central Texas and the eastern corner of the Panhandle, and another pocket of 35–40 species occurred in far western Texas. Most of the rest of the state contained 15–25 species of rodents with the entire west-central part and up to the Panhandle containing <15 species.

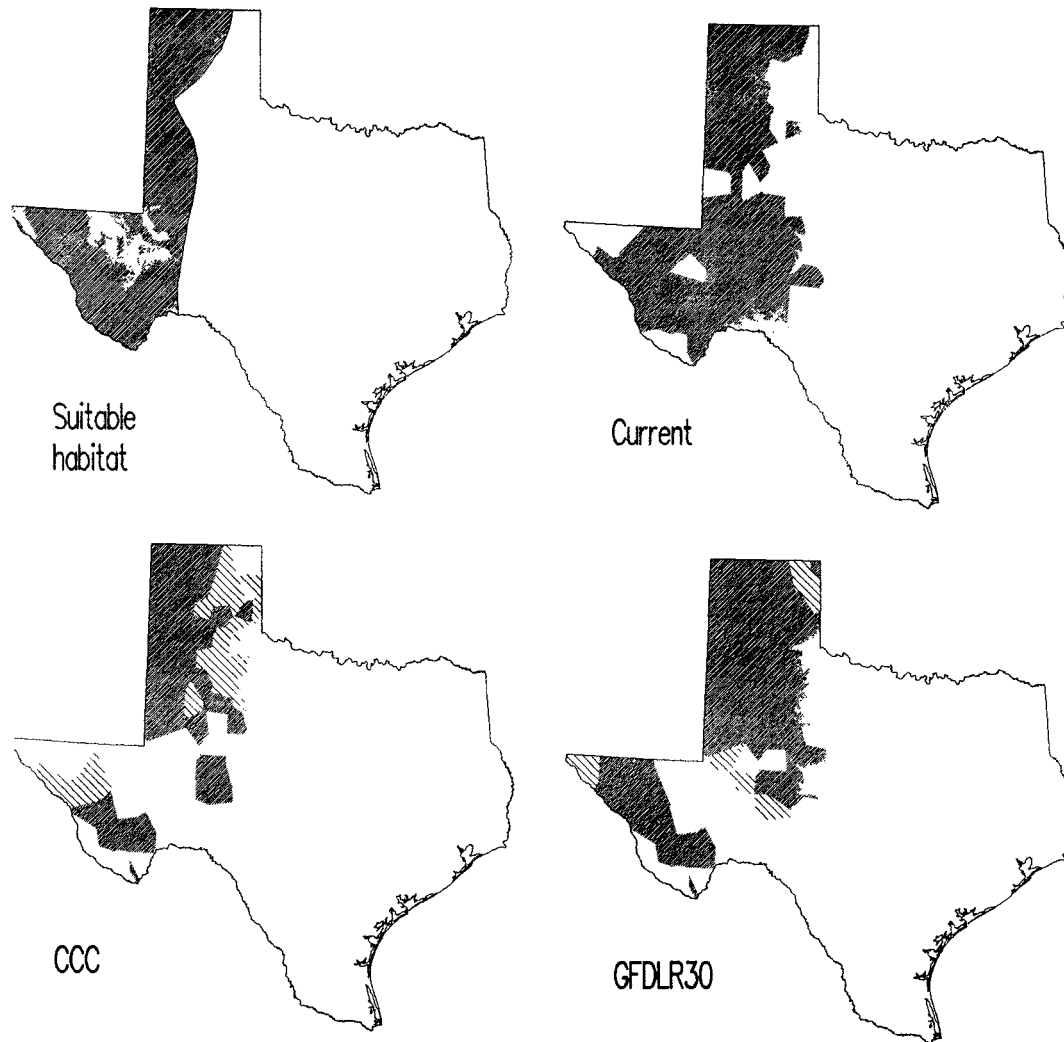


FIG. 4.—Geographic distribution of *Geomys personatus*. See Fig. 1 for description.

