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

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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This thesis has been read by each member of the thesis committee and has been found to be satisfactory regarding content, English usage, format, citations, bibliographic style, and consistency, and is ready for submission to the College of Graduate Studies.

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TABLE OF CONTENTS

LIST OF TABLES

Table Page

LIST OF FIGURES

Figure Page

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, is 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 then 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° 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° 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 insulation 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_2 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 (CO_2) is the most common greenhouse gas but methane (CH_4), nitrous oxide (N_20), ozone (O_3), water vapor (H_20), and chlorofluorocarbons (CFCs) are radiatively important gases as well. The atmospheric concentrations of CO_2, CH_4, and N_20 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_2 and a 180% increase in CH_4 in the earth's atmosphere (Root & Schneider 1993). Atmospheric concentrations of CO_2 (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, propellents, 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_2 (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_2 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_2 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_4 is 20 times more effective at trapping heat than CO_2 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_2 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_2 (Raymo 1992; Hobbs & Hopkins 1991). This shows that an increase in CO_2 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° C in 20 years would necessitate migration rates of 7.5 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 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 km yr $^{-1}$. This still falls short of the 7.5 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 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° 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° 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° 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_2 to establish a reference climate. Then simulations of increased levels of atmospheric CO_2 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 uncertanties 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 Scuiridae. 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 eastern Washington and Oregon to elevations well up in the mountains of western Montana, and northward several hundred miles into British Columbia and Alberta (Manville 1959). The distribution of *S. richardsonii* is from the Rocky Mountain front in western Montana east to western Minnesota, and reaching as far south as central South Dakota and as far north as British Columbia (Hall 1980).

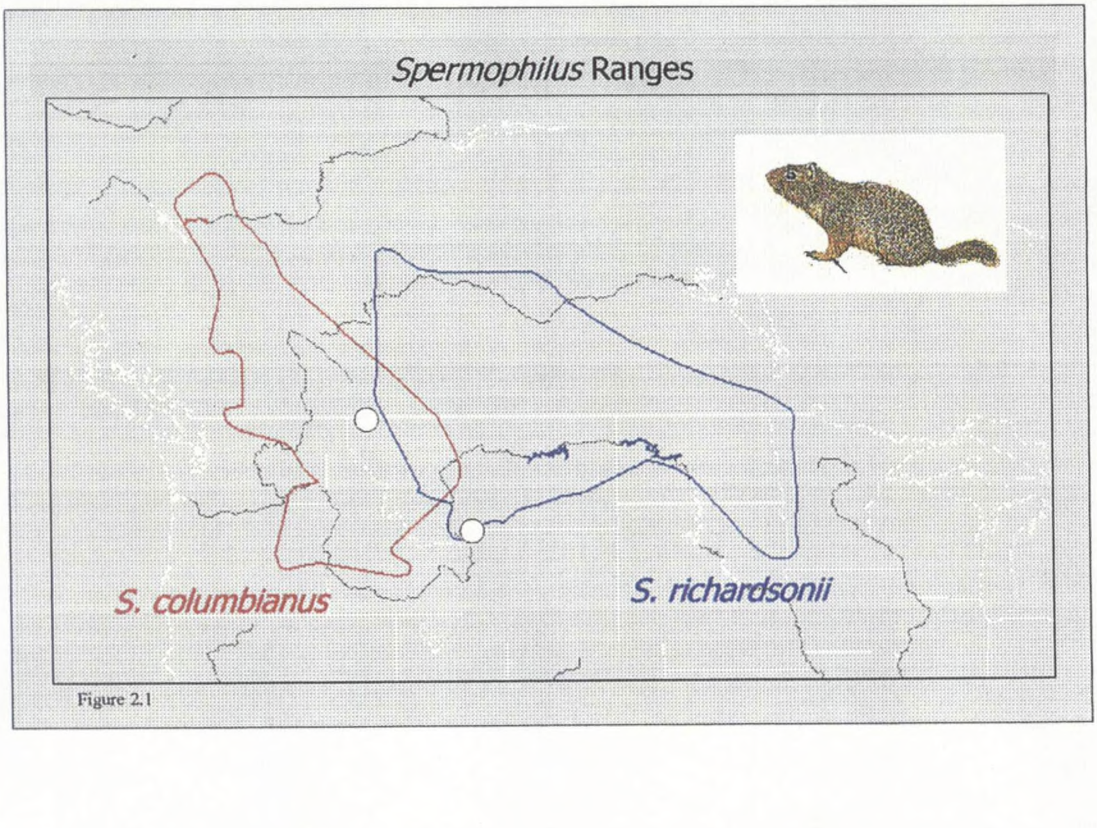


Figure 2.1. Geographic ranges of *Spermophilus columbianus* and *S. richardsonii*.

Natural History

Morphology

S. columbianus is one of the largest of the ground squirrels with adult females weighing between 275-629 g and males 394-820 g. Total length of adult females is 333-385 mm with tail length being an average of 106 mm. Males range from 330-388 mm with average tail length of 101 mm (Smith 1993). The upperparts are mottled gray or grayish brown with the legs, feet and underparts dark fulvous or tawny. Tails may have a white-tinge dorsally while the front of the head is reddish-brown with a white ring surrounding the eye (Manville 1959). The lifespan of Columbian ground squirrels is 4-5 years (Rue 1967).

S. richardsonii is smaller with females weighing between 273-375 g and males 271-609 g. Adult female total length ranges from 284-306 mm with tail length being an average of 72 mm. Males are between 279-332 mm in length with an average tail length of 79 mm (Smith 1993). *S. richardsonii* pelage is sandy brown and speckled with darker hairs to give a mottled appearance on the back. The underparts are lighter in color (Smith 1993). Rue (1967) states that Richardson's ground squirrels also live 4-5 years but Michener (1977) contends that they have a shorter lifespan than Columbian ground squirrels.

Habitat Associations

Spermophilus species inhabit open, grassy landscapes where foraging and burrowing are possible (Manville 1959). *S. columbianus* is found in and around alpine and subalpine meadows, the periphery of cultivated land, and areas where flooding is frequent (Elliott & Flinders 1991) at altitudes ranging from 212-2424 m (Manville 1959); although Michener (1977) says it is a mountain species and is restricted to elevations of 1150-2500 m. *S. columbianus* is found on any slope or area that has been cleared by a disturbance, such as fire or avalanche. They are less often in rocky areas or herbfields but readily use clearcuts (Elliott & Flinders 1991).

S. richardsonii is a prairie species where elevation ranges from 450-1300 m (Michener 1977). Its habitat is described as well-drained prairie, pasture, river terrace or cultivated field. Unlike *S. columbianus, S. richardsonii* will colonize grainfields and will not confine itself to the periphery (Michener 1977).

Burrow Sites

Burrows are an important facet of ground squirrel biology, providing protection from predators, shelter from inclement weather, and a relatively stable microenvironment for hibernation. Hibernacula are burrows used for the specific purpose of hibernation (Young 1989).

S. columbianus burrows are usually in areas with many grasses, clumps of shrubs, and a variety of flowering plants. The topsoil is humus, organic matter, with a mixture of pebbles and stones 0.30 m thick. Beneath the topsoil usually lies a clay layer followed by sand, gravel or rock below (Manville 1959). The burrow tends to be about 4.5 m long, but has been reported to be as long as 20 m (Nowak & Paradiso 1983), and angles in at 45° until it levels off about 0.30 m below the surface (Manville 1959). Hibernacula depth varies between .33-.77 m (Young 1990).

Elliott and Flinders (1991) state that *S. columbianus* burrow placement depends on soil moisture, aspect, drainage and slope. Unless the burrows are constructed on steep slopes, drainages must also be built (Manville 1959). Columbians are densely populated in well-drained areas with south-facing slopes. The choice for this exposure is presumably because there is less snow, allowing earlier emergence (Michener 1977).

S. columbianus seems to occur in soil with a higher percentage of rock fragments than *S. richardsonii* (see Chapter 3). *S. richardsonii* prefers sandy loam or gravely soils where they build burrows which are 3.6-15.0 m in length, 75 mm in diameter and 0.75 to 2.0 m deep (Nowak & Paradiso 1983). They have several chambers and an average of eight entrances with the main one having a mound (Nowak & Paradiso 1983). The burrow is usually about 1.2-1.5 m below the entrance (Knox et al. 1983).

The depth of hibernacula in *Spermophilus* is determined by several factors. Deeper hibernacula provide better protection against predators but then also require digging out through a thicker layer of frozen soil. Respiratory gas exchange may also be a factor since diffusion of gases may be hindered by cold, wet soil. Winter soil temperatures are also warmer at greater depths. Squirrels take advantage of snow-covered areas to build their burrows where they are more insulated (Young 1989).

Annual Cycle

Obligate seasonal hibernation is characteristic of most North American marmotine species (this classification includes marmots, ground squirrels and prairie dogs) whose ranges occur north of 30° N latitude. The annual cycle can be divided into the active and inactive (hibernation) seasons. A predictable sequence of events occurs following vernal (spring) emergence from their burrows: breeding, gestation, lactation, juvenile emergence, prehibernatory fattening, autumnal immergence (Michener 1984) and hibernation. The pattern is reset upon emergence from variable degrees of winter dormancy (Tomich 1982). Although all hibernating marmotines exhibit the same pattern, some species have shorter active seasons of about 4 months (e.g. *S. columbianus*) and others have longer active seasons of about 7-8 months (e.g. *S. richardsonii*) (Michener 1984).

Active Season

Emergence

The time at which species terminate hibernation and appear aboveground is partly dependent on latitude and altitude. Low-elevation species (e.g., *S. richardsonii*) resume activity in January to March, whereas high-elevation species (e.g., *S. columbianus*) emerge in April to May (Michener 1984). Within a species, emergence tends to be later at higher elevations, more northerly latitudes, and more continental locations. Aspect also plays a role in affecting the time of emergence such that animals on southwest-facing slopes emerge earlier than those on northeast-facing slopes (Michener 1984).

For several species of hibernating ground squirrels, time of spring emergence and, hence, emergence by juveniles from natal burrows is dependent on local climatic factors (Michener 1977), such as aridity (Manville 1959), snow cover, snow depth, air temperature and soil temperature (Michener 1984). Ground squirrels resume aboveground activity later in snowy or cold years, compressing the total emergence period, with all individuals appearing within a shorter period than in warmer years. When winter weather persists beyond the usual time of spring emergence, however, ground squirrels do eventually come aboveground again despite unfavorable cold or snowy conditions (Michener 1984). Michener (1984) explains this two-stage threshold:

> Early in the year animals do not respond to warm ambient conditions that later are sufficient to initiate resumption of surface activity, and late in the year animals emerge despite cool ambient conditions that earlier were insufficient to cause emergence. Two selection factors probably constrain the time over which vernal emergence occurs. First, early emergers that resume homeothermy when food is scarce and inclement weather is common experience high mortality. Second, offspring born to animals that emerge and breed late have low survival.

Typically adult males emerge 1-2 weeks prior to females in obligately hibernating species (Michener 1984). Age does not affect time of emergence in *Spermophilus* species in which both sexes are sexually mature at time of emergence at 11 months old. Such is the case with *S. richardsonii* with the emergence sequence being males > (before) females. Columbian ground squirrels do not mature sexually until their second year, however. Therefore, the emergence schedule for *S. columbianus* is adult male > adult female > yearlings (males and females). There are some hypotheses regarding earlier emergence by males than females. Because males generally hibernate in isolation from females, they have to assess the location of the females, an activity only possible aboveground. This extra time is also believed to allow males to establish territories in anticipation of breeding as well as to allow for the completion of spermatogenesis (Michener 1984).

In a two year study, Michener (1977) found that Columbian ground squirrels showed less difference in time of emergence between years suggesting that flexibility in their emergence pattern is less important than it is for Richardson's ground squirrels.

Still, it is not known how ground squirrels, which hibernate several feet underground in a microhabitat that does not immediately respond to ambient conditions, determine when aboveground conditions are suitable for resumption of activity (Michener 1977). Ground squirrels experience an endogenous rhythm of alternating bouts of torpor and arousal during the hibernation period, with arousals increasing in duration and frequency as the season winds down. This pattern appears to increase the probability that an animal is homeothermic and, therefore, can monitor and respond to ambient conditions (Michener 1984).

Reproduction

Breeding occurs within a few days after emergence with young emerging from their natal burrows in early May (Weddell 1991). The onset of breeding may be controlled by seasonal temperatures. Breeding occurs earliest in those years with an early, mild spring (Michener 1977). For example, Michener found that after three years of normally cold spring seasons, *S. richardsonii* advanced their breeding season by 10 days to coincide with warmer weather (Tomich 1982). *S. richardsonii* in the southern part of the range breed earlier than those in the northern part of their range (Michener 1977).

Breeding does not occur until 1 to 2 years of age (Michener 1977). Ground squirrels are promiscuous with the males mating with as many females as possible (Rue 1967). Columbians have 1 litter of 2-15 per year with an average of 4 (Nowak & Paradiso 1983) and gestation of 24 days (Rue 1967). Richardson's have litters of 5-8 per year (Rue 1967) with an average of 7.5 (Nowak & Paradiso 1983) after a gestation period of 25 days (Rue 1967). However, gestation in *S. richardsonii* has been documented at lengths from 17 days to 26 days (Michener 1977).

According to Michener (1977), *S. richardsonii* females, on average, produce more young per litter than do *S. columbianus*. However, the total number of litters produced in a lifetime is probably smaller for *S. richardsonii* since they have a shorter lifespan (Michener 1977). Ground squirrels have 4-7 pairs of mammae. Hibernating species are weaned at 22-35 days as opposed to nonhibernating species which are weaned at 48 days (Tomich 1982).

By June juveniles, which were born blind and naked, are one-third grown and active (Rue 1967). They add considerably to the population density at this time (Michener 1984). By September *S. richardsonii* is full grown and cannot be distinguished from adults (Rue 1967). This early maturation process is an adaptation for those species which must be able to store fat quickly and make the most of available foods before the hibernation season resumes (Tomich 1982). *S. columbianus* juveniles may be able to store sufficient fat but require an additional one or two active seasons to attain adult size (Michener 1984).

Prehibernatory Fattening

Spermophilus diet has great variety but is chiefly vegetable in nature (Manville 1959). Strictly diurnal in habits, they waste no time during the summer months to prepare for the next hibernation. Generally they eat succulent vegetation when available (Manville 1959; Phillips 1984). Later in the season they consume foods with high water content such as insects and animal matter, including their own species (Manville 1959). Stems and heads of oats, rye, clover, barley and garden vegetables are eaten in croplands (Tomich 1982). Dry foods (e.g., seeds) rarely compose the majority of the diet in any season (Phillips 1984). Squirrels seldom drink and probably obtain much of their required water from moist vegetation or succulent foods (Manville 1959), which are 68 to 77% water but may drop to 7 to 10% water in the dry season, and arthropods and vertebrates, which have 60 to 75% water content (Phillips 1984). Many habitats that ground-dwelling sciurids inhabit rarely have standing water, therefore, food may be the only source of water for these animals. Water may be preformed or a product of the oxidation of hydrogen in food (Phillips 1984).

They rely almost entirely on stored fat during long their hibernation. Shaw (1926) noted that 21 of 41 Columbian ground squirrel hibernacula contained caches. If they do cache, their stashes only consist of wild seeds or bulbs, even when in cultivated areas. Usually only one kind of food is stored in one cache and may serve as an important food source before new growth appears in spring (Knox et al. 1983). Ground squirrels may store food but only eat it once they awaken in the spring (Nowak & Paradiso 1983). Caching in underground storage may boost the water level in seeds (Phillips 1984).

Immergence

The active season for Columbian ground squirrels is only about 90-100 days per year, thereby, making hibernation account for 70% of the year (Elliott & Flinders 1991). Ground squirrels have a strong tendency for diurnality and the total time above ground decreases with the season (Elliott & Flinders 1991). In early spring, much of the time is spent above ground in the warmer daylight hours. Shaw (1925) believes early spring activity is controlled by temperature alone. As the season progresses, however, activity becomes bimodal with peaks in the morning and late afternoon hours. The midday heat prevents activity otherwise (Knox & Hoffman 1983). Richardsons avoid the heat and stay in their burrows if it gets above 90° F (Rue 1967). Davis (1939) states that activities are controlled by the sum total of daylight hours.

The time and sequence of autumnal immergence vary among species. For species with short active seasons, all cohorts immerge within a period of a few weeks. Species with long active seasons have some cohorts enter hibernation 2-3 months in advance of other cohorts in the same population (Michener 1984). The general sequence of autumnal immergence in most *Spermophilus* species is adult male > (before) adult female > subadult > juvenile (Michener 1984). This pattern holds for *S. richardsonii*, however, it is an extreme case of staggering of immergence among cohorts. Adult males typically go underground in June to mid-July, adult females in late July to August, and juveniles in September to early October. This asychnrony in immergence schedules means that juveniles spend most of the first year of their lives independent of adults of either sex (Michener 1984). Asynchronous immergence of cohorts is common to species living in habitats with relatively long growing seasons, such as in prairie species like *S. richardsonii*. High elevation species, such as *S. columbianus*, exhibit synchronous immergence of cohorts because its habitat has a short growing season (Michener 1984).

The timing of immergence seems to be an adaptation for individual survival. Once an animal has attained a sufficient fat reserve to survive the hibernation season, it will immerge. Continued activity could result in increased chances of water or heat stress, or obesity which can restrict rapid movement (Michener 1984).

Inactive Season

Hibernation

Hibernation is a mechanism by which organisms are able to survive harsh winter conditions when food is virtually nonexistent. By depositing fat during the prehibernatory period and by making adjustments in metabolism and reproductive expenditures, obligate hibernators can hibernate as an alternative to winter endothermy (Phillips 1984). Shaw (1925) and Manville (1959) suggest that hibernation is induced by the drying of vegetation. The beginning of hibernation is also determined by the accumulation of fat in the body. In general, hibernation is believed to be effected by temperature, latitude and local weather (Knox et al. 1983).

