



Effects of climate on ground squirrel species distribution  
by Angela Victoria Kociolek

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in  
Biological Sciences  
Montana State University  
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Abstract:

Paleoecologic records suggest a correlation between climate and mammalian species distribution. Community reorganization through the past 40,000 years apparently occurred as species tracked optimum conditions individually in response to environmental change. The reaction of species in the past therefore suggests that, as a result of human-induced global warming, significant species range shifts can be expected.

To more fully understand the response of individual species to global warming, two ground squirrel species (*Spermophilus columbianus* and *S. richardsonii*) were examined through correlation analyses to determine if climate is the most important variable controlling the extent of their ranges and, if so, which specific climatic parameters were important. Available data sets (VEMAP, FAUNMAP, and others) were overlain using ARC/INFO to study the macro-scale relationships that exist between the species ranges and biotic and abiotic gradients.

The distributions are mostly allopatric with *S. columbianus* inhabiting the Glacier-Waterton Ecosystem (GWE) but not the Greater Yellowstone Ecosystem (GYE) and *S. richardsonii* inhabiting the GYE but not the GWE. Each species range correlates with a different climatic parameter during opposite seasons. The *S. columbianus* range corresponds with high precipitation during the inactive season (fall-spring). *S. richardsonii* shows a correlation with high temperature during the active season (summer). Soil composition may also play a role. Analyses did not yield significant results for correspondence of species ranges with vegetation cover, topography or other climatic parameters.

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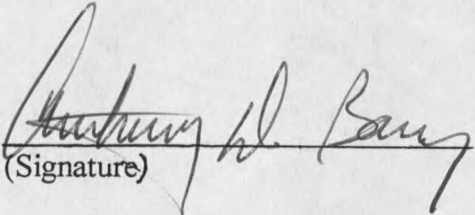
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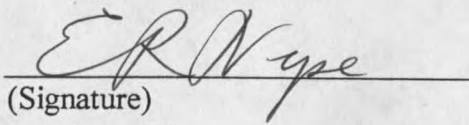
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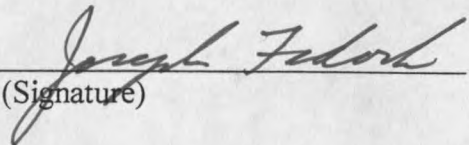
  
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## ABSTRACT

Paleoecologic records suggest a correlation between climate and mammalian species distribution. Community reorganization through the past 40,000 years apparently occurred as species tracked optimum conditions individually in response to environmental change. The reaction of species in the past therefore suggests that, as a result of human-induced global warming, significant species range shifts can be expected.

To more fully understand the response of individual species to global warming, two ground squirrel species (*Spermophilus columbianus* and *S. richardsonii*) were examined through correlation analyses to determine if climate is the most important variable controlling the extent of their ranges and, if so, which specific climatic parameters were important. Available data sets (VEMAP, FAUNMAP, and others) were overlain using ARC/INFO to study the macro-scale relationships that exist between the species ranges and biotic and abiotic gradients.

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## CHAPTER 1

CLIMATE CHANGE AND ITS EFFECTS  
ON SPECIES DISTRIBUTION

Climate, interacting with other physical and biotic attributes of a landscape, has long been thought to be important in delimiting the distribution of mammals (Davis 1939; Krebs 1972; Hunter et al. 1988). A connection between biota and climate, in turn, implies that a significant change in the climatic conditions will elicit a response from the biota. There are four ways in which a species might respond to a climate change. A species may (1) migrate to track shifting climate zones, (2) tolerate the change, or (3) adapt by experiencing microevolutionary change (Stott 1994). Historically there has been another common reaction: extinction (Hibbard et al. 1965; Barnosky 1989; Graham & Grimm 1990). Any of these possible responses except (2) has the potential of changing plant and animal communities. Therefore, biotic response to environmental change becomes a critical issue in the face of ongoing global warming which is predicted to continue into the next century as a result of the greenhouse effect.

The greenhouse effect is a natural phenomenon caused by the presence of certain gases in the earth's atmosphere. While these gases are transparent to solar, high energy (short-wave) radiation, they are relatively opaque to terrestrial, low energy (long-wave)

radiation. Therefore, they effectively trap energy causing the earth's surface to be warmer than it would be otherwise (Hobbs & Hopkins 1991). Without the greenhouse effect it would be approximately 38° C cooler (Hobbs & Hopkins 1991; Callander 1995). When people talk about global warming, however, they are generally referring to the enhanced greenhouse effect caused by the burning of fossil fuels and other human activities. Little disagreement exists in the scientific community that the greenhouse effect is real (Root & Schneider 1993), although some controversy about the magnitude of warming exists.

