

Resource Partitioning and Ecomorphology across Levels of Biological Organization
in Spiny Lizards, genus *Sceloporus*

By

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Abstract

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This dissertation focuses primarily on closely-related species' coexistence and how it is both a function and a driver of phenotypic evolution. To understand how phenotypic diversity evolves in relation to a species' interactions and evolutionary history, I focus on ecomorphology—an organism's ecological role and morphological adaptations. My dissertation uses field and museum-based methods to quantify the dynamics of ecomorphological evolution within the genus *Sceloporus*, a radiation of ~100 lizard species, and how it influences species' resource use and distributions, from sites to landscapes to continents, and from populations to communities to the entire genus.

Chapter I of my dissertation examines the relationship between resource use and phenotypic variation among four species of co-occurring lizards in a sky island system, the Chiricahua Mountains of southeastern Arizona. This isolated environment provides an opportunity to quantify resource use where forces of selection are expected to be strong. I quantified niche use of 300+ co-occurring lizards across multiple axes to determine their relative importance and found that perch height and type explained most variance between species, but I also uncovered variation in the temporal and thermal activity of these interacting species. By measuring phenotypic traits for all individuals, I found that species differed in traits associated with climbing ability, suggesting a coevolved relationship between physical traits and divergent niches.

In Chapter II, I explored another resource axis along which many co-occurring species differentiate by quantifying the trophic ecology of the *Sceloporus* species in the Chiricahua Mountains. Using DNA metabarcoding, I found significant differences in species' diets concomitant with their respective ecologies as uncovered in Chapter 1. As sit-and-wait predators, diet is a function of microhabitat, underscoring the importance of spatial niche partitioning in allowing co-occurrence in this system.

In Chapter III, I examined the dynamics of ecomorphological evolution in *Sceloporus* and its role in facilitating coexistence between congeners. By collecting ecological and morphological data for 80 taxa from 300+ specimens at 5 museums, I found that multivariate morphology is a good predictor of ecology and that *Sceloporus* species occur in six ecological modes with

associated morphologies (ecomorphs). I show that the evolution of arboreality at the base of a rapid radiation led to further ecological and morphological evolution. Examination of the spatial distribution of ecomorphology revealed a pattern of spatial overdispersion: across their range *Sceloporus* assemblages are comprised of more ecomorphs than expected by chance, suggesting ecological and morphological diversity play a key role in spatial sorting.

Together, the results of my dissertation suggest that across the *Sceloporus* radiation, ecology and morphology have evolved in concert and these traits influence the spatial distribution of populations, species, and assemblages.

For the blue bellies, who started this all.

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PREFACE

How closely-related species coexist given that they are likely to be ecologically similar as a result of shared evolutionary history has been a major question in biology since Darwin (1859). Our understanding of coexistence typically relies on interacting species offsetting their resource usage on one or more axes to settle at an allowable level of overlap, otherwise known as resource partitioning (Schoener 1974). Contemporary niche theory focuses on the effects of co-occurring consumers and provides a useful lens for quantifying species' resource use along relevant axes to understand co-occurrence (Letten et al. 2017). Examining multiple niche axes simultaneously can further reveal the relative importance in facilitating coexistence.

In many cases, assemblages of closely-related species reveal distinct forms associated with their respective ecological strategies (Williams 1972). For example, cichlid fishes with different feeding strategies have distinct mouth morphologies (Kocher 2004), and *Anolis* lizards reveal variation in limb and digit morphologies reflective of microhabitat (Losos et al. 1998). This relationship between an organism's ecology and its morphology, or ecomorphology (Arnold 1983), is useful in understanding how phenotypic variation accumulates within and between species and how it relates to broader ecological end evolutionary patterns. Examining ecomorphology in a phylogenetic and spatial context can lead to further insights about the role that processes such as interspecific competition have played in the diversification history of a given group. For instance, whether sister taxa have shared or divergent ecomorphologies can suggest the mechanism of divergence (Rundell and Price 2009). Similarly, whether ecomorphologically similar species tend to occur in sympatry or in allopatry can suggest whether patterns such as habitat filtering or limiting similarity, respectively, tend to structure communities (Webb et al. 2002). Finally, many striking examples of ecomorphs are the result of parallel or convergent evolution, underscoring an element of determinism in the way that natural selection acts upon phenotypes (Losos 2009; Gillespie et al. 2018).

Many landmark studies of ecomorphological evolution and resource partitioning occur on islands. As relatively isolated, closed systems, often with limiting resources, forces of selection on islands can be incredibly strong and lead to rapid cases of evolution (Shaw and Gillespie 2016). Sky islands, or mountains surrounded by vastly different lowland ecosystems, have similar properties and thus make excellent natural laboratories for studies of ecomorphology and resource partitioning (McCormack et al. 2009).

To understand how closely-related species coexist as a function of their ecomorphology, I focus on spiny lizard (genus *Sceloporus*). With over 100 species described, a range encompassing much of North and Central America where species often occur in sympatry, and habitat variation from the High Sierra to gypsum sand dunes to deserts, *Sceloporus* lizards provide an excellent opportunity to understand how ecological and morphological diversity accumulate and interact to shape patterns of coexistence (Hall 2009; Leaché et al. 2016; Roll et al. 2017).

In the following chapters, I present an empirical investigation of resource use between co-occurring species as it relates to phenotypic traits. Chapters I and II quantify resource use along the axes of structural habitat, activity time, substrate temperature, and diet among co-occurring *Sceloporus* lizards in a sky island system. Chapter III takes a broader approach by examining the ecology and morphology of the entire genus and asking how ecomorphological diversity has evolved and influences co-occurrence patterns.

By combining field and museum studies, my dissertation provides a rare opportunity to understand whether shared mechanisms underscore patterns of resource use, ecology-morphology relationships, and patterns of coexistence across spatial scales and levels of biological diversity.

CHAPTER I

Phenotypic diversity facilitates niche partitioning in a sky island assemblage of spiny lizards

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Abstract

If closely-related species should be more similar and, therefore, more likely to compete for resources, why do we see so many examples of species-rich congeneric communities in nature? To avoid competition, many species possess suites of traits associated with resource use—or ecomorphologies—that promote niche differentiation with co-occurring species. Yet, the axes through which niche partitioning evolve and the traits involved are still poorly understood in most systems. Island systems, in which species interactions can form strong forces of selection due to limited resources, provide valuable insights into how ecomorphological diversity contributes to coexistence. Here, we examined axes of resource use and morphological traits that facilitate niche partitioning in a community of spiny lizards (genus *Sceloporus*) in a sky island system, the Chiricahua Mountains of southeastern Arizona. By quantifying structural, temporal, and thermal niche use for over 300 co-occurring lizards from four species over three field seasons, we show that sympatric species diverge primarily in perch height and type but also in thermal and temporal resource use. Our results also demonstrate interspecific divergence in a suite of phenotypic traits known to covary with ecology in other lizard radiations, including body size, scale size, hindlimb length, foot length, and dorsal coloration. Studies of niche partitioning and ecomorphology, especially of closely-related species, deepen our understanding of how diverse communities assemble and how morphological diversity accumulates across the tree of life, and our findings highlight the importance of examining multiple axes of resource use to better understand these processes.

Introduction

Despite theoretical predictions and empirical observations that closely-related species should be ecologically similar and therefore more likely to compete for resources (Schoener 1974; Violle et al. 2011), there are abundant examples of species-rich congeneric communities in nature. Mechanisms of species coexistence rely on assumptions of divergent niches (Schoener 1974). While the niche concept has undergone many iterations from a species' habitat (Grinnell 1917) to its function (Elton 1927) to the set of factors allowing persistence (Hutchinson 1957), contemporary niche theory focuses on resource use and the effects of co-occurring consumers (Letten et al. 2017). According to limiting similarity, species may overlap along some resource axes while differentiating along others, settling at an allowable level of niche overlap that permits coexistence (Volterra 1928; MacArthur and Levins 1967). Understanding community assembly and dynamics therefore requires a quantitative understanding of resource use among co-occurring species along major niche axes (Pianka 1973).

Studies of species' morphologies as related to their resource use (ecomorphology) inform our understanding of how both characteristics evolve and their interactions (Arnold 1983). To facilitate partitioning of available resource space, many coexisting species exhibit divergent ecomorphologies (Losos 1990). In assemblages of closely-related species, ecomorphology can reveal tradeoffs between ecological opportunity and extrinsic and intrinsic limitations (Emerson and Gillespie 2008). Island communities, with limiting resources and typically large distances from source populations, can provide relatively isolated, closed systems in which to study how species interact and partition ecological space (Shaw and Gillespie 2016). Studies of island assemblages such as the Caribbean *Anolis* lizards, Galapagos finches, and Hawaiian *Tetragnatha* spiders have shown that ecomorphological diversity facilitates coexistence and often evolves as a direct result of competitive interactions (Schoener 1968; Grant 1986; Gillespie et al. 2018). Other island assemblages are formed by the repeated colonization of ecologically diverse species (Emerson and Gillespie 2008); when sister taxa are ecomorphologically similar, it can limit their ability to coexist (Kozak et al. 2005; Lovette and Hochachka 2006). Island communities therefore provide an opportunity to understand how ecomorphology evolves across closely-related species and promotes, or hinders, diverse resource use.

Habitats with discrete boundaries, such as lakes or sand dunes, can act like islands by filtering out species (Verheyen et al. 2003; Nosil and Reimchen 2005; Bolnick and On 2008; Des Roches et al. 2016; Ford et al. 2016). "Sky islands"—isolated mountains separated by distinctly different lowland habitats—often have analogous eco-evolutionary dynamics to oceanic and lake islands (reviewed in McCormack, Huang, & Knowles, 2009). Their isolation also allows for replicate studies, as in other island systems. Many sky islands are also home to endemic species that cannot persist in the surrounding habitat and may have difficulty dispersing to other sky islands. The Madrean Sky Islands, a chain of high-elevation mountain peaks surrounded by the low-elevation Sonoran and Chihuahuan deserts that occur between the Mogollon Rim in Arizona and New Mexico, USA, and the Sierra Madre Occidental in Sonora, Mexico (Warshall 1995), are one such system. The Chiricahua Mountains, one of the largest in the Madrean sky islands complex, are home to a wide variety of endemic taxa and a community of four spiny lizard (genus *Sceloporus*) species that are regularly found in syntopy.

Here, we examined spatial (Pianka 1966), temporal (Simon and Mittermeier 1976; Gordon et al. 2010), and thermal (Grover 1996) niche partitioning between four co-occurring sky island *Sceloporus* species (*S. clarkii*, *S. jarrovi*, *S. slevini*, and *S. virgatus*) and quantified the phenotypic traits associated with their respective ecologies. Spatial niche partitioning is a key driver of divergence in many lizard radiations, with repeated evolution of habitat-associated forms appearing in many diverse clades (Pianka 1966; Losos 1990). Partitioning of activity time can reduce competition for other resources, such as food or space, and thereby promote coexistence (Schoener 1974; Gordon et al. 2010). Different thermal physiologies in ectotherms can provide distinct responses to abiotic conditions, manifesting as unique niche exploitation and enabling sympatry (Smith and Amarasekare 2018). Examining multiple niche axes simultaneously provides an opportunity to quantify the relative importance of each in allowing coexistence between similar, co-occurring species (Schoener 1974).

The *Sceloporus* lizards of the Chiricahua Mountains are survivors of historical climate warming that drove lowland populations between the Madrean Sky Islands and their core range in the Sierra Madre Occidental to extinction (Tennesen and Zamudio 2008; Bryson et al. 2012; Wiens et al. 2019). The Chiricahua Mountains are, thus, at or near the northern extent of the ranges of *S. virgatus*, *S. jarrovi*, and *S. slevini*, and there is evidence that the Chiricahua populations of these three species are genetically distinct from other populations (Tennesen and Zamudio 2008; Bryson et al. 2012; Wiens et al. 2019). Given the isolated nature of the *Sceloporus* species in the Chiricahua Mountains relative to other parts of their ranges, we expect community dynamics in this system to play out much as they would on an oceanic island. We conducted a field study over three consecutive seasons to determine if and how the sympatric *Sceloporus* lizards partition niche space along key resource axes in this system.

In his seminal paper on resource partitioning, Schoener (1974) laid out a series of questions that studies should seek to answer to improve our understanding of how ecological communities partition resources. Question one asks about the mechanism of competition and how predation and reproductive isolation may play a role in driving interspecific differences. To assess the main mechanism of competition, we quantified the relative importance of resource use along major axes of competition among lizards in general. We also examined the degree of color-matching against utilized backgrounds, a predator avoidance mechanism that can also promote differential microhabitat use between species (Lillywhite et al. 1977; Gillis 1989; Cooper Jr. and Wilson 2010; Pérez i de Lanuza and Carretero 2018). Because the genes implicated in cryptic coloration affect the colorful ventral patches many *Sceloporus* species use for communication and recognition (Quinn and Hews 2003; Robertson and Rosenblum 2009; Zúñiga-Vega et al. 2021), coloration is a key trait for understanding the influence of both predation and reproductive isolation on niche differentiation. Questions two, three, and five ask about the spacing and relative importance of niche axes and how axis importance may change with increasing species numbers (Schoener 1974). We address these questions by comparing the importance of resource dimensions between two and three-species communities, across environments, and in different combinations of syntopic species. Further, these data are used to address question four—whether niches are complementary—and question seven—how niche distance compares between species pairs. To address question six—the relationship between niche differentiation and phenotypes—we quantified body size (Rivera et al. 2021), hindlimb length (Losos 1994; Losos et al. 1997), foot morphology (Losos 1990; Yuan et al. 2018), scale size (Sinervo et al. 2010; Oufiero et al. 2011; Wegener et al. 2014), and head dimensions

(García-Rosales et al. 2019), all of which are ecologically-important traits in other lizard radiations. These seven questions have seldom been addressed in single studies, yet doing so can illuminate how niche partitioning evolves and regulates species diversity.

Methods

Study System

Comprised of about 40 mountains, the Madrean sky islands are named for the enclaves of Madrean pine-oak habitat that occur between a “sea” of Sonoran and Chihuahuan desert. The variety of biotic communities in proximity provides important habitat refuge for many species and is home to some of the most biodiverse communities in the region (Cahalane 1939; Spector 2002). The highest point of the Chiricahua Mountains, one of the largest mountain ranges in the Madrean Sky Islands, reaches nearly 3000m, and the range itself contains five life zones. This land is ancestral Chiricahua Apache territory and is now owned and managed by the United States Forest Service and the National Park Service.

We chose three sites along an elevational gradient based on occurrence records of *Sceloporus clarkii*, *S. jarrovi*, *S. slevini* and *S. virgatus* and to represent unique biotic communities—from the foothills to high elevation the sites are referred to, respectively, as the Madrean oak woodland (5600’), Madrean pine-oak forest (6800’), and montane conifer forest (8220’; Fig. 1.1). Though some references include *S. bimaculosus* and *S. cowlesi* as potential parts of the Chiricahua community, we found them very infrequently and exclusively in the intermontane desert sea and therefore did not include them in this study. Other lizards in the area include whiptails (genus *Aspidoscelis*), horned lizards (genus *Phrynosoma*), tree lizards (genus *Urosaurus*), and alligator lizards (genus *Elgaria*); we selected sites specifically where *Sceloporus* lizards were the most abundant lizards. With the exception of tree lizards (Bergeron and Blouin-Demers 2020), we expect the other lizards present do not overlap in niche space with *Sceloporus*, as they have distinct dietary niches (Pianka and Parker 1975), foraging styles (widely foraging, *Aspidoscelis*, vs. sit-and-wait in *Sceloporus*), and habitat preferences (*Phrynosoma* and *Elgaria* are obligately terrestrial species). We recorded observations of each non-*Sceloporus* species, but, since there were so few, they were not included in this study.

Field Surveys

In 2019, 2020, and 2021, we surveyed for *Sceloporus* lizards in the Madrean oak, Madrean pine-oak, and montane conifer habitats of the Chiricahua Mountains, each of which contains a unique combination of species. Animal care and field surveys were approved by the University of California Berkeley’s Institutional Animal Care and Use Committee (Protocol AUP-2019-02-11797), collection permits were issued by Arizona Game and Fish Department (LIC#SP653941, SP404320, and SP407158), and land access was granted by Coronado National Forest, Douglas Ranger District. We surveyed sites at different times of day from 0600h to 1800h and across the active summer season from May to August to account for variation in the thermal environment and the temporal activity of these species. Within each site we selected four 300m transects at the same elevation and orientation, chosen to maximize spatial co-occurrence of *Sceloporus* species and to minimize effects on other long-term studies in the area. During the survey period we randomized which sites were visited on a given day and the order in which we

walked the transects. We standardized survey effort (given by person search-hours) between the three elevational sites. Lizards were caught by hand or with a lizard lasso. We recorded snout-vent length (SVL), tail length, and body mass and identified the sex of each lizard by visually inspecting the base of the tail, postanal scales, and color patches on the chin and belly. Lastly, we gave all lizards temporary, unique marks and returned them to their original perches; lizards were not recaptured.

Niche Characterization

For each lizard caught, we recorded environmental data to characterize its spatial, thermal, and temporal niche. We recorded perch height and width using a flexible tape measure, substrate temperature (T_S) using a handheld infrared thermometer (Etekcity Infrared Thermometer 749), and perch type (i.e., rock, tree, leaf litter, bunchgrass). We recorded field body temperature, T_B , by pressing the infrared thermometer to the lizard's cloaca immediately after capture (Rosenblum 2005; Herczeg et al. 2008; Gilbert and Lattanzio 2016). For all niche comparisons, we used T_S rather than T_B , as lizards actively thermoregulate and therefore choose perch sites partially based on thermal properties. We recorded activity time as when we first observed the lizard either basking, displaying, or actively foraging (lizards in shelters were not considered active) rather than its time of capture.

Ecological Niche Partitioning

To characterize ecological niche partitioning, we performed an analysis of variance (ANOVA) for each of the three niche axes (perch height, T_S , and activity time) for each site. Transects within sites (Madrean oak woodland, Madrean pine-oak, and montane conifer forest) were pooled to provide sample sizes with sufficient statistical power. Before proceeding with ANOVA, we checked for normality using histograms and log-transformed any distributions that were not normally distributed. For perch height, which had many zero values (lizards found on the ground, 0m), we added a constant value (+1m) to all values before log transformation. Activity time was converted from military time to minutes past midnight to create a continuous distribution. Next, we checked the assumption of equal variances by computing per-species standard deviations for all three niche axes per site. We then conducted the ANOVAs using the 'aov' function in the 'stats' R package (R Core Team 2021); we included species and sex as predictors in our models. When ANOVAs were significant, we then performed post-hoc comparisons using Tukey's Honest Significance Difference (HSD) test between species and sexes. To estimate effect sizes, we calculated eta-squared values (η^2), which are used for analysis of variance tests and can be interpreted like R^2 values. For perch type, which was a categorical count distribution for each species based on use of different available substrates in each habitat, we used chi-squared tests to assess whether each species used one or several substrate types more than expected. As not all substrates were equally represented at a given site, we used the total distribution of substrates used by all lizards in a given site as a null distribution.

We calculated the mean distance in niche space between all species by taking their values along the quantitative niche axes—perch height, T_S , and activity time—standardizing values to a scale from 0 to 1, and calculating the three-dimensional distance between them. We also calculated the niche standard deviation for each species and the ratio between them, following question seven of Schoener (1974). To understand how variable intraspecific niche use is across sites and in the presence of different species, we compared the niche axes between different sites for two of our study species: *S. jarrovi*, which was found at all three sites, and *S. virgatus*, which

was found in Madrean oak and pine-oak habitats. We performed the ANOVAs with location and sex as variables and implemented Tukey's HSD post-hoc analyses for significant ANOVA results.

Color Differences and Substrate Matching

In the field, we took color-standardized photos of each lizard's dorsum, venter, and perch site using a Nikon D3500 digital camera coupled with a macro lens (AF-S DX Micro Nikkor 85mm F3.5 ED VR; Nikon Corporation., Japan). Images were recorded using the manufacturer's raw image format (.NEF). Depending on light conditions we added two Speedlight R-200 (Nikon) flashes parallel to the lizard. For standard exposure values, we used an incident light-meter Sekonic L308X-U (Seiko Electric Industries Co., Japan). To avoid harsh shadows and reflections, the lizard and X-Rite ColorChecker (X-Rite Inc., Grand Rapids, MI) used for color correction (see below) were placed inside of a 60 x 60 x 60cm translucent photography tent that helped diffuse ambient and speedlight flash. An additional handheld 60 x 90 cm foldable diffuser was used to limit direct sunlight and shadows in the photography tent. Perch sites were photographed with the X-Rite ColorChecker under the handheld diffuser.

Raw images were white balance and color corrected using the white balance tool in Adobe Lightroom Classic CC (Adobe Inc., California) and the 10% neutral grey target in the X-Rite ColorChecker Passport. If needed, minimal exposure correction was made by correcting mid-tones of the ColorChecker image histogram. Images were cropped to remove the ColorChecker and exported as full resolution sRGB JPEG with compression quality setting at 100%. The phenotypic area for analysis included the dorsum and venter between the fore- and hindlimbs.

We then read photos into R v3.6.1 using the 'getHistList' function in the package 'colordistance' to calculate average hue, saturation, and value (HSV) for the dorsum, venter, and perch site of each lizard (Weller and Westneat 2019). HSV measures of color more closely approximate vertebrate color vision than other color spaces (Endler and Mielke 2005; Endler 2012). Value is a measure of brightness (hereafter referred to as brightness), which vertebrates use to detect motion; we therefore predict that if lizards in this system select substrates on which they are more cryptic, dorsal brightness should predict perch brightness. Hue is a measure of dominant reflected wavelength, and saturation represents the relative intensity, or purity, of a color as a percentage. We tested for interspecific differences in dorsal and ventral HSV color using ANOVA. We then used linear models to assess the relationship between dorsal color components and perch color components. As body temperature can affect melanin-based coloration in *Sceloporus* lizards (Langkilde and Boronow 2012; Assis et al. 2020), we included T_B as a covariate in our analysis.

Morphological Measurements

To obtain morphometric measurements of ecologically-relevant body traits, we imported photos into Adobe Photoshop (Adobe Inc., California) and used the linear measurement tool and the scalebar in the X-Rite Color Checker Passport to measure snout-vent length, head width, head length, forelimb length (humerus plus radioulna), hindlimb length (femur and tibiofibula), and longest toe length (hindfoot fourth toe) in centimeters. From photos we recorded whether individuals had enlarged postanal scales to corroborate field sex identification. We counted the number of dorsal and ventral scales in a 1cm² square to estimate scale size following (Wegener et

al. 2014). All measurements were performed by at least two independent measurers and averaged.

Ecomorphology

We performed a principal components analysis (PCA) on our morphometric measurements to evaluate how species were distributed within morphological space. As body size accounted for much of the variation between species, we performed two PCAs, one with raw trait values and one with the residuals of regressions for each trait against body size. We further tested how traits varied between species and sexes using ANOVA and performed post-hoc analyses using Tukey's HSD for significant comparisons. Rather than explore every trait, we selected a handful of morphological traits known to vary in meaningful ways between lizard ecomorphs in other radiations: hindlimb length is correlated with perch diameter and height in *Anolis* lizard ecomorphs in both natural and experimental populations (Losos 1994; Losos et al. 1997) as is foot morphology (Losos 1990; Yuan et al. 2018). Scale size covaries with microhabitat conditions, especially humidity, as scales are thought to reduce evaporative water loss (Sinervo et al. 2010; Oufiero et al. 2011; Wegener et al. 2014). Head dimensions, especially width, correlate with bite force and diet preferences in many lizards, including some *Sceloporus* species (García-rosales et al. 2019). For all traits except SVL, we used body size corrected residuals. We estimated effect sizes as η^2 . Next, we used linear regressions to determine whether habitat use is explained by morphology. We regressed the individual ecologically-relevant traits as well as the first PC axis from the PCA of the raw morphological traits (PC1) on the three ecological niche axes we measured; we included species and sex as predictors in each analysis.

