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Sarah Elizabeth. James
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Patterns of Habitat, Microhabitat, and Body Size Distribution in a Lizard Assemblage

By Sarah E. James

A Thesis
Submitted to the Faculty of Graduate Studies and Research through the Department of Biological Sciences in Partial Fulfillment of the Requirements for the Degree of Master of Science at the University of Windsor

Windsor, Ontario, Canada
2002

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Abstract

I investigated habitat use within an assemblage of four phrynosomatine lizards (\textit{Sceloporus graciosus}, \textit{S. undulatus}, \textit{Urosaurus ornatus}, and \textit{Uta stansburiana}) that are commonly syntopic in the pinyon-juniper woodland habitat on the elevated mesas of western Colorado. Lizard populations were censused within Colorado National Monument, U.S.A., during the summer months of 1989, 1990, 1991, 1992, 2000 and 2001. Microhabitat characteristics surrounding capture points were recorded in 1990, 1992 and 2000, and captures were classified into one of two distinct habitats in 2001. All four species used dead trees more frequently than live trees, despite an opposite pattern of availability. Overall density of the lizard community in 2001 was much greater in rock habitats, which were associated with numerous deadfalls, than in surrounding flatland habitats containing more live than dead vegetation. Despite observed preferences and associations with dead vegetation and rock habitats, all four species coexist in both rock and flatland habitats. I examined microhabitat use as a possible explanation for their broad syntopy and found two microhabitat niche differences apparent over time: the microhabitat niche of \textit{S. graciosus} was distinguished from those of other species by the use of more open flat sandy areas with less rock, and the microhabitat niche of \textit{U. ornatus} was distinguished by higher perch height and more vertical substrate. Although these differences may influence the coexistence of these ecologically similar species, significant changes in relative abundance of the species over time suggest non-equilibrium coexistence. While the species coexist across habitats and partition microhabitat within each, I found lizards within each species to separate between flatland and rock habitats by age and size. The majority of small, hatchling lizards were observed in the flatland and the majority of adult lizards were observed in the rock
habitat. Ontogenetic habitat shifts may explain the observed distributions of all species between habitats, with hatchlings dispersing into flatland to avoid aggression and predation from adult lizards in the rock habitat, and returning when they have attained adult body size, have reduced predation risk, and are presumably more able to compete within social hierarchies.
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Chapter I

General Introduction
Patterns of habitat use in animal species are a consequence of regional, historical and local processes. At the regional scale, geographical pools and dispersal abilities of species determine the availability of colonists that supply local habitats (Ricklefs 1987; Ricklefs and Schluter 1993). At a finer scale, the presence of necessary resources in the form of food, shelter, reproductive opportunities, and thermal microenvironments will also determine where an animal may reside (Morin 1999).

Although a habitat may provide all of these resources, the presence of other species must also be considered, because competition and predation may inhibit the establishment of potential residents. Priority effects and assembly rules may also be important in determining whether a species resides in a given habitat (Gilpin et al. 1986; Drake 1991). During the 1970s and 1980s, a prominent theory of species coexistence dominated ecological research. Known as the theory of limiting similarity (MacArthur and Levins 1967; May and MacArthur 1972), it proposed that species must either possess or evolve niche differences in order to coexist. By this theory, establishment of a species in a habitat already occupied by an ecologically similar species requires either pre-existing niche differences, or the evolution of niche differences, in the form of food, habitat or temporal specializations, resulting from competition for limiting resources.

This classical theory of community organization invokes the principle of equilibrium dynamics, where species' relative abundance and niche relationships are approximately constant through time. However, there are alternate mechanisms of coexistence for non-equilibrium communities, in which species' relative abundances are changing, and this permits the coexistence of ecologically similar species. First, temporally variable relative abundances may lead to the coexistence of similar species rather than competitive niche differentiation because pressures from neighbouring species
would be unpredictable (Hubbell and Foster 1986). Second, coexistence of similar species may occur in an assemblage where living space is a highly variable resource. Once space is available, it is allocated randomly, as a lottery, which no species can consistently win (Sale 1977). Third, density-independent mortality resulting from storms, fires, droughts or other large events that reduce the numbers of a wide variety of similar organisms without regard to size, species identity, or density, can prevent competitive exclusion by reducing population sizes (Huston 1994). Finally, similar species may also co-occur without niche differentiation as a result of intraspecific aggregations, because aggregation would intensify intraspecific competition more than interspecific competition, thereby facilitating coexistence (Atkinson and Shorrock 1981; Hanski 1981). In each case, non-equilibrium dynamics predict changes in relative abundance and species composition within assemblages of species.

The presence of conspecifics may also influence habitat selection, by facilitating or inhibiting establishment. Dispersing individuals may prefer to settle next to established conspecifics rather than in isolated habitat of equal quality, using the presence of conspecifics as a cue to both habitat and territory quality (Stamps 1988; Ray et al. 1991). Facilitation or conspecific cuing may then result in higher densities than expected based on environmental suitability alone. Alternatively, intraspecific competition (Klemetsen and Dahl-Hansen 1995), aggressive interactions resulting from social hierarchies (Law 1991; Rayor and Uetz 1993), and intraspecific predation risks (Stamps 1983) may discourage establishment in habitats already occupied and result in occupation of vacant sites of equal or lesser quality.

When selecting a habitat, animals must weigh the costs of competition and predation with the benefits of high resource quality or availability and reproductive
opportunities. Optimality theory predicts that the selected habitat will maximize the ratio of benefits to costs, thereby maximizing an individual’s fitness. In some cases, maximizing growth rates may maximize fitness (Werner et al. 1983b), while in others fitness may be maximized by minimizing predation or mortality risks (Kotler et al. 1991). However, animals are often forced to make trade-offs between maximizing growth rates and minimizing mortality risk, because higher quality foraging habitats may have greater mortality risks (Werner et al. 1983a; Nonacs and Dill 1990). Because the benefits and costs associated with habitat use often change with size as individuals become less susceptible to predation, or better able to compete or exploit resources, habitat use may change during ontogeny in order to continue to maximize net benefits (Werner and Gilliam 1984). These ontogenetic habitat shifts typically appear with juveniles using lower risk habitats, although sacrificing energy gain in doing so (Sih 1982). As they age, and increase in body size, the maturing individuals shift into habitats where growth rates are higher and mortality rates are lower. The net appearance of species showing ontogenetic habitat shifts is the age/size-segregation of individuals between habitat types.

Other models of optimal habitat choice predict differences in the distribution of numbers of individuals among habitat types. Individuals may balance the costs and benefits of available habitats and distribute themselves among habitats such that more individuals occur in higher quality habitats, and fewer individuals occur in habitat of lower quality. However, there are no expected differences in the fitness of individuals among habitats. This is the premise of the Ideal Free Distribution (Fretwell and Lucas 1970). However, territoriality or social hierarchies within species may lead to the pre-emption of better quality habitats by more dominant individuals (Pulliam and Danielson 1991), resulting in unequal fitness among individuals as some are forced into suboptimal
habitats because higher quality habitats become saturated. Such source-sink dynamics (Pulliam 1988) may lead to greater densities in suboptimal habitats (sinks), and lower population densities in the habitats which are the source of the dispersers.

This thesis presents the results of a 2-year investigation into the responses of four species of phrynosomatine lizard to their habitat in western Colorado. I carried out field studies of lizard habitat use and coexistence within the pinyon-juniper woodland on the elevated mesas of western Colorado, U.S.A., during the summer months of 2000 and 2001. Four phrynosomatine (family Iguanidae, subfamily Phrynosomatinae) lizard species are commonly syntopic in this area. Tree lizards, *Urosaurus ornatus* (Baird and Girard 1852), are one of the most widespread and abundant North American lizards, found throughout the western United States and northwestern Mexico in a variety of habitats ranging from desert riparian to pinyon-juniper woodlands (Stebbins 1966). The eastern fence lizard, *Sceloporus undulatus* (Bosc and Daudin 1801), is also widespread across North America, and is found throughout the eastern and central United States, west to Utah, and south to northern Mexico (Stebbins 1966). This species occupies a wide-variety of habitats, from forests and woodlands to open flatlands and rocky areas. The side-blotched lizard, *Uta stansburiana* (Baird and Girard 1852), is one of the most abundant lizards in the arid and semi-arid regions of the southwestern United States, inhabiting desert areas with sand or rock substrate, as well as flatland and sandy washes with rock and scattered trees and bushes (Stebbins 1966; Tinkle 1967). The sagebrush lizard, *Sceloporus graciosus* (Baird and Girard 1852), is found throughout the western United States in sagebrush, pinyon-juniper woodlands, forests and open flatlands (Tinkle 1973, and Marcellini and Mackey 1970) and is most abundant at elevations above 1500 m. Earlier studies of these lizards have focused primarily on the ecology (Tinkle 1967;
Tinkle 1973; Rose 1976; Tinkle and Dunham 1983; M'Closkey et al. 1990) and
behaviour of individual species (Deslippe et al. 1990; Deslippe and M'Closkey 1991;
Martins 1993; Carpenter 1995; Smith and John-Alder 1999), or on the similarities or
interactions of one species with others outside this assemblage (Milstead 1970; Dunham
1980; Vitt et al. 1981; Grover 1996). Few studies have examined interactions among
any of these species (Ferguson 1971; Tinkle 1982). Previous work within this
assemblage has examined spatial overlap among species (M'Closkey and Hecnar 1994)
and colonization of density sinks (M'Closkey et al. 1997, 1998), but knowledge of niche
patterns among the species is lacking. As members of the same sub-family, these species
have similar life histories, activity times, foraging strategies and prey use (Hammerson
1999). The coexistence and broad syntopy of these species despite their many similarities
led to my investigations into their distributions, microhabitat use and behaviour.

In Chapter II of this thesis, I examine the patterns of microhabitat use of each
species in the assemblage and include data from previous studies in this area to identify
microhabitat niche differences through time. Many studies have used niche partitioning
and complementarity to explain the coexistence of similar species. Here I comment on
differences among species in other dimensions of the fundamental niche, in light of the
microhabitat use patterns observed, but I also discuss how temporal changes in relative
abundance may allow coexistence.

In Chapter III, I describe age- and size-related habitat use for all species and
examine behavioural differences in S. undulatus between habitats in attempts to explain
size distributions. Dominance hierarchies, conspecific aggression and size-related
predation risks are identified as potential factors leading to the habitat segregation of
hatchling and adult lizards.
In Chapter IV, I examine the relationship between lizard distribution and ecological succession within local habitats, and I discuss the conservation implications of the observed associations with respect to the United States National Fire Plan and Federal land maintenance policies.

In Chapter V, I summarize the results of my investigations.
Chapter II

Patterns of microhabitat use in a sympatric lizard assemblage
Abstract

The distribution of animals among habitats and microhabitats has frequently been used to examine patterns of niche overlap. I characterized microhabitat differences within an assemblage of four phrynosomatine lizards (*Sceloporus graciosus*, *S. undulatus*, *Urosaurus ornatus*, and *Uta stansburiana*) that are commonly syntopic in the pinyon-juniper woodland habitat on the elevated mesas of western Colorado. Lizard populations were censused during the summer months of 1989, 1990, 1991, 1992, 2000 and 2001, and microhabitat characteristics of areas surrounding capture sites were recorded in 1990, 1992 and 2000, within Colorado National Monument, U.S.A. Discriminant function analysis (DFA) of microhabitat features extracted one or two significant roots each year, explaining between 55 and 89% of the microhabitat variation observed among species. Planned comparisons of canonical scores revealed two significant microhabitat niche differences apparent in all years. First, the microhabitat niche of *S. graciosus* was distinguished from other species by having more flatland and less rock, indicating the use of more open flat sandy areas within the pinyon-juniper woodland by this terrestrial species. Second, the microhabitat niche of *U. ornatus* was distinguished from those of all other species by higher perch height and more vertical substrate, indicating this species’ arboreality. Although the observed differences in microhabitat may influence the coexistence of these ecologically similar species, changes in relative abundance of the species over time suggest alternative mechanisms of coexistence.

Introduction

Ecologists have investigated patterns of species diversity and the mechanisms of community assembly for many years (Cody 1968; Pianka 1973; Schoener 1974;

Many studies have focused on the method of resource partitioning among sympatric species (Schoener 1974; Meffe and Sheldon 1988; Ortega-Rubio 1991; Bergallo and Rocha 1994; Howard and Hailey 1999; Faria and Almada 2001) in an effort to understand community structure. Studies of niche patterns emphasize the importance of spatial, trophic, and temporal dimensions in distinguishing niches of many taxa, including ants (Albrecht and Gotelli 2001), crustaceans (Croker 1967), fish (Genner et al. 1999), lizards (Pianka et al. 1979; Patterson 1992; Vitt and de Carvalho 1995; Vitt et al. 1999; Vitt et al. 2000), birds (Cody 1968, 1973; Edington and Edington 1972), and marsupial (Jones and Barmuta 2000) and placental mammals (Fedriani et al. 1999; Brannon 2000).

In spite of the criticisms of the interpretation of classical theories of competition and community structure (Strong et al. 1984), there is renewed interest in more comprehensive investigations of niche partitioning and coexistence (Ben-David et al. 1995; Vitt and de Carvalho 1995; Genner et al. 1999; Albrecht and Gotelli 2001). Specifically, recent studies have examined the complementary roles of morphology, phylogeny, habitat and microhabitat use, and temporal activity in patterns of community structure and niche partitioning (Ricklefs and Schluter 1993; Brown 1995; Brannon 2000; Jones and Barmuta 2000; Vitt et al. 2000). In addition, there is increased
recognition of mechanisms of coexistence that are alternatives to resource partitioning (Sale 1977; Atkinson and Shorrocks 1981; Hanski 1981; Hubbell and Foster 1986; Huston 1994; James and Shine 2000). These non-equilibrium explanations of community dynamics predict changes in relative abundance and species composition within communities.