### Community Composition Models

At any one time, the species that compose a community coexist as a result of physical, biological and historical variables. Until recently, it was believed that a community is a tightly-linked and highly coevolved assemblage which will shift together in response to an environmental change. A community was thought to be analogous to an organism, reproducing parts of itself after a disturbance such as fire, logging or climate change like a lizard which has lost its tail (Clements 1949). Huntley and Webb (1989), however, contend that communities are not static but are merely temporary assemblages of species brought together when the prevailing environmental conditions suit their needs (Hobbs & Hopkins 1991). According to this dynamic community ecology model, communities are assemblages of species which respond differentially to environmental

change (Graham 1992). If conditions change, species respond individually and form new species assemblages. Each species may respond by migrating in different directions, at different times, and at different rates according to their own tolerances (Graham & Mead 1987). Moreover, most modern communities in temperate regions are less than 10,000 years old (Graham & Grimm 1990). Even excluding extinct taxa, the composition of communities in the geologic past was not the same as modern ones. Many communities were composed of species that are now geographically allopatric and appear to be ecologically incompatible today (Graham & Mead 1987).

### The Influence of Climate on Biota

Biogeographic texts, such as MacArthur (1972), have highlighted the importance of climate in the patterning of plant and animal ranges at regional and continental scales (Hobbs & Hopkins 1991). Consistently, the climatic factors of temperature and precipitation appear to be key influences on biota in general (Hobbs & Hopkins 1991; Chown & Smith 1993).

Temperature affects many aspects of physiology and development in animals (Hughes & Westoby 1994). Most mammals have a deep-body temperature that ranges from 35 to 40° C, values that essentially mimic the upper end of the range of typical temperatures encountered in the atmosphere. The physiological mechanisms of mammals are well adapted to heat conservation but they are less adapted to heat dissipation.

Thermoregulation in hot conditions is achieved by storing excessive heat, behavioral activity or evaporative cooling. If these processes do not work, the animal's water store becomes depleted. In many species, hyperthermia can occur if ambient temperatures rise above the deep-body temperature by as little as 5° C (Oke 1978). In plants, a 1° C increase corresponds to an increase in respiration of approximately 10-30 % (Hughes & Westoby 1994).

Temperature has also been shown to influence body size over evolutionary time. Smith et al. (1995) used preserved fecal pellets to estimate the size of the bushy-tailed woodrat (*Neotoma cinerea*) since the last glacial maximum. Bergmann's rule states that large body size is an advantage in conserving heat while small body size aids in dissipating heat. As expected, the woodrat showed microevolutionary changes by becoming smaller during times of deglaciation and increased warming (Smith et al. 1995). Similarly, studies of pocket gopher (*Thomomys talpoides*) craniodental material from the late-Holocene show a plastic response to climatic change in that they were smaller during the Medieval Warm Period than at any other time spanned by the deposit (Hadly 1997).

The sex ratio of certain reptiles is influenced by temperature. Slight departures of less than 2° C from incubation temperatures may result in entirely female or entirely male phenotypes. Species with this type of temperature-dependent sex determination (TDSD) are more susceptible to rapid climate change than those without TDSD. One possible reason for the extinction of many Mesozoic reptiles could be a regional warming event



which skewed the ratio completely, blocked reproduction, and ended in the local extinction of the species (Stott 1994).

Precipitation affects evaporation rates and humidity levels which may, in turn, affect the fecundity of organisms. For example, locusts, aphids, and moths become more fecund when humidity rises. Aridity also affects megafauna like elephants by influencing their habitat use. In the rainy season, female elephants congregate in large herds on the plains. This gives the dominant bull the opportunity to sire many offspring. In the dry season, females break into smaller groups near swamps and instead copulate with lower ranking, younger bulls. This climate-induced behavior change can have pronounced consequences on the genetics of the population (Roberts 1988).

### Biotic Response to Climate Change

Biota often respond to climatic extremes rather than mean values. For example, minimum winter temperature might control the northern limit of a species range while the maximum summer temperature might control the southern limit (Graham & Mead 1987). Changes in temperature and moisture will not necessarily affect a species the same way in all parts of its range. At the northern edge, changes in temperature can expand a species range but at the southern edge changes are likely to shrink the current range. Episodic events can also trigger distribution shifts, or the response of a species can be the result of a climatic impact at one particular phase of the life cycle (Roberts 1988).

Many relationships between different species, such as those between plants and their pollinators, will be disrupted if the partners in the relationship have different climatic tolerances (Hughes & Westoby 1994). A species which depends on certain plants for nutrition and others for cover may be faced with different components of its habitat migrating in different directions at different rates. The biotic response is not expected to be a mere displacement of an existing community but a rearrangement of species forming new community assemblages (Hobbs & Hopkins 1991).

In general, the broader the existing range of a species, the better will be its chance to cope with climatic change. The extent to which components of the fauna can adapt to rapid climate change will depend on their physiological tolerances, habitat specificity and their dispersal ability (Hobbs & Hopkins 1991). Most species are capable of living in a wider range of physical environments than they currently inhabit, as is demonstrated by zoos. The organism survives as long as competition is kept at a minimum. However, any change that favors a particular species will hinder other species with which it competes (Hughes & Westoby 1994). Species that are early successional, highly dispersible or good colonizers will fare best (Hughes & Westoby 1994) in the face of changing environmental regimes. Therefore, weedy species, that is, any species that attains a new dominance enabling it to competitively exclude other organisms, may become even more important because of their superior colonizing abilities (Hobbs & Hopkins 1991).