Results

Field Surveys

We captured 323 lizards across the three sites at low, mid, and montane conifer forest. Standardized search effort between the three sites resulted in comparable sample sizes between sites but not necessarily between species (Table 1.1). Though sample sizes were uneven due to the relative rarity and difficulty of capturing *S. clarkii*, standard deviations were comparable for all niche axes at all sites.

Ecological Niche Partitioning

We found strong evidence for partitioning of perch height between species across all sites (Fig. 1.2). In the Madrean oak woodland, species differed significantly in perch height ($F = 20.445$, $p < 0.001$, $\eta^2 = 0.286$), with *S. clarkii* and *S. jarrovii* perching higher off the ground than *S. virgatus* ($p < 0.001$ for both, Fig. 2A). The two large species, *S. jarrovii* and *S. clarkii*, did not differ significantly in perch height ($p = 0.945$, Fig. 2A). In the Madrean pine-oak habitat, we also found significant perch height differences between species ($F = 145.22$, $p < 0.001$, $\eta^2 = 0.620$), and *Sceloporus jarrovii* again perched significantly higher than *S. virgatus* ($p < 0.001$). In the montane conifer forest, *S. jarrovii* perched significantly higher than *S. slevini* ($F = 241.149$, $p < 0.001$, $\eta^2 = 0.702$). We did not find any evidence of perch height partitioning by sex, either within or between species.

We also found evidence for thermal niche partitioning—in the montane conifer forest, *S. slevini* used significantly cooler perches than *S. jarrovii* ($F = 10.102$, $p = 0.003$, $\eta^2 = 0.054$). We did not find significant differences in T_s at either of our other study sites (Fig 1.2). On the

temporal axis, *S. clarkii* was active significantly earlier than *S. jarrovii* and *S. virgatus* ($F = 12.273$, $p < 0.001$, $\eta^2 = 0.175$) in the Madrean oak woodland. In the montane conifer forest, *S. slevini* was active later in the day than *S. jarrovii* ($F = 5.631$, $p = 0.021$, $\eta^2 = 0.095$). We did not find a significant difference in activity time between *S. jarrovii* and *S. virgatus* in the Madrean pine-oak habitat (Fig. 1.2).

Interspecific niche distances ranged from 0.094 between *S. slevini* and *S. virgatus* to 0.402 between *S. clarkii* and *S. slevini* (Table 1.2). *Sceloporus jarrovii* and *S. virgatus* occupy more intermediate distances to the other species in niche space. Among the niche axes we measured, we found that perch height exhibited the greatest ranges in both means and standard deviations between the four species (Table 1.3).

We also uncovered several statistically significant relationships between species and their chosen substrate types, particularly for *S. jarrovii* and *S. slevini*. In the Madrean oak woodland, *S. jarrovii* was significantly more likely to perch on rocks than other substrates ($\chi^2 = 11.405$, $p = 0.009$). In the Madrean pine-oak habitat, *S. jarrovii* used rocks more than any other substrate as well; however, given that rocks were also the most available substrate, this was not statistically significant ($\chi^2 = 3.823$, $p = 0.147$). In the montane conifer forest, where logs are more abundant and rocks are scarce, *S. jarrovii* strongly preferred to use logs compared to perching on the ground ($\chi^2 = 28.91$, $p < 0.001$). *Sceloporus virgatus* exhibited no preference in the Madrean oak woodland but in the Madrean pine-oak habitat preferred to perch on rocks compared to the ground, logs, or trees ($\chi^2 = 7.647$, $p = 0.021$). *Sceloporus clarkii* exhibited no significant preference between perch types in any habitat. *Sceloporus slevini* strongly preferred bunchgrass to other substrates, including the ground (non-bunchgrass), logs, and rocks ($\chi^2 = 77.4$, $p < 0.001$).

Between sites, *S. jarrovii*, which occurred at all three sites, was consistent in its perch height and T_s . The only difference we observed for this species between sites was in activity time, with lizards in the pine-oak habitat active later in the day compared to either the oak woodland or montane conifer forest ($F = 4.224$, $p = 0.017$, $\eta^2 = 0.810$). *Sceloporus virgatus* exhibited consistent T_s between the two sites at which it was found but perched higher and was active earlier in the day in the oak woodland compared to the pine-oak forest ($F = 8.98$, $p = 0.003$, $\eta^2 = 0.073$; $F = 4.10$, $p = 0.046$, $\eta^2 = 0.048$).

Morphological Measurements

We found that species differed significantly in several ecologically-relevant morphological traits, including body size, head width, hindlimb length, fourth toe length, and scale size, and these traits significantly predicted niche use, particularly perch height. All traits except for body size were taken as residuals of a regression against body size (e.g., body size corrected). All species pairs differed significantly in SVL, except the two smallest species, *S. virgatus* and *S. slevini*. *S. clarkii* is the largest followed by *S. jarrovii* ($F = 211.038$, $p < 0.0001$, $\eta^2 = 0.727$). *Sceloporus slevini* and *S. virgatus* had narrower heads than *S. jarrovii*, with *S. slevini* having the narrowest head ($F = 10.622$, $p < 0.001$, $\eta^2 = 0.116$). *Sceloporus slevini* had significantly shorter hindlimbs than all other species ($F = 30.614$, $p < 0.0001$, $\eta^2 = 0.281$). The fourth toe length differed significantly between species ($F = 21.17$, $p < 0.0001$, $\eta^2 = 0.225$): *S. clarkii* had the longest toe length, followed by *S. jarrovii*, then *S. virgatus*, and finally *S. slevini* (all $p < 0.001$). All species pairs differed in scale size ($F = 33.90$, $p < 0.0001$, $\eta^2 = 0.296$), with the exception of *S. slevini* and *S. virgatus*. *Sceloporus clarkii* had the largest scales (all $p < 0.001$), and *S. jarrovii* had larger scales than *S. slevini* and *S. virgatus* ($p = 0.002$; $p < 0.001$).

respectively). Sex predicted intraspecific differences in SVL, with females of all species being larger than males ($F = 4.762$, $p = 0.030$, $\eta^2 = 0.005$), but was not a significant predictor of differences in any other traits.

Ecomorphology

The PCA plots revealed delimitation in morphospace between the four species (Fig. 1.3). Before body size correction, *S. jarrovii* and *S. slevini* are clearly differentiated along PC1, while *S. clarkii* stands out from the other species on PC2, and *S. slevini* and *S. virgatus*, the two smallest species, are also differentiated along PC2. *Sceloporus jarrovii* occupies the largest region of morphospace and *S. clarkii* the smallest, though the latter is likely an artefact of small sample size. *Sceloporus slevini* also clusters tightly in morphospace, and, to a lesser extent, so does *S. virgatus* (Fig. 1.3A), but much less so after body size correction (Fig. 1.3B).

PC1 of the raw morphology PCA (Fig. 1.3A), which largely correlated negatively with body size and explained 91.5% of the overall variance in trait values, significantly predicted perch height ($p < 0.0001$, $F = 39.42$, $R^2 = 0.452$, slope = -0.166) and T_s ($p < 0.0001$, $F = 6.346$, $R^2 = 0.1216$, slope = 1.392) but not activity time ($p = 0.118$, $F = 1.77$, $R^2 = 0.016$, slope = 0.004; Fig. 4). Larger lizards perched higher and preferred cooler temperatures but did not have a significant relationship with activity time (Fig. 1.4). We tested individual traits against niche axes and found that body size and body size corrected head width, hindlimb length, fourth toe length, and dorsal scale size were all positively correlated with perch height (all $p < 0.001$, all $R^2 > 0.55$) and negatively correlated with T_s (all $p < 0.015$, all $R^2 > 0.05$).

Color Differences and Substrate Matching

We uncovered significant differences between species at each site for dorsal and ventral coloration (Fig. 1.5). Dorsal hue differed significantly between *S. virgatus* and *S. jarrovii* in the Madrean pine-oak habitat ($p < 0.001$) and between *S. jarrovii* and *S. slevini* in the montane conifer forest ($p = 0.004$). Dorsal saturation also varied between species: in the Madrean Oak woodland, *S. virgatus* and *S. clarkii* ($p = 0.025$), in the Madrean Pine-Oak, *S. virgatus* and *S. jarrovii* ($p = 0.002$), and in the Montane Conifer Forest, *S. slevini* and *S. jarrovii* ($p < 0.001$) all differed significantly in saturation. In brightness/value, *S. virgatus* and *S. jarrovii* differed significantly in the Madrean oak woodland and pine-oak habitats ($p < 0.001$, both). In the montane conifer forest, *S. slevini* and *S. jarrovii* differed significantly in brightness ($p < 0.001$). Sex and body temperature were not significant predictors of dorsal hue, saturation, or value for any species or sex at any site.

Ventral hue differed significantly between *S. virgatus* and *S. clarkii* ($p = 0.017$) in the Madrean oak woodland, between *S. virgatus* and *S. jarrovii* in the Madrean Oak Woodland ($p < 0.001$) and in the pine-oak habitat ($p < 0.001$), and between *S. slevini* and *S. jarrovii* in the montane conifer forest ($p < 0.001$). *Sceloporus virgatus* differed in ventral saturation from *S. clarkii* in the Madrean oak woodland ($p = 0.020$) and from *S. jarrovii* in the pine-oak habitat ($p = 0.001$). *Sceloporus slevini* and *S. jarrovii* differed in ventral saturation as well in the montane conifer forest ($p = 0.001$). Ventral brightness differed between *S. virgatus* and *S. jarrovii* in the Madrean oak woodland ($p < 0.001$) and in the pine-oak habitat ($p < 0.001$). *Sceloporus slevini* and *S. jarrovii* also differed significantly in ventral brightness ($p < 0.001$).

Our linear models revealed significant links between lizard coloration and substrate coloration. Dorsal saturation predicted perch saturation for *S. slevini* ($T = 3.0$, $p < 0.001$, $R^2 = 0.38$). Dorsal brightness predicted perch brightness for *S. slevini* and *S. virgatus* ($T = -2.548$, $p = 0.014$; $T = -2.378$, $p = 0.018$). For *S. slevini*, ventral saturation significantly predicted perch saturation ($T = 3.650$, $p < 0.001$, $R^2 = 0.38$), and ventral brightness predicted perch brightness ($T = 2.378$, $p = 0.018$, $R^2 = 0.018$).

Discussion

Studying congeneric assemblages in isolated environments provides a powerful opportunity to examine how niche differences and ecomorphologies evolve in relation to community processes. Here, we quantified resource use, phenotypes, and the relationships between them for four *Sceloporus* species that have been stranded on montane sky islands by ancient climate warming to better understand how closely-related species interact in resource-limited environments. Our findings, aimed at answering seven fundamental questions to comprehensively address the key factors involved in differential resource use (Schoener 1974), shed new light on how congeneric species evolve to partition niche space.

1) *What is the mechanism of competition? What is the relative importance of predation? Are differences likely to be caused by pressures toward reproductive isolation?*

Across all sites, species differed most in perch height and type, suggesting the main mechanism of competition is space, specifically access to perch sites that lizards use for thermoregulatory behavior, advertising to potential mates, and signaling defense of territories. This complements previous work demonstrating that structural microhabitat is a key axis of competition for lizard communities (Parker and Pianka 1973; Losos 1995; Bergeron and Blouin-Demers 2020). The *Sceloporus* species in the two-species communities in the Madrean pine-oak and montane conifer forest habitats differed significantly in both perch height and type. In the three-species Madrean oak woodland, *S. jarrovii* and *S. clarkii* differed significantly from *S. virgatus* in perch height but did not differ significantly from each other. They did, however, differ significantly in activity time, suggesting the main mechanism of competition is still space and that to make use of the same perches, the two species must partition the times at which they occupy them.

In addition to competition for space driving differences in perch height, *S. virgatus* and *S. jarrovii* have been shown to differ in perch height and use as a function of predator-escape strategy (Cooper and Avalos 2010), so predation, too, is likely an important driver of niche partitioning in this system. Another predation-avoidance adaptation found in many reptiles is coloration that matches common substrates, or crypsis (Norris and Lowe 1964). In other *Sceloporus* lizards, dorsal color matching has been shown to influence preferred substrate use differentially between species, thereby contributing to niche partitioning (Lillywhite et al. 1977). We uncovered significant differences between species in all color components for dorsal and ventral coloration, indicating that these could be important traits influencing both habitat selection and interspecific recognition (and, therefore, reproductive isolation). Though body temperature is known to affect melanin-based coloration in reptiles (Sherbrooke et al. 1994), we did not recover a significant effect of T_B on color for any species or either sex, suggesting that adaptive color differences outweigh plastic effects in this system.

Of all color components, dorsal brightness has been demonstrated to predict perch and substrate brightness in other *Sceloporus* (Orton and McBrayer 2019). Vertebrates use differences in brightness to detect motion, putting dorsal brightness under strong selective pressure. We recovered a significant relationship between dorsal brightness and perch brightness for the two smallest species, *S. slevini* and *S. virgatus*. Differences in anti-predator strategy are implicated in the degree of substrate matching, with species that prefer to flee relying less on crypsis (Orton and McBrayer 2019). *Sceloporus slevini* has the shortest hindlimbs relative to its body size, and limb length affects sprinting capability in lizards (Losos 1990; Sinervo and Losos 1991). This species may, therefore, rely more on crypsis than flight behavior, thus subjecting it to stronger pressure for substrate matching. Additionally, the blue and orange ventral patches of *S. slevini* were significantly negatively correlated with perch color in saturation and value. This suggests dual selective pressures acting upon this species: strong color matching for crypsis on the dorsum while maintaining color contrast on the venter, likely for intraspecific signaling as in other *Sceloporus* (Robertson and Rosenblum 2009; Hews and Martins 2013).

Despite that *S. clarkii* is a strongly arboreal species and has a greenish-blue dorsum, we did not uncover a signal of substrate matching for this species along any color axis. Of all species, *S. clarkii* is most likely to be affected by detection bias by human observers as these lizards tend to perch very high in trees and are only observed while basking lower on tree trunks. Selection for color matching may be stronger in the treetops where they are more visible to overhead, avian predators. *Sceloporus jarrovi*, similarly, is superficially cryptic on the granite boulders where it often perches; however, in this system it also readily makes use of trees and logs, potentially swamping any color matching relationship.

Overall, we do not posit that niche partitioning is driven by reproductive isolation in this system. Competition for perch sites, which is important in many aspects of lizard behavior (e.g. thermoregulation, foraging, predator escape) in many systems, appears to play a strong role in niche partitioning among these *Sceloporus*.

2) Are niches (utilizations) regularly spaced along a single dimension?

For two species, *S. slevini* and *S. clarkii*, niche use is very narrowly spaced along the axes of perch height and type (Fig. 1.2). Bunchgrass lizards, *S. slevini*, were nearly always found perched low to the ground in or around bunchgrass clusters, though at one of our transects (Rustler Park) where bunchgrass was scarce they used other vegetation. Individuals of *S. clarkii* were likely to be found perched high among trees. The other two species appear more generalist and varied their niche use: *S. jarrovi* preferred to perch on medium-to-high rocks where available in the oak woodland and pine-oak forest and shifted to using logs in the montane conifer forest where rocks were scarce. *Sceloporus virgatus* appears even more generalist in its perch choice, selecting the ground, logs, rocks, and trees in roughly equal proportions to their availability. Despite using a variety of substrates, they perched lower to the ground (or on the ground) compared to the other species with which they co-occur, suggesting that perch height may be more important than type to *S. virgatus*. In general, species are spaced along the perch height axis with *S. slevini* preferring the lowest perches (mean = 0.009), followed by *S. virgatus* (mean = 0.034), with *S. jarrovi* (mean = 0.184) and *S. clarkii* (mean = 0.393) both using high perches. Hence, we find that niche partitioning along the primary axis of perch height is irregular, with the normalized mean distance between *S. jarrovi* and *S. clarkii* almost an order of magnitude greater than the mean distance between *S. slevini* and *S. virgatus* (Table 1.2). Along

with their differences in niche breadth along this axis, this suggests that competition for perch height is not evenly balanced among these four species and that resource use along the perch height axis is not evenly partitioned.

3) *How many dimensions are important, and is there a tendency for more dimensions to be added as species number increases?*

We found that all three niche axes explored here were important in various communities. Perch height and type varied most significantly across all communities, both two and three-species communities (Fig. 1.2; Table 1.3). In the montane conifer forest, we also found evidence for thermal and temporal partitioning (Fig. 1.2). Likely, these three axes are inter-related; the thermal environment varies among perches and across the day. *Sceloporus slevini* preferred the lowest substrate temperatures of any in this study; regulating their activity time and substrate use may therefore be behavioral modifications to achieve desired temperatures. In comparative works, close relatives of *S. slevini* (*scalaris* group) also revealed lower field body temperatures than many other *Sceloporus* species (Andrews 1998), suggesting thermal constraints may be shared within this group. *Sceloporus virgatus* and *S. slevini* have been shown to maintain constant body temperatures despite fluctuating air temperatures throughout the seasons (Smith and Ballinger 1994; Ballinger and Congdon 1996), underscoring the importance of active thermoregulation for these lizards. Though studies that quantify T_B , T_{pref} , and T_S are numerous for individual species in this system (Smith and Ballinger 1994; Andrews 1998), more comparative work is needed to fully understand the scope of thermal partitioning as it relates to other ecological requirements and preferences.

Within the three-species community in the Madrean Oak Woodland, we uncovered differences in activity time between *S. jarrovii* and *S. clarkii*. Population genomic data and distributional analyses have suggested that *S. jarrovii* excludes *S. clarkii* from high elevations and is thus the greater competitor despite being a smaller bodied species (Wiens et al. 2019). The later activity time of *S. clarkii* compared to *S. jarrovii* could be an effect of competitive exclusion by *S. jarrovii*, which occupy basking sites during prime hours of the day. These two species have similar perch height and type preferences; therefore, a third axis of differentiation, time, is invoked to avoid competition. Hence, we found that perches (both perch height and type) constituted an important resource axis across all of our study communities, particularly for the two-species communities, but that, indeed, an additional axis (activity time) was critical in the three-species community.

4) *Is dimensional separation complementary?*

Two sets of species pairs overlap along the main niche axis of perch height—*S. jarrovii* and *S. clarkii*, and *S. virgatus* and *S. slevini*—and there is some evidence for complementarity as a result of this overlap. The former species pair overlaps spatially in only one habitat, the Madrean oak woodland. Here, they partition time to avoid competing over perch sites. Across all three sites, Yarrow's spiny lizard (*S. jarrovii*) was relatively consistent in perch height and type, and interspecific differences appear more related to habitat availability than competitive forces with other lizards. This suggests that *S. jarrovii* may be excluding *S. clarkii* from high-elevation sites (Wiens et al. 2019). In many other sites across the region, Clark's spiny lizards are observed using a broader range of perches and heights, though a preference for high perches is still

noticeable (EPW, pers. obs.); more work must be done to determine if competition by *S. jarrovii* is the major causal mechanism driving niche reduction in the Chiricahua Mountains.

Between the two smaller species, *S. virgatus* and *S. slevini*, both species perch low to the ground or often, on the ground. They are narrowly allotopic in this system, and competition for space may limit their ability to coexist. Given the more generalist nature of *S. virgatus*, it is possible that their presence at high-elevation sites could negatively affect *S. slevini*; further study is needed to assess the competitive interactions between these two species.

5) *Which dimensions are utilized, how do they rank in importance, and why? How do particular dimensions change in rank as species number increases?*

We found the largest effect sizes in interspecific differences in perch height, cementing it as the most importance axis of niche differentiation within the system writ large. Consistent with other lizard radiations borne out of competition for space (e.g. *Anolis*) we see differentiation in phenotypic traits associated with climbing and perching abilities in this system, with those species preferring high perches having longer limbs and digits than the ground-dwelling species. This suggests evolution specifically associated with partitioning of perch height.

We also uncovered a role for thermal and temporal partitioning in the two-species montane conifer forest. However, as discussed above (see 3. How many dimensions are important?), this may be more related to the specialist tendencies and requirements of *S. slevini*, especially their preference for cooler substrates. Species composition, and especially the presence of specialists, may therefore influence the relative importance of niche axes in this system more than species richness alone. The temporal axis comes into play again in our three-species community, in which *S. clarkii* and *S. jarrovii* share perch height preferences, and thus partition the use of perches throughout the day. This community supports the idea that as more species co-occur, more axes of differentiation are needed to support them.

6) *What is the relation of dimensional separation to difference in phenotypic indicators? To what extent does the functional relation of phenotype to resource characteristics constrain partitioning?*

Previous studies have focused on the role of body size as a major axis of variation within *Sceloporus* (Warheit et al. 1999) and suggest differences in body size may facilitate sympatry for some species and constrain it for others (Rivera et al. 2021). By adding additional morphological traits to our analyses, we have identified several potentially key traits that *Sceloporus* lizards use to access divergent niche space. *Sceloporus slevini* possesses shorter hindlimbs and the shortest fourth toe compared to all other species. Limb and digit reduction, concomitant with body elongation, are common trademarks of ground-dwelling and fossorial species (Bergmann and Irschick 2010; Grismer et al. 2018), and we rarely observed Slevin's bunchgrass lizards anywhere but on the ground or in a bunchgrass cluster (Fig. 1.2). The next smallest species, *S. virgatus*, overlapped somewhat with *S. slevini* in morphospace but differed by having longer hindlimbs, both before and after body size correction (Fig. 1.3 A&B). *Sceloporus virgatus* is also more generalist than *S. slevini* and was often observed perching on small objects. *Sceloporus clarkii* was both the largest and had the longest fourth toe of all species; large body size is common in canopy dwelling lizards, and toe length is a strong predictor of climbing ability (Losos 1990). In our observations, *S. clarkii* was strongly arboreal and exhibited the greatest overall perch heights. *Sceloporus jarrovii* exhibits strongly saxicolous characters consistent with

its preference of tall rock perches where available, including large and strongly keeled scales that can help them wedge into rock crevices (Chapple 2003), large body size, and long toe lengths. Our data present a compelling case to consider the species in the Chiricahua Mountains as representing a set of differentially habitat-adapted species, consistent with ecomorphologies observed in other lizard radiations (Williams 1972; Grismer et al. 2018; Meiri 2018). We find more evidence that phenotypic differences facilitate resource partitioning than constrain it.

7) *What is the distance between mean position of niches?*

Interspecific niche distances reveal which species are most, and least, similar in resource use. The most similar are *S. slevini* and *S. virgatus*; both relatively small-bodied ground dwellers, though the latter has a wider niche overall. The most distinct species in niche space are *S. slevini* and *S. clarkii*; the grass-dwelling tendencies of the former species have given it the narrowest niche overall, while the secretive but mostly arboreal tendencies of *S. clarkii* have created a similarly narrow niche, but in the opposite direction. Both *S. virgatus* and *S. jarrovi* have somewhat generalist tendencies, as revealed by middling niche distances to all other species (Table 1.2; Table 1.4). Distances in niche space support the conclusions drawn by the other questions herein: the species in the Chiricahua community partition niche space along consistent axes of perch height and type, and where those are not sufficient, or when specialist tendencies influence niche use, temporal and thermal niche partitioning come into play.

Conclusion

By quantifying niche use along multiple axes for a community of congeneric species, we have revealed the relative importance of each niche dimension in enabling co-occurrence. Microhabitat partitioning is one of the most common axes of differentiation amongst vertebrate communities, including lizards; however, had we focused solely on spatial resource use, we would have missed the important thermal and temporal differences that support the communities of spiny lizards in the Madrean sky islands. Furthermore, we uncovered strong links between ecology and morphology, and we found that traits most associated with climbing, such as body size, limb and digit lengths, are also some of the most differentiated between our focal species, suggesting evolution for differential microhabitat use. Understanding how species, and especially closely-related species, partition resources and structure communities remains a focal point in evolutionary biology. Our results underscore a need for further investigations that examine multiple niche axes simultaneously along with a wide variety of putatively important phenotypic traits to further our understanding of how and why such vast diversity has evolved across the tree of life.

