Grasshopper Diversity and Community Ecology

in the Madrean Sky Islands of Arizona

by

Elena Palka-Flores

A Thesis Presented in Partial Fulfillment
of the Requirements for the Degree
Master of Science

Approved September 2024 by the
Graduate Supervisory Committee:

Jay Taylor, Chair
Nico Franz
Andrew Johnston
Marion Le Gall

ARIZONA STATE UNIVERSITY

December 2024

ABSTRACT

The Madrean sky islands are a group of approximately 60 mountain ranges extending from southeastern Arizona to northern Sonora. Grasshoppers were surveyed in 2023 in six of these mountain ranges to assess their diversity and community structure in relation to habitat, elevation and geography. In total, 43 species were collected, with the most abundant being *Trimerotropis pallidipennis*, *T. modesta*, *Melanoplus sanguinipes* and *M. desultorius*. Analysis of this data revealed that grasshopper community structure and diversity differed between habitats and to a lesser extent mountain ranges. In general, grasshopper diversity decreased with elevation and grasshopper community structure was most strongly associated with elevation and latitude. Intraspecific and interspecific morphological variation were also studied within these communities, revealing that the size and shape of several species varied in association with elevation and sampling date. Although there was extensive overlap between the distributions of morphological traits of grasshopper assemblages in different habitats, both size and several shape-related features differed significantly between some habitats. Lastly, the proportion of flightless grasshoppers within these assemblages was found to be positively correlated with elevation and negatively correlated with latitude.

TABLE OF CONTENTS

Page

LIST OF TABLES iii

LIST OF FIGURES iv

CHAPTER

1 INTRODUCTION 1

General overview of Orthopteran biology 1

Natural history of Orthoptera in the Sonoran Desert 3

Orthoptera in the Madrean Sky Islands 8

Aims of this Study 12

2 METHODS 13

Study Sites 13

Sampling Dates 15

Orthoptera Sampling 15

Plant Surveys and Habitat Classification 16

Adventitious Sampling 17

Identification of Orthoptera 18

Measurements 18

Disposition of Specimens 22

Data Analysis 22

3 GRASSHOPPER DIVERSITY AND COMMUNITY STRUCTURE 30

Plant Surveys and Habitat Classification 30

Grasshopper Diversity and Abundance 32

Community Structure: Unconstrained Ordination 42

Community Structure: Constrained Ordination 48

Community Structure: Subadults and Subfamilies 53

Sex Ratios 57

Page

Adventitious Samples 58

4 MORPHOLOGICAL VARIATION 60

Intraspecific Morphological Variation 60

Interspecific Morphological Variation 68

Flightlessness 76

5 DISCUSSION 79

Diversity and Geographical Structure of Grasshopper Communities 79

Grasshoper Community Structure and Habitat 81

Disturbance 85

Morphological Variation 87

Limitations 90

Implications for Future Research 92

REFERENCES 94

APPENDIX

A COLLECTION LOCATIONS AND DATES 97

B ORTHOPTERA SPECIES LISTS 101

C SUPPLEMENTARY MATERIAL FOR CHAPTER 3 105

D SUPPLEMENTARY MATERIAL FOR CHAPTER 4 121

E PHOTOGRAPHS OF SELECT ORTHOPTERA 140

F SUPPLEMENTARY POPULATION DATA 145

LIST OF TABLES

Table		Page
3.1	List of Grasshopper Species Collected	33
3.2	Abundance and Diversity of Grasshoppers per Focal Site	35
3.3	Correlation of Adult and Juvenile Abundance	57
4.1	Intraspecific Variation in Body Length	62
4.2	Intraspecific Variation in Morphological Principal Components	65
4.3	Intraspecific Morphological Variation across Habitats	72
4.4	Incidence of Flightlessness	77
A1	Collection Locations and Dates	98
B1	Caelifera Species List	102
B2	Ensifera Species List	104
C1	Plant Cover Data	106
C2	Species Abundance by Mountain Range	108
C3	Species Sampling Density by Habitat	109
C4	Species Abundance by Collecting Period	110
C5	Estimated Total Species Richness	111
C6	Variance Explained by Environmental Variables in tb-RDA	114
C7	Variance Explained by Axes in tb-RDA	114
C8	Species Loadings in tb-RDA	115
C9	Variance Explained by Environmental Variables in tb-RDA of Subfamily Data	118
C10	Variance Explained by Axes in tb-RDA of Subfamily Data	118
C11	Subfamily Loadings in tb-RDA	118
C12	Adult Sex Ratios by Species	119
D1	Summary Statistics of Morphological Measurements	122
D2	% Intraspecific Morphological Variance Explained by Principal Components	128
D3	Loadings of Intraspecific Morphological Variables on PC1	129

Table Page

D4 Loadings of Intraspecific Morphological Variables on PC2 130

D5 Loadings of Intraspecific Morphological Variables on PC3 131

D6 % Interspecific Morphological Variance Explained by Principal Components 132

D7 Loadings of Interspecific Morphological Variables on Principal Components 132

D8 Subfamily Composition by Habitat 133

D9 Distribution of Morphological Traits by Subfamily 133

D10 Body Length Variation Across Habitats 136

D11 Variation of PC1 Across Habitats 137

D12 Variation of PC2 Across Habitats 138

D13 Variation of PC3 Across Habitats 139

F1 Adult Count Data for the Chiricahua Mountains 147

F2 Adult Count Data for the Huachuca Mountains 149

F3 Adult Count Data for the Pinal Mountains 151

F4 Adult Count Data for the Pinaleño Mountains 152

F5 Adult Count Data for the Santa Catalina Mountains 155

F6 Adult Count Data for the Santa Rita Mountains 157

F7 Adult Abundance and Species Richness by Site 159

LIST OF FIGURES

Figure		Page
1.1	External Anatomy of a Female Grasshopper	2
1.2	Abdomen of a Male Grasshopper	2
1.3	Map of the Madrean Archipelago	9
1.4	Plant Communities in the Madrean Sky Islands	10
2.1	Map of the Sampling Locations	14
2.2	Antennal Shapes in the Caelifera	19
2.3	Dorsal Anatomy in the Oedipodinae	19
2.4	Head Anatomy of a Grasshopper	20
2.5	Grasshopper Hind Leg Anatomy	20
2.6	Anatomy of the Grasshopper Pronotum	21
2.7	Grasshopper Ventral Anatomy	21
3.1	Principal Coordinates Analysis of Tree Cover Data	31
3.2	Rarefaction Curves by Mountain Range	37
3.3	Abundance and Diversity Per Site by Mountain Range	40
3.4	Abundance and Diversity Per Site by Habitat	41
3.5	NMDS by Mountain Range	44
3.6	NMDS by Habitat	45
3.7	tb-RDA of Species Counts	49
3.8	tb-RDA of Subfamily Counts	55
4.1	Interspecific Size Variation by Habitat	70
4.2	Interspecific Shape Variation by Habitat	71
4.3	Interspecific Size and Shape Variation by Habitat and Subfamily	75
C1	Dendrogram of Sky Island Grasshopper Assemblages	112
C2	Principal Coordinates Analysis of Sky Island Grasshopper Assemblages	113
C3	Residual RDA Correlogram	117

Figure Page

D1 Interspecific Size Variation by Subfamily 134

D2 Interspecific Shape Variation by Subfamily 135

E1 Photographs of Female *Acantherus piperatus* 141

E2 Photographs of Male *Boopedon flaviventris* 142

E3 Photographs of Male *Arethaea* sp. 143

E4 Photographs of Female *Insara apache* 144

CHAPTER 1

INTRODUCTION

General overview of Orthopteran biology

Orthoptera (Latreille, 1793) is an order of insects that are recognizable by their usually saltatorial locomotion, with long hind legs that are adapted for jumping. The most diagnostic morphological character of the order is a pronotum that extends over the pleural sclerites on the sides of the prothorax, known as a cryptopleuron (Song, 2018). The name Orthoptera means “straight-winged” in Ancient Greek, referring to the wing shape of many flying species. The order is distributed worldwide, and contains at least 30 families and more than 26,000 described species (Song, 2018). The oldest known insect species assigned to Orthoptera in the fossil record date back over 300 million years ago to the Carboniferous period. Species in this order have hemimetabolous life cycles, in which they hatch as nymphs that gradually grow larger into adults. Orthoptera have biting-chewing mouthparts (mandibles), which grind solid food before it enters the digestive tract. Most species of Orthoptera have sideways-facing compound eyes, which allow them to detect approaching predators. Like all other insects, Orthoptera also have an upside-down triangle of simple eyes (ocelli) that sense changes in light. The insect orders that are most closely related to Orthoptera are Phasmatodea (stick and leaf insects), Mantodea (mantises), and Blattodea (cockroaches and termites).

The order Orthoptera contains two recognized suborders named after the shape of the characteristic female ovipositors, which are Ensifera (Ander, 1939) (“sword-bearing”) and Caelifera (Ander, 1939) (“chisel-bearing”). Female Ensifera have needle-shaped or laterally compressed, often long ovipositors with six valves that project from the lower abdomen near the cerci, while males lack a projection. The ovipositors of female Caelifera are situated at the end of the last abdominal segment, and consist of four short, tapered prongs that open and close on both dorsal and ventral sides; while the male abdomen ends in noticeable plates on the ventral side. As a general rule, Ensifera have thin antennae that often exceed their body length and small, spherical

compound eyes; while Caelifera have thick antennae that are less than the body length and large, oval-shaped compound eyes. These differences reflect the most common lifestyles of each suborder, as Ensifera are mainly nocturnal with poor eyesight, and rely on touch and smell as their primary senses; while Caelifera are diurnal and more sight-oriented.

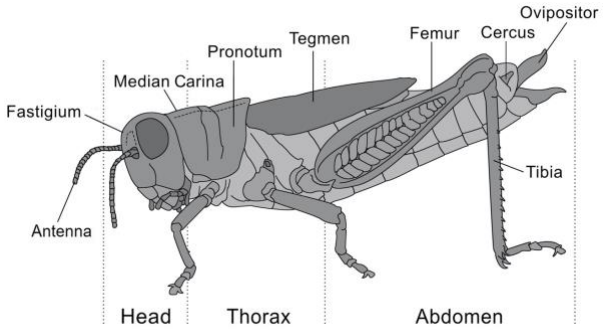


Figure 1.1. External anatomy of a female grasshopper in the family Acrididae (Caelifera), showing the order's distinctive pronotum, and the ovipositor shape and thick antennae that are diagnostic of the suborder (Haberski et al., 2021).

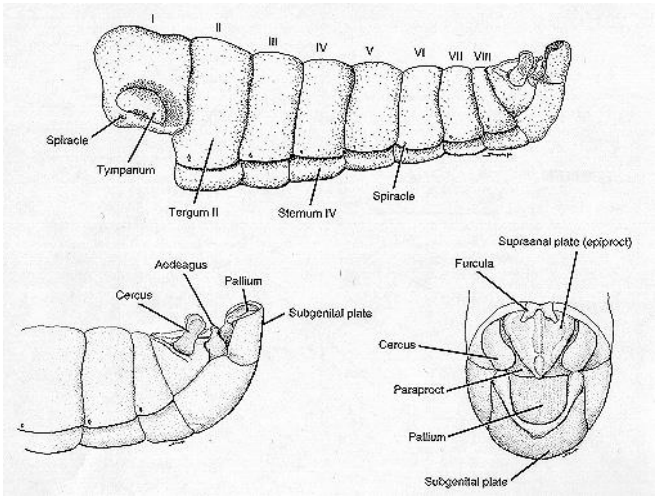


Figure 1.2. Abdomen of a male grasshopper in the family Acrididae (Caelifera), showing the rounded plates on the last two segments (University of Wyoming).

Most Orthoptera have a sense of hearing with a tympanum located on their legs, and some families (mostly in the suborder Ensifera) are known for sound production by males using their wings, which is known as stridulation when done on the ground or on a perch, or crepitation when done in flight. Some families that have lost wings have also lost the tympanum, and sound production has not evolved again independently in any species that lack hearing (Song et al., 2020).

A small number of *Gryllus* (Linnaeus, 1758) individuals with long wings are able to fly short distances, although this may be due to intraspecific variation rather than a trait of specific *Gryllus* species. Similarly, some Caelifera species in the subfamily Melanoplinae, such as *Melanoplus lakinus* (Scudder, 1878) and *Phoetaliotes nebrascensis* (Thomas, 1872) are usually flightless with short wings, but have long-winged individuals that are capable of flying as well. In some other genera such as *Arethaea* (Stål, 1876), only males have wings that are long enough for them to fly.

Natural History of Orthoptera in the Sonoran Desert

In Arizona, at least 294 species of Orthoptera in 14 families have been recorded (Palka-Flores, Franz and Johnston, unpublished). The family with the most species in the state is Acrididae, particularly the subfamilies Gomphocerinae, Melanoplinae and Oedipodinae. The most common species of grasshopper in Arizona appears to be *Trimerotropis pallidipennis* (personal observations), followed by *Schistocerca nitens*, both of which can be seen year-round. The southeastern portion of Arizona has the highest overall concentration and diversity of Orthoptera, due to the ecological heterogeneity of the region. Some species of Orthoptera found in southeastern Arizona are thought to be endemic to the state or else only range into a portion of Sonora across the border. The majority of these putatively endemic species belong to the family Rhaphidophoridae, which has an especially high level of species diversity in the Madrean Sky Islands, with a number of species restricted to high elevations in individual ranges such as the Santa Rita, Huachuca, and Chiricahua Mountains.

Most species of Orthoptera in Arizona are semelparous and reproduce during autumn before dying, with eggs overwintering in diapause and nymphs hatching in spring when the ambient

temperature is warmer. However, some species overwinter as either nymphs or adults, including small numbers of *Schistocerca nitens*, a common grasshopper species in much of Arizona. Grasshopper nymphs may also prefer to feed on different types of plants than adults (Skinner, 1995), possibly because nymphs do not have functional wings and cannot disperse between plants as effectively as flying adult grasshoppers.

Many grassland and woodland ecosystems in the US, including southeast Arizona, have been heavily disturbed by livestock overgrazing, wildfires, plowing, and introduced grasses (Fielding, 1993) which may benefit some species of Orthoptera while causing population declines of others. Livestock overgrazing and plowing reduce the cover of forage grasses and allow those that are of little forage value and not used as host plants by grasshoppers to proliferate, which reduces their overall numbers. The desert grasslands of southeastern Arizona have not recently evolved in the presence of bison, which are important grazers of grasslands in much of central North America, making them particularly vulnerable to the effects of livestock grazing (Debano, 2006). Overall abundance of insects was found to be lower in grazed grasslands, although there was no significant difference in species richness and diversity between grazed and ungrazed sites (Debano, 2006). While grasshoppers may use introduced grasses as host plants, native grasses are important for maintaining diverse ecosystems, however they may also allow grasshoppers to reach densities at which they are considered pests. Density and species diversity of grasshoppers in slightly disturbed rangelands dominated by native perennial grasses such as blue grama (*Bouteloua gracilis*) are greater than in highly disturbed rangelands dominated by a mix of native and introduced annual grasses, as only early hatching species of grasshoppers can survive on annual grasses before they become dry in May. Perennial grasses provide food and habitat for both early-hatching and late-hatching species of grasshoppers, which may support a high enough population density to cause outbreaks of grasshoppers on rangelands (Pfadt, 1982). Annual grasses, particularly introduced ones that die before the onset of summer, also increase the frequency of fires from human factors, as they provide an expansive cover of fuel.

While the frequency of natural fires caused by lightning strikes in desert grasslands has likely decreased since European colonization (McPherson, 1995), the danger of wildfires caused by vehicle engines, unattended campfires, and cigarette butts has increased significantly during years when the monsoon fails because of fluctuations in annual precipitation driven by climate change. A study at the Appleton-Whittell Research Ranch in southeastern Arizona (Bock & Bock, 1991) found that while the densities of both nymph and adult grasshoppers in burned plots declined by 60% over the first year following a wildfire, grasshoppers were able to repopulate by the second year. However, grasshopper species of the family Oedipodinae such as *Arphia pseudonietana* and *Trimerotropis pallidipennis*, which prefer bare ground, as well as *Melanoplus gladstoni*, which feeds on herbs rather than grasses, became more abundant soon after the fire (Bock & Bock, 1991).

Another factor that may be affecting the distribution and diversity of Orthoptera in Arizona is climate change. Studies show that climate change is slowing the maturation rates of Orthoptera, as increasing temperatures lead to more plant biomass and lower levels of nutrients in the soil (Kaspari et al., 2022), Rising temperatures may be causing shifts in plant communities of mountain ranges such as the Madrean Sky Islands. Species turnover of Orthoptera due to climate change has been found to be highest in wet and mesic grasslands, while overall species richness has been increasing in calcareous grasslands as they are colonized by generalist species of Orthoptera (Löffler et al., 2019). Most grasslands and woodlands in southeastern Arizona are semi-arid and rely on rainfall from the monsoon season as a water source, making the effects of climate change on Orthoptera communities particularly significant in this region.

In addition to climate change, predation by birds may affect Orthoptera community structure, as many species of birds prefer to eat medium-sized insects, thus reducing competition with smaller insects (Branson, 2005). Southeastern Arizona is famous for its diversity of bird species, many of which do not occur anywhere else in the US, but no studies of bird predation on any orders of insects have been conducted there. Bird species that were noted in Branson's (2005) study in eastern Montana include Western Meadowlarks (*Sturnella neglecta*), Horned Larks (*Eremophila alpestris*), Vesper Sparrows (*Pooecetes gramineus*), and Grasshopper Sparrows

(*Ammodramus savannarum*), all of which are present in southeastern Arizona during summer when insects are readily available. Another study by Bock et al. (1992) at the Appleton-Whittell Research Ranch noted Grasshopper Sparrows (*Ammodramus savannarum*), Cassin's Sparrows (*Peucaea cassinii*), Botteri's Sparrows (*Peucaea botterii*), and Eastern Meadowlarks (*Sturnella magna*) as predators of grasshoppers at the research site. Of these, the Grasshopper and Botteri's Sparrows were also noted to extensively feed on grasshoppers, and 95% of the insect species that the Cassin's Sparrow fed to its young at the research site were grasshoppers of the family Acrididae (Bock et al., 1992). While birds at the Appleton-Whittell Research Ranch limited the abundance of grasshoppers, they did not serve as keystone predators because there was no significant difference in the vegetation between the researchers' grasshopper enclosures that excluded birds and the surrounding areas where birds were present (Bock et al., 1992). Unlike Branson's (2005) findings, Bock et al. (1992) did not find evidence that bird predation on grasshoppers at this location mediated competition between different grasshopper species. One species that was notably not affected by bird predation at the Appleton-Whittell Research Ranch was *Dactylotum bicolor*, which has aposematic coloration and is unpalatable to most predators (Bock et al., 1992).

A study by Caplan (1966) has shown that the grasshopper species *Melanoplus bivittatus*, *Melanoplus differentialis*, and *Melanoplus lakinus*, all of which occur in southeastern Arizona, feed on the same grasses and other host plants. However, each of these three sympatric species shows preferences for particular plant species sufficient enough for them to occupy different niches and reduce competition with one another (Caplan, 1966). Grass genera that these species of grasshoppers were found to commonly feed on in Colorado which also grow in southeastern Arizona include *Sporobolus*, *Elymus*, *Dactylis*, *Avena*, and *Agrostis*. Of the plants that Caplan (1966) fed to grasshoppers in her research, the majority were introduced species, which could introduce a significant bias into the study. The only native plants offered were sand dropseed (*Sporobolus cryptandrus*), prickly poppy (*Argemone intermedia*), western ragweed (*Ambrosia psilostachya*), giant ragweed (*Ambrosia trifida*), and prairie rose (*Rosa arkansana*). All three *Melanoplus* species used in the study showed at least a slight preference for oats and orchard

grass, while both *M. bivittatus* and *M. differentialis* also strongly preferred poison hemlock, common dandelion, and yellow salsify. Both *M. differentialis* and *M. lakinus* preferred redtop, while *M. bivittatus* and *M. lakinus* preferred white sweet clover. Only *M. bivittatus* showed a preference for a native plant, which was prickly poppy. Caplan's (1966) results could have implications for the food preferences of grasshoppers in southeastern Arizona, where many of the preferred host plants in Colorado have also been introduced and are found among native grasses and forbs. However, further research using a greater variety of native host plants rather than introduced plants is needed to better understand how different species of Orthoptera occupy their own dietary niches in the same habitats, especially in sites that are minimally disturbed and primarily vegetated by native plants.

Common native North American food plants for Orthoptera listed by University of Wyoming that can also be found in Arizona include grama grasses (*Bouteloua* sp.), needlegrasses (*Hesperostipa* sp.), penstemon (*Penstemon* sp.), scarlet globemallow (*Sphaeralcea coccinea*), saltbushes (*Atriplex* sp.), sagebrushes (*Artemesia* sp.), ragweeds (*Ambrosia* sp.), groundsels (*Senecio* sp.), lupines (*Lupinus* sp.), pepperweeds (*Lepidium* sp.), and buckwheats (*Eriogonum* sp.) (University of Wyoming). Mesquite (*Prosopis* sp.) and palo verde (*Parkinsonia* sp.) are the primary host plants for *Insara elegans* (Scudder, 1900), a common katydid species of the Chihuahuan, Sonoran, and Mojave Deserts whose wing pattern mimics the compound leaves of the aforementioned tree genera. Widely introduced plant species in the US that Orthoptera also feed on include alfalfa (*Medicago sativa*), sweet clovers (*Melilotus* sp.), common dandelion (*Taraxacum officinale*), prickly lettuce (*Lactuca serriola*), cheeseweed mallow (*Malva parviflora*), wild oat grass (*Avena fatua*), wheatgrasses (*Agropyron* sp.), and barley grasses (*Hordeum* sp.) (University of Wyoming). The grasshopper subfamilies Gomphocerinae and Oedipodinae are mainly grass feeders, while the subfamilies Cyrtacanthacridinae and Melanoplinae prefer forbs and shrubs as food plants.

Orthoptera in the Madrean Sky Islands

The Madrean Sky Islands are a group of approximately 60 small mountain ranges extending from southeastern Arizona and extreme southwestern New Mexico to northeastern Sonora and extreme northwestern Chihuahua, lying northwest of the Sierra Madre Occidental (Figure 1.3). This region is known for its diverse flora and fauna not found anywhere else in the US. Altitudes in the Madrean Sky Islands range from 915 to 3300 meters above sea level, with a variety of plant communities at different elevations (Figure 1.4). These include hot and dry desert grasslands, warm and moist chaparral, oak woodlands, pine-oak woodlands, pine forests, and cool and wet mixed coniferous forests.

This region contains the greatest species diversity of Orthoptera in the state, thanks to its varied habitats and topography, as well as its transitional location between the Rocky Mountains to the north and the Sierra Madre Occidental to the south. The grasshopper families Acrididae and Romaleidae are mostly found among grasses and forbs at low to mid elevations. Acridid grasshoppers in the subfamily Oedipodinae thrive in these grasslands, while those in the subfamilies Gomphocerinae, Melanoplinae, and Cyrtacanthacridinae find suitable host plants at a variety of elevations from grasslands all the way to mixed conifer forests. The Sky Islands also harbor several endemic species as each mountain range contains oak woodlands and coniferous forests surrounded by desert grasslands, chaparral, and mesquite woodlands. Examples of Orthoptera species that are endemic to the Madrean Sky Islands include *Melanoplus pinaleno*, *Melanoplus chiricahuae*, and *Eumorsea pinaleno*. Orthoptera species that have only been collected in the Madrean Sky Islands but are thought to also occur further south in the Sierra Madre Occidental include *Insara apache*, *Poecilotettix pantherinus* (F. Walker, 1870), and *Eumorsea balli*.

With one exception, extensive insect surveys in the Madrean Sky Islands to date have focused on other insect orders, with Orthoptera as incidental collection records. Meyer et al. (2015) conducted pitfall trapping in the Santa Catalina Mountains to investigate how the structure and composition of assemblages of ground-dwelling arthropods vary along an elevational gradient. This study focused on four taxa, including grasshoppers and crickets, beetles, centipedes and

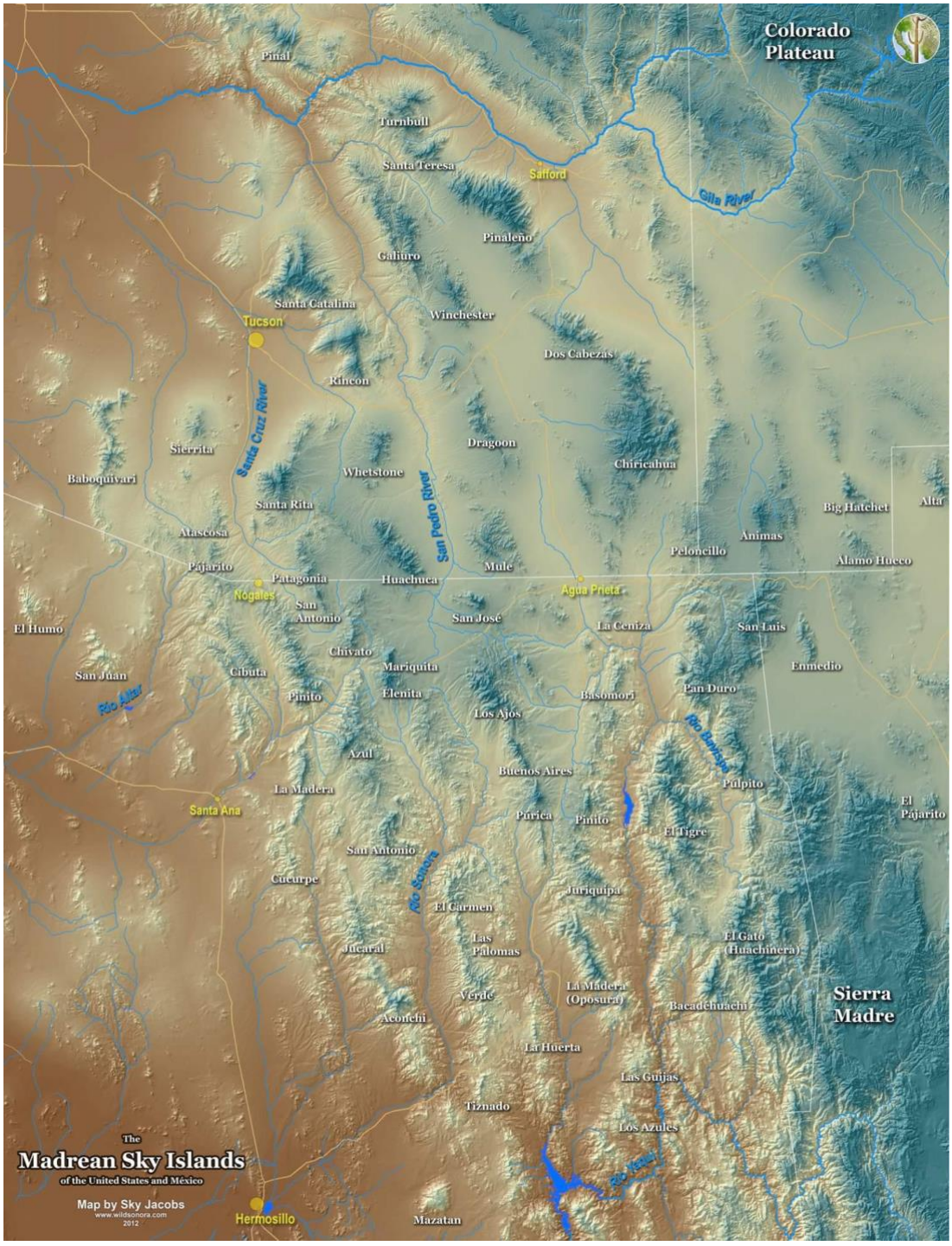


Figure 1.3. Map showing the location and names of the Madrean Sky Islands in the United States and Mexico (Jacobs, 2012).

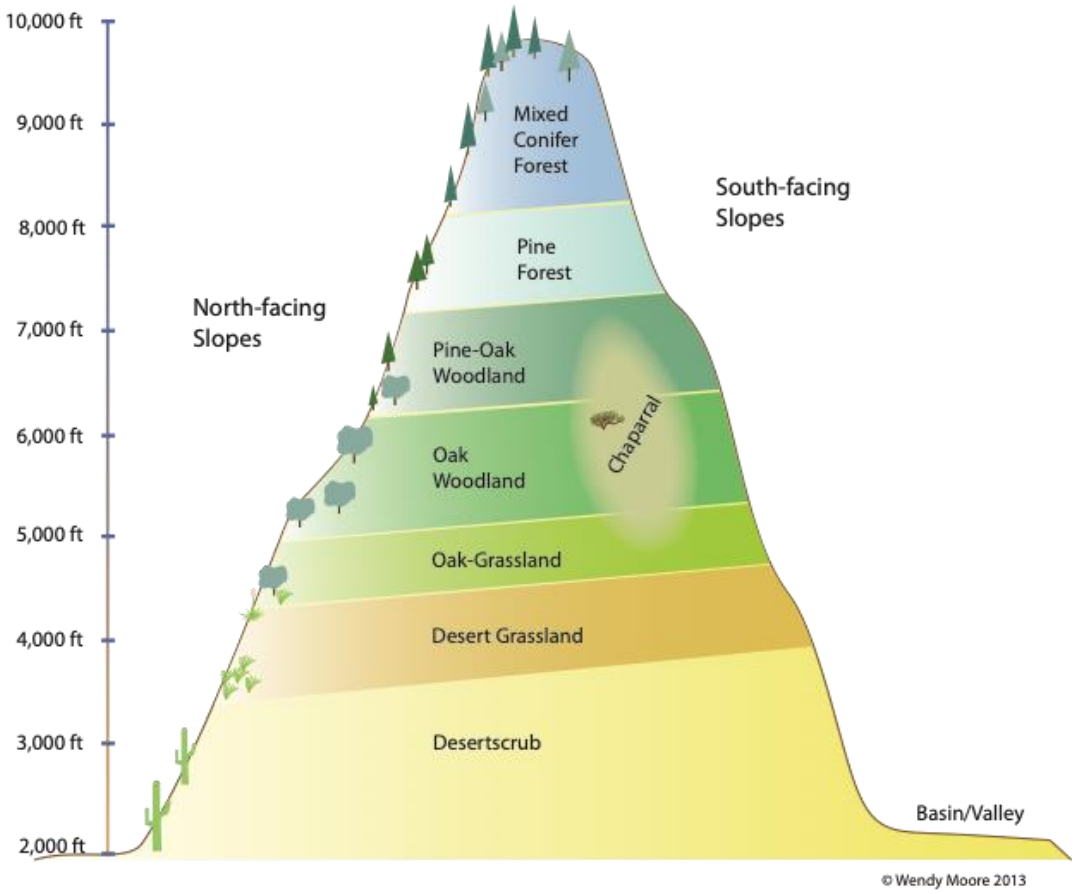


Figure 1.4. Plant communities by elevation in a typical Madrean sky island Moore, 2013).

millipedes, and spiders. In total, 523 individuals belonging to 25 species/morphospecies of Orthoptera were collected, with most species belonging to the families Acrididae and Gryllidae (15 and 4 species, respectively). These authors found that the species richness of Orthoptera tended to decline with elevation, with 18 species being collected in grassland, 7 in chaparral, 7 in pine-oak woodland, 4 in pine forest and 4 in mixed coniferous forest. Furthermore, most (55%) species were collected in only one biome, although the only adjacent biomes that harbored significantly different Orthoptera communities were pine forest and pine-oak woodland.