In previous studies of lizard populations on the Colorado plateau (M'Closkey et al. 1997, 1998), an assemblage of four species of phrynosomatine lizard was repeatedly observed in pinyon pine and juniper habitat in the Colorado National Monument. However, there is no information on the patterns of microhabitat use within this assemblage. Experimental reduction of lizard numbers in this fauna revealed no differences among species in the rates of recolonization and establishment (M'Closkey et al. 1997). In this chapter, I present a more comprehensive analysis of ecological relationships among these syntopic lizard species. I provide information on differences in body size patterns and the associated differences in microhabitat partitioning, and the consistency of relative abundance of the species across temporal and spatial scales.

Methods

Study Area

I worked at The Colorado National Monument (39°6'15" N, 108°43'45" W, elevation 1750m), Colorado, U.S.A., during the morning hours (0830 – 1300h) of August 2000 and had access to data collected in the same area, by the same methods, during late May, 1990, and late May and early June, 1992. The predominant habitat is pinyon pine (Pinus edulis) and juniper (Juniperus utahensis) woodland, with a sandy substrate interspersed with exposed flat rock, numerous tree falls, and Entrada sandstone ledges
reaching up to 2 m in height. Field work was carried out at 2 replicate study areas each year, in the same area and pinyon-juniper woodland habitat as the density manipulations (M’Closkey et al. 1997, 1998), but isolated from them so as not to confound the interpretation of microhabitat patterns with the experimental work. Within each study area, 2-3 study plots were established. Due to the nature of the terrain, plot area could not be standardized, so wandering belt transects containing structural features likely to be included in lizard territories and home ranges, such as tree falls and rock ledges, were used in order to maximize potential contact with lizards (M’Closkey and Heenar 1994). Each transect varied from 250-900 m in total length and spanned approximately 15 m in width.

Lizards and Data Collection

Four species of diurnal phrynosomatine lizard are commonly syntopic in the pinyon-juniper woodland habitat on the elevated mesas of western Colorado. The fence lizard, *Sceloporus undulatus* (Bosc and Daudin 1801) is both saxicolous (rock-dwelling) and arboreal (M’Closkey et al. 1998) and is the largest of the lizards, with a mean snout-vent length (SVL) of 63 mm. The sagebrush lizard, *Sceloporus graciosus* (Baird and Girard 1852) is the next largest with a mean SVL of 56 mm, and is terrestrial (Marcellini and Mackey 1970). The side-blotched lizard, *Uta stansburiana* (Baird and Girard 1852) and the tree lizard, *Urosaurus ornatus* (Baird and Girard 1852), are similar in SVL (44 mm and 46 mm, respectively), but differ in that the former is terrestrial and the latter is saxicolous and arboreal (Hammerson 1999). All four species are sit-and-wait, opportunistic insectivores (Hammerson 1999). Male *U. ornatus*, *S. undulatus* and *S. graciosus* are territorial and actively defend their home areas against other males, while
male *U. stansburiana* are only weakly territorial and may overlap home ranges (Hammerson 1999). Two species of teiid lizard (*Cnemidophorus tigris* (western whiptail; Baird and Girard 1852) and *Cnemidophorus velox* (plateau striped whiptail; Springer 1928)) are also commonly syntopic with this assemblage; however, whiptails are very different from phrynosomatine lizards in both their foraging mode and territory defence (see Hammerson 1999; Pianka 1973) and were not included in this study.

Each year, the lizard fauna at each study area was censused using mark-recapture. Upon capture of each lizard, sex was determined by examination of postanal scales, and a distinct temporary paint mark was provided. Lizards were then released at the point of initial observation. In 2000, snout-vent length (SVL) to the nearest 1 mm and mass to the nearest 0.1 g were also recorded for all captures. My research protocol in handling the lizards was approved by the University of Windsor Animal Care Committee under the mandate of the Canadian Council on Animal Care. Each time a lizard was seen or captured, a description of the microhabitat was noted within a 5-m radius of the initial point of observation. Capture point substrate type and perch height of the focal lizard were recorded. The number of each tree species, as well as tree condition, was recorded each year, and tree volume was visually estimated in 1992 and 2000. Tree condition was recorded as live or dead, and if dead, standing or prone. I assessed rock structure (ranging from flat rock to rock walls) in 1990 and 2000, and estimated % rock cover in 1992 and 2000.

A single census consisted of 3 researchers conducting a thorough search of all plots in an area 1-2 times within the same day, each census requiring approximately 9 person hours. The number of censuses each year varied from 5-6 per study area. Although the number of censuses varied among years, relative abundances observed each
year are believed to be representative of relative population sizes due to the thorough
nature of the censuses, and relatively high recapture rates (> 64%) by the end of each
yearly study period.

During the spring and summer months from 1989 to 1992, as well as in 2000 and
2001, lizard populations were censused at a total of 5 replicate study areas. The census
periods spanned 45 days in 1989, 18 days in 1990, 59 days in 1991, 25 days in 1992, 17
days in 2000, and 39 days in 2001. The census data formed the basis of comparison of
lizard relative abundance.

**Statistical analyses**

For each year of the study, all microhabitat characteristics were initially
transformed (ln for continuous, square root for discrete). Because of the large number of
“0” observations for many of the variables, transformed data were not normally
distributed, but otherwise met the assumptions of a principal component analysis (PCA).
Deviations from normality do not necessarily bias the analysis, as long as the distributions
are reasonably unskewed (Legendre and Legendre 1998). My transformations
sufficiently reduced the skew to minimize the risk of bias in the analysis.

For each year, transformed microhabitat characteristics were entered into a PCA
to reduce the number of microhabitat variables. Principal components (PCs) were then
varimax raw rotated to obtain a clear pattern of factor loadings. Next, rotated principal
component scores were entered into a discriminant function analysis (DFA). DFA
extracts roots or axes (linear combinations of the original variables) that maximize the
differences among groups relative to the variation within groups. The canonical scores
along extracted roots were then used to characterize the microhabitat niche of each
species. Finally, planned comparisons in a MANOVA of canonical scores examined differences between species and univariate ANOVAs determined which root(s) contributed to contrasts.

Body mass and SVL measurements were ln-transformed to reduce deviations from normality. Planned comparisons in a MANOVA of transformed SVL and body mass measurements (excluding those of hatchling lizards) from 2000 were then used to examine differences in body size among the four lizard species, as indicators of possible prey size differences. Regression analysis of ln SVL and ln mass, and comparison of the resulting regression coefficients, were used to identify differences in body plan (e.g. long and slim vs. long and heavy) among species. I used Kruskal-Wallis ANOVA of ranks to compare the relative abundance of each species over all study areas, and for one study area that was censused each year (Window Rock), among years using data from censuses in 1989, 1990, 1991, 1992, 2000, and 2001. All analyses were performed using STATISTICA (StatSoft Inc. 1998).

Results

Lizard Relative Abundance

During 6 years, from 1989 through 2001, lizard populations were censused at 5 replicate study areas, resulting in 13 complete censuses. In only one census was a species (U. stansburiana) missing. The constancy of species composition in this assemblage across study areas indicates the broad syntopy of these species, with virtually no species turnover among study areas.

The relative abundance of the species over time varied greatly for all study areas, and for Window Rock alone (Fig. 2.1). A Kruskal-Wallis ANOVA revealed no
significant difference in abundance rank among species for either case (p = 0.496 and p =
0.187, respectively), indicating the high variability in relative abundance among years and
the lack of numerical dominance by any species over time (Fig. 2.2). Over the study
period, the relative abundance of U. ornatus varied from 11 to 59%, that of S. graciosus
and S. undulatus ranged from 8 to 56% and 21 to 45%, respectively, and that of U.
stansburiana ranged from 8 to 38%.

**Body Size Differences**

Planned comparisons within a MANOVA on SVL and body mass measurements
of adult and sub-adult lizards (Table 2.1), indicated that S. undulatus was larger than all
other species (p < 0.000001 in all cases, Table 2.2). S. graciosus was in turn was larger
than U. stansburiana (p < 0.01, Table 2.2), and had greater mass than U. ornatus (p_{mass} <
0.01, Table 2.2). U. stansburiana differed from U. ornatus based on SVL alone (p_{SVL} <
0.01, Table 2.2). There were significant correlations between mass and SVL for all
species (Table 2.1, Fig. 2.3). Regression coefficients (Table 2.1) were significantly
different for all species (p < 0.000001), with those of U. ornatus and U. stansburiana
being significantly less than S. undulatus (p < 0.00001 and p < 0.00001, respectively) and
S. graciosus (p < 0.01 and p < 0.05, respectively). Neither U. ornatus and U.
stansburiana nor S. undulatus and S. graciosus differed in regression coefficients. These
findings suggest a difference in body plan among species, such that U. ornatus and U.
stansburiana have a relatively lower body mass for a given SVL than S. undulatus and S.
graciosus, and are thus longer and more slender in body shape.
**Lizard Microhabitat**

In 1990, microhabitat characteristics were recorded for 188 lizards. The relative abundance of lizards was 78 *S. graciosus*, 46 *S. undulatus*, 36 *U. stansburiana*, and 28 *U. ornatus*. In 1992, 115 lizards were observed, including 41 *U. ornatus*, 33 *S. undulatus*, 30 *S. graciosus*, and 11 *U. stansburiana*. During 2000, I recorded microhabitat characteristics for 155 lizards, consisting of 68 *U. stansburiana*, 58 *S. undulatus*, 20 *U. ornatus*, and 9 *S. graciosus*. A summary of the microhabitat characteristics recorded each year, with descriptive statistics for each is presented in Appendix 1. All species were observed to emerge early in the morning and retreat around mid-day when temperatures exceeded 30 °C. There appears to be little opportunity for significant differences in times of activity.

For 1990, DFA of rotated principle component scores extracted two significant roots that explained 95.3% of the variation in PC scores among species (Fig. 2.4), which in turn explained 75.0% of the variation in microhabitat among species. Thus, overall, DFA explained 71.5% of the variation in microhabitat among species. Root 1 was positively correlated with PC1 (standardized coefficient = 0.954), which represented perch height and capture point substrate type (PC1 loadings = 0.925 and 0.892, respectively), and explained 71.1% of the variation in PC scores, and 53.3% of the variation in microhabitat features, among species. Root 2 was negatively correlated with PC2 (standardized coefficient = -0.997), which was positively correlated with the number of live pine (PC2 loading = 0.728) and negatively correlated with the degree of rock development (PC2 loading = -0.615), and explained 24.2% of the observed variation in PC scores, and 18.2% of the variation in microhabitat features, among species. The mean canonical scores for each species with respect to these roots are given in Table 2.3.
In 1990, the microhabitat of *U. ornatus* was characterized by higher perch height and more vertical substrate (more live or dead trees) compared to the microhabitats of all other species (*p* < 0.000001 in all cases, Table 2.4). The microhabitat of *S. graciosus* was characterized by less live pine and more flatland compared to other species' microhabitats (*p* < 0.05 in all cases, Table 2.4), and distinguished further from the microhabitat of *U. stansburiana* by having higher perch height and more vertical substrate (*p* < 0.05, Table 2.4). *S. undulatus* and *U. stansburiana* did not differ significantly in microhabitat use.

For 1992, DFA of rotated principle component scores extracted one significant root, which explained 65.0% of the variation in PC scores among species (Fig. 2.5), which in turn explained 85.0% of the variation in microhabitat among species. Overall, DFA explained 55.3% of the variation in microhabitat among species. The one root was negatively correlated with PC2 (standardized coefficient = -0.754), which was positively correlated with the amount of sandy substrate (PC2 loading = 0.860) and negatively correlated with the amount of rock (ledge rock, PC2 loading = -0.810; and flat rock, PC2 loading = -0.768). Table 2.3 contains mean canonical scores for each species with respect to this root. The microhabitat of *S. graciosus* was characterized by more sandy substrate and less rock than all other species (*p* < 0.05 for all cases, Table 2.4). No other microhabitat differences were significant.

Results from the 2000 analyses are quite similar to those of 1990 but are presented separately because of small variations in the microhabitat features recorded. DFA of rotated principal component scores from data collected in 2000 extracted two significant roots, which explained 98.0% of the variation in PC scores among species (Fig. 2.6), which in turn explained 90.8% of the variation in microhabitat among species. Overall, DFA explained 89.0% of the variation in microhabitat among species. Root 1 was
negatively correlated with PC8 (standardized coefficient = -0.849), which represented perch height and capture point substrate type (PC8 loadings = 0.875 and 0.896, respectively), and accounted for 72.9% of the variation in PC scores, and 66.2% of the variation in microhabitat features, among species. Root 2 was positively correlated with PC5 (standardized coefficient = 0.592) which represented the amount of rock cover and rock structure (PC5 loadings = 0.907 and 0.947, respectively), negatively correlated with PC4 (standardized coefficient = -0.521) which represented the number and mean volume of dead prone pine (PC4 loadings = 0.947 and 0.933, respectively), and negatively correlated with PC6 (standardized coefficient = -0.507) which was in turn negatively correlated with the number and mean volume of live juniper (PC6 loadings = -0.916 and -0.920, respectively). Root 2 accounted for 25.1% of the variation in PC scores, and 22.8% of the variation in microhabitat features, among species. Mean canonical scores are shown in Table 2.3.