One of the most remarkable traits of *S. columbianus* is its long and erratic period of dormancy. Long before winter seems imminent they disappear underground. Ground squirrels burrow beneath the frost line where they hibernate. Adaptations to climatic conditions during hibernation are massive food consumption, fat storage, and a high degree of reduction in metabolic functions (Tomich 1982).

In the torpid condition, their temperature drops from normal 98° to about 40°. While they are true hibernators, ground squirrel hibernation is marked by periodic arousal between bouts of torpor. The bouts of torpor are longest and most frequent in midhibernation (Michener 1977).

Studies on Alberta populations of *S. columbianus* have elicited significant differences in overwinter survival between high and low elevation with high elevation populations having higher overwinter survival. At high elevations, nearly all hibernacula were located on level terrain beneath shrubby ground cover or in shallow depressions which collected snow drifts. Low elevation hibernacula were located on a more varied terrain. The high hibernacula had finer textured, poorly drained soil while low ones had coarse and well-drained soil (Young 1989).

Table 2.1. Differences between *Spermophilus columbianus* and *S. richardsonii*.

	S. COLUMBIANUS	*S. RICHARDSONII*
MORPHOLOGY		
weight (g)	275-820	333-388
length (mm)	273-609	279-332
pelage	mottled gray with darker underparts	sandy brown, dark speckled with lighter underparts
LIFE HISTORY		
lifespan (years)	4-5	< 4-5
reproductive age (years)	2	1
litter size	2-15; mean = 4	5-8; mean = 7.5
HABITAT		
elevation (m)	212-2500	450-1300
burrow depth (m)	.33-.77	.75-2.0
soil type	clay; sand; gravel; rock	sandy loam; gravely soils
vegetation type	(sub)alpine meadow; periphery of cultivated land	prairie; pasture; river terrace; cultivated land

Behavior

Ground squirrels are diurnal and colonial. When there is one squirrel, others are not far away. *S. columbianus* are especially more socially inclined than most other North American squirrels. Constantly alert, ground squirrels warn other members of the colony when a predator approaches and will scurry into the closest burrow no matter whom it belongs to. They have an acute sense of hearing and also rely heavily on sight for the detection of danger. They are highly vocal and can be heard for several hundred yards. Normal gait is a series of leaps or a quick dash (Manville 1959).

Columbians are not as gregarious as Richardson's, preferring to have their own burrows. Still, like other ground squirrels, they live in colonies that may extend for miles. This colonization helps the survival of the species because members of the group are always on alert for danger while the rest are feeding (Rue 1967).

Home Range and Dispersal

Ground squirrels tend to have small to moderate home ranges. The requirements for food, shelter and life's processes usually occur within a certain area, however, that area may change according to daily or seasonal needs (Tomich 1982). Out of 11 *S. columbianus* individuals monitored, only 3 were detected outside of an area 0.65 ha in two seasons. The greatest measured distance of travel by any individual was 128 m (Tomich 1982). The author did not mention the sex or age of the individuals monitored, however. Columbian ground squirrels disperse as yearlings so they do not leave their natal site until after the first winter (Boag & Murie 1981). Juvenile male *S. columbianus* shift their centers of activity more than females do (Weddell 1991). Pre-reproductive males tend to disperse greater distances and establish themselves farther from their natal sites. The longest known dispersal of *S. richardsonii* was 9.6 km in only 72 hours (Holekamp 1984).

Colonial behavioral patterns play a role in the dispersal of ground squirrels (Eisenberg 1981). While they are capable of traversing relatively large distances, individuals will only settle within close range of conspecifics or their burrows. Sciurid (squirrel) social behavior is based on polygynous mating and proximity of female kin (Weddell 1991). Occupied sites are more likely to receive immigrants than unoccupied sites, thus, isolated yet suitable patches separated by development or agriculture can cause deleterious effects on *Spermophilus*. This behavioral mechanism provides an optimal balance between outbreeding and inbreeding but is not suited for colonization of fragmented habitats (Weddell 1991).

Economic Importance

Ground squirrels were a substantial food item for early Americans, and the skins were used sometimes to make clothing (Tomich 1982). Now, ground squirrels are of economic importance because they are seen as pests by agriculturists. Being prolific to begin with, *S. richardsonii* became even more abundant with the expansion of agriculture. The conversion of natural prairie lands to crops improved the conditions for these animals. It was estimated that there were 600,000,000 in 1900. They became a nuisance to farmers which led the US Biological Survey to develop a poisoning program to eradicate them. Records show that 4,000 could be killed in one square mile and, still, they could not be controlled (Rue 1967). Once farming is discontinued at a site ground squirrel (*S.*

beecheyi) populations decline, and within about 6 years, they will abandon the site completely (Tomich 1982).

In the case of *S. columbianus,* however, increased dryland cultivation reduced and fragmented wildlife habitat. Until the late 1800s, for example, the meadow steppe of east-central Washington and northern Idaho was almost continuous potential ground squirrel habitat (Weddell 1991). Young (1989) postulated that availability of hibernacula may be a limiting factor for some populations facing decreased habitat availability.

Ecological Importance

Ground squirrels comprise a large part of the prey base for badger, grizzly bear, weasel, coyote, fox, bobcat, cougar, golden eagle and hawks. In Alberta, Canada Swainson's hawks (*Buteo swainsoni*) and Richardson's ground squirrels, its main prey, have precisely coterminous ranges. In a study by Houston and Schmutz (1995) it was shown that a population decline in Swainson's hawks coincided with a drastic decrease in the number of Richardson's ground squirrels. As semi-fossorial creatures, they are good aerators of soil. Ground squirrels are also an important host of ticks that carry Rocky Mountain spotted fever and the plague (Manville 1959).

CHAPTER 3

COMPARATIVE STUDY OF FOREARM MORPHOLOGY

The Richardson's ground squirrel (*Spermophilus richardsonii*) tends to be a plains species while the Columbian ground squirrel (*S. columbianus*) inhabits the mountains. Aside from this generalization, it is unknown what controls the boundary of the distribution ranges of each of these species. Chapter 4 describes some potential environmental controls on the boundaries; this chapter explores whether functional morphological attributes of the species influence where they can live.

The degree of soil rockiness (percent of mineral rock fragments) is a gradient that appears to separate the ranges of *S. columbianus* and *S. richardsonii,* with *S. columbianus* living in mountainous areas characterized by a considerably higher percentage of rock fragments than is found in the plains habitat of *S. richardsonii* (VEMAP 1995). *S. columbianus*, over most of its range, inhabits an area with a high degree of rockiness in the soil ranging from 19-21% while *S. richardsonii* inhabits those areas with a lower degree of rockiness (8-16%) (Figure 3.1). This chapter tests the hypothesis that a

Percent Volume of Mineral Rock Fragments

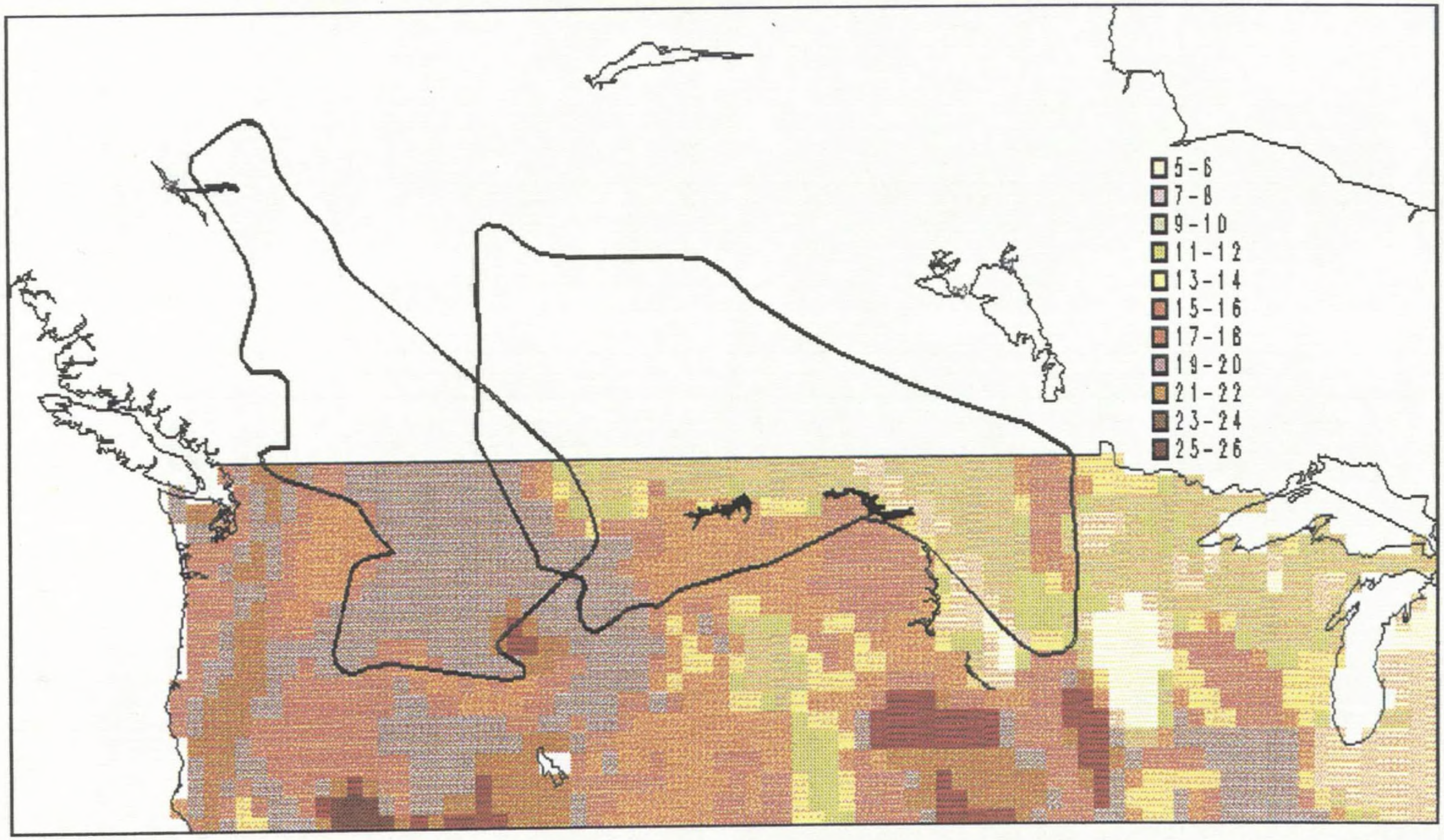


Figure 3.1

functional morphological adaptation, i.e., the ability to dig easily in rocky soils, helps to separate the geographic ranges of the two species.

Fossorial vertebrates, such as ground squirrels, that dig in firm soil must be capable of exerting great force against the substrate. Their skeletal and muscular systems generally show adaptations that produce large out-forces ($\mathbf{F_o}$) for movements relevant to digging. $\mathbf{F_o} = \mathbf{F_i L_i / L_o}$ where $\mathbf{F_i}$ is the in-force and $\mathbf{L_i}$ and $\mathbf{L_o}$ are the input and output-levers, respectively. Total length from the hinge (joint) to the point where a bone exerts a force represents the output lever ($\mathbf{L_o}$), while length from a relevant joint to a muscle insertion point represents the input lever ($\mathbf{L_i}$) (Hildebrand 1974). The efficiency of this lever system can be analyzed by comparing the length of $\mathbf{L_i}$ and the length of $\mathbf{L_o}$. The longer the input portion ($\mathbf{L_i}$), the higher the $\mathbf{L_i/L_o}$ ratio, and the more efficient that lever system is in producing more output force for a given input force (Barnosky 1981; Hildebrand 1974).

There are three ways to increase the output force ($\mathbf{F_o}$). Reducing the $\mathbf{L_o}$ increases the $\mathbf{F_o}$. Therefore, most expert diggers have short necks and limbs with short distal segments. For example, the radius is nearly always shorter than the humerus. Increasing the $\mathbf{L_i}$ also increases the $\mathbf{F_o}$. Therefore, the muscles used in digging tend to be inserted far from the joints they turn. Increasing the $\mathbf{F_i}$ also increases the $\mathbf{F_o}$, that is, diggers have enormous muscles and rugged bones (Hildebrand 1974). This study examines mainly $\mathbf{L_i}$ and $\mathbf{L_o}$ ratios, but also examines qualitative information about muscle size that is interpreted from the size of the muscle attachment areas.

S. richardsonii tends to be a smaller species than *S. columbianus* with a body weight of 271-609g versus 275-820g and a body length of 279-332mm versus 330-388mm. Hence, *S. columbianus* is generally a more robust, stronger animal which is consistent with its ability to dig better in rockier soils. This study is designed to compare the forearm lever potentials of the two species to further determine whether functional anatomical differences may give *S. columbianus* a competitive edge in rockier soils.

Materials and Methods

The bones associated with the forearm muscles used in digging are the sternum, scapula, humerus, radius, ulna, manus and digits. The associated muscles are responsible for extension and retraction of the humerus, pronation and supination (rotation) of the manus, and flexion of the digits. Muscles involved are listed in Table 3.1, as are the origins and insertions for the muscles (Table 3.1). Postcranial material was measured using a digital caliper to one hundredth of a millimeter. A roughly equal number of male and female adult specimens of each species were randomly selected from available material. Adult specimens were confirmed by one or more of the following criteria: sealed sutures on cranium, eruption and wear on third molars, and attached epiphyses on long bones. A few ambiguous specimens were measured but noted as possible subadults. Species, gender, locality, specimen number, and laterality were recorded for each.

Table 3.1. Digging muscles and their insertion points.

	INSERTIONS POINTS ON BONES				
MUSCLES	SCAPULA	STERNUM	HUMERUS	ULNA	MANUS/ DIGITS
Teres Major (retraction & rotation of humerus)	posterior edge of proximal end		teres tubercle on proximal end, medial side		
Deltoids (retraction of humerus)	acromion process		deltoid crest		
Pectoralis (retraction of humerus)		along the length	along the length of the shaft		
Infraspinatus (retraction of humerus)	posterior scapular spine and infraspinous fossa		lateral epicondyle		
Spinodeltoideus (retraction)	posterior scapular spine and infraspinous fossa		lateral epicondyle		
Triceps (extension of the ulna)	distal posterior end		lateral proximal end; medial shaft	olecranon process	
Pronators; Supinators (pronation; supination of digits)			lateral epicondyle to radius; lateral epicondyle		manus
Flexors (flexion of digits)			medial epicondyle		digits

adapted from Gilbert 1976

Measurements of the scapula, humerus and ulna reflecting the muscle origins and insertions and consequent lever systems are shown in Figure 3.2. Table 3.2 lists those measurements taken on each skeletal element. Data from the left and the right bones were included in each statistical test, unless that particular bone was immeasurable. Therefore, the sample size is generally twice as large as the number of individuals actually sampled. Sample size may differ from measurement to measurement because bones may have been missing or broken in certain specimens.

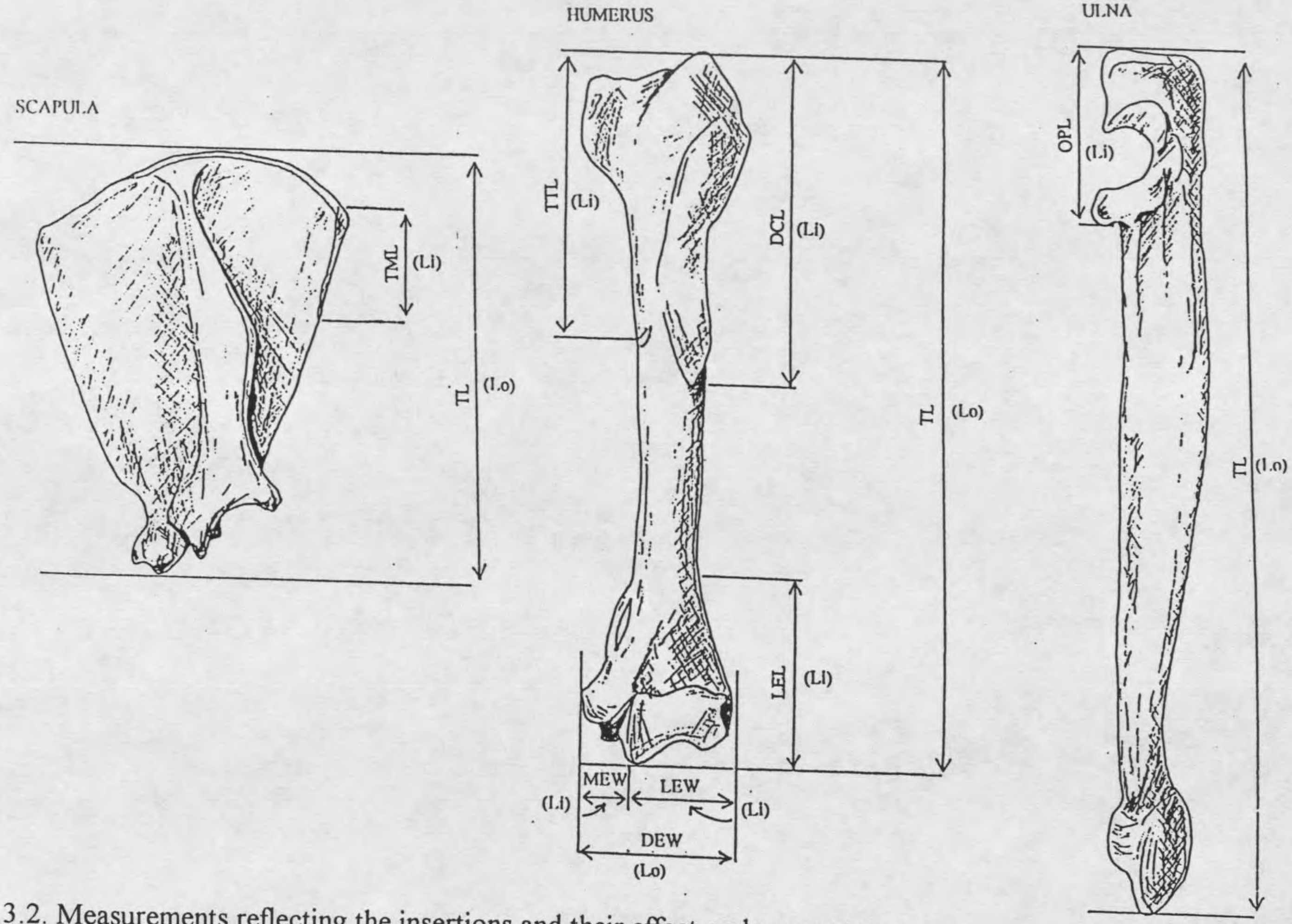


Figure 3.2. Measurements reflecting the insertions and their effect on lever systems.
TL-total length, TML-teres major length, DCL-deltoid crest length, TTL-teres tubercle length, DEW-distal end width, MEW-medial epicondyle width, LEW-lateral epicondyle width, OPL-olecranon process length; Li-input lever, Lo-output lever.