The only other studies to investigate Orthoptera communities in upland habitats in southeastern Arizona were those conducted by Carl and Jane Bock and colleagues in the Sonoita Valley, which lies at an elevation of 1300-1600 m between the Santa Rita and Huachuca Mountains. The predominant plant communities present here include grasslands and oak-mesquite savannas. Two of these studies (Bock & Bock, 1991; Bock et al. 1992) were conducted on the Appleton-Whittell Research Ranch and focused on grasshopper ecology in ungrazed grasslands at an elevation of 1300-1400 m; these are discussed in detail above. In addition, Bock et al. (2006) studied the impact of urbanization on grasshopper communities in the wider Sonoita Valley. A total of 41 grasshopper species were encountered along a set of 48 transects in both grazed and ungrazed areas. Although grasshopper species richness was not found to be significantly associated with either grazing or development, the authors found that grasshopper abundance was highest on exurban plots with livestock. Finally, Bock et al. (2007) investigated the relationship between species richness, evenness and abundance of multiple taxa including flowering plants, grasshoppers, butterflies, lizards, birds and rodents across a set of 48 plots in this same region. A total of 31 grasshopper species were encountered in this study, which found that grasshopper abundance was significantly positively correlated with species richness, but significantly negatively correlated with evenness. In contrast, evenness and species richness were uncorrelated.

Despite the lack of comprehensive studies of Orthoptera in the Madrean Sky Islands, several important discoveries of Orthoptera have been made in the last five decades. In 1988, the katydid species *Microcentrum latifrons* was described from the holotype collected in Portal

(Spooner, 1988). In 2009, the grasshopper species *Dichroplus notatus* was recorded in the US for the first time, from specimens collected in the Huachuca Mountains (Behrstock and Sullivan, 2011). In 2014, the katydid species *Bucrates weissmani* was described from specimens collected in the Quinlan, Santa Rita, Huachuca, and Dragoon Mountains in 1990, 2001, and 2013 (Walker, 2014). In 2019, the cricket species *Anaxipha hyalicetra* was described from specimens collected in the Atascosa and Pajarito Mountains in 2013 and 2014 (Cole and Funk, 2019), with photographs being taken in the Patagonia Mountains later that year (BugGuide). Also in 2019, the taxonomy of crickets in the genus *Gryllus* inhabiting the US was revised, with some of the new species described from specimens collected in various Madrean Sky Islands (Weissman and Gray, 2019). In 2020, the first live photos of the pygmy mole cricket species *Ellipes monticolus* were taken in the Chiricahua Mountains, with notes about its behavior, including its habit of making shallow burrows at the surface of sandy areas near water (Woo, 2020).

Aims of this Study

This study had several overlapping aims, including (1) to provide a contemporary survey of grasshoppers in the Madrean Sky Islands of Arizona, (2) to characterize the structure of grasshopper communities in this region in relation to elevation, habitat, plant coverage and geography, (3) to characterize intraspecific and interspecific morphological variation in grasshoppers in relation to these factors, and (4) to provide pinned specimens and photographs of several grasshopper species lacking or poorly represented in the ASU Hasbrouck Insect Collection. In addition, although not primary aims of this study, we also (5) characterized the ectoparasitic and phoretic mite fauna associated with the grasshoppers collected in this study, and (6) documented and attempted to collect other Orthoptera taxa encountered in the field.

CHAPTER 2

METHODS

Study Sites

Orthoptera were collected in six mountain ranges, which were selected both because they offer road access to higher elevations and because they span most of the latitudinal and longitudinal range of the Madrean archipelago in Arizona (Figure 2.1). These include the Pinal Mountains, which are sometimes regarded as the northernmost of the Madrean Sky Islands (Brusca & Moore, 2013), the Pinaleño Mountains, the Santa Catalina Mountains, the Chiricahua Mountains, the Santa Rita Mountains, and the Huachuca Mountains. An initial series of collecting sites was chosen during the first visit to each mountain range according to the following heuristics. We attempted to select one site for each 100 m band of elevation, beginning in either desert grassland or oak savanna at an elevation between 1300 – 1500 m above sea level and extending to as high an elevation as was accessible from the road. We looked for sites that were simultaneously accessible from the road and which contained habitat that was not directly altered by the construction of the road. We also gave preference to sites that were relatively level and which contained an open understory permitting easy passage on foot and the use of sweep nets.

These criteria led to the selection of 11 sites in the Pinal Mountains, 15 sites in the Pinaleño Mountains, 13 sites in the Santa Catalina Mountains, 11 sites in the Chiricahua Mountains, 9 sites in the Santa Rita Mountains, and 12 sites in the Huachuca Mountains. Although we were able to collect Orthoptera from each of these sites during the initial visits in June and July, concern about the feasibility of completing this many transects during the monsoon season (when afternoon thunderstorms are common at higher elevations) led us to reduce the number of collecting sites to a maximum of 11 in each mountain range. This reduction was accomplished by excluding several sites that were unproductive during the first visit, typically because these were either covered by a closed canopy on either side of the road or were on steep slopes that made collecting difficult. We refer to the remaining sites as our focal sites and we restrict all ecological analyses to data collected

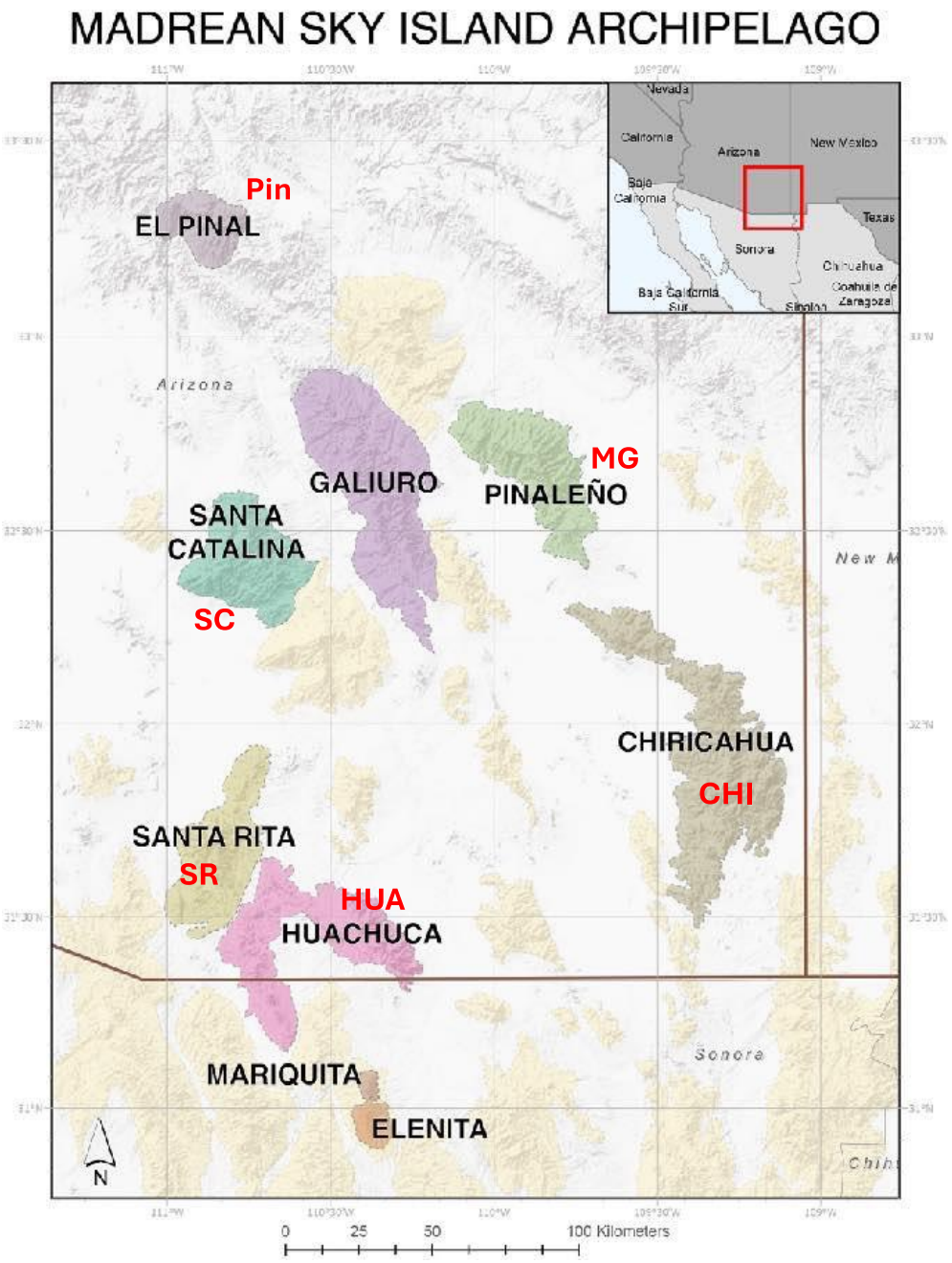


Figure 2.1. Map showing the six Madrean Sky Islands sampled in this study (modified from Piña Páez et al., 2023). Codes: Chi - Chihuahua; Hua - Huachuca; Pin - Pinal; MG - Pinaleño; SC - Santa Catalina; SR - Santa Rita.

at these sites. Detailed information about the collecting sites (focal and excluded) is provided in Appendix A (Table A1).

Sampling Dates

The Madrean Sky Islands receive a significant proportion of their annual rainfall during a summer monsoon season that usually lasts from late July to early September in southeast Arizona, with a duration that typically decreases with latitude. Although many insect species are most abundant (as adults) during the monsoon, some species peak in abundance either before or after this season. For this reason, we sampled each mountain range on three different dates, including one visit during June or July before the start of the monsoon season, one between late July and mid-September during the monsoons, and one from late September to early November after the monsoons. In particular, each focal site was sampled on three dates. The sampling dates for each location are recorded in Appendix A.

Orthoptera Sampling

Grasshopper surveys in grassland and prairie habitats are commonly performed by sweeping a net through the top layer of vegetation in an arc of 180°. Sampling effort can then be standardized by having collectors complete a fixed number of sweeps per site, often along linear transects (Evans and Bailey, 1993). Although we had originally intended to use such a protocol in this study, the variation in ground cover across collecting sites made this impractical. We encountered two difficulties. On the one hand, the density of shrubs and cacti was high enough at many sites that it was impossible to sweep at regular intervals along transects at these sites. On the other hand, most sites also included a significant amount of nearly bare ground where grasshoppers were frequently observed resting on soil or rock. Although these individuals could be captured by bringing the net directly down on top of them, they would simply flush if the net was swept laterally through what little vegetation was present at such points.

For these reasons, we adopted the following sampling protocol. At each site, two individuals (E.P.F. and J.E.T.) collected grasshoppers using a combination of lateral sweeps where feasible and targeted capture otherwise. Grasshoppers resting on the ground could often be collected directly as described above, while grasshoppers perched on shrubs and cacti that could not be captured directly would frequently flush onto the ground when approached by the collectors where they could be captured. Sampling effort was at least partially standardized by having each collector sample grasshoppers for exactly 20 minutes at each site. In addition, we sampled on opposite sides of the road, avoiding overlap, and we sampled within 100 m of a central point which was used to designate the location of the site. Accordingly, the maximum area sampled per site was approximately 30,000 m^2, although in practice we usually sampled much smaller areas than this due to inaccessible terrain at some sites and the time required to capture grasshoppers at sites where they were abundant.

After capture, grasshoppers and other Orthoptera were first placed in kill jars containing ethyl acetate, and then later transferred to plastic containers which were stored in a cooler for transport back to the lab. Upon arrival, these specimens were initially stored in a refrigerator for up to a week until they could be examined for mites, after which they were transferred to vials containing 95% ethanol which were stored at -20°C. Representative male and female specimens of each species were also photographed using microscope cameras to show diagnostic characters such as pronotum texture or male cerci.

Plant Surveys and Habitat Classification

The vegetation at each focal site was characterized both in terms of ground cover and tree cover using the following protocol. We selected five non-overlapping 10 m-long linear transects spanning the area where grasshoppers were collected and then recorded the ground and tree cover at 1-meter intervals along each transect for a total of 50 points. At each point, we recorded whether the ground was covered by grass, by ferns (principally common bracken - *Pteridium aquilinum*), by forbs (sensu lato, including herbaceous non-graminoid plants, woody shrubs, cacti, agaves and

yuccas), or was bare. Where grass or ferns were covered by forbs, we recorded the site as being occupied by a forb. We also recorded the tree cover (if any) at each point, using the following categories: mesquite (*Prosopis* spp.), manzanita (*Arctostaphylos* spp.), oak (*Quercus* spp.), deciduous-other, juniper (*Juniperus* spp.), pine (*Pinus* spp.), coniferous-other (mainly *Pseudotsuga menziesii* and *Abies concolor*), or treeless. The deciduous-other category was broad and included many species such as quaking aspen (*Populus tremuloides*), desert kidneywood (*Eysenhardtia orthocarpa*), and buckthorn (*Frangula* sp.). Ground cover and tree cover were measured separately, so that for example a site could simultaneously be recorded as being covered by grass and by pine. All plant surveys were conducted during the third post-monsoon season visit to each focal site and the data collected from the five transects surveyed at each focal site was used to estimate the proportion of each class of ground and tree cover in the immediate vicinity of the sampling area.

In addition, we assigned each focal site to one of five broad habitat categories, reflecting the composition of the tree community in the vicinity of the site: desert grassland, oak, pine-oak, mixed coniferous forest, and disturbed. This classification is coarser than those typically given in detailed descriptions of Madrean plant communities (see Figure 1.3); for example, we lumped Ponderosa pine forest and mixed coniferous forest into a single category (conifer). This was done both to avoid having few focal sites per category and because the plant communities vary continuously rather than discretely, making it difficult to delineate between finer habitat categories. We also included a disturbed category to accommodate three sites where most trees have either been removed by fire (Pin7, SC11) or appear to have been cleared to prevent forest fires (Pin11). The habitat assignment for each site is specified in Appendix A.

Adventitious Sampling

In addition to the timed collections made at the focal sites, we also collected Orthoptera opportunistically. These included Ensifera collected by sweep netting at the focal sites, as well as additional grasshoppers encountered away from the focal sites (e.g., at Proctor Road and in Florida

Canyon in the Santa Rita Mounts). Furthermore, because we stayed overnight in the Pinaleño Mountains, Chiricahua Mountains, and Huachuca Mountains, we were able to observe and collect some nocturnally active Orthoptera in these mountain ranges. This additional material was not included in the ecological analyses that follow in the next chapter, but we do include these records in the species lists provided in Appendix B and we comment on the more notable records.

Identification of Orthoptera

I identified specimens to the lowest taxonomic level possible based on the most accurate descriptions and existing photographs of the pronotum (plate at the top of the thorax), forewings (also known as tegmina), hindwings, and also male cerci for the subfamily Melanoplinae. To get a better view of these morphological characteristics, I viewed specimens under a dissecting microscope. For reference, I used BugGuide (Iowa State University) and the adult grasshopper identification key by Grasshoppers of the Western US (IDTools). A series of images illustrating key anatomical features used to identify grasshoppers to species is provided below (Figures 2.2 - 2.7).

Measurements

On each individual specimen, I used a millimeter ruler to measure the total length (from head to wing tips on long-winged specimens), body length (from head to abdomen tip), body height, body width, wing length, wing width, pronotum length, hind femur length, hind femur width, hind tibia length, head height, head width, eye length, and antenna length. I also recorded the eye shape, as that could indicate whether the species primarily relies on vision or on other sensory functions such as touch and smell.

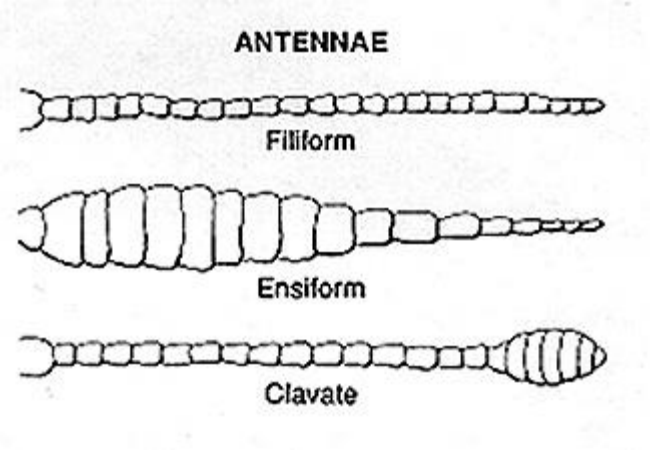


Figure 2.2. Three different antenna shapes found in the suborder Caelifera which are useful for identification. Most species in this suborder have filiform antennae, while some genera in the subfamily Gomphocerinae have ensiform or clavate antennae (University of Wyoming).

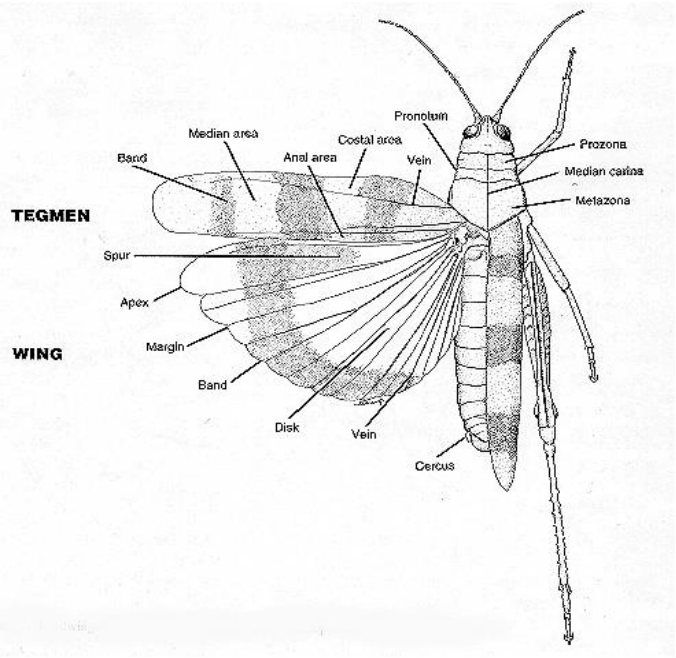


Figure 2.3. Wings, pronotum, and cerci of a grasshopper in the subfamily Oedipodinae (University of Wyoming).

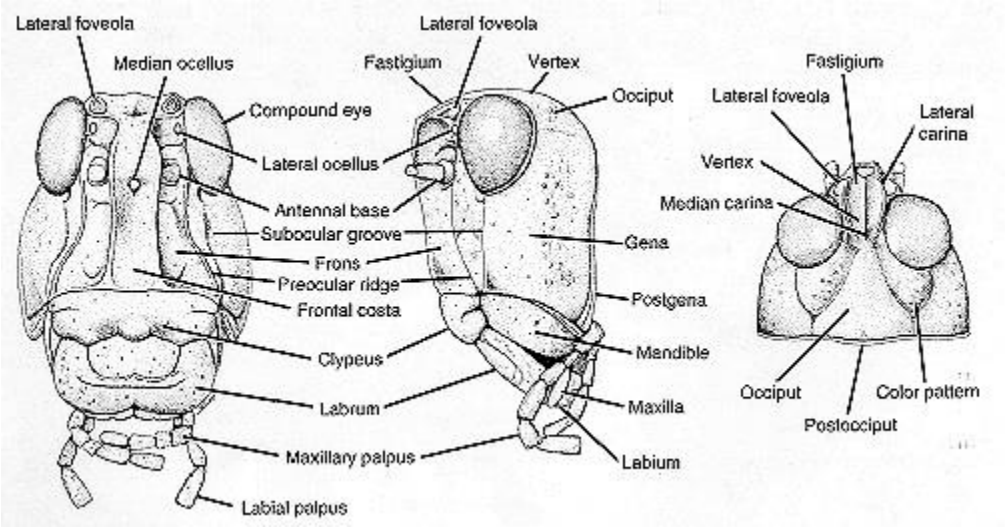


Figure 2.4. Head anatomy of a grasshopper (University of Wyoming).

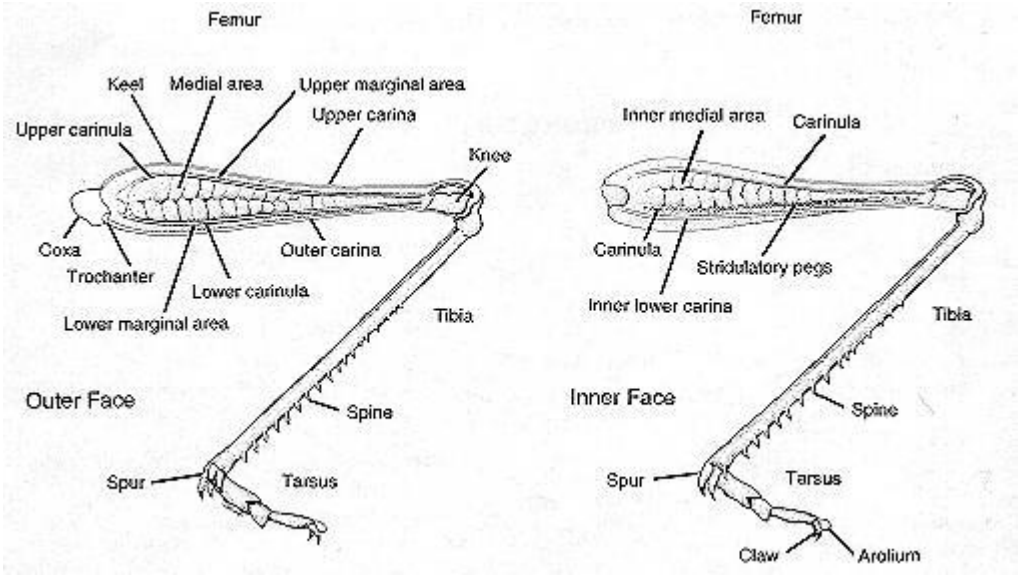


Figure 2.5. Grasshopper hind leg anatomy (University of Wyoming).

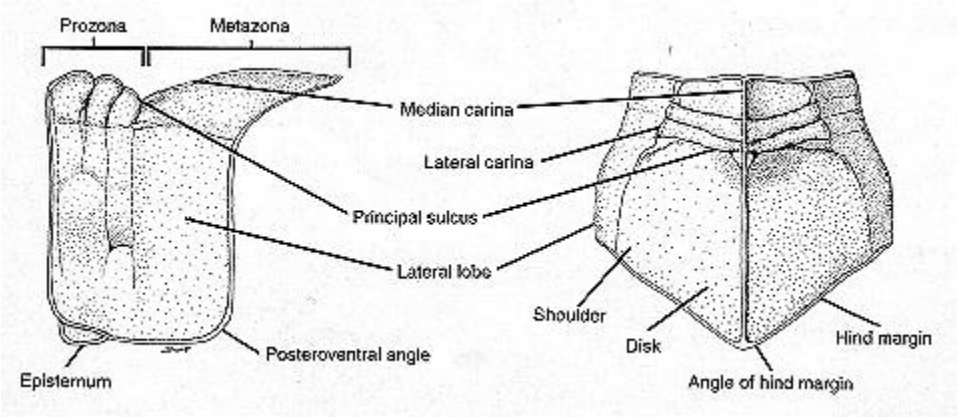


Figure 2.6. Anatomy of the grasshopper pronotum, showing the cryptopleuron (lateral lobes that are characteristic of the order Orthoptera), as well as the sulci and carinae that are useful for identifying species (University of Wyoming).

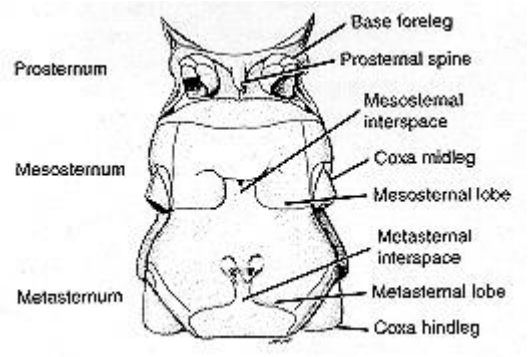


Figure 2.7. Grasshopper Ventral Anatomy (University of Wyoming).

Disposition of Specimens

Voucher specimens representing a male and female of each species collected (if available) have been pinned and will be donated to the ASU Hasbrouck Insect Collection.

Data Analysis

Most statistical analyses were carried out in R version 4.4.0 using the package vegan version 2.6-6.1 (Oksanen et al. 2024). We give a general overview of these analyses here and provide more detailed descriptions in the Results section as appropriate. Where frequentist statistical tests were performed, we treated results with p-values less than $\alpha = 0.01$ as statistically significant.

The tree coverage data was compared between habitats using non-parametric permutational multivariate analysis of variance tests (PERMANOVA) applied to the distance matrix containing the square roots of the Bray-Curtis dissimilarities between each pair of focal sites. The Bray-Curtis statistic quantifies the dissimilarity between the composition of two assemblages and was calculated using the vegan function *vegdist* applied to the untransformed tree coverage data. Although the Bray-Curtis dissimilarity is non-metric due to violation of the triangle inequality, it can be converted to a metric by square root transformation, as was done here. We then used the vegan function *adonis2* to perform the PERMANOVA tests, which assess whether two or more groups of objects in a metric space differ in their centroids or dispersions. Since PERMANOVA tests are sensitive to differences between the dispersions of sites around their centroids, we also tested for homogeneity of multivariate dispersions among habitats using the non-parametric PERMDISP procedure implemented in the vegan function *betadisper*, with the bias adjustment for small sample sizes. All permutation tests were performed using 9999 permutations. Lastly, we performed a principal coordinates analysis (PCoA) of the Bray-Curtis dissimilarity matrix to visualize the heterogeneity of the tree coverage data across sites. The PCoA was plotted in two dimensions and did not require correction for negative eigenvalues.

Grasshopper diversity was quantified using several standard metrics, including both the species richness (number of species) and the effective species richness, the latter being calculated as e^H, where H is the Shannon diversity index, which depends on both the number of species present in a sample as well as their frequencies. Evenness was quantified using Pielou's index J, which is equal to the ratio H/log(S), where S is the actual species richness. Because rare or difficult-to-capture species may be missing from sample data, particularly when sample sizes are small, we used three methods to estimate the actual species richness of the grasshopper assemblages. The 2'nd order Jackknife estimator attempts to estimate the number of missing species using the number of species that were sampled just once or twice; we calculated this using the XXX function implemented in vegan. We also calculated two rarefaction-based estimators of total species richness using the R package iNEXT version 3.0.1 (Hsieh et al., 2016). The abundance-based estimate was obtained by resampling individuals, whereas the incidence-based estimate was obtained by resampling sampling units, which in our case correspond to the focal sites. This package was also used to plot abundance- and incidence-based rarefaction curves for the individual mountain ranges and individual habitats. Lastly, we used non-parametric Kruskal-Wallis tests to assess whether the distributions of adult and juvenile grasshopper abundance and of species richness and effective species richness per site differed amongst mountain ranges or habitats. Where significant results were obtained, we then used Dunn's test to perform post-hoc pairwise comparisons. For the latter, we used Hochberg's method to adjust the significance level when performing multiple tests.

We investigated the structure of the grasshopper communities in relation to habitat and geography using both constrained and unconstrained ordination. For the purposes of these analyses, we combined the three grasshopper samples collected at each site during the three sampling periods. Thus, each assemblage consisted of all of the adult grasshoppers collected at a given site during visits that took place prior to the monsoons, during the monsoons, and after the monsoons. Although we lose information about seasonal variation in community structure by taking this approach, we also substantially reduce the number of sampling units that need to be omitted

from distance-based analyses due to an absence of adult grasshoppers; indeed, whereas 32 of the 183 samples (17%) contained no adult grasshoppers, only one of the 61 focal sites (1.6%) lacked adult grasshoppers when we combined the data from the three sampling periods.

We used non-metric multidimensional scaling (NMDS) applied to the Bray-Curtis dissimilarities between the adult grasshopper assemblages at the 61 focal sites to visualize the structure of these assemblages in relation to mountain range and habitat. NMDS was performed using the vegan function *metaMDS*, with 30 random starts and both two and three dimensions. NMDS performs an unconstrained ordination based on a distance matrix by assigning each object in the data set to a location in a low-dimensional Euclidean space in such a way that the rank order of the Euclidean distances between objects is as close as possible to the rank order of the distances in the original distance matrix. Thus, objects that are closer in the NMDS plot are likely to be closer (or more similar) to one another according to the original metric. Although there is no guarantee that the two rank orders will be identical, the quality of the representation can be assessed by calculating the stress of the ordination. Ordinations with stresses less than 0.10 are generally considered to be good, those with stresses between 0.1 and 0.2 are considered to be adequate, and those with stresses in excess of 0.2 are considered to be at risk of misinterpretation (Clarke, 1993).

We also investigated the structure of the grasshopper assemblages at a coarser geographical scale by combining the data from all of the focal sites located within individual sky islands. This produced six grasshopper assemblages, whose relationships to one another were characterized using three approaches. First, we used Ward's method to hierarchically cluster the aggregated community data based on the square root of the Bray-Curtis dissimilarity; this was done using the R function *hclust* with the method *ward.D2*. We also visualized the relationships between the six assemblages by performing a principal coordinates analysis of the distance matric containing the square root-transformed Bray-Curtis dissimilarities; this was done using the function *pcoa* implemented in the R package ape version 5.8. Lastly, we used a Mantel test to assess whether the ecological distance between grasshopper communities located on different sky islands

is correlated with the geographical distance between the sky islands. We defined the geographical distance between each pair of sky islands to be the geodesic distance between the highest elevation focal sites in those mountain ranges. These sites were chosen as proxies for the mountain ranges themselves as they tend to be fairly centrally located within each mountain range. Geodesic distances were calculated using the function *geodist* (with measure = geodesic) in the package geodist version 0.1.0 applied to the latitudinal and longitudinal coordinates of the sites that were measured in the field. The Mantel test was performed using the R function *mantel*, with Spearman's rank correlation as the test statistic; with only six data points, the significance of the test statistic was calculated exactly through exhaustive permutation of the distances (719 permutations).