Transitional Statement

The previous chapter examined the relationship between co-occurring species' phenotypes (e.g., color, morphology) and their resource use along three major axes. These analyses uncovered a strong relationship between habitat partitioning and phenotypic traits, suggesting a coevolved relationship. The next chapter examines the diet of co-occurring species in the same system and assesses the significance of dietary partitioning in context with findings from this chapter.

Figures and Tables

Figure 1.1 Map of study locations in the Chiricahua Mountains of Arizona, USA (A), representative habitat shots for each study area (B), and photos of the four focal species in this system (C).

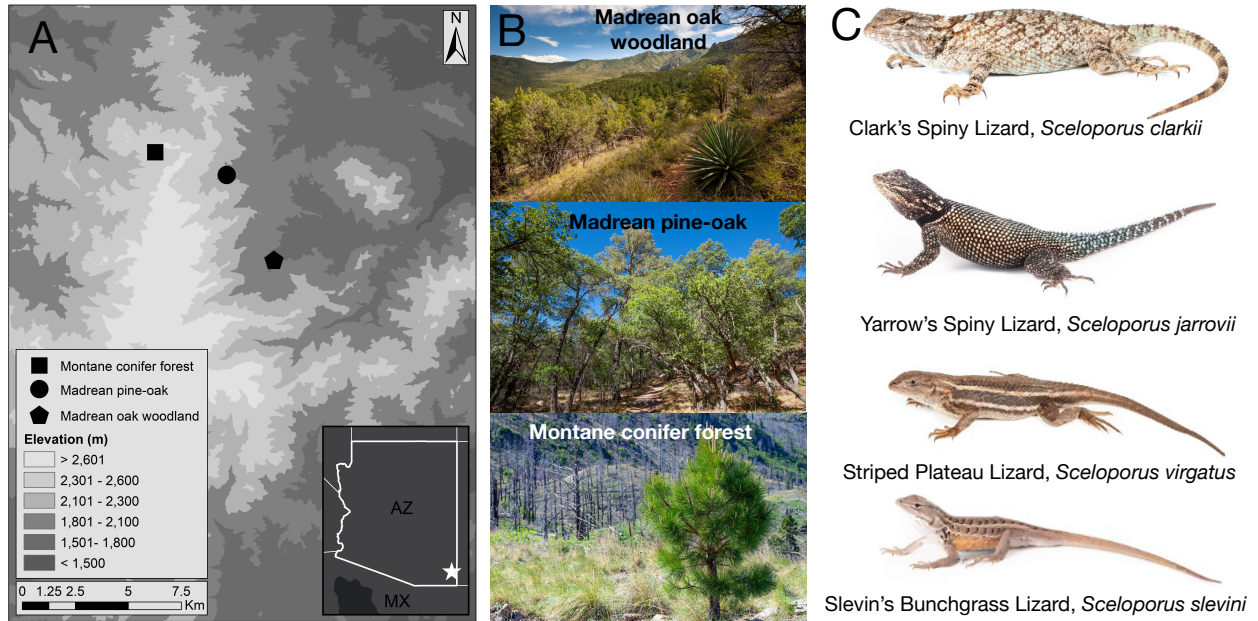


Figure 1.2 Niche use along the four major axes (perch height, T_s , activity time, and perch type) across all sites by the four *Sceloporus* species. Perch height (A, E, I) and perch type (D, H, L) are the major axes of niche differentiation, as they vary significantly between species at each site. Lizards' chosen T_s differ in the montane conifer forest (J) but not at the other sites (B, F), and activity time differs between species in the Madrean oak woodland (C) and montane conifer forest (K), but not in the Madrean pine-oak habitat (G). b-g = bunchgrass.

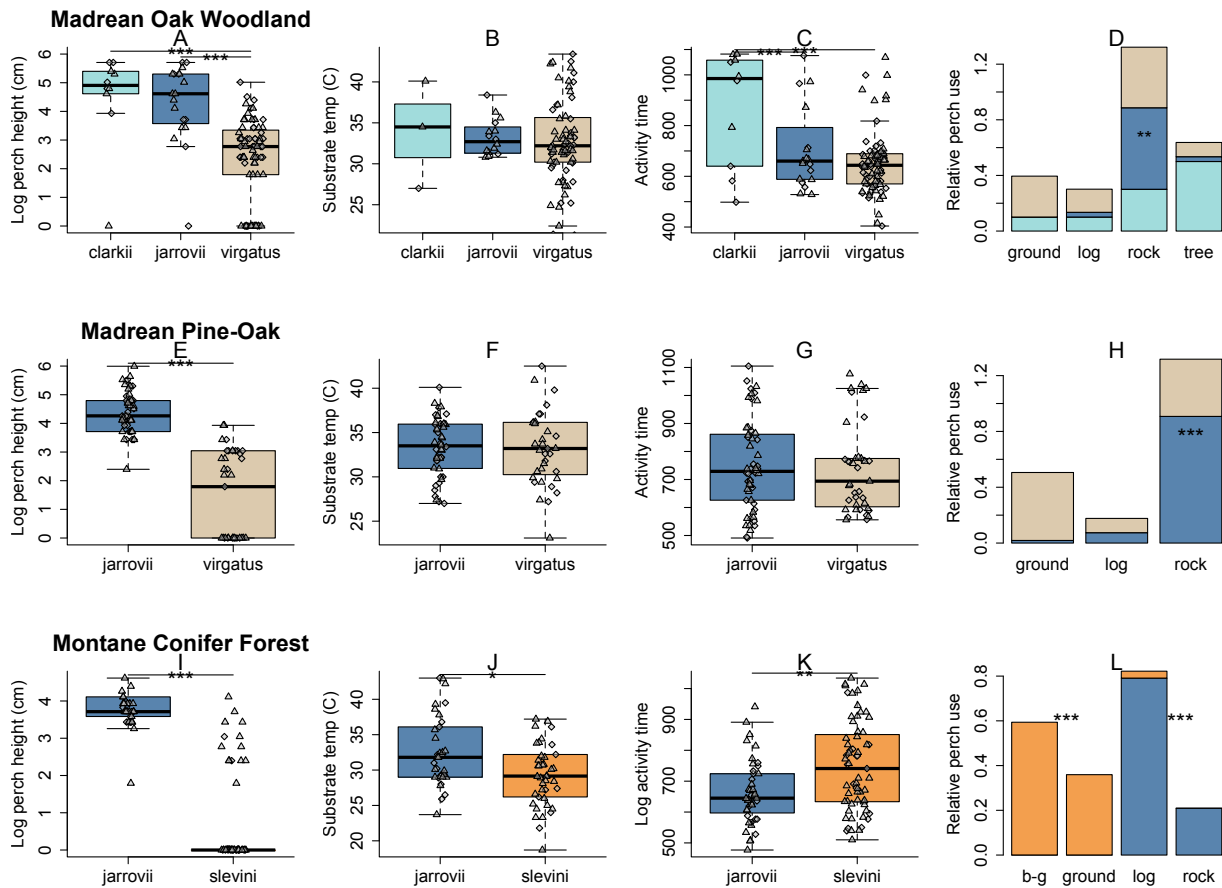


Figure 1.3 Principal component scores and corresponding axis loadings for both raw morphological traits (A) and residuals of traits from a regression against body size (B) show delimitation in morphospace between the four *Sceloporus* species. Though differences in body size account for much of the morphological variation between species (A), body size corrected traits such as hindlimb length (B, PC1) and scale size (B, PC2) reveal variation between species. Despite balanced sample sizes for all species except *S. clarkii*, *S. jarrovii* occupies the largest region of morphospace in both analyses.

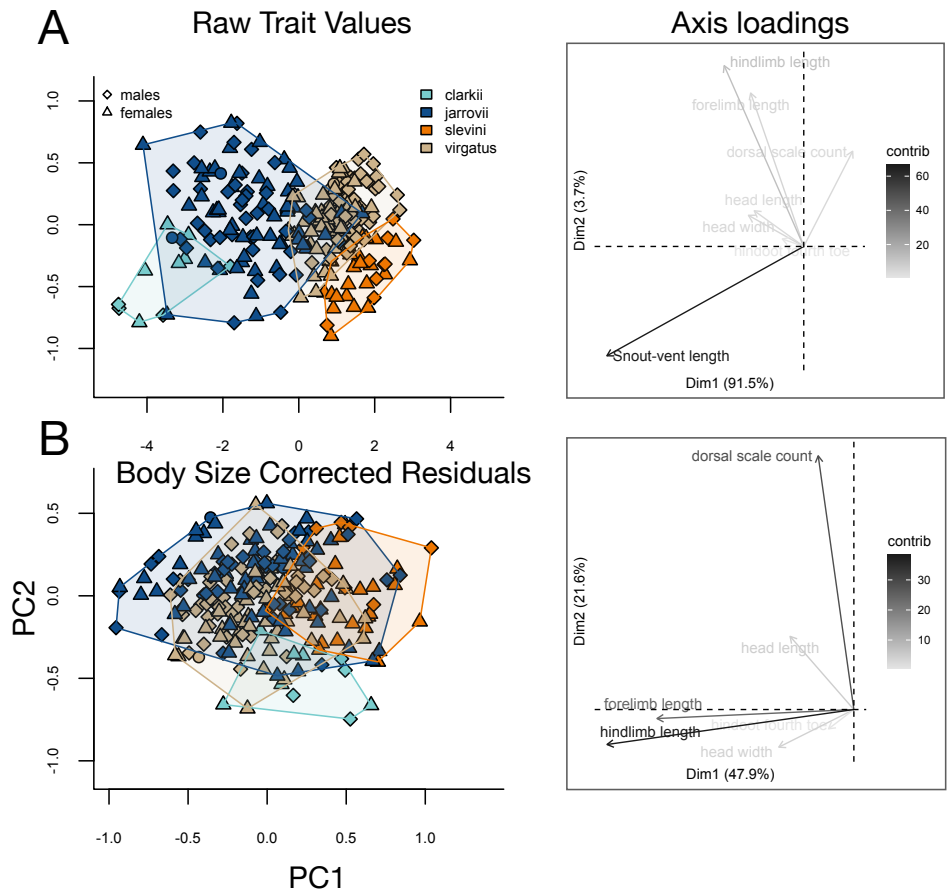


Figure 1.4 Regressions of morphological PC1 (raw trait values, see Fig. 3A) against the three major niche axes reveals that morphology strongly predicts habitat use for perch height and substrate temp but not activity time for the four *Sceloporus* species.

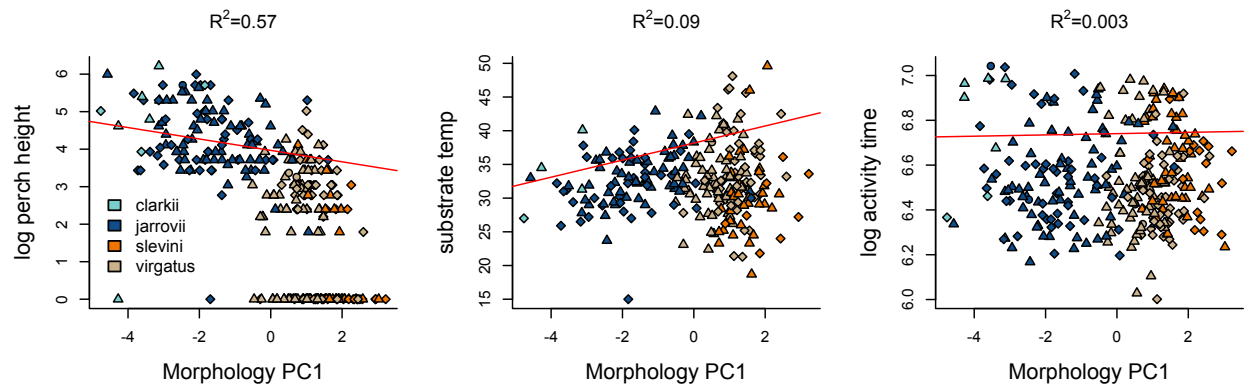


Figure 1.5 Dorsal (A) and ventral (B) lizard color along the axes of hue, saturation, and value (brightness) reveal differentiation in color space between the four *Sceloporus* species, especially in brightness on the dorsum and hue on the venter.

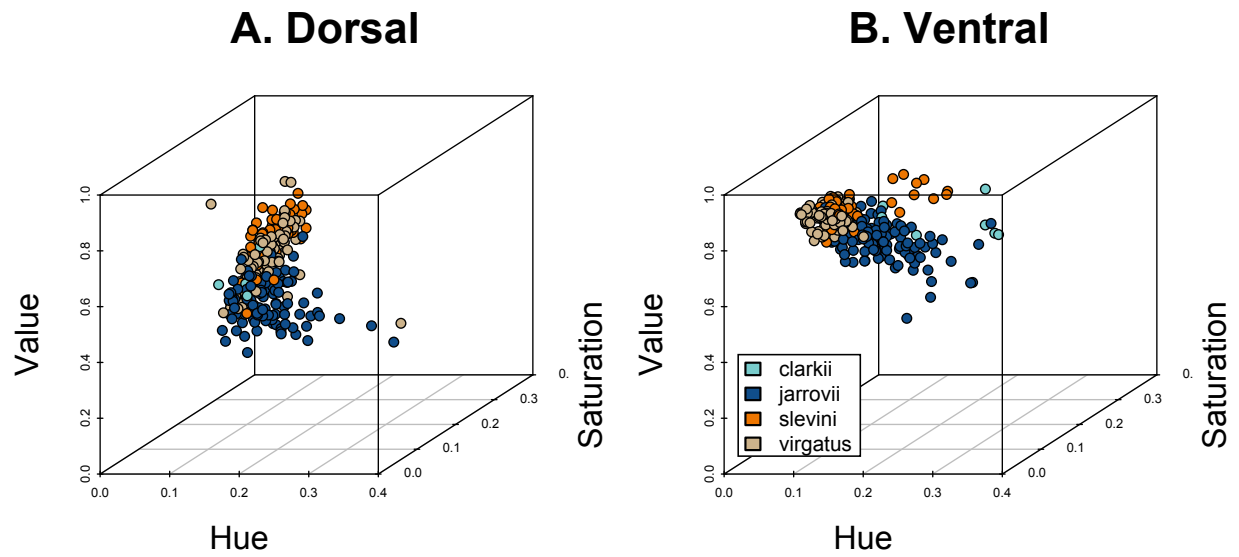


Table 1.1 Counts of individual lizards from our four study species, genus *Sceloporus*, at our three study sites in the Chiricahua Mountains, Arizona, USA.

species	Study Location		
	Madrean oak woodland	Madrean pine-oak	Montane conifer forest
<i>S. virgatus</i>	80	39	0
<i>S. jarrovii</i>	27	56	43
<i>S. clarkii</i>	12	0	0
<i>S. slevini</i>	0	0	64
total	119	95	109

Table 1.2 Niche distances between all species pairs taken as the distance in three-dimensional space for the quantitative niche axes: perch height, T_s , and activity time. Each niche axis was standardized prior to distance calculations. Species vary in niche distance from greatest, *Sceloporus clarkii* and *S. slevini*, to most similar, *S. slevini* and *S. virgatus*.

Standardized pairwise niche distance			
	<i>S. jarrovii</i>	<i>S. slevini</i>	<i>S. virgatus</i>
<i>S. clarkii</i>	0.250	0.402	0.396
<i>S. jarrovii</i>		0.186	0.153
<i>S. slevini</i>			0.094

Table 1.3 Normalized means and standard deviations for each species along the three quantitative niche axes, as well as the ratio between niche position and niche standard deviation, as discussed in Schoener (1974).

species		Niche axis			Niche position
		Perch height	Substrate temp.	Activity time	
<i>S. clarkii</i>	Mean	0.393	0.669	0.758	0.589
	s.d.	0.275	0.111	0.211	0.284
<i>S. jarrovii</i>	Mean	0.184	0.659	0.621	0.481
	s.d.	0.173	.0849	0.136	0.257
<i>S. slevini</i>	Mean	0.009	0.605	0.655	0.402
	s.d.	0.022	0.117	0.127	0.32
<i>S. virgatus</i>	Mean	0.034	0.668	0.590	0.428
	s.d.	0.043	0.106	0.122	0.298

Table 1.4 The ratio of niche distance and niche standard deviation for each species pair as discussed in Schoener (1974) Q7; results are given as the niche distance between the two species divided by niche width of the species on the vertical axis.

Niche distance (d) over niche variance				
	<i>S. clarkii</i>	<i>S. jarrovii</i>	<i>S. slevini</i>	<i>S. virgatus</i>
<i>S. clarkii</i>		0.880	1.415	1.394
<i>S. jarrovii</i>	0.973		0.723	0.595
<i>S. slevini</i>	1.256	0.581		0.293
<i>S. virgatus</i>	1.328	0.513	0.315	

CHAPTER II

Dietary niche partitioning of three Sky Island *Sceloporus* lizards as revealed through DNA metabarcoding

This manuscript has been previously published.

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Abstract

Lizard diets are highly diverse and have contributed to the diversification, biogeographical distributions, and evolution of novel traits across this global radiation. Many parts of a lizard's ecology—including habitat preferences, foraging modes, predation risks, interspecific competition, and thermal constraints, among others—interact to shape diets, and dietary niche partitioning simultaneously contributes to co-occurrence within communities. We used DNA metabarcoding of fecal samples to identify prey items in the diets of three sympatric *Sceloporus* lizards in the Madrean Sky Islands of Arizona, USA. We found evidence for dietary niche partitioning between interacting species concomitant with their respective ecologies. We also compared diet composition between populations to understand how conserved or plastic species' diets are between different environments. Our findings suggest that habitat generalists are also diet generalists in this system, while the same may be true for specialists. The identification of prey items to much lower taxonomic levels than previously documented further reveals hidden diversity in the diets of these species and underscores the utility of metabarcoding for understanding the full complexity of lizard diets.

Introduction

Feeding ecology is one of the most essential aspects of an organism's life and plays a key role in the evolution of biodiversity. Incredible diversity in diet, levels of dietary specialization, and feeding modes and strategies have evolved across the tree of life (Fryer and Iles 1972; Schluter 1993; Lovette et al. 2002). Diet evolution is governed simultaneously by ecological opportunity and competition (Schluter 2000b), and dietary divergence represents an important form of resource partitioning that can enable species co-occurrence (Pianka 1973; Schoener 1974; Kartzinel et al. 2015; Ford et al. 2016). In squamate reptiles, dietary shifts are sufficiently important as to influence diversification (Vitt and Pianka 2005; Grundler and Rabosky 2021), structure assemblages (Losos 1994; Vitt and Pianka 2005), and promote the evolution of novel morphologies (Savitzky 1981; Vitt and Zani 1996).

Other aspects of an organism's ecology and behavior intersect with patterns of prey consumption. Microhabitat preferences or requirements, thermal constraints, competitive interactions, and predation risks can all influence spatial and temporal foraging opportunities (Svanbäck and Bolnick 2007; Gordon et al. 2010; Lopez-darias et al. 2012; Novosolov et al. 2018). Because prey species are not evenly distributed across landscapes, these factors influence the diet items available to predator species. Dietary niche partitioning within communities is often a result of these many interacting elements and can enable sympatry by reducing competitive overlap (Pianka 1973; Schoener 1974).

Many studies focus on how interspecific diet differs within communities (Pacala and Roughgarden 1985; Vitt and Carvalho 1995; Serrano-Cardozo et al. 2008), but fewer examine at the consistency of diet composition between populations of the same species. While some species may specialize so heavily that the absence of favored prey items is enough to limit distributions (Pianka and Parker 1975), other, more opportunistic feeders may have substantially different diets based on local prey availability between sites, even when those species are dietary generalists overall. Studies that incorporate diet analyses of multiple populations across different environmental settings can further our understanding of how much dietary plasticity exists within species, how the structure of predator communities is influenced by the structure of prey communities, and how spatial variation in prey availability can influence the co-occurrence of predator species (Taverne et al. 2019).

Recent studies using molecular approaches have revealed previously hidden diversity in animal diets (Kartzinel and Pringle 2015; Gil et al. 2020). Though taxonomic databases are still incomplete, their utility for characterizing dietary composition is proven in cases where morphological identification of diet items is difficult or impossible (Taberlet et al. 2012). Morphological studies of stomach contents can also be biased by the different rates of digestion between prey items based on size, hardness, and composition (Carretero 2004). DNA metabarcoding for diet analysis using fecal matter is a technique that enables identification of prey items without invasive methods, such as stomach flushing, bleeding, or specimen collection (Walker et al. 2016, 2019; Martínez-Fonseca et al. 2022). For sensitive species or species of conservation concern, it remains the most promising avenue for understanding dietary diversity.

We used DNA metabarcoding to investigate the diets of three congeneric lizard species inhabiting the Madrean Sky Islands region in southeastern Arizona. The striped plateau lizard, *Sceloporus virgatus*, is a small-to-medium-bodied habitat generalist that utilizes a variety of low perches, from small rocks and logs to dwelling on the ground (Smith 1996). Slevin's bunchgrass

lizard, *S. slevini*, is also small-bodied, though more elongate, has reduced limbs compared to *S. virgatus*, and is almost exclusively grass-dwelling (Ballinger and Congdon 1981). These two species are narrowly allotopic in this system but overlap in spatial niche and ecomorphological space (Westeen et al. 2023). Yarrow's spiny lizard, *S. jarrovi* is a medium-to-large lizard that is strongly saxicolous and occasionally arboreal (Simon and Middendorf 1976). It is syntopic with the two smaller species but retains a distinct microhabitat and temporal niche from *S. slevini*; it overlaps somewhat spatially and temporally with *S. virgatus* (Westeen et al. 2023). *Sceloporus virgatus* and *S. jarrovi* are sit-and-wait predators (Weiss 2001; Watters 2009); foraging habits for *S. slevini* have not been recorded but likely also conform to sit-and-wait predation given their shy nature and affinity for bunchgrass clusters (EPW, pers. obs). Given the differences in spatiotemporal niche use among these species and their sedentary predation habits, we predict that interspecific dietary niche partitioning will be evident. More specifically, we predict that *S. slevini* will have the narrowest dietary niche due to its high habitat-specificity and will overlap more in dietary niche space with *S. virgatus*, the other small-bodied ground-dweller, than it will with *S. jarrovi*. We collected fecal samples from 228 lizards from the Chiricahua Mountains and Appleton Whittell Research Ranch, Arizona, USA to examine how diet composition varies among these three species and between populations within each species. We then quantified intraspecific and interspecific niche breadth and compositional overlap to understand how these lizards utilize this important resource axis and how dietary niche partitioning may contribute to species interactions in syntopy.

Methods

Field Surveys

We collected fecal samples from adult individuals of *Sceloporus jarrovi*, *S. slevini*, and *S. virgatus* in the Chiricahua Mountains and Appleton-Whittell Research Ranch, AZ from 2019-2022 (Fig.2.1, Table 2.1). Sites within the Chiricahua Mountains included Cave Creek Canyon, comprised of Madrean Oak Woodland habitat; Turkey Creek, within the Madrean pine-oak habitat band; and Barfoot Park, an area of Montane Conifer Forest near the highest peaks of this mountain range. The Appleton-Whittell Research Ranch (AWRR) in the Sonoita Plain, AZ, is a semi-desert grassland that supports relict populations of *S. slevini* (Bock et al. 1990; Smith et al. 1998; d'Orgeix et al. 2011). Despite the relatively long geographic distance between these two sites, they represent two of the closest habitat patches for *S. slevini* in this region, as this species exhibits a very disjunct range overall (Watkins-Colwell et al. 2003).