DISCUSSION

We modeled distributions of rodents in Texas before and after simulated climate change, using general circulation models to predict climates and models of climate-vegetation associations to predict vegetation changes that followed. We determined that the impact of climate change on rodents would be greatest in eastern Texas if the climate becomes warmer and wetter (GFDLR30), but greatest in western and southern Texas if the climate becomes warmer and drier (CCC). This result is be-

cause forest habitats in eastern Texas were predicted to expand under the wetter climate, whereas desert and shrub habitats in western and southern Texas were predicted to expand under the drier climate. Similarly, we found that life-history variables (e.g., habitat type or diet) that were correlated with changes in size of range, location, or composition of habitat also reflected broad changes in relative distribution of vegetation types. For example, in the wetter climate, rodents that live in swamp-marsh habitats used more new habitats as these be-

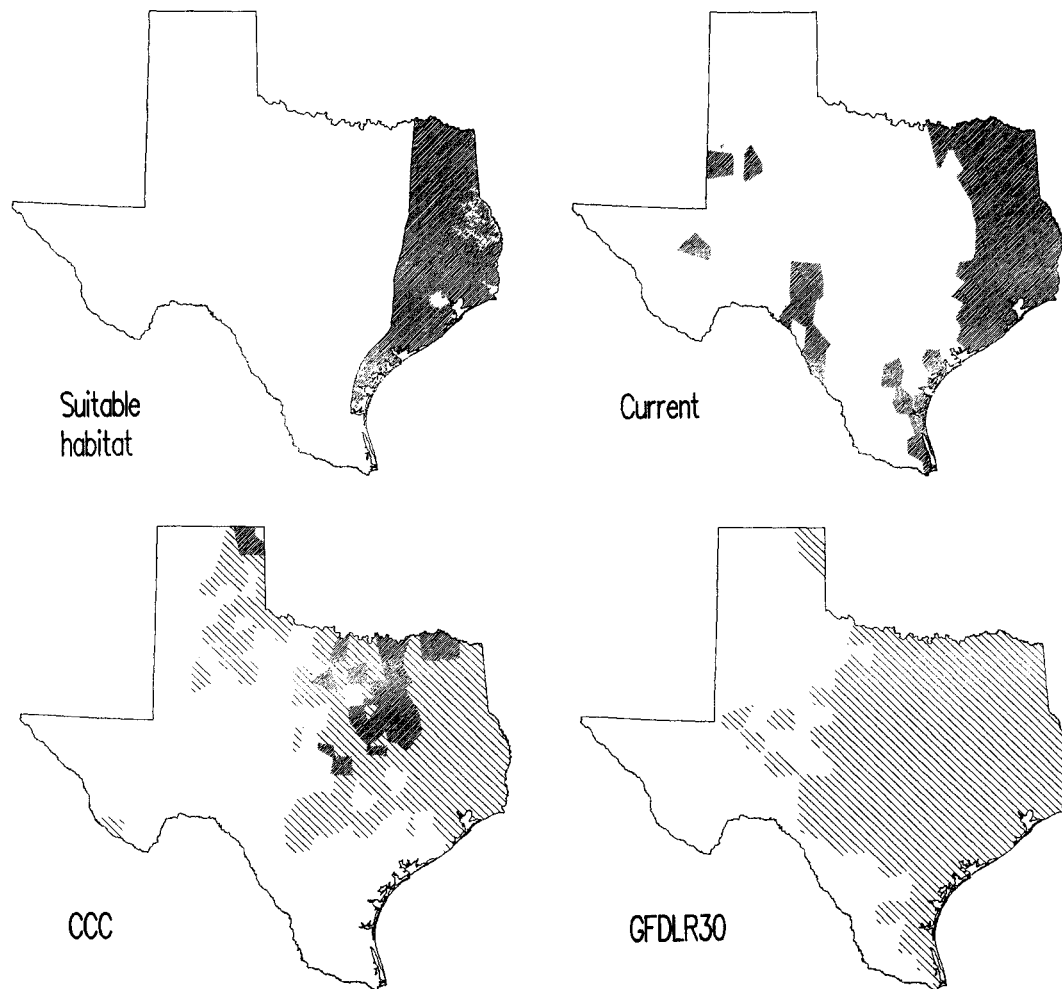


FIG. 5.—Geographic distribution of *Oryzomys palustris*. See Fig. 1 for description.