Table 3.2. Measurements taken on each bone type.

SCAPULA	HUMERUS	ULNA
total length (tl)	total length	total length
length of teres major insertion (tml)	length of deltoid crest (dcl)	length of olecranon process (opl)
	proximal length to teres tubercle (ttl)	
	width of distal end (dew)	
	width of medial epicondyle (mew)	
	width of lateral epicondyle (lew)	
	length of lateral epicondyle (lel)	

Ratios of $\mathbf{L_i/L_o}$ were calculated for each measurement, with the numerator and denominator for each lever system defined as illustrated in Figure 3.2. These ratios appear to be normally distributed (Figures 3.3a-g). A two-tailed, two sample student's t-test assuming equal variances (0.05 probability level) was performed to test for significance between the mean ratios for the two species for each measurement type.

The null hypothesis (H_o) is: the mean ratio for *S. columbianus* is equal to the mean ratio for *S. richardsonii* (for a particular measurement). The alternative hypothesis (H_a) is: the mean ratio for *S. columbianus* is not equal to the mean ratio for *S. richardsonii* (for a particular measurement). The direction of difference between means was observed and noted when the t-test indicated significant differences.

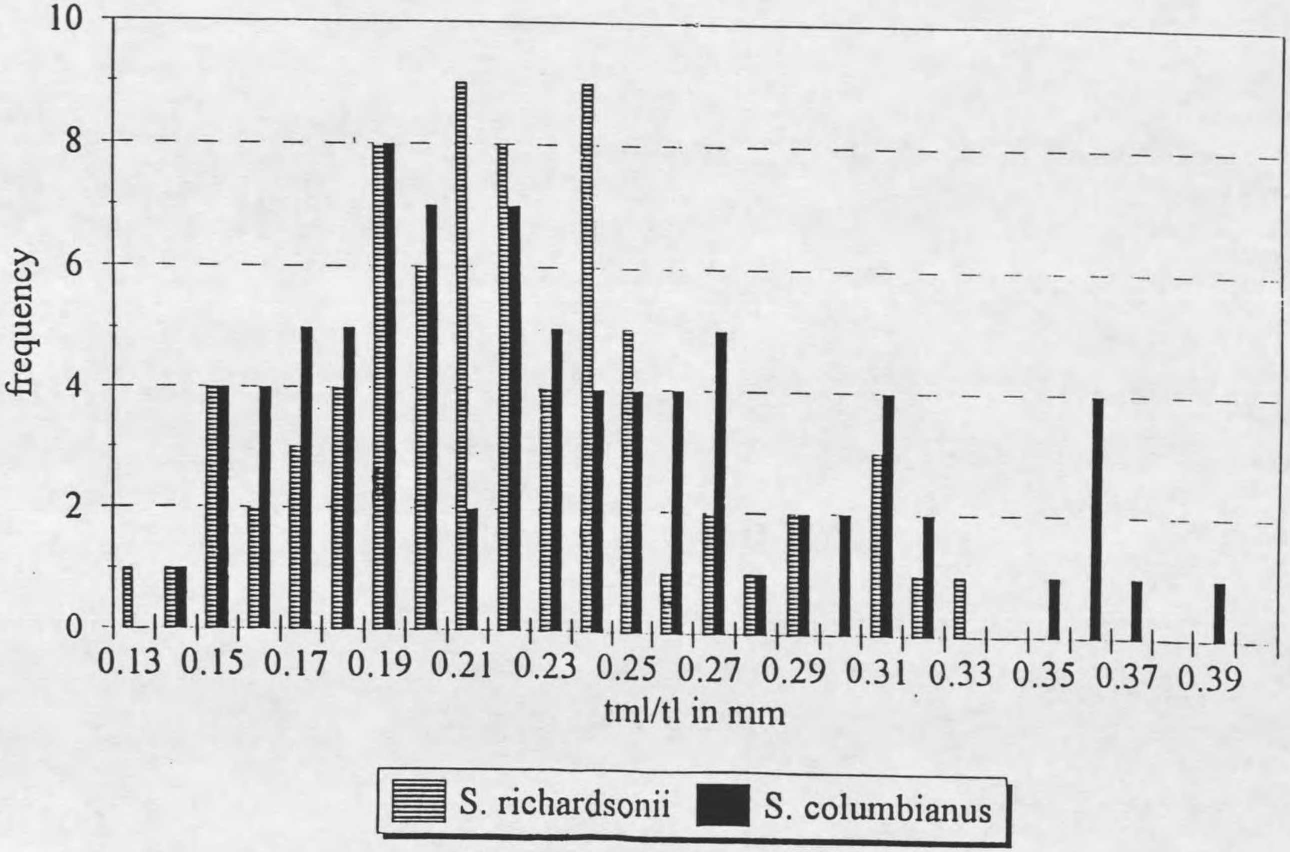


Figure 3.3a. Teres major length/total length of scapula; refers to size of the teres major.

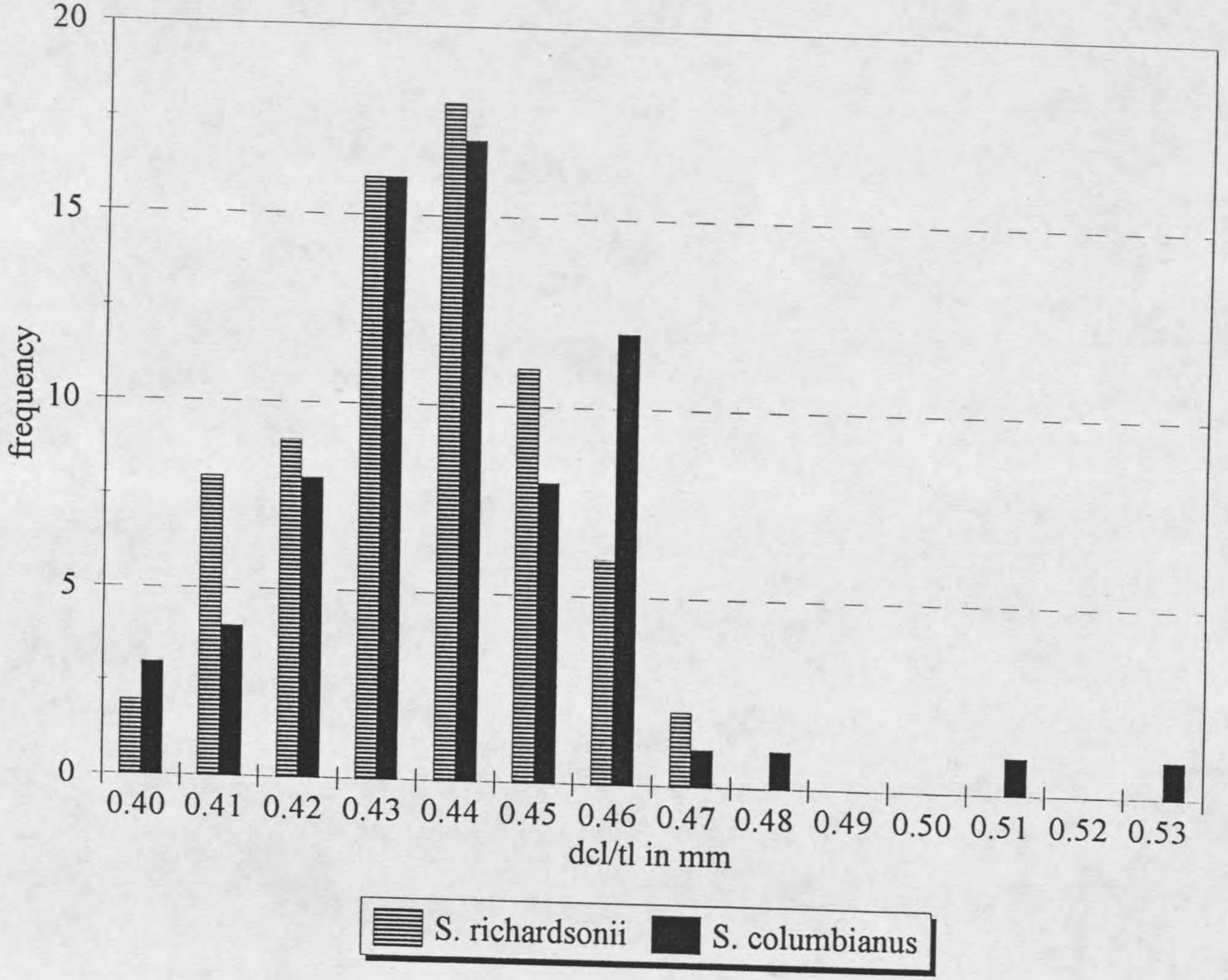


Figure 3.3b. Deltoid crest length/total length of humerus; refers to lever arm for retraction of humerus.

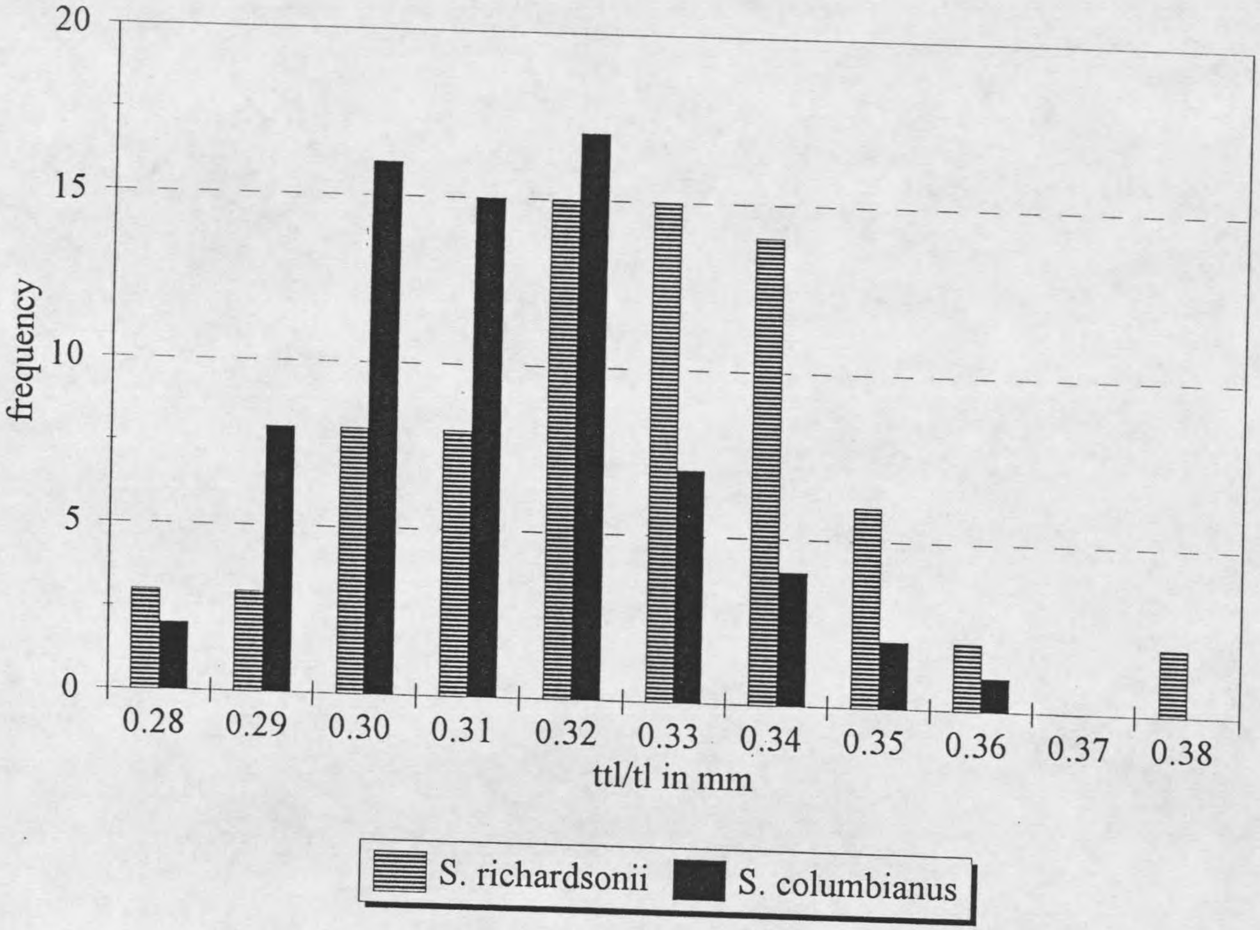


Figure 3.3c. Teres tubercle length/total length of humerus; refers to lever arm for rotation and retraction of humerus.

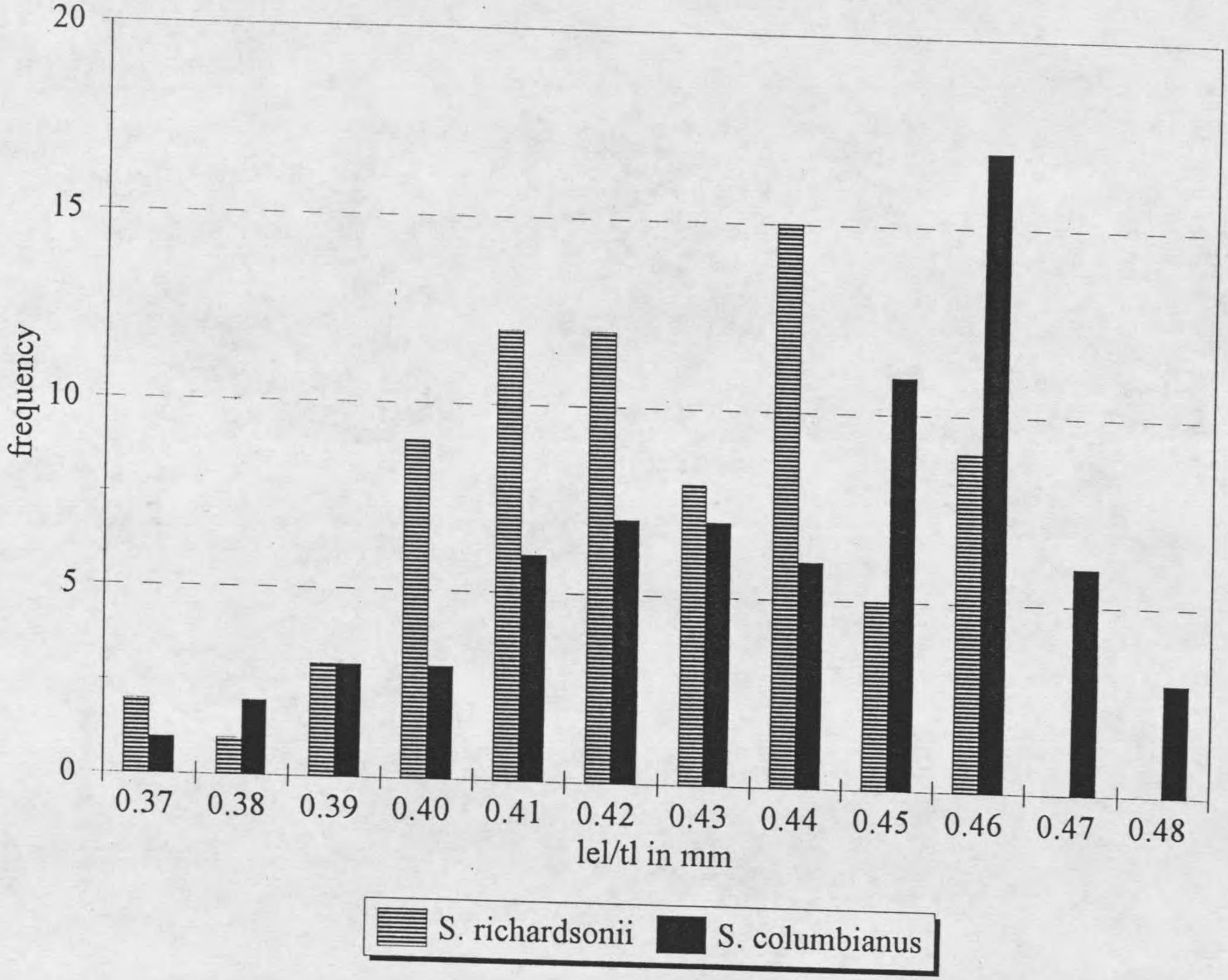


Figure 3.3d. Lateral epicondyle length/total length on humerus; refers to size of the muscle attachment area for retraction of humerus, pronators and supinators of digits.