Migration has historically been associated with the movement of animals but it also applies to plant species which have moved across the landscape in response to climate

change (Huntley & Webb 1989; Hobbs & Hopkins 1991). Little thought has been given to the actual method of spread. Most commonly, it is assumed species will move in fronts but it is possible that a spread can occur from an established foci and move outward from it. Saltatory as opposed to progressive movements may also occur (Hobbs & Hopkins 1991). Rates of species movements vary greatly depending on the mode of dispersal in the case of plants and agility in the case of animals (Hobbs & Hopkins 1991).

### Floral Response

Fossil pollen grains from terrestrial plants occur abundantly and almost ubiquitously in the organic sediments in lakes and peat bogs providing a rich source of information about the terrestrial environment of the past (Davis 1969). Pollen studies illustrate vegetation response to past climate change and indicate that species respond in an individualistic manner rather than as intact communities (Davis 1969; Grimm 1983; Webb 1987). Contour maps of pollen percentages have been produced with the large number of palynological (fossil pollen) sites in Europe and eastern North America for different periods. These maps document the past distribution of tree populations and illustrate the individualistic behavior of species through time. Taxa were sympatric at some times and allopatric at others. For example, beech (*Fagus*) and hemlock (*Tsuga*) essentially have congruent ranges today. About 12,000 years ago, after the Wisconsinan glaciation, these taxa had separate ranges with beech on the southeastern Coastal Plain

and hemlock in the southern Appalachians. During the next 4,000 years, hemlock migrated northward along the Appalachians, while beech moved north along the Coastal Plain. For the next two millennia, both taxa moved westward through the Great Lakes region and began establishing their modern ranges. So, their existence as important co-dominators of the forest has only existed for the past 6,000 years (Graham & Grimm 1990).

Huntley mapped vegetation units based on pollen samples for 1000-year intervals from sites throughout Europe. His work showed the ephemeral nature of vegetation types as they appear, disappear and sometimes reappear at different times and places. This paleoecological study helps to support that species, as opposed to communities, move differentially in response to changing climate thereby forming new species assemblages (Graham & Grimm 1990). Not only does each species respond differently to climate, but each is also differentially sensitive to seasonal variations in temperature and moisture within its range and at its range boundary. No single climatic parameter controls the distribution, temporally or spatially, of a pollen type or plant species (Webb 1987).

Entire habitat types have been documented to change as a result of climate change. Around 6,000 years ago, within a span of 100 years, the vegetation around Cold Water Cave, Iowa changed from forest to prairie. This change was associated with a temperature rise of approximately 3° C (Stott 1994).

While changes in climate are believed to be responsible for corresponding shifts in vegetation ranges as shown through palynological evidence, Grimm (1983) cautions that other variables may also be playing a role. In his study on the Big Woods region of Minnesota he found he could not reconstruct past climate on the basis of changes in vegetation patterns alone. Vegetation patterns were spatially heterogeneous in response to the same climatic event, meaning that other nonclimatic variables such as water levels or fire disturbance were interacting with the force of climate (Grimm 1983).

Vegetation response to climate has usually lagged behind rapid climate changes by hundreds or thousands of years (Root & Schneider 1993; Hobbs & Hopkins 1991). This may be a result of the inability to migrate fast enough or because soil development is not rapid enough to allow vegetation to survive in tandem with rapid climate change (Hobbs & Hopkins 1991). Flora may be restricted to migrating along elevational gradients in response to climate changes since topography can channel or block dispersal and affect local climate (Grimm 1983; Hobbs & Hopkins 1991). Migration by plants is by propagules of sexually mature individuals which further accentuates the lag effect. Newly established individuals must wait until maturity to allow propagules to further colonize (Hobbs & Hopkins 1991). Even if they reach a suitable site, existing mature individuals may prohibit establishment of propagules unless a disturbance such as fire clears them out (Hobbs & Hopkins 1991).

### Faunal Response

There is also zoogeographic evidence for the dynamic community model. The Pleistocene (late-Quaternary) climate changes about 17,000 years ago provide a natural experiment from which to detect general responses of terrestrial organisms to an abrupt global climate change (Graham & Grimm 1990). Paleoecological data from the Pleistocene illustrate that climatic changes can spur changes in community composition (Barnosky 1989). Forty-three North American mammal genera became extinct near the end of this epoch, and other organisms adjusted by withdrawing to the north or south in response to changes in seasonality (Guilday et al. 1978; Barnosky 1989). For example, sites have been located where three small mammal species all coexisted but now have almost completely disjunct ranges, all having moved in different directions. The northern bog lemming (*Synaptomys borealis*) shifted north, the prairie dog (*Cynomys* sp.) shifted west and the eastern chipmunk (*Tamias striatus*) extended east (Graham 1988).