came available, whereas rodents that live in dry shrubland used fewer new habitat associations as this habitat type became more restricted. Under either climate scenario, granivores and herbivores used fewer new habitat associations that entered the state after climate change than did omnivores and insectivores, as did terrestrial rodents compared with fossorial or arboreal rodents. In both cases, rodents used fewer new habitats if they had closer ties to particular plant types.

We determined the error in our assessment of active habitats by measuring the proportion of actual capture points that were included in habitats that we defined as

preferred for each species. Inclusion of all capture points would reflect a perfect match between our determination of actual habitats and the actual habitats of the animals. For rodents, an average of 98% of capture points was included in our determination of suitable habitats (Table 1). This result is comparable with other groups that we have studied (98% for bats—Scheel et al. 1996; 100% for lagomorphs and insectivores—Cameron and Scheel 1993). Together, these results demonstrated a nearly total match between habitats known to be occupied and the suitable habitats depicted by TPW vegetation associations.

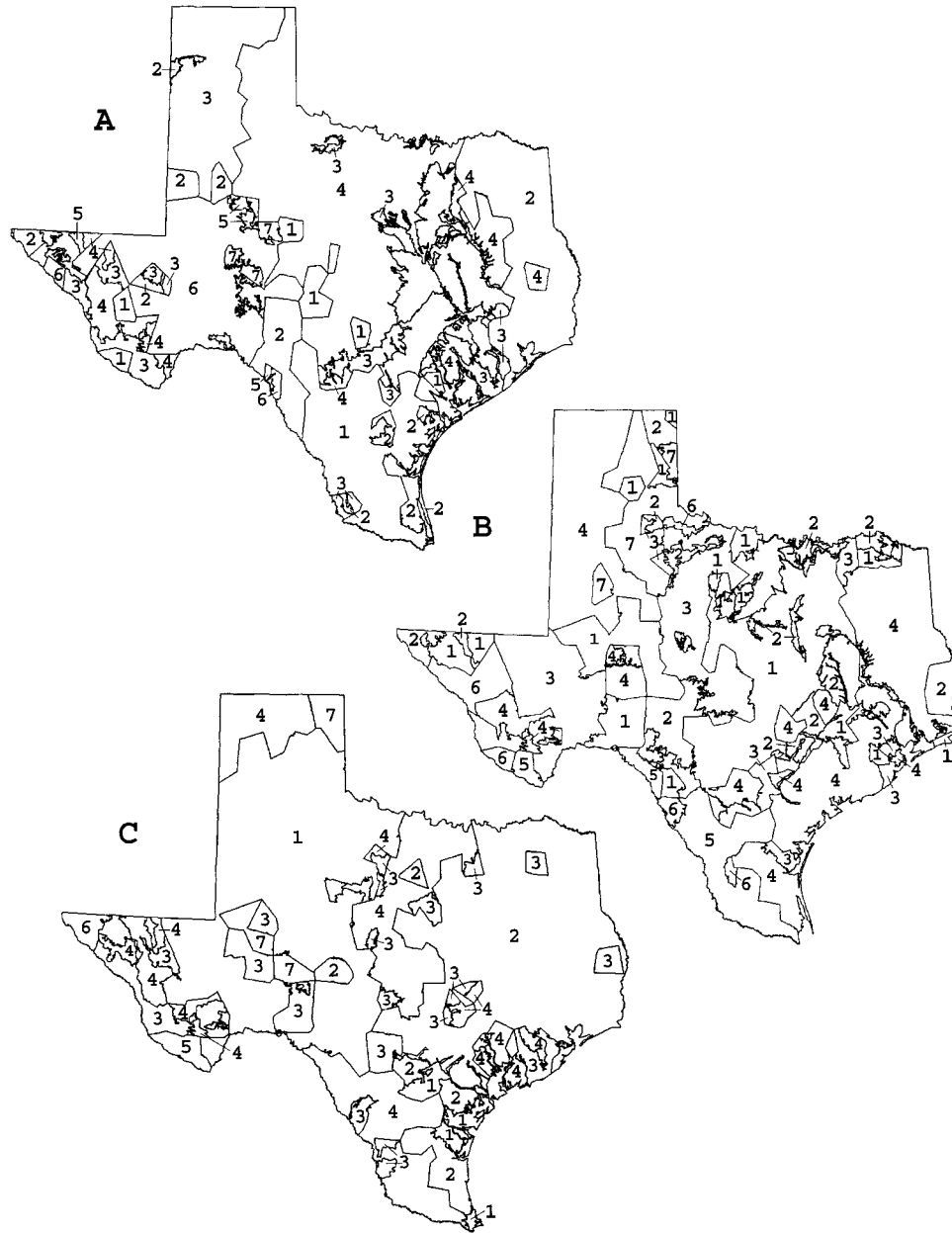


FIG. 6.—Distribution of species richness under A) current, B) Canadian Climate Centre (CCC)-modeled, and C) Geophysical Fluid Dynamics Laboratory (GFDLR30)-modeled climatic conditions. The number of species are arranged in categories: 1 = <15, 2 = 15–19, 3 = 20–24, 4 = 25–30, 5 = 30–34, 6 = 35–39, and 7 = >40 species.

Liberty is taken when outer boundaries of geographic ranges of species are constructed for maps of geographic distribution, with the common criterion being that

all marginal capture points are included. For those species with relatively few capture locations, the known limits of geographic distributions are more tenuous. Few