We used transformation-based redundancy analysis (tb-RDA) to investigate the relationship between the grasshopper assemblages at the focal sites and the elevation, vegetation, and latitude and longitude of these sites. The vegetation data for each site consisted of the ground and tree cover data described earlier. Redundancy analysis performs a constrained asymmetric ordination of a set of response variables based on their linear relationships with a set of explanatory variables. We note that the resulting ordination is based on the predicted values of the response variables obtained from the explanatory variables using a linear model inferred from the full data. We first applied a Hellinger transformation to the grasshopper community data using the vegan function *decostand*; this transformation converts absolute abundances to relative abundances and then applies a square root transformation that reduces the impact of highly abundant species. We then conducted two redundancy analyses, one using no explanatory variables and the other using all 13 explanatory variables (latitude, longitude, elevation, as well as nine plant cover variables), both performed using the vegan function *rda*. Because many of the explanatory variables were not significantly associated with the response data in the full analysis, we next used the vegan function *ordiR2step* to perform forward variable selection. This function adds variables one at a time to a regression-based model so that it maximizes the adjusted R^2, halting whenever this statistic begins to decrease. We also repeated these analyses using two subsets of the grasshopper community data obtained by omitting species that were either very abundant or very rare in the samples. The

rationale for omitting the most abundant species is that these were mostly very widespread and thus may obscure relationships that the remaining species have with the explanatory variables. On the other hand, the rationale for omitting the very rare species is that these were so restricted in their distributions that they essentially just added noise to the community data. Lastly, we used the function *resassoc.cca* in the R package natto version 0.3 (unpublished, but available at https://github.com/jarioksa/natto) to create a correlation heat map showing the residual associations between species left over after accounting for the predicted community composition using the best-fitting linear model identified using forward variable selection. This plot can be used to visualize associations between species that are not explained by the environmental variables and which could be attributed to other ecological processes such as environmental filtering or inter-specific competition.

Because we were only able to consistently identify grasshopper nymphs to subfamily, these were not included in the analyses of grasshopper community structure described above. However, we did perform transformation-based redundancy analysis using the counts of adult and subadult grasshoppers in each subfamily as response variables. This allowed us to compare the impact of the explanatory variables on grasshopper abundance both between life stages (adult vs. subadult) and between subfamilies. We also used Kendall's rank correlation test to directly assess whether the abundances of adult and subadult grasshoppers per site within each subfamily were significantly correlated.

We performed binomial tests to assess whether the proportions of adult male and adult female grasshoppers of each species were significantly different from 0.5. For these tests, we used the overall numbers of males and females of each species collected in all 61 focal sites. Although the adult sex ratio could vary spatially, as could collecting biases, the numbers of adult grasshoppers of individual species collected at individual sites were almost never large enough to be able to detect even extreme skews in the sex ratio. However, we did use the binomial test to assess whether the overall proportions of adult male and adult female grasshoppers were significantly different from 0.5. Likewise, we also used this test to assess whether the number of

species in which females outnumbered males was significantly different from the number of species in which males outnumbered females. These last two tests were conducted to look for evidence of a consistent sex ratio bias that could not be detected using the counts from individual species due to small sample sizes.

We summarized intraspecific variation in the twelve morphological characters measured on adult grasshoppers by calculating the sample mean and sample standard deviation of each trait in each species. Because most grasshopper species are somewhat sexually dimorphic (in size and shape), we calculated these statistics separately in females and males. We then used multiple linear regression to investigate how the size and shape of the more abundant grasshopper species varied in relation to elevation, sampling date and mountain range. Elevation and sampling date were both treated as quantitative variables, the latter being expressed as the number of days from the beginning of the year, whereas the mountain range was treated as a categorical variable with six levels. These analyses were restricted to the nine species in which we had measured at least ten individuals of each sex. Four morphological traits were investigated. We first performed multiple linear regressions of body length as the response variable, treating males and females separately. By performing separate regressions for the two sexes, we are able to identify sexually dimorphic relationships between body length and the explanatory variables, although this comes at the cost of reduced power to detect those relationships that are similar in the two sexes due to the reduced sample size.

Because quantitative morphological traits are often strongly correlated with size, it would be inefficient to simply repeat these regression analyses with each of the remaining 11 traits. Instead, we used principal components analysis to identify a small number of linear combinations of these traits that capture much of the measured morphological variation within each species and which are uncorrelated with one another. One approach that can be used to partially disentangle variation in shape-related components from variation in size is to perform principal components analysis on log-transformed morphological data (Klingenberg 2016). The principal component that accounts for the greatest proportion of variance in the data is then interpreted as a measure of size,

while the remaining components (which are orthogonal to the first component) capture different aspects of shape. Often the first component lies close to the diagonal of the trait space, with approximately constant loadings for most morphological traits. Traits with loadings that differ greatly from this constant are those that have different allometric scaling relationships with size.

We applied this approach to each of the nine abundant species using the following 12 morphological traits: body length, height and width, tegmen length and width, pronotum length, hind femur length and width, hind tibia length, head height and width, and antenna length. Each trait was first log-transformed, then centered and standardized, and then principal components analysis was performed on the resulting data. Less than two percent of the measured individuals were missing data for one or more traits, usually due to missing or broken limbs or antennae, and these were excluded from further analysis. Here we analyzed conspecific females and males together so that we could take advantage of the larger sample size and so that the resulting components would be directly comparable between the two sexes. We then performed multiple linear regressions of the individual scores on the first three principal components (ranked according to the total variance explained in the log-transformed trait data) against sex, elevation, sampling date, and mountain range. Sex was included as a categorical variable to allow for the possibility of different intercepts for females and males for each principal component. However, because we did not include interaction terms between sex and the other explanatory variables, these regressions assumed that environmental and geographical variation were similar on a log scale in both sexes.

We used a different approach to examine if and how the distribution of morphological traits within grasshopper assemblages varied across habitats. We again focused on four traits, including body length as well as the first three principal components obtained by analyzing the same log-transformed morphological data as above. However, having observed that intraspecific variation in these traits between females and males often exceeds interspecific variation between individuals of the same sex, here we opted to analyze males and females separately. Unlike the intraspecific analyses, subdividing by sex did not lead to unacceptably small sample sizes in this case because the data included individuals from all 41 species. Furthermore, by comparing the trait loadings on

each of the three leading principal components in females and males, we were able to confirm that these components measured similar morphological features in both sexes. We then used non-parametric Kruskal-Wallis tests to assess whether the distribution of each trait in each sex differed amongst habitats, followed by Dunn's test with Hochberg's correction to perform post-hoc pairwise comparisons when justified. We also repeated these analyses three more times using only those individuals belonging to each of the three most abundant subfamilies (Gomphocerinae, Melanoplinae, and Oedipodinae). Note, however, that these latter analyses used the individual scores from the original community-wide principal components analyses, i.e., we did not repeat the principal components analyses themselves. This was done to investigate the extent to which changes in the assemblage-wide trait distributions between habitats were mirrored within the sub-assemblages containing species from individual subfamilies.

As many grasshopper species are wholly flightless, we investigated the relationship between the proportion of flightless individuals within sites and either elevation or habitat using binomial regression. Two regressions were performed, one using elevation, latitude and longitude as explanatory variables and the other using habitat, latitude and longitude as explanatory variables. In both cases, we analyzed the proportion of the non-Oedipodine adult grasshoppers that were flightless. Oedipodinae was excluded from this analysis because there are no flightless species within this subfamily within our region and thus its inclusion in the total counts would have been confounding if Oedipodine abundance was separately affected by any of the explanatory variables. The binomial regressions were performed using the R function *glm*, with the logit link function.

CHAPTER 3

GRASSHOPPER DIVERSITY AND COMMUNITY STRUCTURE

Plant Surveys and Habitat Classification

The percent ground and tree cover by different categories of plants is reported for each focal site in Table C1 (Appendix C), along with the habitat classification which was based on our subjective assessment of the tree community in the vicinity of the collecting location. Permutational multivariate analysis of variance of the tree cover data using the Bray-Curtis dissimilarity index indicates that tree cover differs significantly amongst habitats (PERMANOVA: $R^2 = 0.517$, $F_{4,56} = 15.015$, $p < 10^{-4}$), although this could be due to differences in either the centroids or the dispersion of the data. We tested for homogeneity of the multivariate dispersion amongst habitats using the PERMDISP2 procedure implemented in the function *betadisper* in the R package vegan. Although the standard version of this test was insignificant ($F_{4,56} = 1.448$, $p = 0.231$), a repeat analysis using the recommended bias correction for small sample sizes was significant ($F_{4,56} = 2.916$, $p = 0.029$), indicating that the within-habitat dispersion of tree cover dissimilarities differs amongst habitats. Since the latter result was sensitive to sample size, we repeated these analyses with the three sites classified as disturbed omitted from the data. This second round of tests indicated that the distribution of tree cover differed significantly amongst the four natural habitat classes (PERMANOVA: $R^2 = 0.520$, $F_{3,54} = 9.534$, $p < 10^{-4}$), while the multivariate dispersion did not, even with the bias correction for small sample size ($F_{3,54} = 1.116$, $p = 0.351$). Combined, these two tests allow us to infer that the typical composition of the tree cover data collected at the focal sites differs amongst the sites classified as grassland, oak, pine-oak or coniferous habitats. This is further reflected in an ordination of the tree cover data collected at the focal sites using principal coordinates analysis (PCoA) applied to Bray-Curtis dissimilarity. As can be seen in Figure 3.1, the convex hulls of the points assigned to each of the four natural habitats are disjoint from one another. In contrast, we see some overlap between the hull enclosing the three disturbed sites with the hulls

enclosing sites assigned to the grassland and oak habitats, which we attribute to the presence of a few oaks in two of the disturbed sites and the lower overall density of trees in both the disturbed and grassland sites.

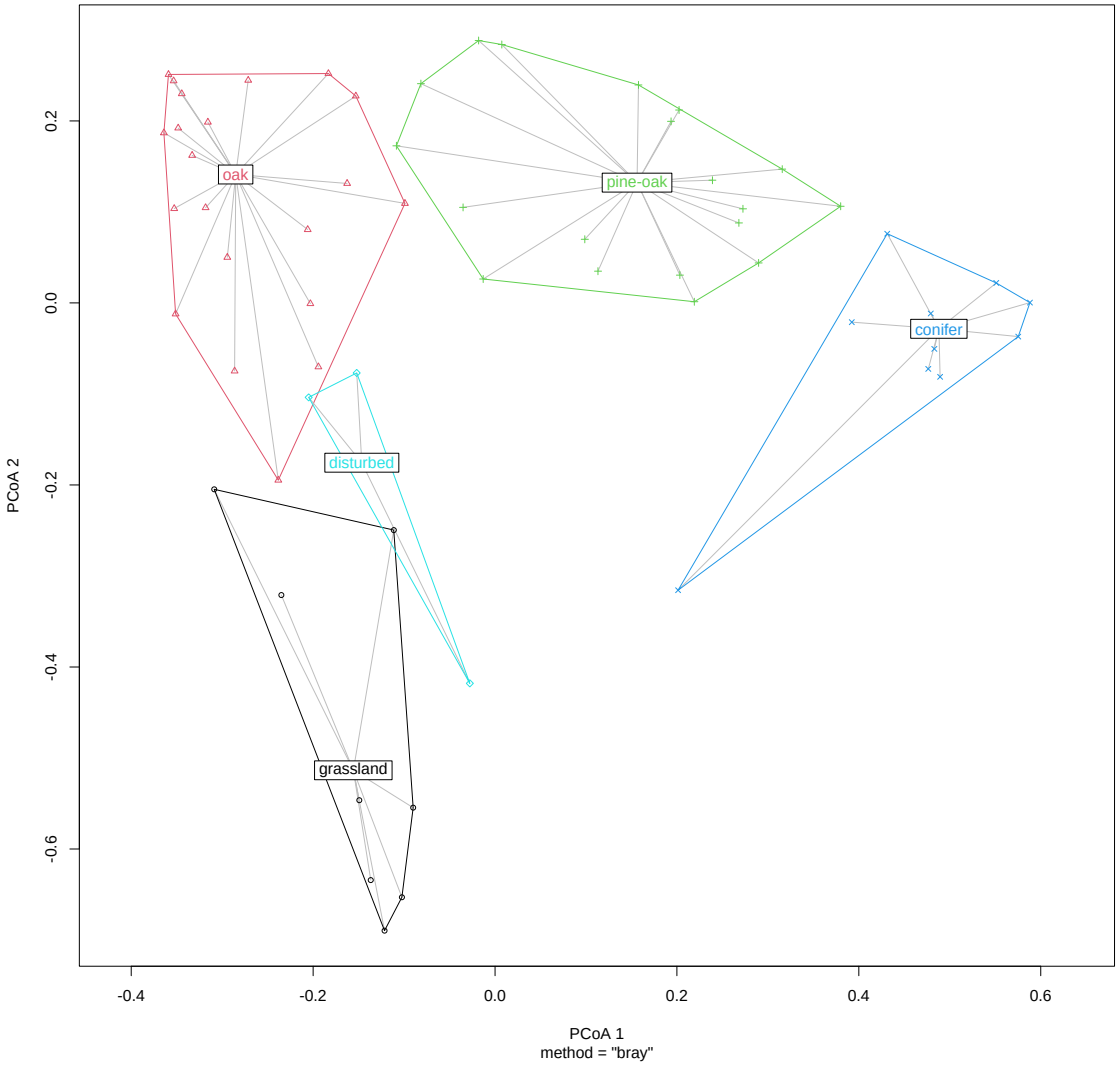


Figure 3.1. Ordination of tree cover data at all focal sites using principal coordinates analysis applied to Bray-Curtis dissimilarity. Sites are colored according to habitat type and enclosed in convex hulls, while the centroid of each habitat is indicated by the habitat name enclosed in a box.

Grasshopper Diversity and Abundance

In total, 1,307 grasshoppers, including 991 adults and 316 nymphs, were collected at the 61 focal sites. All adult grasshoppers were identified to species (Table B1), which included a single species (*Phrynotettix tshivavensis*) in the family Romaleidae (lubber grasshoppers) as well as 40 species in the family Acrididae (short-horned grasshoppers). The latter family included species from three subfamilies, including 18 species in the subfamily Gomphocerinae, 13 species in the subfamily Oedipodinae, and 10 species in the subfamily Melanoplinae. We also collected a single nymph in the genus *Schistocerca*, representing a fourth subfamily Cyrtacanthacridinae, and it is possible that additional unidentified species may have been represented in the juvenile grasshoppers in our samples. However, since we were unable to identify many juvenile grasshoppers to species, we restrict our discussion of species diversity to the adult grasshoppers in the focal samples and defer consideration of the juveniles to a later section. Two additional grasshopper species were collected outside of the focal sites and are described in the section on adventitious collecting.

Table 3.1 shows the overall abundance, incidence (% occupancy), and distribution of these species; additional tables showing how the abundance of individual species varied across mountain ranges, habitats, and collecting periods are provided in Appendix C (Tables C2 - C4, respectively) and the raw count data is provided in Appendix F. As expected, the species abundance distribution is strongly skewed, and the four most abundant species, *Trimerotropis pallidipennis, Melanoplus sanguinipes, T. modesta* and *M. desultorius*, account for nearly 60% of all of the adult grasshoppers in the focal samples. The most abundant species, *T. pallidipennis*, was especially widespread, having been collected at over 90% of the focal sites, including all six mountain ranges, all five habitats, and from the lowest to the highest elevations sampled. No other species was collected at more than 40% of the focal sites, although eight additional species were present in at least 20% of the focal sites. At the other extreme, seven species were represented by single individuals, while a further six species were represented by just two individuals.

Species	total adults	occup. (%)	mountain ranges	habitats	min, max elevation (m)
Acantherus piperatus	2	3.3	SR	gr, oak	1348 - 1632
Achurum sumichrasti	21	16.4	all - Pin	gr, oak, p-o	1348 - 1969
Ageneotettix deorum	16	14.8	all - SC	gr, oak	1332 - 1660
Amblytropidia mysteca	17	16.4	all - Pin, SC	gr, oak, p-o	1348 - 1874
Amphitornus coloradus	34	26.2	all - SC	gr, oak, p-o	1348 - 2159
Boopedon flaviventris	2	3.3	SR	gr, oak	1348 - 1632
Cibolacris parviceps	3	3.3	Pin	gr, oak	1332 - 1433
Eritettix simplex	1	1.6	Chi	oak	1669
Horesidotes cinereus	3	3.3	Hua, MG	oak	1565 - 1742
Mermiria bivittata	1	1.6	SR	gr	1348
Mermiria texana	16	13.1	Chi, Hua, MG	gr, oak, p-o	1454 - 2246
Opeia obscura	4	6.6	Hua, SR	gr, oak, p-o	1348 - 2159
Paropomala pallida	21	9.8	all - Pin, SR	gr, oak	1362 - 1565
Procorypha snowi	22	9.8	Hua, SR	gr, oak, p-o	1348 - 1948
Psoloessa texana	33	29.5	all	gr, oak, p-o, con	1332 - 2770
Rhammatocereus viatorius	2	3.3	Hua, SC	oak, con	1466 - 2322
Syrbula montezuma	30	31.1	all	gr, oak, p-o	1332 - 2246
Barytettix humphryesii	8	11.5	Hua, MG, SR	gr, oak	1348 - 1827
Conalcea huachucana	41	31.1	all	oak, p-o, con, dist	1660 - 2690
Hesperotettix viridis	24	6.6	MG, Pin	gr, oak	1332 - 1660
Melanoplus desultorius	80	39.3	all	all	1454 - 2567
Melanoplus flavidus	2	3.3	MG, Pin	gr	1332 - 1362
Melanoplus franciscanus	3	1.6	Pin	con	2322
Melanoplus lakinus	1	1.6	SR	gr	1348
Melanoplus pictus	1	1.6	Pin	p-o	2101
Melanoplus sanguinipes	132	34.4	all - Hua, SR	all	1332 - 2770
Phoetaliotes nebrascensis	21	8.2	SC, SR	gr, oak, p-o	1429 - 2054
Arphia conspersa	20	18.0	all - Pin	oak, p-o, con	1669 - 2770
Arphia pseudonietana	1	1.6	SR	oak	1632
Conozoa carinata	13	13.1	all - SR	gr, oak, p-o, con	1332 - 2590
Lactista azteca	2	3.3	Pin, SR	gr, con	1429 - 2301
Lactista gibbosus	1	1.6	MG	con	2770
Leprus wheeleri	3	4.9	Chi, Hua, SR	oak, p-o	1765 - 2159
Mesostegma plattei	7	6.6	Chi, MG	oak, p-o	1660 - 2246
Tomonotus ferruginosus	5	4.9	Chi, Hua	oak, p-o	1640 - 1948
Trimerotropis cyaneipennis	21	21.3	all	oak, p-o, con	1742 - 2770
Trimerotropis inconspicua	1	1.6	SC	p-o	2270
Trimerotropis modesta	93	32.8	all - SR	oak, p-o, con, dist	1565 - 2770
Trimerotropis pallidipennis	278	91.8	all	all	1327 - 2770
Xanthippus corallipes	3	3.3	MG, SC	gr, dist	1362 - 2567
Phrynotettix tshivavensis	2	3.3	Pin	con, dist	2301 - 2373

Table 3.1. List of grasshopper species collected in the focal sites showing the total number of adults, the proportion of sites (% occupancy), the mountain ranges and habitats, and the minimum and maximum elevations where collected. Habitat codes: gr: grassland; oak; p-o: pine-oak; con: coniferous; dist: disturbed.

To gain insight into how individual species are distributed across habitats, we calculated the mean number of adults collected per site in each habitat for each of the 41 grasshopper species (Table C3). Here we show the standardized abundance rather than the absolute abundance because of the disparity in the number of sites in each habitat class, as discussed below. The number of species achieving their peak sampling density in each of the habitats was 18 in the grasslands, 9 in oak-associated habitats, 4 in pine-oak forest, 7 in coniferous forest, and 3 in the disturbed habitats. Although these numbers need to be viewed cautiously given the potential for distortion by the many species that were sampled only once or twice, they suggest that grasshopper diversity within the region is highest in the grasslands and then tends to decline with elevation until reaching the coniferous forest, where it increases slightly. Nonetheless, there are several grasshopper species that were relatively abundant in high elevation habitats and absent or rare in the grasslands. These include *H. cinereus*, *M. plattei* and *T. ferruginosus* in oak woodland and chaparral, *P. nebrascensis* in pine-oak forest, and *A. conspersa*, *T. cyaneipennis*, and *T. modesta* in coniferous forest. One species, *M. sanguinipes*, was most abundant in disturbed habitats, but it was also the second most abundant species (per site) in coniferous forest and the fourth most abundant species in pine-oak forests. Although we are uncertain whether the apparent rebound in grasshopper abundance and diversity at high elevations is real, this could be due to the relatively high frequency of meadows that occur in proximity to coniferous forests, perhaps because of topographical features (e.g., a higher proportion of relatively flat land at higher elevations) or because of forest fires.

The seasonal variation in the total counts of individual species is shown in Table C4. Although overall grasshopper abundance was greatest in the pre-monsoon collecting period, this pattern was mainly due to peaks in the abundance of just two species, *T. pallidipennis* and *M. sanguinipes*. Excluding species that were collected only once or twice, 7 species were most abundant during the pre-monsoon period, 16 species were most abundant during the monsoons, and no species was most abundant during the post-monsoon period, although we collected equal numbers of *A. deorum* during and after the monsoons. This data suggests that the diversity of adult

grasshoppers in this region is greatest during the monsoons, possibly in response to the increasing plant productivity that occurs during that period. Lastly, we note that *T. pallidipennis* numbers

range/habitat	sites	N_{ad}	N_{nym}	S	D	J
Chiricahuas	10	181	31	20	12.3	0.84
Huachucas	10	162	38	22	9.6	0.73
Pinal	11	170	41	18	5.9	0.61
Pinaleño	11	185	73	23	13.8	0.84
Santa Catalina	10	116	45	16	4.4	0.54
Santa Rita	9	166	88	22	11.6	0.79
grassland	8	151	114	25	14.7	0.88
oak	21	320	123	31	14.4	0.78
pine-oak	19	265	39	22	9.9	0.74
coniferous	10	189	17	14	6.9	0.73
disturbed	3	66	23	7	2.3	0.44
pre-monsoon	61	481	163	29	7.6	0.60
monsoon	61	366	143	29	17.6	0.85
post-monsoon	61	144	10	23	10.5	0.75
total	61	991	316	41	15.0	0.73

Table 3.2. Abundance and diversity of grasshoppers collected at the 61 focal sampling sites. N_{ad} and N_{nym} are the counts of adult and sub-adult grasshoppers. S is the species richness (adults only), $D = e^H$ is the effective number of species, and J is Pielou's evenness metric.

recovered somewhat in the post-monsoon period after decreasing precipitously from their pre-monsoon high, giving rise to a bimodal abundance distribution that was unique to this species.

Table 3.2 shows how the overall abundance and diversity of grasshoppers varied between mountain ranges, habitats, and collecting periods. With one exception, the samples collected in each mountain range were similar in overall abundance and species richness, with each mountain range containing approximately half (18 - 23 species) of the total species pool sampled across the region. For unknown reasons, we collected significantly fewer adult grasshoppers in the Santa Catalina Mountains, which also had the lowest overall species richness of the six mountain ranges. Both species diversity, here characterized by the effective number of species ($D = e^H$), and the overall evenness ($J = H/\ln(S)$) of the grasshopper assemblages varied to a greater extent across mountain ranges. Both indices were exceptionally low in the Santa Catalina and Pinal Mountains,

at least in part because the grasshopper communities sampled in each of these two mountain ranges were dominated by a single species, *T. pallidipennis* in the former and *M. sanguinipes* in the latter, these accounting for over 50% of the adult grasshoppers collected in each mountain range (Table C2). In contrast, grasshopper diversity was much more even in the remaining four mountain ranges, although the ratio of the effective number of species to the observed number (D/S) varied from around 0.44 in the Huachuca Mountains to 0.6 in the Pinaleño Mountains.

Grasshopper abundance and diversity also differed amongst the five habitats sampled, although to some extent these differences can be attributed to variation in the number of sites sampled within each habitat, which ranged from 3 sites within disturbed habitats to 21 sites within oak-associated habitats. However, whereas the correspondence between sampling effort and total adult abundance appears to be strong, this was not the case with either the actual or the effective number of species. For example, although only 8 sites were located within grassland, this habitat class had the highest effective number of species and the second highest actual number of species. Grassland grasshopper communities also had the highest evenness index compared with the other habitats, which appeared to become moderately less even with elevation. Species richness and diversity were smallest within the disturbed habitat, as was evenness, mainly due to *M. sanguinipes* which accounted for nearly 80% of all adult grasshoppers collected within this habitat (Table C3).

Although direct comparison between different mountain ranges or different habitats is confounded by variation in sampling effort, we can attempt to control for the latter effect in several ways. One approach is to estimate the true species richness of the assemblage by using either the abundance or the incidence data to estimate the number of species that were not sampled despite being present in the area surveyed. In general, these estimates are sensitive to the assumptions made about the relationship between the number of unsampled species and the number of species that were sampled only once or a few times. Since it is unclear which if any of these estimators is best suited for our data, we have used three different methods to estimate the total species richness of grasshoppers in each mountain range, each habitat, and throughout the entire region (Table C5). Two of these methods are based on extrapolation of rarefaction curves and we show both the

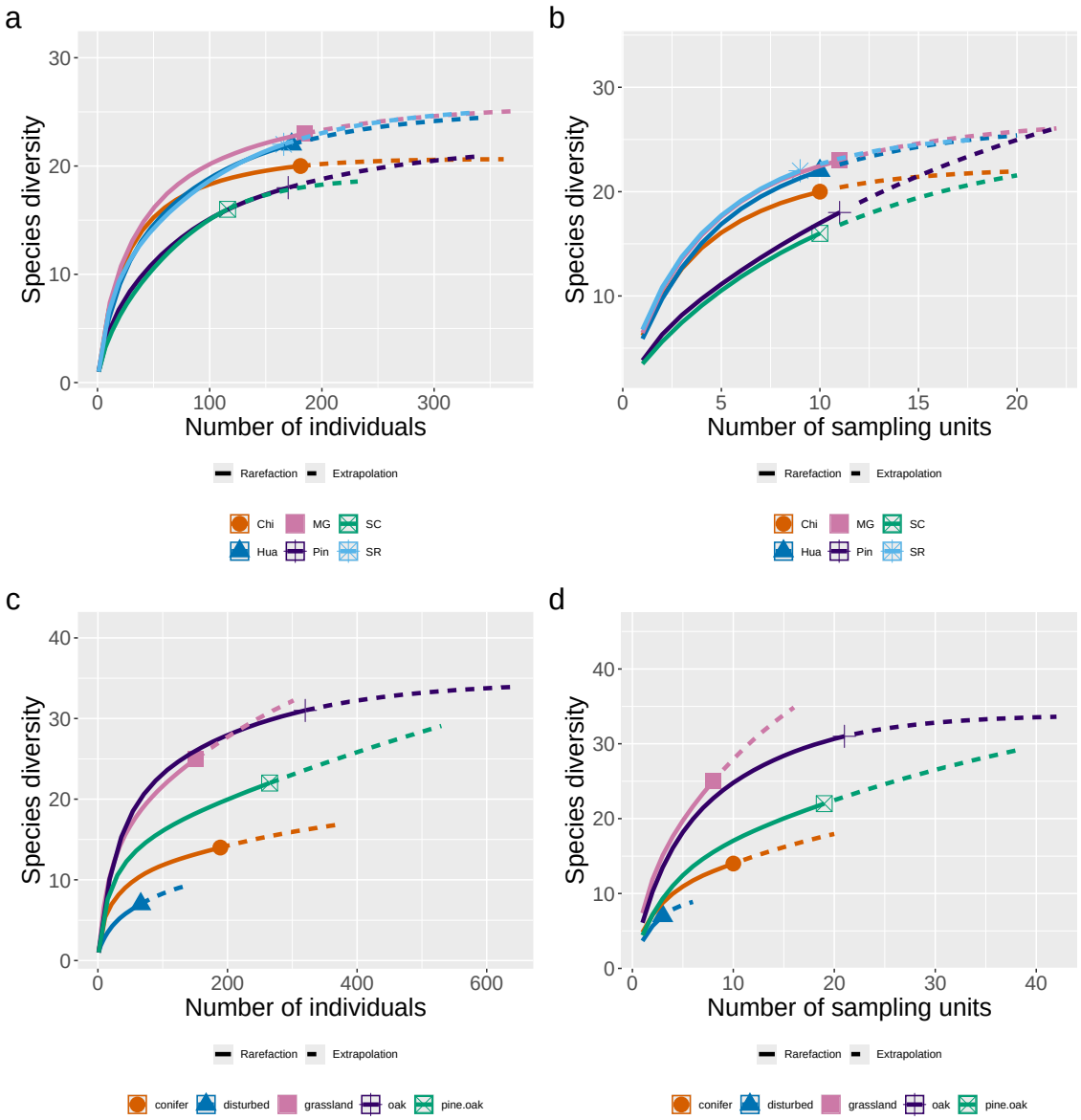


Figure 3.2. Rarefaction curves for grasshopper species richness in individual mountain ranges (a, b) and individual habitats (c, d). Panels a and c show abundance-based curves, while panels b and d show incidence-based curves.

abundance-based and incidence-based rarefaction curves for each mountain range and each habitat in Figure 3.2.

All three estimates of total species richness for the entire region (meaning the six Madrean Sky Islands included in the study but excluding the lower elevation desert habitats that were not sampled) are similar, ranging from 44 to 48, suggesting that the 41 species that were sampled may relatively complete. On the other hand, because the 95% confidence intervals for the two rarefaction-based estimates are quite large, with upper limits of 58 and 65, we cannot be very confident that we haven't missed numerous species. Indeed, we know of six additional grasshopper species that are missing from our focal samples, including two species that were collected opportunistically and four other endemic species that we missed entirely. Combined with the 41 species that we did collect, this brings the grasshopper community to 47 species, which is in line with the estimated species richness.

Turning to the individual sky islands, we see that the three methods give similar estimates of total species diversity for four of the mountain ranges (Table C5). The estimated total species richness is on the order of 25 – 30 species in the Huachuca, Pinaleño and Santa Rita Mountains, but is somewhat lower (21 – 25 species) in the Chiricahua Mountains. Furthermore, these estimates are much smaller than both the observed and the estimated regional species pool, suggesting that numerous grasshopper species present in the region are absent from each individual mountain range. In contrast, the discrepancies between the three estimates are much larger in the case of the Pinal and Santa Catalina Mountains. This may be because the grasshopper assemblages collected on these two mountain ranges were each dominated by one very abundant species, while many other species were collected at only one or two sites on each mountain range. This would explain why the abundance-based rarefaction estimates of total species richness are so much lower than the corresponding incidence-based rarefaction estimates. It may also explain why the incidence-based rarefaction curves for these two mountain ranges eventually cross the rarefaction curves for the other four mountain ranges, despite initially being dominated by these curves when the number of sampling units is small (Figure 3.2 b).

We face similar difficulties when using estimated species richness to compare amongst habitats. On the one hand, the three estimators give similar results for four of the habitats, suggesting that the total species richness decreases from 44-50 in the grasslands to 34-37 in oak-associated habitats, 20-25 in coniferous forests, and 10-11 in disturbed habitats. In particular, the rank order of these four habitats by estimated total species richness is the same irrespective of which estimator is used, and both the abundance-based and incidence-based rarefaction curves for these habitats are largely non-intersecting (Figure 3.2 c,d). Unfortunately, the same is not true for the pine-oak habitat, for which the estimated total species richness varies from 37 to 54 depending on the choice of estimator. It also appears that the rarefaction curves for the pine-oak habitat will eventually cross those obtained for the oak habitat, making it difficult to determine which of these two habitats has greater total grasshopper diversity.