The microhabitat of *U. ornatus* was characterized by higher perch height and more vertical substrate (more prone and dead standing trees) compared to microhabitats of all other species (p < 0.000001 in all cases, Table 2.4). The microhabitat of *S. graciosus* was characterized by less rock cover and structure (mostly flatrock, if any), more dead prone pinyon, and less live juniper compared to all other species' microhabitats (p < 0.01 in all cases, Table 2.4). The microhabitat of *S. graciosus* was further distinguished from that of *S. undulatus* by having lower perch height and more horizontal substrate than that of the latter species (p < 0.05, Table 2.4). *S. undulatus* and *U. stansburiana* did not differ significantly in microhabitat.

Roots extracted from DFA gave significant separation among species; however, owing to the covariate structure of the original microhabitat characteristics, comparisons
of single field variables provide poor interspecific separation in some cases (Appendix 1).
In all years, microhabitats did not differ significantly between sexes within a species; thus
the results are for both male and female lizards.

In summary, highly significant differences in microhabitat were apparent among
most species pairs each year, although no significant differences in microhabitat occurred
between S. undulatus and U. stansburiana.

Discussion

Habitat-level and regional differences in species’ distributions often reflect
differences in their phylogenetic relationships (Vitt and Zani 1996). Vitt et al. (2000),
have reported high niche overlap in closely related lizard species. The phrynosomatine
lizards I investigated are syntopic on virtually all of R.T. M’Closkey’s long-term study
plots. Therefore, the emphasis of my investigations was at the microhabitat level. Two
major microhabitat differences were observed during the study period. First, the
microhabitat of S. graciosus was distinguished from those of other species by having
more flatland (less rock structure) and less rock (Fig. 2.4, 2.5, 2.6). My results indicate
that S. graciosus occupied the more open (less pine in 1990, less juniper in 2000), flat
sandy areas within the pinyon-juniper woodland. More dead prone pinyon pine in this
species’ microhabitat compared to others in 2000, would provide cover and perch sites
for this ground dwelling lizard, further distinguishing this species from more saxicolous
and arboreal species. Indeed, the terrestrial S. graciosus had lower perch heights and
more horizontal substrate than the saxicolous and arboreal S. undulatus in 2000 (Table
2.4). The microhabitat niche of S. graciosus was also distinguished from U.
stansburiana (1990, Table 2.4), on the basis that S. graciosus occupied higher perches
and more vertical substrate. This was due to *U. stansburiana* perching almost entirely on rock or bare ground and *S. graciosus* perching relatively more often on dead prone trees. In this sense, *S. graciosus* is the more "arboreal" of the terrestrial species.

Second, in 1990 and 2000, the microhabitat niche of *U. ornatus* was distinguished from all other species by higher perches and more vertical substrate (Figs. 2.4, 2.6), both of which are indications of the arboreality of this species. Correlations between habitat use and body shape have been observed among populations of this species in structurally distinct habitats (Herrel *et al.* 2001), and the long slender body plan of *U. ornatus* is well-adapted to tree-dwelling. Although this long and slim body plan distinguished *U. ornatus* from *S. undulatus* and *S. graciosus*, it was not significantly different from the body plan of the terrestrial *U. stansburiana* (Fig. 2.3, Table 2.1). Thus, the body plan differences observed in this study do not distinguish between species with respect to arboreal and terrestrial microhabitat use, but may reflect the ability of a species to exploit a given microhabitat at a finer scale. For instance, the long slender body plan of *U. ornatus* may allow its agile use of higher perches and more vertical substrates than the heavier arboreal *S. undulatus*, and the relatively slender body plan of *U. stansburiana* may permit the use of smaller crevices in rock or dead prone trees for shelter than can be used by the larger terrestrial *S. graciosus*. In both 1990 and 2000, *U. ornatus* was observed primarily on dead standing or prone trees, occasionally on rock, but never on bare ground. In 1992, *U. ornatus* was only observed in dead standing or dead prone trees, but microhabitat differences with other species were not significant. The arboreal microhabitat of *U. ornatus* distinguished it from other species in the pinyon-juniper woodland habitat.

Although statistically significant microhabitat niche differences occurred among all species pairs other than *S. undulatus* and *U. stansburiana*, substantial overlap in
microhabitat is apparent among species in Figures 2.4, 2.5 and 2.6. This similarity among species reflects the spatial design of this study. Field-assessed differences in microhabitat use were recorded for all species within the same habitat, and, therefore, the overall similarity among species (Figs. 2.4, 2.5, 2.6) is primarily due to their syntopy and the dominance of the landscape by relatively few prominent features (number of trees, rock cover, rock structure). The microhabitat differences observed suggest that combinations of microhabitat features that are likely important in foraging, basking, and territory exploration distinguish the microhabitat niche characteristics of these lizards.

My goal was to provide a comprehensive assessment of niche patterns in a closely related lizard assemblage. I did not explicitly search for niche complementarity, although recent investigations have done so (Patterson 1992; Jones and Barmuta 2000; Vitt et al. 2000). However, my results allow a commentary on the presence of species differences in other niche dimensions. A large volume of both comparative and experimental studies on a variety of vertebrates and invertebrates have found separation among sympatric species in the spatial, trophic and temporal dimensions (Pianka et al. 1979; Winemiller and Pianka 1990; Patterson 1992; Ben-David et al. 1995; Vitt and Zani 1996; Genner et al. 1999; Vitt et al. 1999; Jones and Barmuta 2000; Albrecht and Gotelli 2001). Niche complementarity within the spatial dimension may distinguish the niches of similarly-sized *U. ornatus* and *U. stansburiana*, which overlapped in microhabitat in 1992. These species are known to differ with respect to vertical microhabitat structure and results from 1990 and 2000 support this: *U. ornatus* is arboreal and *U. stansburiana* is terrestrial. Sea birds and woodland passerines also partition vertical microhabitat, partitioning depth under water (Cody 1973) and foraging height (Edington and Edington 1972), respectively. Similarities among lizards in this assemblage in the spatial dimension may
be complemented by ecological segregation in the temporal or trophic dimensions, reducing actual or potential competition between species.

However, my field studies revealed that all four species are active at the same time on a daily basis, most likely due to constraints imposed on ectothermic activity by the thermal environment of the region. Turner (1974) similarly found daily activity periods of *S. graciosus* and *S. undulatus* to be almost identical. In addition, seasonal activity times are also very similar (see Hammerson 1999), indicating that the temporal dimension is of relatively little importance in the niche separation of this assemblage. Many studies on lizards have provided similar results. Pianka *et al.* (1979), Patterson (1992), and Vitt *et al.* (2000) found no temporal niche separation for desert, grassland and tropical lizards, respectively.

The trophic dimension is another source of possible differentiation among species. Many studies have revealed that species that overlap in habitat often differ in the trophic dimension (Schoener 1974). This has been reported for birds (Cody 1968), fish (Zaret and Rand 1971; Genner *et al.* 1999), crustaceans (Croker 1967) and lizards (Schoener 1968; Pianka *et al.* 1979). However, the four lizard species in this assemblage have similar sit-and-wait, opportunistic foraging strategies, and they all eat insects. Although I did not have stomach content data to examine this pattern, lizard body size has been found to be correlated with size of prey eaten (Pianka 1969; Turner 1974; Pianka and Pianka 1976; Ortega-Rubio 1991; Vitt and Zani 1996). Therefore, I examined body size differences among the lizard species, as indicators of possible prey size differences. *S. undulatus* was larger than all other species (Table 2.2, Fig. 2.3), indicating that overlap in microhabitat niche between *S. undulatus* and *U. stansburiana* in all years, and between *S. undulatus* and *U. ornatus* in 1992, may be complemented by differences in trophic
niche. However, lizard body size-prey size correlations are not universal (Schoener 1968; Schoener and Gorman 1968; Rose 1976; Patterson 1992). In spite of the body size differences within this guild, the lizard species probably overlap substantially in prey use. The limited range of body sizes within the assembly may preclude opportunities for diet specialization.

The ultimate source of niche differences in coexisting species has often been attributed to competitive interactions through coevolution (MacArthur and Levins 1967) or by virtue of pre-existing niche differences. However, the differences I observed among species are not likely based on current interspecific competition, in spite of numerous studies demonstrating interspecific competition in lizards (Petren and Case 1996; Pacala and Roughgarden 1982). First, I rarely observe interspecific encounters among members of this guild. Second, observed competition in communities involving these species is either rare (Dunham 1980) or absent (Milstead 1970; Tinkle 1982; M'Closkey and Baia 1987). To my knowledge, there is only one published account of competitive interaction among any of the four species reported here. Ferguson (1971) observed one aggressive interaction out of five interspecific interactions between S. graciosus and S. undulatus. Third, M'Closkey et al. (1997)'s experimental reduction of lizard numbers revealed no significant difference among species in rates of recolonization, but differences in recolonization were detected at the intraspecific level (size structure within species; M'Closkey et al. 1998). These results suggest that interspecific interactions (priority effects and space pre-emption) are not important in the assembly process of this lizard guild. My findings of relative constancy of microhabitat niche differences and overlap, despite changes in relative abundance and total lizard numbers over time, adds support to this argument, and suggests that the microhabitat
differences observed are independent of density, at least for the population sizes observed in 1990, 1992 and 2000. Experimental studies on *U. ornatus* and *S. merriami* (Dunham 1980) however, suggest an important role of lizard density in competitive interactions.

The interpretation of classical niche theory has typically excluded other mechanisms of species coexistence, in particular the class of mechanisms referred to as non-equilibrium coexistence or dynamics. These model systems include competitive lotteries for space (Sale 1977; Chesson and Warner 1981), drift in species’ abundance without niche differentiation (Hubbell and Foster 1986), density-independent mortality in competition-based communities (Huston 1994), and coexistence on identical resources by intraspecific aggregation (Atkinson and Shorrocks 1981; Hanski 1981). Each mechanism predicts changes in relative abundance, and in some cases, changes in species composition within communities. In Huston’s simulation models, periodic density-independent mortality reduces dominance competition by causing non-synchronous population changes among species. In this lizard guild, the repetition of the four-species assembly, through time and across study areas, reveals very high constancy in species composition. However, the lack of significant difference among species in their abundance ranks (Fig. 2.2), supports the frequent shifts in relative numbers that characterize non-equilibrium systems (Chesson and Case 1986).

The patterns of microhabitat and body size differences shown here may be of less importance in coexistence than the shifts in relative abundance of the lizard species. Investigation of niche patterns must simultaneously evaluate theories of non-equilibrium dynamics. This research program requires detailed knowledge of species composition and relative abundance within communities.
Table 2.1. Body size measurements and regression results (hatchlings excluded). SVL is given in mm and mass in g. p-values, adjusted $r^2$ and regression coefficients (b) shown result from the regression of ln SVL and ln mass.

<table>
<thead>
<tr>
<th>Species</th>
<th>SVL Mean</th>
<th>Range</th>
<th>SD</th>
<th>Mass Mean</th>
<th>Range</th>
<th>SD</th>
<th>n</th>
<th>$r^2$</th>
<th>b</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>S. undulatus</td>
<td>62.5</td>
<td>50.0-78.0</td>
<td>1.1</td>
<td>9.3</td>
<td>5.2-17.0</td>
<td>1.4</td>
<td>31</td>
<td>0.953</td>
<td>2.48</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>S. graciosus</td>
<td>47.5</td>
<td>40.0-56.0</td>
<td>1.1</td>
<td>4.6</td>
<td>3.0-7.2</td>
<td>1.3</td>
<td>7</td>
<td>0.956</td>
<td>2.49</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>U. stansburiana</td>
<td>44.6</td>
<td>40.0-49.0</td>
<td>1.0</td>
<td>3.6</td>
<td>2.7-4.6</td>
<td>1.1</td>
<td>36</td>
<td>0.440</td>
<td>1.45</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>U. ornatus</td>
<td>46.2</td>
<td>42.0-52.0</td>
<td>1.1</td>
<td>3.6</td>
<td>2.9-4.3</td>
<td>1.1</td>
<td>12</td>
<td>0.304</td>
<td>1.08</td>
<td>&lt; 0.01</td>
</tr>
</tbody>
</table>
Table 2.2. Results of planned comparisons in MANOVA of body size measurements, with univariate ANOVA results illustrating which measurement(s) are responsible for contrasts. Contrasts are arranged to highlight differences of one species versus all others, with species arranged in order of decreasing body size. Significant univariate results are in bold type.

<table>
<thead>
<tr>
<th>MANOVA</th>
<th>ANOVA</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>SVL</td>
</tr>
<tr>
<td></td>
<td>Wilk's lambda</td>
</tr>
<tr>
<td>S. undulatus vs S. graciosus</td>
<td>0.709</td>
</tr>
<tr>
<td>U. ornatus</td>
<td>0.306</td>
</tr>
<tr>
<td>U. stansburiana</td>
<td>0.222</td>
</tr>
<tr>
<td>S. graciosus vs U. ornatus</td>
<td>0.850</td>
</tr>
<tr>
<td>U. stansburiana</td>
<td>0.936</td>
</tr>
<tr>
<td>U. ornatus vs U. stansburiana</td>
<td>0.794</td>
</tr>
</tbody>
</table>
Table 2.3. Mean canonical scores for significant roots \((p < 0.05)\) extracted by discriminant function analysis. Number of individuals observed each year is given in the last column.