studies have plotted actual (i.e., corrected for preferred habitat) ranges. We made this correction with the geographic information system and found that the average amount of suitable habitat was 62% of the geographic ranges (cf. 88% for Insectivora and Lagomorpha, 56% for Chiroptera, and 71% for Rodentia in eastern Texas—Cameron and Scheel 1993; Cameron et al. 1997; Scheel et al. 1996).

Another type of error could be introduced because the Holdridge model of current vegetation communities may not satisfactorily describe suitable habitat distributions. We assessed how robust the Holdridge model was in predicting geographic extent of suitable habitats by comparing Holdridge-modeled areas with actual habitats under current climatic conditions. Total error was divided into overshoots and undershoots. Of the 4 orders that we have analyzed, average total error for Rodentia (23.8%) was surpassed only by that for Insectivora (28.5%), with lower errors for Lagomorpha (22.5%) and Chiroptera (15.9%—Cameron and Scheel 1993; Scheel et al. 1996). Primary errors for those groups were in overshoot (average = 20.7%), not undershoot (average = 1.9%). Overshoot errors averaged 21.8% for rodents, 14.3% for bats, 26.8% for insectivores, and 20.0% for lagomorphs. The error was lower for bats largely because they were restricted by roosts, which our model handled well (Scheel et al. 1996). However, size of geographic and habitat-corrected range was correlated positively with overshoots, indicating that our model was less successful for wide-ranging species. That result meant that our models consistently erred by about 20% in predicting more area occupied than actually was occupied. Some of this error was because, on average, Holdridge polygons were larger than TPW polygons, and conversion from TPW to Holdridge habitat designations de facto resulted in larger occupied habitats. Therefore, species occurring in larger parts of the state (e.g., with larger geographic ranges) had higher overshoot errors (more

mismatching between Holdridge and TPW) than did species with smaller ranges.