Lizards were captured by hand or lasso and processed in the field. Individuals were given a unique mark and released at their point of capture to ensure that lizards were not resampled for this study. Through intensive sampling efforts, we were able to exceed a target of twenty individuals per population (Rato et al. 2022) for all of our studied populations (Table 2.1). Lizards were captured across the active season (April – September) to document a summary of total spring-summer diet. Samples were collected directly from the cloaca and placed into RNALater or ethanol for preservation. Many lizards will defecate when captured, but in some cases, it was necessary to gently palpate lizards by hand or using a piece of foam following McGee et al. (2019) to induce defecation. Animal care and field surveys were approved by the University of California Berkeley and Virginia State University Institutional Animal Care and Use Committees (Protocol AUP-2019-02-11797 to EPW at UC Berkeley; Protocol 2017-100 to CAD at Virginia State University), collection permits were issued by Arizona Game and Fish

Department (LIC#SP653941, SP404320, SP407158, SP808336 to EPW; LIC#SP652734 to CAD), and land access was granted by Coronado National Forest, Douglas Ranger District.

Sample Processing

We pooled fecal samples by population, resulting in 6 sample pools (Table 2.1). Pooled fecal samples were processed at Northern Arizona University's Pathogen and Microbiome Institute. We extracted genomic DNA using a QIAamp Fast DNA Stool Mini kit (Qiagen, Valencia, CA, USA) following the human DNA analysis protocol, allowing lysis to occur for 30 min at 70 °C, and then eluting DNA to 100 µL. To target arthropods, we amplified a short-section (~185 bp insert) of cytochrome oxidase subunit I (COI) using the ANML primer set (forward: LCO1490, reverse: CO1-CFMRA) (Jusino et al. 2019). Primers were pre-modified with 5' universal tails (Colman et al. 2015) for preparing sequencing libraries in a later PCR step. The first PCR was run in 15 µL reaction volumes with 3 µL of genomic DNA, 8.46 µL of PCR grade water, 1.5 µL 10X Mg-free PCR buffer (Invitrogen, Thermo Fisher Scientific, Waltham, MA, USA), 1.5 mM MgCl₂, 0.2 mM each dNTP, 0.2 µM each primer, 0.16 µg/µL bovine serum albumin (Ambion Ultrapure BSA), and 0.03 U/µL PlatinumTaq DNA polymerase (Invitrogen, Thermo Fisher Scientific). We also included a negative template control (NTC) whereby PCR-grade water was added as template to a reaction instead of genomic DNA. Thermal cycling included initial denaturation at 94 °C for 5 min, 5 cycles of 94 °C for 1 min, 45 °C for 1.5 min, and 72 °C for 1 min, 35 cycles of 94 °C for 1 min, annealing at 50 °C for 1.5 min, and 72 °C for 1 min, with a final extension cycle of 72 °C for 5 min. PCR product was subsequently used as template to a second PCR to add unique 8 bp indices for dual indexed, paired-end sequencing and to make the amplicon flow-cell ready (Colman et al. 2015). An index was only used once per sample. Reactions were run in 25 µL volumes with 2 µL amplicon template, 12.5 µL 2X Kapa HiFi HotStart ReadyMix (Roche Sequencing, Wilmington, MA, USA), 8.5 µL PCR-grade water, and 1 µL each index primer (10 µM initial concentration). Thermal cycling conditions included an initial denaturation at 98 °C for 2 min, followed by 8 cycles of 98 °C for 30 s, 60 °C for 20 s, and 72 °C for 5 min, concluding with a final extension step of 72 °C for 5 min. Amplified PCR product was then sequenced on an Illumina MiSeq V2 Micro 300 cycle kit with 30% PhiX with 3.5 pM of the pooled amplicon libraries.

Sequencing reads were processed in QIIME2 v2022.2 (Bolyen et al. 2019). Priming regions were removed using cutadapt v4.0 (Martin 2011) to isolate the fragment of interest. Using DADA2 (Callahan et al. 2016), we removed low quality reads, denoised and merged paired-end reads, and then filtered out PCR chimeric reads. DADA2 was run with both R1 and R2 reads truncated to 125 bp and with the expected error parameter (--p-max-ee-f, --p-max-ee-r) set to 4.0. Amplicon sequence variants were then post-clustered de novo into operational taxonomic units (OTUs) using Vsearch v2.7.0 (Rognes et al. 2016) at 98.5% similarity (O'Rourke et al. 2021). OTUs were cross-referenced against the National Center for Biotechnology Information's (NCBI) GenBank database (Benson et al. 2009) using BLAST (Altschul et al. 1990), classified to phylum using least common ancestor (LCA) assignment in MEGAN v6 (Huson et al. 2007), and only OTUs assigned to Arthropoda and Chordata were retained for analysis (Sanchez 2021). Although the focus of our study was on diet, the ANML primers may also co-amplify host COI sequences and can allow for host verification in a fecal sample. Arthropod and chordate OTUs were then classified using a naïve-Bayes machine learning classifier (Bokulich et al. 2018) that was trained against a previously validated reference library (O'Rourke et al. 2020, 2021). The reference library ("fullCOI_db" available at

<https://osf.io/qju3w/files/osfstorage>) consists of all available invertebrate and vertebrate COI sequences assembled from the Barcode of Life Database (Ratnasingham and Hebert 2007) and NCBI GenBank (Benson et al. 2009). The reference library was already trimmed to the ~185 bp ANML insert and made non-redundant through LCA (described here: <https://github.com/devonorourke/tidybug/>). We retained classifications above a threshold of 70% bootstrap support. The complete OTU table may be found in Appendix 1.

Existing and Novel Diet Records

We tabulated existing diet records for adult lizards of our three study species from the literature. We recorded results from any study that identified diet items for any of the three species (Simon 1975; Ballinger and Ballinger 1979; Barbault et al. 1985; Goldberg and Bursey 1990; Watters 2008; Gadsden et al. 2011; Bergeron and Blouin-Demers 2020). We also consulted field guides for the region (Degenhardt et al. 1996; Jones and Lovich 2009; Holycross et al. 2022), which corroborated data from the literature but generally did not add records. Existing diet records may be found in Appendix 2. We did not consider studies in which lizards were fed or had their diets supplemented, nor did we consider diets of neonate lizards, which can differ significantly from adult conspecifics (Watters 2010).

We cross-referenced OTU identification with known arthropod records from the area during the spring and summer (May – August), which matches the temporal sampling of our study (Simon 1975; Ballinger and Ballinger 1979; Watters 2010). Simon (1975) sampled both available arthropods and lizard prey items and found that all available prey types were ingested over the season with the exception of Neuropterans (net-winged insects). We therefore used the total composition of prey items ingested by the three species as a proxy for available prey items in the environment. We identified all OTUs to the lowest taxonomy possible based on reference libraries. For comparisons of dietary breadth and composition, we used both the complete set of OTUs as well as a subset of OTUs that were able to be identified to order level (hereafter, order level).

Evidence on whether sequence (read) numbers are interpretable as abundances is mixed but this process is generally discouraged as there are many potential factors affecting how much DNA results from prey items that are independent of prey biomass (Clare 2014; Deagle et al. 2019; Lamb et al. 2019; Di Muri et al. 2020). Therefore, we considered diet items based on OTUs as either present or absent in each pooled diet sample.

Inter and Intraspecific Niche Breadth and Overlap

We calculated total dietary niche breadth for each species by pooling the two populations per species and calculating Levin's index of niche breadth,

$$Bn[j] = \frac{1}{R} \frac{1}{\sum(p[i]^2)},$$

where R is the number of different environments and p[i] is the proportion of taxon j in environment i (Levins 1968). Following Pianka (1986), we consider the lizards as the 'environments' and the available food items as the taxa. The proportion of prey items was calculated as the number of prey OTUs present in each lizard species' diet compared to total OTUs for all three species. We first used all prey OTUs to calculate breadth and overlap metrics; then we used only the subset of prey items able to be identified to order level. To convert niche

width to a standardized scale from 0 to 1 (specialist to generalist, respectively), we used the following equation:

$$B_A = \frac{Bn[j]-1}{R-1}.$$

We also calculated niche width using the Shannon-Weiner Diversity Index:

$$H' = -\sum(p_j \log p_j),$$

where p_j is the proportion of samples containing resource j (Colwell and Futuyma 1971). We then standardized the measure as

$$J' = H' / \log(n).$$

We chose these two indices to provide complementary measures of niche breadth; Levin's index gives more weight to common resources used, while the Shannon-Weiner Index weights rare resources more heavily. For dietary niche breadth, the use of Levin's index of niche breadth is largely advocated over other indices (Hurlbert 1978), so we base most of our discussions around this metric. We then compared diet breadth based at OTU and order resolution between species using Kruskal-Wallis tests and Dunn tests for post-hoc analyses, where appropriate (Van Den Berge et al. 2022).

We calculated niche overlap based on dietary composition between species using MacArthur and Levin's index

$$M_{jk} = \frac{\sum(p_{ij} p_{ik})}{\sum(p_{ij})^2},$$

where M_{jk} is the overlap of species k on species j , p_{ij} is the proportion of resource i relative to the total resources used by species j , p_{ik} is the proportion of resource i out of the total resources used by species k , and n is the total number of resource states (MacArthur and Levins 1967). We also calculated Pianka's index,

$$O_{jk} = O_{kj} = \frac{\sum(p_{ij} * p_{jk})}{\sqrt{(\sum((p_{ij})^2) \sum((p_{jk})^2))}}$$

for total dietary overlap between species (Pianka 1973), where p_i , p_j , and p_k are the same as in MacArthur and Levin's index. We compared dietary composition among species using a X^2 test with Monte Carlo simulation (2,000 replicates) (Clare et al. 2014).

We then calculated niche breadth and overlap using these metrics for the interacting populations at two specific sites, Turkey Creek and Barfoot Park. Finally, we compared dietary composition between the two sites (populations) for each of the three species using Pianka's niche overlap metric. We assessed if populations had different dietary compositions using X^2 tests with Monte Carlo simulation (2,000 replicates) (Clare et al. 2014).

Results

Sample Processing

None of the negative controls prepared with our samples amplified. We obtained 120704 paired raw-end reads (mean = 20117.22, S.D. = 3091.01); after cleaning and retaining only

arthropods and chordates, 105996 reads remained (mean = 17666, S.D. = 4799.12). We detected 53 unique OTUs across all levels of biological organization among our six sample pools (which each contained 32–44 individual lizard samples; Table 2.1), including some co-amplification of the host species, which was excluded for a total of 51 prey OTUs. 42 OTUs were identifiable to order level and spanned 8 orders including Araneae, Coleoptera, Diptera, Hemiptera, Hymenoptera, Isopoda, Lepidoptera, and Orthoptera. 32 OTUs were identified to family level, 21 were identified to genus level, and 10 were identified to species level (Appendix 1). Due to incomplete genetic reference libraries for this taxonomic group (arthropods), we cross-checked the classifications against existing records of arthropod taxa and found that all identified OTUs represent taxa present in the study area. Furthermore, all identifiable OTUs matched existing prey records for these lizards at order level except for two; Watters (2008) documented termites (Order Blattodea, infraorder Isoptera) and Simon (1975) identified a gastropod, both in the stomach of *S. jarrovii* individuals, which were not present in our samples (Appendix 2). Only one family uncovered in this study has been identified previously: formicid ants were present in the diets of *S. jarrovii* and *S. virgatus* (Watters 2008; Gadsden et al. 2011). Some records mentioned lower taxonomy by common name only (e.g., ‘spiders’; Appendix 2).

Interspecific Niche Breadth and Overlap

Our study species differed significantly in dietary niche breadth by OTU ($X^2 = 11.137$, $p = 0.003$) with *S. virgatus* having the greatest niche breadth compared to *S. jarrovii* ($Z = 2.66$, $p = 0.015$) and *S. slevini* ($Z = 3.073$, $p = 0.006$; Table 2.2). *Sceloporus jarrovii* and *S. slevini* did not differ significantly in niche breadth ($Z = 0.409$, $p = 0.682$) despite having different dietary compositions (Table 2.2; Fig. 2.2). When diet items were subset to order level, *S. virgatus* still revealed the greatest niche breadth (Table 2.2), but this was not statistically significant ($X^2 = 2.574$, $p = 0.2761$).

Species differed significantly in dietary composition at the order level ($X^2 = 29.926$, $p = 0.0134$). Compositional niche overlap was highest between the two more generalist species, *S. virgatus* and *S. jarrovii* (Fig. 2.3; Table 2.3), and lowest between *S. jarrovii* overlaps very little with *S. slevini*, both in terms of overall dietary composition (Table 2.3) and site-specific diets at Barfoot Park (Fig. 2.3). In this system, *Sceloporus slevini* and *S. virgatus* are narrowly allotopic; despite not occurring at the same sites, they had moderate dietary overlap (Table 2.3).

Intraspecific Niche Overlap

Populations within species differed in dietary composition, though not significantly ($X^2 = 9.4735$, $p = 0.096$). *Sceloporus slevini* had the least dietary overlap between its two sites, followed by *S. jarrovii*; *S. virgatus* had the highest level of overlap (Table 2.4). For *S. jarrovii* and *S. slevini*, high elevation populations (Barfoot Park, 2505 m) revealed greater dietary richness compared to low elevation sites despite similar sample sizes (Fig. 2.4).

Novel Diet Records

Our results introduce more specificity into the identification of prey categories: previously, the vast majority of records were identified only to order level (Appendix 2). The following families that we detected have not been identified previously by name in the diets of these lizards: for *S. jarrovii* Acrididae, Armadillidiidae, Cecidomyiidae, Elateridae, Geometridae and Gryllidae; for *S. slevini* Formicidae, Lycosidae, Rhopalidae, Scarabaeidae, and Tachinidae; and for *S. virgatus*

are Acrididae, Armadillidiidae, Lycosidae, and Rhyparochromidae. Additionally, all of the records we identified to the genus or species levels are novel for these lizard species. Novel records are indicated in Appendix 1.

Discussion

With the use of DNA metabarcoding, we recovered a great deal of dietary richness, including previously unreported families, genera, and species, in the diets of three *Sceloporus* lizard species in southeastern Arizona. By using samples taken across the spring and summer, we obtained a dietary summary during a period of prey abundance. We found evidence for dietary niche partitioning between interacting species as well as intraspecific differences in diet between populations.

Interspecific Niche Breadth and Overlap

Dietary breadth and composition varied between the three species (Table 2.2; Fig. 2.2), providing evidence that dietary partitioning may structure interactions in this system. Previous work on the diets of *S. virgatus* and *Urosaurus ornatus*, two lizards similar in size and ecology, found very few differences in diet (Bergeron and Blouin-Demers 2020). The differences in diet we uncovered between the three *Sceloporus* species match what is known about niche partitioning more generally in this system. We previously showed that perch height and type were significantly different between species in this system (Westeen et al. 2023). Given the nature of these species as sit-and-wait predators, it follows that these microhabitat differences lead to different availability of prey, which in turn contribute to the dietary differences we observed. Evidence for optimal foraging theory is limited in lizards, including explicit studies of these species (Stamps et al. 1981; Watters 2010); lizards generally eat prey items in relation to their availability in this system. Therefore, we suspect that most differences in diet in this system are due to differences in microhabitat and localized prey availability. Contrary to our prediction that the two small, ground-dwellers—*S. slevini* and *S. virgatus*—would overlap most in diet composition, we found the highest overlap between *S. jarrovii* and *S. virgatus* (Table 2.3). These two species are more generalist in their habitat as they occupy perches from the ground level up into trees and rocks, perhaps providing more opportunities for the two species to overlap in foraging areas. However, overlap between *S. slevini* and *S. virgatus* was similar; these two species have very similar spatial niches (Westeen et al. 2023), and their dietary niche overlap is consistent with this. This similarity may limit their ability to co-exist, and as such they are narrowly allotopic in this system. We also found that *S. virgatus* had the broadest dietary niche width of our three study species (Table 2.2), consistent with a role as a generalist predator. Furthermore, we found that the dietary niche of *S. virgatus* overlapped with the two other species more than they did with one another (Table 2.3). This supports the idea that *S. slevini* and *S. jarrovii* maintain distinct dietary niches from one another, while *S. virgatus* exhibits a broad dietary niche that encompasses some of the dietary diversity of both *S. jarrovii* and *S. virgatus*.

Analyses at OTU and order levels provide similar but complementary information. For instance, niche breadth at OTU resolution suggests that *S. jarrovii* feeds more broadly than *S. slevini*, whereas at order level the opposite pattern is observed (Table 2.2). Different OTUs may represent the same taxa and therefore overestimate measures of richness and breadth while underestimating dietary overlap. Yet only using prey items to the order level can sacrifice specificity and therefore underestimate the degree of dietary partitioning occurring in this system. For example, prey items in the same order can vary substantially in size and ecology,

such as small-bodied weevils and large Scarab beetles that are both Coleopterans, further contributing to dietary preferences and partitioning. Previous work in this system has shown that gape width is related to prey size selection (Bursey and Goldberg 1993); though prey size is not an aspect of the current study, future work may consider the relationship between individual-level diet and predator ecomorphology and how size selection of prey may reduce interspecific competition as it does intraspecific competition (Simon 1976). As taxonomic databases continue to grow, analyses at OUT resolution will provide the most complete dietary information; until then, subsetting OTUs to those which can be identified to a more ecologically pertinent group, such as family or order, remains a useful addition to OUT-level analyses.

Intraspecific Niche Overlap

We also uncovered differences in diet composition between populations of the same species (Fig. 4), though they were not statistically significant. *Sceloporus slevini* is a microhabitat specialist and exhibited the least dietary overlap between sites (Pianka overlap = 0.338): the two sites are geographically distant (121km straight-line distance), situated at different elevations (Table 2.1), possess markedly different vegetation (semi-desert grassland vs. montane conifer forest), and have different temperature regimes. Given these differences in habitat, populations may have very different access to prey communities between sites. Despite also being the smallest species and the species with the narrowest gape width per body (Westeen et al. 2023) size, spiders and especially wolf spiders in the family Lycosidae appeared in the diet *S. slevini* at both sites (Fig. 4). Existing studies on the diet of *S. slevini* are rare; Newlin (1976) found hemipterans and ants to be the most significant diet categories by volume. Barbault et al. (1985) found beetles, ants, hemipterans and grasshoppers to contribute significantly to diets in Durango, Mexico, though given current taxonomy and distributions, it is possible that these results do not represent *S. slevini* but another member of the *S. scalaris* group, *S. brownorum* (Grummer and Bryson 2014). Neither report spiders as contributing significantly to the diet of this species; observational studies would be a welcome follow-up to understand how often spiders are consumed.

For *S. jarrovii* the two sites we sampled are in close geographic proximity (3.3km straight-line distance), yet population-level diet overlap (Pianka overlap = 0.396) is similar to that of *S. slevini* (Pianka overlap = 0.338), which had substantially more distance between populations. We previously uncovered differences in microhabitat use by *S. jarrovii* between these sites (Westeen et al. 2023), which may contribute to the divergence in diet between populations. Previous works report Hymenopterans, especially ants, as major diet items (Barbault et al. 1985; Goldberg and Bursey 1990; Watters 2008). Formicid ants were present at both sites occupied by *S. jarrovii* but not consumed; they were consumed by *S. slevini* and *S. virgatus*, however (Fig. 4), perhaps serving as evidence of a competitive effect or a difference in prey availability in each species' preferred microhabitat.

Taken together, our findings on the dietary niche breadth and overlap between populations in *S. jarrovii* and *S. slevini* suggest that although they exhibit very similar levels of dietary niche breadth at the species level (Table 2.2), and population-level diet overlap within each species (Table 2.4), their diet composition is structured in very different ways (Fig. 2.2, Fig. 2.3). Analyses of dietary niche that are conducted only at the species level may overlook important differences in how diet composition varies between populations.

The most habitat- and dietary-generalist, *S. virgatus* reveals greater dietary overlap between sites than the other two species (Table 2.4; Fig. 2.4). With the greatest overall dietary niche width, it may be easier to find overlap between populations given the sheer number of diet items consumed at each site. However, we do see two categories that stand out as relatively important in the diet for this species at both sites: Hymenopterans, namely ants, and Orthopterans, namely grasshoppers. Previous works underscore the importance of Hymenopterans as a prey item; Bergeron and Blouin-Demers (2020) found that they comprise >75% of prey items consumed, while Watters (2008) found that formicid ants comprised about 50% of observational consumptions and 30% of stomach contents.

Novel Diet Records

The dietary diversity uncovered in this study complements previous work that examined prey items from the stomachs of the three species herein (Appendix 1). The use of metabarcoding allowed us to achieve finer resolution of prey identification in most instances, while avoiding stomach flushing that can potentially impact the health of lizards, especially of the small-bodied *S. slevini* that has already suffered severe population reductions at both sites herein (Bock et al. 1990; Ballinger and Congdon 1996; Smith et al. 1998; d’Orgeix et al. 2011). An interesting next step would be to pair observational studies or microscopic identification with metabarcoding to further understand how size selection of prey—an important factor at least for *S. jarrovii* (Simon 1976) and likely for the other species as well—structures diets within and between species. We hope that the utility of DNA metabarcoding in this study inspires other researchers to employ this method to document prey items of lizards in different contexts.

Conclusion

The use of DNA barcoding enabled us to capture dietary breadth and composition of three lizards, including one species, *S. slevini*, for which other methods (stomach flushing, collecting) would be inadvisable due to their small size and sensitive nature. We document previously unknown diet items and reveal both interspecific and intraspecific dietary differences. Interspecific prey consumption appears related to differences in microhabitat and may contribute to patterns of sympatry between species. Future studies will benefit from comparisons between sexes, across seasons, from volumetric analyses of prey items to reveal relative abundance and from prey-size analyses to further illuminate the drivers of dietary niche partitioning in this system and among squamate species in general. Further, an understanding of interspecific dietary partitioning can provide critical information for resource managers to optimize the long-term survival of these three species and serve as a template for other sympatric species.

Transitional Statement

This chapter examined differences in diet between co-occurring species and uncovered dietary novelty for all three species examined. The results of my first two chapters together suggest that by being sit-and-wait predators that partition habitat space, the *Sceloporus* lizards of the Chiricahua Mountains are also partitioning diet resources. Examining these resource axes together can help inform the relative importance of each in facilitating sympatry. In the next chapter, I will examine the relationship between ecology and morphology across the entire genus and ask what role ecomorphology plays in enabling sympatry at broader spatial scales.

Figures and Tables

Figure 2.1 Study system including three sites in the Chiricahua Mountains and one in the Sonoita Plain, AZ, USA. Focal species are depicted to the right: *Sceloporus jarrovi* is a large-bodied saxicolous species, *S. slevini* is a small-bodied grass dweller, and *S. virgatus* is a small-to-medium terrestrial generalist.