<table>
<thead>
<tr>
<th>Year</th>
<th>Species</th>
<th>Root 1</th>
<th>Root 2</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>1990</td>
<td><em>U. ornatus</em></td>
<td>1.424</td>
<td>-0.145</td>
<td>28</td>
</tr>
<tr>
<td></td>
<td><em>S. undulatus</em></td>
<td>-0.267</td>
<td>-0.514</td>
<td>46</td>
</tr>
<tr>
<td></td>
<td><em>S. graciosus</em></td>
<td>-0.077</td>
<td>0.393</td>
<td>78</td>
</tr>
<tr>
<td></td>
<td><em>U. stansburiana</em></td>
<td>-0.597</td>
<td>-0.083</td>
<td>36</td>
</tr>
<tr>
<td></td>
<td><strong>Total</strong></td>
<td></td>
<td></td>
<td>188</td>
</tr>
<tr>
<td>1992</td>
<td><em>U. ornatus</em></td>
<td>-0.002</td>
<td></td>
<td>41</td>
</tr>
<tr>
<td></td>
<td><em>S. undulatus</em></td>
<td>0.373</td>
<td></td>
<td>33</td>
</tr>
<tr>
<td></td>
<td><em>S. graciosus</em></td>
<td>-0.626</td>
<td></td>
<td>30</td>
</tr>
<tr>
<td></td>
<td><em>U. stansburiana</em></td>
<td>0.598</td>
<td></td>
<td>11</td>
</tr>
<tr>
<td></td>
<td><strong>Total</strong></td>
<td></td>
<td></td>
<td>115</td>
</tr>
<tr>
<td>2000</td>
<td><em>U. ornatus</em></td>
<td>-1.563</td>
<td>-0.233</td>
<td>20</td>
</tr>
<tr>
<td></td>
<td><em>S. undulatus</em></td>
<td>-0.005</td>
<td>0.131</td>
<td>58</td>
</tr>
<tr>
<td></td>
<td><em>S. graciosus</em></td>
<td>0.837</td>
<td>-1.429</td>
<td>9</td>
</tr>
<tr>
<td></td>
<td><em>U. stansburiana</em></td>
<td>0.353</td>
<td>0.146</td>
<td>68</td>
</tr>
<tr>
<td></td>
<td><strong>Total</strong></td>
<td></td>
<td></td>
<td>155</td>
</tr>
</tbody>
</table>
**Table 2.4.** Significant results of planned comparisons in MANOVA of canonical scores, with univariate ANOVA results illustrating which roots are responsible for contrasts. Contrasts are arranged to highlight differences of one species versus all others. Significant univariate results are in bold type. Non-significant multivariate results are not shown.

<table>
<thead>
<tr>
<th>Year</th>
<th>Contrast</th>
<th>Wilk's lambda</th>
<th>p</th>
<th>F</th>
<th>p</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>MANOVA</td>
<td></td>
<td></td>
<td>ANOVA</td>
<td>Root 1</td>
<td>Root 2</td>
<td></td>
</tr>
<tr>
<td>1990</td>
<td><em>U. ornatus</em> vs <em>S. undulatus</em></td>
<td>0.779</td>
<td>0.000000</td>
<td>49.880</td>
<td>0.000000</td>
<td>2.369</td>
<td>0.125496</td>
</tr>
<tr>
<td></td>
<td><em>S. gracidosus</em></td>
<td>0.778</td>
<td>0.000000</td>
<td>46.437</td>
<td>0.000000</td>
<td>5.960</td>
<td>0.015578</td>
</tr>
<tr>
<td></td>
<td><em>U. stansburiana</em></td>
<td>0.741</td>
<td>0.000000</td>
<td>64.372</td>
<td>0.000000</td>
<td>0.060</td>
<td>0.807009</td>
</tr>
<tr>
<td></td>
<td><em>S. gracidosus</em> vs <em>U. ornatus</em></td>
<td>0.778</td>
<td>0.000000</td>
<td>46.437</td>
<td>0.000000</td>
<td>5.960</td>
<td>0.015578</td>
</tr>
<tr>
<td></td>
<td><em>S. undulatus</em></td>
<td>0.881</td>
<td>0.000009</td>
<td>1.062</td>
<td>0.304104</td>
<td>23.791</td>
<td>0.000002</td>
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<td>6.670</td>
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<td>1992</td>
<td><em>S. gracidosus</em> vs <em>U. ornatus</em></td>
<td></td>
<td></td>
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Figure 2.1. Relative abundance of species at Window Rock through time. Changes in the relative abundance of species at this one study area are virtually identical to changes observed over all sites across the same time period.
Figure 2.2. Mean values and variation of the relative abundance of species at Window Rock over time. Means are shown in black, boxes represent the mean +/- one standard error, and whiskers represent the mean +/- one standard deviation. The size of boxes and whiskers, and overlap of each among species indicates the high variability in relative abundance among years and the lack of dominance by one species over time, respectively.
Figure 2.3. In mass-In SVL regression. Mass and SVL are positively correlated for all species (Table 2.1) and regression coefficients of *U. ornatus* and *U. stansburiana* were significantly lower those of *S. undulatus* and *S. gracilis*. 
Figure 2.4. 1990 microhabitat niches based on canonical scores along 2 significant roots extracted from a discriminant function analyses of 5 rotated principle components representing 9 microhabitat characteristics. Roots 1 and 2 account for 53.3% and 18.2%, respectively, of the variation in microhabitat among species. 95% confidence ellipses are shown.
Figure 2.5. 1992 microhabitat niches based on canonical scores along 1 significant root extracted from a discriminant function analyses of 9 rotated principle components representing 21 microhabitat characteristics. Root 1 accounts for 55.3% of the variation in microhabitat among species. Means and 95% confidence bands are shown.
Figure 2.6. 2000 microhabitat niches based on canonical scores along 2 significant roots extracted from a discriminant function analysis of 8 rotated principal components representing 16 microhabitat characteristics. Roots 1 and 2 account for 66.2% and 22.8% respectively of the variation in microhabitat among species. 95% confidence ellipses are shown. Note that numerical axes are reversed to highlight root similarities with 1990 microhabitat niches.
Chapter III

Patterns of body size and habitat use in a lizard assemblage
Abstract

I quantified differences in the distributions and behaviour of four territorial species of phrynosomatine lizard (*Urosaurus ornatus*, *Uta stansburiana*, *Sceloporus undulatus*, and *Sceloporus graciosus*) between 2 habitat types on the elevated mesas of western Colorado. Community lizard density was greater on rock ridges dissecting pinyon-juniper woodland than in the surrounding flat open areas. The frequency of community level interactions, or behaviours directed towards another lizard of any species, was similarly greater in the rock compared to the flatland habitat for *S. undulatus*. Snout-vent length distributions of *S. undulatus*, *U. ornatus* and *U. stansburiana* differed between habitats, with larger lizards residing in the rock habitat. Distributions of hatchling lizards of all species between habitats were the opposite of those expected based on the distributions of conspecific adult females, with the majority of adult females residing in the rock habitat and the majority of hatchlings in the flatland. Flatland indices of juvenile recruitment (number of hatchlings per adult female) approximated average clutch size for *U. ornatus* and *U. stansburiana* despite known high rates of juvenile mortality in these species. I suggest ontogenetic habitat shifts may explain the observed age and size distributions of all species between habitats. Hatchlings may disperse from rock to flatland to avoid aggression and predation from adult lizards in the rock habitat, and return when they have attained larger body size and reduced predation risk, and are presumably more able to compete within social hierarchies.

Introduction

The distribution of mobile animals within their geographic range is dependent not only on dispersal abilities, but also on the distribution of resources, predators, and
competitors. In theory, animals select habitats based on maximizing net energy gains, and habitat use may reflect decisions on how to balance conflicting demands associated with the need to forage and reproduce, but also to avoid predators (Werner and Hall 1988; Dahlgren and Eggleston 2000). Studies have shown that animals select habitats based upon either minimizing mortality risks (Kotler et al. 1991), or maximizing growth rates (Werner et al. 1983b; Nonacs and Dill 1990). However, better quality foraging habitats (with higher potential growth rates) often have a greater risk of predation, forcing animals to make trade-offs between maximizing foraging profitability and minimizing predation risk when selecting habitats (Werner et al. 1983a; Bland and Temple 1990; Cowlishaw 1997; Downes 2001). When trade-offs occur, animals are predicted, and have been shown, to choose habitats where the ratio of mortality risk to growth rate is minimized, thereby maximizing net energy gain (Werner and Gilliam 1984; Nonacs and Dill 1990; Dahlgren and Eggleston 2000).

Because an animal's energetic requirements, susceptibility to natural enemies, and ability to both compete and acquire resources change with body size, many species exhibit habitat shifts during ontogeny (Werner and Gilliam 1984). This is especially apparent in species with major life-history changes during development, but has also been noted in aquatic (Sih 1982, Werner and Hall 1988; Dahlgren and Eggleston 2000; Faria and Almada 2001) and terrestrial organisms (Stamps 1983; Law 1991; Rayor and Uetz 1993) in which size is the only major difference between adults and juveniles. Size-specific predation risks often lead to smaller, younger individuals residing in more protected habitats, thereby minimizing predation risk, but usually also sacrificing better quality food resources until they are large enough to avoid predation (Stamps 1983; Werner and Gilliam 1984; Werner and Hall 1988). Dominance or social position is
positively related to both size (Stamps 1983, 1984; Zucker and Murray 1996) and habitat quality (Ferner 1974; Fox et al. 1981). In addition, conspecific aggression that results from dominant-subordinate interactions may also lead to size or age class differences in habitat distributions within a species (Bradshaw 1971; Schall 1974; Law 1991; Rayor and Uetz 1993). Ideally, individuals would distribute themselves in order to maximize their fitness by balancing the costs of intra- and interspecific interactions with the foraging benefits that each habitat confers (Fretwell and Lucas 1970). When social hierarchies allow some individuals to achieve greater than average fitness, source-sink systems may develop as higher quality habitat becomes saturated and subordinates are forced into sub-optimal habitats (Pulliam and Danielson 1991). Even without saturation, aggressive exclusion may lead to almost complete separation of dominant and subordinate individuals between habitats.

During my field work in 2000, I observed apparent habitat differences in the distribution of numbers and age structures of 4 phrynosomatine lizard species. All four species had access to two major juxtaposed habitat types that appeared to differ in lizard density. Hatchlings of all species were observed almost entirely in one habitat, whereas the majority of adults were observed in the second more densely populated habitat type. My objectives were to quantify these differences in lizard density and age structure distributions and to determine if habitat differences in behavioural interactions within and among species may be contributing to these distributions.
Methods

Study Area

I worked at the Colorado National Monument (39°6'15" N, 108°43'45" W, elevation 1750 m), Colorado, U.S.A., during the morning hours (0830-1300 h) of August and early September 2001. The predominant habitat is pinyon pine (Pinus edulis) and juniper (Juniperus utahensis) woodland, with a sandy substrate interspersed with exposed flat rock and Entrada sandstone ledges reaching up to 2 m in height. Within the pinyon-juniper woodland I focused on lizards in two distinct habitat types. The flatland habitat consisted of the open, flat regions of the woodland, with very little rock structure and relatively few fallen dead trees. The rock habitat consisted of the elaborate rock ridges and associated deadfall that dissect the flatland regions. Field work was conducted at 2 replicate study areas (Window Rock and Distant View), approximately 1 km apart. Due to the nature of the terrain, I could not standardize the area of each habitat type within each study area, but rather chose wandering belt transects through each such that both habitat types were included. Because the habitat types are intermixed I established a 2-m buffer zone extending into the flatland around each rock ridge in the rock habitat. This zone was created to include lizards that I observed to move up to 2 m from the ridge in order to bask in the surrounding flatland. At Window Rock (WR), I searched 7751 m² of flatland habitat and 2936 m² of rock and at Distant View (DV), 20038 m² and 1466 m² of flatland and rock habitat, respectively.

Lizards

Four species of diurnal phrynosomatine lizard commonly occur in the pinyon-juniper woodland habitat on the elevated mesas of western Colorado. The fence lizard,
*Sceloporus undulatus* (Bosc and Daudin 1801) is both arboreal and saxicolous (rock-dwelling) (Turner 1974; M’Closkey *et al.* 1998) and is the largest of the lizards, with a mean snout-vent length (SVL) of 63 mm. The sagebrush lizard, *Sceloporus graciosus* (Baird and Girard 1852) is the next largest, with a mean SVL of 56 mm, and is terrestrial (Marcellini and Mackey 1970; Turner 1974). The tree lizard, *Urosaurus ornatus* (Baird and Girard 1852) and the side-blotched lizard, *Uta stansburiana* (Baird and Girard 1852), are similar in SVL (46 mm and 44 mm, respectively), but differ in that the former saxicolous and arboreal while the latter is terrestrial (Hammerson 1999). Despite this distinction between saxicolous, arboreal and terrestrial, I have observed all 4 species to use rocks and dead trees as perch and foraging sites. Oviposition by these species may occur in rock crevices filled with sand as well as in soft sand at the base of trees (M’Closkey *et al.* 1990). All four species are sit-and-wait, opportunistic insectivores (Hammerson 1999).

Male *U. ornatus* (M’Closkey *et al.* 1987a, 1987b), *S. undulatus* (Ferguson 1971; Ferner 1974; Hammerson 1999), and *S. graciosus* (Deslippe and M’Closkey 1991) are territorial and actively defend their home areas against other males. Observations of two distinct populations of *U. stansburiana* indicated territoriality and aggression within each sex in Texas, but territory overlap and only weak aggression in Colorado (Tinkle 1969). Female *U. ornatus* have been reported as both territorial (Mahrt 1998) and unaggressive and nonterritorial (M’Closkey *et al.* 1987a; Deslippe *et al.* 1990a, 1990b). Studies of *U. stansburiana* indicate territoriality and dominance relationships within juveniles (Fox *et al.* 1981). Within species, dominance hierarchies have also been observed for *U. ornatus* (Deslippe *et al.* 1990a), *U. stansburiana* (Tinkle 1969), and *S. undulatus* (Ferner 1974) with dominance being correlated largely with age and size (Tinkle 1969; Deslippe *et al.*
1990a; Carpenter 1995; Zucker and Murray 1996). Cannibalism occurs within *U. stansburiana* (Wilson 1990) and *S. undulatus* (M'Closkey, pers. obs.), and has been suggested for *S. graciosus* (Hammerson 1999). Adult *S. undulatus* are known to prey on *S. graciosus* hatchling lizards as well (Turner 1974).