In their study at Baker Bluff Cave, Tennessee, Guilday et al. (1978) found that the stratigraphic column contained small mammal species associated with two different biomes. The lower (older) deposits contained species normally found in temperate areas, whereas the upper (younger) sediments were composed of boreal species. This transition suggests a change from a closed to an open-canopy characteristic of temperate and boreal forests, respectively. The thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*) and the yellow-cheeked vole (*Microtus xanthognathus*) were among those species found

together in the upper stratigraphic layer. Today the thirteen-lined ground squirrel is confined to the mid-western prairie and the yellow-cheeked vole inhabits the boreal taiga (Guilday et al. 1978).

In another example derived from Pleistocene evidence, the northern pocket gopher (*Thomomys talpoides*) inhabited southwestern Wisconsin, more than 600 km east of its modern distribution. It inhabited western Iowa until at least 14,800 years ago. Then the Late Wisconsin climate change caused this species to shift its range further west. Conversely, the same climate changes caused the least shrew (*Sorex* sp.) to shift eastward while the collared lemming (*Synaptomys* sp.) moved from a widespread distribution south of the Laurentide ice sheet during the Wisconsin to almost 1,600 km farther north in response to climate warming (Graham & Grimm 1990). These examples are characteristic of the responses of mammalian fauna throughout the world.

Information from the studies of Pleistocene climate change and biotic change demonstrates that each species responded differently according to their own tolerances and paces, which yielded new communities (Roberts 1988) as the Pleistocene gave way to the Holocene. The timing of these Pleistocene community changes also coincided with human settlement (Barnosky 1989) in some cases, which itself was a response to climate change in North America since humans immigrated through the ice-free corridor as the Cordilleran and Laurentide ice sheets retreated.

Modern Studies

Ranges of species can often be tied to some limiting factor. If an animal is strongly linked to certain vegetation, the speed with which it shifts its range is largely dependent on the rate at which the plants do. Essentially, the herbivores will only be able to migrate as fast as the plants they depend on. Also a factor is the rate at which an organism is capable of dispersing (Root & Schneider 1993). If an animal is linked to temperature, as in the case of the eastern phoebe (*Sayornis phoebe*), it will be able to expand northward as quickly as its dispersal mechanisms allow. However, physiological limitations may ultimately restrict any more movement. Again, using the eastern phoebe as an example, the northern boundary is tightly correlated with the  $-4^{\circ}\text{C}$  isopeth (Root & Schneider 1993) because the eastern phoebe's basal metabolic rate can only be effective above that temperature. If the temperature drops below  $-4^{\circ}\text{C}$ , the bird cannot function properly (Root & Schneider 1993). While other birds have shown similar range adjustments, their high degree of mobility makes it difficult to interpret significance of climate in limiting their range (Graham & Grimm 1990). In cases of extreme climatic events, massive die-offs may occur as is cited in James (1962), where the crash of eastern bluebird, house wren, eastern phoebe, and hermit thrush is attributed to severe winter cold snaps (Root & Schneider 1993).

Caughley et al. (1987) have demonstrated that the distribution of two kangaroo species is, in major part, influenced by climate, which controls their ability to find water,



shelter and food. Both the eastern grey kangaroo (*Macropus giganteus*) and the western grey kangaroo (*M. fuliginosus*) are closely associated with seasonality of rainfall. They overlap in areas of uniform seasonality of rainfall but *M. giganteus* occurs where summer rainfall predominates and *M. fuliginosus* occurs where winter rainfall predominates. Since climate change has influenced distribution of macropods in the past, it is reasonable to develop climate-based models to predict the distributional responses of these species in the future. If winter rainfall contracts to the south, as predicted by four out of five general circulation models (see Climate Models, p. 22) used in the study, *M. fuliginosus* would also contract to the south. *M. giganteus* could extend a considerable distance to the west of its current distribution. This all implies, however, that other conditions are also met. In this case, an increase in the frequency of summer rain, and a persistence in the heterogeneity of habitat in the face of climate change are needed (Stott 1994).

An in situ climate manipulation experiment, designed to mimic the predicted global warming scenario, showed a shift from a forb-dominated montane meadow to one dominated by sagebrush (*Artemisia*) (Harte & Shaw 1995). Still, there is a high degree of uncertainty surrounding predicted biotic response to rapid climate change (Hobbs & Hopkins 1991).

### Comparing the Past with the Future

During the Pleistocene, the earth warmed between 3 to 5° C, an amount similar to the predicted rates for the enhanced greenhouse effect. During the Quaternary (which the Pleistocene comprised a portion of), the global climate fluctuated substantially and frequently enough to produce more than 20 glacial/interglacial cycles. These changes were closely linked with periodic fluctuations in solar insolation that result from astronomical variations involving the tilt of the earth's axis, the precession of equinoxes and the obliquity of the orbit around the sun (Milanokovitch cycles) (Webb 1987). The natural fluctuations in the levels of atmospheric CO<sub>2</sub> is probably associated with these glacial/interglacial cycles although some question remains (Hunter et al. 1988). The Pleistocene changes, however, may have been spread out over a few thousand years, not compressed into a half century (Roberts 1988) (see Rates and Effects of Warming, p. 17). While the Pleistocene record may add insight, one cannot compare the past directly with the predicted future because the rate of change of human-induced global warming may be greater than rates of warming as a glacial period gives way to an interglacial period (Graham & Grimm 1990). The forecasted temperature increase exceeds that of any period in the last 120,000 years (Root & Schneider 1993). Graham and Grimm (1990) caution against reliance on the past to predict future patterns for the very reason that future climates may be out of the existing domain to which species are adapted.