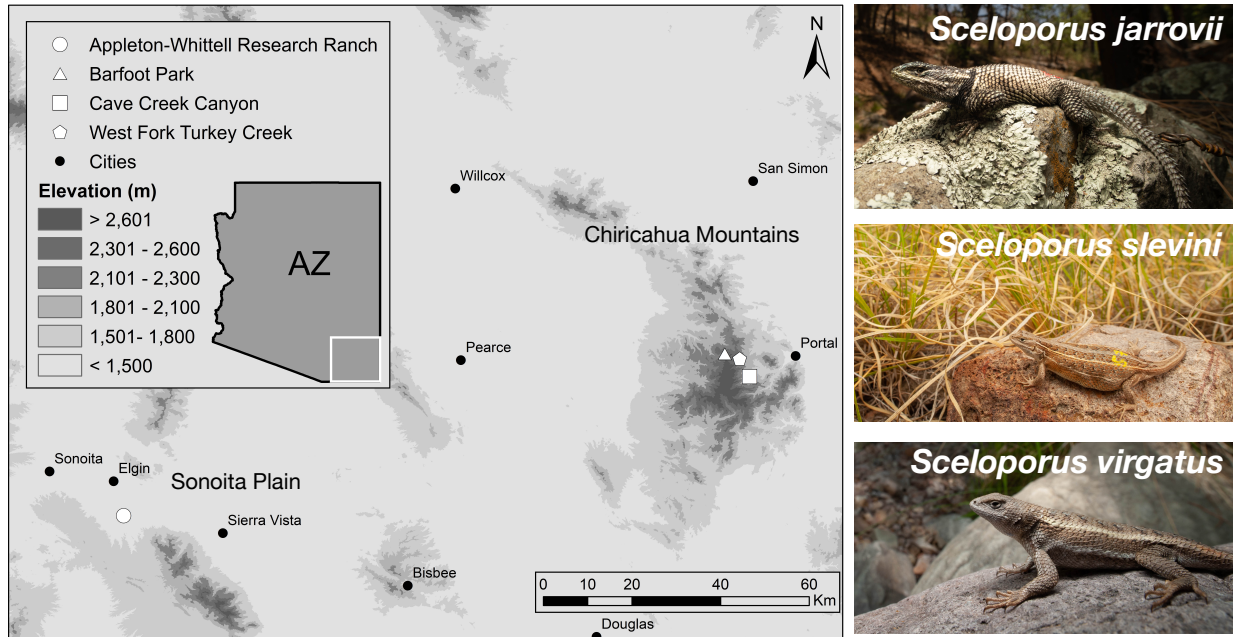


Figure 2.2 Diet items recovered in this study as given by the number of OTUs per prey order. The height of each colored segment represents the number of OTUs identified within the diet of each lizard species. When family, genus, or species-level identification was possible from OTUs, those taxa are listed within the corresponding bar unit. Numbers in parentheses indicate number of OTUs corresponding to that category. Bar units without text indicate OTUs that we were not able to identify past order level. *Sceloporus virgatus* consumed all prey orders but one and shows substantial overlap with the other two species, while *S. jarrovii* and *S. slevini* overlap in only two prey orders. Inset Venn diagram shows summarized overlap between the three species at order level.

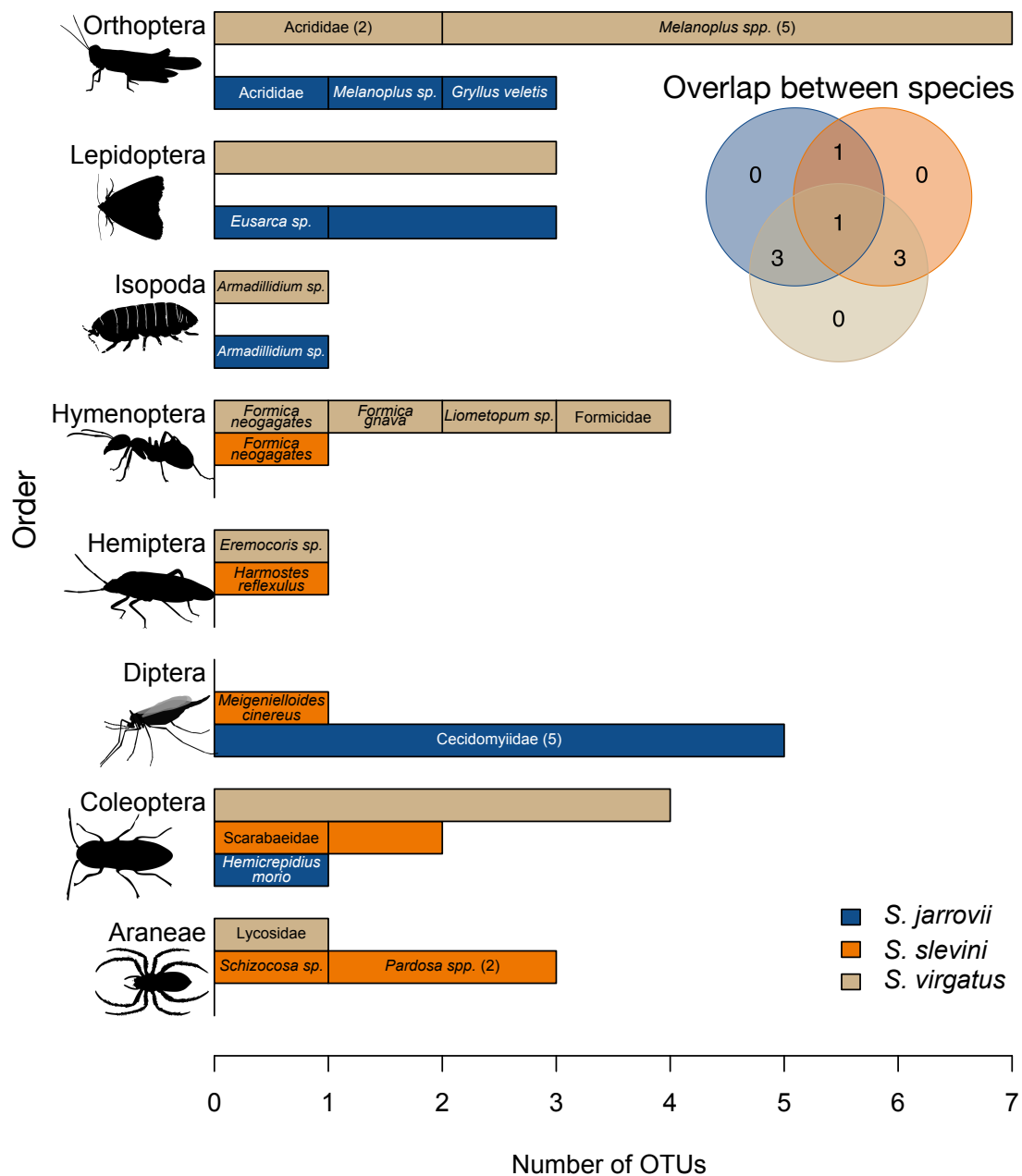


Figure 2.3 Site-specific comparisons reveal dietary niche partitioning between the two sets of syntopic species. Top: Bar height represents number of OTUs identified from each species corresponding to that order. Bottom: Venn diagrams show the number of diet categories by order unique and shared between sets of interacting species.

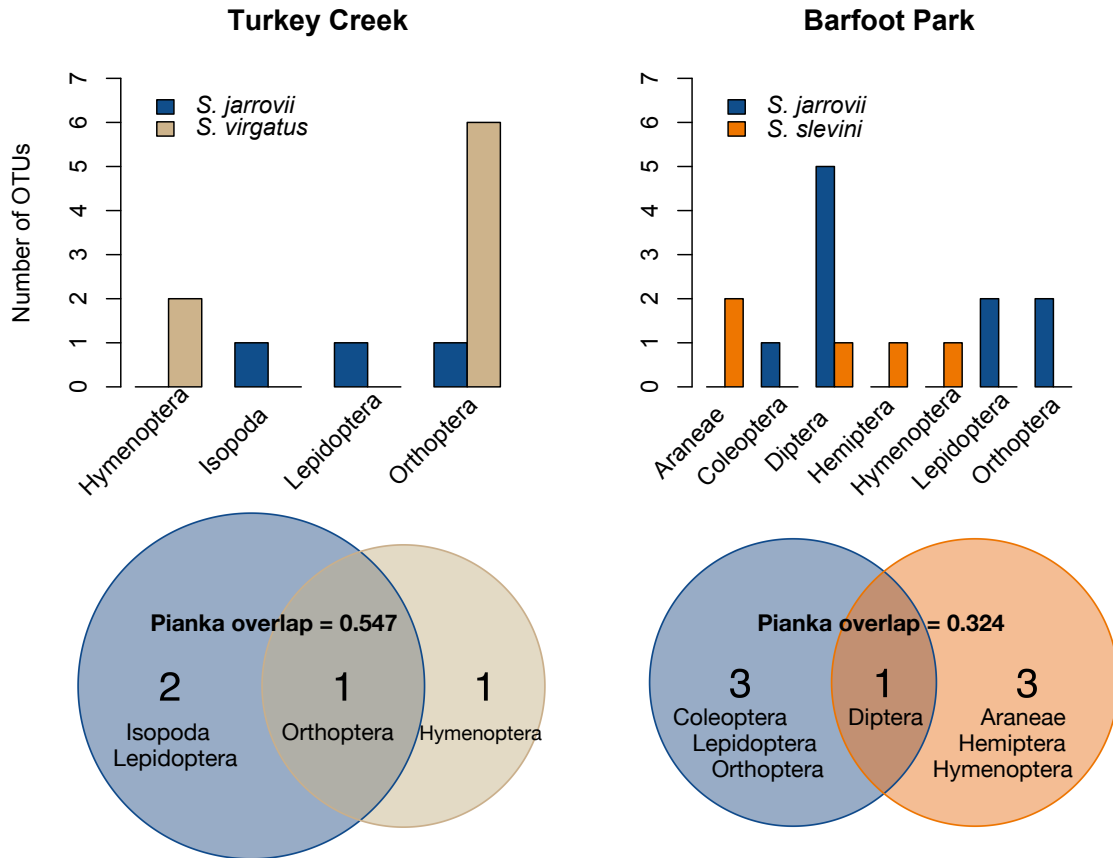


Figure 2.4 Colored bar height corresponds to the number of OTUs per order within the diet of each population. Unlabeled bars indicate OTUs unable to be identified beyond order level. Lizard diets vary by population; all species exhibit differences between populations, but the greatest differences are observed for *S. slevini*, followed by *S. jarrovi* and then *S. virgatus*. For each species, its respective low elevation site (LE) is plotted to the left and high elevation site (HE) to the right. AWRR = Appleton Whittell Research Ranch.

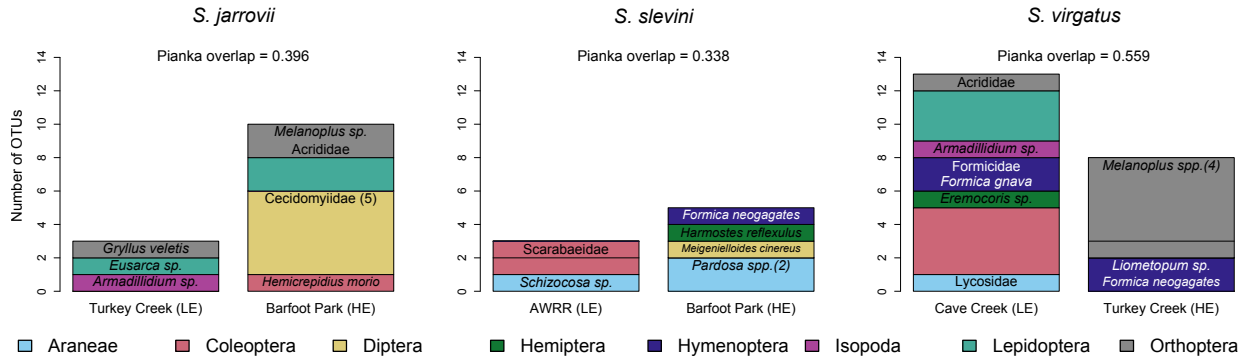


Table 2.1 Samples included in the study, by species and population. Each species is represented by two populations with paired low and high elevation sites.

Species	Site	Habitat	Elevation (m)	No. of samples
<i>S. jarrovii</i>	W. Fork Turkey Creek, Chiricahua Mtns, Cochise County, AZ	Madrean pine-oak	2070	42
<i>S. jarrovii</i>	Barfoot Park, Chiricahua Mtns, Cochise County, AZ	Montane conifer forest	2505	39
<i>S. slevini</i>	Barfoot Park, Chiricahua Mtns, Cochise County, AZ	Montane conifer forest	2505	38
<i>S. slevini</i>	Appleton Whittell Research Ranch, Sonoita Plain, Santa Cruz County, AZ	Semi-desert grassland	1430	32
<i>S. virgatus</i>	Cave Creek Canyon, Chiricahua Mtns, Cochise County, AZ	Madrean oak woodland	1700	44
<i>S. virgatus</i>	W. Fork Turkey Creek, Chiricahua Mtns, Cochise County, AZ	Madrean pine-oak	2070	33

Table 2.2 Total dietary niche breadth for the three species (populations pooled) based on OTU identification and order and included in the study. *Sceloporus virgatus* exhibits the most dietary generalism, as indicated by the largest niche width across all metrics.

Species	Std. Levin's Index (OTU)	Std. Shannon's Index (OTU)	Std. Levin's Index (Order)	Std. Shannon's Index (Order)
<i>S. jarrovii</i>	0.28	0.688	0.393	0.692
<i>S. slevini</i>	0.24	0.652	0.429	0.718
<i>S. virgatus</i>	0.54	0.847	0.534	0.822

Table 2.3 Dietary niche overlap by OTU and prey order for each pair of species included in the study. *Sceloporus virgatus* overlaps more with *S. jarrovii* and with *S. slevini* than *S. jarrovii* and *S. slevini* do with one another.

Species pairs	Pianka's Niche Overlap (OTU)	Levin's Niche Overlap (OTU)	Pianka's Niche Overlap (Order)	Levin's Niche Overlap (Order)
<i>S. jarrovii</i> – <i>S. virgatus</i> Syntopic	0.195	0.143	0.541	0.481
<i>S. jarrovii</i> – <i>S. slevini</i> Syntopic	0.000	0.000	0.261	0.252
<i>S. slevini</i> – <i>S. virgatus</i> Allotopic	0.052	0.035	0.415	0.381

Table 2.4 Dietary niche overlap by prey order between the two populations for each species. Populations did not share any OTUs between sites but shared multiple diet items at order level.

Species	Pianka's Niche Overlap (Order)	Levin's Niche Overlap (Order)
<i>S. jarrovii</i>	0.396	0.4
<i>S. slevini</i>	0.338	0.24
<i>S. virgatus</i>	0.559	0.492

CHAPTER III

Ecomorphology is associated with speciation and community composition in *Sceloporus* lizards

Abstract

Closely-related species can impose strong forces of selection on one another, leading to dramatic examples of phenotypic evolution. Resource partitioning is one such process that can promote the use of novel resources between co-occurring species to reduce competitive overlap and thereby drive phenotypic divergence. Quantifying the relationship between ecology and morphology across species can reveal how ecological opportunity and evolutionary constraint interact to shape patterns of phenotypic evolution and how phenotypic diversity can facilitate co-occurrence. We explored the dynamics of ecomorphological evolution in relation to speciation and community composition in *Sceloporus* lizards, a speciose group that spans North and Central America, where species often occur in sympatry. Using data for 80 taxa, we demonstrate strong relationships between multivariate morphology and ecology, finding that *Sceloporus* species occur in six ecological modes with associated morphologies (ecomorphs). We found that the evolution of arboreality was a major transition that expanded morphospace, allowed for further ecological novelty, and is associated with increased speciation rates. Across much of the range of the genus, ecomorphs are spatially overdispersed, suggesting that interspecific competition may limit the ability of similar species to coexist. However, ecomorphs have different constraints on sympatry: smaller-bodied habitat specialists appear limited in their ability to co-occur, whereas generalists and scansorial species co-occur readily, suggesting that for more ecomorphologically similar species, limits on co-occurrence may be higher. By quantifying ecomorphological diversity across a diverse radiation, our results shed new light on how phenotypic variation accumulates and its implications for coexistence between closely-related species.

Introduction

What drives the evolution of phenotypic diversity, and what are its consequences? Habitat partitioning that leads to phenotypic differentiation is often a key first stage in vertebrate radiations (Streelman and Danley 2003). Notable examples are *Anolis* lizards where specialized limb, digit, and toe morphologies are associated with vertical habitat partitioning (Losos et al. 1998), stickleback fishes that have repeatedly evolved benthic and limnetic forms (Bolnick and On 2008), and Darwin's finches where divergence between ground and tree clades gave way to further phenotypic novelty (Grant and Grant 2003). Dissecting this relationship between organismal ecology and morphology, or ecomorphology, can provide insights into the interplay of adaptive phenotypic evolution, speciation, and community dynamics (Arnold 1983). Divergent ecomorphology can facilitate the use of unique resources, thereby reducing competitive overlap in sympatry (Pianka 1974; Schoener 1974; Pacala and Roughgarden 1985). Ecomorphological divergence may be particularly important for facilitating coexistence between closely-related species, which would otherwise typically be ecologically and morphologically similar (Schluter 2000a).

Ecological opportunity, which comes in many forms (Losos and Mahler 2010), creates the potential for diversifying selection to generate phenotypic diversity. For example, arrival to new areas such as islands or lakes can allow lineages to exploit novel resources (Nosil and Reimchen 2005; Mahler et al. 2010; Refsnider et al. 2015), which is often aided by competitor or predator release (Schluter 1988). Ecological opportunity need not result from geographic shifts or expansion, though—for example, accessing novel microhabitat within a lineage's existing range can also provide sufficient opportunity to promote phenotypic novelty (Ford et al. 2016).

Access to novel niche space can result from the evolution of key phenotypic diversity. Hence, phenotypic evolution itself may generate ecological opportunity (e.g., bats evolving powered flight), while in other cases ecological opportunity may arise first and allow for subsequent phenotypic evolution (Losos and Mahler 2010). Further, many radiations reveal a suite of divergent traits that interact to improve whole organism performance and allow access to novel niche space (Losos et al. 1998; Schluter 2000b; Wainwright et al. 2012; Yuan and Westeen 2024). Examinations of both multivariate morphology and ecology can therefore help us better understand how and when phenotypic evolution leads to niche diversification.

Comprehensively understanding ecomorphological evolution requires characterizing the spatial and phylogenetic context in which it occurs. Examining these together can uncover the roles that factors such as interspecific competition have played in the diversification history of different groups. For example, whether phenotypic traits are shared or divergent between sister taxa can suggest whether neutral or deterministic forces, respectively, have played a role in shaping their evolution (Rundell and Price 2009). Similarly, quantifying the distribution of phenotypic diversity across space can provide insights into community sorting mechanisms and the selective pressures acting on niche evolution. Ecomorphologically diverse communities are often formed when similar species are limited in their ability to co-occur (e.g., limiting similarity), whereas communities of ecomorphologically similar species can reveal that species with certain traits are more successful in a given environment (e.g., habitat filtering) (Webb et al. 2002).

Sceloporus lizards are a diverse, species-rich clade with a geographic distribution throughout North and Central America in which species often occur in sympatry (Hall 2009;

Rivera et al. 2021). With over 100 described species, they are the most speciose genus in the family Phrynosomatidae. *Sceloporus* lizards exhibit a great deal of ecological variation, inhabiting a broad range of habitats such as lowland deserts, cloud forests, high alpine forests, grasslands, and sand dunes (Roll et al. 2017). The diversification history of this group has been the subject of extensive study, and there is known rate heterogeneity with a period of rapid diversification in one clade (hereafter, the rapid radiation) beginning 20-25Mya (Leaché et al. 2016). If phenotypic evolution is associated with speciation in this group, we might expect species in the rapid radiation to be more ecomorphologically divergent. Recent work has suggested that ecomorphological diversity reduces competitive overlap between *Sceloporus* species in sympatry (Westeen et al. 2023) and that communities tend to be phylogenetically clustered but exhibit body size diversity (Rivera et al. 2021). Hence, *Sceloporus* lizards provide an excellent opportunity to study phenotypic evolution in relation to ecology, phylogenetic history, and interspecific interactions.

Here, we examine the relationship between ecology and morphology across *Sceloporus* and how ecomorphology is related to speciation and community composition in this diverse radiation. We collected data on the morphology, ecology, and geographic distribution of 80 taxa to answer the following questions: (1) what is the relationship between ecology and morphology across this group? (2) What is the tempo and mode of ecomorphological evolution? And (3) what is the spatial distribution of ecomorphological diversity? Examining how ecomorphological diversity arises and its role in structuring co-occurrence patterns can provide a more complete understanding of the causes and consequences of phenotypic evolution.

Methods

Data

We collected morphological data from from a total of 330 field-caught lizards and museum specimens, spanning a total of 80 *Sceloporus* taxa (Appendix III). Permits for field-collected data were granted to EPW (AZGFD LIC#SP653941, SP404320, SP407158, SP808336, NMDGF #3780) and IJW (CA SC-8436). Ethanol-preserved individuals came from the Museum of Vertebrate Zoology (MVZ) at the University of California, Berkeley, the California Academy of Sciences (CAS), and the Museum of Natural History at the University of Colorado, Boulder (UCM). We obtained digital photographs of additional specimens via VertNet from the Museum of Comparative Zoology at Harvard University and from UCM as part of the oMeso project (NSF Award No. 2001474).

We measured a suite of morphological traits from all specimens: body size as given by snout-to-vent length (SVL), head length, head width, body width, humerus length, radioulna length, forefoot length, forelimb length, femur length, tibiofibular length, hindfoot fourth toe length, hindfoot length, hindlimb length, and dorsal scale count following Wegener et al. (2014). We selected these measures because they are commonly associated with performance and/or ecology in lizards. Body size is associated with locomotion and jumping (Losos 1990), thermal physiology (Rubalcaba and Olalla-Tárraga 2020; Claunch et al. 2021), climate and microhabitat (Adolph 1990; Losos 1990), and prey size (Vitt and Zani 1996). Limb lengths, and especially hindlimbs, are associated with perch height and diameter (Losos 1994; Losos et al. 1997), as is foot morphology (Losos 1990). Longer limbs are also associated with increased sprint speed (Arnold 1983; Losos and Sinervo 1989; Sinervo and Losos 1991; Reilly and Delancey 1997). Head width is associated with bite force and dietary breadth (García-Rosales et al. 2019). Scale

counts are associated with climate and are thought to reduce evaporative water loss (Oufiero et al. 2011; Wegener et al. 2014)

We took standardized digital photographs of all specimens and measured morphology from these images. EPW photographed specimens on a white background with a ruler in the frame for scaling, using a Nikon D3500 digital camera coupled with a Nikkor AF-P 18-55mm lens. We used a polarizing filter coupled with two Neewer CN-160 LED lights with linear polarization sheets attached to them to remove any glare on wet (e.g., ethanol-preserved) specimens.

We collected measurements in Adobe Photoshop by setting a custom scalebar based on the ruler in each photo. All measurements were replicated by at least two independent reviewers or by the same reviewer at separate timepoints. We averaged measurements per specimens, and any measurements that differed by more than 10% of the average measurement value were discarded for inconsistency. Once we had the mean measurement for each trait per specimen, we then calculated species averages for each trait, resulting in a single set of measurements for each species. Finally, we regressed all morphological traits against body size (SVL) using phylogenetic regressions and used the residuals in downstream analyses as body size-corrected measures (Revell 2012).

We used ecological data from the literature to define habitat categories that each species occupies (Olberding et al. 2016; Meiri 2018; Heimes 2022). We classified habitat into six categories: arboreal, saxicolous (e.g., rock-dwelling), generalist, terrestrial, vegetation-dwelling, and sand-dwelling, following Olberding et al. (2016). Arboreal species are defined as those that predominantly perch in trees. Saxicolous, or rock-dwelling, species include those that primarily use rocks, including boulders, rocky outcroppings, and canyon walls. Generalists are defined as species with evidence for three or more habitat preferences (e.g., arboreal, saxicolous, and terrestrial). Terrestrial species may use a variety of objects as perches but predominantly perch low to the ground. The vegetation class refers to the “bunchgrass” group (*scalaris* clade) of lizards that are strongly associated with bunchgrass clusters in which they take refuge (Ballinger and Congdon 1996). Finally, the sand category represents two species, *S. arenicolus* and *S. woodi*, as well as the White Sands form of *S. cowlesi* that exclusively inhabit sand dunes or sand “islands” in the case of *S. woodi*.

For some analyses, we reduced this categorization scheme into two categories representing the major variation in ecology: predominantly scansorial (arboreal and saxicolous), and predominantly terrestrial (terrestrial, vegetation, and sand), with generalist species classified on a case-by-case basis (Foster et al. 2018). Hereafter, we refer to these ecological groupings as “full scheme” and “reduced scheme” for the six and two category classifications, respectively. Ecological groupings are not intended to explain the totality of species’ habitat use but rather to represent general trends.