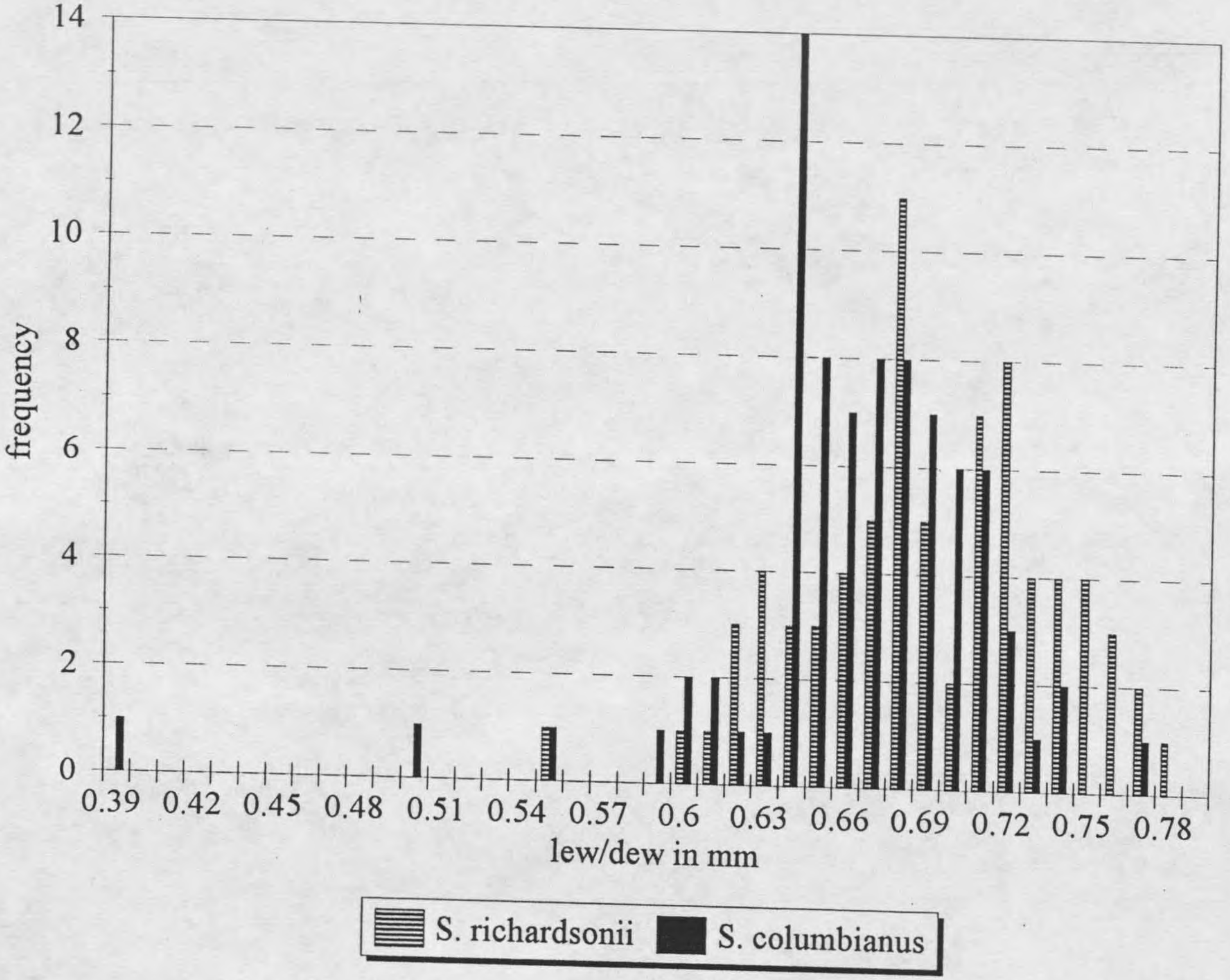


Figure 3.3e. Lateral epicondyle width/ total width of humerus; refers to size of muscle attachment area for retraction of humerus, pronators and supinators of digits.

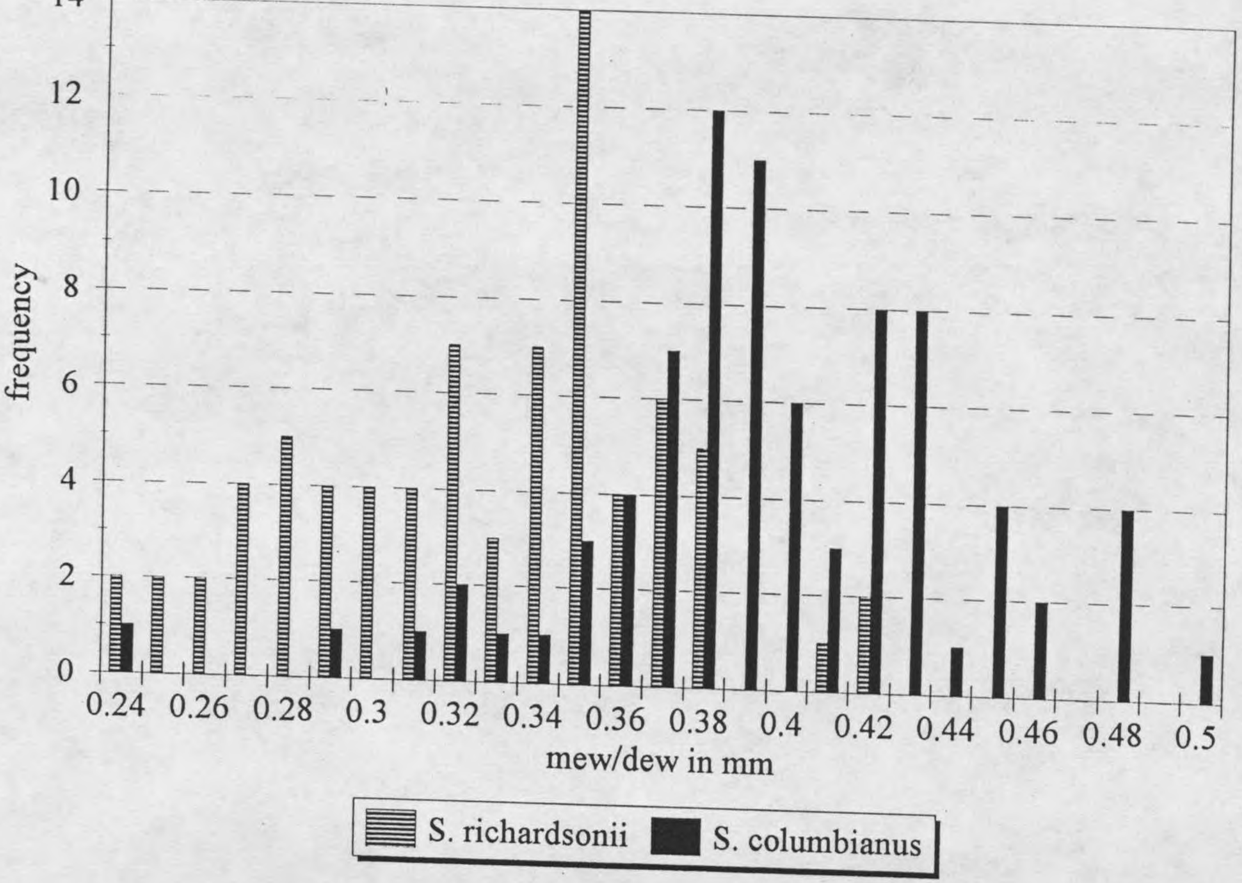


Figure 3.3f. Medial epicondyle width/total width of humerus; refers to attachment area of muscle for flexion of digits.

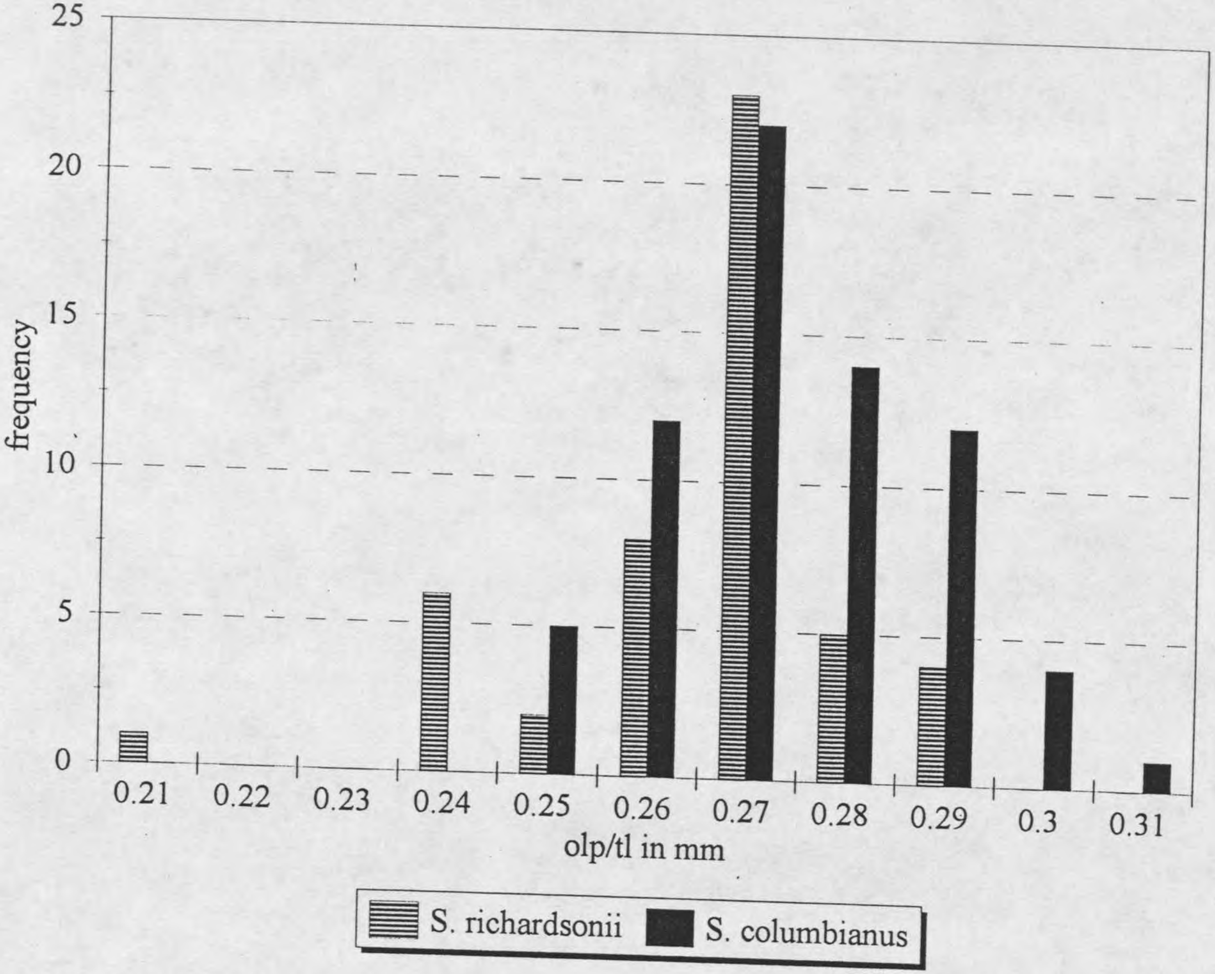


Figure 3.3g. Olecranon process length/total length of ulna; refers to lever arm for extension of ulna.

Results and Discussion

Descriptive statistics for the seven sets of ratios are listed in Table 3.3. Five out of the seven t-tests yielded significant results (Table 3.4). The null hypothesis could not be rejected for the size of the teres major insertion on the scapula (ratio of teres major length/total length ratio of the scapula). This indicates no difference in the size of this muscle relative to scapula size for the two species. Neither is there a significant difference in retraction efficiency of the deltoids, indicated by the deltoid crest length/total length ratio of the humerus.

The null hypothesis was rejected for the five remaining tests suggesting there is a difference in the lever potentials of the two species. In three out of five cases, *S. columbianus* had a significantly higher lever potential than did *S. richardsonii*. The mean ratios for the lateral epicondyle length and the medial epicondyle width of the humerus, and the olecranon process length of the ulna versus the total length (width) were greater in *S. columbianus*. This implies that the relative efficiency of the infraspinatus, spinodeltoideus, triceps, and flexors are all greater in *S. columbianus*, allowing this species to more efficiently produce output forces for retraction of the humerus, extension of the forearm, and flexion of digits.

However, the mean ratios for the teres tubercle length and the lateral epicondyle width versus the total length (width) of the humerus are greater in *S. richardsonii*. The lateral epicondyle width measurement in effect cancels out the higher potential initially

Table 3.3. Descriptive statistics of each ratio for *Spermophilus columbianus* and *S. richardsonii*.

STATISTIC	S. COLUMBIANUS	S. RICHARDSONII
SCAPULA		
teres major length/total length		
mean	**0.2385**	0.2227
standard deviation	0.0611	0.0437
variance	0.0037	0.0019
count	83	75
HUMERUS		
deltoid crest length/total length		
mean	**0.4451**	0.4420
standard deviation	0.0215	0.0179
variance	0.0004	0.0003
count	72	76
teres tubercle length/total length		
mean	0.3173	**0.3398**
standard deviation	0.0167	0.0208
variance	0.0002	0.0004
count	72	76
lateral epicondyle length/total length	**0.4431**	0.4297
mean	0.0268	0.0223
standard deviation	0.0007	0.0004
variance	72	76
count		
medial epicondyle width/total width		
mean	**0.4009**	0.3822
standard deviation	0.0447	0.0410
variance	0.0020	0.0016
count	81	76
lateral epicondyle width/total width		
mean	0.6677	**0.6959**
standard deviation	0.0519	0.0455
variance	0.0026	0.0020
count	81	76
ULNA		
olecranon process length/total length		
mean	**0.2796**	0.2703
standard deviation	0.0138	0.0151
variance	0.0001	0.0002
count	70	49

Table 3.4. Results of two-tailed, two sample t-tests for significance of difference between mean ratios for each measurement type.

	SCAPULA TML/TL	HUMERUS DCL/TL	TTL/TL	LEL/TL	LEW/DEW	MEW/DEW	ULNA OPL/TL
P-value	0.0657	.3335	2.7E-11	.0011	.0004	.0070	.0007
significant at .05 level?	no	no	yes	yes	yes	yes	yes

TL-total length, TML-teres major length, DCL-deltoid crest length, TTL-teres tubercle length, DEW-distal end width, MEW-medial epicondyle width, LEW-lateral epicondyle width, OPL-olecranon process length.

shown for *S. columbianus* in terms of the lateral epicondyle measurement because they both refer to the same purpose of retraction of the humerus and pronation and supination of the digits.

S. richardsonii appears more efficient in the aspects of rotation and retraction controlled by the teres major. The teres major is one of the least important muscles in retracting the forearm in scratch diggers with most of this action being accomplished by the other retractors noted in Table 3.1 (Barnosky 1981; Hildebrand 1974). Since there is no significant difference between the species in terms of retraction of the humerus, it appears *S. columbianus* has a digging advantage over *S. richardsonii* by having a higher lever potential for the extension of the ulna and for the flexion of digits.

Conclusion

S. columbianus has a more efficient digging forearm, which may give it a competitive advantage in rocky soils. This is consistent with this *S. columbianus* inhabiting an area with a higher percent of mineral rock fragments than that of *S. richardsonii*.

However, digging abilities do not explain why *S. columbianus* seems to be *restricted* to an area with a high degree of rockiness. Presumably, if an animal can dig in rocky soil, it can also dig in less rocky soil. This suggests that some factor other than functional morphology is keeping *S. columbianus* from expanding its range into the plains, even though digging abilities may be keeping *S. richardsonii* out of the mountains.

Other than functional morphological considerations, possibilities for limiting the range of *S. columbianus* include various climatic factors, vegetation, and physiological constraints, among others. These potential controls on the species ranges are explored in Chapter 4.

CHAPTER 4.

A CASE STUDY OF THE EFFECTS OF CLIMATE ON GROUND SQUIRREL SPECIES DISTRIBUTION: A GIS APPROACH

Much attention has recently focused on how organisms respond to climate change in light of human-induced global warming. While it is uncertain to what extent global temperature will change, climate models coupled with an understanding of the ecology, behavior, evolutionary history and physiology of organisms are necessary to project the biological consequences of whatever climate changes do occur. There is generally a mismatch in scales in relating climatic studies to ecological studies, with the biological component rarely encompassing an area larger than the size of a playing field and the resolution of climatic studies being the size of Colorado. Only a handful of studies have tried to bridge the gap between small scale single-species studies and large-scale biogeographic data to explain distribution patterns (Root & Schneider 1993). This study uses data from both of these scales to address what parameters correlate with the distribution of two ground squirrel species, the Columbian ground squirrel (*Spermophilus columbianus*) and Richardson's ground squirrel (*S. richardsonii*), of western North America (Figure 4.1). Information on the evolutionary and natural history of these species, coupled with information gathered on continental scales is used to explore mechanisms that might explain any observed correlations between climatic parameters and geographic distribution of these mammalian species, or if instead, distributions are more strongly limited by some parameter not linked to climate.