Anticipated changes are believed to happen too fast for evolutionary processes like natural selection to take place.

### Global Warming

Global warming, also known as the greenhouse effect, is a natural phenomenon in which certain gases allow high energy solar radiation to enter the earth's atmosphere but prevent the re-radiated low energy waves from escaping. The energy which is trapped then heats the earth's surface, effectively causing a climatic change. Human activities (e.g., burning of fossil fuels, agricultural activities, cement production, and forest harvest) produce these gases at higher rates than would naturally occur. This enhanced greenhouse effect is believed to be capable of causing substantial biotic reorganization around the globe.

### The Greenhouse Gases

Carbon dioxide ( $\text{CO}_2$ ) is the most common greenhouse gas but methane ( $\text{CH}_4$ ), nitrous oxide ( $\text{N}_2\text{O}$ ), ozone ( $\text{O}_3$ ), water vapor ( $\text{H}_2\text{O}$ ), and chlorofluorocarbons (CFCs) are radiatively important gases as well. The atmospheric concentrations of  $\text{CO}_2$ ,  $\text{CH}_4$ , and  $\text{N}_2\text{O}$  have been maintained at constant levels for centuries by a balance of natural fluxes into and out of the atmosphere (Callander 1995). Greenhouse gas injections over the past

150 years, however, have spurred a 25% increase in CO<sub>2</sub> and a 180% increase in CH<sub>4</sub> in the earth's atmosphere (Root & Schneider 1993). Atmospheric concentrations of CO<sub>2</sub> (averaged over several years) are currently rising by 0.4% per year. The rise in these concentrations is a direct result of human activities. The concentration of human-made CFCs (i.e., blowing agents, solvents, propellants, and refrigerants) (Sulzman et al. 1995) not present in the pre-industrial atmosphere have also increased (Callander 1995). Methane, nitrous oxide and CFCs combined, may affect temperature as much as CO<sub>2</sub> (Hobbs & Hopkins 1991). Nitrogen and oxygen, the major components of the atmosphere, do not interact with long-wave radiation and play no part in the greenhouse effect (Callander 1995).

### Historical Background

The fact that the perturbation of adding greenhouse gases to the atmosphere will alter the climate in some way is well-established. The warming effect of greenhouse gases in the atmosphere was first detected by Jean-Baptiste Fourier in 1827, while the first calculation of the effect of doubling the CO<sub>2</sub> concentrations was made by Arrhenius, a Swedish scientist, almost a century ago. His estimate of a global average temperature increase was 5 to 6° C, not very different from current estimates which have been calculated using more advanced techniques (Callander 1995).

Since then, in 1988, the Intergovernmental Panel on Climate Change (IPCC), formerly the World Meteorological Organisation (WMO) and the United Nations

Environmental Programme (UNEP), successfully engaged the world's experts in many fields to study the science of climate and the effects of climate change. The overall message they portray is "that many human and natural systems are vulnerable to the magnitude and/or rates of climate change likely over the next century". They also played a role in the negotiation of the UN Framework Convention on Climate Change which was signed in June 1992 in Rio de Janeiro, Brazil, by more than 150 countries (Callander 1995).

#### The Rate and Effects of Warming

The debate concerning the enhanced greenhouse effect arises when trying to translate the accumulation of greenhouse gas emissions to a change in temperature (Root & Schneider 1993). Essentially, the question is not whether greenhouse gases are going to affect the climate, but rather, how much and how soon (Hughes & Westoby 1994). The estimated temperature increase by the middle of the next century ranges between 1.5 and 4.5° C (IPCC 1990). If the earth does get 3° C warmer, it will be the warmest period in 100,000 years (Schneider & Londer 1984). If it gets 4° C warmer, it will be the warmest period in 40 million years (Barron 1985).

There are three important ways in which a gas can contribute to the enhanced greenhouse effect. The first factor is its ability to absorb radiation. The second is the lifetime of the gas. Eventually all the gases will react with other atmospheric constituents

and will be decomposed by ultraviolet radiation. The only exception is carbon dioxide which is removed by processes on earth, photosynthesis being the most important.

The third factor is the total mass of the gas added to the atmosphere. Even though CO<sub>2</sub> is a relatively weak greenhouse gas on a per molecule basis, the sheer amounts of it being emitted through anthropogenic activities makes it the most dominant contributor to the enhanced greenhouse effect (Callander 1995). CH<sub>4</sub> is 20 times more effective at trapping heat than CO<sub>2</sub> while CFCs are 12,000 times more effective (Sulzman et al. 1995).