**Data Collection**

At each study area, I censused the lizard fauna using mark-recapture. Upon capture of each lizard, I determined the sex by examination of postanal scales, recorded snout-vent length (SVL) to the nearest 1 mm, and mass to the nearest 0.1 g, and provided a distinct temporary paint mark. Lizards were captured with a noose or by hand and were released at the point of initial observation. Both male and female lizards with a SVL less than or equal to 35 mm were classified as hatchlings (see Figs 3.3, 3.4, 3.5; Tinkle 1965). Each time a lizard was seen or captured, I recorded the habitat type, as well the number of other lizards within a 5-m radius of the point of capture. A single census consisted of 2 researchers conducting a thorough search of both habitat types in a study area 1-2 times within the same day, with each census covering the same area and requiring approximately 8 person-hours. Ten censuses were completed at each of Distant View and Window Rock. Some hatchlings were not captured due to the difficult and time-consuming nature of their capture; however, habitat type and the number of other lizards nearby were always recorded. For the purposes of body size analysis, these lizards were assigned the mean SVL of captured conspecific hatchlings (Table 3.1).

Between censuses I also carried out behavioural observations of *S. undulatus*. I watched 39 lizards (17 in flatland and 22 in rock) for a total time of 34 hours (16 h 20 min and 17 h 40 min in flatland and rock habitats, respectively). The number of observations
was approximately equal between study areas (18 at DV and 21 at WR) and both sexes were well represented (22 females and 17 males). All observations occurred during the morning hours of August and September 2001. *S. undulatus* was chosen due to ease of observation of this large saxicolous lizard as well as the need to obtaining sufficient sample sizes in each habitat at each study area. Upon location of a target individual, the lizard was allowed to settle for 5 minutes before data collection commenced. All previously unmarked lizards were marked following observation. Lizards were observed from a distance of greater than 5 m, by a single observer, for a period ranging from 15 – 120 minutes. During the observation period the frequency of the following behaviours was recorded: feeding strikes, undirected movement, undirected push-ups, conspecific push-ups, conspecific head nods, conspecific chasing and being chased, conspecific biting (or being bitten), and heterospecific pushups. Behaviours classified as undirected meant that no other lizard was visible to the observer. When another lizard was present, its identity and distance were recorded and behaviour towards this lizard was classified as either conspecific or heterospecific. Undirected movement was defined as a movement or series of movements greater than one body length, and push-ups and head nods were counted once whether they occurred singly or in series. Push-ups were the only observed behaviour directed towards a heterospecific.

**Data analyses**

All marked lizards were classified by the habitat type in which they were caught, and in the case of capture and recapture in different habitat types, lizards were counted as half in each. Lizards recaptured in the same habitat were only counted once.
Density was determined at the community level because my interest was in the potential frequency of encounter and interaction both among and within species due to similarities in foraging, habitat use, and territoriality. I determined community lizard density using two measures. First, lizard density was calculated for each census from the number of newly marked individuals and the area searched. Although this provided independent estimates of density, they did not meet the assumptions of parametric statistics. Therefore, a Mann-Whitney U test was used to identify differences in density both between habitats and between study areas. A second measure of community density, the number of lizards within a 5-m radius of the capture point of a target lizard, was also examined for differences both between habitats and between study areas. Because of the non-normality of the data, a Mann-Whitney U test was used.

In order to quantify the observed differences in age structure between habitats, a goodness of fit χ² test was used to examine the distribution of hatchlings between habitats compared to that expected from the distribution of adult females.

The distribution of lizard body size between habitats was also quantified for each species. Because SVL is highly correlated with body mass (r² = 0.939), I used the SVL distribution to characterize body size patterns. Deviations from normality, despite transformation, required the use of the Kolmogorov-Smirnov test on ln SVL differences between habitats and study areas. Because I was unable to divide lizards caught in both habitats for this analysis, lizards were classified based on the habitat in which they were initially marked.

Behavioural differences between habitats were examined through both individual and combined behaviours. Observations were summarized as the frequency of each
behaviour / hr and tested for normality. When deviations from normality were not improved by square-root transformation, a Mann-Whitney U test was employed to examine differences in the frequency of each behaviour (untransformed) between habitats and between study areas. Behaviours were also combined into activities / hr (the sum of all behaviours / hr), undirected activities / hr (undirected movements + undirected push-ups / hr), directed activities / hr (all activities directed towards another lizard of any species / hr), and top 3 activities / hr (the sum of the most common behaviours (undirected movement, undirected push-ups and feeding strikes) / hr). Because these combinations include activities that are not always independent, Mann-Whitney U tests were used to determine if differences in these groups of behaviours occurred between habitats or study areas. Multiple observations on a single lizard were combined, except in the case of observations in different habitats, for which observations were treated independently. One outlier was removed from the behavioural analyses on the basis of significant Dixon's tests for feeding strikes / hr (p < 0.01) and undirected movements / hr (p < 0.05), and consequently for activities / hr (p < 0.01), undirected activities / hr (p < 0.05) and top 3 activities / hr (p < 0.01). All analyses were performed using STATISTICA (StatSoft Inc. 1998).

Results

During the censuses I marked 199 lizards (Table 3.2), comprising 108 lizards in flatland and 91 in rock habitats. Eleven lizards were observed in both habitats at least once. Table 3.2 summarizes the number of marked adults as well as the total of marked and unmarked hatchlings, giving an estimate of the minimum number of lizards alive. Because the rate of hatchling recapture was quite low (6.9%), and I observed many
hatchlings I did not capture, I included unmarked hatchlings for the most realistic estimate of the minimum number of hatchlings alive.

**Lizard Density**

Both measures of community lizard density were significantly greater in the rock habitat. The density of newly marked lizards each day was almost ten times greater in the rock (Z = 4.25, p < .0001) than in the flatland habitat (Table 3.3), and the number of lizards within a 5-m radius of a target lizard was more than three times greater in the rock (Z = -4.21, p < 0.0001) than in the flatland habitat (Table 3.4). No differences in community lizard density occurred between study areas. Differences in density between habitats cannot be attributed to lower catchability (probability of sighting or capturing a lizard known to be alive) in the flatland habitat, because the lower structural complexity in the flatland habitat increased the ease with which search and capture occurred.

**Adult Female and Hatchling Distributions**

I found strikingly significant differences in hatchling and adult female distributions between the two habitats. Hatchling distribution between habitats was significantly different from that of adult females for *S. undulatus, U. stansburiana* and *U. ornatus* (Table 3.5, p < 0.001 in all cases), with the majority of hatchlings residing in the flatland habitat (Fig. 3.1) and the majority of adult females residing in the rocky habitat (Fig. 3.2). Although all hatchling *S. gracioso*s were observed in flatland habitat, the small sample size for this species (Table 3.2) resulted in a lack of significant difference in hatchling and adult female distributions. The distribution of *U. stansburiana* hatchlings
between study areas was significantly different from that of adult females ($\chi^2 = 6.07$, $p < 0.05$); however, no other differences in age distribution occurred between study areas.

**SVL Differences Between Habitats**

SVL distributions differed between habitats for *S. undulatus*, *U. ornatus*, and *U. stansburiana* (Table 3.6), with larger lizards residing in the rock habitat and smaller lizards residing in the flatland habitat (Figs 3.3, 3.4, 3.5). In the rock habitat, 93% of *S. undulatus* had SVLs greater than 50 mm, whereas only 51% of flatland lizards were this large (Fig. 3.3). Similarly, 100% of rock-dwelling *U. ornatus* had SVLs greater than 40 mm, whereas the majority (63%) of flatland lizards were smaller than this (Fig. 3.4). Study area differences in ln SVL distribution occurred only for *U. stansburiana* ($p < 0.01$), thus for this species each site was tested individually for differences in SVL distributions between habitat types. *U. stansburiana* had significant differences in SVL distribution between flatland and rock habitats at Distant View, with 82% and 30% of lizards having SVLs greater than 40 mm in the rock and flatland habitats, respectively; however, no differences were found at Window Rock (Table 3.6). The SVL distribution of *S. graciosus* was not significantly different between habitats due to small sample sizes (Table 3.6) and the absence of hatchling SVLs in this analysis (Table 3.1).

**Lizard Behaviour**

Mann-Whitney U tests on each individual behaviour for *S. undulatus* revealed no significant difference (Figs 3.6-3.11). However, analysis of directed activities / hr, a measure of the frequency of interactions at the community level, indicated a greater
frequency of interactions in the rock habitat \((Z = -2.10226, \ p < 0.05; \ \text{Fig. 3.12})\). All other combined behaviour frequencies (Figs. 3.13-3.15) did not differ between habitats and no significant differences in behaviour occurred between study areas. Only two aggressive interactions (chasing, biting) were observed in 34 hours of observation. Both occurred in rock habitat and involved a male aggressor and a female subordinate, of which one had a greater SVL and one a smaller SVL than the aggressor. There was no difference in behavioural frequencies between sexes and the timing of behavioural observations did not differ between habitats.

**Discussion**

My results confirmed my previous observations. Lizards residing in rock habitat differed from those in flatland in both size and number. Rock habitats had greater community lizard density, larger lizards, more adult females and fewer hatchlings than the less populated surrounding flatland habitat. *S. undulatus* in rock habitats also had a higher frequency of behavioural interaction.

The distribution of animals between habitats depends on dispersal and the ability of animals to assess their environment and make habitat choices. Population density is frequently used as an index of relative habitat quality (Schall 1974; Schoener and Schoener 1980) with greater density indicating optimal habitats, although the opposite may be true in other model systems (Pulliam 1988; Pulliam and Danielson 1991). Models of optimal behaviour, such as the ideal free distribution, apply to animals that balance the costs of intraspecific competition with the benefits of high-quality habitat, and redistribute themselves between habitats such that each animal has the same fitness (Fretwell and Lucas 1970). Optimal choice by individuals results in greater densities in
higher quality habitat. However, constraints on optimal habitat selection can lead to the evolution of a dispersal system where there is a net movement of individuals from a population where mean fitness is high (source) to a population where mean fitness is low (sink) (Pulliam 1988). In territorial species, individuals may be able to preempt high-quality habitats forcing others into those of lower quality (Pulliam and Danielson 1991). Such dynamics could potentially lead to higher densities in sub-optimal habitats, outside the fundamental niche of a species (Pulliam 1988; Pulliam and Danielson 1991).

Therefore, greater community density in the rock habitat does not permit the conclusion that it is a higher quality habitat than the flatland. However, through visual assessment alone, the greater structural complexity of the rock habitat would indeed seem to make it ideal, with many more perch sites, refuges, and thermal microenvironments provided by rock ledges, crevices, and associated dead fall than the more homogeneous flatland. Measurements of growth rates, fecundity and survival differences between habitat types would allow quantification of habitat quality.

While the observed distribution of lizard densities is consistent with expectations from optimal habitat selection, the predominance of large lizards in the rock habitat and of smaller lizards in the flatland suggests that their distribution between habitats is not consistent with the Ideal Free Distribution (Fretwell and Lucas 1970). These species are territorial (Tinkle 1969; Ferguson 1971; Ferner 1974; M'Closkey et al. 1987a, 1987b; Deslippe and M'Closkey 1991) and exhibit dominance hierarchies based on size and experience (Fox et al. 1981; Deslippe et al. 1990a; Carpenter 1995; Zucker and Murray 1996). Interactions due to dominance hierarchies within species may generate size-biased dispersal from the rock habitat into the flatland, such that juvenile lizards are excluded based on their low position in the hierarchy, and relegated to sub-optimal sites, resulting
in apparent source-sink dynamics. Fox et al. (1981) suggest that agonism from *U. stansburiana* adults towards juveniles expanding their home ranges is minimal; however, studies of adult-juvenile interactions in these species are lacking. Within juvenile *U. stansburiana*, older juveniles may aggressively exclude smaller juveniles from higher quality territories (Fox 1978). Within adult male *U. ornatus*, dominant individuals aggressively exclude smaller conspecifics (Deslippe 1989), and will inhibit the activity of subordinates by displaying or attacking active individuals (Deslippe et al. 1990a). In general, conspecific aggression is usually more pronounced at higher densities (Fox 1975; Wildy et al. 2001) and in populations with high size variation (Fox 1975; Polis 1981). Because size variation within *U. stansburiana* would be the smallest of the lizards reported here, potential aggression between adults and juvenile lizards may be minimal for this species. There would be greater potential for conspecific aggression in *S. undulatus* and *S. graciosus* because of the greater size difference between adults and hatchlings.

However, I observed only two aggressive interactions in my behavioural observations of *S. undulatus*, and although they both occurred in the higher density rock habitat, the aggressor was not necessarily the larger lizard and neither subordinate was a hatchling. Dominance may be signalled primarily through body size and territorial displays, making aggressive interactions and their observation less common in this species. Deslippe et al. (1990a) found that aggressive interactions in *U. ornatus* were infrequent compared to ritualized displays. Social interactions are less frequent during the post-breeding season (Smith and John-Alder 1999), thus the timing of my behavioural observations (late summer) would have further reduced the frequency of interactions that occurred earlier in the summer. Indeed, with the exception of basic movement, feeding,
and undirected push-ups (Figs 3.6, 3.7, and 3.8), frequencies of observed behaviours were very low (Figs 3.9, 3.10, and 3.11). Seasonal decreases in the frequency of interactions may account for the lack of significant differences between habitats for most behaviours. Further observations throughout the breeding and post-breeding seasons are required to determine the true degree of behavioural differences between habitats. The greater frequency of all activities, in *S. undulatus*, directed towards both conspecifics and heterospecifics observed in the rock habitat (Fig 3.12) reflects the greater community density and potential for interaction both within and between species in this habitat. However, to my knowledge, there is only one record of an aggressive interaction between any of the species in this assemblage (Ferguson 1971), suggesting that intraspecific competition plays a much greater role in the community dynamics of these species than does interspecific competition.