An alternative approach to comparing grasshopper abundance and diversity among mountain ranges or habitats is to focus on the distribution of counts or species per site. This avoids the need to use extrapolation-based estimates, but it also means a shift from considering gamma diversity to alpha diversity. Figure 3.3 shows the distribution of adult abundance, juvenile abundance, observed species richness and effective species richness per site in each mountain range. Visual inspection of this figure suggests that, on average, similar numbers of adult grasshoppers (14 - 22) and similar numbers of juvenile grasshoppers (2 - 4) were collected per site in each mountain range, although adult abundance appears to have been somewhat lower in the Santa Catalina Mountains and somewhat higher in the Santa Rita Mountains. However, a formal non-parametric test for differences in the medians of these distributions across mountain ranges was not significant for either stage (adult abundance: χ_5^2 = 3.616, p = 0.606; juvenile abundance: χ_5^2 = 2.741, p = 0.740). In contrast, both the median number of species and the median effective number of species collected per site appear to be lower in the Pinal and Santa Catalina Mountains than in the other mountain ranges. In both cases, the Kruskal-Wallis test is significant (species richness: χ_5^2 = 11.786, p = 0.038; effective species richness: χ_5^2 = 16.294, p = 0.006), indicating that alpha diversity varies between mountain ranges. A post hoc analysis using Dunn's test with the

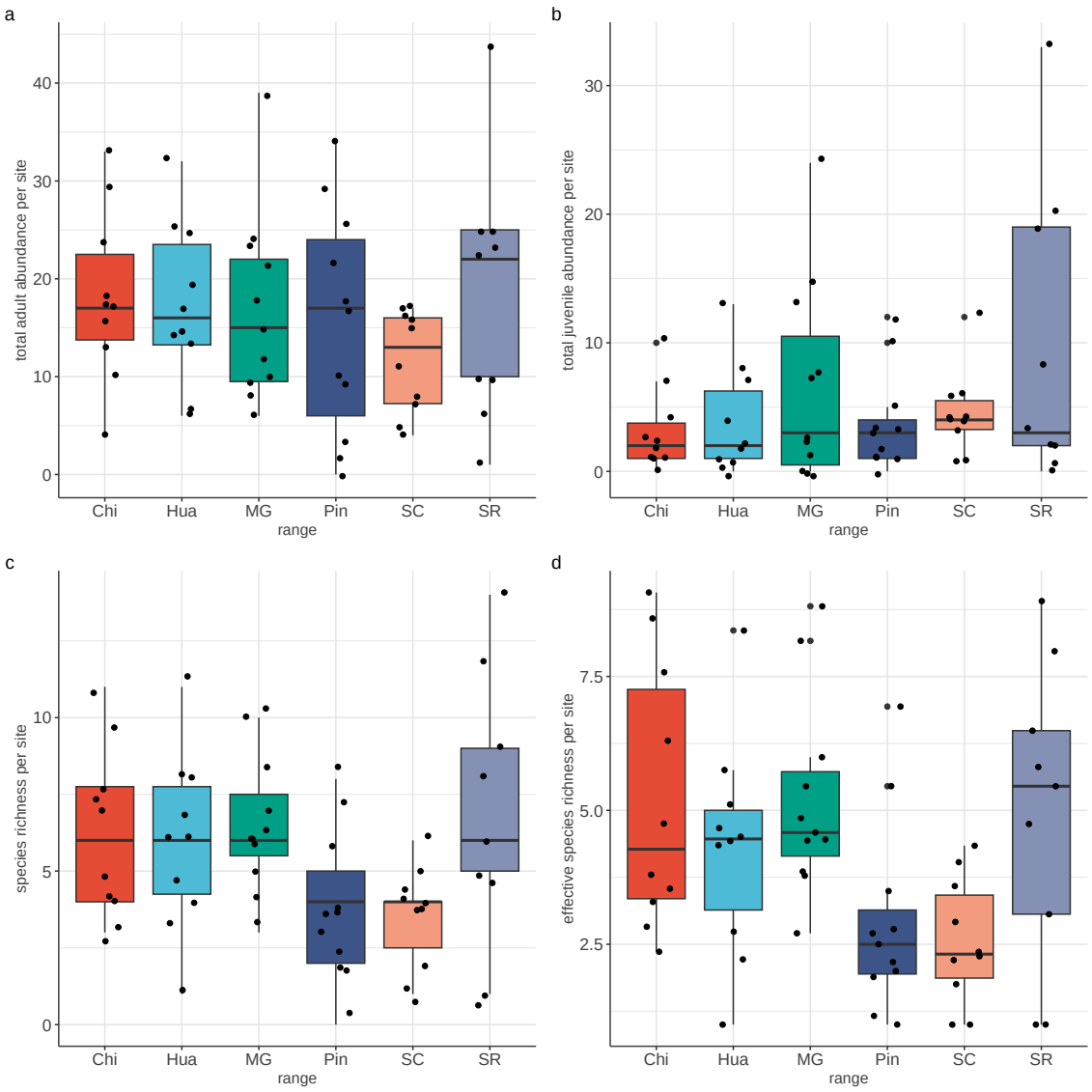


Figure 3.3. Comparison of adult and juvenile abundance (a, b) and actual and effective species richness (c, d) per site across mountain ranges.

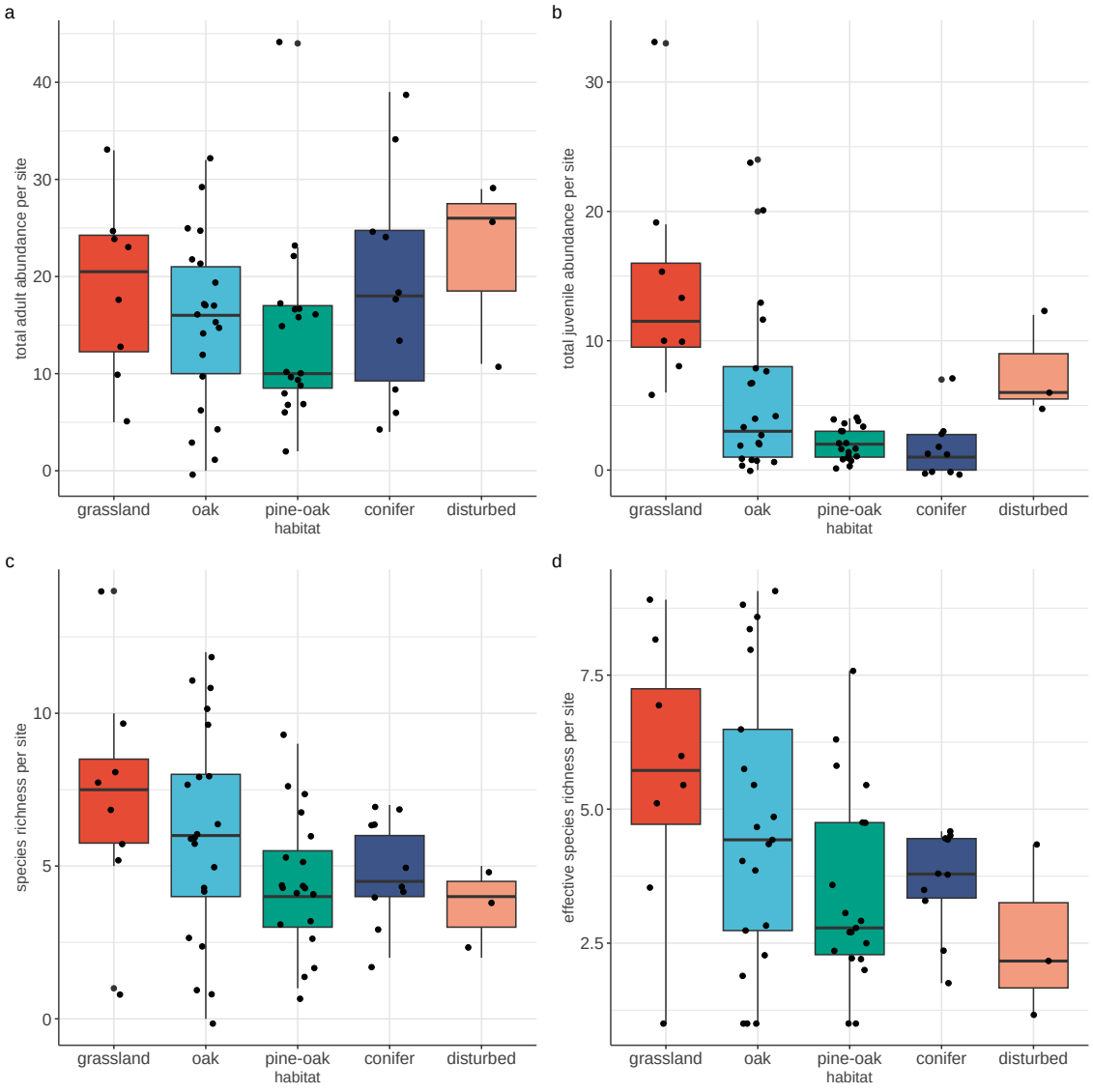


Figure 3.4. Comparison of adult and juvenile abundance (a, b) and actual and effective species richness (c, d) per site across habitats.

Hochberg adjustment for multiple testing did not identify any significant pairwise differences in species richness per site among mountain ranges, but it did indicate that the effective species richness per site was significantly different between the Pinaleño and Santa Catalina Mountains ($Z = 2.994$, $p_{adj} = 0.041$) and marginally non-significantly different both between the Pinaleño and Pinal Mountains ($Z = 2.673$, $p_{adj} = 0.098$) and between the Chiricahua and Santa Catalina Mountains ($Z = 2.697$, $p_{adj} = 0.098$).

We carried out similar comparisons of habitats using the distributions of adult abundance, juvenile abundance, species richness and effective species richness per site, which are illustrated in Figure 3.4. Although visual examination of these plots suggests that adult and juvenile abundance being much higher in grassland and disturbed habitats than in the other three habitats, in this case the Kruskal-Wallis test did not provide evidence for a significant difference in the distribution of adult abundance across habitats ($\chi_4^2 = 4.888$, $p = 0.299$), but did indicate a highly significant difference in the distribution of juvenile abundance ($\chi_4^2 = 24.411$, $p < 10^{-4}$). Furthermore, a post hoc analysis using Dunn's test indicates that juvenile abundance per site was significantly higher in grassland habitat than in either oak habitat ($Z = 2.741$, $p_{adj} = 0.049$), pine-oak habitat ($Z = 4.040$, $p_{adj} = 0.00048$) or coniferous habitat ($Z = 4.214$, $p_{adj} = 0.00025$). Furthermore, although the median species richness and median effective species richness both appear to decrease as we pass from lower elevation to higher elevation habitats (grassland, oak, pine-oak and conifer) and also are smallest in disturbed habitats, the Kruskal-Wallis test was only marginally significant in both cases (species richness: $\chi_4^2 = 7.616$, $p = 0.107$; effective species richness: $\chi_4^2 = 7.907$, $p = 0.095$). In general, these distributions were highly dispersed around their medians, with many sites containing either very few or very many species.

Community Structure: Unconstrained Ordination

Unconstrained ordination can be used to project high-dimensional community data into lower dimensional spaces in ways that may help reveal the biological and environmental processes

shaping community structure. We used non-metric multidimensional scaling (NMDS) to map the adult grasshopper assemblages obtained at the 61 focal sites to a two-dimensional plot such that proximity in the NMDS diagram reflects ecological similarity as quantified by the Bray-Curtis index. Individual species can also be added to the ordination diagram as abundance-weighted averages of the sites in which they occur. The stress of the best fitting NMDS diagram was 0.172, which indicates an adequate correspondence between the rank orders of the NMDS distances and the Bray-Curtis dissimilarities. Because ordination diagrams that show both sites and species tend to be cluttered and difficult to interpret, we have plotted the NMDS diagram four times to emphasize different features of the data. Note, however, that all four plots are based on the same ordination.

Figure 3.5 shows two plots of the NMDS diagram that emphasize the structure of the grasshopper assemblages in relation to the six mountain ranges that were sampled. The upper panel (Figure 3.5a) shows both the sites, which have been enclosed in convex hulls corresponding to each mountain range, as well as the species, which are labeled and represented by inverted red triangles. We see that there is extensive overlap between these hulls, indicating that similar grasshopper assemblages can be found throughout the region. In fact, there is a non-empty intersection between all six hulls centered around the origin (0,0) of this plot. Although most species fall within regions of overlap between two or more of the hulls, the 11 species that were sampled in just one mountain range lie near the periphery of the plot. The species are omitted from the lower panel (Figure 3.5), which instead shows the labeled sites as well as the centroid of each cluster of sites belonging to the same mountain range. In the lower panel (Figure 3.5), we have plotted only the sites, which are now labeled, as well as the centroid of each cluster of sites belonging to the same mountain range. This plot suggests that despite the extensive overlap between the grasshopper assemblages found on different mountain ranges, there is some geographical structure as well. In particular, we note that the second axis (NMDS2) tends to separate the more northern mountain ranges (the Pinal and Pinaleño Mountains) from the more southern ranges. Interestingly, the second axis also seems to separate sites according to elevation, at least within mountain ranges, with higher elevation sites tending to be positioned higher up along this axis. This

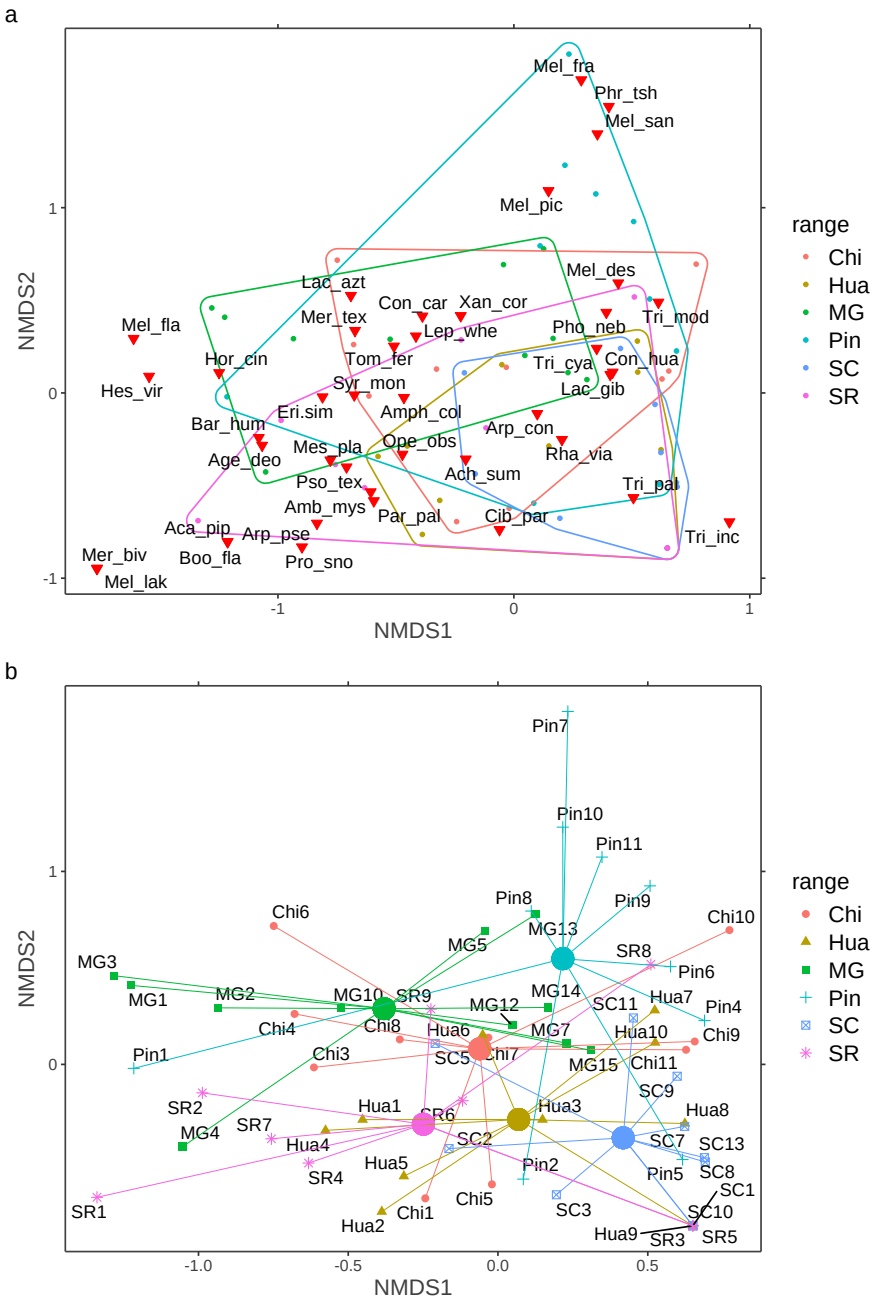


Figure 3.5. Non-metric multidimensional scaling diagram of the grasshopper assemblage data collected from each focal site. (a) Sites belonging to the same mountain range are enclosed in convex hulls, while species are labeled and marked by inverted red triangles. (b) Spider plot showing the centroid of each cluster of sites from the same mountain range.

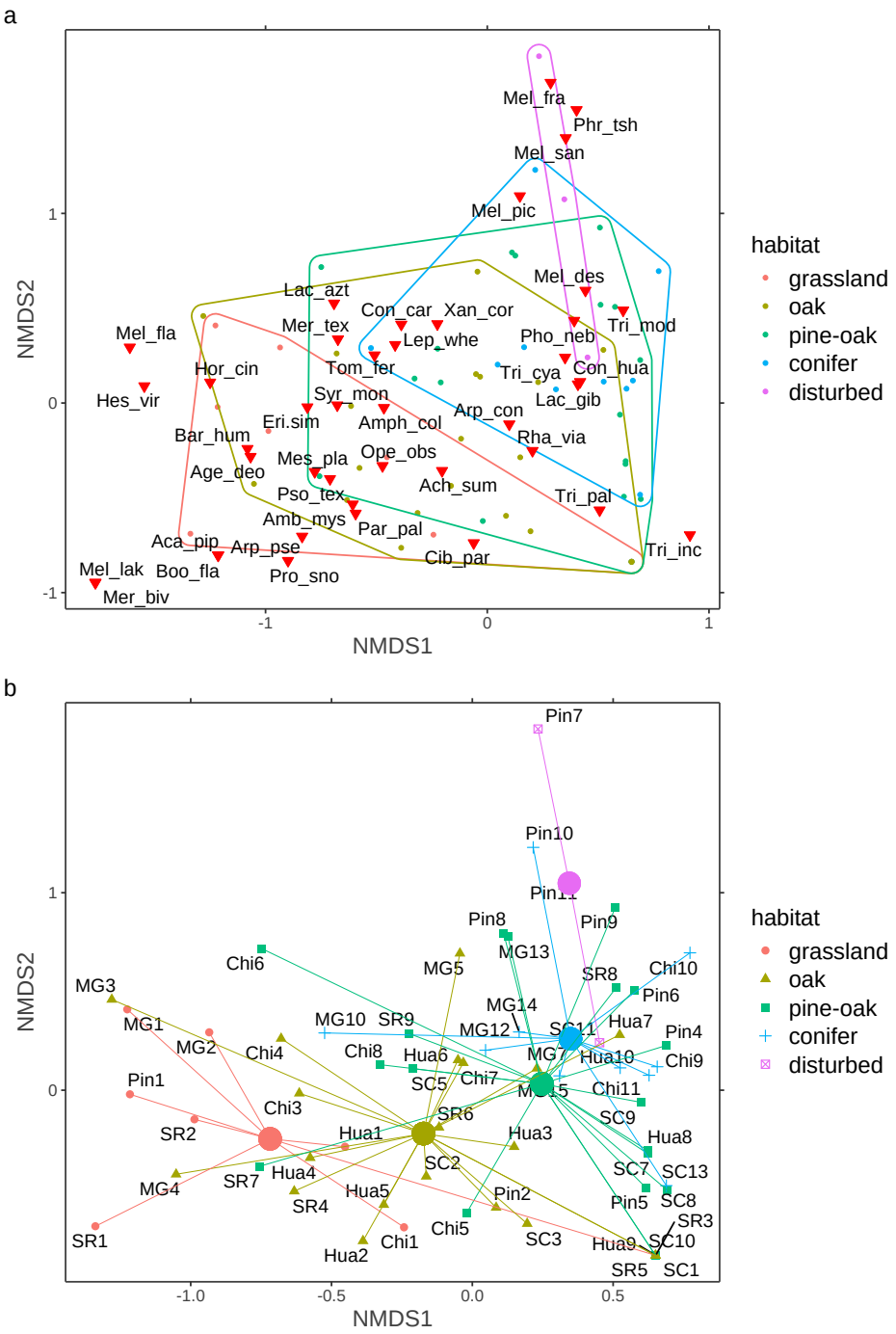


Figure 3.6. Non-metric multidimensional scaling diagram of the grasshopper assemblage data collected from each focal site. (a) Sites belonging to the same habitat are enclosed in convex hulls, while species are labeled and marked by inverted red triangles. (b) Spider plot showing the centroid of each cluster of sites from the same habitat.

is reminiscent of the observation that plant communities at higher elevations within the Madrean Sky Islands tend to be more similar to plant communities found at higher latitudes.

The same NMDS diagram is shown in Figure 3.6, but now we emphasize the structure of the grasshopper assemblages in relation to the five habitat classes. We again plot both sites and species in the upper panel (Figure 3.6a), with sites belonging to the same habitat class now enclosed in convex hulls. Although each habitat-specific hull overlaps several others, there is much less overlap than in Figure 3.5a and there is no overlap between the hulls corresponding to the grassland and coniferous habitats. Furthermore, the hulls corresponding to the undisturbed habitats are sequentially arranged in such a way that we progress from lower to higher elevation habitats as we pass from the lower left portion of the NMDS diagram to the upper right. This observation suggests that the grasshopper assemblages are at least positively associated with the plant assemblages that we used to assign sites to habitat classes, although the correspondence is only partial since the grasshopper data does not lead to a perfect partitioning of these sites according to habitat in the same way that the tree cover data does in Figure 3.1. We also observe that the grasshopper assemblages at the three sites that were classified as disturbed lie in the upper right-hand corner of the ordination diagram, either within or near to the convex hulls corresponding to the pine-oak and coniferous communities. Since all three of these sites are located at elevations at which we would expect them to be covered by pine-oak or coniferous forest, this observation suggests that the grasshopper assemblages at these sites remain similar to those that may have existed prior to the disturbance. At the same time, the peripheral location of the point corresponding to site Pin 7 indicates that the grasshopper assemblage at this site has likely been affected by the disturbance. Lastly, we note that the lower left-hand corner of the NMDS diagram (Figure 3.5b, 3.6b) contains a point that corresponds to five different sites (Hua9, SC1, SC10, SR3 and SR5) and three different habitats (grassland, oak and pine-oak). Examination of the raw community data reveals that the grasshopper assemblages that were collected at these five sites contained only the common species *T. pallidipennis*, which therefore accounts for some of the overlap between the convex hulls corresponding to different mountain ranges and different habitats.

We further explored the geographical structure of the Madrean grasshopper communities by aggregating the grasshopper abundance data collected at different sites within the same mountain range. This produced a community matrix with six sampling units corresponding to each of the mountain ranges surveyed in this study. We reasoned that the aggregated data should better reflect geographical structure both because it averages out the habitat-based structure seen in local assemblages and because it should also reduce the impact of sampling variance. We analyzed this data in three ways. First, we used Ward's method to infer a dendrogram for the aggregated grasshopper assemblages found in the six mountain ranges, using the square root of Bray-Curtis dissimilarity as a metric. This is shown in Figure C1 (Appendix C), which reveals that the two northern-most assemblages found in the Pinal and Pinaleño Mountains form one cluster, while the remaining four southern assemblages form a second cluster. However, while there is additional structure within this second cluster, it does not appear to reflect the geographical proximity of the four southern mountain ranges. For example, the Huachuca Mountain assemblage clusters with the Chiricahuas despite the former mountain range being much closer to the Santa Rita Mountains. We then conducted a Mantel test to formally test whether the ecological distances between the aggregated grasshopper assemblages are positively correlated with the geographical distances between the corresponding mountain ranges. For the latter, we used the geodesic distances between the highest elevation sites that were sampled in each pair of mountain ranges; we note that these sites tend to be approximately centrally located within each mountain range and serve as good proxies for the mountain ranges themselves. The Mantel test was only marginally significant ($r = 0.4$, $p = 0.072$), which is suggestive of a weak relationship between geographical and ecological distances, although we note that even a relatively small number of discrepancies in the rank order of the two metrics will lead to loss of significance due to the small number of mountain ranges being tested. Lastly, we conducted a principal coordinates analysis on the dissimilarity matrix obtained by calculating the square root of the Bray-Curtis dissimilarity between each pair of aggregated grasshopper assemblages. Figure C2 shows the resulting ordination diagram using the first two coordinates, which together accounted for approximately 78% of the variation in the data.

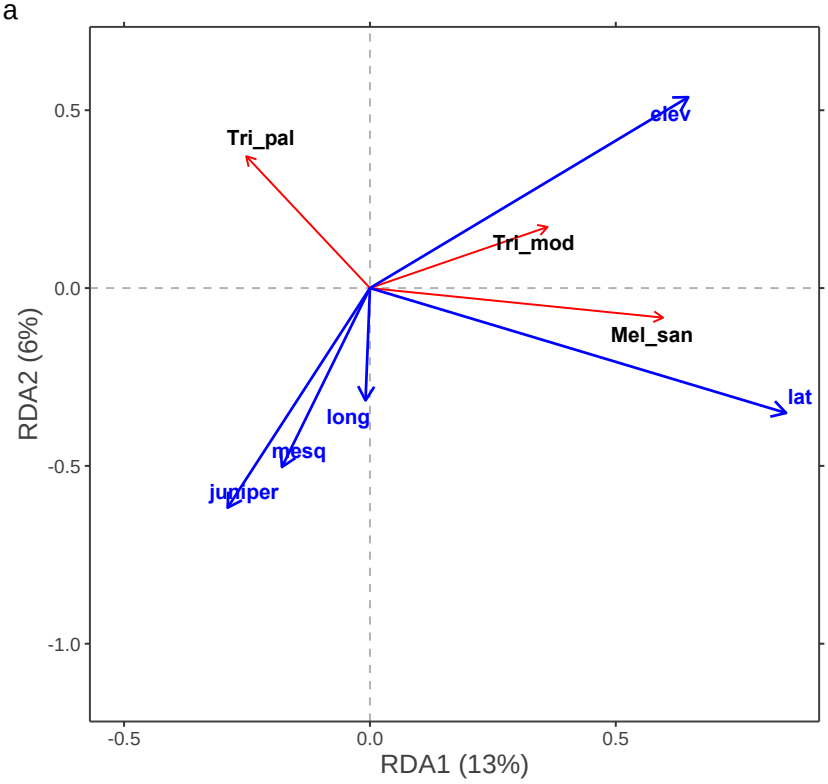
We see that the first coordinate (which is plotted along the y-axis in the ordination diagram) accurately ordinates the assemblages according to their relative latitudinal positions. However, the second coordinate only poorly matches the longitudinal positions of the corresponding mountain ranges. Indeed, while four of the mountain ranges are positioned close to the origin of axis 2, the assemblages corresponding to the Santa Rita and Santa Catalina Mountains are positioned on opposite sides of the origin even though both mountain ranges are located to the west of the other four ranges.

Community Structure: Constrained Ordination

While non-metric multidimensional scaling is a useful tool for visualizing the structure of complex data sets, it does not allow us to either formally test if community structure depends on environmental or geographical variables or quantify these relationships if they do exist. For this reason, we used transformation- based redundancy analysis (tb-RDA) to examine how the grasshopper assemblages at the focal sites depended on vegetative cover, elevation, and latitude and longitude. After applying the Hellinger transformation to the grasshopper assemblage data, we used forward variable selection to identify those variables that explained a significant fraction of the variation in the transformed data. This procedure selected just five variables, including latitude, longitude, elevation, the proportion of coverage by juniper trees, and the proportion of coverage by mesquite trees, which collectively accounted for approximately 21% of the variation in the grasshopper assemblages (R^2 = 0.274, R^2_{adj} = 0.207). Latitude and elevation each accounted for approximately 8.2% and 5.6% of the variation (adjusted R^2) respectively, while the remaining variables each accounted for less than 3% of the variation (Table C6). Of the five RDA axes that were formed from linear combinations of the explanatory variables, four were found to explain statistically significant fractions of the variation in the grasshopper assemblages (Table C7).

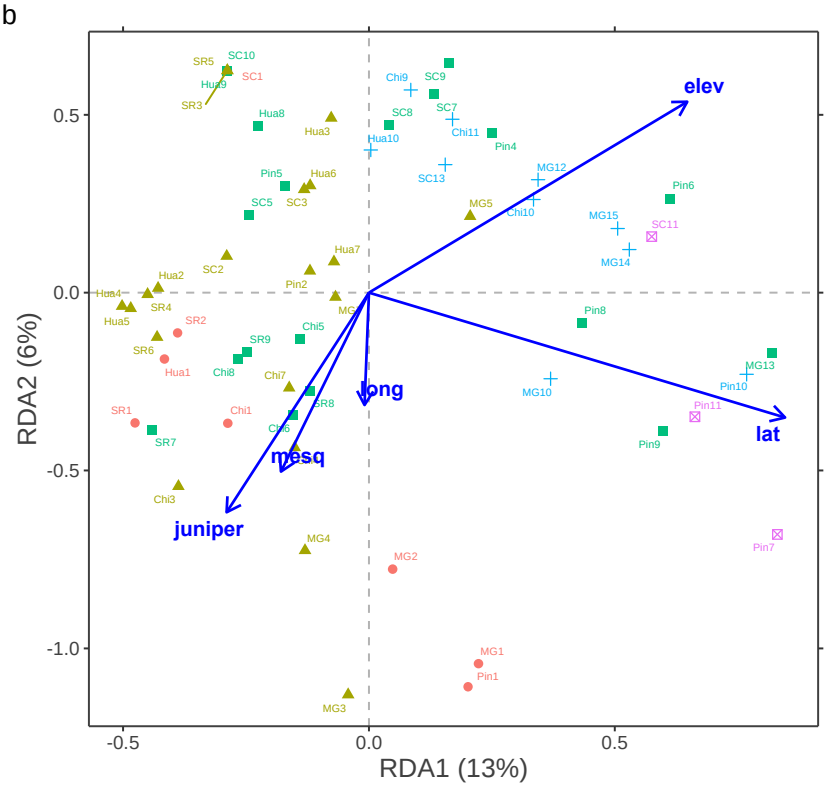
Figure 3.7 shows two RDA triplots corresponding to the model identified by the forward selection procedure, both with the type 2 scaling in which the angle formed between the vectors corresponding to any two variables is proportional to the statistical correlation between those

a



range
Chi
Hua
MG
Pin
SC
SR

b



habitat
grassland
oak
pine-oak
conifer
disturbed

Figure 3.7. tb-RDA triplots of the grasshopper community data. Both plots use the type 2 scaling, with sites represented by colored symbols, species represented by red inverted triangles, and explanatory variables represented by blue arrows. Sites are colored either according to mountain range (a) or habitat (b). We also include red arrows in (a) indicating the three species with the strongest correlations with the environmental variables.

variables. In the upper panel (Figure 3.7a), we have colored the sites according to mountain range to highlight the geographical structure identified by the RDA, which has a latitudinal component, as previously recognized, and a weaker, but significant longitudinal component. Most species (shown as inverted red triangles) have weak and statistically insignificant correlations with the RDA axes (Table C8), but the three species that were most strongly correlated with the explanatory variables are designated by red vectors in the upper panel. Comparing the directions of the red vectors with those of the blue vectors, we see that the distributions of these three species depend on elevation and geography in different ways. On the one hand, while the distribution of *T. pallidipennis* is nearly uncorrelated with elevation, it has a moderately strong negative correlation with both latitude and longitude, indicating that the density of this species tends to increase towards the southwest, at least within our study area. In contrast, both *T. modesta* and *M. sanguinipes* have moderately strong positive correlations with elevation and latitude, with the former species being more strongly correlated with elevation and the latter more strongly correlated with latitude. It is perhaps unsurprising that these three species were also the most abundant in our samples since the power to detect correlations between density and environmental factors will generally increase with sample size. In fact, most of the species with statistically significant environmental correlations in Table B4 are those with sample sizes exceeding 20 individuals. However, the converse does not hold. For example, it is notable that the fourth most abundant species, *M. desultorius/aridus*, shows no correlation with the selected explanatory variables (Table C8: $r = 0.017$; $p = 0.610$), as is also the case with two other relatively common species, *C. huachucana* and *A. conspersa*.