We downloaded species range data from the Global Assessment of Reptile Distributions (GARD) dataset, which provides range polygons based on occurrence records and expert opinion (Roll et al. 2017). We pruned a time-calibrated phylogeny for *Sceloporus* (Leaché et al. 2016) to contain only taxa for which we collected morphological data. Given the distinct phenotypic and genetic nature of the White Sands form of *S. cowlesi*, we manually added a branch to the phylogeny of Leaché et al. (2016) using divergence times from Laurent et al. (2016). This

resulted in 80 taxa for which we had morphology, ecology, and phylogenetic data and 77 for which we conducted geographic range analyses.

What is the relationship between ecology and morphology?

To assess the relationship between ecology and morphology, we performed a phylogenetic principal components analysis (pPCA) (Revell 2012). A strong relationship between these variables will manifest as putative ecomorphs occupying different parts of morphospace. We then examined PC loadings to evaluate which morphological traits captured different axes of the variance between species. We used phylogenetic analysis of variance (ANOVA) to test whether univariate morphological traits differ between ecological groups (Revell 2012).

Then, we examined whether we can predict ecology based on multivariate morphology using linear discriminant analysis (LDA) (Venables and Ripley 2002). We performed all analyses on the entire tree and on only the rapid radiation to test the hypothesis that species in the rapid radiation are more morphologically differentiated than the stem group. We also performed all analyses using the full and reduced ecology classification schemes.

Next, we examined evidence for ecomorphological convergence across the *Sceloporus* tree. We first used ‘SURFACE,’ which searches for Ornstein-Uhlenbeck (OU) adaptive optima using a stepwise model-fitting procedure and retains only optima which can be justified under a stated information theoretic criterion (e.g., AICc) (Ingram and Mahler 2013). This approach is useful for identifying the total number of convergence events because the same optimum can be found across the phylogeny; when independent lineages share an optimum, convergence is detected. For the SURFACE analysis, we used principal component axes 1 and 2 (PC1 and PC2) (Ingram and Mahler 2013). We also computed the strength of convergence as the Wheatsheaf index (w), which examines phenotypic distance in relation to phylogenetic distance (Arbuckle et al. 2014). We computed w for all ecological groupings, using PC1 and PC2 as our phenotypic data, and conducted 1,000 bootstrap replicates to estimate a P-value using the ‘windex’ package (Arbuckle and Minter 2015).

What are the dynamics of ecomorphological evolution?

To quantify the degree to which phylogenetic history influences ecological mode, we calculated phylogenetic signal using the delta approach of Borges et al. (2019). We calculated phylogenetic signal for morphology, as given by PC1, as Blomberg’s K , the ratio of observed to expected phenotypic variance under Brownian motion (BM), and Pagel’s λ , a scaling factor for correlations between species relative to a Brownian motion expectation (Pagel 1994; Blomberg et al. 2003; Revell 2012).

We analyzed disparity through time (DTT) to assess how morphological disparity, given by the first two PC axes, is distributed within and among subclades (Harmon et al. 2008; Pennell et al. 2014). Higher values of relative disparity (given by the Morphological Disparity Index, MDI) indicate greater morphospace occupied within subclades compared to the group’s overall disparity, whereas low values indicate morphological variation is distributed between subclades and can suggest constrained evolution (Harmon et al. 2003). Additionally, we calculated MDI separately for the stem group and the rapid radiation (Guillerme 2018).

To better understand the dynamics of morphological evolution within *Sceloporus*, we fit a series of models of evolution to our trait data. First, we fit three univariate models using PC1 as our metric of morphology, which largely represents body size (Harmon et al. 2008; Pennell et al. 2014). The three models include Brownian motion, a random walk; Ornstein-Uhlenbeck (OU), a random walk where characters return to a single optimum; and an Early Burst (EB) model in which the overall rate of evolution slows as time progresses. We implemented multivariate models using all 13 measures of body form in ‘mvMORPH’ using a penalized likelihood approach for high-dimensional data (Clavel et al. 2015). We fit the same three models, BM, OU, and EB, for multivariate data.

To evaluate the evolutionary dynamics of ecological states, we then conducted maximum-likelihood ancestral state reconstruction and transition rates (q) estimation using the ‘ace’ function in the R package ‘ape’ (Paradis and Schliep 2019). We performed ancestral state reconstructions using the equal rates, symmetrical, and all rates different models and compared models using AIC scores and pairwise-likelihood tests. In addition, we performed stochastic character mapping implemented in ‘SIMMAP’ to estimate the number of transitions between ecological states (Huelsenbeck et al. 2003; Revell 2012). We performed 999 simulations and averaged the number of transitions across all simulations. To compare with our maximum-likelihood ancestral state reconstruction, we also calculated the posterior probability of each ancestral state by summarizing across simulations.

To assess whether ecology is associated with speciation across *Sceloporus*, we tested for trait-dependent speciation using a series of state-dependent speciation and extinction models in the ‘Hidden State Speciation and Extinction’ framework (HiSSE, Beaulieu and O’Meara 2016). This framework is advantageous because it allows both observed characters and concealed (hidden) states, which reduce the prevalence of type I errors common to other SSE family models (Rabosky and Goldberg 2015; Beaulieu and O’Meara 2016). SSE methods in general are sensitive to states that have evolved only once or few times and can lead to spurious results when these traits are modeled (Maddison and FitzJohn 2015). Therefore, we used the reduced scheme for ecology that classified species as either predominantly terrestrial or scansorial. We built four models: the null model included equal rates for speciation (λ), extinction (μ), and transitions (q) and did not include hidden states. Second, the ‘hidden state’ model included two hidden states and allowed λ and μ to vary as functions of the unobserved states only. Third, our ‘ecology’ model allowed all three parameters to vary with ecological state. Fourth, our ‘ecology + hidden’ model allowed all three parameters to vary with ecology state as well as two hidden states. All models were fit using the ‘hisse’ package in R.

What is the spatial distribution of ecomorphological diversity?

To visualize the spatial distribution of *Sceloporus* diversity we constructed maps of *Sceloporus* species richness and ecomorph richness at 5 arc-minute resolution, which represents a horizontal resolution of ~9km at the equator. We used the GARD dataset, which provides range polygons based on occurrence records and expert opinion (Roll et al. 2017), and functions developed in Davis Rabosky *et al.* (2016) to create our maps.

Next, we investigated whether the distribution of ecomorphology is spatially overdispersed (a tendency for different ecomorphs to co-occur, as in limiting similarity), underdispersed (a tendency for same ecomorphs to co-occur, as in habitat filtering), or neutral with respect to species richness. To do so, we used spatial autoregressive (SAR) models

implemented in the package ‘spdep’ to map the distribution of residuals of a linear regression of ecomorph richness on species richness while accounting for spatial autocorrelation (Bivand and Wong 2018). We constructed the neighbors list using polygons for each species’ range and computing both overlapping and contiguous polygons; for contiguous polygons, we specified that more than one boundary point must be shared to be considered neighbors. We excluded island endemics (*S. angustus*, *S. becki*, *S. grandaevus*) from community analyses as they are the sole *Sceloporus* inhabitants of their respective islands. We then mapped the residuals of our resulting model; ecomorphological overdispersion with respect to species richness will result in positive residuals, underdispersion will result in negative residuals, and a neutral relationship will result in a residual of 0.

To further assess whether ecomorphs are more spatially overdispersed than expected by chance, we conducted a permutation test by shuffling ecomorph assignments among species (while keeping the distribution of range polygons fixed) and re-running SAR models 1000 times to generate a null distribution. We compared the slopes of the shuffled distributions to the observed slope and calculated a one-tailed p-value as the number of instances that a simulated slope was greater, indicating a stronger relationship, than the observed slope, divided by the number of simulations.

To investigate whether ecomorphs had different constraints on sympatry, we calculated range overlap for every pair of species in our dataset. We used a 20% range overlap threshold as a proportion of the focal species range size (Pigot and Tobias 2013; Shi et al. 2018; Yuan et al. 2022). We then calculated for each species how many times it overlapped with species of the same ecomorph and the proportion of the total number of species with which it overlaps to account for differences in overall range size between species. Ecomorphs with more constraints on limiting similarity should overlap with species of their own ecomorph class less than those of other ecomorph classes. We then computed the overlap between all pairs of ecomorphs and visualized these relationships using a heatmap (R Core Team 2021). We compared this with a heatmap of overlap in morphospace between ecological groups to evaluate how ecomorphological similarity may influence co-occurrence.

Results

Data

We collected morphological data from 330 individual *Sceloporus* lizards, including field-caught animals and ethanol-preserved specimens spanning 79 species plus the ecologically-unique White Sands form of *S. cowlesi*. The number of specimens measured per species ranged from 1 to 16 with an average of 3.7. After pruning a time-calibrated phylogeny for *Sceloporus* (Leaché et al. 2016), our dataset included 80 taxa for which we had morphological, ecological, and phylogenetic data and 77 for which we conducted geographic analyses. All morphological traits were significantly correlated with body size (all $p < 0.05$), so we used residuals of a phylogenetic regression against body size in downstream analyses.

What is the relationship between ecology and morphology?

We found that ecological groups classified by habitat usage (arboreal, $n = 19$; saxicolous, $n = 20$; generalist, $n = 15$; terrestrial, $n = 14$; vegetation, $n = 9$; and sand, $n = 3$) occupy different regions of morphospace, with some being more distinct than others (Fig. 3.1C). Our first PC

axis, PC1, explained 86% of the variance in morphology, and body size loaded highly onto this axis (Table 3.1). Hindlimb length, hindfoot length, and forelimb length all loaded highly onto PC2, which explained 6.5% of the variance (Table 3.1). In our phylomorphospace plot (Fig. 3.1C), vegetation morphs cluster tightly in a position with the smallest body size and reduced limbs and digits. The sand morphs all cluster with their sister species but, in general, occupy the space adjacent to vegetation and terrestrial morphs. Terrestrial morphs cluster tightly and overlap with some generalists and stem-group scansorial species. Generalists occupy the center of morphospace and exhibit the greatest variance along PC2. Arboreal and saxicolous morphs achieve the largest body sizes and overlap the most of any groups; however, the saxicolous species occupy two separate portions of morphospace, with the stem group saxicolous species clustering with terrestrial and generalist species, while species in the rapid radiation cluster with arboreal species (Fig. 3.1C). The stem group, overall, is restricted in morphospace, occupying only 25% of morphospace, clustering with low scores on PC1 and intermediate to high scores on PC2, representing small body size and average to elongated limbs.

Species in the rapid radiation occupy novel morphospace (89% of total morphospace) compared to the stem group; for instance, arboreal morphs reveal high scores along PC1 representing the evolution of larger body size compared to stem group species. Vegetation morphs, on the other hand occupy, unique morphospace with low scores on both PC axes, representing small bodies and reduced limbs (Fig. 3.1C). When species are grouped into a reduced scheme with only two ecological categories, scansoriality (arboreal and saxicolous) and terrestriality (terrestrial, sand, and vegetation), we see even greater separation in morphospace, particularly within the rapid radiation.

Several univariate measures of morphology were significantly predicted by ecological classification. Arboreal morphs are significantly larger than generalist, terrestrial, sand, and vegetation morphs ($t < -3.38$ and $p < 0.05$ in all comparisons). Hindlimb length also differed significantly, with vegetation morphs having shorter hindlimbs for their body size compared to generalist and terrestrial morphs (all $t < -3.23$, $p < 0.05$), as did hindfoot length, with vegetation morphs again having smaller feet compared to arboreal, generalist, and terrestrial morphs (all $t < -3.34$, $p < 0.05$). Vegetation morphs also had significantly shorter fourth toes than arboreal, generalist, and sand morphs (all $t < -3.77$, all $p < 0.05$).

Linear discriminant analysis predicted ecology from multivariate morphology (using our full scheme) with an accuracy of 68% for all species, which increased to 78% when only the rapid radiation was examined. The most miscategorized groups were arboreal and saxicolous. Using the reduced ecology scheme, accuracy jumped to 91% for the full tree and 96% for the rapid radiation)

The SURFACE analysis identified eight phenotypic shifts across all species, with multiple convergent and divergent regimes. SURFACE detected a novel phenotypic regime (indicated by a divergent shift) at the base of the rapid radiation. The entirety of the bunchgrass clade was also considered divergent to the rest of the rapid radiation. The stem group consists of a single phenotypic regime except for the two island endemic species, *S. angustus* and *S. grandaevus*, which were considered divergent. We found terrestrial ($w = 2.769$, $p = 0$), sand ($w = 6.61$, $p = 0.047$), and vegetation ($w = 1.825$, $p = 0.03$) ecomorphs to be phenotypically convergent according to the Wheatsheaf index.

What are the dynamics of ecomorphological evolution?

Our analysis did not detect a significant phylogenetic signal for ecological class (full scheme, $\Delta A=7.13$, $p = 0.19$, reduced scheme, $\Delta A=2.99$, $p = 0.4$). For our SIMMAP analysis, the symmetrical model was identified as the best fit for the full ecology dataset ($\Delta AIC = 9$). We estimated an ancestral state for the crown group *Sceloporus* using the full ecological scheme as terrestrial (0.504), generalist (0.182), or saxicolous (0.178), based on the scaled likelihood at the root (other probabilities < 0.05 , Fig. 3.2A). We recovered 51.78 transitions between ecological states across the tree, with the most frequent transitions occurring as terrestrial to generalist states (10.86 transitions) and back (9.57 transitions; Fig. 3.2B). We found that arboreality evolved a single time at the base of the rapid radiation (posterior probability = 0.90).

Under the reduced ecology scheme, our best fit model was an equal rates model ($\Delta AIC = 22$). We found more support for a terrestrial ancestor (scaled likelihood at the root = 0.611) than a scansorial ancestor (scaled likelihood = 0.389). We recovered 21.29 transitions over the tree, with slightly more (12.4 transitions) being from scansoriality to terrestriality than vice versa.

From our analyses of phylogenetic signal in morphology (given by PC1), we obtained a value of $\lambda = 0.793$ and a value of $K = 0.676$. We found that univariate morphology, given by PC1, best fit an OU model of evolution (AIC weights: BM = 0.052, OU = 0.929, EB = 0.017; Parameters from OU model: $\sigma^2= 0.371$, $\alpha= 0.048$). Multivariate morphology, analyzed in ‘mvMORPH,’ also best fit an OU model of evolution. Our DTT analysis yielded an MDI statistic of -0.0967 for the whole tree for PC1 and 0.475 for PC2, and neither significantly differed from a simulated null distribution ($p = 0.153$ and $p = 0.994$, respectively). However, we found that MDI differed significantly with the stem group having lower disparity (mean = 1.080) compared to the rapid radiation (mean = 4.35, $p < 0.001$). The best fit model for our HiSSE analysis was the ecology + hidden model (Table 3.2), suggesting that ecological mode is associated with increased speciation rates, but that effect is secondary to an unmeasured state. Our parameter estimates support heterogeneous transition rates (Fig. 3.2B).

What is the spatial distribution of ecomorphological diversity?

We found that the spatial distribution of ecomorphological diversity is correlated with species diversity ($R^2 = 0.812$, $p < 0.001$), and both ecomorph and species richness peak in Mexico (Fig. 3.3A). Our SAR model revealed a slope of $\beta= 0.520$, suggesting that for every two species in a given grid cell, or “community,” roughly one additional ecomorph is found. The distribution of residuals reveals that, across much of the range of *Sceloporus*, there are more ecomorphs than expected based on species richness. Areas of high species richness show positive residuals, while large temperate areas where only a handful of species occur (e.g., the United States of America, excluding the desert southwest) are effectively neutral with respect to comparisons based on species richness. Our permutation test also revealed that ecomorphs are significantly spatially overdispersed compared to null expectations ($p = 0.023$).

Our comparisons of co-occurring congeners by ecomorph category revealed that vegetation, sand, and terrestrial ecomorphs are less likely to co-occur with species of their same ecomorph type than arboreal and saxicolous ecomorphs (all $p < 0.001$). Examinations of overlap between all pairs of ecomorphs in geographic space and morphospace reveal different constraints on sympatry. Vegetation, sand, and terrestrial ecomorphs overlap in morphospace but are

unlikely to co-occur in geographic space, whereas arboreal, saxicolous, and generalist ecomorphs overlap in morphospace and often co-occur geographically (Fig. 3.3 E,F).

Discussion

To understand how phenotypic diversity evolves in closely-related species and how it can enable co-occurrence, we examined ecomorphology in a diverse and widespread group of lizards. As a critical first step, our results demonstrate a strong relationship between ecological mode and multivariate morphology. We found that a shift to arboreality at the base of a rapid radiation is associated with increased speciation and the evolution of both phenotypic and ecological novelty. Consequently, we found that ecomorphology plays a role in community composition across the range of the genus, with a predominant pattern of overdispersion of ecomorphs suggesting that limiting similarity may structure communities. Our study provides new insights into the evolution of ecomorphological diversity and its consequences for speciation processes and coexistence in closely-related species.

What is the relationship between ecology and morphology?

We found a strong relationship between ecology and morphology, with both our univariate (ANOVAs) and multivariate (PCA, LDA) analyses underscoring that body size and limb lengths are key traits that differ between *Sceloporus* ecomorphs (Table 3, Fig. 3.1C). Across lizard diversity, the relationship of body size and limb lengths is associated with microhabitat due to the functional basis of these traits (Foster et al. 2018). In Iguanian lizards, longer limbs are typically associated with increased sprint speeds (Losos and Sinervo 1989; Sinervo and Losos 1991) and are associated with perch diameter in some *Anolis* lizards (Kolbe 2015). We found that generalist and terrestrial *Sceloporus* species typically have longer limbs for their body size (Fig. 3.1C), and these species likely use running as their predominant means of predator escape (Cooper and Avalos 2010). Arboreal and saxicolous species may instead use crevices or shuttle to the opposite side of their tree or boulder (Cooper and Avalos 2010), thus reducing the need to optimize sprint speed and perhaps favoring climbing ability. Arboreal and saxicolous morphs reveal variation in relative limb lengths (Fig. 3.1C), suggesting lability in this trait; investigating the relationship of limb lengths to climbing and sprinting abilities across *Sceloporus* ecomorphs will be an interesting next step. We also found that vegetation ecomorphs are morphologically similar to terrestrial ecomorphs and have comparable body sizes but exhibit significant reduction in limb length, foot length, and fourth toe length (Fig. 3.1C). Unlike terrestrial sprinters, these species are known to duck into bunchgrass clusters for refuge rather than flee (Bock et al. 1990; Westeen et al. 2023). Thus, relative limb length appears to be a key trait differentiating *Sceloporus* ecomorphs, with some specialized morphs also revealing divergent foot morphology.

Beyond ecology morphology associations, we also uncovered evidence for evolutionary convergence within some ecomorph classes including the terrestrial, sand, and vegetation groups. However, the index used (w) is agnostic to process, and parallelism is indistinguishable from convergence (Arbuckle et al. 2014): the vegetation modality has evolved only once and therefore represents morphological conservatism rather than convergence. We did not detect a signal of convergence among generalists, likely due to the spread in traits across species. The saxicolous category is the only one that appears to represent two distinct phenotypes—stem group saxicolous species are small bodied, small scaled, with relatively long limbs for their body size, while saxicolous species in the rapid radiation reveal larger bodies, larger scales, and variation in limb lengths. Our examinations of ecomorphological variation across the phylogeny underscore

the mosaic pattern of phenotypic evolution in this group: some ecological groups are highly conserved (vegetation), some are highly convergent (sand, terrestrial), some are highly labile (generalist), and one class reveals two distinct phenotypes (saxicolous).

What are the dynamics of ecomorphological evolution?

We detected a moderate level of phylogenetic signal for morphology ($\lambda = 0.793$, $K = 0.676$) but a non-significant signal for ecology, suggesting that while morphology may be constrained by phylogenetic history, ecology may be more labile. Our models of evolution and our DTT analyses suggest that morphological variation is distributed among subclades rather than within them, and that morphological evolution in *Sceloporus* has accumulated gradually, with an increase in disparity occurring in the rapid radiation. We found that the ancestral *Sceloporus* was most likely a terrestrial species and that arboreality evolved a single time at the base of the rapid radiation (~20-25Mya). Arboreality then gave way to multiple other modalities, including a one-way transition to vegetation dwelling (Fig. 3.2B).

We found that species in the rapid radiation exhibited higher morphological disparity concomitant with the evolution of ecological novelty, especially arboreality, which then led to the evolution of the vegetation modality and re-evolution of the saxicolous mode (Fig. 3.1C, Fig. 3.2A). This is consistent with results that larger body size evolved at the base of the rapid radiation and has been retained, as most arboreal species are large-bodied, and rapid radiation saxicolous species are similarly large-bodied (Rivera et al. 2021). Our trait-dependent speciation analyses further revealed that speciation rates are faster in scansorial taxa (Fig. 3.2C). Thus, the transition to arboreality, coincident with the rate shift at 20-25Mya, may have been a key transition in *Sceloporus* that opened additional ecological and morphological space, allowing for faster speciation.

Sceloporus evolved in the northern United States and Canada (Lawing et al. 2016), likely invading Mexico only within the last 5 million years when the habitat became suitable (Rivera et al. 2020). Other lizards within the Nearctic guild are predominantly terrestrial (e.g., horned lizards, skinks, alligator lizards, whiptails, night lizards), or saxicolous (e.g., collared lizards, rock lizards, desert iguanas). Arboreal lizards in this region include those in the genera *Urosaurus* (e.g. bush and tree lizards) and *Anolis*, the latter of which are found largely in the southern part of this range and arrived only in the Miocene (Glor et al. 2005). Therefore, the arboreal niche where *Sceloporus* evolved was likely largely unoccupied and may have provided the initial opportunity for ecomorphological diversification.

Our findings that transitions between generality and terrestriality occurred frequently across the *Sceloporus* tree suggest that these two states as especially labile. The fastest transition we detected occurred from sand back to generalism, suggesting the highly specialized sand ecomorphology may not be a successful long-term strategy given the limited availability of sand habitat (Fig. 3.2B). Of all the ecological modes, arboreality is the source of most transitions to other ecologies (Fig 3.2C), again suggesting that the evolution of arboreal ecomorphology played a critical role in enabling adaptive diversification in this group.

Arboreality has evolved many times in squamate reptiles (Miller and Stroud 2021) and could be associated with increased speciation by opening up new ecological space (Bars-Closel et al. 2017, but see De Alencar et al. 2017 and Harrington et al. 2018 for examples of arboreality constraining morphological evolution in snakes). However, in agamid lizards, arboreality is not

associated with diversification (Yuan and Westeen 2024), and one study found that terrestriality, rather than arboreality, is associated with ecomorphological differentiation (Collar et al. 2010). Thus, the evolution of arboreality across squamate reptiles appears to be an opportunity in some cases and a constraint in others; in *Sceloporus*, we find evidence that it provided sufficient opportunity for further morphological and ecological novelty to evolve.

What is the spatial distribution of ecomorphological diversity?

We found evidence for spatial overdispersion of ecomorphs, suggesting that competitive exclusion may play a role in community assembly in *Sceloporus*. Across the range of *Sceloporus*, species are unevenly distributed, with higher species richness occurring from Mesoamerica to Central America (Fig. 3.3B), broadly following the latitudinal diversity gradient, where diversity increases near the tropics (Hillebrand 2004), and Rappaport's rule, where species at higher latitudes have larger ranges and less turnover (Stevens 1989). Rivera *et al.* (2021) showed that *Sceloporus* are phylogenetically clustered across the landscape and that heterogeneous environments—which can provide more opportunities for allopatric speciation to occur—are positively associated with species richness. Community composition patterns observed today are likely a reflection of these allopatric speciation modes coupled with moderate levels of dispersal, potentially to reduce competitive overlap, though other modes of speciation cannot be ruled out. Some areas of very high species richness (e.g. north-central Mexico) are underrepresented with ecomorphs, which is likely an artifact of having only 5 possible ecomorphs that can co-occur in a given area, whereas species richness can reach 12 or even 14 (at the scale of our 5 arc-minute map). Tropical mountains with high species richness may offer additional microhabitat heterogeneity and niche space, such that species occupying same ecomorph class in these regions may actually differ sufficiently in their ecologies to offset competitive overlap (Janzen 1967).