Competitive exclusion of juveniles by adults in optimal habitats has been used to explain habitat segregation of age classes in other vertebrate and invertebrate species. Schall (1974) found higher proportions of smaller whiptails (*Cnemidophorus arubensis*) in sub-optimal habitats and suggested that strong intraspecific competition between young and adult whiptails may result in dispersal of young into zones less favoured by adults, until the opportunity to replace adults lost through mortality occurs. Bradshaw (1971) observed similar habitat separation between juvenile and adult agamid lizards (*Amphibolurus ornatus*), with the majority of juveniles being displaced to marginal habitats by continual territorial harassment from adult males. Dominant Australian water skinks (*Eulamprus quoyii*) were aggressive towards smaller individuals of the same species, and obtained more food and better sites than subordinates, suggesting that larger skinks may also initiate the movement of juveniles to more marginal habitats (Law 1991).
In colonial web-building spiders (*Metepeira incrassata*), larger individuals aggressively defend spots in the core of the colony where predation risk is low, forcing immature spiders to reside on the high-risk periphery of the colony (Rayor and Uetz, 1993).

Habitat separation of hatchling and adult lizards may be further encouraged by the predation risk hatchlings face from adults. The consumption of hatchling or juvenile lizards by conspecific adults has been observed for *U. stansburiana* (Tinkle 1967; Wilson 1990) and *S. undulatus* (M'Clokey, *pers. obs.*), and has been suggested for *S. graciosus* (Hammerson 1999). The size difference between adult and hatchling *U. ornatus* would make cannibalism possible in this species as well. Although intraspecific predation is rarely documented in iguanid lizards (Polis 1981), it may be more common than is usually recognized (Wilson 1990). Interspecific predation by adult *S. undulatus*, the largest lizard, on hatchling *S. graciosus* occurs (Turner 1974) thus predation on the smaller species would also be possible. Cannibalism and interspecific predation within this assemblage would allow alternate energy sources when resources are low, and serve to reduce competition in highly populated areas (Wildy *et al.* 2001; Polis 1981). The affiliation of all species of hatchling lizards with the lower density flatland habitat compared to that of adult lizards with the rock habitat, would reduce the risk of cannibalism or interspecific predation. Collared lizards (*Crotaphytus collaris*) are known predators of all sizes of these species in rock habitats; however none was resident within my study areas. Other known predators of these species in this area (striped whipsnake (*Masticophis taeniatus*), midget faded rattlesnake (*Crotalus viridis concolor*), whiptails (*Cnemidophorus tigris*), scorpions, and various birds and mammals (see Hammerson 1999)) could prey on all sizes of lizards in both habitats, perhaps with greater success in the more open flatland. Higher densities of juveniles in the flatland may actually indicate
that refuge from predators, other than lizards, is less important. Stamps (1983, 1988) observed *Anolis aeneus* to migrate from shady areas to clearings soon after hatching, and return when they reach sub-adult size. She attributes this ontogenetic change in habitat use to the restriction of important predators of juvenile lizards, adult *Anolis richardi* and adult conspecifics, to shady habitats. During previous studies in this area, R.T. M'Closkey observed a similar habitat shift in juvenile *Crotaphytus collaris* away from rock outcrops where dominant males reside, presumably due to both dominance relations and risk of cannibalism.

Therefore, an ontogenetic habitat shift may occur, with hatchling lizards moving from the rock habitat into the flatland soon after hatching, returning only once they are better able to compete for space and when the risk of cannibalism has been reduced. In a study of hatchling dispersal, Doughty and Sinervo (1994) observed *U. stansburiana* hatchlings to disperse long distances within the first month of life from the highly populated rock outcrops, where they were released in the spring, into ground squirrel holes in the surrounding fields. This resulted in habitat separation of adults and hatchlings until autumn when juveniles returned to the outcrops. Pounds and Jackson (1983) found perch height to be positively correlated with SVL in *S. undulatus undulatus* in southwestern Alabama, suggesting an ontogenetic shift in microhabitat utilization in this species. Deslippe and M'Closkey (1991) observed an opposite pattern of ontogenetic microhabitat segregation for *S. gracilis*, in which juveniles are arboreal and adults are terrestrial. To my knowledge, no other ontogenetic habitat shifts for these species have been documented.

I did not observe the physical movement of hatchlings during my census work, although the nature of my search and focus of my behavioural observations were not
designed for this purpose. I propose this as a possible explanation for the distribution of size classes between habitats and offer evidence that would support this possibility: Because the majority of adult females reside in the rock habitat, and oviposition occurs within a female's home range (Tinkle 1965; M’Closkey et al. 1990), I would expect more hatchlings in the rock habitat. However, the opposite was found. The number of hatchlings per adult female in the flatland was approximately equal to the average clutch size for *U. ornatus* and *U. stansburiana* (Hammerson 1999) (Fig. 3.1). Naturally high juvenile mortality in all species (Tinkle 1965; Tinkle and Dunham 1983; Hammerson 1999), makes this ratio of hatchlings to adult females highly unlikely without some influx of hatchling lizards into the flatland habitat. Movement of hatchlings into the flatland from the nearby rock habitat would account for this pattern as well as for the extremely low number of hatchlings per adult female in the rock habitat. The latter may also be due to higher hatchling mortality in the rock habitat, and I cannot distinguish these alternatives. Previous studies of hatchling dispersal for *U. stansburiana*, the smallest and least dispersive of these species, have given mixed results. *U. stansburiana* hatchlings disperse long distances (median ~100 m) in rock habitat and short distances (median ~ 20 m) in chaparral community in California (Doughty and Sinervo 1994), but only move between 6 and 42 m in Mesa County, Colorado (Tinkle 1967) and less than 7 m in Winkler Co., Texas (Tinkle 1965), from hatching until sexual maturity was attained. The nature of the habitat mosaics in my study area would allow hatchlings of all species to disperse between the rock and surrounding flatland habitats with even minimal dispersal distances.

Size and age-related changes in habitat association in other lizards (Bradshaw 1971; Schall 1974; Stamps 1983; Law 1991), fish (Werner and Hall 1988; Klemetsen and
Dahl-Hansen 1995; Dahlgren and Eggleston 2000; Faria and Almada 2001), and invertebrates (Sih 1982; Rayor and Uetz 1993). reflect the changes in selective pressures operating on different size classes within a species. In most cases, smaller individuals reside in vegetation or other protective habitats that often contain poorer food resources, then move into more exposed, riskier habitats as adults when they are less susceptible to predation. Many of these studies examine trade-offs between predation risks and foraging or growth rates, and habitat associations suggest the importance of size-specific predation risk for many species. In this study, juveniles and adults of each species overlap in prey items, with larger individuals able to prey upon the same prey as juveniles, as well as larger items. Foraging rates for all lizard sizes may differ between habitats due to differences in microhabitat structure and encounter rates with prey; however, arthropod abundance in this area did not differ between sites occupied and unoccupied by S. graciosus (Deslippe and M'Closkey 1991). Arthropod distribution did not affect the distribution of tree lizards in the Sonoran desert (M'Closkey et al. 1990) and similar results in other lizard studies (Ballinger 1977; Ruby 1986; M'Closkey et al. 1987a) suggest arthropod distribution is not associated with lizard distribution.

Density manipulations within this assemblage (M'Closkey et al. 1997, 1998) resulted in rapid and essentially simultaneous colonization of experimentally created density sinks by all four species from adjacent habitats, suggesting that former residents had excluded others from their territories. Colonizing S. undulatus and U. ornatus were smaller than those removed (M'Closkey et al. 1998), and size-dependent dominance relationships were invoked to explain this pattern of size-biased dispersal. Non-significant size differences between colonizing and pre-removal S. graciosus and U. stansburiana were attributed to microhabitat segregation of S. graciosus juveniles
(arboreal) and adults (terrestrial) (Deslippe and M'Closkey 1991), and the terrestrial habit of *U. stansburiana*, compared to similar arboreal microhabitat use for all sizes of *S. undulatus* and *U. ornatus*.

In the present study, the lack of size separation between habitats at Window Rock for *U. stansburiana*, despite a terrestrial habit for all ages, is not surprising. *U. stansburiana* has nearly an annual population turnover (Tinkle 1965) and thus there may be little intraspecific competition between adults and surviving offspring, and therefore no need for great dispersal. In long-lived lizards such as *S. undulatus* and *S. graciosus*, there may be more competition between young and adults than short-lived species, producing greater dispersal and potential size differences between habitats. Differences in age and size distributions of *U. stansburiana* between study areas may be the result of greater intraspecific competition and aggression due to greater densities in the Distant View rock habitat, or different habitat mosaics at Distant View allowing dispersal of more hatchlings in this study area.

In summary, the distribution of lizards between the two habitats may result from aggressive exclusion and predation of hatchlings by adult lizards in rock habitats, and subsequent dispersal of hatchling lizards into the surrounding flatland. The low densities and small size of lizards in the flatland habitat suggest that most hatchlings do not remain once adult body size is attained, but rather return to the rock habitat when they have reduced risk of predation, and are presumably more able to compete within dominance hierarchies.

Long-term observational studies of immigration, emigration, fecundity, and survivorship in flatland and rock habitats would allow identification of ontogenetic habitat shifts and indicate whether this size-biased dispersal results in source-sink
dynamics.
Table 3.1. Number of hatchlings captured for each species and study area. Mean SVLs were assigned to uncaptured hatchlings for the analysis of body size (SVL) distribution.

<table>
<thead>
<tr>
<th>Species</th>
<th>Study Area</th>
<th># Hatchlings</th>
<th>Mean SVL</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>U. ornatus</em></td>
<td>WR</td>
<td>5</td>
<td>27.2</td>
</tr>
<tr>
<td></td>
<td>DV</td>
<td>4</td>
<td>28.5</td>
</tr>
<tr>
<td><em>U. stansburiana</em></td>
<td>WR</td>
<td>5</td>
<td>33.6</td>
</tr>
<tr>
<td></td>
<td>DV</td>
<td>9</td>
<td>30.8</td>
</tr>
<tr>
<td><em>S. undulatus</em></td>
<td>WR</td>
<td>2</td>
<td>29.5</td>
</tr>
<tr>
<td></td>
<td>DV</td>
<td>2</td>
<td>33.0</td>
</tr>
<tr>
<td><em>S. graciousus</em></td>
<td>WR</td>
<td>0</td>
<td>-----</td>
</tr>
<tr>
<td></td>
<td>DV</td>
<td>0</td>
<td>-----</td>
</tr>
</tbody>
</table>
Table 3.2. Number of marked adult lizards and marked and unmarked hatchlings for each species in each habitat. Fractions represent lizards that were caught in both habitats and divided such that a half lizard was counted in each habitat type.

<table>
<thead>
<tr>
<th>Species</th>
<th>Habitat</th>
<th># Adults</th>
<th># Hatchlings</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>U. ornatus</em></td>
<td>Flatland</td>
<td>5.5</td>
<td>10</td>
<td>15.5</td>
</tr>
<tr>
<td></td>
<td>Rock</td>
<td>10.5</td>
<td>0</td>
<td>10.5</td>
</tr>
<tr>
<td><em>U. stansburiana</em></td>
<td>Flatland</td>
<td>16</td>
<td>33.5</td>
<td>49.5</td>
</tr>
<tr>
<td></td>
<td>Rock</td>
<td>36</td>
<td>13.5</td>
<td>49.5</td>
</tr>
<tr>
<td><em>S. undulatus</em></td>
<td>Flatland</td>
<td>18</td>
<td>16</td>
<td>34</td>
</tr>
<tr>
<td></td>
<td>Rock</td>
<td>27</td>
<td>2</td>
<td>29</td>
</tr>
<tr>
<td><em>S. graciosus</em></td>
<td>Flatland</td>
<td>5</td>
<td>4</td>
<td>9</td>
</tr>
<tr>
<td></td>
<td>Rock</td>
<td>2</td>
<td>0</td>
<td>2</td>
</tr>
</tbody>
</table>
Table 3.3. Mean density of newly marked lizards
(S. undulatus, S. gracious, U. stansburiana, U. ornatus)
per m² per census. The number of censuses (n) was divided
equally between study areas.

<table>
<thead>
<tr>
<th>Habitat</th>
<th>Mean</th>
<th>SD</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>Flatland</td>
<td>2.37 × 10⁻¹</td>
<td>1.96 × 10⁻¹</td>
<td>20</td>
</tr>
<tr>
<td>Rock</td>
<td>21.14 × 10⁻¹</td>
<td>25.27 × 10⁻¹</td>
<td>20</td>
</tr>
</tbody>
</table>
Table 3.4. Mean number of lizards (*S. undulatus*, *S. gracilis*, *U. stansburiana*, *U. ornatus*) within a 5-m radius of any target lizard. *n* is the total number of lizards observed during all censuses.

<table>
<thead>
<tr>
<th>Habitat</th>
<th>Mean</th>
<th>SD</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>Flatland</td>
<td>0.10</td>
<td>0.30</td>
<td>164</td>
</tr>
<tr>
<td>Rock</td>
<td>0.34</td>
<td>0.64</td>
<td>230</td>
</tr>
</tbody>
</table>
Table 3.5. Results of a $\chi^2$ test of observed vs expected hatchling distributions between habitats, based on the distributions of adult females for each species.