When categorized according to life-history characteristics, substrate type and habitat significantly affected overshoots, whereas taxa, body size, or food did not. For substrate, fossorial rodents had the largest overshoot error (average = 33%, with *G. attwateri*, *G. knoxjonesi*, and *G. texensis* exceeding 50%; Table 2). We followed the literature by including in our geographic information system models that fossorial rodents were limited primarily by soil type. However, these species may be limited by other factors such as microclimate or interspecific effects that were not included in the models. If true, we would have mapped the species into suitable soils outside their actual range; hence large overshoots would have occurred. For habitat, *O. plaustris* and *O. cousei* in swamp-marsh habitats had much lower overshoot errors than did rodents in other habitats, probably because they are wetland specialists. This result may be because wetland TPW habitats were mapped into few Holdridge types, thereby reducing the tendency toward overshoots.

Average size of habitat-corrected range increased dramatically for rodents under both CCC and GFDLR30 (Fig. 1; Table 3). The average increase in size of range was greater under GFDLR30 (=3.52-fold) than under CCC (=2.39-fold). Although predicted increase in average temperature (3–4°C) was similar between these 2 climatic models, GFDLR30 predicted an average increase in rainfall of 30%, whereas rainfall under CCC was predicted to decrease by 6% (Cameron and Scheel 1993). Under GFDLR30, rainfall was predicted to increase by 60–80% for central, north-central, south-central, and west-central Texas. In addition, under GFDLR30, numerous tropical vegetation associations were predicted to move into Texas (Cameron and Scheel 1993). The combination of increased rainfall and tropical vegetation types accounted for the increased geographic ranges for rodents under GFDLR30. For example, rodents in

moist or low-lying habitats (e.g., *O. palustris*; Fig. 5) showed marked increases in geographic range under GFDLR30, whereas rodents characteristically in drier habitats (e.g., *C. hispidus*; Fig. 3) had larger geographic ranges under CCC.

Conversely, geographic range of insectivores and lagomorphs decreased under both CCC (average size of range compared to current range for lagomorphs = 0.82; for insectivores = 0.84) and GFDLR30 (average size of range compared to current range for lagomorphs = 0.81; for insectivores = 0.89—Cameron and Scheel 1993). The only species to increase was the southern short-tailed shrew (*Blarina carolinensis*), whose range increased 35% under GFDLR30, perhaps in response to increased rainfall and tropical habitats as for rodents, but no effect was found of climate change on the geographic distribution of the eastern mole (*Scalopus aquaticus*) or the swamp rabbit (*Sylvilagus aquaticus*). The range of tree-roosting and roost-generalist bats increased in response to changes in the amount of tropical and subtropical forest and woodland vegetation (Scheel et al. 1996). These findings suggest that rodents may be more adaptable to changes in vegetation associations because their ranges increased to accommodate new habitats and, consequently, they would be less affected by GCC than would lagomorphs, insectivores, or bats.

No significant difference was found in the ratio of suitable habitat under either climatic scenario to current conditions for any life-history characteristic (Table 2). However, a significantly greater proportion of suitable habitats for forest-dwelling rodents occurred under future climates because grasslands were replaced by forests and woodlands (Cameron and Scheel 1993). For both models, the ratio of suitable habitat after GCC to the current amount of suitable habitat was greater for species with smaller geographic and habitat-corrected ranges, indicating that these habitat-specialists responded more to GCC than did wide-ranging habitat generalists.