Furthermore, we found that ecomorphs may have different constraints on sympatry—while arboreal, saxicolous, and generalist morphs appear to co-occur readily, smaller morphs such as the terrestrial, vegetation, and sand morphs are less likely to be found in the same community (Fig. 3.3 E,F). This may be the result of allopatric speciation, especially within the *scalaris* clade (of which all members are vegetation morphs) and in which diversification appears tied to volcanism in the Trans-Mexican Volcanic Belt region (Bryson et al. 2012). However, vegetation morphs are also the most ecologically and morphologically similar (Fig. 3.1C), and therefore constraints on limiting similarity may be higher. Similarly, the sand morphs are the only *Sceloporus* in most parts of their specialized and restricted ranges (*S. arenicolus* in the Mescalero Sand Dune blowouts of New Mexico and Texas, *S. cowlesi* at White Sands, and *S. woodi* in the sandhill paleoislands of Florida) but do co-occur with terrestrial and generalist species in parts of their range. This echoes results found by Rivera *et al.* 2021 that smaller species are more likely to occur with larger species (compared to small species) than expected by chance, whereas larger species had no such constraints and co-occurred with other large species readily. Many small-bodied species are also habitat specialists, which may be the underlying reason for their constraints on sympatry.

Of all combinations, generalists occur with other generalists the most. This could be due in part to many of these species having larger ranges across temperate zones (e.g., *S. undulatus*, *S. occidentalis*, *S. graciosus* (Roll et al. 2017)) or because these species often exhibit lability in habitat use (Sinervo and Losos 1991) such that they can offset their resource use in sympatry.

The high degree of overlap between scansorial (arboreal and saxicolous) morphs may be a function of greater vertical space to partition, as in *Anolis* lizards (Williams 1972; Losos et al. 1998; Losos 2009). Our use of aggregated polygons could overestimate community membership; however, the fact that our results support those found using occurrence data (Rivera et al. 2021) are promising. Studies that continue to quantify closely-related species' interactions, performance abilities, and resource use in sympatry, and their relationships to morphology, will deepen our understanding of how interspecific interactions and phenotypic diversity shape patterns of community composition.

Conclusions

Our results show that ecomorphological evolution is associated with speciation and community composition in a diverse and widespread lizard radiation. We found that body size and relative limb and digit lengths differ between *Sceloporus* ecomorphs in ways consistent with functional differences in sprinting and climbing performance expected by their habitat utilization. The evolution of one of these ecomorphological forms, arboreality, is linked to an increase in speciation rate and led to further ecomorphological diversification, suggesting that some morphological shifts can precipitate the rapid accumulation of additional phenotypic novelty. Together, our results suggest that phenotypic evolution itself can create sufficient ecological opportunity, even without a shift in a lineage's geographic range or an environmental change in resource availability, to enable the rapid evolution of ecomorphological and species diversity.

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Figures & Tables

Figure 3.1 A. Phylogeny of *Sceloporus* lizards from (Leaché et al. 2016); bar length at tips represents relative body size, given by SVL, and colored by ecology. The rapid radiation is denoted by purple branches. B. Exemplar ecomorphs reveal phenotypic convergence and/or conservatism. C. Phylomorphospace for species in this study, visualized using the first two principal components of a phylogenetic PCA. Convex hulls group species by ecology. Photos 1-11 by EPW, photo 12 ©Joel Sartore/ Photo Ark.

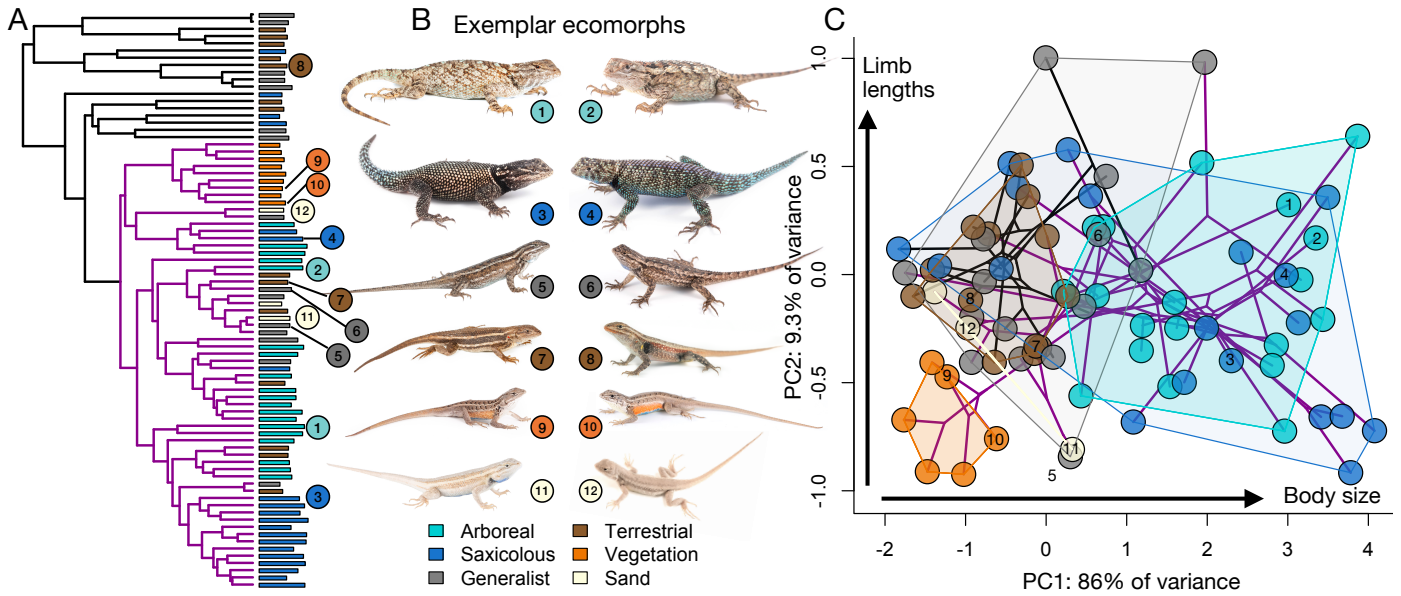


Figure 3.2 A. Maximum likelihood ancestral character estimates for ecology are shown on a phylogeny of *Sceloporus* studied here. Tip labels correspond to ecological mode. B. Transition rates between ecological modes. Arrows are colored by transition rate, with red being faster, and labelled with estimated mean number of transitions between states. C. Model-averaged speciation rates from our best fit HiSSE model. Outer colors indicate speciation rate, with red being faster. Inner colors represent the ecological mode using the binary characterization.

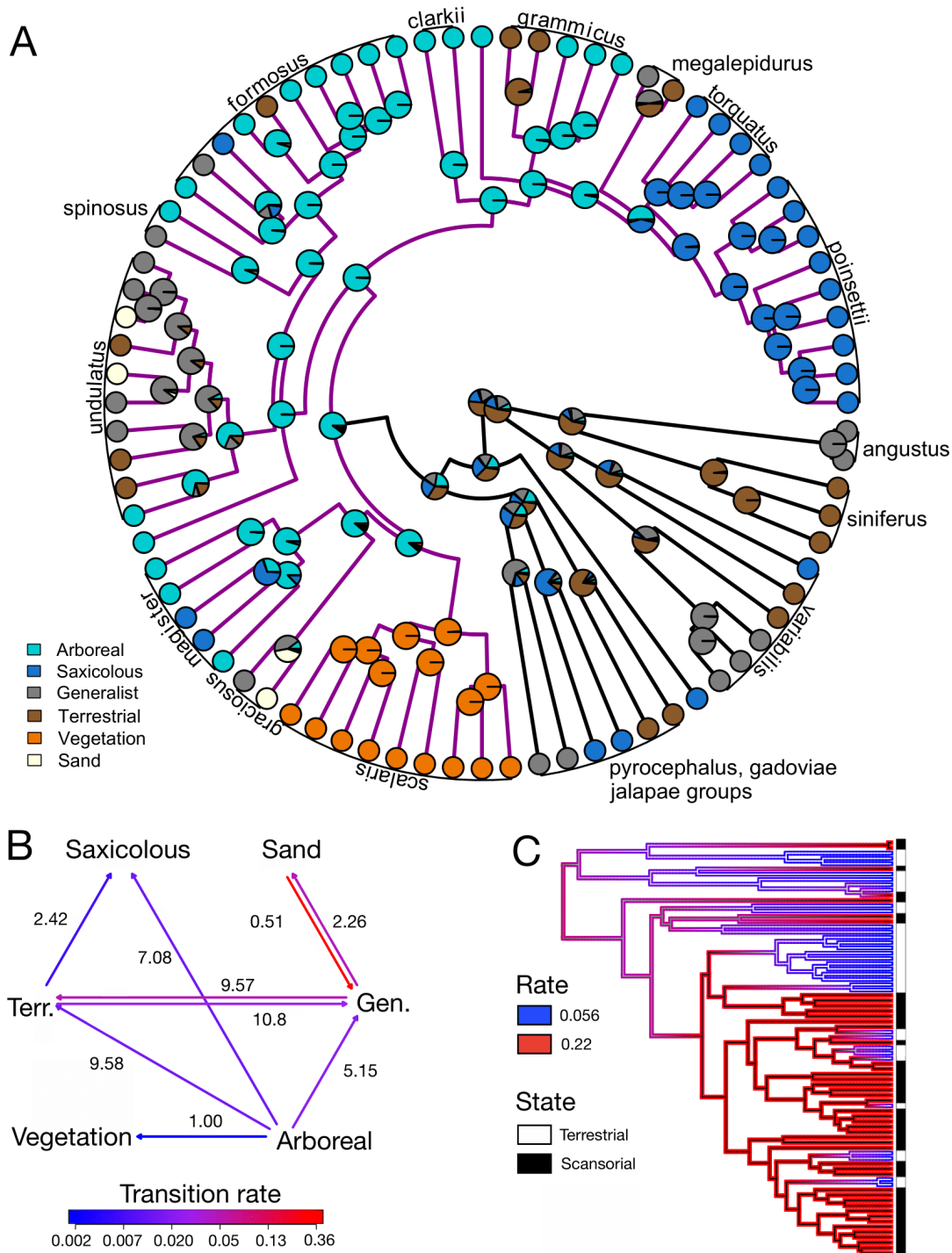


Figure 3.3 A. Ecomorph richness peaks in the southwestern United States and Central Mexico. B. Species richness also peaks in the same areas, with richness reaching 14 species per 5-minute grid cell in some areas. C. Residuals of a regression of ecomorph richness on species richness reveal that across much of the range of the genus, *Sceloporus* ecomorphs are spatially overdispersed. D. Distribution of slopes from our permutation test show that the observed distribution (slope indicated by red line) is stronger than expected by chance. E. Heatmap of geographic overlap by ecological group. F. Heatmap of morphological overlap by ecological group.

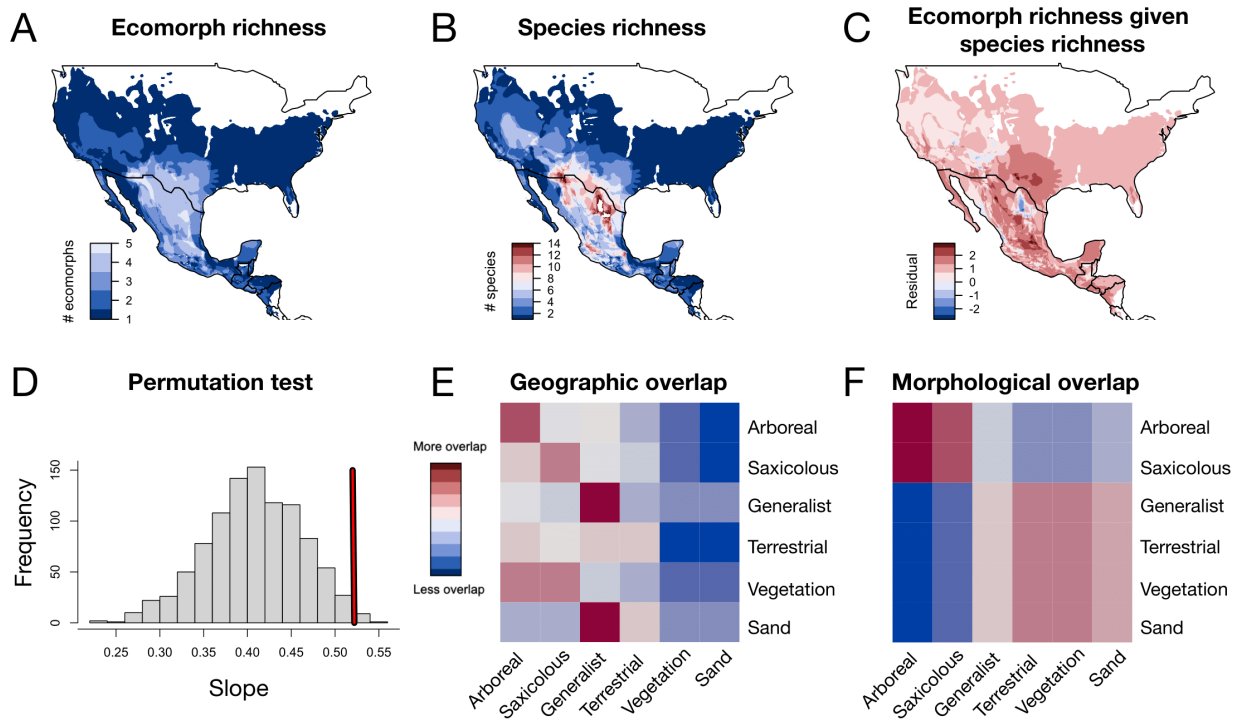


Table 3.1 Principal component axis loadings based on a phylogenetic PCA for species in this study.

	PC1	PC2
<i>Percent variance explained</i>	86%	9.3%
Snout-vent length (SVL)	0.999	0
Head length	0.025	0.238
Head width	0.044	0.277
Body width	0.011	-0.165
Humerus length	0.277	0.468
Radioulna length	-0.056	0.516
Forefoot length	0	0.505
Forelimb length	0.141	0.559
Femur length	-0.102	0.837
Tibiofibular length	0.004	0.908
Hindfoot fourth toe	0.092	0.487
Hindfoot length	0.056	0.759
Hindlimb length	-0.054	0.94
Dorsal scale count	-0.106	-0.009

Table 3.2 HiSSE model selection comparing ecology (terrestrial and scansorial) and parameter estimate results, including log-likelihoods, AIC, difference in AIC with minimum value (Δ AIC) and parameter estimates for speciation rate dewlap absent (λ_0), dewlap present (λ_1) and with hidden states (λ_A and λ_B). Other parameter estimates are not shown as they were not relevant to the goals of this study.

	logL	AIC	Δ AIC	λ_{0A}	λ_{1A}	λ_{0B}	λ_{1B}
Null	-307.82	623.62	-9.36	0.0568	0.1005	--	--
Hidden	-304.54	619.08	-4.82	0.1039	0.1039	0.0191	0.0191
Ecology	-305.75	623.50	-9.24	0.0848	0.0848	--	--
Ecology + Hidden	-297.13	614.26	0	0.0557	0.2176	0	0.0203

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Appendix I

Diet records, as given by identified OTUs, recovered from fecal samples in this study. OTUs that were unidentifiable to order level were removed from consideration, as were OTUs representing the host species.

Species	Site	Reads	Kingdom	Phylum	Class	Order	Family	Genus	Species	Confidence	Novel Record?
<i>Sceloporus jarrovii</i>	Barfoot Park	502	Animalia	Arthropoda	Insecta	Diptera	Cecidomyiidae			0.748	Yes
<i>Sceloporus jarrovii</i>	Barfoot Park	5676	Animalia	Arthropoda	Insecta	Diptera	Cecidomyiidae			0.719	Yes
<i>Sceloporus jarrovii</i>	Barfoot Park	4992	Animalia	Arthropoda	Insecta	Orthoptera	Acrididae			0.997	Yes
<i>Sceloporus jarrovii</i>	Barfoot Park	802	Animalia	Arthropoda	Insecta	Lepidoptera				0.998	
<i>Sceloporus jarrovii</i>	Barfoot Park	696	Animalia	Arthropoda	Insecta	Diptera	Cecidomyiidae			0.993	Yes
<i>Sceloporus jarrovii</i>	Barfoot Park	131	Animalia	Arthropoda	Insecta	Orthoptera	Acrididae	Melanoplus		0.724	Yes
<i>Sceloporus jarrovii</i>	Barfoot Park	391	Animalia	Arthropoda	Insecta	Diptera	Cecidomyiidae			0.832	Yes
<i>Sceloporus jarrovii</i>	Barfoot Park	1115	Animalia	Arthropoda	Insecta	Coleoptera	Elateridae	Hemicrepidius	<i>Hemicrepidius morio</i>	0.92	Yes
<i>Sceloporus jarrovii</i>	Barfoot Park	321	Animalia	Arthropoda	Insecta	Lepidoptera				0.999	
<i>Sceloporus jarrovii</i>	Barfoot Park	288	Animalia	Arthropoda	Insecta	Diptera	Cecidomyiidae			0.986	Yes
<i>Sceloporus jarrovii</i>	Turkey Creek	1048	Animalia	Arthropoda	Insecta	Orthoptera	Gryllidae	Gryllus	<i>Gryllus veletis</i>	0.999	Yes
<i>Sceloporus jarrovii</i>	Turkey Creek	1780	Animalia	Arthropoda	Insecta	Lepidoptera	Geometridae	Eusarca		0.81	Yes

<i>Sceloporus jarrovi</i>	Turkey Creek	3554	Animalia	Arthropoda	Malacostraca	Isopoda	Armadillidiidae	Armadillidium	Ambiguous_taxa	0.834	Yes
<i>Sceloporus slevini</i>	Barfoot Park	2	Animalia	Arthropoda	Insecta	Diptera	Tachinidae	Meigenielloides	<i>Meigenielloides cinereus</i>	0.997	Yes
<i>Sceloporus slevini</i>	Barfoot Park	16363	Animalia	Arthropoda	Arachnida	Araneae	Lycosidae	Pardosa		0.977	Yes
<i>Sceloporus slevini</i>	Barfoot Park	8	Animalia	Arthropoda	Insecta	Hymenoptera	Formicidae	Formica	<i>Formica neogagates</i>	0.857	Yes
<i>Sceloporus slevini</i>	Barfoot Park	56	Animalia	Arthropoda	Arachnida	Araneae	Lycosidae	Pardosa		0.975	Yes
<i>Sceloporus slevini</i>	Barfoot Park	95	Animalia	Arthropoda	Insecta	Hemiptera	Rhopalidae	Harmostes	<i>Harmostes reflexulus</i>	0.999	Yes
<i>Sceloporus slevini</i>	AWRR	18731	Animalia	Arthropoda	Insecta	Coleoptera				0.875	
<i>Sceloporus slevini</i>	AWRR	92	Animalia	Arthropoda	Insecta	Coleoptera	Scarabaeidae			0.824	Yes
<i>Sceloporus slevini</i>	AWRR	2016	Animalia	Arthropoda	Arachnida	Araneae	Lycosidae	Schizocosa	<i>Schizocosa sp.</i> 4GAB	0.996	Yes
<i>Sceloporus virgatus</i>	Cave Creek	43	Animalia	Arthropoda	Insecta	Hymenoptera	Formicidae	Formica	<i>Formica gnava</i>	0.999	Yes
<i>Sceloporus virgatus</i>	Cave Creek	74	Animalia	Arthropoda	Insecta	Coleoptera				0.82	
<i>Sceloporus virgatus</i>	Cave Creek	54	Animalia	Arthropoda	Insecta	Coleoptera				0.868	
<i>Sceloporus virgatus</i>	Cave Creek	23	Animalia	Arthropoda	Insecta	Orthoptera	Acrididae			0.997	Yes
<i>Sceloporus virgatus</i>	Cave Creek	511	Animalia	Arthropoda	Insecta	Lepidoptera				0.998	
<i>Sceloporus virgatus</i>	Cave Creek	47	Animalia	Arthropoda	Insecta	Coleoptera				0.864	
<i>Sceloporus virgatus</i>	Cave Creek	3	Animalia	Arthropoda	Insecta	Hymenoptera	Formicidae			0.922	

<i>Sceloporus virgatus</i>	Cave Creek	56	Animalia	Arthropoda	Insecta	Coleoptera					0.774	
<i>Sceloporus virgatus</i>	Cave Creek	11	Animalia	Arthropoda	Insecta	Lepidoptera					0.999	
<i>Sceloporus virgatus</i>	Cave Creek	35	Animalia	Arthropoda	Insecta	Lepidoptera					0.996	
<i>Sceloporus virgatus</i>	Cave Creek	5	Animalia	Arthropoda	Arachnida	Araneae	Lycosidae				0.999	Yes
<i>Sceloporus virgatus</i>	Cave Creek	4	Animalia	Arthropoda	Insecta	Hemiptera	Rhyparochromidae	Eremocoris			0.999	Yes
<i>Sceloporus virgatus</i>	Cave Creek	72	Animalia	Arthropoda	Malacostraca	Isopoda	Armadillidiidae	Armadillidium	Ambiguous_taxa		0.834	Yes
<i>Sceloporus virgatus</i>	Turkey Creek	412	Animalia	Arthropoda	Insecta	Orthoptera	Acrididae	Melanoplus			0.873	Yes
<i>Sceloporus virgatus</i>	Turkey Creek	378	Animalia	Arthropoda	Insecta	Orthoptera	Acrididae				0.85	Yes
<i>Sceloporus virgatus</i>	Turkey Creek	127	Animalia	Arthropoda	Insecta	Orthoptera	Acrididae	Melanoplus			0.926	Yes
<i>Sceloporus virgatus</i>	Turkey Creek	145	Animalia	Arthropoda	Insecta	Hymenoptera	Formicidae	Formica	<i>Formica neogagates</i>		0.857	Yes
<i>Sceloporus virgatus</i>	Turkey Creek	1777	Animalia	Arthropoda	Insecta	Hymenoptera	Formicidae	Liometopum			0.999	Yes
<i>Sceloporus virgatus</i>	Turkey Creek	3826	Animalia	Arthropoda	Insecta	Orthoptera	Acrididae	Melanoplus			0.981	Yes
<i>Sceloporus virgatus</i>	Turkey Creek	2197	Animalia	Arthropoda	Insecta	Orthoptera	Acrididae	Melanoplus			0.724	Yes
<i>Sceloporus virgatus</i>	Turkey Creek	412	Animalia	Arthropoda	Insecta	Orthoptera	Acrididae	Melanoplus			0.952	Yes

Appendix II

Existing diet records collated from a literature search. We considered diet records of free-ranging adult lizards of the three species (*S. jarrovi*, *S. slevini*, or *S. virgatus*); studies in which lizards were fed or had their diets supplemented were not considered.