The predicted changes in the global physical environment in response to rapid global warming can be described as primary, secondary and tertiary effects (Hobbs & Hopkins 1991). The primary effects include major increases in CO<sub>2</sub> and other greenhouses gases. Ambient temperature may increase with the highest increases being greatest at the high latitudes. Montane and high latitude ecosystems may experience especially dramatic changes because of the sensitivity of regional climate to snow or ice cover. Vegetation growth and nutrient availability is sensitive to the timing of snowmelt, soil and air temperatures, length of growing season, and midsummer soil drying (Harte & Shaw 1995). A temperature flux such as the one predicted would trigger changes in rainfall patterns, vegetation types and soil chemistry while increasing the frequency of extreme climatic events (Peters 1992). Global mean precipitation may increase by 3-11%, with increases in the tropics and redistributions in the mid-latitudes. It is important to note that while the world is undergoing a steady increase in temperature due to greenhouse-gases, the response will not be uniform. The middle portions of continents have a

relatively low heat retaining capacity, thus an equilibrium in climate will be reached more rapidly in those areas (Hobbs & Hopkins 1991).

Secondary effects include a rise in sea level as a consequence of thermal expansion of the ocean water bodies. A rise of 3-10 cm per decade is predicted (Sulzman et al. 1995). Increasing temperatures could lead to increased evapotranspiration and alter water availability (Hobbs & Hopkins 1991).

The tertiary effects will stem from social consequences of climate change. An increase in water demand, the incidence of pests and pathogens, and changes in rates and pattern of land degradation, fragmentation, and fire regimes are slated to occur (Hobbs & Hopkins 1991). Climatic fluctuations can drastically affect agricultural regions by decreasing production (Roberts & Lansford 1979) or by shifting regions entirely. Thus, the social implications of climate-induced food shortages can have ramifications around the globe (Roberts & Lansford 1979).

Studies of gases trapped in bubbles in ice cores show fluctuations in temperature over the last 16,000 years and correlated with that is a flux in CO<sub>2</sub> (Raymo 1992; Hobbs & Hopkins 1991). This shows that an increase in CO<sub>2</sub> is coupled with an increase in temperature. The potential biological changes are not just spurred by temperature itself but by the rate at which that temperature increases (Root & Schneider 1993). The rate of climate change has accelerated since the Pleistocene (Root & Schneider 1993), largely because of the great amounts of fossil fuels burned since the onset of the Industrial Revolution. This rate is especially important because if it is faster than dispersal and

establishment rates of affected species, then certain species could be extirpated (Root & Schneider 1993). Rapid rate of change can force variations in mean and extreme climate statistics. Any alteration of character of extreme weather events could be biologically significant. It should be recognized that human-induced changes happen on a scale of decades while species response to those changes is on a scale of centuries (Root & Schneider 1993).

An increase in global temperature of  $1^{\circ}\text{C}$  in 20 years would necessitate migration rates of  $7.5\text{ km yr}^{-1}$ . This is considerably greater than any estimated past migration rates for plants. Individual species of plants have been estimated to move as much as  $2\text{ km yr}^{-1}$  but these are the maximum distances expected except for rare long distance dispersal events. These estimated rates are averages of long time intervals between pollen samples. The actual spread may have occurred as a series of episodes of spread (Hobbs & Hopkins 1991).

Keeping pace with changing climate zones may also be an issue with animals, depending on the species. Many birds are capable of traversing thousands of miles during their yearly migrations. Some mammals, including the armadillo (*Dasypus novemcinctus*), the cotton rat (*Sigmodon hispidus*), the opossum (*Didelphis virginiana*), and the racoon (*Procyon lotor*) have been extending their ranges northward (perhaps in response to the present warming cycle) with the latter having extended its range from eastern Colorado to the Rocky Mountains within 50 years (Vaughan 1972), a migration rate of  $5.5\text{ km yr}^{-1}$ . This still falls short of the  $7.5\text{ km yr}^{-1}$  rate said to be necessary for species to keep up with



increasing global temperature. Even flying insects, although they appear to be mobile, may experience trouble. Dennis and Shreeve (1991) have estimated that to keep up with climate change moving polewards at  $6 \text{ km yr}^{-1}$ , an adult butterfly with a lifespan of five days would have to travel 200 m/h, 6 h/day throughout its life. Many butterflies that have been surveyed by mark-recapture have daily movements of less than 50 m (Hughes & Westoby 1994). Natural migration rates generally are at an order of magnitude too slow to keep up with predicted changes. Due to the rapidity in which future climate changes are predicted to occur, up to 60 times faster than previous warmings (Hughes & Westoby 1994), it seems likely that only a subset of extant species will be able to migrate at a suitable rate.