Movement of geographic ranges for rodents was somewhat greater under CCC (average overlap = 54%) than under GFDLR30 (average overlap = 61%). Movement was significantly different among climatic models for Geomyidae (GFDLR30 = 62%; CCC = 53%), Heteromyidae (GFDLR30 = 63%; CCC = 44%), and Sciuridae (GFDLR30 = 68%; CCC = 58%; Table 2). Average overlap for rodents was lower than that for lagomorphs (CCC = 91%; GFDLR30 = 94%), insectivores (CCC = 83%; GFDLR30 = 84%—Cameron and Scheel 1993), or bats (CCC = 86%; GFDLR30 = 73%—Scheel et al. 1996), indicating that, on average, rodents moved more in response to GCC than species in the other mammalian orders, particularly during the drier (CCC) climate. Such range expansion allowed incorporation of a high percentage (54–84%) of new habitats in future ranges of all taxa (see below and Tables 2 and 3).

For rodents, no effect of life-history traits was found on movement of ranges (Table 2), but ranges of species with larger geographic and habitat-corrected ranges moved less in response to GCC than did those of species with smaller ranges. That result was an artifact of our study area. Species with larger ranges were more constrained by the political boundary of Texas and, therefore, showed less movement in response to GCC than did species with smaller ranges. Overlap was significantly lower for rodents in forest and swamp-marsh habitats, indicating that species in these habitats moved more.

The amount of new vegetation associations in ranges of rodents was about 60% for CCC and 64% for GFDLR30 (Table 3). Area occupied by new vegetation types always was higher under GFDLR30 than under CCC, especially for Geomyidae (GFDLR30 = 76%; CCC = 66%). This result is because more vegetation types were present under the wetter GFDLR30 scenario. Ranges of insectivores and lagomorphs contained about the same amount of new

vegetation associations under CCC (insectivores = 67%; lagomorphs = 62%) but contained more new vegetation associations under GFDLR30 (insectivores = 78%; lagomorphs = 76%—Cameron and Scheel 1993). *B. carolinensis* occupied all new habitats under both climatic scenarios and *S. aquaticus* occupied all new habitats under GFDLR30. That result was in spite of the fact that, on average, ranges of lagomorphs and insectivores moved less than did those of rodents, and those ranges contained a lower proportion of suitable habitat after GCC than did those of rodents. For bats, about 50% of the range consisted of new vegetation types (CCC = 54%; GFDLR30 = 55%), with ranges of tree-roosting bats containing significantly more new habitat than did ranges of cavity or generalist roosters (Scheel et al. 1996).

No significant difference was found among taxa or body mass categories in proportion of the range occupied by new vegetation types for rodents (Table 2). However, ranges of insectivorous and omnivorous rodents contained significantly more new vegetation types than did ranges of herbivores and granivores under GFDLR30. Not only were more habitat types present in the wetter (GFDLR30) scenario, but herbivores and granivores had less restrictive habitat associations and, consequently, used more new habitats (Table 2). From a biological perspective, this result suggests that insectivores—omnivores would increase more under wetter conditions, whereas granivores—herbivores would increase more under drier conditions.

In addition, ranges of arboreal and fossorial rodents contained more new vegetation types than did ranges of terrestrial species. That finding led to the conclusion that fossorial rodents such as pocket gophers were most (positively) impacted by GCC. For CCC, no differences were found among habitat types in amount of new vegetation after GCC. However, for GFDLR30, ranges of rodents in arid-shrub habitats contained the least new habitat, whereas ranges of ro-

dents in swamp-marsh habitats contained the most new habitat. That result occurred because the wetter climate scenario contained more types of mesic habitat and few types of arid habitat. Contrary to the findings for suitable size and movement of ranges in response to GCC, no significant relationship was found between size of range and amount of new vegetation in ranges after GCC.

The impact index measured the response of individual species to GCC by summing change in amount of suitable habitat, shift in location of range, and proportion of new vegetation types in their range. A high index indicated greater impact. That is, in response to GCC, the proportion of $2 \times \text{CO}_2$ habitat to current habitat increased, the geographic range exhibited little overlap with the current location, and the range contained a large area comprised of new vegetation types. We predict that impacted species would be most plastic to climatic changes, and would be least likely to suffer negatively from GCC; in general, such species were found in forest and swamp-marsh habitats (Table 2). Conversely, species that were least impacted (e.g., the same or less-suitable habitat than currently, little movement of geographic range, and a small proportion of new vegetation types) would be expected to suffer most under changing environmental conditions; those species generally were in arid-shrub, grassland, and mesic-brush habitats in western and central Texas (Table 2).