<table>
<thead>
<tr>
<th>Species</th>
<th>$\chi^2$</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>U. ornatus</td>
<td>22.00</td>
<td>$&lt; 0.00001$</td>
</tr>
<tr>
<td>U. stansburiana</td>
<td>18.85</td>
<td>$&lt; 0.0001$</td>
</tr>
<tr>
<td>S. undulatus</td>
<td>13.70</td>
<td>$&lt; 0.001$</td>
</tr>
<tr>
<td>S. graciosus</td>
<td>1.33</td>
<td>$&gt; 0.05$</td>
</tr>
</tbody>
</table>
Table 3.6. Mean SVLs for each species by habitat and for *U. stansburiana*, by study area. P-values indicate the results of a Kolmogorov-Smirnov Test on ln SVL distributions between habitats.

<table>
<thead>
<tr>
<th>Species</th>
<th>Habitat</th>
<th>Mean</th>
<th>SD</th>
<th>n</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>S. undulatus</em></td>
<td>Flatland</td>
<td>46.1</td>
<td>1.4</td>
<td>37</td>
<td>p &lt; 0.001</td>
</tr>
<tr>
<td></td>
<td>Rock</td>
<td>62.7</td>
<td>1.2</td>
<td>28</td>
<td></td>
</tr>
<tr>
<td><em>U. ornatus</em></td>
<td>Flatland</td>
<td>34.7</td>
<td>1.3</td>
<td>16</td>
<td>p &lt; 0.025</td>
</tr>
<tr>
<td></td>
<td>Rock</td>
<td>47.8</td>
<td>1.1</td>
<td>11</td>
<td></td>
</tr>
<tr>
<td><em>S. graciosus</em></td>
<td>Flatland</td>
<td>54.3</td>
<td>1.1</td>
<td>5</td>
<td>p &gt; 0.10</td>
</tr>
<tr>
<td></td>
<td>Rock</td>
<td>51.5</td>
<td>1.0</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td><em>U. stansburiana</em> (DV)</td>
<td>Flatland</td>
<td>35.8</td>
<td>1.2</td>
<td>37</td>
<td>p &lt; 0.001</td>
</tr>
<tr>
<td></td>
<td>Rock</td>
<td>42.9</td>
<td>1.2</td>
<td>33</td>
<td></td>
</tr>
<tr>
<td><em>U. stansburiana</em> (WR)</td>
<td>Flatland</td>
<td>37.0</td>
<td>1.1</td>
<td>12</td>
<td>p &gt; 0.10</td>
</tr>
<tr>
<td></td>
<td>Rock</td>
<td>40.9</td>
<td>1.1</td>
<td>19</td>
<td></td>
</tr>
</tbody>
</table>
Figure 3.1. Number of hatchlings per adult female in flatland and rock habitats.
Figure 3.2. Number of adult females per m² of area searched in flatland and rock habitats.
Figure 3.3. SVL distributions of *S. undulatus* in flatland and rock habitats. x-axis values (in mm) represent the mid-point of each class.
Figure 3.4. SVL distributions of *U. ornatus* in flatland and rock habitats. *x*-axis values (in mm) represent the mid-point of each class.
Figure 3.5. SVL distributions of *U. stansburiana* (DV) in flatland and rock habitats. x-axis values (in mm) represent the mid-point of each class.
Figure 3.6. Frequency distribution of the number of feeding strikes / hr for *S. undulatus* in flatland and rock habitats. x-axis values represent the maximum value in each class.
Figure 3.7. Frequency distribution of the number of undirected movements / hr for *S. undulatus* in flatland and rock habitats. x-axis values represent the maximum value in each class.
Figure 3.8. Frequency distribution of the number of undirected push-ups/h for *S. undulatus* in flatland and rock habitats. x-axis values represent the maximum value in each class.
Figure 3.9. Frequency distribution of the number of conspecific push-ups/hr for *S. undulatus* in flatland and rock habitats. x-axis values represent the maximum value in each class.
Figure 3.10. Frequency distribution of the number of conspecific head nods/hr for *S. undulatus* in flatland and rock habitats. x-axis values represent the maximum value in each class.
Figure 3.11. Frequency distribution of the number of interspecific push-ups/hr for _S. undulatus_ in flatland and rock habitats. x-axis values represent the maximum value in each class.
Figure 3.12. Frequency distribution of directed activities / hr for *S. undulatus* in flatland and rock habitats. Directed activities is the sum of all activities directed towards another lizard (conspecific push-ups, conspecific head nods, conspecific chasing and being chased, conspecific biting (or being bitten), and heterospecific pushups). x-axis values represent the maximum value in each class.
Figure 3.13. Frequency distribution of activities / hr for *S. undulatus* in flatland and rock habitats. Activities is the sum of all behaviours. x-axis values represent the maximum value in each class.
Figure 3.14. Frequency distribution of undirected activities / hr for *S. undulatus* in flatland and rock habitats. Undirected activities is the sum of undirected movements and undirected push-ups. x-axis values represent the maximum value in each class.
Figure 3.15. Frequency distribution of the top 3 activities / hr for *S. undulatus* in flatland and rock habitats. Top 3 activities is the sum of undirected movements, undirected push-ups and feeding strikes. x-axis values represent the maximum value in each class.
Chapter IV

Lizard microhabitat and fire fuel management
Abstract

Many animal species respond to changes in habitat structure during ecological succession. For some species, dead vegetation is important microhabitat necessary for survival and reproduction. I compared the use of three categories of tree: living, dead standing and dead prone, within and among four species of phrynosomatine lizard (Sceloporus undulatus, Sceloporus graciosus, Urosaurus ornatus, and Uta stansburiana) on the Colorado Plateau during 1990, 1992 and 2000. All four species used dead trees (both prone and standing) more frequently than live trees, despite an opposite pattern of availability. U. ornatus used dead standing more often than dead prone trees, reflecting this lizard’s arboreal nature. Tree use did not differ among species and the species by tree category interaction was not significant. Current policy mandates the removal of dead vegetation and debris on U.S. Federal lands as basic maintenance in order to decrease fire risk. Active removal of “fuel” may limit the local distribution, abundance, and diversity of these lizards, which include dead trees in their microhabitat for shelter, perching, foraging, courting, and defending territories.

Introduction

As a response to an overwhelming fire season in the United States during 2000, fire management and fuel reduction strategies are being reinforced, with the 2001 budget for hazardous fuel reduction almost three times what it was in 2000 (Laverty et al. 2001). Fuel reduction includes removal of undesired or excess live and dead vegetation through thinning, prescribed fire and other removal methods, in order to reduce the likelihood of ignition and spread of fire (Laverty and Williams 2000). While highest priority for these efforts has been assigned to areas that are subject to intense fires, are in close proximity to
municipal watersheds, or contain threatened or endangered species, maintenance of
healthy ecosystems by preventing the accumulation of fuels is also considered critical to
the U.S. National Fire Plan (Laverty and Williams 2000).

However, dead vegetation serves as key microhabitat for many species, including
insects (Smith 1996), small mammals (Nordyke and Buskirk 1991), lizards (Vitt 1974;
Mushinsky 1992; M’Closkey 1997), and cavity-nesting waterfowl (Pierre et al. 2001).
These species use dead vegetation for shelter (Mushinsky 1992), food (Smith 1996),
foraging and perch sites (M’Closkey 1997), nesting (Pierre et al. 2001) and over-
wintering (Vitt 1974). For these species, dead vegetation is important microhabitat for
local distribution and activity. Animals respond to changes in the plant community
during ecological succession, and community species composition has been found to
differ with successional stage (Fox 1982; Lunney et al. 1991; Mushinsky 1992;
Greenberg et al. 1994). Removal of specific microhabitat may have serious consequences
for biological diversity (Primack 1993). Furthermore, widespread habitat loss may lead
to metapopulation and regional extinctions.

During previous studies in Colorado, M’Closkey and Hehnar (1994) and
M’Closkey et al. (1998) observed preferential use of dead trees relative to live trees by
four species of phrynosomatine lizard. My objectives were to quantify this preference, to
examine differences in use among the species, and to explore the conservation
implications of such findings.
Methods

Study Area and Lizards

I worked at Colorado National Monument (39°6'15" N, 108°43'45" W, elevation 1750m), Colorado, U.S.A., during 2000 and had access to data collected in the same area during 1990 and 1992. The predominant habitat is pinyon pine (*Pinus edulis*) and juniper (*Juniperus utahensis*) woodland, with a sandy substrate interspersed with exposed flat rock and Entrada sandstone ledges. In this habitat, I studied the microhabitat use of four sympatric species of phrynosomatine lizard. *Sceloporus undulatus* (eastern fence lizard) and *Urosaurus ornatus* (tree lizard) are both saxicolous (rock-dwelling) and arboreal (M’Closkey *et al.* 1998; Hammerson 1999), and *Sceloporus graciosus* (sagebrush lizard) and *Uta stansburiana* (side-blotched lizard) are primarily terrestrial (Marcellini and Mackey 1970; Hammerson 1999). Despite this distinction between arboreal and terrestrial lizards, all four species use dead trees as perch sites, although this is less common in the terrestrial species.

Field Procedures

During late May 1990, late May and early June 1992, and August 2000, 10, 21, and 15 person-days, respectively, were spent searching the pinyon-juniper woodland for lizards. In order to obtain sufficient sample sizes, a minimum of 2 randomly selected study areas were searched each year. In each area structural features likely to be included in lizard territories were searched, in order to maximize potential contact with lizards. Each year, the lizard fauna was censused using mark-recapture. My data collection in 2000 involved the same methods as those used in 1990 and 1992. I captured each lizard I encountered, determined the sex by examination of postanal scales, provided a distinct
temporary paint mark, and released the lizard at the initial point of observation. Each
time I saw or captured a lizard, a description of the microhabitat was recorded within a 5-
m radius of the initial point of observation. I recorded capture point tree type as well as
the number of trees (pinyon and juniper) in the surrounding radius in each of three
categories: living, dead standing, and dead prone. Live trees less than 1 m in height were
not recorded, because I never observed lizards using them. Recaptures were not included
in the analysis, thereby eliminating multiple observations on the same individuals.

Data analyses

For each species, I calculated the proportion of each tree category (living, dead
prone, and dead standing) used from the number of captures on each type of tree and the
total number of available trees at the capture site and within its radius. These proportions
were arcsine transformed and analyzed by two-way ANOVA to test for differences in use
among species, among tree categories, and for an interaction between species and
category. Replicate study sites were necessarily pooled to obtain sufficient sample sizes.
However, microhabitat use among years was independent and was thus treated as three
replicates of use for each species and each category of tree. Planned comparisons
examined differences in percent use of each tree category within and among species. All
analyses were performed using STATISTICA (StatSoft Inc. 1998).

Results and Discussion

Percent use was highly significantly different among the three categories of tree (p
< 0.000001), but not among lizard species (Table 4.1). There was no significant tree
category by species interaction (Table 4.1). Despite greater availability of live trees, all
species had much greater percent use of dead (both prone and standing) trees (Table 4.2, Figs. 4.1, 4.2, 4.3, 4.4). *U. ornatus* was the only species that differed in the use of dead standing and dead prone trees (*p* < 0.05, Table 4.2), using dead standing juniper and pine more often than prone (Fig. 4.1). A similar preference was apparent for *S. undulatus* (Fig. 4.2), but was not significant. M’Closkey (1997) found that *U. ornatus* similarly prefer dead standing to dead prone or live saguaro cactus (*Carnegiea gigantea*) in Arizona.

Both *U. ornatus* and *S. undulatus* use arboreal microhabitat, often in conjunction with rock, for perching and basking, territory surveillance and defense, feeding, shelter, and refuge from predators (Pounds and Jackson 1983; Deslippe 1989; Hammerson 1999). Because dead pinyon and juniper are preferred to living trees, dead vegetation must be an important component of these species’ microhabitat. As dead trees become available through ecological succession, lizards shift their territory and home range boundaries to exploit this important microhabitat (M’Closkey 1997).

Although I expected the terrestrial species (*S. graciosus* and *U. stansburiana*) to use more dead prone than dead standing trees, no significant preference between these categories was found (Table 4.2, Figs. 4.3, 4.4). Dead prone trees are more accessible to terrestrial lizards, and they have been observed in use as shelter and refuge for these species. With the exception of *S. graciosus* in 2000, small sample sizes were not due to fewer lizards, but rather were because many lizards were captured on rock or ground, which were not included in this analysis. Despite relatively small sample sizes of terrestrial lizards (Table 4.2), those that were captured in trees showed the same preferential use of dead compared to live trees as the two arboreal species (*U. ornatus* and *S. undulatus*).
During the course of my studies in Colorado, I have observed concentrations of all four species in areas with numerous dead juniper and pine, and comparatively few individuals in the surrounding open habitat, which contained relatively few dead trees. My results indicate that such concentrations of dead prone and standing trees may be significant microhabitat for these species. Use of dead vegetation by these species has also been reported in other studies. Adolph (1990) showed that *S. graciosus* in the San Gabriel Mountains of southern California use woody debris extensively, and that off-ground perches such as logs and stumps are used far more often than expected on the basis of availability. *S. undulatus* in Louisiana and Alabama coastal plain are often associated with logs, and areas occupied by this lizard contain significantly more logs than other areas within the same habitat (Pounds and Jackson 1983). *U. ornatus* over-winters in dead vegetation, forming large aggregations under the bark of dead mesquite stumps in Arizona (Vitt 1974). Lillywhite and North (1974) report on the use of charred branches of woody plants by *S. occidentalis*, indicating the importance of woody debris and suggesting the importance of fire for a *Sceloporus* species.