The same RDA triplot is shown in the lower panel (Figure 3.7b), but here the sites have been labeled and colored to highlight their habitat associations. We can see that there is some segregation of grasshopper assemblages sampled in different habitats along the RDA axes. For example, those assemblages that were sampled in coniferous habitats are largely concentrated in the upper right-hand corner, whereas those that were sampled in grassland habitats tend to be concentrated in the lower left-hand corner. However, as was the case in the NMDS plot shown in Figure 3.6a, we see extensive overlap between assemblages that were sampled in habitats that tend to merge along elevational gradients, e.g., between grasshopper assemblages in oak and pine-oak habitats. It is also notable that the percent coverage by the tree taxa that characterize these higher elevation habitats, namely oak, pine and conifers, were not included in the best-fitting model identified by forward variable selection. Mesquite trees generally were restricted to lower elevation sites that were classified as grassland and indeed the grasshopper assemblages that were sampled in grassland habitats are mostly concentrated in the direction of the blue arrow corresponding to percent coverage by mesquite trees. However, it is surprising that neither percent coverage by grasses nor percent coverage by forbs were included in the best-fitting model shown here.

Although the five explanatory variables identified by redundancy analysis of the grasshopper abundance data are statistically significant, the amount of variation in grasshopper assemblages explained by these variables, both individually and collectively, is low. For this reason, we repeated this analysis using two modified data sets constructed by omitting species that were either very abundant or very rare in our samples. For example, since we lack sufficient information to identify environmental variables that are correlated with the density of species that were only sampled in one site, we might expect the inclusion of these species in the community data to reduce the amount of variance explained by the best fitting model. To test this hypothesis, we repeated the redundancy analysis using a community data set from which we had excluded each of the eight grasshopper species that had been collected at only one site. Forward variable selection using the restricted data set retained the same five explanatory variables that were identified in the original

analysis using the full data set. However, the adjusted R^2 for the best-fitting model only increased from 0.207 to 0.210, with similarly minor changes in the percentage of variance explained by the individual variables. Alternatively, since the most abundant species in the grasshopper community greatly outnumber the other species, we might expect redundancy analysis of the full data set to mainly identify environmental variables that are correlated with these most abundant species. This could explain, for example, why we might fail to recover percent coverage by grass or forbs as important explanatory variables of community structure even if these variables are significantly associated with many of the species in the community. To test this second hypothesis, we again repeated the redundancy analysis, but now using a community data set from which we had excluded the two most abundant species, *T. pallidipennis* and *M. sanguinipes*. In this case, forward variable selection did retain a different set of explanatory variables in the best fitting model, including elevation, percent coverage by grass, percent coverage by conifers, and percent coverage by junipers. However, the adjusted R^2 for the best-fitting model decreased from 0.207 to 0.151, and the percent coverage by grass explained less than 3% of the variation in the structure of the reduced community. In other words, simplifying the data by removing the most abundant species did not lead to a tighter correlation between the environmental variables and grasshopper community structure.

There are several possible explanations for the fact that the best fitting RDA model explains so little of the variation in grasshopper community structure, none of which are mutually exclusive. Because our sample sizes are so low, we expect the grasshopper abundance data to be noisy, possibly obscuring any real associations between community structure and environmental and geographical covariates. Alternatively, these relationships can be obscured by biological processes such as demographic stochasticity and ecological drift, by interspecific competition or facilitation, and by dispersal limitation, either in the present or the past. Lastly, the model itself used in the redundancy analysis may be inadequate, either because we have failed to measure relevant environmental variables or because the relationships between grasshopper community structure and the measured variables are non-linear and therefore not captured by redundancy analysis,

which assumes linear relationships between the dependent and independent variables. Although we have not tried to formally discriminate between these different possibilities, which would require much more sophisticated analytical techniques, we did attempt to informally assess the degree to which the residual variation in grasshopper community structure left over after the best-fitting RDA model has been applied is structured. If random sampling alone is responsible for the low percentage of variation explained by the best-fitting RDA model, then we would expect the residual variation to be uncorrelated amongst species. However, this does not appear to be the case, as can be seen in Figure C3, which shows a residual correlation plot for the 41 grasshopper species that were collected in the focal sites. Indeed, there are many species pairs for which the residuals are either very strongly positively correlated (shown in blue), indicating that they occur together more frequently than expected by chance, even after environmental and geographical affects are accounted for by the best-fitting RDA model, or strongly negatively correlated (shown in red), indicating that they occur together much less frequently than expected by chance even after these other effects have been accounted for. Unfortunately, it is unclear how to assess the significance of these residual correlations without constructing a much more complicated model. Furthermore, even if the larger correlations are significant, this alone does not allow us to deduce which processes are responsible for generating these correlations.

Community Structure: Subadults and Subfamilies

Our inability to identify many of the subadult grasshoppers to species prevented us from including information on nymph abundance in the preceding analyses of community structure. However, since we were able to identify both nymphs and adults to subfamily, we repeated the redundancy analysis and forward variable selection procedure using the counts of grasshopper adults and nymphs in each subfamily in each focal site. The number of nymphs in each subfamily was determined by summing the numbers of nymphs identified to each species in that subfamily and then adding to that tally the number of nymphs that were identified to that subfamily despite not being identified to species. We excluded two subfamilies from this analysis due to their rarity in

our samples: Cyrtacanthacridinae, which was represented by a single subadult individual, and Romaleinae, which was represented by two adults. Thus, this analysis is based on the counts of adults and nymphs in the remaining three Acridid subfamilies: Gomphocerinae, Melanoplinae and Oedipodinae.

Figure 3.8 shows the triplot obtained from redundancy analysis of the subfamily data using the explanatory variables retained after forward variable selection. This procedure selected three of the five variables that were identified in the analysis of the adult grasshopper data, including elevation, latitude, and the proportion of coverage by juniper trees, which collectively accounted for approximately 28% of the variation in the subfamily data (R^2 = 0.320, R^2_{adj} = 0.284). Elevation accounted for approximately 19.8% of the variation (adjusted R^2), while elevation and % juniper coverage each accounted for 5.9% and 2.5% of the variation, respectively (Table C9). Of the three RDA axes that were formed from linear combinations of the explanatory variables, two were found to explain statistically significant fractions of the variation in the subfamily data (Table C10).

The triplot shown in Figure 3.8 as well as the RDA axis loadings listed in Table C11 reveal that the three Acridid subfamilies depend on the ordination variables in distinct ways. The adult and subadult Gomphocerinae had very similar distributions, both being negatively correlated with elevation and, to a lesser extent, with latitude. Adult and subadult Oedipodinae also shared somewhat similar distributions, both being positively correlated with elevation, but while adult abundance was also negatively correlated with latitude and generally strongly associated with the explanatory variables (r = 0.906), subadult abundance was only weakly associated with these variables (r = 0.142), likely due to the small number of Oedipodine nymphs collected overall (23 nymphs vs. 448 adults). Lastly, the vectors corresponding to adult and subadult Melanoplinae are nearly orthogonal to one another in the ordination space, indicating that these have very different relationships with the explanatory variables. While adult Melanoplines were positively associated with latitude and, to a lesser extent, with elevation, Melanopline nymphs were negatively associated with elevation and nearly uncorrelated with latitude. Given that we collected moderately large numbers of both adults and nymphs in this subfamily, it seems unlikely that the observed difference

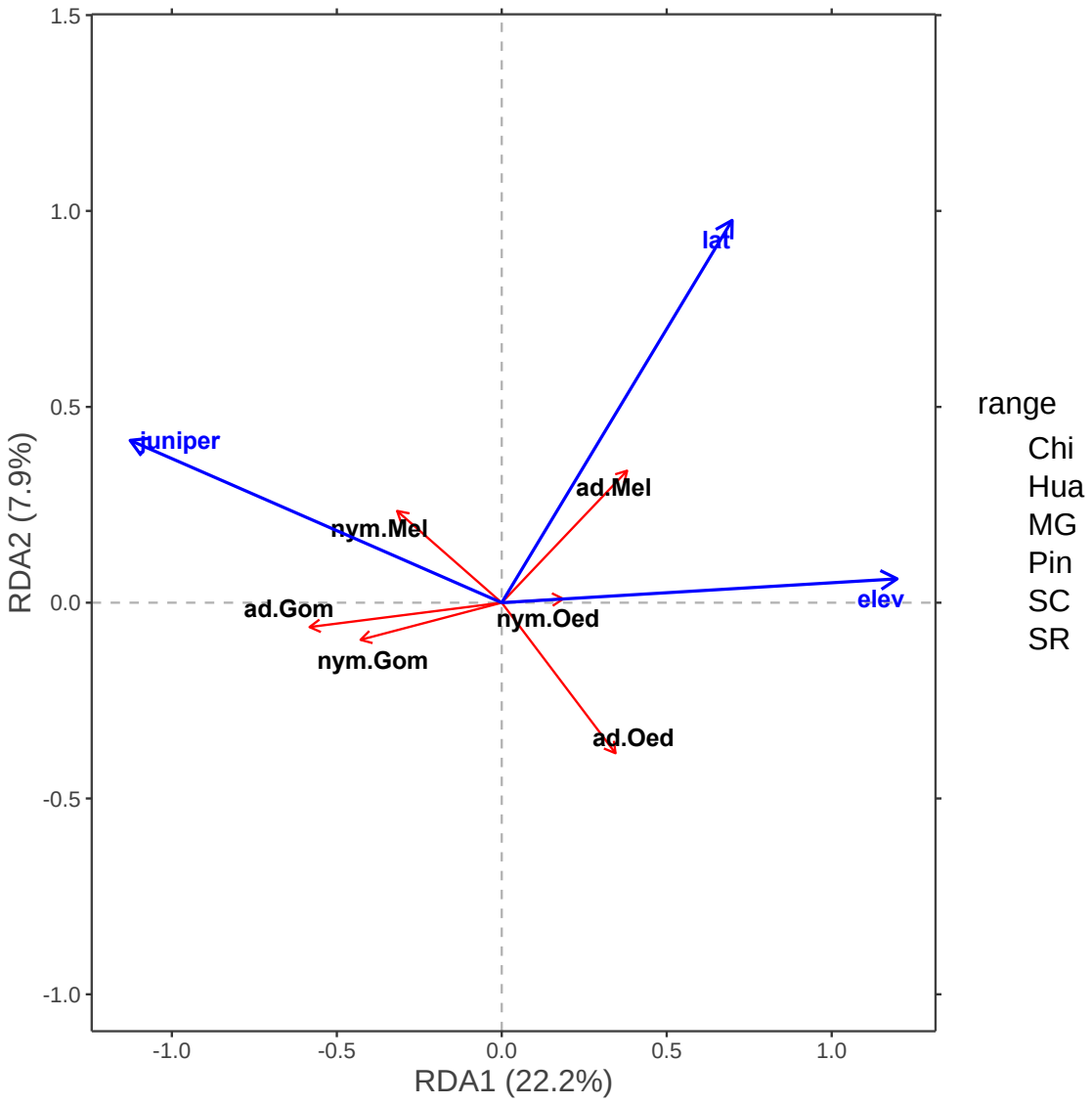


Figure 3.8. tb-RDA triplot of the adult and subadult counts within subfamilies. The triplot is shown with the type 2 scaling, with sites represented by colored symbols, taxa represented by red arrows, and explanatory variables represented by blue arrows.

is spurious. However, it should be emphasized that since the RDA explanatory variables together account for less than 30% of the variance in the subfamily data, the overall association between adult and subadult abundance may be much stronger than is apparent in the RDA diagram. To assess whether this is the case, we applied Kendall's rank correlation test to each of the subfamilies as well as to the overall numbers of nymphs and adult (Table 3.3). In each case, we found that the numbers of nymphs and numbers of adults were positively and at least marginally significantly correlated, although in general the correlation was weak except within the Gomphocerinae.

The triplot shown in Figure 3.8 as well as the RDA axis loadings listed in Table C11 reveal that the three Acridid subfamilies depend on the ordination variables in distinct ways. The adult and subadult Gomphocerinae had very similar distributions, both being negatively correlated with elevation and, to a lesser extent, with latitude. Adult and subadult Oedipodinae also shared somewhat similar distributions, both being positively correlated with elevation, but while adult abundance was also negatively correlated with latitude and generally strongly associated with the explanatory variables ($r = 0.906$), subadult abundance was only weakly associated with these variables ($r = 0.142$), likely due to the small number of Oedipodine nymphs collected overall (23 nymphs vs. 448 adults). Lastly, the vectors corresponding to adult and subadult Melanoplinae are nearly orthogonal to one another in the ordination space, indicating that these have very different relationships with the explanatory variables. While adult Melanoplines were positively associated with latitude and, to a lesser extent, with elevation, Melanopline nymphs were negatively associated with elevation and nearly uncorrelated with latitude. Given that we collected moderately large numbers of both adults and nymphs in this subfamily, it seems unlikely that the observed difference is spurious. However, it should be emphasized that since the RDA explanatory variables together account for less than 30% of the variance in the subfamily data, the overall association between adult and subadult abundance may be much stronger than is apparent in the RDA diagram. To assess whether this is the case, we applied Kendall's rank correlation test to each of the subfamilies as well as to the overall numbers of nymphs and adult (Table 3.3). In each case, we found that the

numbers of nymphs and numbers of adults were positively and at least marginally significantly correlated, although in general the correlation was weak except within the Gomphocerinae.

taxon	τ	p-value
Acrididae	0.189	0.042
Gomphocerinae	0.603	9.1×10^{-9}
Melanoplinae	0.215	0.028
Oedipodinae	0.208	0.049

Table 3.3. Correlation of adult and juvenile abundances using Kendall's rank correlation test.

Sex Ratios

Because the sex of adult grasshoppers can be reliably determined from the presence or absence of an ovipositor, we were able to investigate whether our samples contained an excess of either adult male or adult female grasshoppers. Such an excess, if present, could be due either to an actual skew in the adult sex ratio or to sex-biased capture probabilities. For example, male grasshoppers are typically smaller than females and have proportionately longer wings, making them stronger fliers that may be less likely to be captured by sweep netting.

Table C12 shows the observed proportion θ_{fem} of adult female grasshoppers for each species collected in the focal sites, the 95% confidence interval for the actual proportion θ of females, and the p-value obtained via a two-sided binomial test of the null hypothesis that $\theta = 0.5$. The null hypothesis was rejected in two cases: both *P. pallida* and *T. modesta* had male-biased sex ratios. In two other species, *P. texana* and *M. sanguinipes*, the proportion of females was marginally significantly different ($p < 0.05$) from 0.5, and we note that the first species exhibited a female-biased sex ratio. However, having conducted 41 independent tests, we would expect two tests on average to be marginally significant at this level, which suggests that both of these results are spurious. In fact, after applying Bonferroni's correction for multiple tests, we are led to conclude that none of the species had an observed sex ratio that was significantly different from parity.

At the same time, since the power to detect deviations from the null hypothesis is strongly dependent on sample size and since we collected small numbers of most species, it is also possible

that several species had skewed adult sex ratios that we failed to detect. We investigated this possibility in two ways. First, we applied the binomial test to the total number of adult females and adult males collected in the focal sites. Although we collected fewer females than males (472 vs. 519), the observed proportion of females (θ_{fem} = 0.48) was not significantly different from 0.5 (p = 0.14), suggesting that males were only slightly more prevalent in our samples than would be expected by chance if males and females were present in equal frequencies and equally likely to be captured. We also used the binomial test to assess whether the number of species in which fewer females were collected than males was significantly different than the number that would be expected under the null hypothesis. Of the 41 species collected at the focal sites, five species had equal numbers of males and females, 19 species had an excess of females, and 17 species had an excess of males. Excluding the five ties, the probability that 19 or more species have an excess of the same sex is p = 0.87 under a two-sided binomial test, which does not allow us to reject the null hypothesis. Thus, apart from a few species, our data does not support the existence of a significant skew in the sex ratio of the captured grasshoppers.

Adventitious Samples

A female *Insara apache* (Rehn, 1907) was collected at Mount Graham during the June 30 night sample, which may represent the northernmost range limit of this poorly known species that has only one other record from the Pinaleño Mountains, and has also been documented in the Huachuca, Santa Rita, and Rincon Mountains. During the same night sample, an unidentified male specimen of the also poorly known genus *Arethaea* Stål, 1876; in addition to a female *Schistocerca shoshone* (Thomas, 1873) were collected as well. During all night samples in the Pinaleño, Chiricahua, and Huachuca Mountains, many unidentified individuals of the genera *Gryllus* Linnaeus, 1758 and *Ceuthophilus* Scudder, 1862 were also collected. A single *Trimerotropis modesta* was collected in desert grassland at the base of the Chiricahua Mountains during the October 7 night sample, which is an unusually low elevation for the species. Although normally found in high-elevation coniferous forest, *T. modesta* is a flying species that may be capable of

dispersing between different Sky Islands. While birding on Proctor Road at the base of the Santa Rita Mountains on July 15, a male *Tomonotus mexicanus* Saussure, 1861 was spotted and collected along with a female *Psoloessa texana* Scudder, 1875 and a female *Amphitornus coloradus* (Thomas, 1873). *T. mexicanus* is rare in the US, and only known to occur north of Mexico from a small number of records in the Baboquivari, Rincon, Santa Rita, and Huachuca Mountains.

Insects from several other orders related to Orthoptera that were collected adventitiously during the July 1 night sample on Mt. Graham include an unidentified male cockroach of the genus *Arenivaga* Rehn, 1903 and an unidentified male mantis of the genus *Litaneutria* Saussure, 1892. Other mantises were also collected during day samples, which included unidentified males and females of the genus *Yersiniops* Hebard, 1931 in the Chiricahua Mountains on August 6. a male *Stagmomantis gracilipes* at Mt. Lemmon on May 20, and a female *S. gracilipes* at Mt. Graham on July 1.

CHAPTER 4

MORPHOLOGICAL VARIATION

Intraspecific Morphological Variation

Table D1 (Appendix D) shows the mean and the standard deviation of the twelve morphological characters that were measured on the adult grasshoppers captured in this study. We report separate statistics for males and females due to the pronounced sexual size dimorphism exhibited by many Orthoptera. In general, adult females were longer than adult males, and the ratio of the mean body length of males to the mean body length of females in our samples varied from 0.51 for *Xanthippus corallipes* (albeit based on a single male) to 0.96 for *Melanoplus sanguinipes*, with a mean ratio of 0.74 across all species for which data was available.

Apart from sex, intraspecific variation in adult morphology may be influenced by environmental conditions, phenology, and population membership. To gain insight into the determinants of intraspecific variation in length, we conducted multiple linear regressions of body length against elevation, sampling date, and mountain range (treated as a categorical factor) for those species in which at least 10 individuals of each sex had been measured. (We excluded species with smaller sample sizes because these generally had been collected in relatively few samples, limiting the amount of variation in the explanatory variables.) The results of these analyses are summarized in Table 4.1, which suggests that the relationship between body length and the explanatory variables is generally weak and idiosyncratic. Indeed, only four of the regressions are statistically significant ($p < 0.01$), although there are two additional cases in which one of the explanatory variables is significantly associated with body length even though the regression itself is only marginally significant ($p < 0.05$).

The best supported relationships were found in the two *Trimerotropis* species. In *T. pallidipennis*, body length was negatively associated with collection date in both males and females, such that individuals collected later in the season were on average approximately 3 mm shorter for every additional 100 days. In contrast, in *T. modesta*, body length was negatively correlated with

elevation, with males being 2 mm shorter and females 2.5 mm shorter for every 1000 m gain in elevation. However, males in this latter species also exhibited significant geographical variation, being approximately 2 mm longer on average in the Pinaleño Mountains than in the other ranges. In contrast, female body length in *T. modesta* did not differ significantly between mountain ranges. Notably, body length did not vary significantly with elevation in *T. pallidipennis*, despite its near ubiquity in our samples at all elevations, which may be a consequence of the species' high dispersal capacity.

In two other species, the relationship between length and the explanatory variables was significant in only one of the two sexes. Adult male *M. sanguinipes* were on average 3.7 mm shorter in the Santa Catalina Mountains than in the other ranges, while adult female *H. viridis* that were collected later in the year were shorter on average than those collected on an earlier date. Unfortunately, given the small sample sizes available (especially in *H. viridis*), it is difficult to assess whether these sex-dependent differences are genuine or spurious. It is noteworthy that the only species in which the relationship between body length and the explanatory variable was both statistically significant and fully concordant between the two sexes was also the most abundant in our samples. Likewise, in both species in which we found evidence of geographical variation in body length in one sex but not the other, it is the sex with the larger sample size that appears to differ between mountain ranges.

We also carried out principal components analyses of the log-transformed morphological data to identify a small number of linear combinations of traits that capture much of the measured morphological variation in each species, including features that are related to shape. Scree plots indicate that the first three principal components explain at least 84% of the variance in the morphological data in all species except *M. sanguinipes*, in which only 70.1% is explained (Table D2). As expected, the first component (PC 1) accounted for a majority of the morphological variance, although the actual percentage explained ranged from a low of 53.6% in *M. sanguinipes* had the same loading on this component (as would be expected if every trait had the same scaling relationship with size), then since the components are normalized, the loadings would all be equal

Species	sex	n	elev (km)	date (days)	mountain range					adj. R^2	p
					Hua	Pin	MG	SC	SR		
A. coloradus	f	16	0.137	0.008	2.63	1.31	1.35		1.76	0.12	0.336
	m	19	-0.447	0.014	1.35	-1.92	1.76		2.25	0.22	0.174
P. texana	f	30	0.483	0.051	0.92	0.24	-0.43	0.30	0.51	0.13	0.186
	m	14	-0.115	-0.006		0.72	1.09	0.34	1.45	0.04	0.450
S. montezuma	f	11	7.930	-0.017	0.19	-0.82	-0.70		0.04	0.19	0.391
	m	19	2.424	-0.016	0.59		3.05	1.66	1.46	0.14	0.261
C. huachucana	f	22	-0.782	-0.012	0.19	0.87	0.07	0.39	-0.38	-0.41	0.995
	m	16	-1.223	-0.023	0.99	-2.62			-0.21	-0.16	0.706
H. viridis	f	13	-4.165	**-0.124**		-1.17				0.56	0.014
	m	11	1.064	0.045		-1.71				0.06	0.377
M. desultorius	f	40	-1.514	0.019	1.74	-1.67	-0.63	-3.84	-0.44	0.07	0.245
	m	42	-1.839	-0.011	0.96	0.37	-1.35	-0.26	1.17	0.11	0.145
M. sanguinipes	f	56	-1.982	0.007		-0.19		-1.78		0.07	0.108
	m	80	0.346	-0.009		-0.91	-1.64	**-3.70**		0.13	0.010
T. modesta	f	33	**-2.519**	0.006	0.54	-0.47	-0.37	0.53		0.23	0.043
	m	60	**-2.021**	-0.006	1.68	0.25	**1.77**	2.11		0.46	0.0002
T. pallidipennis	f	152	-0.389	**-0.035**	0.41	0.56	-0.60	-0.56	0.23	0.29	$<10^{-9}$
	m	147	-0.271	**-0.027**	-0.03	-1.65	-0.43	-0.29	0.21	0.20	$<10^{-5}$

Table 4.1. Multiple linear regression of body length (mm) on elevation (km), collection date (days since Jan 1), and mountain range. Cells beneath each covariate show the estimated slope. The penultimate column gives the adjusted R^2 for the full model and the last column gives the p-value for the F-test of the full model. Estimates that differ significantly ($p < 0.01$) from 0 are shown in bold font.

to $1/\sqrt{12}$, which is approximately 0.289. In fact, the average loading on PC 1 across all 12 traits and all nine species is 0.280, with a standard deviation of 0.070 (Table D3). This suggests that the first component can be interpreted as a proxy for size in this analysis. However, there are several traits with consistently low loadings on this component. This is most apparent for antennal length, for which the loadings on PC 1 vary from -0.107 in *H. viridis* to 0.204 in *T. pallidipennis*, with a mean of 0.093. These values indicate that antennal length grows much more slowly with size (sub-linearly) in these species than do the remaining traits. Tegmen width also shows evidence of sub-linear scaling with size in most of species; for this trait, the loadings on PC 1 vary from 0.138 in *S. montezuma* to 0.292 in *T. pallidipennis*, with a mean of 0.226. The remaining instances of traits with apparently anomalous scaling are restricted to just a few species and include hind femur width in *A. coloradus*, *P. texana* and *H. viridis* as well as head width in *M. sanguinipes*, *M. desultorius* and *T. pallidipennis*.

The second component (PC 2) accounted for between 5.8% and 11% of the morphological variation and can be regarded as a shape-related feature which is uncorrelated with size (as measured by the first component). Although the loadings of the morphological traits on this component are more variable between species than those on PC 1, the second component does seem to capture some features that are shared between species (Table D4). In particular, the trait most strongly related to PC 2 in each of the nine species is antennal length, for which the loadings range from 0.593 in *A. coloradus* to 0.924 in *T. modesta*, with a mean loading of 0.809. None of the remaining traits have as consistent or as strong an association with the second component, but other traits that show evidence of anomalous size scaling through their loadings on PC 1 also tend to have relatively large loadings on PC 2, although these differ in sign between species. For example, tegmen width has a large positive loading on PC 2 in both *A. coloradus* and *S. montezuma*, but it has a large negative loading in *M. sanguinipes*. Notably, these are also the three species in which the loading of tegmen width on PC 1 was smallest. In summary, the second component is most strongly associated with antennal length, but it also captures species-specific deviations in other traits with anisometric size scaling.

Unsurprisingly, the interpretation of the third component (PC 3), which accounted for between 2.6% and 9.4% of the morphological variation in each species, is even more idiosyncratic. Although no single trait consistently had the highest loading on this component in all nine species, tegmen width had the highest loading in five species and the second or third highest loading in three other species, and it also had the highest average loading (0.608) out of all twelve traits (Table D5). Several other traits had relatively high loadings (both positive and negative) on this component, but these varied between species in a manner that did not suggest an obvious biological explanation. We therefore interpret the third component as being positively associated with tegmen width, but also having species-specific associations with other traits.

Because the remaining components explained even less of the morphological variation and appear to have completely idiosyncratic associations with the morphological traits in different species, we restricted our regression analyses to the first three principal components. In addition to elevation (in km), sampling date (in days since 1 Jan), and mountain range, we also included sex as an explanatory variable in these regressions to allow for the possibility of sexual dimorphism in the principal components, which were calculated using the combined morphological data obtained from both males and females. The results of these analyses are presented in Table 4.2.

In every species, the size-related first component has a statistically significant negative association with male sex, reflecting the fact that the males of these species are smaller on average than females. This difference is smallest in *M. sanguinipes* and greatest in *S. montezuma*, consistent with the previously observed interspecific variation in body length sexual dimorphism. In four species, sex was the only explanatory variable significantly associated with PC 1. However, in the remaining five species, the first component was also significantly associated with at least one additional explanatory variable. In four of these species, these associations are negative, indicating a tendency for body size to decrease on average with elevation (*T. modesta*, *M. desultorius*) or date (*T. pallidipennis*) or both elevation and date (*M. sanguinipes*). In contrast, PC 1 and elevation significantly positively associated in *S. montezuma*, indicating that this species tends to be larger on average at higher elevations. However, unlike the preceding four species, which generally had

Species	PCA axis	sex (male)	elev (km)	date (days)	range					adj. R^2	p
					Hua	Pin	MG	SC	SR		
A. coloradus	1	**-4.645**	0.440	0.011	2.13	-0.01	1.44		1.80	0.77	$<10^{-7}$
	2	0.950	-0.117	0.015	0.99	0.38	1.10		1.15	0.25	0.03
	3	-0.343	-1.220	0.013	-0.76	1.43	0.37		0.17	0.01	0.43
P. texana	1	**-6.263**	0.033	0.006	-0.25	1.12	-0.08	-0.37	-0.37	0.91	$<10^{-15}$
	2	0.033	0.467	-0.017	-0.10	-0.02	-0.26	-1.70	-0.66	0.12	0.14
	3	0.371	0.814	**0.022**	0.34	0.77	0.61	**1.46**	**1.21**	0.37	0.002
S. montezuma	1	**-6.511**	**2.579**	-0.025	0.51	-0.09	1.33	1.55	1.56	0.93	$<10^{-11}$
	2	-0.006	0.944	-0.026	-0.84	-0.80	0.52	0.83	0.97	0.15	0.17
	3	0.015	-0.612	0.006	0.11	0.27	0.29	-0.16	-0.13	-0.25	0.97
C. huachucana	1	**-4.613**	-1.044	-0.022	-1.08	-2.26	-0.47	1.40	-1.55	0.46	0.001
	2	0.159	-0.690	-0.007	-0.43	-1.67	-1.28	-0.41	-0.23	0.28	0.02
	3	0.092	-0.472	-0.003	-0.62	0.12	-0.66	-0.16	-1.03	0.03	0.36
H. viridis	1	**-5.184**	-0.723	-0.022		-0.36				0.76	$<10^{-5}$
	2	0.579	-1.862	-0.012		-0.74				0.12	0.18
	3	0.122	1.315	0.018		-0.35				0.07	0.26
M. desultorius	1	**-4.551**	**-3.786**	-0.005	0.47	-1.55	-2.08	-2.00	-0.24	0.65	$<10^{-14}$
	2	**1.116**	**-1.755**	-0.002	0.04	-0.89	-0.89	-1.05	-0.15	0.43	$<10^{-7}$
	3	-0.091	0.103	-0.001	**0.73**	0.31	0.14	0.65	0.19	0.08	0.08
M. sanguinipes	1	**-1.403**	**-1.352**	**-0.019**		0.05	0.75	-1.19		0.15	$<10^{-3}$
	2	**1.269**	0.101	**-0.007**		0.08	-0.11	-0.71		0.39	$<10^{-11}$
	3	**0.932**	-0.185	0.000		-0.46	-0.15	0.19		0.29	$<10^{-7}$
T. modesta	1	**-4.701**	**-3.089**	-0.011	**1.52**	-0.57	**1.97**	1.12		0.85	$<10^{-15}$
	2	**0.803**	**-1.410**	**-0.010**	-0.64	**-0.84**	0.26	0.46		0.43	$<10^{-8}$
	3	**0.331**	**-0.719**	**0.011**	-0.16	-0.09	-0.02	-0.09		0.34	$<10^{-6}$
T. pallidipennis	1	**-4.718**	-0.342	**-0.027**	-0.02	-0.03	-0.24	-0.45	-0.33	0.71	$<10^{-15}$
	2	**0.611**	0.167	**-0.008**	0.05	**-0.77**	-0.24	-0.19	-0.07	0.32	$<10^{-15}$
	3	-0.084	0.028	0.000	0.00	**-0.57**	0.10	0.01	-0.17	0.04	0.02

Table 4.2. Multiple linear regressions of the first three principal components on sex, elevation (km), collection date (days since Jan 1), and mountain range. Cells beneath each covariate show the estimated slope. The penultimate column gives the adjusted R^2 for the full model and the last column gives the p-value for the F-test of the full model. Estimates that differ significantly ($p < 0.01$) from 0 are shown in bold font.

their highest densities in coniferous forests at elevations above 2200 m, *S. montezuma* was most abundant in grassland and oak-associated habitats and did not extend above 2250 m in our samples. We found evidence for statistically significant variation in the first component only in *T. modesta*, which is larger on average in the Huachuca and Pinaleño Mountains.