For instance, considering temperature alone,  $1^\circ \text{C}$  is equivalent to a latitudinal shift of 150 km, or an elevational shift of 250 m. For certain species with habitats at lower altitudes this elevational shift may be enough but what about those that run out of mountain? The entire habitat of the mountain pygmy possum (*Burramys parvus*), for example, will be lost with only  $1^\circ \text{C}$  of warming (Hughes & Westoby 1994). At present scientists are unsure how much of a temperature change will occur but even a low estimate of  $.6^\circ \text{C}$  by the next century can produce major reorganizations in communities (Root & Schneider 1993).

## Climate Models

Scientists estimating future climate changes have utilized general circulation models (GCMs). These computer simulations use mathematics to represent the complex physical and chemical interactions among the atmosphere, oceans, ice, land and biota (Root & Schneider 1993). GCMs are capable of including feedback processes, such as those involving water vapor and carbon storage of vegetation, but their representations of these are quite simplified when compared with the real world (Sulzman et al. 1995).

The most widely known GCMs have been developed at several institutions in North America and Europe over the last three decades (Appendix A). Most GCMs represent the earth and its atmosphere with a 3-D grid system. The horizontal spacing between grid points ranges from 4-8° latitude and 5-10° longitude with 2-11 vertical layers extending approximately 30 km above the earth's surface. The geographic features of the earth's surface in a model is affected by the grid size. For example, the United States topography is smoothed to the extent that the western mountain regions are represented by a single dome centered over the Great Salt Lake, Utah. Other limitations include the fixed state of transient features such as vegetation types which do not evolve in response to simulated climate change (Sulzman et al. 1995).

GCMs are not meant to be predictive tools but heuristic ones which are used to assess the sensitivity of the climate system to human-induced increases of greenhouse gases. First, a control run is made with present levels of CO<sub>2</sub> to establish a reference climate. Then simulations of increased levels of atmospheric CO<sub>2</sub> are entered for multiple

years and are compared with the control (Sulzman et al. 1995). According to Root & Schneider (1993) (*italics mine*):

Simulating one year of weather in 30-minute "time steps" with the crude resolution of 4.5° latitude by 7.5° longitude and ten vertical layers (nearly 20,000 "grid boxes" around the globe) takes approximately 10 hours (*to run*). Such a grid cannot resolve the Sierras and Rocky Mountains as separate mountain chains. Refining the resolution to 50 x 50 km grid squares would so dramatically increase the number of computations that it would take on the order of one year of current generation computer time to calculate one year's weather statistics. Obviously, many important imponderables in the models are unlikely to be resolved before significant climatic changes are felt, and certainly not before we are committed to potentially significant long-term environmental and societal effects.

GCMs were designed to study global rather than regional climate responses. The reason is that the models can realistically represent global patterns of temperature and precipitation but the simplified topographical and precipitation-generating processes distort climatology at the coarser regional scale (Sulzman et al. 1995).

Despite the uncertainties associated with GCMs, they are currently the only estimates available regarding human-induced climate change that are based on physics rather than conjecture (Sulzman et al. 1995). The global society does not have the luxury of time in this instance. We must make due with the information we have already to understand potentially detrimental effects of rapid climate change on ecosystems (Root & Schneider 1993).

### Conservation Implications

One major issue surrounding global climate change is the effect it will have on the world's biota (Hobbs & Hopkins 1991). While much effort has been put forth in establishing nature reserves, little attention has been given to allowing for the effects of climate change. The reserves would serve well if climate remained stable but it does not (Hobbs & Hopkins 1991; Huntley 1994). Reserves set aside to conserve particular species or assemblages under existing climatic conditions may no longer be able to serve as suitable habitat under a rapidly changing climatic regime that spurs range shifts and community disassembly (Hobbs & Hopkins 1991). Many more species could go extinct, and the reshaping of ranges could be more drastic (Root & Schneider 1993). If biota are to persist in face of global climate change, it will be necessary for species to track optimum conditions across the landscape by migration (Hobbs & Hopkins 1991).

It is generally accepted that the formation of corridors are beneficial in that they allow gene flow (Hughes & Westoby 1994) and migration from one place to another, thereby providing a safety net which gives biota more options in face of rapid climate change (Hobbs & Hopkins 1991) and decreases the rate of extinction of semi-isolated groups (Hughes & Westoby 1994). There has been much discussion about the role of corridors in facilitating movements of biota. Hobbs & Hopkins (1991) point out it is "now almost an article of faith that they do". However, little evidence actually exists that

species use corridors in this way. Instead it is believed that the continuum of effectiveness of corridors is from 0%, which effectively blocks all movements (unpassable terrain), to 100%, which allows all species to pass. In between these extremes, corridors act as selective filters allowing certain species to pass while not letting others. For example, a salt marsh corridor will let salt tolerant species pass but not non-salt tolerant species (Hobbs & Hopkins 1991).