We determined that suitable habitats for *O. cousei* and *M. mexicanus* would not occur in the state under $2 \times \text{CO}_2$ scenarios and, hence, concluded that those species would go extinct. Although species may extend their ranges northward under GCC, none moved out of the state. Furthermore, of the rodents found in Mexico whose current ranges are ≤ 500 km from Texas, only 5 (*Tamias dorsalis*, *Orthogeomys hispidus*, *Oryzomys fulvescens*, *Reithrodontomys sumichrasti*, and *R. mexicanus*—Hall 1981) do not currently occur in Texas. Thus, we

would expect relatively few new species to move into Texas from the south as a result of GCC.

Impact was greatest under CCC but was not affected by any life-history characteristic (Table 2). Among the most impacted species was a fossorial rodent (*G. personatus*). Conventional wisdom would dictate that a rodent tied to a particular habitat characteristic, that is, soil type or texture, might be less responsive to climate change and might be more in danger of negative impacts. In the case of *G. personatus*, movement onto suitable soil types populated with new, suitable vegetation, led to expansion of the range under GCC (Fig. 4). On the other hand, GCC may affect soil characteristics, indicating that changes in this biogeographic feature may affect future distribution of fossorial mammals (Scharpenseel et al. 1990).

Results from 2 climatic scenarios produced differences in distribution of rodents compared with current conditions. Amount of suitable habitat was less, movement of ranges was more, and proportion of new habitats was less under CCC than under GFDLR30, reflecting the drier conditions and smaller expansion of mesic-shrub than forest and wet habitats under CCC. These patterns held for separation of data by life-history characteristics (e.g., taxa, food type, substrate, and body mass) and demonstrated the variation expected under different scenarios of climatic warming. The ratio of suitable habitat during GCC relative to the current climate was much higher for rodents than for insectivores, lagomorphs, or bats. In addition, of the orders analyzed, ranges of rodents moved the most, whereas the area of new vegetation was about the same under both scenarios of GCC. Finally, richness increased in the Panhandle under both scenarios of GCC, increased in the east under the wet scenario (GFDLR30), remained high in western Texas, and declined in central Texas under the drier (CCC) scenario.

Our results indicated that the type of cli-

mate change, as well as its severity, would effect rodent distributions. The impact on rodents differs depending on whether the overall climate becomes drier or wetter. In the former scenario, many species of rodents may decrease their size of range as forests become less common and new unsuitable grass and shrub habitats invade the state (Texas may become more suitable for grazing and less suitable for growing crops susceptible to rodent infestation). In the latter scenario, granivores and herbivores may be excluded in the face of expanding forests, whereas arboreal, and to some extent fossorial, rodents take advantage of the new habitats predicted to enter the state. Packard (1995) had similar findings from analyzing the impact of GCC on biodiversity in Texas and concluded that regional diversity in the state required that these geographic regions be considered individually when assessing potential effects of GCC. In particular, she argued that analyses of fragmentation and isolation of protected areas must be considered to assess regional effects of GCC. We agree with this perspective, and suggest that studies at regional scales such as Packard's and ours can be incorporated into gap analyses (Scott et al. 1991, 1993) at the state and multistate level to understand further the impact of GCC, not only on individual species but also on community organization and structure. We also echo the conclusion of Graham et al. (1996) that responses of individual species are a manifestation of their life histories, and, thus, species respond to changes in environmental gradients in a Gleasonian manner. By virtue of this observation alone, composition and structure of communities will change with GCC.

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