In light of the relationship between PC 1 and size, it is of interest to compare these results with those obtained via direct regression of body length on the explanatory variables. Although every effect that was statistically significant in both males and females in this first set of analyses remained significant in the regressions using PC 1 as a dependent variable, this was not the case with those effects that showed a sex-dependent pattern. For example, while body length in *H. viridis* females was negative associated with sampling date, there was no significant association between PC 1 and sampling date in this species. Similarly, *M. sanguinipes* males were shorter on average in the Santa Catalina Mountains, but we found no evidence of geographical variation involving the first component in this species. These discrepancies have several possible explanations. One is that these associations are genuinely sex-dependent and therefore invisible to the PCA-based analyses which allowed for a sex-dependent intercept but did not incorporate interactions involving sex and the other explanatory variables. The other possibility is that some of these associations are spurious, i.e., false positives, which are suppressed in the PC-based analyses that make use of larger data sets, combining information from both sexes and from 11 different traits. Indeed, Table 3.5 shows the results of nearly 126 separate tests, one for every combination of the nine species, two sexes and up to seven explanatory variables, and thus we would expect on average for one to two of these tests to yield a false positive result at a level of $\alpha = 0.01$.

Perhaps the more striking difference between these two analyses is the larger number of statistically significant results that were obtained when regressing PC 1 against the explanatory variables. We performed nearly 72 separate tests involving this component (one for each of nine species and up to eight explanatory variables per species) and so we would expect there to be nearly one false positive result on average. In fact, the PCA-based regressions identified five statistically significant effects that were not detected in the first set of regressions, four of which

involved elevation or sampling date. Although some of these may be false positives, the probability of obtaining five or more false positive results from 72 tests at this level of significance is less than 0.001, which suggests that not all of these results are spurious. In fact, there are several reasons why we might expect the PCA-based regressions to have greater sensitivity than the regressions using body length alone. As alluded to above, the analysis of the combined data from males and females will have greater power to detect any effects that are shared between the sexes. Likewise, because the first component is determined from 11 different morphological traits, it may be less affected by measurement error. A third possibility is that the first component is intrinsically more strongly correlated with some of the explanatory variables because it more fully captures size variation between individuals, e.g., because PC 1 depends on size variation in multiple anatomical structures rather than body length alone.

In contrast, statistically significant relationships involving the second principal component were only identified in the four most abundant species. In all four species, PC 2 was significantly positively correlated with male sex, suggesting that males in these species have disproportionately long antennae relative to their size when compared with females. In fact, Table D1 reveals that the antennae are about 10 - 15% longer on average in males than in females in both *Melanoplus* species, while there is no significant difference between males and females in the two *Trimerotropis* species, despite females generally having larger bodies in all of these species. Since this appears to be true of most of the grasshopper species that we sampled (Table D1), the failure to detect a correlation between PC2 and sex in the other five species analyzed here may be due to the smaller sample sizes available for these species. In contrast, in the four most abundant species, the second component was also negatively correlated with either elevation (*M. desultorius*) or date (*M. sanguinipes* and *T. pallidipennis*) or both elevation and date (*T. modesta*). This indicates that individuals of these species living at higher elevations or at later times of the year tend to have disproportionately shorter antennae, as well as other species-specific differences in shape.

As expected, the relationship between the third component and the explanatory variables was species-specific. There is evidence for sexual dimorphism in this component in only two

species, *M. sanguinipes* and *T. modesta*, in both of which PC 3 is significantly positively correlated with male sex. As tegmen width had a large positive loading on PC 3 in both species, this observation suggests that males in these species have disproportionately wider forewings on average than females, which is confirmed in Table D1. The third component was also negatively associated with elevation and positively associated with collection date in *T. modesta*, but the only other species to show a significant association with either elevation or date was *P. texana*, in which PC 3 was positively associated both with collection date and with two of the mountain ranges, including the Santa Catalina and Santa Rita Mountains. Curiously, neither the first nor the second component were significantly associated with any of the explanatory variables other than sex in this species, suggesting that much of the morphological variation in *P. texana* involved tegmen width, which had a large positive loading on PC 3.

Interspecific Morphological Variation

We also investigated the extent to which the distribution of morphological characters within grasshopper assemblages varied among habitats. Although intraspecific variation along environmental and other gradients may contribute to community-wide patterns, the much greater degree of interspecific variation in these morphological traits makes it likely that any such patterns will be mainly due to changes in taxonomic composition, as we discuss below. For these analyses, we focused on four measures of morphological variation, including body length and the first three principal components obtained from the 12 log-transformed morphological traits that were investigated in the preceding section. In light of the substantial sexual dimorphism evident in Table D1, we analyzed females and males separately. Table D6 shows the percent variance explained in each sex by the first three components of the principal components analysis, while Table D7 shows the loadings of the 12 morphological traits on each of these three components in females and males. Collectively, these components explained over 85% of the morphological variance in each sex, with the size-related first component being somewhat more variable in females and the shape-related second component being somewhat more variable in males. Furthermore, despite

the sexual dimorphism in shape between the two sexes, the character loadings on the first three components are similar.

The first component is mainly related to size, with relatively uniform loadings for each character in each sex. In females, the mean loading on PC 1 (calculated across the 12 traits) is 0.288 with a standard deviation of 0.025, while in males the corresponding statistics are 0.287 and 0.036. Antennal length and tegmen length have relatively low loadings in both sexes, suggesting that these two characters scale sub-linearly with body size across species. This deviation is more pronounced for antennal length in males (loading = 0.205) than in females (loading = 0.268), whereas the opposite pattern is seen with tegmen length (loading of 0.226 in females vs. 0.257 in males). In general, large-bodied species such as *X. corallipes* and *T. pallidipennis* had large values along this axis, while small-bodied species such as *P. pallida* and *M. desultorius* had small values. The second component is related to shape, with relatively large positive loadings for body length, head height, antennal length and both hind tibia length and hind femur length, and similarly large negative loadings for body width, head width and hind femur width. Gomphocerines occupied positions at both extremes of this axis, with relatively slender species such as *P. snowi* and *A. sumichrasti* having the highest values, while relatively short and thick species such as *P. texana* and *A. deorum* had the lowest values. The third component mainly captures variation in the relative size of the tegmen and has large positive loadings for tegmen length and width in both females and males. The species with the highest values along this axis were mainly Gomphocerines and Oedipodines such as *P. texana* and *T. pallidipennis*, respectively, while those with the lowest values were mainly flightless Melanoplines such as *C. huachucana*, *B. humphreysii* and *M. desultorius*.

Boxplots illustrating the variation of body length and the first three principal components across the five habitats are shown in Figures 4.1 and 4.2. These show that, in general, there is extensive overlap between the trait distributions found in different habitats; in particular, it is not the case that the majority of individuals found in one habitat are larger or more skewed along one of the principal component axes than the majority of individuals found in another habitat. Furthermore, although the medians of the trait distributions do differ between habitats, with one exception, these

do not appear to be monotonically increasing or decreasing along an elevational gradient. The exception is that the median of the first principal component in male grasshoppers does increase from low elevation to high elevation habitats, although the distributions in the two uppermost habitats (pine-oak and coniferous forests) are very similar.

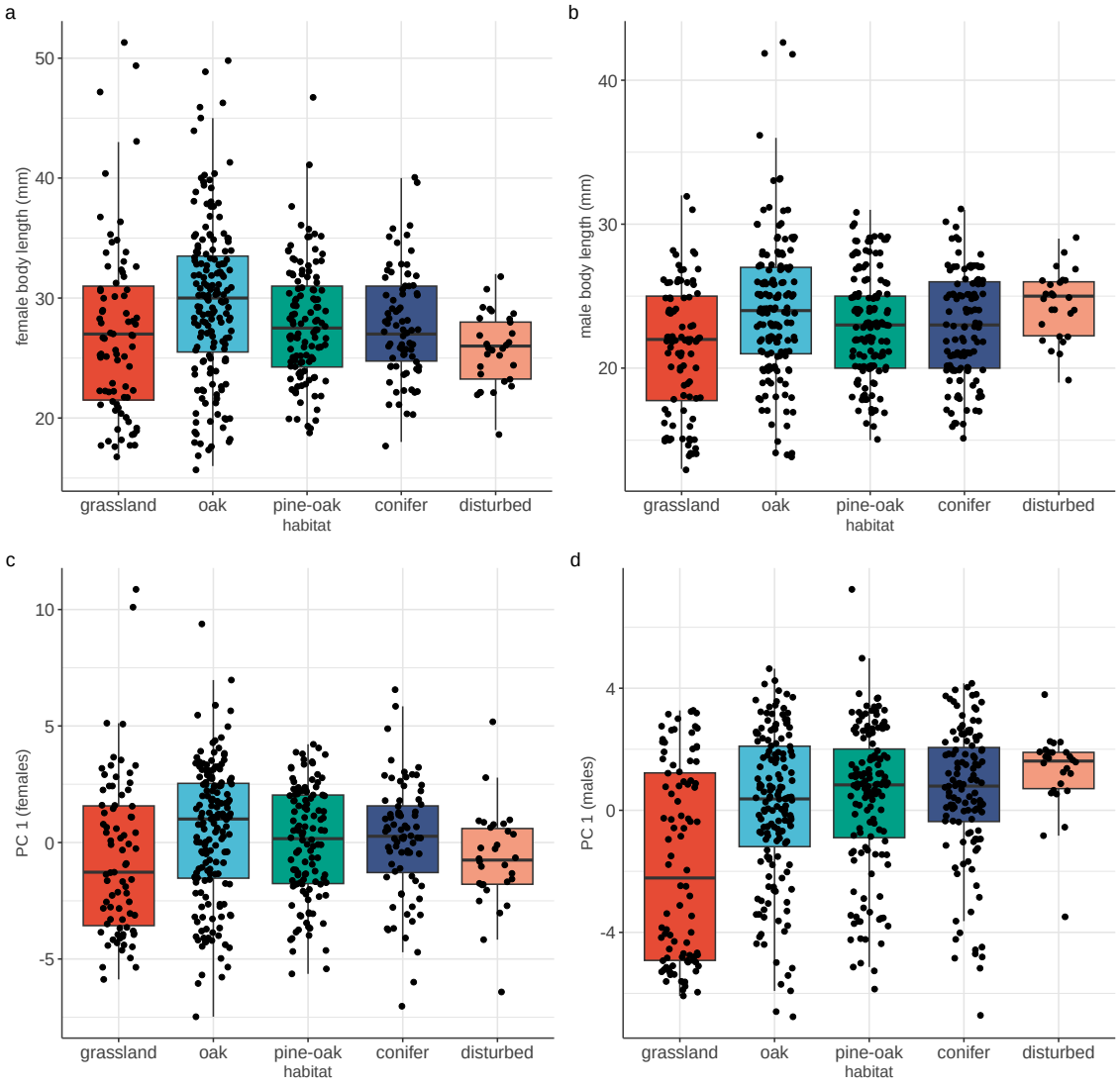


Figure 4.1. Boxplots illustrating the distribution of adult body length (mm) and the first principal component in females and males in the five different habitat classes. Each point corresponds to an individual adult grasshopper.

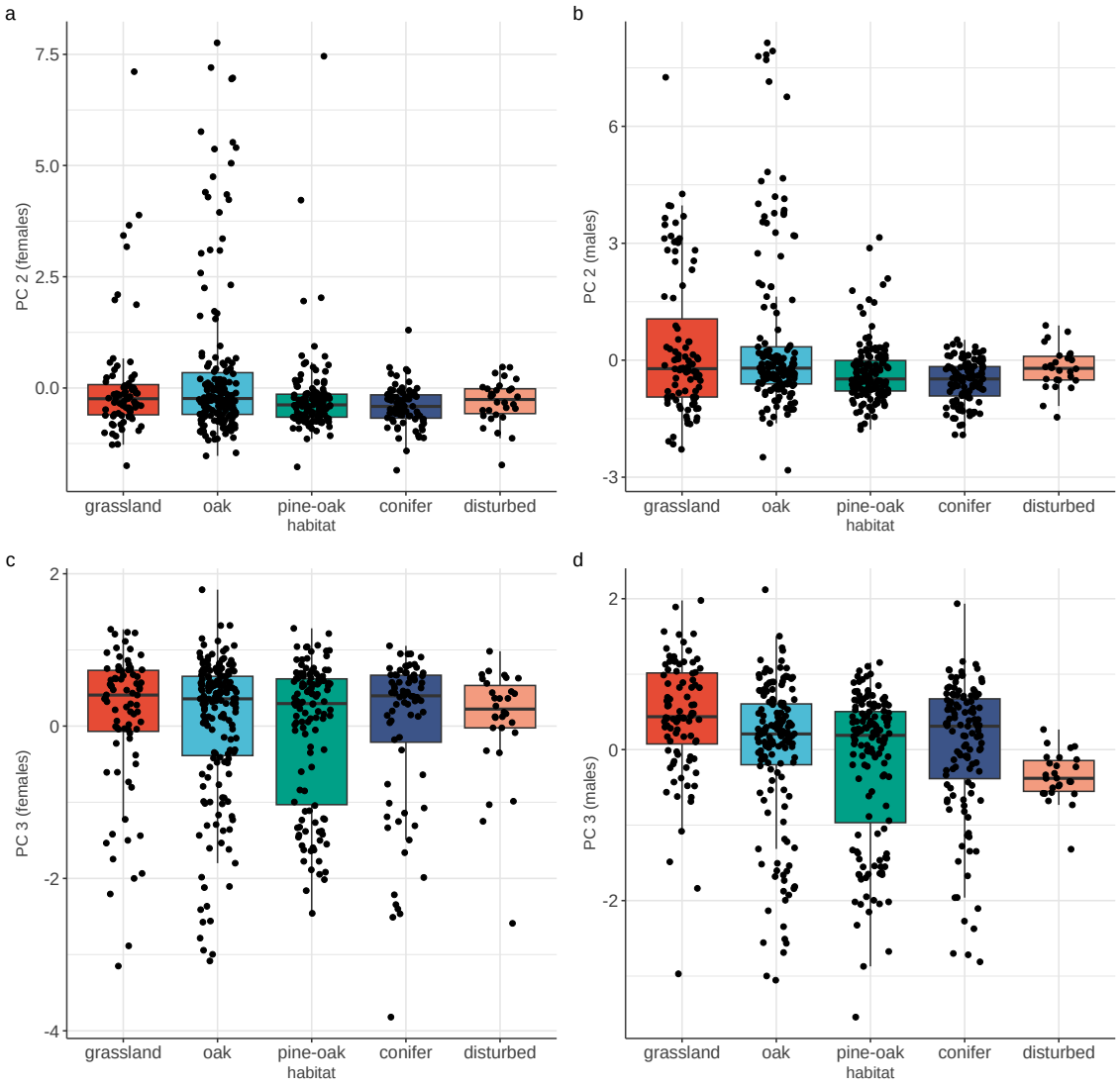


Figure 4.2. Boxplots illustrating the distribution of the second and third principal components in females and males in the five different habitat classes. Each point corresponds to an individual adult grasshopper.

trait	sex	habitat					p
		grassland	oak	pine-oak	conifer	disturbed	
n	f	79	170	118	75	31	
	m	92	152	136	119	26	
body length (mm)	f	27.1 ± 7.3^{a}	30.0 ± 6.8^{b}	27.9 ± 4.8^{ab}	27.8 ± 4.6^{ab}	25.7 ± 3.0^{a}	10^{-4}
	m	21.2 ± 4.5^{a}	23.7 ± 4.2^{b}	23.0 ± 3.6^{ab}	22.8 ± 3.6^{ab}	24.4 ± 2.4^{b}	10^{-4}
PC 1	f	-0.66 ± 3.35^{a}	0.41 ± 2.90^{b}	-0.03 ± 2.39^{ab}	0.12 ± 2.50^{ab}	-0.73 ± 2.11^{ab}	0.006
	m	-1.79 ± 3.18^{a}	0.11 ± 2.49^{b}	0.40 ± 2.41^{b}	0.51 ± 2.25^{b}	1.24 ± 1.34^{b}	10^{-6}
PC 2	f	0.04 ± 1.32^{ab}	0.37 ± 1.84^{a}	-0.21 ± 0.97^{ab}	-0.41 ± 0.46^{b}	-0.31 ± 0.49^{ab}	0.023
	m	0.36 ± 1.84^{ac}	0.53 ± 2.14^{a}	-0.32 ± 0.80^{bc}	-0.55 ± 0.55^{b}	-0.20 ± 0.54^{abc}	10^{-4}
PC 3	f	0.09 ± 0.95^{a}	0.02 ± 0.96^{a}	-0.09 ± 0.95^{a}	-0.02 ± 1.04^{a}	0.08 ± 0.73^{a}	0.671
	m	0.43 ± 0.78^{a}	-0.03 ± 0.99^{b}	-0.20 ± 1.00^{b}	0.02 ± 0.92^{b}	-0.36 ± 0.32^{c}	10^{-7}

Table 4.3. Mean and standard deviation of adult body length (mm) and the first three principal components in males and females grouped by habitat. The p-value was calculated using the Kruskal-Wallis test which assesses whether the distribution of each trait differs across habitats. Distinct superscripts indicate pairs of habitats with significantly different trait distributions according to a post-hoc Dunn test. n, sample size for each habitat category.

do not appear to be monotonically increasing or decreasing along an elevational gradient. The exception is that the median of the first principal component in male grasshoppers does increase from low elevation to high elevation habitats, although the distributions in the two uppermost habitats (pine-oak and coniferous forests) are very similar.

We used the Kruskal-Wallis test and, where appropriate, the Dunn test to test for differences between the trait distributions in different habitats. These results, along with the mean and the standard deviation of each trait in each habitat, are reported for females and males in Table 4.3. With the exception of the third principal component in female grasshoppers, the Kruskal-Wallis test was statistically significant, indicating that the most of the trait distributions do differ between at least some of the habitats. However, in general, there is little evidence of concordance in trait variation either between the sexes or among the four traits. The one pattern that does stand out is that grasshoppers of both sexes tend to be significantly larger in oak-associated habitats than in grasslands, whether we measure size in terms of body length or using the first principal component (PC 1). In females, these two traits are also smaller on average in the other three habitats, but most of these differences are not statistically significant, apart from female body length in disturbed habitats which is significantly smaller than in the oak-associated habitats. In contrast, male grasshoppers in the disturbed habitats were significantly larger than those in the grasslands.

The shape-related traits show similar heterogeneity in their distributions across habitats. The second principal component was significantly larger in both females and males in oak-associated habitats than in coniferous forests, likely due to the rarity of Gomphocerines at higher elevations, but this trait did not differ significantly between oak-associated habitats and grasslands in either sex. Lastly, the third component, which was associated with tegmen size, did not differ significantly between habitats in females, but in male grasshoppers this trait was significantly larger in grasslands and significantly smaller in disturbed habitats than in the remaining three habitats.

As suggested above, some of the differences in the trait distributions between habitats can be attributed to variation in the relative proportions of the three most prevalent Acridid subfamilies (Table D8). Table D9 shows the mean and the standard deviation of each of these four traits in

males and females in these three subfamilies, as well as the results of Kruskal-Wallis tests that demonstrate that the distribution of each trait in each sex differs significantly among subfamilies, with most pairwise comparisons being significant as well according to post-hoc Dunn tests. These differences are also illustrated in Figures D1 and D2, which shows, for example, that Oedipodines tend to be larger and longer than the other two families, that Gomphocerines tend to be more slender on average, and that Melanoplines have proportionately smaller tegmina.

One motivation for examining trait variation across habitats within subfamilies is to determine the extent to which morphological differences between habitats are consistent amongst subfamilies. If we do observe consistent changes in trait distributions across subfamilies, then this suggests that the set of species within each subfamily that is able to survive within a given habitat may be determined by a similar set of environmental filters. To assess whether this is the case, we compared the mean value of each trait in each habitat across subfamilies; these are plotted in Figure 4.3, along with the overall mean for the entire grasshopper assemblage. Likewise, we report the mean and the standard deviation for each trait in each subfamily in each habitat in Tables D10-D13 and we again used the Kruskal-Wallis test and post-hoc Dunn test to assess whether these distributions differ significantly from one another. Figure 4.3 suggests that, in general, there is little consistency between subfamilies in the shifts in trait distributions across habitats. For example, the previously noted increase in body length as we pass from the grasslands into oak-associated habitats appears to be driven entirely by an increase in the body length within the Gomphocerinae and is not evident in the other two subfamilies. More generally, a comparison of the sets of significantly differing trait distributions shown in Table reveals little consistency among subfamilies, even in those cases where the Kruskal-Wallis tests indicate significant differences within multiple subfamilies.

One surprising aspect of this data is that the trait distributions more often differed significantly between habitats in male grasshoppers than in female grasshoppers (Tables D10-D13 Of the twelve trait and subfamily combinations analyzed here, two were significantly different in females, while nine were significantly different in males. However, the reasons for this are unclear.

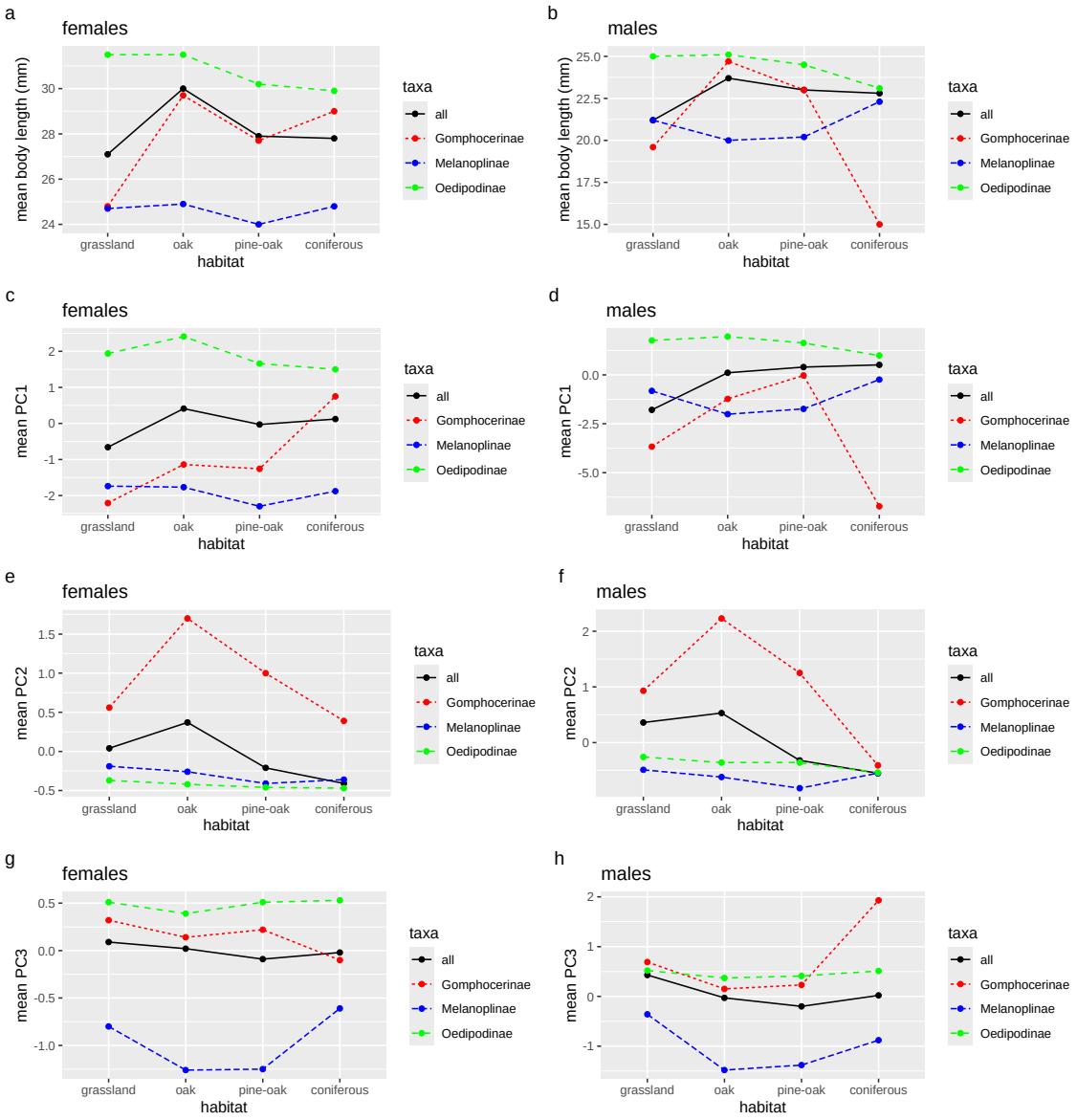


Figure 4.3. Mean body length and principal components (PC1 - PC3) in females and males grouped by subfamily and habitat. Additionally, the black curves show the overall mean of each trait in females and males for the full grasshopper assemblage in each habitat.

For example, the distribution of male body lengths differed significantly between habitats in all three subfamilies, whereas the distribution of female body lengths did not differ significantly between habitats in any subfamily. Within the Gomphocerinae, the differences between the mean body lengths in the grasslands and oak-associated habitats are almost identical (~4.9 mm) in both females and males, but the standard deviations of these distributions are much higher in females than in males, suggesting that the lack of significance in females may be due to greater overall variability. In contrast, within the Melanoplinae, the mean female body length barely differs between the oak-associated habitats and the disturbed habitats, whereas male body length is on average 4.2 mm greater in the latter than in the former. It is tempting to attribute these differences to the smaller number of female grasshoppers for which we had morphological data (females: 473; males: 525), but this seems unlikely given that the sample sizes of the two sexes differ only by about 10%. At present, we do not have a compelling explanation for this observation.

Flightlessness

Nine flightless species of grasshoppers were collected in the focal sites, including two Gomphocerines (*B. flaviventris*, *P. snowi*), six Melanoplines (*B. humphreysii*, *C. huachucana*, *M. desultorius*, *M. franciscanus*, *M. lakinus*, *P. nebrascensis*) and one Romaleid (*P. tshivavensis*). These species varied widely both in abundance and prevalence: four were only collected at one or two sites in a single mountain range, while two others (*C. huachucana* and *M. desultorius*) were in the top five most abundant species in our samples and were collected in all six mountain ranges. In total, flightless species were represented by 180 adults which were sampled in 41 of the 61 focal sites.

We used binomial regression to assess how the proportion of flightless individuals collected in each site varied in relation to elevation, latitude and longitude. We performed two analyses, one using habitat as a categorical explanatory variable and the second using elevation (in km) as a quantitative explanatory variable. Latitude and longitude (in degrees) were also included as

explanatory variables in both regressions. Because none of the Oedipodine grasshoppers sampled in this study are flightless, we used the number of non-Oedipodine adult grasshoppers sampled at each site as the total count per site in the binomial model. Had we not excluded Oedipodinae from these counts, our analyses would potentially be confounded by direct associations between the explanatory variables and Oedipodine abundance unrelated to flightlessness.

model	latitude (deg)	longitude (deg)	elevation (km)	habitat				AIC
				oak	pine-oak	conifer	disturbed	
1	**-0.739**	-0.391		0.281	**0.865**	**0.925**	-0.091	197.2
2	**-0.841**	**-0.429**	**0.800**					198.3

Table 4.4. Binomial regression analyses of the proportion of flightless grasshoppers per site. Estimates that differ significantly ($p < 0.01$) from 0 are highlighted in bold font.

The results of these analyses are summarized in Table 3.7. In both regressions, the proportion of flightless individuals is significantly negatively associated with latitude, indicating that the overall proportion of flightless individuals tends to increase towards the south within our study area. Flightlessness was also significantly negatively associated with longitude in the first analysis and was marginally significantly ($p = 0.017$) negatively associated with this variable in the second analysis. In the regression using habitat as a categorical explanatory variable, the proportion of flightless individuals was significantly higher by a factor of 2.3 - 2.5 in both the pine-oak and coniferous habitats than in the other habitats, which did not significantly differ from one another. Similarly, in the regression using elevation as an explanatory variable, flightlessness was significantly positively associated with elevation, such that the probability that a randomly sampled non-Oedipodine grasshopper is flightless increases by approximately 2.2-fold for every 1000 m gain in elevation.

Both analyses provide evidence that the relative abundance of flightless grasshoppers increases with elevation within the Madrean Sky Islands, as might have been expected given the inventory of flightless species provided above. Two of the flightless species - *M. franciscanus* and

P. tshivavensis - were only collected at higher elevations, while three of the most abundant species on this list reached their peak densities in either pine-oak or coniferous forest. Indeed, there are four flightless grasshopper species which are thought to be endemic to the Madrean Sky Islands and which are primarily found in higher elevation habitats; these include *Melanoplus chiricahuae* Hebard, 1922, *M. pinaleno* Hebard, 1937, *Eumorsea balli* Hebard, 1935 and *E. pinaleno* Rehn & Grant, 1959, none of which were collected in this study. Despite having three more parameters, model 1 has a slightly lower AIC score than model 2, suggesting that habitat (as categorized here) may be a slightly better predictor of the proportion of flightless grasshopper species within an assemblage than elevation. In particular, although the three sites that we classified as disturbed were all at high elevations and surrounded by pine-oak and coniferous forests, the proportion of flightless grasshoppers in these sites was actually slightly lower than in most of the low-elevation grassland sites. However, we are unable to say whether the paucity of flightless grasshoppers in these sites was due to dispersal limitation, environmental filtering or chance.