In order for corridors to be effective in allowing climate-induced biotic movement, they must be oriented in such a way that biota can track environmental changes (Hobbs & Hopkins 1991). They must radiate in all directions or at least along bioclimatic gradients. Designers must strike a balance between establishing a network of corridors in all directions and allowing for enough interior habitat for edge sensitive species (Hobbs & Hopkins 1991). We cannot yet predict how the greenhouse effect will influence regional patterns but assuming climatic changes will most likely follow existing climatic gradients, corridors should ideally run parallel to these gradients (Hobbs & Hopkins 1991). This may be valid for temperature gradients but precipitation patterns are more variable and may not necessarily follow existing gradients (Hobbs & Hopkins 1991).

In addition to the direct effects of these large scale climatic changes, wildlife will also endure another major stress. Modern land use has so fragmented the natural environment, that, while migration may once have provided a solution, environmental routes for dispersal are now limited compared to prehistoric times (Root & Schneider 1993). There are real constraints for biota to migrate because most potential habitats are

now extremely fragmented as a consequence of human activities during the past 200 years. Rural intensification, urban expansion and industrialization all compound the loss of available habitat. Humans have modified the natural landscape to the point where just fragments of natural resources remain in an otherwise heavily-modified landscape (Hobbs & Hopkins 1991).

Climate change can easily be treated as less urgent than other conservation problems but the future era of moving climate zones will demand fundamental reorganization of conservation practices. The rate and magnitude of future climate changes seem likely to be a threat to biodiversity in coming decades on a par with, and compounded by, habitat destruction (Hughes & Westoby 1994). Sustaining species will move from a local to a continent-wide scale, often using locations where they do not currently exist. Allowing for abiotic gradients and preserving as much physical diversity as possible will allow organisms to choose for themselves where they can survive and reproduce themselves in the face of environmental change (Hunter et al. 1988; Graham 1988; Hughes & Westoby 1994). Placing reserves along elevational, latitudinal or climatic gradients on a continental scale, while encompassing a diverse array of soil types, geology and landforms, will give species the maximum chance to migrate with changing climatic zones (Hughes & Westoby 1994).

Assuming preserving critical ecosystems is a priority, there are several things the global society can do. Limits to harvesting, curtailing of urban expansion, minimization of converting land to agriculture, conservation of resources, and seeking long term benefits

as opposed to short term profits will all better the globe's current state of affairs. We should strive for more efficient use and production of fossil fuels and termination of CFC use. All these actions affect global climate change. Even if the global community cannot decrease greenhouse injections to 60% like IPCC recommends, any slow down of emissions will help because it is the rate of change in temperature that is critical (Root & Schneider 1993). Still, all of these suggestions are reactive. We must seek to educate and change our attitudes if we are to mitigate the effects of our actions.

CHAPTER 2  
EVOLUTIONARY AND NATURAL HISTORY  
OF STUDY ORGANISMS

Performing an analysis of how climate might affect a certain species requires knowledge of its evolutionary and natural history. Information presented here (summarized in Table 2.1) will be used to interpret the correlations seen in the studies that follow (see Chapters 3 and 4).

Squirrels are classified as Class Mammalia, Order Rodentia, Family Scuridae. Like other rodents, squirrels have ever-growing incisors used for gnawing in the upper and lower jaws and have no canines (Rue 1967). Their family name comes from the Greek words *skia* (shade) and *oura* (tail); "shade-tail" describes the way a squirrel holds its bushy tail over its back (Gotch 1979). Often mistakenly called "gophers", ground squirrels are in the genus *Spermophilus* (formerly *Citellus*) (Nowak & Paradiso 1983) meaning "seed-loving" (Gotch 1979).



### Evolutionary History

The geologic range of Family Sciuridae is from the Oligocene to Recent in Europe and North America; Miocene to Recent in Asia; and Pleistocene to Recent in South America and Africa (Mclaughlin 1984).

Chromosomal analysis suggests the Columbian ground squirrel (*Spermophilus columbianus*) became a species 0.47 million years before present (m.y. B.P.) while the Richardson's ground squirrel (*S. richardsonii*) became a species 0.01 m.y. B.P. (Nadler et al. 1983). The earliest fossil record for *S. columbianus* is in the Sangamonian division within the Rancholabrean land-mammal age; the Sangamonian dates to 0.50 m.y. B.P. The site is at an elevation of 1,584 m in the Snake River Plain of Wasden, Idaho. The earliest record for *S. richardsonii* is from middle to late Irvingtonian land-mammal age, about 0.70 m.y. B.P. The site at Cudahy, Kansas is characterized by numerous northern forms such as *S. richardsonii* (Kurten & Anderson 1980). While the chromosomal and fossil data provide similar estimates for the origin of *S. columbianus* as a species, the two lines of data for *S. richardsonii* are inconsistent. *S. richardsonii* could not have originated as a species only 0.01 m.y. B.P. as chromosomal evidence indicates, if fossil specimens demonstrate the species' presence by 0.70 m.y. B.P.

The geographic ranges of *Spermophilus columbianus* and *S. richardsonii* abut and overlap in the foothills of the Rocky Mountains (Michener 1977) (Figure 2.1). *S. columbianus* occupies a large range from the higher grassy plateaus and sagebrush plains of





















































































































































