species	life stage	Phylum	Subphylum	Class	Order	Family/Suborder	study location	method of ID	citation
<i>Sceloporus virgatus</i>	adult	Arthropoda	Hexapoda	Insecta	Coleoptera		Chiricahua Mtns, AZ -Middle Fork, Cave Creek	Manual ID of fecal pellets	Bergeron & Blouin-Demers 2020, Copeia
<i>Sceloporus virgatus</i>	adult	Arthropoda	Hexapoda	Insecta	Diptera		Chiricahua Mtns, AZ -Middle Fork, Cave Creek	Manual ID of fecal pellets	Bergeron & Blouin-Demers 2020, Copeia
<i>Sceloporus virgatus</i>	adult	Arthropoda	Hexapoda	Insecta	Hemiptera		Chiricahua Mtns, AZ -Middle Fork, Cave Creek	Manual ID of fecal pellets	Bergeron & Blouin-Demers 2020, Copeia
<i>Sceloporus virgatus</i>	adult	Arthropoda	Hexapoda	Insecta	Homoptera		Chiricahua Mtns, AZ -Middle Fork, Cave Creek	Manual ID of fecal pellets	Bergeron & Blouin-Demers 2020, Copeia
<i>Sceloporus virgatus</i>	adult	Arthropoda	Hexapoda	Insecta	Hymenoptera		Chiricahua Mtns, AZ -Middle Fork, Cave Creek	Manual ID of fecal pellets	Bergeron & Blouin-Demers 2020, Copeia
<i>Sceloporus virgatus</i>	adult	Arthropoda	Hexapoda	Insecta	Lepidoptera		Chiricahua Mtns, AZ -Middle Fork, Cave Creek	Manual ID of fecal pellets	Bergeron & Blouin-Demers 2020, Copeia
<i>Sceloporus virgatus</i>	adult	Arthropoda	Hexapoda	Insecta	Orthoptera		Chiricahua Mtns, AZ -Middle Fork, Cave Creek	Manual ID of fecal pellets	Bergeron & Blouin-Demers 2020, Copeia
<i>Sceloporus virgatus</i>	adult	Arthropoda	Chelicerata	Arachnida	Araneae		Chiricahua Mtns, AZ -Middle Fork, Cave Creek	Manual ID of fecal pellets	Bergeron & Blouin-Demers 2020, Copeia
<i>Sceloporus virgatus</i>	adult	Arthropoda	Crustacea	Malacostraca	Isopoda		Chiricahua Mtns, AZ -Middle Fork, Cave Creek	Manual ID of fecal pellets	Bergeron & Blouin-Demers 2020, Copeia

<i>Sceloporus virgatus</i>	adult	Arthropoda	Chelicerata	Arachnida		Chiricahua Mtns, AZ - John Hands and Herb Martyr CGs	Manual ID of stomach contents	Watters 2008, Herp. Review
<i>Sceloporus virgatus</i>	adult	Arthropoda	Hexapoda	Insecta	Coleoptera	Chiricahua Mtns, AZ - John Hands and Herb Martyr CGs	Manual ID of stomach contents	Watters 2008, Herp. Review
<i>Sceloporus virgatus</i>	adult	Arthropoda	Hexapoda	Insecta	Formicidae	Chiricahua Mtns, AZ - John Hands and Herb Martyr CGs	Manual ID of stomach contents	Watters 2008, Herp. Review
<i>Sceloporus virgatus</i>	adult	Arthropoda	Hexapoda	Insecta	Heteroptera	Chiricahua Mtns, AZ - John Hands and Herb Martyr CGs	Manual ID of stomach contents	Watters 2008, Herp. Review
<i>Sceloporus virgatus</i>	adult	Arthropoda	Hexapoda	Insecta	Hymenoptera	Chiricahua Mtns, AZ - John Hands and Herb Martyr CGs	Manual ID of stomach contents	Watters 2008, Herp. Review
<i>Sceloporus virgatus</i>	adult	Arthropoda	Hexapoda	Insecta	Lepidoptera	Chiricahua Mtns, AZ - John Hands and Herb Martyr CGs	Manual ID of stomach contents	Watters 2008, Herp. Review
<i>Sceloporus virgatus</i>	adult	Arthropoda	Hexapoda	Insecta	Diptera	Chiricahua Mtns, AZ - John Hands and Herb Martyr CGs	Feeding observation	Watters 2008, Herp. Review
<i>Sceloporus virgatus</i>	adult	Arthropoda	Hexapoda	Insecta	Orthoptera	Chiricahua Mtns, AZ - John Hands and Herb Martyr CGs	Feeding observation	Watters 2008, Herp. Review
<i>Sceloporus jarrovi</i>	adult	Arthropoda	Chelicerata	Arachnida		Chiricahua Mtns, AZ - John Hands and Herb Martyr CGs	Manual ID of stomach contents	Watters 2008, Herp. Review

<i>Sceloporus jarrovii</i>	adult	Arthropoda		Chilopoda			Chiricahua Mtns, AZ - John Hands and Herb Martyr CGs	Manual ID of stomach contents	Watters 2008, Herp. Review
<i>Sceloporus jarrovii</i>	adult	Arthropoda	Hexapoda	Insecta	Coleoptera		Chiricahua Mtns, AZ - John Hands and Herb Martyr CGs	Manual ID of stomach contents	Watters 2008, Herp. Review
<i>Sceloporus jarrovii</i>	adult	Arthropoda	Hexapoda	Insecta	Diptera		Chiricahua Mtns, AZ - John Hands and Herb Martyr CGs	Feeding observation	Watters 2008, Herp. Review
<i>Sceloporus jarrovii</i>	adult	Arthropoda	Hexapoda	Insecta	Hymenoptera	Formicidae	Chiricahua Mtns, AZ - John Hands and Herb Martyr CGs	Manual ID of stomach contents	Watters 2008, Herp. Review
<i>Sceloporus jarrovii</i>	adult	Arthropoda	Hexapoda	Insecta	Isoptera		Chiricahua Mtns, AZ - John Hands and Herb Martyr CGs	Feeding observation	Watters 2008, Herp. Review
<i>Sceloporus jarrovii</i>	adult	Arthropoda	Hexapoda	Insecta	Lepidoptera		Chiricahua Mtns, AZ - John Hands and Herb Martyr CGs	Manual ID of stomach contents	Watters 2008, Herp. Review
<i>Sceloporus jarrovii</i>	NA	Arthropoda	Hexapoda	Insecta	Orthoptera		Baboquivari Mtns, AZ - Kitt Peak	Manual ID of stomach contents	Goldberg & Bursey 1990. J. Herpetol.
<i>Sceloporus jarrovii</i>	NA	Arthropoda	Hexapoda	Insecta	Hemiptera		Baboquivari Mtns, AZ - Kitt Peak	Manual ID of stomach contents	Goldberg & Bursey 1990. J. Herpetol.
<i>Sceloporus jarrovii</i>	NA	Arthropoda	Hexapoda	Insecta	Homoptera		Baboquivari Mtns, AZ - Kitt Peak	Manual ID of stomach contents	Goldberg & Bursey 1990. J. Herpetol.
<i>Sceloporus jarrovii</i>	NA	Arthropoda	Hexapoda	Insecta	Coleoptera		Baboquivari Mtns, AZ - Kitt Peak	Manual ID of stomach contents	Goldberg & Bursey 1990. J. Herpetol.

<i>Sceloporus jarrovii</i>	NA	Arthropoda	Hexapoda	Insecta	Lepidoptera	Baboquivari Mtns, AZ - Kitt Peak	Manual ID of stomach contents	Goldberg & Bursey 1990. J. Herpetol.
<i>Sceloporus jarrovii</i>	NA	Arthropoda	Hexapoda	Insecta	Diptera	Baboquivari Mtns, AZ - Kitt Peak	Manual ID of stomach contents	Goldberg & Bursey 1990. J. Herpetol.
<i>Sceloporus jarrovii</i>	NA	Arthropoda	Hexapoda	Insecta	Hymenoptera (ants)	Baboquivari Mtns, AZ - Kitt Peak	Manual ID of stomach contents	Goldberg & Bursey 1990. J. Herpetol.
<i>Sceloporus jarrovii</i>	NA	Arthropoda	Hexapoda	Insecta	Hymenoptera (other)	Baboquivari Mtns, AZ - Kitt Peak	Manual ID of stomach contents	Goldberg & Bursey 1990. J. Herpetol.
<i>Sceloporus jarrovii</i>	NA	Arthropoda	Chelicerata	Arachnida		Baboquivari Mtns, AZ - Kitt Peak	Manual ID of stomach contents	Goldberg & Bursey 1990. J. Herpetol.
<i>Sceloporus jarrovii</i>	NA	Arthropoda		Diplopoda		Baboquivari Mtns, AZ - Kitt Peak	Manual ID of stomach contents	Goldberg & Bursey 1990. J. Herpetol.
<i>Sceloporus slevini</i>	NA	Arthropoda	Hexapoda	Insecta	Homoptera	Southeastern AZ	NA	Newlin 1974 Angelo State University, Unpub. Dissertation
<i>Sceloporus slevini</i>	NA	Arthropoda	Hexapoda	Insecta	Hemiptera	Southeastern AZ	NA	Newlin 1974 Angelo State University, Unpub. Dissertation
<i>Sceloporus slevini</i>	NA	Arthropoda	Hexapoda	Insecta	Hymenoptera (ants)	Southeastern AZ	NA	Newlin 1974 Angelo State University, Unpub. Dissertation
<i>Sceloporus slevini</i>	NA	Arthropoda	Hexapoda	Insecta	Coleoptera	Durango, Mexico - La Michiliá	Manual ID of stomach contents	Barbault et al. 1985, Oecologia
<i>Sceloporus slevini</i>	NA	Arthropoda	Hexapoda	Insecta	Orthoptera	Durango, Mexico - La Michiliá	Manual ID of stomach contents	Barbault et al. 1985, Oecologia
<i>Sceloporus slevini</i>	NA	Arthropoda	Hexapoda	Insecta	Lepidoptera	Durango, Mexico - La Michiliá	Manual ID of stomach contents	Barbault et al. 1985, Oecologia

<i>Sceloporus slevini</i>	NA	Arthropoda	Hexapoda	Insecta	Hymenoptera		Durango, Mexico - La Michiliá	Manual ID of stomach contents	Barbault et al. 1985, Oecologia
<i>Sceloporus slevini</i>	NA	Arthropoda	Hexapoda	Insecta	Hymenoptera (ants)		Durango, Mexico - La Michiliá	Manual ID of stomach contents	Barbault et al. 1985, Oecologia
<i>Sceloporus slevini</i>	NA	Arthropoda	Hexapoda	Insecta	Hemiptera		Durango, Mexico - La Michiliá	Manual ID of stomach contents	Barbault et al. 1985, Oecologia
<i>Sceloporus slevini</i>	NA	Arthropoda	Hexapoda	Insecta	Diptera		Durango, Mexico - La Michiliá	Manual ID of stomach contents	Barbault et al. 1985, Oecologia
<i>Sceloporus slevini</i>	NA	Arthropoda	Chelicerata	Arachnida		Araneida	Durango, Mexico - La Michiliá	Manual ID of stomach contents	Barbault et al. 1985, Oecologia
<i>Sceloporus slevini</i>	NA	Plants					Durango, Mexico - La Michiliá	Manual ID of stomach contents	Barbault et al. 1985, Oecologia
<i>Sceloporus slevini</i>	NA	Arthropoda		Chilopoda			Durango, Mexico - La Michiliá	Manual ID of stomach contents	Barbault et al. 1985, Oecologia
<i>Sceloporus jarrovi</i>	NA	Arthropoda	Hexapoda	Insecta	Coleoptera		Durango, Mexico - La Michiliá	Manual ID of stomach contents	Barbault et al. 1985, Oecologia
<i>Sceloporus jarrovi</i>	NA	Arthropoda	Hexapoda	Insecta	Orthoptera		Durango, Mexico - La Michiliá	Manual ID of stomach contents	Barbault et al. 1985, Oecologia
<i>Sceloporus jarrovi</i>	NA	Arthropoda	Hexapoda	Insecta	Lepidoptera		Durango, Mexico - La Michiliá	Manual ID of stomach contents	Barbault et al. 1985, Oecologia
<i>Sceloporus jarrovi</i>	NA	Arthropoda	Hexapoda	Insecta	Hymenoptera		Durango, Mexico - La Michiliá	Manual ID of stomach contents	Barbault et al. 1985, Oecologia

<i>Sceloporus jarrovii</i>	NA	Arthropoda	Hexapoda	Insecta	Hymenoptera (ants)		Durango, Mexico - La Michiliá	Manual ID of stomach contents	Barbault et al. 1985, Oecologia
<i>Sceloporus jarrovii</i>	NA	Arthropoda	Hexapoda	Insecta	Hemiptera		Durango, Mexico - La Michiliá	Manual ID of stomach contents	Barbault et al. 1985, Oecologia
<i>Sceloporus jarrovii</i>	NA	Arthropoda	Hexapoda	Insecta	Diptera		Durango, Mexico - La Michiliá	Manual ID of stomach contents	Barbault et al. 1985, Oecologia
<i>Sceloporus jarrovii</i>	NA	Arthropoda	Chelicerata	Arachnida		Araneida	Durango, Mexico - La Michiliá	Manual ID of stomach contents	Barbault et al. 1985, Oecologia
<i>Sceloporus jarrovii</i>	NA	Plants					Durango, Mexico - La Michiliá	Manual ID of stomach contents	Barbault et al. 1985, Oecologia
<i>Sceloporus jarrovii</i>	adult	Arthropoda	Hexapoda	Insecta	Coleoptera		Durango, Mexico - Las Piedras Encimadas	Manual ID of stomach contents	Gadsden et al. 2011, Southwestern Naturalist
<i>Sceloporus jarrovii</i>	adult	Arthropoda	Hexapoda	Insecta	Hemiptera		Durango, Mexico - Las Piedras Encimadas	Manual ID of stomach contents	Gadsden et al. 2011, Southwestern Naturalist
<i>Sceloporus jarrovii</i>	adult	Arthropoda	Hexapoda	Insecta	Homoptera		Durango, Mexico - Las Piedras Encimadas	Manual ID of stomach contents	Gadsden et al. 2011, Southwestern Naturalist
<i>Sceloporus jarrovii</i>	adult	Arthropoda		Isoptera			Durango, Mexico - Las Piedras Encimadas	Manual ID of stomach contents	Gadsden et al. 2011, Southwestern Naturalist
<i>Sceloporus jarrovii</i>	adult	Arthropoda	Hexapoda	Insecta	Hymenoptera	Formicidae	Durango, Mexico - Las Piedras Encimadas	Manual ID of stomach contents	Gadsden et al. 2011, Southwestern Naturalist
<i>Sceloporus jarrovii</i>	adult	Arthropoda	Hexapoda	Insecta	Diptera		Durango, Mexico - Las Piedras Encimadas	Manual ID of stomach contents	Gadsden et al. 2011, Southwestern Naturalist

<i>Sceloporus jarrovii</i>	adult	Arthropoda	Hexapoda	Insecta	Orthoptera	Durango, Mexico - Las Piedras Encimadas	Manual ID of stomach contents	Gadsden et al. 2011, Southwestern Naturalist
<i>Sceloporus jarrovii</i>	adult	Arthropoda	Chelicerata	Arachnida	Araneae	Durango, Mexico - Las Piedras Encimadas	Manual ID of stomach contents	Gadsden et al. 2011, Southwestern Naturalist
<i>Sceloporus jarrovii</i>	NA	Arthropoda	Hexapoda	Insecta	Coleoptera	Chiricahua Mtns, AZ - 7mi SW Portal	Manual ID of stomach contents	Ballinger & Ballinger, 1979, Southwestern Naturalist
<i>Sceloporus jarrovii</i>	NA	Arthropoda	Hexapoda	Insecta	Hemiptera	Chiricahua Mtns, AZ - 7mi SW Portal	Manual ID of stomach contents	Ballinger & Ballinger, 1979, Southwestern Naturalist
<i>Sceloporus jarrovii</i>	NA	Arthropoda	Hexapoda	Insecta	Diptera	Chiricahua Mtns, AZ - 7mi SW Portal	Manual ID of stomach contents	Ballinger & Ballinger, 1979, Southwestern Naturalist
<i>Sceloporus jarrovii</i>	NA	Arthropoda	Hexapoda	Insecta	Lepidoptera	Chiricahua Mtns, AZ - 7mi SW Portal	Manual ID of stomach contents	Ballinger & Ballinger, 1979, Southwestern Naturalist
<i>Sceloporus jarrovii</i>	NA	Arthropoda	Hexapoda	Insecta	Hymenoptera	Chiricahua Mtns, AZ - 7mi SW Portal	Manual ID of stomach contents	Ballinger & Ballinger, 1979, Southwestern Naturalist
<i>Sceloporus jarrovii</i>	NA	Arthropoda		Chelicerata	Arachnida	Chiricahua Mtns, AZ - 7mi SW Portal	Manual ID of stomach contents	Ballinger & Ballinger, 1979, Southwestern Naturalist
<i>Sceloporus jarrovii</i>	NA	Arthropoda		Chilopoda		Chiricahua Mtns, AZ - 7mi SW Portal	Manual ID of stomach contents	Ballinger & Ballinger, 1979, Southwestern Naturalist
<i>Sceloporus jarrovii</i>	NA	Arthropoda	Hexapoda	Insecta	Coleoptera	Chiricahua Mtns, AZ - Barfoot and Rustler Parks	Manual ID of stomach contents	Ballinger & Ballinger, 1979, Southwestern Naturalist
<i>Sceloporus jarrovii</i>	NA	Arthropoda	Hexapoda	Insecta	Homoptera	Chiricahua Mtns, AZ - Barfoot and Rustler Parks	Manual ID of stomach contents	Ballinger & Ballinger, 1979, Southwestern Naturalist

<i>Sceloporus jarrovii</i>	NA	Arthropoda	Hexapoda	Insecta	Hemiptera	Chiricahua Mtns, AZ - Barfoot and Rustler Parks	Manual ID of stomach contents	Ballinger & Ballinger, 1979, Southwestern Naturalist
<i>Sceloporus jarrovii</i>	NA	Arthropoda	Hexapoda	Insecta	Diptera	Chiricahua Mtns, AZ - Barfoot and Rustler Parks	Manual ID of stomach contents	Ballinger & Ballinger, 1979, Southwestern Naturalist
<i>Sceloporus jarrovii</i>	NA	Arthropoda	Hexapoda	Insecta	Lepidoptera	Chiricahua Mtns, AZ - Barfoot and Rustler Parks	Manual ID of stomach contents	Ballinger & Ballinger, 1979, Southwestern Naturalist
<i>Sceloporus jarrovii</i>	NA	Arthropoda	Hexapoda	Insecta	Orthoptera	Chiricahua Mtns, AZ - Barfoot and Rustler Parks	Manual ID of stomach contents	Ballinger & Ballinger, 1979, Southwestern Naturalist
<i>Sceloporus jarrovii</i>	NA	Arthropoda	Hexapoda	Insecta	Hymenoptera	Chiricahua Mtns, AZ - Barfoot and Rustler Parks	Manual ID of stomach contents	Ballinger & Ballinger, 1979, Southwestern Naturalist
<i>Sceloporus jarrovii</i>	NA	Arthropoda	Chelicerata	Arachnida		Chiricahua Mtns, AZ - Barfoot and Rustler Parks	Manual ID of stomach contents	Ballinger & Ballinger, 1979, Southwestern Naturalist
<i>Sceloporus jarrovii</i>	NA	Arthropoda	Chelicerata	Arachnida; Solfugae		Chiricahua Mtns, AZ - Barfoot and Rustler Parks	Manual ID of stomach contents	Ballinger & Ballinger, 1979, Southwestern Naturalist

Appendix III

Institutional catalogue numbers for all individual specimens included in Chapter III. Specimens are housed at the Museum of Vertebrate Zoology (MVZ; University of California, Berkeley, California), Museum of Comparative Zoology (MCZ; Harvard University, Cambridge, Massachusetts), and the University of Colorado Museum (UCM; Boulder, Colorado).

MCZ127036; MCZ127049; MCZ136523; MCZ177824; MCZ21093; MCZ34321; MCZ53920; MCZ53923; MCZ54104; MCZ56014; MVZ100476; MVZ104060; MVZ104097; MVZ104120; MVZ104138; MVZ104139; MVZ104141; MVZ104256; MVZ104257; MVZ106264; MVZ106413; MVZ109497; MVZ109504; MVZ114719; MVZ117344; MVZ129256; MVZ129257; MVZ129258; MVZ129272; MVZ129280; MVZ129281; MVZ129292; MVZ129293; MVZ129323; MVZ129324; MVZ129325; MVZ129326; MVZ129327; MVZ129959; MVZ131506; MVZ131508; MVZ132912; MVZ137084; MVZ137095; MVZ137099; MVZ137104; MVZ142032; MVZ144153; MVZ144154; MVZ144155; MVZ144156; MVZ144167; MVZ144176; MVZ144177; MVZ144178; MVZ144179; MVZ146919; MVZ146920; MVZ147972; MVZ147973; MVZ147974; MVZ147982; MVZ149965; MVZ150090; MVZ150113; MVZ159452; MVZ159453; MVZ159926; MVZ159929; MVZ160080; MVZ160081; MVZ160142; MVZ160148; MVZ16393; MVZ164292; MVZ164294; MVZ176938; MVZ177746; MVZ17824; MVZ17857; MVZ180229; MVZ180230; MVZ180232; MVZ180236; MVZ180238; MVZ180320; MVZ182389; MVZ185653; MVZ185656; MVZ187524; MVZ196095; MVZ205131; MVZ215592; MVZ22382; MVZ22386; MVZ22387; MVZ22388; MVZ225525; MVZ225540; MVZ226199; MVZ229647; MVZ230690; MVZ232623; MVZ236291; MVZ236294; MVZ237348; MVZ24342; MVZ249155; MVZ253034; MVZ253483; MVZ272348; MVZ275606; MVZ275611; MVZ275618; MVZ275619; MVZ279498; MVZ279499; MVZ279504; MVZ279508; MVZ279792; MVZ279793; MVZ279933; MVZ279935; MVZ279939; MVZ279940; MVZ279945; MVZ279955; MVZ280001; MVZ280007; MVZ280016; MVZ280018; MVZ280027; MVZ280028; MVZ292304; MVZ292314; MVZ30167; MVZ32255; MVZ32256; MVZ36750; MVZ36756; MVZ36807; MVZ36808; MVZ36815; MVZ38713; MVZ39400; MVZ40174; MVZ40175; MVZ41017; MVZ44697; MVZ50697; MVZ50700; MVZ50701; MVZ53753; MVZ53754; MVZ53755; MVZ53759; MVZ56286; MVZ56289; MVZ56298; MVZ57227; MVZ57228; MVZ59100; MVZ59115; MVZ59116; MVZ59130; MVZ60143; MVZ65658; MVZ66452; MVZ66465; MVZ67020; MVZ67021; MVZ67040; MVZ67044; MVZ67045; MVZ67054; MVZ67080; MVZ67083; MVZ67096; MVZ67098; MVZ67099; MVZ67131; MVZ67174; MVZ67175; MVZ67176; MVZ67416; MVZ68817; MVZ71245; MVZ71252; MVZ71257; MVZ71948; MVZ71949; MVZ71950; MVZ71967; MVZ72309; MVZ72649; MVZ73432; MVZ75795; MVZ76644; MVZ76645; MVZ76646; MVZ76647; MVZ76648; MVZ76696; MVZ76697; MVZ76698; MVZ76699; MVZ76744; MVZ7786; MVZ7789; MVZ78257; MVZ78265; MVZ78269; MVZ78294; MVZ78299; MVZ79201; MVZ79207; MVZ79389; MVZ79877; MVZ79878; MVZ79910; MVZ79921; MVZ80039; MVZ80343; MVZ80353; MVZ8184; MVZ82897; MVZ8853; MVZ8866; MVZ96755; MVZ96757; MVZ96760; MVZ96926; MVZ96929; MVZ96930; MVZ96941; MVZ96946; MVZ96983; MVZ96984; MVZ98806; UCM16667; UCM16684; UCM287426; UCM28753; UCM28976; UCM31334; UCM38354; UCM39832; UCM41120; UCM41544; UCM44424; UCM45886; UCM47114; UCM47121; UCM47356; UCM48370; UCM48371; UCM48377; UCM48889; UCM48893; UCM49646; UCM50029; UCM50656; UCM51088; UCM59252; UCM59253; UCM60316; UCM60947; UCM60948; UCM60975; UCM61211; UCM61274; UCM64191; UCM64194; UCM64195; UCM64700; UCM65985; UCM66329; UCM66656; UCM66658; UCM66804; UCM66812; UCM66813; UCM66837; UCM66848; UCM67229; UCM67263; UCM67264; UCM67270; UCM8774; UCM8831; UCM8902; UCM8969