Additionally, three flightless genera of Ensifera were collected, which are *Ceuthophilus* (Scudder, 1862) (species unknown), *Eremopedes* (Cockerell, 1898) (species unknown), and *Obolopteryx brevihastata* (Morse, 1902).

CHAPTER 5

DISCUSSION

Diversity and Geographical Structure of Grasshopper Communities

To the best of our knowledge, this is the first dedicated survey of grasshopper communities in the Madrean sky islands of southern Arizona since Ernest Tinkham's investigations in 1938 - 1942 (Tinkham, 1947). We collected 43 species in total, all but one belonging to the family Acrididae. For comparison, a recent compilation of Orthoptera species reported in Arizona (Palka Flores et al., unpublished) includes 207 species of grasshoppers distributed across five families: Acrididae (187 spp.), Romaleidae (7 spp.), Eumastacidae (5 spp.), Tanaoceridae (1 sp.), and Tetrigidae (7 spp.). Thus, our samples include over 20% of the species diversity reported for the entire state, despite having been collected in mountain ranges that together cover less than 2% of the total area of the state (approximately 4,000 km^2 out of 295,000 km^2). This illustrates the high species diversity supported by the Madrean sky islands.

Grasshopper diversity was much lower in the samples collected from the individual sky islands, ranging from 16 species in the Santa Catalina Mountains to 23 in the Pinaleño Mountains. Although rarefaction curves (Figure 3.2; Table C5) suggest that these samples probably significantly underestimate the diversity within each sky island, even the estimated total species richness of the individual sky islands, which ranges from 19 to 36, is much lower than either the observed or the estimated total species richness of the entire region. There are several possible reasons for this. The minimum and maximum elevations sampled differed between sky islands, either due to variation in the elevation of the base and summit (e.g., the bases of the Chiricahua and Huachuca Mountains were above 1400 m on the sides that we sampled) or due to access limitations (e.g., the Mt. Hopkins Rd. in the Santa Rita Mountains is gated just below 2200 m). Since some grasshopper species were collected only at very low or very high elevations, these species may be missing from inventories on sky islands where these elevations were not sampled. For example, although *T. modesta* was relatively common at higher elevations on the other five sky

islands, we did not encounter this species in the Santa Rita Mountains, where we had limited access to this species' preferred habitat. Likewise, since each mountain range was generally sampled along a single route determined by road access, we were unable to comprehensively sample habitats on both north- and south-facing slopes on individual sky islands, which often differ in plant composition and microhabitats (Brusca & Moore, 2013). For these reasons, we believe that the grasshopper inventories reported for the individual sky islands are very likely to be incomplete.

Despite these limitations, analysis of the grasshopper count data did reveal some evidence for geographical structure of grasshopper communities across the region which would be consistent with reduced diversity within individual sky islands. Although community dissimilarity was only marginally significantly ($p = 0.07$) positively correlated with geographical distance, a principal coordinates analysis of the aggregated grasshopper assemblage for each mountain range generated an ordination that is strikingly similar to the geographical map of the corresponding mountain ranges (Figure C2). The one striking discrepancy is in the relative positions of the Chiricahua and Santa Rita Mountains, which are inverted in the ordination compared with the geographical map. However, this may be an artifact of not having sampled sites at higher elevations in the Santa Rita Mountains, causing this assemblage to appear to be more distinct from the other assemblages than it actually is. Similarly, latitude and longitude were both identified as significant explanatory variables in the redundancy analysis of the site-specific assemblage data (Figure 3.7), while latitude was retained as a significant explanatory variable in the redundancy analysis of the abundances of adult and subadult counts by subfamily (Figure 3.8). These analyses, which are based on relative abundance, suggest that grasshopper communities in the Madrean sky islands are at least weakly geographically structured, although they do not indicate whether this is due to dispersal limitation or spatially autocorrelated environmental filtering.

One observation that suggests that environmental filtering may be at least partially responsible for the geographical structure is that the effects of latitude and elevation on grasshopper community structure were positively correlated in both redundancy analyses, indicating some similarity between grasshopper assemblages at higher elevations and those at

higher latitudes. For example, two of the three species that had the highest relative abundance within coniferous forests, *M. sanguinipes* and *T. modesta*, also were most abundant in the three northernmost sky islands sampled in this study, the Pinal, Pinaleño and Santa Catalina Mountains (Tables C2 and C3). This was generally not true of *T. pallidipennis*, which was the most abundant species in coniferous forests and somewhat less abundant in the two northernmost mountain ranges than in the others; however, this species was widespread in all habitats and its abundance was uncorrelated with elevation (Figure 3.7). Likewise, most of the species that were only sampled in one mountain range belonged to one of two groups: those that were sampled in pine-oak or coniferous forest in one of the three northern sky islands, including *M. franciscanus*, *M. pictus* and *P. tshivavensis* in the Pinal Mountains, *L. gibbosus* in the Pinaleño Mountains, and *T. inconspicua* in the Santa Catalina Mountains, and those that were sampled in grassland or oak-associated habitats in one of the southern sky islands, including *A. piperatus*, *B. flaviventris*, *M. bivittata*, *M. lakinus* and *A. pseudonietana* in the Santa Rita Mountains, and *E. simplex* in the Chiricahua Mountains. The only exception to this pattern was *C. parviceps*, which was collected in grassland and oak-associated habitats in the Pinal Mountains. These associations suggest that the latitudinal gradient in grasshopper community structure may be related to temperature or some other variable correlated with temperature, with an excess of more cold-adapted species occurring in the north.

Grasshopper Community Structure and Habitat

Consistent with a recent study that used pitfall traps to survey ground-dwelling arthropods in the Santa Catalina Mountains (Meyer et al., 2015), we found that grasshopper species diversity in the Madrean sky islands tended to decrease with elevation, being highest in the grasslands and lowest in coniferous forest (Table 3.2). The evenness of the communities found in different habitats also decreased slightly with elevation, with the greatest difference being observed between the grasslands and the other three undisturbed habitats. This pattern was not repeated when considering grasshopper species richness, which was higher in oak-associated habitats (31) than in the grasslands (25), but a direct comparison is confounded by the different numbers of sites that

were sampled in these two habitats (21 in oaks vs. 8 in grasslands). However, estimated species richness (which accounts for sampling effort or sample size) did tend to decrease with elevation (Table C5), although the estimates for pine-oak woodland were highly variable, with some estimates exceeding those obtained for oak woodland and chaparral.

Curiously, we obtained a somewhat different result when using the assemblages collected at each site to assess how α-diversity varies across habitats. Since every focal site was sampled on three occasions, these indices are not confounded by sample size. Instead, what we find is that median adult abundance, species richness, and species diversity per site all decrease with elevation as we pass from the grasslands to pine-oak forests, but then increase again in coniferous forests (Figure 3.4). Although none of these differences are statistically significant, we believe that the apparent increase in local grasshopper abundance and diversity at the highest elevations is real and that our selection of sampling sites may have inadvertently concealed this pattern. Whereas it was generally easy to find suitable sites for sampling grasshoppers in grassland, oak woodland, and coniferous forest, this was often not the case in pine-oak forests, which tended to occur on much steeper slopes than other plant communities. In contrast, because they occur closer to the summit, coniferous forests tended to occupy flatter areas and often were adjacent to meadows that contained relatively high numbers of grasshoppers. Since we tried to select sampling locations where we would be likely to encounter grasshoppers, our count data probably underestimates the habitat-wide differences in grasshopper diversity and abundance that may have been more apparent had sampling sites been selected at random. Unfortunately, random sampling, although preferable for some reasons, would probably also have greatly reduced the number of grasshoppers sampled in the study and adversely impacted other objectives.

The composition of grasshopper communities also varied between habitats. Although there were no abundant species restricted to just one habitat, only five species were collected in all four undisturbed habitats, including *P. texana*, *M. desultorius*, *M. sanguinipes*, *C. carinata*, and *T. pallidipennis*. Excluding species that were only collected in one or two sites, the sampling densities of most species were unimodal with respect to elevation when sites were grouped by habitat type

(Table C3). The most common pattern was for a species to have its highest density in the grasslands and then decrease monotonically with elevation; this was observed in 12 species, all belonging to the subfamilies Gomphocerinae and Melanoplinae. Six species, including three Gomphocerines and three Oedipodines, were most abundant in oak-associated habitats, with sampling densities decreasing at both higher and lower elevations. As noted previously, only one species - *P. nebrascensis* - was most abundant in pine-oak forest. This is a normally flightless species that feeds almost exclusively on grasses and which is typically found in tallgrass prairie (Brust et al., 2020). We collected this species in just two of the sky islands, with the majority of individuals coming from a single sample collected during the monsoon period in pine-oak forest in the Santa Rita Mountains. Although the forest at this site was mostly intact, there was also a large gully alongside the road which was moist and which supported some tall grass that this species was likely feeding on. Finally, six species, including three Melanoplines and three Oedipodines, were most abundant in coniferous forest, with densities monotonically decreasing towards lower elevations. There was only one species that was neither rare nor abundant in all four undisturbed habitats that could not be assigned to one of these four habitat-associated groups. *A. coloradus* was approximately equally abundant in grassland, oak-associated habitat, and pine-oak forest. This species normally breeds in grasslands but has been observed as a vagrant to high elevation sites in Colorado (Brust et al., 2020). Thus its occurrence in pine-oak forest in our study may also be due to vagrancy.

We also observed pronounced differences in the relative frequencies across habitats of the three most abundant subfamilies (Table D8). Whereas the Gomphocerinae as a group decreased in frequency with elevation, accounting for nearly half of the adult grasshoppers sampled in the grasslands but less than 2% of those sampled in coniferous forest, both the Melanoplinae and the Oedipodinae tended to increase in frequency with elevation. Although both of these subfamilies were present at similar frequencies in the grasslands, the more rapid increase in the frequency of the Oedipodinae with elevation ensured that it was always more abundant (on average) than the Melanoplinae, except in the disturbed sites. It is unclear what is driving the

changes in the relative frequencies of these three subfamilies across habitats, but it is notable that the densities of the Gomphocerinae and Oedipodinae are negatively correlated, both as adults and subadults (Figure 3.8). Although we don't have direct knowledge of the diets of these species in Arizona, many species in these two subfamilies are thought to be grass feeders, whereas many of the species in the Melanoplinae either feed on forbs or are generalists (Capinera et al., 2004; Brust et al., 2020). This raises the possibility that the inverse relationship seen between the Gomphocerinae and the Oedipodinae in this region may be driven in part by competition for shared food resources. Interspecific competition between grasshoppers for food has been documented in experimental field environments (Ritchie & Tilman, 1992; Belovsky & Slade, 1995; Beckerman, 2000), although the importance of interspecific competition in regulating herbivore populations has also been strongly challenged (Hairston et al., 1960).

Despite the pronounced change in the taxonomic composition of grasshopper communities in different habitats, redundancy analysis did not reveal a particularly strong relationship with elevation, geographical location, or any of the plant cover variables (Figure 3.7). Community composition depended most strongly on latitude and elevation, as previously discussed, but these two variables together accounted for less than 14% of the variation in grasshopper community structure. Longitude, as well as mesquite and juniper coverage, were also significantly associated with community structure, but collectively these only accounted for an additional 7% of the variation. Surprisingly, community composition was not significantly associated with either the percentage of bare ground or the percent coverage by grasses or forbs, despite the importance of grasses and forbs in the diets of many of these species or the fact that many of the grasshoppers present in this study can often be found resting on bare ground.

There are several reasons that could explain the weakness of these relationships. The plant coverage data that we collected was coarse, with large numbers of taxa being lumped into single categories. This may be particularly problematic for the forb coverage data, which included essentially all non-gramineous, non-arboreal vascular plants encountered in our survey area. However, we believe that sample size is probably an even more important limiting factor. On

average, only 16 adult grasshoppers were collected at each site, with a standard deviation of 9.6, indicating that the grasshopper assemblages at many of the sites were based on relatively few individuals. With such small numbers, even the species composition at individual sites will be strongly impacted by sampling randomness, introducing a significant variance component that will necessarily be unrelated to the explanatory variables. Combining multiple sites would help alleviate this problem and probably explains why we see such a strong pattern in the relative proportions of the three subfamilies when comparing different habitats (which, with the exception of the disturbed category, are based on at least 8 different sites). Unfortunately, with only 61 sites, any meaningful aggregation of sites would reduce the number of communities to be compared with the environmental variables to such a small number that we would again be unable to resolve any relationships between community structure and the explanatory variables.

Disturbance

We classified three collecting sites as disturbed due to the absence of trees caused by wildfire or clearance (Tables A1.3, A1.5). All three sites were at elevations which would have originally harbored pine-oak forest or coniferous forest, as was confirmed by nearby areas with standing trees, and with one exception all of the grasshopper species collected in these sites were species that were also collected in other high-elevation habitats. Especially abundant was *M. sanguinipes*, which we collected in large numbers at both disturbed sites in the Pinal Mountains in June, but not in subsequent visits. In fact, these two counts were the highest for any species throughout the study. This species, which is commonly known as the migratory grasshopper, is known to be highly mobile, especially in Arizona and New Mexico, and swarms have been encountered at elevations up to 4,000 m above sea level (Brust et al., 2020). As it is a mixed feeder of grasses and forbs, its abundance at these disturbed sites in not surprising. Most of the remaining individuals collected in the disturbed sites also belonged to species, such as *T. pallidipennis* and *T. modesta*, that are strong fliers which were common at high elevations. However, there were four exceptions to this observation. We only collected three *X. corallipes* at focal sites in this study

(although others were encountered adventitiously), two of which were in low-elevation grassland sites and one in a high-elevation disturbed site. *X. corallipes* is known as a strong flier which inhabits a wide range of habitats in the western United States, including areas above timberline (Brust et al., 2020). In contrast, the remaining three species, *C. huachucana*, *M. desultorius*, and *P. tshivavensis*, are flightless, but all three were present at other high-elevation sites in the same mountain ranges where they were collected at the disturbed sites, suggesting that only short-range movements would have been required to colonize the disturbed patches. Despite these occurrences, the majority of the species encountered in either pine-oak or coniferous forests were not collected in the disturbed sites, resulting in a much lower species richness in the latter habitat. Furthermore, due to the exceptionally high abundance of *M. sanguinipes*, species diversity in the disturbed habitat was also much lower than in the remaining habitats.

It should also be acknowledged that the classification of sites into the disturbed and undisturbed categories is somewhat artificial. Indeed, all of the 61 focal sites were adjacent to roads and many of the grasshoppers that we collected were found either on the road itself or on disturbed surfaces next to the road, e.g., in parking turnoffs. Although we deliberately surveyed undisturbed surfaces at every site, the proximity to disturbed areas means that even away from the road we may have collected grasshoppers whose presence was influenced by the road itself. For example, we have already seen that the presence of a roadside gully may have been responsible for the presence of the species *P. nebrascensis* at a high-elevation site in the Santa Rita Mountains. This is a major limitation of this study and it means that we cannot infer that the grasshopper assemblages that we have documented are identical to those that would have been present in the Madrean sky islands prior to the construction of roads. On the other hand, the fact that we do see clear distinctions between the grasshopper communities in low- and high-elevation habitats suggests that at least some of the species that we have collected are likely to have been present in these habitats even in the absence of anthropogenic modification of the landscape. In addition, most species were not collected directly on roads or immediately adjacent surfaces and many

species were either exclusively or primarily collected on native vegetation, which also provides some evidence that these may be 'natural' members of these montane communities.

Morphological Variation

Due to limited sample sizes, we were only able to assess intraspecific morphological variation in nine of the species that we collected. Although no pattern was consistent across all nine species, body size, measured either in terms of body length or using a principal components analysis of twelve log-transformed morphometric characters, varied significantly in relation to elevation in four of these species (Tables 4.1 and 4.2). In three species, including *M. desultorius*, *M. sanguinipes*, and *T. modesta*, this relationship was negative, indicating that individuals living at higher elevations tend to be smaller. This pattern is the opposite of that predicted by Bergmann's rule, which states that individuals living in colder environments should be larger on average than conspecifics living in warmer environments and therefore predicts that body size should be positively associated with latitude and elevation. In fact, the evidence for Bergmann's rule is much weaker in insects than in endothermic vertebrates, with most studies finding no evidence of clinal variation in body size (Shelomi, 2012) and many studies in Orthoptera finding evidence for the converse Bergmann's rule as observed here (Blanckenhorn & Demont, 2004; Ciplak et al., 2008; Whitman, 2008). Curiously, body size was significantly positively associated with elevation in only one species in our study, *S. montezuma*, which also tended to be less abundant at higher elevations, unlike the three high-elevation specialists in which body size followed a counter-Bergmann trend. This suggests that body size could be negatively correlated with density in all four species, perhaps due to intraspecific competition. We have not explicitly tested this hypothesis with our data, but we believe that this is a direction worth pursuing, albeit with larger samples.

We did find that body size was negatively associated with sampling date in two species, *T. pallidipennis* and *M. sanguinipes*, with this trend being particularly strong in the former species. As the abundance of both of these species decreased over time, this pattern is unlikely to be related to intraspecific competition. We can also rule out changes in the proportion of gravid females as a

primary cause in *T. pallidipennis* since the trend was significant in both males and females when body length was used as a proxy for size (Table 4.1). Unfortunately, because we were unable to mark individuals and follow them throughout the season, we are unable to determine whether this trend is due to size-biased survival (with larger individuals dying at higher rates than smaller individuals) or shorter developmental times resulting in smaller body sizes in individuals emerging as adults later in the season.

We also found evidence for significant intraspecific variation in several shape-related variables in some species, although these too appeared to be species-specific. Of particular note, antenna length appeared to scale anisometrically in all nine species, increasing sublinearly with body length, and having the highest loading of all measured characters on the second principal component (Tables D3 and D4). This component was sexually dimorphic in the four most abundant species in our survey, reflecting the proportionately longer antennae found in males in these species, and it was also significantly negatively associated with either elevation or sampling date or both variables in each of these species. As our analysis assumed a log-linear model for intraspecific variation, these trends in shape-related characters could have been generated by other forms of non-linear size-dependence as might be expected for cuticular structures comprised of a fixed number of segments (Whitman, 2008).

We also investigated interspecific variation in morphology using the complete assemblage of adult grasshoppers in each habitat. We found that both size and shape-related features varied significantly among habitats in both males and females, with somewhat more pronounced variation in males (Table 4.3). For example, the median body length was larger by about 2.5 - 3 mm in individuals living in oak-associated habitats than in the other undisturbed habitats. However, these differences, though statistically significant, were much smaller than the interspecific variation in each trait observed within habitats (Figures 4.1 and 4.2). Furthermore, in general, we did not observe monotonic shifts in trait distributions along elevational gradients, e.g., the distribution of body size did not significantly differ between the lowest- and highest-elevation habitats. In

particular, neither Bergmann's rule nor the converse Bergmann's rule appears to hold at the community level in this study.

To the extent that trait distributions did differ between habitats, these differences were largely driven changes in the taxonomic composition of the grasshopper assemblages. Indeed, we found that the first three principal components obtained from an analysis of the log-transformed morphological data had significantly different distributions in the three most abundant Acridid subfamilies sampled in this study (Table D9; Figures D1 and D2). Furthermore, although some of these trait distributions differed significantly across habitats when we considered individual subfamilies (Tables D10 - D13), in general, this variation was not consistent across of subfamilies (Figure 4.3). Thus we find no evidence that the morphological variation between habitats is due to environmental filters acting consistently on the same traits in multiple taxa.

Lastly, we observed a significant positive association between the proportion of flightless adult grasshoppers and elevation when analyzing non-Oedipodine grasshoppers (Table 4.4). This is consistent with analyses of Orthoptera in other regions, which find that the incidence of flightlessness tends to increase with altitude (Roff, 1990). It has been argued that this association is due either to greater habitat persistence at higher elevations, perhaps due to reduced rates of succession in colder, more restrictive environments, or to greater isolation between suitable habitat patches, such that dispersal becomes increasingly risky. Both of these hypotheses could apply within the Madrean sky islands, although we are unaware of any studies that have specifically tested these hypotheses within this region. Curiously, our study also found that the proportion of flightless individuals is signifcantly negatively associated with latitude within the Madrean sky islands, which is opposite to the pattern documented for Orthoptera and other insect orders in other regions (Roff, 1990). This may be because altitudinal gradients in the Madrean sky islands become less pronounced with increasing latitude in Arizona, such that habitat stability and isolation is less dependent on elevation in the northern sky islands than in the south. We have not attempted to test this hypothesis directly, but it would be interesting to at least determine whether other insect orders show a decreasing incidence of flightlessness within the region.

Limitations

Identification

Due to limited information on many Orthoptera species found in Arizona, and no comprehensive dichotomous keys for the state published since 1942, it is possible that some species in my samples may have been misidentified. The nymph and adult grasshopper keys on Grasshoppers of the Western US (IDTools) are not comprehensive and exclude lesser-known species found in Arizona, so I was not able to use the site as reference for all specimens. In addition, many genera in the suborder Ensifera have cryptic or disputed species, so I was only able to identify most of my specimens in that taxon to genus level. At some sites, the majority of specimens collected were nymphs, which can usually only be reliably identified to subfamily.

Two of the species that were collected are of disputed taxonomy, and not readily distinguishable from the others they have been included within. *Melanoplus desultorius* has been split off from *M. aridus* (Scudder, 1878) by some authors, and encompasses the population from southeastern Arizona. Similarly, *Oecanthus texensis* (Symes & Collins, 2013) has recently been split from *Oecanthus californicus* (Saussure, 1874), and the spots on the first two antenna segments are not sufficient to distinguish them without genetic data.

Each stop was only sampled for 20 minutes, so time constraints limited how many species potentially could have been collected. No individuals of *Brachystola magna* or *Taeniopoda eques* were found, despite those being very large, conspicuous species that become abundant in Arizona's grasslands during the autumn months. Males of the Tettigoniidae species *Insara elegans* (Scudder, 1900) and *Capnobotes fuliginosus* (Thomas, 1872) were heard singing at night, but no individuals were found for collecting.

Many Orthoptera species that are common in desert grasslands surrounding the Madrean Sky Islands were not found in this study. These include *Brachystola magna*, *Taeniopoda eques*, *Boopedon nubilum*, *Dactylotum bicolor*, *Melanoplus femurrubrum*, and *Spharagemon collare*. Various species that are endemic to the region or possibly occur in the Sierra Madre Occidental

were also not found, including *Aztecacris gloriosus* (Hebard, 1935), *Melanoplus chiricahuae* (Hebard, 1922), *Melanoplus pinaleno* (Hebard, 1937), *Leuronotina ritensis* (Rehn, 1912), *Machaerocera mexicana* (Saussure, 1859), *Eumorsea balli* (Hebard, 1935), *Eumorsea pinaleno* (Rehn and Grant, 1958), and *Oecanthus major* (T. J. Walker, 1967). In addition, no Jerusalem crickets (*Ammopelmatus* sp.), which are widespread across the state of Arizona were seen during the adventitious night samples.

Measurements

Because measurements of specimens were taken using a physical ruler rather than software, the measurement precision was only to the nearest ¼ of a millimeter. Due to time constraints, each specimen was only measured once, so I did not have the option to use average calculations from multiple trials on a single specimen.

Plant Communities

While conducting plant surveys at each stop, the notes for each transect did not distinguish between native or introduced grasses and forbs. Grasses are difficult to identify to species in the field, and many genera such as *Poa* (Linnaeus, 1753) have a Holarctic or cosmopolitan distribution with both native and introduced species present in North America.

Calpan (1966) tested the food plant preferences of the grasshopper species *Melanoplus bivittatus*, *M. differentialis*, and *M. lakinus* in Colorado to analyze resource partitioning between them using both grasses and forbs. However, a limitation of this study is that the majority of plant species that were offered are introduced, so further research on grasshopper consumption of plants that are native to North America is needed.

While Orthoptera were found perched on common bracken (*Pteridium aquilinum*), no evidence of them consuming these ferns was observed, suggesting that they may only be feeding on angiosperms at the sample sites. The order Orthoptera predates angiosperms by hundreds of

millions of years in the fossil record, which could indicate a shift in the diet towards angiosperms when they appeared during the Cretaceous Period.

Ecological Factors

A heat wave and drought with record high temperatures occurred during the second half of my sampling period in July of 2023, which significantly reduced both overall abundance of Orthoptera as well as species diversity. In recent years, climate change has caused annual precipitation during Arizona's monsoon season to fluctuate, which affects plant growth and in turn also insect abundance. In the event that the 2023 monsoon season was a success with regular downpour, one would expect much greater diversity and abundance of Orthoptera as the summer progressed. Prior to the heat wave, the grasshopper species *Melanoplus sanguinipes* and *Trimerotropis pallidipennis* were extremely plentiful (with 28 individuals of the former collected at the Pinal 7 site on June 17), possibly due to extended rainfall during early spring, but their abundance crashed after most grasses and forbs dried up in July.

Implications for Future Research

Because this study only took place during the year 2023, it is not sufficient to comprehensively sample all Orthoptera in southeastern Arizona. To reliably document the distribution and abundance of Orthoptera in the region, one would need to sample them from April to November for several years.

As climate change continues to alter annual precipitation and temperature patterns in the Southwest and elsewhere, both the diversity and abundance of Orthoptera is predicted to continue declining with more frequent drought years. While surviving populations adapt to these conditions, changes in phenotype such as body proportions and color that reflect a change in substrates are also likely to occur.

Summer droughts also increase the danger of wildfires, due to widespread vegetation death that provides fuel for lightning strikes, unattended campfires, car engines, and littered

cigarette butts. While Arizona's plant communities in grasslands, woodlands, and conifer forests are adapted to regenerate after lightning fires burn dead vegetation away, fire suppression efforts over the last centuries that have increased tree density have led fires to burn less frequently but more severely. Furthermore, the lowland Sonoran Desert has not experienced fires until recent history, after the introduction of grass species such as buffelgrass (*Cenchrus ciliaris*) that cover large areas of land and wither in summer. Because the native desert plants have not evolved under selection pressure from fires, they do not easily regenerate after being burned by lightning or by human negligence.

Another possibility is that climate change potentially could allow Orthoptera species that are currently only found south of the Mexican border to expand their range northward into the US, which would alter the insect communities of southeastern Arizona. We might also expect species ranges to shift to higher elevations, possibly leading to decreases in the ranges occupied by species restricted to higher elevation habitats. Climate change has already been implicated as a major driver of range shifts in other Orthoptera populations and thus may have impacts within this region as well (Poniatowski et al., 2000).

REFERENCES

Appendix of Common-Scientific Names of Grasshopper Food Plants. *University of Wyoming*, www.uwyo.edu/entomology/grasshoppers/field-guide/ghplants.html#Common-Scientific. Accessed 24 June 2024.

Beckerman, A. P. (2000). Counterintuitive Outcomes of Interspecific Competition Between Two Grasshopper Species Along A Resource Gradient. *Ecology* 81(4): 948-957.

Behrstock, R. A. & Sullivan, P. H. (2011). *Dichroplus notatus* (Orthoptera: Acrididae): A Grasshopper Genus and Species New to the United States. *Journal of Orthoptera Research* 20(1): 35–38.

Belovsky, G. E. & Slade, J. B. (1995). Dynamics of two Montana grasshopper populations: relationships among weather, food, and intraspecific competition. *Oecologia* 101: 383-396.

Blanckenhorn, W. U. & Demont, M. (2004). Bergmann and converse Bergmann latitudinal clines in Arthropods: two ends of a continuum. *Integrative and Comparative Biology* 44: 413-424.

Bock, C. E., & Bock, J. H. (1991). Response of Grasshoppers (Orthoptera: Acrididae) to Wildfire in a Southeastern Arizona Grassland. *American Midland Naturalist* 125(1): 162–167.

Bock, C. E., Bock, J. H., & Grant, M. C. (1992). Effects of Bird Predation on Grasshopper Densities in an Arizona Grassland. *Ecology* 73(5): 1706–1717.

Bock, C. E., Jones, Z. F., & Bock, J. H. (2006). Grasshopper Abundance in an Arizona Rangeland Undergoing Exurban Development. *Rangeland Ecology & Management* 59(6): 640–647.

Bock, C. E., Jones, Z. F., & Bock, J. H. (2007). Relationships between species richness, evenness, and abundance in a Southwestern Savanna. *Ecology* 88(5): 1322–1327.

Branson, D. H. (2005). Direct and Indirect Effects of Avian Predation on Grasshopper Communities in Northern Mixed-Grass Prairie. *Environmental Entomology* 34(5): 1114–1121.

Brusca, R. C. & Moore, W. (2013). *A Natural History of the Santa Catalina Mountains, with an Introduction to the Madrean Sky Islands.* Arizona-Sonora Desert Museum Press.

Brust, Mathew, Jim Thurman, Chris Reuter, Lonnie Black, Robert Quartarone, Amanda J. Redford. 2020. *Grasshoppers of the Western U.S., Edition 4.1.* USDA APHIS Identification Technology Program (ITP). Fort Collins, CO. https://idtools.org/id/grasshoppers/ Accessed 24 June 2024.

BugGuide, University of Iowa, www.bugguide.net/node/view/15740. Accessed 24 June 2024.

Capinera, J. L., Scott, R. D., & Walker, T. J. (2004). Field Guide to Grasshoppers, Katydids, and Crickets of the United States. Cornell University.

Caplan, E. B. (1966). Differential Feeding and Niche Relationships Among Orthoptera. *Ecology* 47(6): 1074–1076.

Ciplak, B., Sirin, D., Taylan, M. S., & Kaya, S. (2008). Altitudinal size clines, species richness and population density: case studies in Orthoptera. *Journal of Orthoptera Research* 17: 157-163.

Cole, J. A., & Funk, D. H. (2019). *Anaxipha hyalicetra* sp. n. (Gryllidae: Trigonidiinae), A New Sword-Tailed Cricket Species from Arizona. *Journal of Orthoptera Research* 28(1): 3–9.

Cigliano, M. M., H. Braun, Eades, D. C. & Otte, D. (2024). Orthoptera Species Files. http://orthoptera.speciesfile.org/ Accessed 13 July 2024.

Debano, S. J. (2006). Effects of Livestock Grazing on Aboveground Insect Communities in Semi-Arid Grasslands of Southeastern Arizona. *Topics in Biodiversity and Conservation* 15: 207–224.

DeBrey, L. D., Brewer, M. J. & Lockwood, J. A. (1998). Grasshoppers of Wyoming and the West. https://www.uwyo.edu/entomology/grasshoppers/rgmanage.html Accessed 20 June 2024.

Evans, E. W. & Bailey, K. W. (1993). Sampling Grasshoppers (Orthoptera: Acrididae) in Utah Grasslands: Pan Trapping versus Sweep Sampling. *Journal of the Kansas Entomological Society*, 66(2): 214–222.

Fielding, D. J. & Brusven, M. A. (1993). Grasshopper (Orthoptera: Acrididae) Community Composition and Ecological Disturbance on Southern Idaho Rangeland. *Environmental Entomology* 22(1): 71-81.