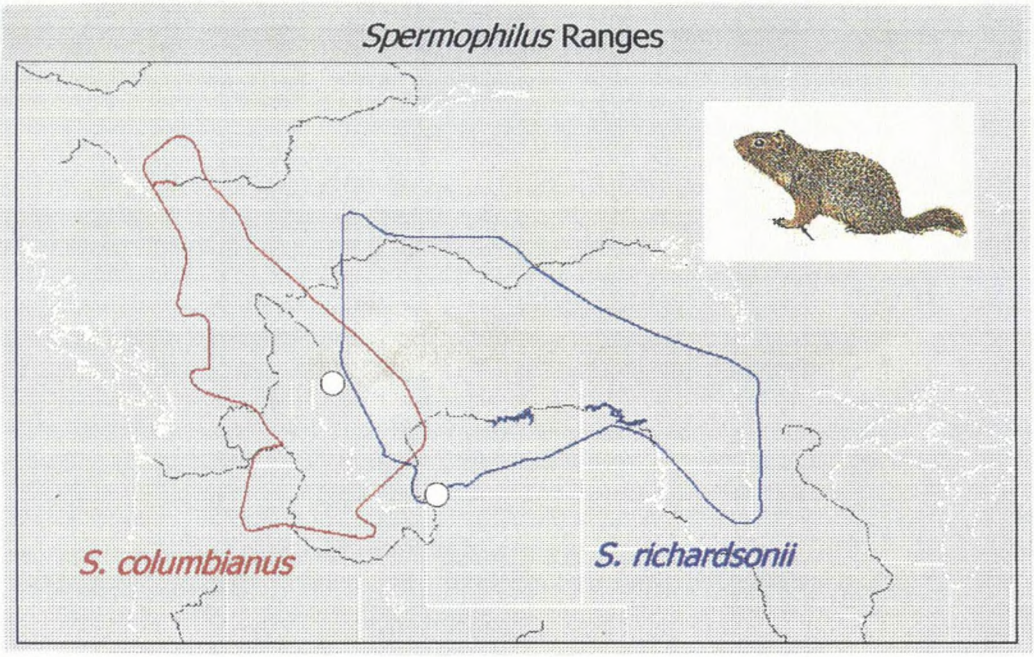


Figure 4.1. Distribution ranges of *Spermophilus columbianus* (left) and *S. richardsonii* (right) of western North America. Black dots denote the approximate location of Glacier National Park in *S. columbianus*' range and Yellowstone National Park in *S. richardsonii*'s range.

S. columbianus and *S. richardsonii* form the basis of this study for the following reasons. (1)The diurnal, fossorial and hibernating lifestyle in both *Spermophilus* species may denote a strong physiological connection with climate. (2) Other studies have identified associations between ground squirrels and climatic parameters (Davis 1939; Knox & Hoffman 1983; Elliott & Flinders 1991). (3)The two species are mostly allopatric with only a small overlap zone. (4) One species is dominant in each of two established nature reserves: *S. richardsonii* in the Greater Yellowstone Ecosystem (GYE) *and S.*

columbianus in the Glacier-Waterton Ecosystem (GWE) (Figure 4.1). They are one of the most abundant small mammals in each of the ecosystems they occur in; thus, climate-induced changes in their range or abundance might be expected to affect species at higher trophic levels.

The purpose of this study is to determine what climatic or (bio)physical parameters may be correlated with the southern half of the distributions of *S. columbianus* and *S. richardsonii.* This information is critical to address the question: 'What is keeping *Spermophilus columbianus* from reaching peak abundance in the GYE and *S. richardsonii* from inhabiting most of the GWE?'

It is hypothesized that climate parameters are critical variables influencing the southern parts of the geographic ranges of *Spermophilus columbianus* and *S. richardsonii.* If climate is the most critical variable, then the distribution of these species will be more significantly correlated to temperature, precipitation, solar radiation, and/or other climatic parameters than any other non-climatic variable (i.e., vegetation type, soil type, elevation, or biological interaction).

The objectives of the study are three-fold: 1. To determine whether certain climatic variables correlate with the geographic ranges of *Spermophilus columbianus* and *S. richardsonii.* 2. To comment briefly on potential ecological, anatomical, and physiological mechanisms that might explain any observed correlations between species ranges and climate. (However, the actual experiments or other analyses required to document exact mechanisms are beyond the scope of this study.) 3. To design a GIS-based methodology that uses existing data from various sources to illustrate and evaluate biotic and abiotic patterns in relation to species ranges.

Materials and Methods

Study Area

The study area includes a major portion of western North America encompassing the ranges of the two species (*Spermophilus columbianus*, approximately 43° to 49° latitude and -110° to -120° longitude; and *S. richardsonii*, approximately 44° to 49° latitude and -94° to -110° longitude) (Figure 4.1). These coordinates represent the southern portions of the species ranges. In some statistical analyses, the study area is actually the conterminous U. S. The study focuses on the southern half of the species distribution because Canadian data presently do not exist in the desired format, and building the data set would be far beyond the scope of this study both in time and cost.

Because both species ranges extend south to approximately the same latitude, the major distributional question in the context of this study is what limits the expansion of each to the east (*S. columbianus*) and west (*S. richardsonii*).

Data Collection

Available digital data sets were obtained from internet-based information that was developed for purposes independent of this study. Species ranges, political and natural features, and a base map were obtained from FAUNMAP, Illinois State Museum in vector (line) format (http://www2.museum.state.il.us/research/faunmap). Climate parameters, soil, vegetation, and elevation for the U.S. were obtained from VEMAP, University Corporation for Atmospheric Research in raster (grid) format (http://www.cgd.ucar.edu/vemap). ARC/INFO Geographic Information System (GIS) software running on a Sun Sparc Station 5 was used to overlay the VEMAP grids with the FAUNMAP polygon coverages of the two ground squirrel species ranges (Appendix B).

The VEMAP grids consist of mean, minimum and maximum monthly temperatures, annual temperature, mean monthly precipitation, annual precipitation, mean monthly solar irradiance, general vegetation type, soil composition and elevation grids. The gridcells are 0.5 degree latitude/longitude and the climatic data were averaged over 20 years (see Appendix C for more information about VEMAP).

Analyses

Visual Correlation Analysis

After ensuring all the data layers were matched in geographic projection, each grid-based layer was overlaid with the polygon coverages of the species ranges to identify visual correlations (Figures 4.2-4.9). The digital output was inspected for patterns of climate factors that coincided with the boundaries of the species ranges or for patterns that varied between ranges. Visual inspection was designed to identify annual trends in climate parameters and correlation of monthly attributes of climate with species ranges. Correspondence of patterns of soil type, vegetation classification, and elevation with species ranges were also inspected.

Statistical Analysis

In order to test the statistical validity of the visual correlation analysis and to analyze the parameters in combination with one another, statistical analyses were used to test correlations between species ranges and the vegetation, elevation, and selected soil and climatic data sets. Spatial autocorrelation statistics using the Statistical Analysis System (SAS) were used to test if there was a significant difference between the values of each parameter when compared between the two species ranges. To ascertain differences among grid cell values between the two species ranges and the zone of overlap, the mixed procedure in SAS was used to identify and compensate for spatial autocorrelation among cells, then to calculate descriptive statistics (mean and t-values) for each range.

To identify which of the various parameters examined in this study most strongly correlate with the species ranges (and zone of overlap), Classification and Regression Trees (CART) was used. This test assesses how the parameters rank among each other in terms of predicting which species will be found in which grid cells.

CART was deemed the most appropriate test to discern the rank importance of examined parameters, inasmuch as it is a conservative assessment that is well-suited to the kind of data available for the VEMAP database. The database includes only mean values for each cell; with the locations or number of values that contributed to each mean being unknown. Because of this, combined with complexities introduced by spatial autocorrelation, statistical tests such as Principal Components Analysis, multivariate regression, or discriminant analyses were deemed unsuitable. Results from these tests are most robust when raw values (rather than means) provide the original data, and when spatial autocorrelation is not a problem. The more conservative approach (CART) was used to minimize the potential of Type II errors. Although additional statistical tests might quantify the differences between strength of correlations, the conclusions and design of this study require only the rank-order information that CART provides.

Finally, comparison of the visual results with the statistical results was performed to determine whether visual determinations were in fact statistically significant, and whether statistical tests found correlations that were not evident visually.

Results and Discussion

Scope

The scope of this study is to discover correlations between broad-scale abiotic and biotic parameters and the southern portions of the ranges of two ground squirrel species. It is important to realize correlation not does equal causation and any correlations established here are based only on speculations of biological mechanisms that might be causative. The only exception involves the test of anatomical links to mineral rock fragments as explained in Chapter 3. Other tests involve experimental physiology and experimental ecology and are beyond the scope of this study.

Limitations

The most obvious limitation of this study is that correlations are noted at only one point in time. The set of parameters examined is discrete and limited only to the U.S.

portion of the ranges. The nature of the VEMAP database itself also has limitations (see *Statistical Analyses*, p. 69). Even with these limitations, a study such as this is an absolutely necessary first step in determining climate's role in limiting geographic distribution. This study took the broad-scale approach, the next step is to perform experimental tests to help make links at smaller scales.

Correlation Analysis

Soil

For each grid, VEMAP provides a modal soil type based on percentages of clay-silt-sand in each grid cell (APPENDIX C). These soil data sets yielded no visual correlations with species ranges. However, the soil data on percent mineral rock fragments did show a correlation with the area encompassed by *S. columbianus* having 19-21% mineral rock fragments and *S. richardsonii* having between 8 and 16 % (Figure 4.2). The overlap zone of the two species is quite variable, with grid cells having 9 to 20 % mineral rock fragments. This correlation seemed so striking as a possible mechanism for limiting *S. richardsonii*'s expansion to the west that a comparative study of forearm lever potentials was undertaken. Chapter 3 discusses the significant results denoting that *S. columbianus* is a more efficient digger, evidenced by more efficient lever potentials and larger forearm muscles than *S. richardsonii* in three out of five measurements.

Percent Volume of Mineral Rock Fragments

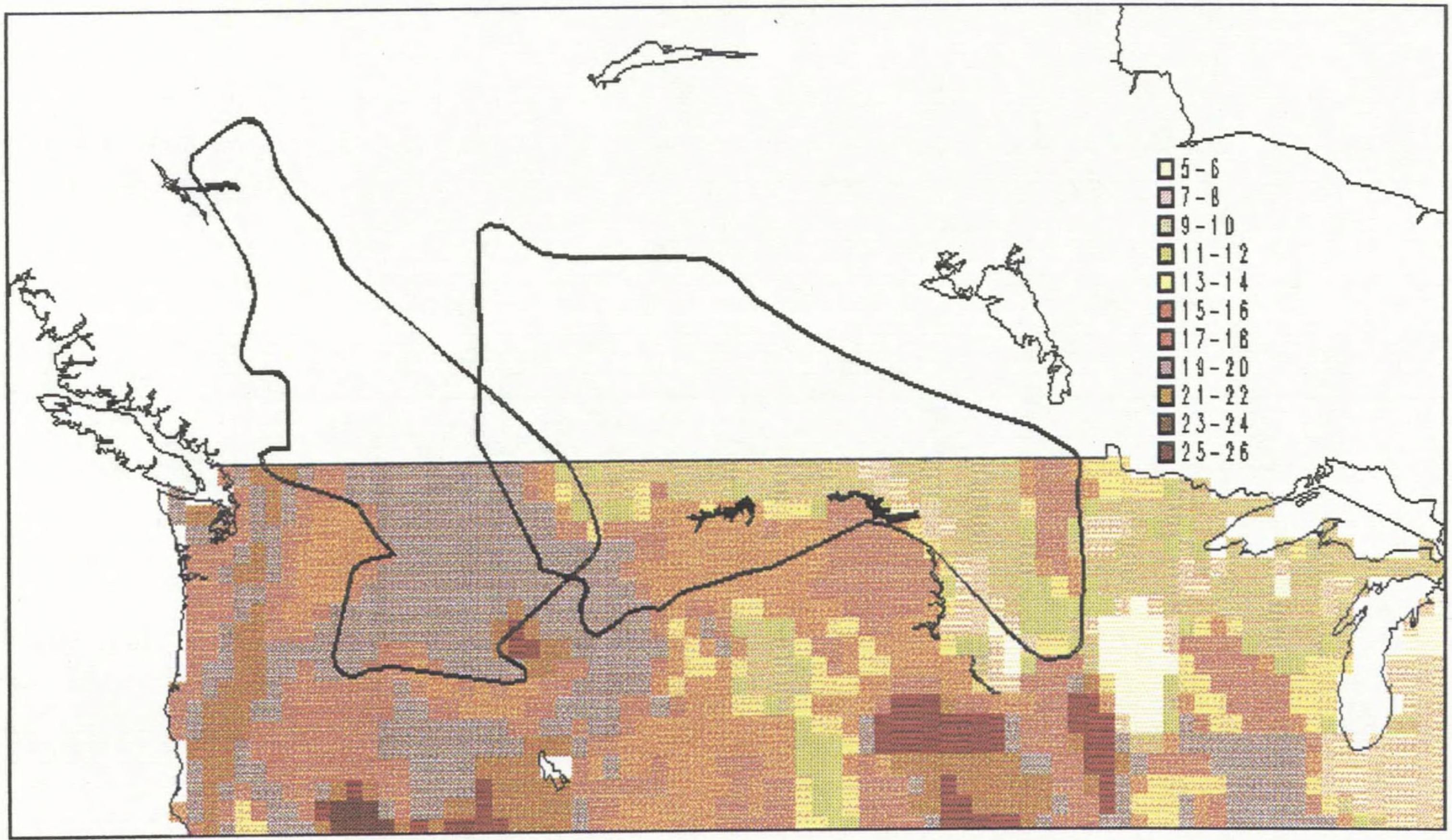


Figure 4.2

Vegetation

VEMAP classifies vegetation within grid cells in terms of dominant life forms and leaf characteristics. *S. columbianus*' habitat is subalpine and alpine meadows amidst conifer forest while *S. richardsonii*'s is mostly grassland (Figure 4.3). While these habitats are different, both species rely on a wide assortment of bulbs, seeds, herbs, insects and carrion. They are restricted to open areas, probably due to their fossorial and social lifestyles, but are not reliant on any one particular vegetative species for nutritition. Therefore, although the two species generally inhabit different vegetational regimes, it seems either species could live in either vegetation type if necessary. Even if vegetation is the proximal limiter of distribution, vegetation itself is ultimately correlated and probably controlled by some of the climate parameters noted below.

Elevation

The elevational gradient appears to increase from the west in *S. columbianus*' range and the east in *S. richardsonii*'s range to the area of overlap in the mountains (Figure 4.4). Elevation appears to be variable within both species' ranges and perhaps the Rocky Mountains are barrier to further expansion in either direction. Elevation correlates with a variety of climatic and vegetational parameters.

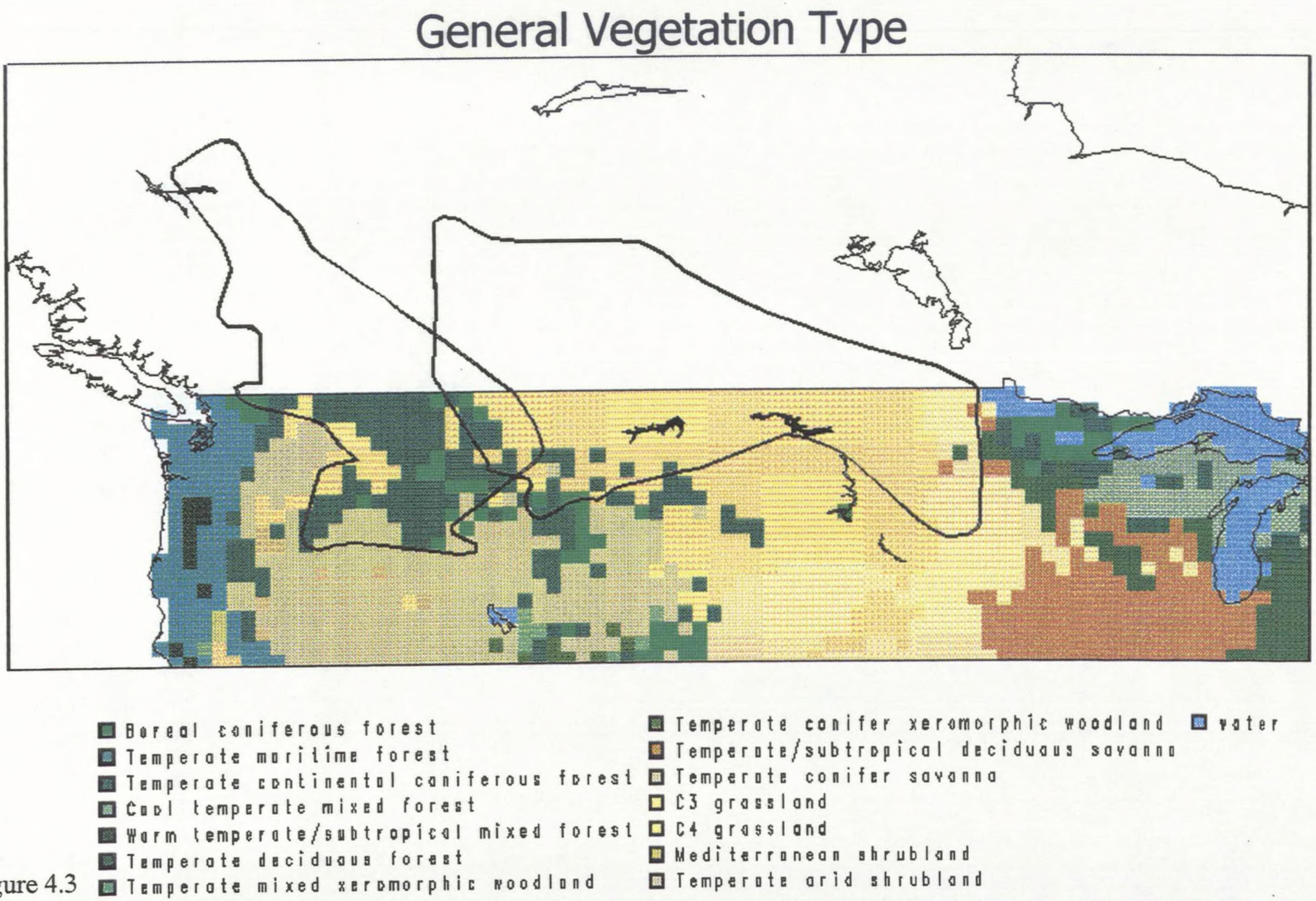

General Vegetation Type
Boreal coniferous forest
Temperate maritime forest
Temperate continental coniferous forest
Cool temperate mixed forest
Warm temperate/subtropical mixed forest
Temperate deciduous forest
Temperate mixed xeromorphic woodland
Temperate conifer xeromorphic woodland
Temperate/subtropical deciduous savanna
Temperate conifer savanna
C3 grassland
C4 grassland
Mediterranean shrubland
Temperate arid shrubland
water