The amount of dead trees in the area is ultimately affected by two factors: ecological succession and removal for fuel reduction. Many parks have a policy to remove dead vegetation and debris as basic maintenance in order to decrease fire risk (National Park Service 2001). Because of the large number and magnitude of fires in North America in 2000, increased precautions are presently being taken to reduce and prevent the accumulation of fuels. Fuel reduction treatments are currently planned for an estimated 1.8 million acres of U.S. Federal lands (Laverty et al. 2001).

However, there is conflict between the need to preserve ecosystems and protect threatened and endangered species by removing fire hazards, and the need to preserve late
successional habitat (potential forest fire fuel) that serves as important microhabitat for a number of species. Community composition has been found to differ with successional stage, as animals respond to changes in plant communities during ecological succession (Smith 1996). When disturbances such as logging, fire, or human interference result in the removal of late successional habitat, community compositions of small mammals (Fox 1982; Haim and Izhaki 1994), and lizards (Lillywhite 1977; Lunney et al. 1991; Mushinsky 1992; Greenberg et al. 1994) are found to change with regeneration time. Through alteration of habitat, these disturbances promote the abundances of some species (Mushinsky 1985) while reducing that of others (Lillywhite 1977; Mushinsky 1992). Loss of late successional habitat could be a large threat to biological diversity because it would reduce the diversity of habitats and microhabitats available (Smith 1996). Loss of even a small area of habitat may lead to larger-scale extinction if the area contained source populations (Pulliam 1988).

My purpose was to assess the response of lizards within habitats to available microhabitat structure provided by trees. My field design did not address the importance of dead vegetation in determining lizard distribution and abundance across habitat types. In addition to trees, lizards also exploit other substrates (rock ledges and rock walls) which no doubt contribute to patterns of lizard distribution and numbers. Indeed, during the study period, 54.4% of all lizards encountered were perched on live or dead trees, while the remaining 45.6% were observed on rock or sandy substrate.

I found that lizards preferentially used dead rather than live trees despite an opposite pattern of availability. The propensity of the lizard fauna to exploit a specific seral stage of succession has clear implications for local species richness. Removal of dead prone trees would reduce shelter available to terrestrial species, possibly making
them more vulnerable to predators. Additional removal of dead standing trees could seriously affect the local abundance and diversity of arboreal species, which spend the majority of their time in these trees, basking, feeding, courting, and defending territories. Few studies have examined the consequences of planned removal of fire fuel by non-fire treatments on local fauna (Lillywhite 1977). Such consequences need to be considered on an individual basis when fire management and fuel reduction plans are implemented.
Table 4.1. Analysis of the use of three categories of tree by four species of lizard. A arcsine transformed percent use of each category of tree were analysed using a two-way ANOVA.

<table>
<thead>
<tr>
<th>Source</th>
<th>df Effect</th>
<th>MS Effect</th>
<th>df Error</th>
<th>MS Error</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species</td>
<td>3</td>
<td>2.08</td>
<td>23</td>
<td>320.28</td>
<td>0.23</td>
<td>0.878</td>
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<td>2</td>
<td>10807.95</td>
<td>23</td>
<td>320.28</td>
<td>33.75</td>
<td>&lt;0.000001</td>
</tr>
<tr>
<td>Species X Tree category</td>
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<td>356.51</td>
<td>23</td>
<td>320.28</td>
<td>1.11</td>
<td>0.385</td>
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Table 4.2. Results of planned comparisons within ANOVA of percent use of three categories of tree by four species of lizard. Use of dead trees (prone and standing) was compared to that of live, and use of dead prone trees compared to that of dead standing trees for each species. Significant results are shown in bold type. Sample sizes for each year are given in the last columns.

<table>
<thead>
<tr>
<th>Species</th>
<th>Contrast</th>
<th>F</th>
<th>p</th>
<th>n</th>
<th>n</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>S. graciosus</em></td>
<td>dead vs live</td>
<td>13.10</td>
<td>0.0014</td>
<td>32</td>
<td>45</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>dead prone vs dead standing</td>
<td>0.20</td>
<td>0.6601</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>S. undulatus</em></td>
<td>dead vs live</td>
<td>17.78</td>
<td>0.0003</td>
<td>12</td>
<td>45</td>
<td>14</td>
</tr>
<tr>
<td></td>
<td>dead prone vs dead standing</td>
<td>3.45</td>
<td>0.0762</td>
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<td></td>
</tr>
<tr>
<td><em>U. ornatus</em></td>
<td>dead vs live</td>
<td>17.12</td>
<td>0.0004</td>
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<td>70</td>
<td>10</td>
</tr>
<tr>
<td></td>
<td>dead prone vs dead standing</td>
<td>4.98</td>
<td>0.0357</td>
<td></td>
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</tr>
<tr>
<td><em>U. stansburiana</em></td>
<td>dead vs live</td>
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<td>0.0003</td>
<td>3</td>
<td>14</td>
<td>5</td>
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<tr>
<td></td>
<td>dead prone vs dead standing</td>
<td>0.25</td>
<td>0.6194</td>
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Figure 4.1. Mean percent use and total percent availability of living, dead standing, and dead prone trees for *U. ornatus* during the study period (1990, 1992, and 2000). Availability was determined from the number of trees in each category that were either capture sites or were in the areas immediately surrounding *U. ornatus* capture sites. Percent use was determined from the number of *U. ornatus* captures on each type of tree and the total number of available trees (capture sites and surrounding areas) of that type for each year. Standard error bars shown reflect variation in percent use among years. The total number of captures on each type of tree for all years appears above percent use data.
Figure 4.2. Mean percent use and total percent availability of living, dead standing, and dead prone trees for *S. undulatus* during the study period (1990, 1992, and 2000). Availability was determined from the number of trees in each category that were either capture sites or were in the areas immediately surrounding *S. undulatus* capture sites. Percent use was determined from the number of *S. undulatus* captures on each type of tree and the total number of available trees (capture sites and surrounding areas) of that type for each year. Standard error bars shown reflect variation in percent use among years. The total number of captures on each type of tree for all years appears above percent use data.
Figure 4.3. Mean percent use and total percent availability of living, dead standing, and dead prone trees for *S. graciosus* during the study period (1990, 1992, and 2000). Availability was determined from the number of trees in each category that were either capture sites or were in the areas immediately surrounding *S. graciosus* capture sites. Percent use was determined from the number of *S. graciosus* captures on each type of tree and the total number of available trees (capture sites and surrounding areas) of that type for each year. Standard error bars shown reflect variation in percent use among years. The total number of captures on each type of tree for all years appears above percent use data.
Figure 4.4. Mean percent use and total percent availability of living, dead standing, and dead prone trees for *U. stansburiana* during the study period (1990, 1992, and 2000). Availability was determined from the number of trees in each category that were either capture sites or were in the areas immediately surrounding *U. stansburiana* capture sites. Percent use was determined from the number of *U. stansburiana* captures on each type of tree and the total number of available trees (capture sites and surrounding areas) of that type for each year. Standard error bars shown reflect variation in percent use among years. The total number of captures on each type of tree for all years appears above percent use data.
Chapter V

Conclusions
My investigations of microhabitat, habitat-dependent body size distributions, and responses to seral stages of ecological succession in phrynosomatine lizards, revealed broad overlap and similarities among species. I discovered an affiliation of all species with vegetation in the late stages of ecological succession. All four species used dead trees (both prone and standing) more frequently than live trees, despite an opposite pattern of availability. Overall density of the lizard community was indeed much greater in rock habitats, which were associated with numerous deadfalls, than in the surrounding open flatland areas that were characterized more by live than dead pinyon and juniper. The preferential use of dead trees, and the distribution of both dead trees and lizard numbers between the two habitat types add support to the notion that rock habitats are of higher quality than flatland. If rock habitats do act as “sources” for the surrounding flatland “sinks”, and if flatland habitats are “true sinks” (relying on immigration to sustain their populations) rather than “pseudosinks” (able to sustain themselves at equilibrium without immigration), there may be serious consequences of fuel reduction practices in this area. Active removal of dead trees or “fuel” could affect the local abundance and diversity of lizards within the rock habitats by reducing the amount of shelter available to the terrestrial lizard species, and the number of sites available to the arboreal species for basking, feeding, courting, and defending territories. The consequences may be much greater because changing source-sink dynamics between rock and flatland habitats may not only affect the local abundance, number and diversity of lizards in the surrounding flatland habitat, but also have serious implications for persistence at the scale of metapopulations. However, the degree to which lizard associations with the rock habitat are based on the presence of dead vegetation rather than the degree of rock structure is not known. A study of lizard distributions, habitat use, fecundity, and survivorship between
rock habitat devoid of dead trees, and rock habitat as I have described it, could identify
the relative importance of rock structure and dead vegetation in the distribution and
abundance of these species.

Despite observed preferences and associations of all four lizard species with dead
vegetation and rock habitats, all species coexist on the mesas of Colorado in both rock
and flatland habitats. Many studies have suggested niche partitioning as a mechanism of
coeexistence of ecologically similar species, and I examined the microhabitat use and
consistency of relative abundance of the species over time as possible explanations for
their broad syntopy. Over 3 study years, 2 major microhabitat niche differences were
consistently observed: the microhabitat niche of S. graciosus was distinguished from the
other species by the use of more open flat sandy areas with less rock, and the microhabitat
niche of U. ornatus was distinguished by higher perch height and more vertical substrate.
Microhabitat differences were observed among all species pairs other than S. undulatus
and U. stansburiana, which may differ in the trophic dimension with respect to prey size.
However, the observed changes in relative abundance of the species over time suggest
that coexistence within this assemblage may not require niche differentiation, but rather
may result from non-equilibrium dynamics.

Intraspecific interactions are often of greater consequence than interspecific
interactions, and strong intraspecific competition may allow coexistence between
competitors in resource-limited environments. I observed greater habitat separation
within than among species. While species were found to coexist across habitats and
partition microhabitat within each habitat, I found lizards within each species to separate
between flatland and rock habitats by age and size. The majority of small, hatchling
lizards were observed in the flatland and the majority of large, adult lizards were
observed in the rock habitat. This size distribution of lizards within each species between the seemingly ideal rock habitat and the suboptimal flatland suggests that residence in the rock habitat may be limited. This limitation, combined with the territorial nature of these species and their potential to form size-based dominance hierarchies, may lead to intraspecific competition for territories within the rock habitat. The subsequent establishment of successful dominants, and the exclusion of hatchling subordinates to the flatland. Strong intraspecific competition for space within habitats, may then also contribute to the coexistence of these four closely-related species.

Further study of this lizard assemblage is warranted to distinguish between ideal and suboptimal habitats, to decipher the existence of source-sink dynamics and ontogenetic habitat shifts, and to determine the importance of dead vegetation in the microhabitats of these species. Long-term observational studies of immigration, emigration, fecundity, and survivorship in flatland and rock habitats would allow identification of the mechanism of ontogenetic habitat shifts and indicate whether this size-biased dispersal results in source-sink dynamics. Behavioural studies of all species throughout the active season would aid in determining the contribution of intraspecific aggression and predation to the distribution of lizards between habitats, and would identify interspecific competition should it occur.
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Appendix 1. Summary of microhabitat characteristics (prior to transformation) used in principle components analyses. Means and standard error are presented for each species. Perch height is given in m and mean tree volumes in 1992 are in m$^3$ (tree height X greatest crown diameter X least crown diameter). Live tree volumes in 2000 were recorded in volume classes based on mean dimension, ranging from 1 (< 1 m) to 4 (4-8 m). Dead tree size in 2000 is in m$^2$ (length X largest diameter). Capture point substrate type is categorical, and was assigned numerical values from 100-107 in 1990, 1-8 in 1992 and 100-105 in 2000, values increasing with verticality of substrate type (e.g. bare ground, rock, dead prone trees, dead standing trees, then live trees). In 1992, if a lizard was observed on only one capture point substrate type, -999 was recorded for the 2nd substrate type. In all years, microhabitat characteristics other than those relating to capture site were recorded within a 5-m radius of the capture site. In 1990, rock structure ranged from 1 (deeply dissected gullies and massive ledges) to 5 (flatland pinyon-juniper woodland - no rock). In 2000, rock development ranged from 1 (erosion exposed flat rock) to 4 (rock walls and scoured washes), and % rock cover ranged from 0 (no rock) to 5 (80-100% cover).

<table>
<thead>
<tr>
<th>Year</th>
<th>Microhabitat characteristic</th>
<th>U. ornatus Mean</th>
<th>U. ornatus SE</th>
<th>S. undulatus Mean</th>
<th>S. undulatus SE</th>
<th>S. gracilis Mean</th>
<th>S. gracilis SE</th>
<th>U. stansburiana Mean</th>
<th>U. stansburiana SE</th>
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<td>1990</td>
<td>perch height</td>
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<td>0.13</td>
<td>0.24</td>
<td>0.08</td>
<td>0.22</td>
<td>0.04</td>
<td>0.02</td>
<td>0.02</td>
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<td>capture point substrate</td>
<td>102.21</td>
<td>0.28</td>
<td>101.63</td>
<td>0.22</td>
<td>101.45</td>
<td>0.20</td>
<td>100.94</td>
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<td>0.73</td>
<td>0.08</td>
<td>0.67</td>
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<td>0.09</td>
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<td>0.05</td>
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<td>0.11</td>
<td>0.26</td>
<td>0.07</td>
<td>0.24</td>
<td>0.05</td>
<td>0.22</td>
<td>0.07</td>
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<td>0.00</td>
<td>0.06</td>
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<td>87.08</td>
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**Vita Auctoris**

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