Figure 4.3


Elevation (m)

Figure 4.4

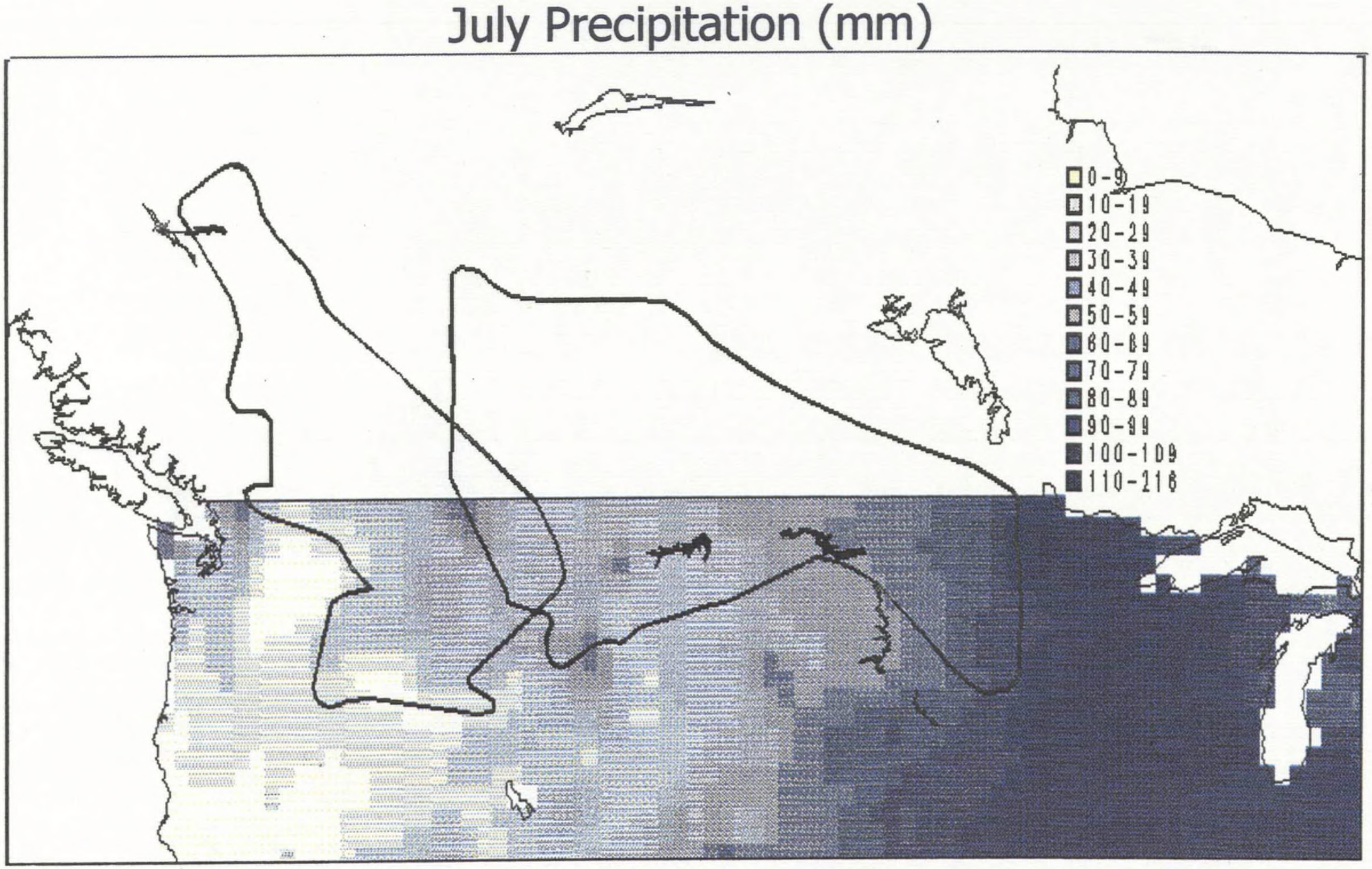
Precipitation

Beginning in April, the average emergence date of both species, there is considerably more precipitation in the range of *S. columbianus* than in that of *S. richardsonii*. From May through the summer, precipitation appears to equilibrate between the two ranges (Figure 4.5). By September, the range of *S. columbianus* starts to receive more precipitation and gets increasingly more through January. A stark difference in precipitation contrasts the two ranges in the winter months (Figure 4.6). *S. columbianus'* range surrounds an area of high precipitation presumably because of its mountainous location. *S. richardsonii*'s range is variable in terms of precipitation.

Snow has good insulative properties, which would keep hibernacula warmer in the winter. If future physiological studies demonstrate *S. columbianus* has higher survivorship than *S. richardsonii* at lower winter temperature, the warmer hibernacula might explain why *S. columbianus* is restricted to an area of high winter precipitation. However, this reasoning would not explain *S. richardsonii*'s absence from areas of high winter precipitation. Other forces must be active in keeping *S. richardsonii* from expanding west.

Temperature

In April there does not appear to be much contrast in temperature values between the ranges of the two species. From May through the summer, however, the range of *S. richardsonii* experiences increasingly warmer temperatures than does *S. columbianus*'



July Precipitation (mm)

Figure 4.5

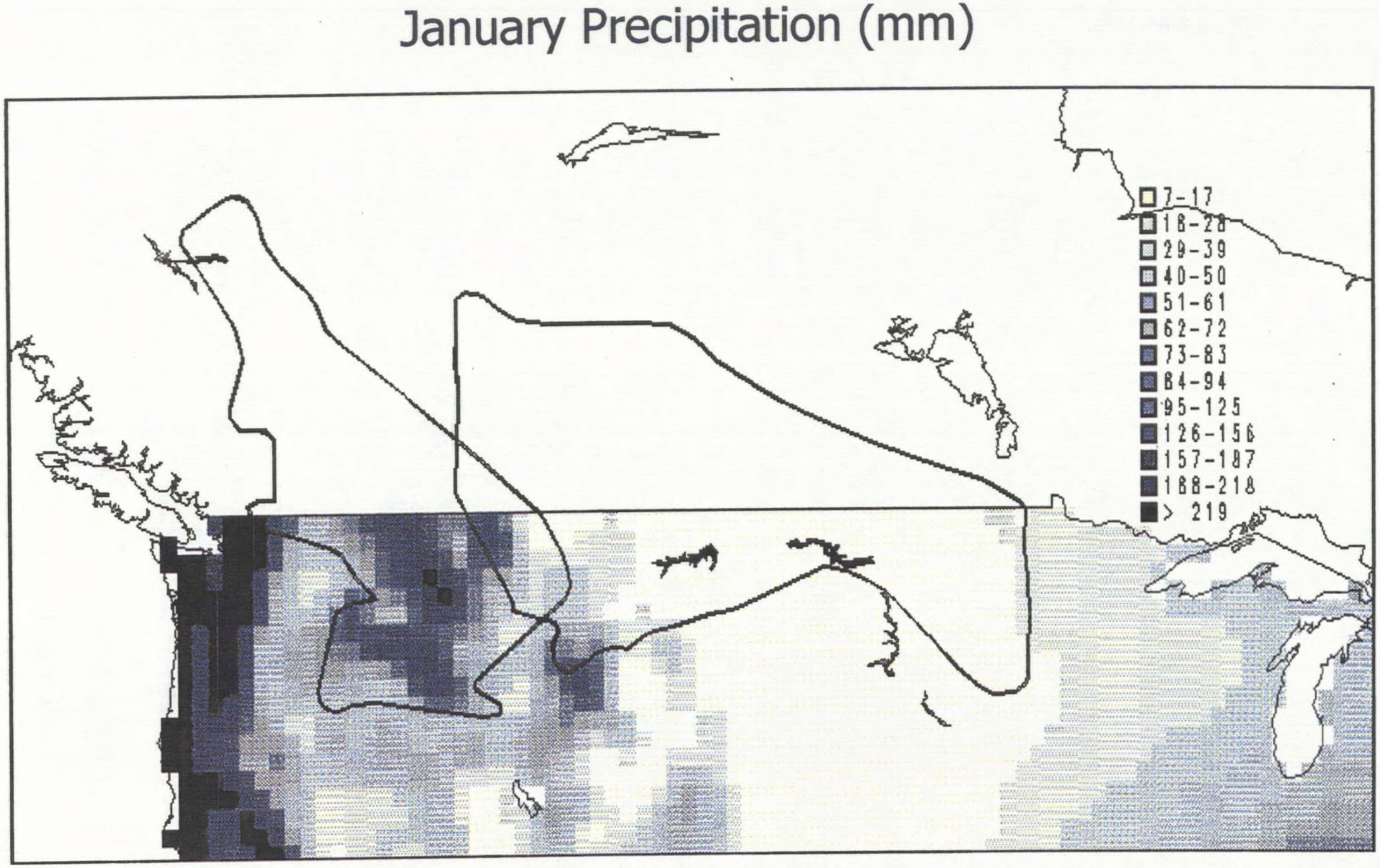
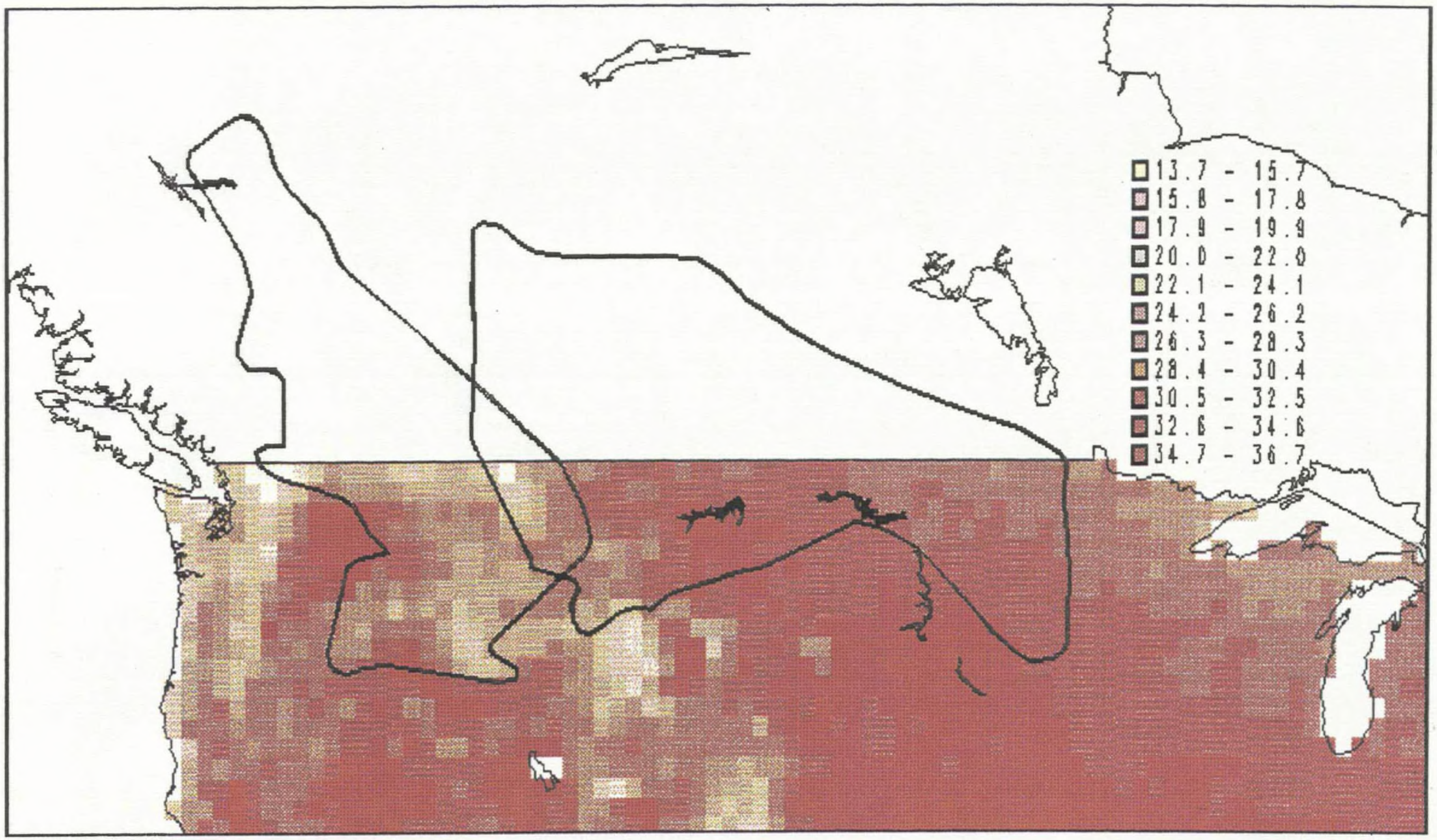

January Precipitation (mm)
7-17
18-28
29-39
40-50
51-61
62-72
73-83
84-94
95-125
126-156
157-187
188-218
> 219

Figure 4.6



Maximum July Temperature (Celsius)

Figure 4.7

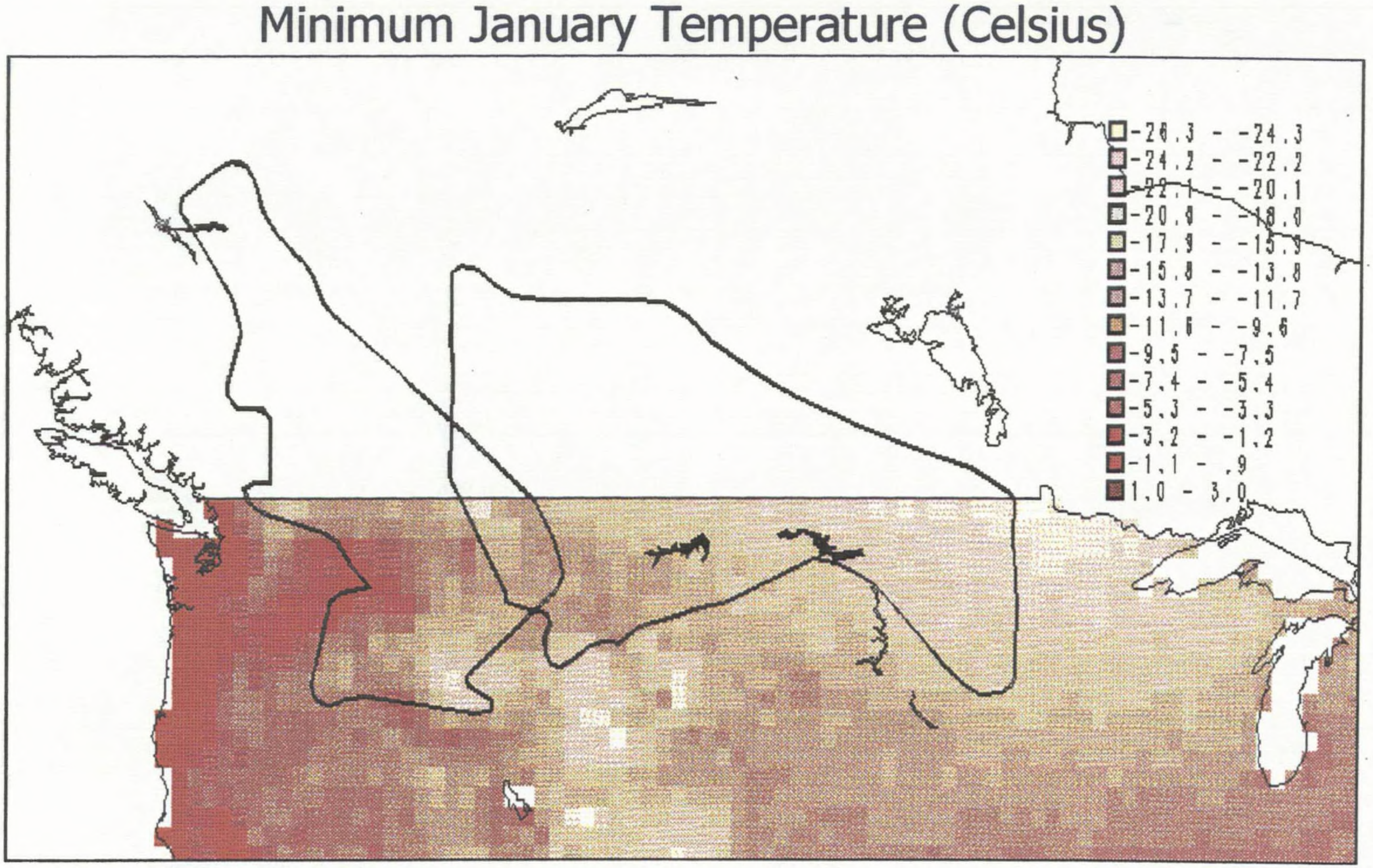

Minimum January Temperature (Celsius)
-26.3 - -24.3
-24.2 - -22.2
-22.1 - -20.1
-20.0 - -18.0
-17.9 - -15.9
-15.8 - -13.8
-13.7 - -11.7
-11.6 - -9.6
-9.5 - -7.5
-7.4 - -5.4
-5.3 - -3.3
-3.2 - -1.2
-1.1 - .9
1.0 - 3.0

Figure 4.8

(Figure 4.7). By September, there is less contrast between the ranges, a pattern that holds through November. In December, there is a shift with the range of *S. columbianus* having higher temperatures than *S. richardsonii*'s until February (Figure 4.8). By March, temperatures equilibrate again.

The range of *S. richardsonii* shows an interesting pattern where it is warmer in the west than the east during the winter but the opposite in the summer. Since the range of *S. richardsonii* seems to experience a wider range of temperature extremes (i.e., minimum January temperature and maximum July temperature), it seems unlikely that the low temperatures in the west just prior to immergence are preventing *S. richardsonii* from expanding into *S. columbianus*' range. Perhaps summer temperature is a surrogate of some other parameter.

Solar Irradiance

Solar irradiance patterns do not conform to the ranges of either species. Annual data (Figure 4.9) shows a correlation of both species with a common isocline at the southern edge of their ranges but that does not explain why one species does not extend more into the other's range.

Table 4.1 provides a qualitative assessment of the strength of each parameter as a mechanism for limiting the expansion of the ranges based on the visual correlation analysis. It lists a subset of all the data layers involved in the analysis; e.g., only those layers which showed a strong visual correlation with species ranges or those thought to be

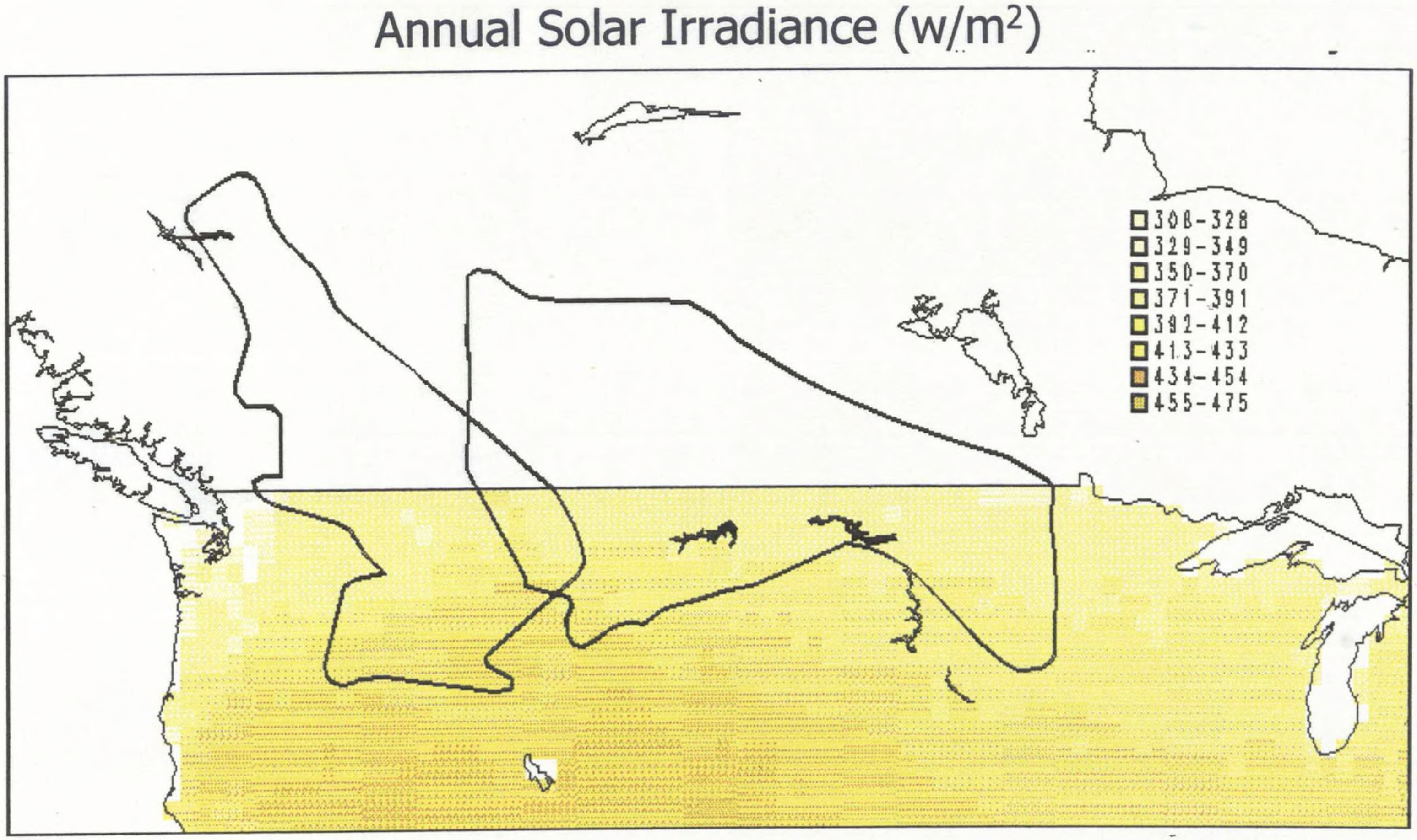

Annual Solar Irradiance (w/m^2)
308-328
329-349
350-370
371-391
392-412
413-433
434-454
455-475

Figure 4.9

potentially important for these species. These qualitative strength assessments are compared to the 'Ranking order' output from CART.

Table 4.1. Qualitative assessment of the strength of each parameter correlative with the ranges based on visual correlation analysis.

Parameter	Qualitative assessment	
	S. columbianus	*S. richardsonii*
Mineral rock fragments	strong	weak
Vegetation	moderate	moderate
Elevation	moderate	moderate
Precipitation (winter)	strong	moderate
Precipitation (summer)	moderate	weak
Temperature (winter)	weak	moderate
Temperature (summer)	moderate	moderate
Solar irradiance	weak	weak

The zone of overlap stretches south from the southeastern portion of Alberta, Canada approximately to the region of Three Forks, Montana, USA. This zone encompasses the area where the Great Plains meet the Rocky Mountains and, therefore, is characterized by varied topography. Vegetation type is comprised of grassland, conifer forest and pockets of deciduous forest. Percent volume of mineral rock fragments is variable, ranging from 9-20%. January precipitation ranges from approximately 10-150 mm while July precipitation ranges from approximately 30-55 mm. Minimum January temperature ranges from approximately -20 to -9 °C with maximum July temperature ranging from approximately 13 to 26 °C.

Statistical Analysis

Range Comparison

Spatially autocorrelated grid cell values for each parameter were averaged as part of one of three data sets: (1) *S. columbianus*' range minus area of overlap with *S.*

richardsonii (squirrel 1), (2) *S. richardsonii*'s range minus area of overlap with *S. columbianus* (squirrel 2), and (3) zone of overlap of both species (squirrel 3). SAS automatically computes an estimate of the deviation of the mean of the third variable, in this case, the zone of overlap of both species (squirrel 3).

The null hypothesis is: the means of squirrel 1 or squirrel 2 do not differ from squirrel 3. That is, the values contained in *S. richardsonii* and *S. columbianus* ranges are not statistically different. The alternative hypothesis is: the means are not equal. That is, the values contained in each range are different.

Two sample t-test results comparing means for each parameter are listed in Table 4.2. It is important to note that the deviation is relative to the intercept, or the overlap zone. Therefore, the mean for the total range for *S. columbianus*, for instance, would be calculated from the values in the overlap zone plus or minus the values in the squirrel 1 zone. The p-values in columns 4 and 6 refer to significance of difference between squirrel 1 (the range of *S. columbianus* only) and the overlap zone, and squirrel 2 (the range of *S. richardsonii* only) and the overlap zone, respectively. This analysis also determines if there is a significant difference among the three data sets (i.e., (squirrel 1) the range of *S. columbianus* only, (squirrel 2) the range of *S. richardsonii* only, and (squirrel 3) the overlap zone. Column 7 refers to the significance of difference among the three means. The mean elevation in *S. columbianus*' range is not statistically different than the elevation in the overlap zone. However, there is undoubtedly a high degree of variability as a result

Table 4.2. T-test results for difference between data sets 1, 2, and 3 for each parameter. Alpha value = 0.05; Degree of freedom =1.

Parameter	Intercept (squirrel 3)	squirrel 1	P-value	squirrel 2	P-value	Overall P-value	significant?
ELEV	1477.12	-86.78	.3498	-726.23	.0001	.0001	yes
MRF	16.96	2.75	.0001	-4.11	.0001	.0001	yes
TNJAN	-140.12	14.95	.0460	-37.53	.0001	.0001	yes
TXJUL	246.68	1.43	.7822	39.65	.0001	.0001	yes
PJAN	45.20	47.97	.0001	-28.54	.0001	.0001	yes
PJUL	41.12	-10.89	.0009	16.19	.0001	.0001	yes
IRRANN	37139.64	1095.85	.0032	-407.47	.2540	.0001	yes

ELEV - elevation, MRF - mineral rock fragments, TNJAN - minimum temperature in January, TXJUL - maximum temperature in July, PJAN - January precipitation, PJUL - July precipitation, IRRANN - annual solar irradiance. (squirrels 1-3 are the range of *S. columbianus* only, the range of *S. richardsonii* only, and the overlap zone, respectively.)

of mountainous relief. The mean elevation of *S. richardsonii*'s range is much lower with a deviation of -726.23 m. Still, according to Figure 4, elevation between the two species ranges does not appear to have that strong of a correlation with species range boundaries when viewed independent of the overlap zone. This overlap zone does appear to be quite different and may be interpreted as a mountainous barrier between the rest of the two geographic ranges.

Mean values for mineral rock fragments vary widely with *S. columbianus*' being significantly higher and *S. richardsonii*'s being significantly lower than that of the overlap zone. Based on the comparative anatomy study in Chapter 3, it appears that the high degree of rockiness may be preventing *S. richardsonii* from expanding west into *S. columbianus*' range. The results for three out of five measurements state *that S. columbianus* is the more efficient digger of the two. Still, mineral rock fragments must not be limiting *S. columbianus* because this species does not inhabit *S. richardsonii*'s range, which is lower in mineral rock fragments and presumably easier for digging.

Winter precipitation, that which influences hibernacula temperature and is the other most significantly different parameter tested, may be the ultimate reason S. columbianus is limited from eastward expansion.

Both temperature values, minimum January temperature (TNJAN) and maximum July temperature (TXJUL), in the range of *S. richardsonii* are significantly different compared to the overlap zone, being an average 37.53 °C cooler in January and 39.65 °C warmer in July. *S. columbianus*' range is not statistically different from the overlap zone in terms of temperature. This is probably due to a maritime effect on the west side of the Rocky Mountains where annual extremes are not as great as more continental areas. Figures 4.7 and 4.8 illustrate a greater temperature difference in July than in January. Temperature may be important in winter too, since there is undoubtedly a threshold of minimum temperature even a hibernating animal can withstand.

Precipitation values are significantly different for both species ranges with the mean for *S. columbianus*' range being an average of 47.97 mm higher and the mean for *S. richardsonii* being 28.54 mm lower in January. Just the opposite occurs in July where *S. columbianus*' range is 10.89 mm lower in precipitation relative to the zone of overlap and *S. richardsonii*'s is 16.19 mm higher. The contrast in January precipitation is clear in Figure 4.6. The high degree of precipitation in January in the range of *S. columbianus* is correlative to massive snow accumulation at high elevations.

While snow acts as an insulator, possibly increasing over-winter survivability in *S. columbianus*, it also prevents foraging until snowmelt. *S. richardsonii* may be at a disadvantage during winter because of colder temperatures and less insulating precipitation in the form of snow but are at an advantage by inhabiting an area which allows earlier foraging and thus, earlier immergence.

Figure 4.9 does not provide an irradiance pattern to distinguish between the two ranges. The SAS results do show, however, that *S. columbianus*' range is statistically different with an annual average of 1095.85 w/m^2 more than the zone of overlap and consequently more annual irradiance than in *S. richardsonii*'s range.

Ranking of Parameters

The parameters were ranked in importance for delineating the conditions between the two ranges using CART. The parameters were ranked with the first being the most important, the second being the next important, and so on. Taking into account the spatial autocorrelation of the data, CART divided the grid cells into progressively detailed categories based on the spread of the data. The test was run two times. The first test used the entire data set from the conterminous U.S. and the second test used the data only from where *S. columbianus* is found alone and where *S. richardsonii* is found alone.

Using the entire conterminous U.S. data set, CART defined the most important parameters in delineating each species range as compared to the rest of the continental U.S. Figure 4.10 illustrates an abbreviated version of the CART output with the nodes being the splitting points and the terminal regions culminating in a series of conditions suitable for either squirrel 1 (*S. columbianus* only), squirrel 2 (*S. richardsonii* only), and squirrel 3 (overlap zone of both species).

Figure 4.10 establishes sets of conditions found within each species range and the overlap zone. Presumably, these conditions, in conjunction with historical contingencies, explain the geographic location of each species. Table 4.4 reiterates the conditions required to find *S. columbianus*, *S. richardsonii* or both.

CART ranked vegetation as the most important variable in defining the ranges of *S. columbianus* and *S. richardsonii* out of all possible ranges in the entire U.S.(Appendices D and E). That is, these species are seldom if ever found mixed forest

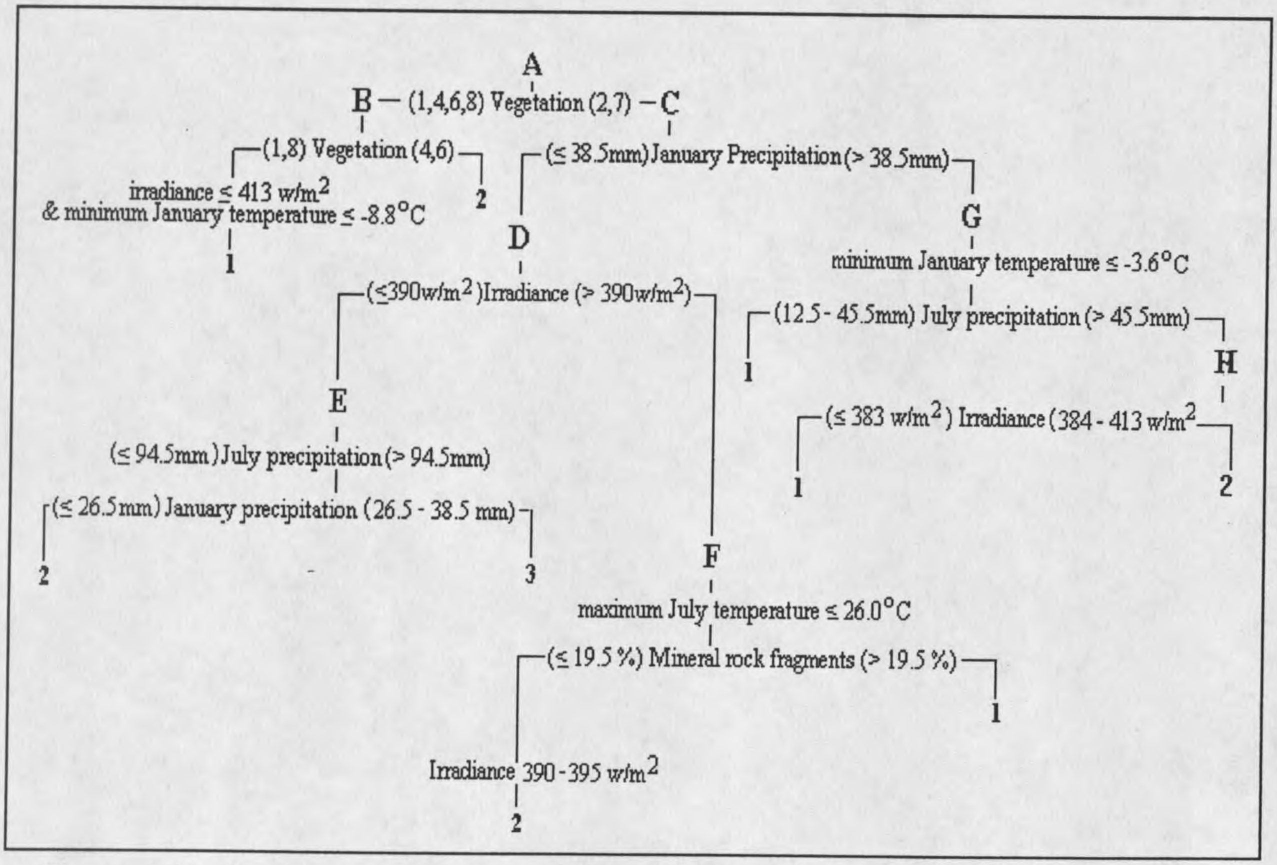


Figure 4.10. Classification tree delineating conditions necessary for the presence of each species. Nodes are marked with capital letters(**A-H**). Bold numbers at terminal regions indicate which species is most likely to be found under stated conditions: **1** = *S. columbianus*, **2** = *S. richardsonii*, **3** = both species.

(3) and woodland (5) (Appendix E). Given certain combinations of non-vegetative parameters, the species are found in either (a) tundra (1), deciduous forest (4), savannah (6) and shrubland (8) which are the branches to the left of node A in Figure 4.10, or (b) conifer forest (2) and grassland (7), the branches to the right of node A in Figure 4.10. However, the species usually are found in conifer forest and grassland (below node C). Vegetation forms the highest-ranking separator of where the species are found. It is important to note that branches to the left (node B) are defined on only one gridcell classified as deciduous forest, and two cells as savannah within the range of *S. richardsonii*. Similarly, only one cell within the range of *S. columbianus* was classified as tundra, and 15 were classified as shrubland.

The majority of the grid cells encompassed by both species range boundaries are found in conifer forest and grassland habitats. While vegetation segregates where *S. columbianus* and *S. richardsonii* are found collectively, it is not very informative in delineating between the ranges. Instead, climate and soil parameters appear to separate the two species.

Node C (Figure 4.10) basically shows that the two species are separated by January precipitation. If January precipitation <= 38.5 mm, then *S. richardsonii* is the typical species found. There are two exceptions, however. Even if January precipitation <= 38.5 mm, if solar irradiance > 390 w/m^2, maximum July temperature <= 26.0 °C, and mineral rock fragments > 19.5 % then *S. columbianus* would be the typical species found.

Similarly, if solar irradiance <= 390 w/m^2, July precipitation > 94.5 mm and January precipitation is between 26.5 and 38.5 mm, then both species are as likely to be found. If January precipitation > 38.5 mm, then *S. columbianus* is the typical species found unless minimum January temperature <=36.5 °C, July precipitation > 45.5 mm and irradiance is 384-413 w/m^2. In this instance *S. richardsonii* would more likely be found.

There is a probability associated with the accuracy in which CART predicted which species would be found under certain conditions. Table 4.3 lists the percent of time CART was correct.

Table 4.3 Probability table of correct predictions by CART for entire U.S. data set.

	Squirrel 1	Squirrel 2	Squirrel 3
% of time CART correctly predicted each species	86.6%	92.7%	24.0%

In Table 4.1, a qualitative assessment was given to each of the parameters identified as important in the visual correlations. January precipitation was given a rating of 'strong' for *S. columbianus*. The visual correlation and statistical analysis agree that winter precipitation is a major delineator between the two species as the January precipitation value of 38.5 mm splits the ranges well. Most of the cells in *S. richardsonii*'s range have <= 38.5 mm while most of the cells in *S. columbianus*' range have > 38.5 mm.

Table 4.4 Conditional requirements for the majority of the cells within the ranges of *S. columbianus* and *S. richardsonii* as determined by CART. This table only relates to the branches under node C (vegetation values of 2 and 7) in the classification tree.

Species range	Sets of conditional requirements	Number of cells within ranges satisfying conditional requirements
S. columbianus only (squirrel 1)	**Set 1**. January precipitation <= 38.5 mm, irradiance <= 390 w/m^2, maximum July temperature <= 26.0 °C and > 19.5 % mineral rock fragments. **Set 2**. January precipitation > 38.5 mm, minimum January temperature <= 3.6 °C, July precipitation 12.5 - 45.5 mm. **Set 3**. January precipitation > 38.5 mm, minimum January temperature <=3.6 °C, July precipitation > 45.5 mm, irradiance <= 383 w/m^2.	**1.** 5 **2.** 88 **3.** 9 total number of cells = 119 88/119 = 73.9 % of cells in *S. columbianus*' range satisfy set #2.
S. richardsonii only (squirrel 2)	**Set 1**. Irradiance <= 390 w/m^2, July precipitation <= 94.5 mm, January precipitation <= 26.5 °C. **Set 2**. January precipitation <= 38.5 mm, irradiance <= 390 w/m^2, July temperature <= 26.0 °C, <= 19.5 % mineral rock fragments, irradiance 390 - 395 w/m^2. **Set 3**. January precipitation > 38.5 mm, minimum January temperature <=3.6 °C, July precipitation > 45.5 mm, irradiance 384 - 413 w/m^2.	**1.** 176 **2.** 1 **3.** 7 total number of cells = 192 176/192 = 91.6 % of cells *in S. richardsonii*' range satisfy set #1.
Zone of overlap of both squirrels (squirrel 3)	**Set 1**. Irradiance <= 390 w/m^2, July precipitation <= 94.5 mm, January precipitation 26.5 - 38.5 °C.	**1.** 9 total number of cells = 25 9/25 = 36.0 % of cells in the zone of overlap satisfy set #1.

When the CART test is run using only the *S. columbianus* and *S. richardsonii* data sets, the results are similar but more concise (Figure 4.11).

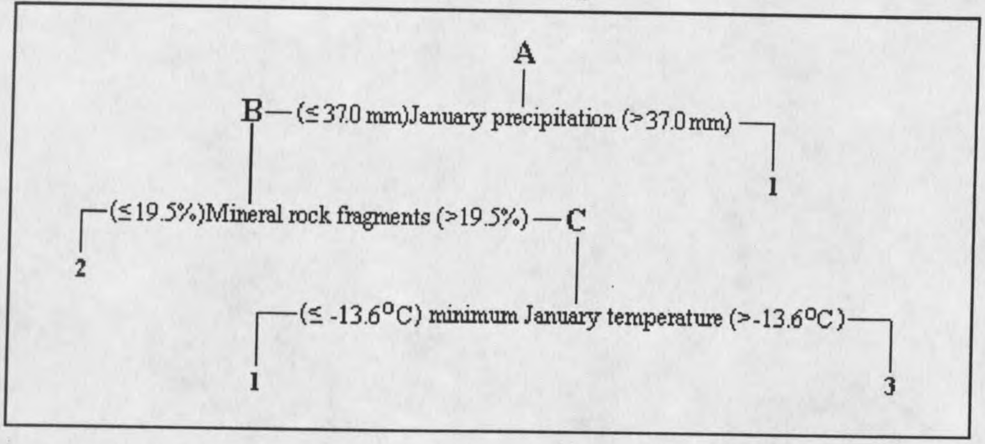


Figure 4.11 Classification tree delineating conditions necessary for the presence of each species. Nodes are marked with capital letters (**A-C**). Bold numbers at terminal regions indicate which species is most likely to be found under stated conditions: **1** = *S. columbianus*, **2** = *S. richardsonii*, **3** = both species.

Not surprisingly, the probability with which CART predicted which species would be found under certain conditions increased with the abbreviated dataset (Table 4.5).

Table 4.5 Probability table of correct predictions by CART for only squirrel data sets.

	Squirrel 1	Squirrel 2	Squirrel 3
% of time CART correctly predicted each species	96.6%	93.8%	16.0%

CART essentially chose those parameters which are most important in delineating the differences between the ranges of *S. columbianus* and *S. richardsonii*. As illustrated in Table 4.6, the distinction in the conditional requirements for these two species is based mainly on splitting one parameter, January precipitation. The majority of the cells within each species range diverge when the value of 37.0 mm of January precipitation is stated as the splitting value.

Table 4.6 Conditional requirements for defining the ranges of *S. columbianus* and *S. richardsonii* as determined by CART.

Species range	Sets of conditional requirements	Number of cells within ranges satisfying conditional requirements
S. columbianus only (squirrel 1)	**Set 1.** January precipitation > 37.0 mm. **Set 2.** January precipitation <= 37.0 mm, >19.5% mineral rock fragments and minimum January temperature <= -13.6 ° C.	**1.** 132 **2.** 7 total number of cells = 119 132/119 = 110.9% of cells in *S. columbianus*' range satisfy set #1. *
S. richardsonii only (squirrel 2)	**Set 1.** January precipitation <= 37.0 mm, <= 19.5% mineral rock fragments.	**1.** 193 total number of cells = 192 193/192 = 100.5% of cells in *S. richardsonii*'s range satisfy set #1. *
Zone of overlap of both squirrels (squirrel 3)	**Set 1.** January precipitation <= 37.0 mm, >19.5% mineral rock fragments and minimum January temperature > -13.6 ° C.	**1.** 4 total number of cells = 25 4/25 = 16.0% of cells in the zone of overlap satisfy set #1.

* Refer to Table 4.5 for probability of correct predictions.

Conclusion

Establishing a relationship between a species and climate is necessary before one can predict how that species may respond to climate change. Analysis of the correlations between these species ranges and broad-scale parameters denote a connection with climate. The collective ranges of *S. columbianus* and *S. richardsonii* correlate with broad vegetation classifications. To characterize each range separately, however, abiotic factors, including climatic and soil parameters, must be explored.

According to this study, *S. columbianus* is restricted to an area of high winter precipitation, less seasonal extremes in temperature, and a high degree of mineral rock fragments. Based on the literature search performed for Chapter 2, some possible mechanisms for each of these correlations is suggested. *Columbianus*' restriction to an area of high winter precipitation may be indicative of the insulative quality of snow. More snow accumulation would keep hibernacula warmer during cold winter temperatures and would not require the animals to dig as deep as those species found in areas of less winter precipitation. This is consistent with the higher percentage of mineral rock fragments, presumably requiring a higher digging efficiency, found in *S. columbianus'* range. The correlation of *S. columbianus'* range with less seasonal temperature extremes may be explained by their short active season as compared to low elevation species (i.e. *S. richardsonii*). While high snow accumulation may enable *S. columbianus* to endure cold winter temperatures, it is possible that extreme summer temperatures are more limiting. By having a shorter active season, *S. columbianus* may be less able to compensate for extreme warm temperatures because they have less time for reproduction and prehibernatory fattening. Physiological studies that determine how mortality relates to hibernacula and other pertinent temperatures are necessary to confirm any of these possible causative mechanisms.

S. richardsonii is restricted to an area of higher summer precipitation (and less winter precipitation), more seasonal extremes in temperature, and a low degree of mineral rock fragments. It is possible that by inhabiting an area with a lower degree of mineral rock fragments, *S. richardsonii* deals with extreme winter temperatures and less snow cover by digging deeper burrows allowed by the finer textured soil. The average burrow depth of *S. richardsonii* ranges from one to three times as deep as *S. columbianus* burrows. This variation in depth could probably be explained by microclimatic conditions, with shallower burrows placed under sites with more snow cover and deeper burrows under sites with less snow cover. The correlation with higher summer precipitation can be linked to the longer active season experienced by *S. richardsonii* which coincides with the longer growing season found at lower elevations. *S. richardsonii*'s adaptation of an early maturation process as compared to *S. columbianus*, along with the longer growing season, allows this species to reproduce at one year as opposed to two years.

Still, more research is necessary to determine or confirm if these suggestions are causative mechanisms for the correlations seen here. The use of FAUNMAP and models of climatic conditions of the past can be used to test whether these relationships hold at different evolutionary times. At a smaller scale, ecological and physiological experiments are necessary to determine if the parameters at the broad-scale still correlate on the smaller-scale.

Assuming that the climatic parameters correlating with the geographic distributions do, in fact, limit the ranges, here are some possible mechanisms by which *S. columbianus* and *S. richardsonii* may adjust to a global warming event. If winter temperature and/or snow cover decreases significantly in the Rockies, a decrease in S. columbianus would be expected. This scenario may have little to do with *S. richardsonii* expanding its range to the west since it may be limited more by soil rockiness. If winter temperature and/or snow cover increased in the Great Plains, an increased overlap between the two ranges would be expected with *S. columbianus* expanding to the east. Perhaps the most interesting thing to note is that different parameters limit each species, denoting an individualistic response of species within similar communities to the same environmental influence.

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APPENDICES

APPENDIX A

GENERAL CIRCULATION MODELS
The most widely used models
developed over the last thirty years*

Goddard Institute for Space Studies (GISS) (Hansen and others 1983, 1984)

National Center of Atmospheric Research (NCAR) (Washington and Meehl 1983, 1984)

United Kingdom Meteorological Office (UKMO) (Mitchell 1983)

Oregon State University (OSU) (Schlesinger and Zhao 1989)

Geophysical Fluid Dynamics Laboratory (GFDL) (Manabe and Wetherald 1980)

Canadian Climate Centre (CCC) (Boer and others 1992)

Colorado State University (CSU) (Randall and others 1991)

Max Planck Institute (MPI) (Cubasch and others 1990)

* from Sulzman et al. 1995

APPENDIX B

STEPS FOR PREPARING THE DATA FOR ANALYSIS

1. Search the Internet for pertinent data in ARC/INFO format. Follow standard file transfer protocol (ftp).

   eg., For VEMAP: ftp.ucar.edu

   ```
   Name: anonymous
   Password: <your_login>
   ftp> cd cgd/vemap
   ftp> get <filename>
   ```

2. Download files to personal account.
3. Create a header specifying the spatial extent for each file (Figure B.1)
4. Convert files from ascii format to grid or polygon format. (In ARC, use *asciigrid* command).
5. Change the projection of the polygon coverages to be compatible with the grids. In this case, lambert to geographic. (In ARC, use *project* command).
6. Overlay grids with polygons. (In ARC, use *mapcomposition*, *mapextent*, *polys*, and *grids* commands).

APPENDIX C

THE VEMAP DATABASE

(Adapted from the Vemap database user's guide
by N. Rosenbloom and T. Kittel, 1996)

Digital climate, vegetation, and soil data were obtained through the Vegetation/Ecosystem Modeling and Analysis Project (VEMAP). VEMAP is an ongoing multi-institutional, international effort whose goal is to evaluate the sensitivity of terrestrial ecosystems and vegetation processes to altered climate forcing and elevated atmospheric CO_2. VEMAP data are in the form of grid coverages of the conterminous U.S. with each cell size equaling 0.5 degree latitude by 0.5 degree longitude. Grid edges are aligned with 1.0 degree and 0.5 degree lat/lon lines with centers at 0.25 and .075 degrees.

The grid's minimum bounding rectangle (MBR) is defined by the following corners: Lower Left Corner => -124.5 degrees longitude, 25.0 degrees latitude; and Upper Right Corner => -67.0 degrees longitude, 49.0 degrees latitude, where negative longitudes are degrees west. The 0.5 degree VEMAP grid contains 5,520 cells, 3,261 of which are within the boundaries of the conterminous U.S. and predominantly covered by land. The other roughly 2,200 cells are either out of the U.S.' physical or political boundaries or are ocean or inland water cells.

Climate Data

The VEMAP dataset includes monthly and annual climate data for the conterminous U.S. including minimum, maximum and mean temperature, precipitation, and solar radiation. Long term monthly mean, minimum, and maximum temperature were interpolated to the VEMAP grid from 4,613 station 1961-1980 normals (NCDC dataset TD-9641). The station values were adiabatically lowered to sea level (Marks and Dozier 1992), interpolated to the 0.5 degree VEMAP grid, and then re-adjusted to the new grid elevation. Daily minimum and maximum temperatures were generated using a daily weather generator (WGEN) for each grid point. Daily temperatures were constrained in the generation process so that monthly means matched the interpolated long-term monthly normals.

Long-term mean monthly precipitation was spatially aggregated from a 10-km gridded U.S. dataset developed using PRISM (Daly et al. 1994). PRISM models precipitation distribution by 1) dividing the terrain into topographic facets of similar aspect, 2) developing precipitation-elevation regressions for each facet type for a given region based on station data, and 3) using these regressions to spatially extrapolate station precipitation to 10-km cells that are on similar facets. Daily precipitation values were generated for each grid point with WGEN. Daily values were constrained such that monthly rainfall accumulations for each grid point matched the long-term monthly means.

Daily mean irradiance for daylight hours was derived from CLIMSIM total incident solar radiation and day length. Monthly and annual values were then calculated.

Vegetation Data

The vegetation data set was compiled by defining the vegetation types physiognomically in terms of dominant lifeform and leaf characteristics and, in the case of grasslands, physiologically with respect to dominance of species with C3 versus C4 photosynthetic pathway. The U.S. distribution of these types is based on a 0.5 degree latitude/longitude gridded map of Kuchler's (1964, 1975) potential natural vegetation.

Soils Data

Soil properties were based on the 10-km gridded EPA Soil Database developed by Kern (1994, 1995) which uses both the USDA Soil Conservation Service (SCS), the National Soil Database (NATSGO) and the United Nations Food and Agriculture Organization soil database (FAO).

Physical consistency in soils data was incorporated by representing a grid cell's soil by a set of dominant (modal) soil properties. Because soil processes are non-linearly related to soil texture and other soil parameters, simulations based on dominant soil profiles and their frequency distribution can account for soil dynamics that would be lost if averaged soil properties were used.

Kern's data was spatially aggregated to the .5 degree grid by cluster analysis which grouped the subgrid 10-km elements into up to 4 modal soil types (Kittel et al. 1995). This way the soil properties are represented by the set of modal soil profiles rather than by an average soil.

APPENDIX D

VEMAP VEGETATION TYPES

TUNDRA
1. Tundra

FOREST
2. Boreal Coniferous Forest
   (Includes Boreal/Temperate Transition & Temperate Subalpine Forests)
3. Maritime Temperate Coniferous Forest
4. Continental Temperate Coniferous Forest
5. Cool Temperate Mixed Forest
6. Warm Temperate/Subtropical Mixed Forest
7. Temperate Deciduous Forest
8. Tropical Deciduous Forest**
9. Tropical Evergreen Forest**

XEROMORPHIC WOODLANDS and FORESTS
10. Temperate Mixed Xeromorphic Woodland
11. Temperate Conifer Xeromorphic Woodland
12. Tropical Thorn Woodland**

SAVANNAS
13. Temperate/Subtropical Deciduous Savanna/Temperate Deciduous Savanna
14. Warm Temperate/Subtropical Mixed Savanna
15. Temperate Conifer Savanna
16. Tropical Deciduous savanna

GRASSLANDS
17. C3 Grasslands (includes short through tall C3 grasslands)
18. C4 Grasslands (includes short through tall C4 grasslands)

SHRUBLANDS
19. Mediterranean Shrubland
20. Temperate Arid Shrubland
21. Subtropical Arid Shrubland

Excluded Surface Types
90 Ice**
91 Inland Water Bodies (includes ocean inlets)
92 Wetlands (includes floodplains and strands)
** means not present in the current distribution of types for the U.S. on the 0.5 degree grid.

APPENDIX E

RECLASSIFIED VEGETATION TYPES

1. Tundra
2. Conifer forest
3. Mixed forest
4. Deciduous forest
5. Woodland
6. Savannah
7. Grassland
8. Shrubland

Note: Vemap vegetation types had to be reclassified for use in CART.