Haberski, A. & Sikes D. (2021). Orthoptera of Alaska: A Photographic Key, New Records, and Synonymy of *Melanoplus gordonae*. *Canadian Journal of Arthropod Identification* 44: 51 pp. doi:10.3752/cjai.2021.44

Hairston, N. G., Smith, F. E., & Slobodkin, L. B. (1960). Community structure, population control, and competition. *American Naturalist* 94: 421-425.

Hsieh, T. C., Ma, K. H. & Chao, A. (2016). iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). *Methods in Ecology and Evolution* 7 (12): 1451-1456.

Kaspari, M., Joern, A., & Welti, E. A. R. (2022). How and Why Grasshopper Community Maturation Rates are Slowing on a North American Tall Grass Prairie. *Biology Letters* 18: 20210510

Klingenberg, C. P. (2016). Size, shape, and form: concepts of allometry in geometric morphometrics. *Development Genes and Evolution* 226: 113-137.

Löffler, F., Poniatowski, D., & Fartmann, T. (2019). Orthoptera Community Shifts in Response to Land-Use and Climate Change – Lessons from a Long-Term Study Across Different Grassland Habitats. *Biological Conservation* 236: 315–323.

McPherson, G. R. (1995). The Role of Fire in the Desert Grasslands. *The Desert Grassland* 130-151.

Meyer, W. M., Eble, J. A., Franklin, K., McManus, R. B., Brantley, S. L., Henkel, J., Marek, P. E., Hall, W. E., Olson, C. A., McInroy, R., Bernal Loaiza, E. M., Brusca, R. C., & Moore, W. (2015). Ground-dwelling arthropod communities of a Sky Island mountain range in southeastern Arizona, USA: Obtaining a baseline for assessing the effects of climate change. *PLOS ONE* 10(9): e0135210.

Oksanen J, Simpson G, Blanchet F, Kindt R, Legendre P, Minchin P, O'Hara R, Solymos P, Stevens M, Szoecs E, Wagner H, Barbour M, Bedward M, Bolker B, Borcard D, Carvalho G, Chirico M, De Caceres M, Durand S, Evangelista H, FitzJohn R, Friendly M, Furneaux B, Hannigan G, Hill M, Lahti L, McGlinn D, Ouellette M, Ribeiro Cunha E, Smith T, Stier A, Ter Braak C, Weedon J (2024). vegan: Community Ecology Package. R package version 2.6-6.1, https://CRAN.R-project.org/package=vegan.

Palka-Flores, E., Johnson, M. A. & Franz, N. (2024). A Current List of the Orthoptera of Arizona. *Unpublished manuscript*.

Piña Páez, C., Carson A. R., Luoma, D. L. & Spatafora, J. W. (2023). Truffles in the sky: The impact of stochastic and deterministic drivers on *Rhizopogon* communities of the Madrean sky island archipelago. *Fungal Ecology* 63: 101245.

Pfadt, R. E. (1982). Density and Diversity of Grasshoppers (Orthoptera: Acrididae) in an Outbreak on Arizona Rangeland. *Environmental Entomology* 11(3): 690–694.

Poniatowski, D., Beckmann, C., Löffler, F., Münsch, T., Helbring, F., Samways, M. J., & Fartmann, T. (2020). Relative impacts of land-use and climate change on grasshopper range shifts have changed over time. *Global Ecology and Biogeography* 29: 2190-2202.

Ritchie, M. E. & Tilman, D. (1992). Interspecific competition among grasshoppers and their effects on plant abundance in experimental field environments. *Oecologia* 89: 524-532.

Roff, D. A. (1990). The Evolution of Flightlessness in Insects. *Ecological Monographs* 60(4): 389-421.

Shelomi, M. (2012). Where are we now? Bergmann's rule sensu lato in insects. *American Naturalist* 180(4): 511-519.

Skinner, K. F. (1995). *Plant and Grasshopper Community Composition: Indicators and Interaction Across Three Spatial Scales.* (thesis).

Song, H. (2018). Biodiversity of Orthoptera. *Insect Biodiversity*, pp. 245–279, https://doi.org/10.1002/9781118945582.ch10.

Song, H. et al. (2020). Phylogenomic Analysis Sheds Light on the Evolutionary Pathways Towards Acoustic Communication in Orthoptera. *Nature Communications* 11 (4939).

Spooner, J. D. (1988). *Microcentrum latifrons*, A New Species of Angular-Winged Katydid from Southwestern United States (Orthoptera, Tettigoniidae, Phaneropterinae). *Transactions of the American Entomological Society* 311-317.

Tinkham, E. R. (1947). New Species, Records and Faunistic Notes Concerning Orthoptera in Arizona. *The American Midland Naturalist* 38(1): 127-149.

Walker, T. J. (2014). A New North American Species of *Bucrates* (Orthoptera: Tettigoniidae: Conocephalinae: Copiphorini). *Journal of Orthoptera Research* 23(1), 69–73.

Weissman, D. B. & Gray, D. A. (2019). Crickets of the Genus Gryllus in the United States (Orthoptera: Gryllidae: Gryllinae). *Zootaxa* 4705, no 1.

Whitman, D. W. (2008). The significance of body size in the Orthoptera: a review. Journal of Orthoptera Research 17(2); 117-134.

Woo, B. (2020). First Natural History Observations of the Canyon Pygmy Mole Cricket, *Ellipes monticolus* (Orthoptera: Tridactylidae). *Journal of Orthoptera Research* 29 (1): 1-7.

APPENDIX A

COLLECTION LOCATIONS AND DATES

code	latitude	longitude	elevation (m)	notes	habitat
Chi1	31.914133	-109.117833	1425	Portal Rd - grassland below Portal	grassland
Chi2	31.890002	-109.168350	1536	FR 42 - Stewart Campground	oak
Chi3	31.887550	-109.208333	1669	FR 42	oak
Chi4	31.898333	-109.221683	1765	FR 42	oak
Chi5	31.901667	-109.233933	1862	FR 42	pine-oak
Chi6	31.908683	-109.250850	1948	FR 42/Paradise Rd. junction	pine-oak
Chi7	31.914183	-109.238582	2013	FR 42	oak
Chi8	31.928567	-109.256717	2246	FR 42	pine-oak
Chi9	31.927433	-109.262533	2359	FR 42D	conifer
Chi10	31.911133	-109.271750	2514	FR 42D - road to Rustler Park	conifer
Chi11	31.918317	-109.274467	2567	FSR 357 - Barfoot Lookout	conifer

Table A1.1. Collecting sites in the Chiricahua Mountains. Grasshoppers were collected on 2 July, 6 August and 8 October 2023.

code	latitude	longitude	elevation (m)	notes	habitat
Hua1	31.45271	-110.25512	1465	unnumbered FSR - grasslands east of SR 92	grassland
Hua2	31.44890	-110.28108	1578	E Carr Canyon Rd	oak
Hua3	31.44451	-110.28561	1640	E Carr Canyon Rd	oak
Hua4	31.43921	-110.28192	1742	E Carr Canyon Rd	oak
Hua5	31.43618	-110.27434	1827	E Carr Canyon Rd - Clark Spring trailhead	oak
Hua6	31.43392	-110.28468	1994	E Carr Canyon Rd - waterfall overlook	oak
Hua7	31.43245	-110.28439	2060	E Carr Canyon Rd	oak
Hua8	31.42996	-110.28294	2157	E Carr Canyon Rd	pine-oak
Hua9	31.42832	-110.30338	2258	Ramsey Vista Campground	pine-oak
Hua10	31.42285	-110.30018	2322	Carr Peak trail	conifer
Hua11	31.42333	-110.29889	2424	Carr Peak trail	conifer

Table A1.2. Collecting sites in the Huachuca Mountains. Grasshoppers were collected on 7 July, 11 August and 11 November 2024.

code	latitude	longitude	elevation (m)	notes	habitat
Pin1	33.341100	-110.824883	1332	Kellner Canyon Rd./FR 651 junction	grassland
Pin2	33.333730	-110.839633	1433	FR 651	oak
Pin3	33.322667	-110.849350	1543	FR 651	oak
Pin4	33.311817	-110.856233	1664	FR 651	pine-oak
Pin5	33.301450	-110.862350	1747	FR 651	pine-oak
Pin6	33.294350	-110.867250	1805	FR 651 - Sulphide del Rey Campground	pine-oak
Pin7	33.284383	-110.853883	1989	FR 651	disturbed
Pin8	33.293733	-110.850200	2101	FR 651	pine-oak
Pin9	33.299500	-110.844800	2180	FR 651	pine-oak
Pin10	33.292683	-110.831300	2301	FR 651	conifer
Pin11	33.282260	-110.822250	2373	FR 651 - Pinal Peak	disturbed

Table A1.3. Collecting sites in the Pinal Mountains. Grasshoppers were collected on 17 June, 19 August and 23 September 2023.

code	latitude	longitude	elevation (m)	notes	habitat
MG1	32.678783	-109.774100	1362	Hwy 366	grassland
MG2	32.673567	-109.782667	1454	Hwy 366	grassland
MG3	32.668283	-109.795050	1565	Hwy 366 - Noon Creek picnic area	oak
MG4	32.666670	-109.802600	1660	Hwy 366	oak
MG5	32.655683	-109.805900	1786	Hwy 366	oak
MG6	32.651417	-109.812883	1844	Hwy 366 - Wet Canyon picnic area	oak
MG7	32.648917	-109.813017	1969	Hwy 366	oak
MG8	32.648667	-109.818567	2005	Hwy 366 - Arcadia Campground	pine-oak
MG9	32.637300	-109.823883	2176	Hwy 366	pine-oak
MG10	32.632400	-109.816850	2254	Hwy 366 - Twilight Campground	conifer
MG11	32.630433	-109.824767	2359	Hwy 366	pine-oak
MG12	32.625633	-109.826067	2482	Hwy 366	conifer
MG13	32.622733	-109.823400	2590	Hwy 366 - Ladybug Saddle	pine-oak
MG14	32.629083	-109.839833	2690	Hwy 366	conifer
MG15	32.656533	-109.861117	2770	Hwy 366 - Shannon Campground	conifer

Table A1.4. Collecting sites in the Pinaleño Mountains. Grasshoppers were collected on 1 July, 5 August and 7 October 2023.

code	latitude	longitude	elevation (m)	notes	habitat
SC1	32.336183	-110.694900	1327	Catalina Hwy - Molino Basin Campground	grassland
SC2	32.339683	-110.717633	1466	Catalina Hwy - Gordon Hirabayashi Campground	oak
SC3	32.348417	-110.722917	1564	Catalina Hwy	oak
SC4	32.363550	-110.712717	1680	Catalina Hwy	pine-oak
SC5	32.372867	-110.692867	1776	Catalina Hwy	pine-oak
SC6	32.373317	-110.702450	1913	Catalina Hwy - Middle Bear Picnic Area	pine-oak
SC7	32.396017	-110.693483	2181	Catalina Hwy - Rose Canyon Camground	pine-oak
SC8	32.401317	-110.694517	2270	Catalina Hwy	pine-oak
SC9	32.407767	-110.704133	2375	Catalina Hwy	pine-oak
SC10	32.410633	-110.714683	2430	Catalina Hwy - Palisades Visitor Center	pine-oak
SC11	32.452450	-110.783183	2567	E Ski Run Rd - burned area	disturbed
SC12	32.447367	-110.785917	2665	E Ski Run Rd	conifer
SC13	32.440733	-110.784000	2743	E Ski Run Rd - Mt. Lemmon peak	conifer

Table A1.5. Collecting sites in the Santa Catalina Mountains. Grasshoppers were collected on 24 June, 30 August and 14 October 2023.

code	latitude	longitude	elevation (m)	notes	habitat
SR1	31.674470	-110.937620	1348	Mt. Hopkins Rd - Montosa Basin	grassland
SR2	31.675920	-110.928380	1429	Mt. Hopkins Rd - Amateur Astronomy Pads	grassland
SR3	31.672470	-110.924500	1568	Mt. Hopkins Rd	oak
SR4	31.670750	-110.914280	1632	Mt. Hopkins Rd	oak
SR5	31.672270	-110.905550	1746	Mt. Hopkins Rd	oak
SR6	31.673890	-110.891390	1874	Mt. Hopkins Rd	oak
SR7	31.670780	-110.889730	1948	Mt. Hopkins Rd	pine-oak
SR8	31.679840	-110.885310	2054	Mt. Hopkins Rd	pine-oak
SR9	31.674530	-110.879870	2159	Mt. Hopkins Rd - gate	pine-oak

Table A1.6. Collecting sites in the Santa Rita Mountains. Grasshoppers were collected on 14 July, 9 September and 4 November 2024.

APPENDIX B

ORTHOPTERA SPECIES LISTS

Caelifera Collected in this Study

Species	Describer/year	Family	Subfamily	Distribution
Schistocerca nitens	(Thunberg, 1815)	Acrididae	Cyrtacanthacridinae	Nearctic/Neotropical
Schistocerca shoshone	(Thomas, 1873)	Acrididae	Cyrtacanthacridinae	Nearctic/Neotropical
Acantherus piperatus	Scudder, 1902	Acrididae	Gomphocerinae	Neotropical
Achurum sumichrasti	(Saussure, 1861)	Acrididae	Gomphocerinae	Neotropical
Ageneotettix deorum	(Scudder, 1876)	Acrididae	Gomphocerinae	Nearctic/Neotropical
Amblytropidia mysteca	Saussure, 1861	Acrididae	Gomphocerinae	Nearctic/Neotropical
Amphitornus coloradus	Thomas, 1873	Acrididae	Gomphocerinae	Nearctic
Boopedon flaviventris	Bruner, 1904	Acrididae	Gomphocerinae	Neotropical
Cibolacris parviceps	F. Walker, 1870	Acrididae	Gomphocerinae	Nearctic/Neotropical
Eritettix simplex	Scudder, 1869	Acrididae	Gomphocerinae	Nearctic
Horesidotes cinereus	Scudder, 1899	Acrididae	Gomphocerinae	Nearctic
Mermiria bivittata	Serville, 1839	Acrididae	Gomphocerinae	Nearctic
Mermiria texana	Bruner, 1889	Acrididae	Gomphocerinae	Nearctic
Opeia obscura	Thomas, 1872	Acrididae	Gomphocerinae	Nearctic
Paropomala pallida	Bruner, 1904	Acrididae	Gomphocerinae	Nearctic
Prorocorypha snowi	Rehn, 1911	Acrididae	Gomphocerinae	Neotropical
Psoloessa texana	Scudder, 1875	Acrididae	Gomphocerinae	Nearctic/Neotropical
Rhammatocerus viatorius	Saussure, 1861	Acrididae	Gomphocerinae	Neotropical
Syrbula montezuma	Saussure, 1861	Acrididae	Gomphocerinae	Nearctic/Neotropical
Barytettix humphreysii	Thomas, 1875	Acrididae	Melanoplinae	Neotropical
Conalcaea huachucana	Rehn, 1907	Acrididae	Melanoplinae	Neotropical
Hesperotettix viridis	Thomas, 1872	Acrididae	Melanoplinae	Nearctic/Neotropical
Melanoplus desultorius/aridus[1]	Scudder 1878/Rehn, 1907	Acrididae	Melanoplinae	Nearctic
Melanoplus flavidus	Scudder, 1878	Acrididae	Melanoplinae	Nearctic
Melanoplus franciscanus	Scudder, 1898	Acrididae	Melanoplinae	Nearctic
Melanoplus lakinus	Scudder, 1878	Acrididae	Melanoplinae	Nearctic/Neotropical
Melanoplus pictus	Scudder, 1897	Acrididae	Melanoplinae	Nearctic
Melanoplus sanguinipes	Fabricius, 1798	Acrididae	Melanoplinae	Nearctic/Neotropical
Phoetaliotes nebrascensis	Thomas, 1872	Acrididae	Melanoplinae	Nearctic

Caelifera Collected in this Study

Species	Describer/year	Family	Subfamily	Distribution
Arphia conspersa	Scudder, 1875	Acrididae	Oedipodinae	Nearctic/Neotropical
Arphia pseudonietana	Thomas, 1870	Acrididae	Oedipodinae	Nearctic/Neotropical
Conozoa carinata	Rehn, 1907	Acrididae	Oedipodinae	Nearctic/Neotropical
Lactista azteca	Saussure, 1861	Acrididae	Oedipodinae	Neotropical
Lactista gibbosus	Saussure, 1884	Acrididae	Oedipodinae	Nearctic/Neotropical
Leprus wheeleri	Thomas, 1875	Acrididae	Oedipodinae	Nearctic/Neotropical
Mestobregma plattei	Thomas, 1873	Acrididae	Oedipodinae	Nearctic
Tomonotus ferruginosus	Bruner, 1905	Acrididae	Oedipodinae	Neotropical
Tomonotus mexicanus	Saussure, 1861	Acrididae	Oedipodinae	Neotropical
Trimerotropis cyaneipennis	Bruner, 1889	Acrididae	Oedipodinae	Nearctic
Trimerotropis inconspicua	Bruner, 1904	Acrididae	Oedipodinae	Nearctic
Trimerotropis modesta	Bruner, 1889	Acrididae	Oedipodinae	Nearctic
Trimerotropis pallidipennis	Burmeister, 1838	Acrididae	Oedipodinae	Nearctic/Neotropical
Xanthippus corallipes	Haldeman, 1852	Acrididae	Oedipodinae	Nearctic/Neotropical
Phrynotettix tshivavensis	Haldeman, 1852	Romaleidae	Romaleinae	Nearctic/Neotropical

Table B1. Caelifera collected in this study. The taxonomy is based on the Orthoptera Species Files (Cigliano et al., 2024).

[1]Some authors distinguish between *Melanoplus desultorius* and *M. aridus*, but this split is not universally recognized.

Ensifera Collected in this Study

Species/Taxon	Describer/year	Family	Subfamily	Distribution
Gryllus sp.	Linnaeus, 1758	Gryllidae	Gryllinae	Nearctic/Neotropical
Oecanthus californicus or O. texensis	Saussure, 1874; Symes & Collins, 2013	Gryllidae	Oecanthinae	Nearctic/Neotropical
Oecanthus exclamationis	Davis, 1907	Gryllidae	Oecanthinae	Nearctic
Hoplosphyrum boreale	Scudder, 1902	Mogoplistidae	Oedipodinae	Nearctic and possibly Neotropical
Ceuthophilus sp.	Scudder, 1862	Rhaphidophoridae	Ceuthophilinae	Nearctic/Neotropical
Conocephalus strictus	Scudder, 1875	Tettigoniidae	Conocephalinae	Nearctic
Orchelimum unispina	Saussure & Pictet, 1898	Tettigoniidae	Conocephalinae	Neotropical
Arethaea sp.	Stål, 1876	Tettigoniidae	Phaneropterinae	Nearctic/Neotropical
Insara apache	Rehn, 1907	Tettigoniidae	Phaneropterinae	Nearctic and possibly Neotropical
Microcentrum californicum	Hebard, 1932	Tettigoniidae	Phaneropterinae	Nearctic/Neotropical
Obilopteryx brevihastata	Morse, 1902	Tettigoniidae	Phaneropterinae	Neotropical
Scudderia sp.	Stål, 1873	Tettigoniidae	Phaneropterinae	Nearctic/Neotropical
Eremopedes sp.	Burmeister, 1838	Tettigoniidae	Oedipodinae	Nearctic/Neotropical

Table B2. Ensifera collected in this study. The taxonomy is based on the Orthoptera Species Files (Cigliano et al., 2024).

APPENDIX C

SUPPLEMENTARY MATERIAL FOR CHAPTER 3

Plant Data

	ground cover (%)				tree cover (%)							
Site	grass	forb	fern	bare	mesq	manz	oak	decid	junip	pine	conif	habitat
Chi1	66	20	0	14	50	0	0	16	0	0	0	grassland
Chi3	96	0	0	4	0	0	26	12	32	4	0	oak
Chi4	92	2	0	6	0	0	38	2	16	10	0	oak
Chi5	94	4	0	2	0	0	36	0	14	20	0	pine-oak
Chi6	74	26	0	0	0	0	18	4	4	8	18	pine-oak
Chi7	54	32	0	14	0	0	22	2	8	4	2	oak
Chi8	62	24	0	14	0	0	28	0	6	6	6	pine-oak
Chi9	56	32	0	12	0	0	4	0	0	16	20	conifer
Chi10	30	32	22	18	0	0	2	0	0	30	4	conifer
Chi11	48	36	6	10	0	0	4	0	0	10	10	conifer
Hua1	62	28	0	10	4	0	0	8	0	0	0	grassland
Hua2	76	8	0	16	0	0	46	0	6	0	0	oak
Hua3	34	0	0	66	0	40	14	16	0	0	0	oak
Hua4	54	0	0	46	0	24	46	20	0	0	0	oak
Hua5	76	10	0	14	0	6	34	0	4	0	0	oak
Hua6	54	16	0	30	0	4	62	4	0	0	0	oak
Hua7	34	6	0	60	0	34	50	0	6	4	0	oak
Hua8	10	18	2	70	0	24	40	0	0	26	0	pine-oak
Hua9	6	12	2	80	0	16	26	0	0	40	4	pine-oak
Hua10	76	16	0	8	0	0	0	6	0	44	0	conifer
Pin1	58	32	0	10	2	0	6	2	2	2	0	grassland
Pin2	14	80	0	6	0	0	10	0	4	0	0	oak
Pin3	30	64	0	6	0	0	20	4	8	8	0	oak
Pin4	20	54	0	26	0	0	14	16	0	32	0	pine-oak
Pin5	46	34	0	20	0	0	16	14	0	34	0	pine-oak
Pin6	20	36	0	44	0	0	14	0	6	56	0	pine-oak
Pin7	40	36	0	24	0	0	4	0	10	0	0	disturbed
Pin8	30	44	0	26	0	0	10	0	8	14	18	pine-oak
Pin9	16	50	0	34	0	0	14	0	0	42	14	pine-oak
Pin10	42	30	0	28	0	0	0	8	4	38	8	conifer
Pin11	10	68	4	18	0	0	12	2	0	0	0	disturbed
MG1	66	28	0	6	46	0	6	2	0	0	0	grassland
MG2	68	18	0	14	28	0	20	0	8	0	0	grassland
MG3	64	20	0	16	2	0	36	6	12	0	0	oak
MG4	60	18	0	22	0	16	46	4	6	2	0	oak
MG5	28	40	0	32	0	18	44	2	0	0	0	oak
MG7	40	24	0	36	0	4	70	0	2	8	0	oak
MG10	48	26	2	24	0	0	2	0	0	14	40	conifer
MG12	18	46	4	36	0	0	0	42	0	0	42	conifer
MG13	26	18	0	56	0	0	28	0	0	20	28	pine-oak
MG14	16	56	0	28	0	0	10	0	0	38	12	conifer
MG15	68	26	2	4	0	0	0	0	0	18	8	conifer

	ground cover (%)				tree cover (%)							
Site	grass	forb	fern	bare	mesq	manz	oak	decid	junip	pine	conif	habitat
SC1	80	12	0	8	10	0	12	4	0	0	0	grassland
SC2	64	24	0	12	6	0	16	0	4	0	0	oak
SC3	60	24	0	16	6	0	28	2	0	0	0	oak
SC5	66	12	0	22	0	0	22	8	6	12	0	pine-oak
SC7	44	28	0	28	0	0	12	0	4	60	0	pine-oak
SC8	44	28	0	28	0	0	22	0	0	24	6	pine-oak
SC9	38	32	2	28	0	0	16	0	0	32	8	pine-oak
SC10	48	28	0	24	0	0	12	4	0	32	2	pine-oak
SC11	32	60	4	4	0	0	0	2	0	0	0	disturbed
SC13	48	34	0	18	0	0	0	0	0	16	22	conifer
SC1	80	12	0	8	10	0	12	4	0	0	0	grassland
SR1	68	30	0	2	20	0	2	2	0	0	0	grassland
SR2	48	46	0	6	28	0	0	2	0	0	0	grassland
SR3	24	56	4	16	6	0	16	30	4	0	0	oak
SR4	66	30	0	4	2	0	40	0	2	0	0	oak
SR5	70	24	0	6	0	4	30	0	4	0	0	oak
SR6	76	16	0	8	0	0	28	24	18	0	0	oak
SR7	42	32	2	24	0	0	16	28	12	26	0	pine-oak
SR8	46	24	0	30	0	0	34	8	16	12	0	pine-oak
SR9	46	40	0	14	0	0	20	38	16	10	4	pine-oak
SR1	68	30	0	2	20	0	2	2	0	0	0	grassland

Table C1. Plant cover data and habitat classification for the 61 focal sites. Explanation of categories: grass - grasses (Poaceae); forb - forbs *sensu lato*, including all non-arboreal, non-grammineous vegetation, excluding ferns; fern - ferns, mainly bracken (*Pteridium aquilinum*); bare - bare ground (dirt or rocks); mesq - mesquite trees (*Prosopis* spp.); manz - manzanita trees (*Arctostaphylos* spp.); oak - oak trees (*Quercus* spp.); decid - all deciduous trees except *Quercus* and *Arctostaphylos*; junip - juniper trees (*Juniperus* spp.); pine - pines trees (*Pinus* spp.); conif - all conifers except pines and junipers.

Grasshopper Abundance by Mountain Range

Species	Chi	Hua	Pin	MG	SC	SR
Acantherus piperatus	0	0	0	0	0	2
Achurum sumichrasti	7	7	0	2	2	3
Ageneotettix deorum	2	2	3	7	0	2
Amblytropidia mysteca	5	8	0	1	0	3
Amphitornus coloradus	5	3	2	7	0	17
Boopedon flaviventris	0	0	0	0	0	2
Cibolacris parviceps	0	0	3	0	0	0
Eritettix simplex	1	0	0	0	0	0
Horesidotes cinereus	0	2	0	1	0	0
Mermiria bivittata	0	0	0	0	0	1
Mermiria texana	9	1	0	6	0	0
Opeia obscura	0	2	0	0	0	2
Paropomala pallida	14	1	0	5	1	0
Procorypha snowi	0	9	0	0	0	13
Psoloessa texana	5	3	4	10	4	7
Rhammatocereus viatorius	0	1	0	0	1	0
Syrbula montezuma	7	8	1	3	1	10
Barytettix humphryesii	0	3	0	2	0	3
Conalcea huachucana	10	10	3	5	2	11
Hesperotettix viridis	0	0	4	20	0	0
Melanoplus desultorius	14	19	15	8	2	22
Melanoplus flavidus	0	0	1	1	0	0
Melanoplus franciscanus	0	0	3	0	0	0
Melanoplus lakinus	0	0	0	0	0	1
Melanoplus pictus	0	0	1	0	0	0
Melanoplus sanguinipes	2	0	90	31	9	0
Phoetaliotes nebrascensis	0	0	0	0	2	19
Arphia conspersa	12	3	0	3	1	1
Arphia pseudonietana	0	0	0	0	0	1
Conozoa carinata	2	1	2	6	2	0
Lactista azteca	0	0	1	0	0	1
Lactista gibbosus	0	0	0	1	0	0
Leprus wheeleri	1	1	0	0	0	1
Mesostegma plattei	4	0	0	3	0	0
Tomonotus ferruginosus	3	2	0	0	0	0
Trimerotropis cyaneipennis	5	6	1	5	2	2
Trimerotropis inconspicua	0	0	0	0	1	0
Trimerotropis modesta	23	10	21	28	11	0
Trimerotropis pallidipennis	50	71	13	28	74	42
Xanthippus corallipes	0	0	0	2	1	0
Phrynotettix tshivavensis	0	0	2	0	0	0
total	181	173	170	185	116	166

Table C2. Species abundance by mountain range. The rows show the total numbers of adult grasshoppers of each species collected in each mountain range.

Grasshopper Relative Abundance by Habitat

Species	grassland	oak	pine-oak	conifer	disturbed
Acantherus piperatus	0.125	0.048	0.000	0.000	0.000
Achurum sumichrasti	0.125	0.905	0.053	0.000	0.000
Ageneotettix deorum	1.375	0.238	0.000	0.000	0.000
Amblytropidia mysteca	0.625	0.524	0.053	0.000	0.000
Amphitornus coloradus	0.750	0.667	0.737	0.000	0.000
Boopedon flaviventris	0.125	0.048	0.000	0.000	0.000
Cibolacris parviceps	0.125	0.095	0.000	0.000	0.000
Eritettix simplex	0.000	0.048	0.000	0.000	0.000
Horesidotes cinereus	0.000	0.143	0.000	0.000	0.000
Mermiria bivittata	0.125	0.000	0.000	0.000	0.000
Mermiria texana	0.375	0.524	0.105	0.000	0.000
Opeia obscura	0.125	0.095	0.053	0.000	0.000
Paropomala pallida	2.375	0.095	0.000	0.000	0.000
Procorypha snowi	1.250	0.524	0.053	0.000	0.000
Psoloessa texana	1.625	0.619	0.211	0.300	0.000
Rhammatocereus viatorius	0.000	0.048	0.000	0.100	0.000
Syrbula montezuma	0.750	0.714	0.474	0.000	0.000
Barytettix humphryesii	0.375	0.238	0.000	0.000	0.000
Conalcea huachucana	0.000	0.571	0.947	1.000	0.333
Hesperotettix viridis	1.625	0.524	0.000	0.000	0.000
Melanoplus desultorius	0.625	1.000	1.684	1.800	1.333
Melanoplus flavidus	0.250	0.000	0.000	0.000	0.000
Melanoplus franciscanus	0.000	0.000	0.000	0.300	0.000
Melanoplus lakinus	0.125	0.000	0.000	0.000	0.000
Melanoplus pictus	0.000	0.000	0.053	0.000	0.000
Melanoplus sanguinipes	1.250	0.095	1.263	4.400	17.333
Phoetaliotes nebrascensis	0.125	0.286	0.737	0.000	0.000
Arphia conspersa	0.000	0.333	0.421	0.500	0.000
Arphia pseudonietana	0.000	0.048	0.000	0.000	0.000
Conozoa carinata	0.375	0.048	0.263	0.400	0.000
Lactista azteca	0.125	0.000	0.000	0.100	0.000
Lactista gibbosus	0.000	0.000	0.000	0.100	0.000
Leprus wheeleri	0.000	0.095	0.053	0.000	0.000
Mesostegma plattei	0.000	0.190	0.158	0.000	0.000
Tomonotus ferruginosus	0.000	0.190	0.053	0.000	0.000
Trimerotropis cyaneipennis	0.000	0.381	0.368	0.600	0.000
Trimerotropis inconspicua	0.000	0.000	0.053	0.000	0.000
Trimerotropis modesta	0.000	0.810	1.684	4.200	0.667
Trimerotropis pallidipennis	3.875	5.095	4.474	5.000	1.667
Xanthippus corallipes	0.250	0.000	0.000	0.000	0.333
Phrynotettix tshivavensis	0.000	0.000	0.000	0.100	0.333
total	18.875	15.238	13.947	18.900	22.000

Table C3. Mean number of adult grasshoppers collected per site by species in the five habitats.

Grasshopper Abundance by Season

Species	pre-monsoon	monsoon	post-monsoon
Acantherus piperatus	0	0	2
Achurum sumichrasti	14	7	0
Ageneotettix deorum	4	6	6
Amblytropidia mysteca	7	10	0
Amphitornus coloradus	15	19	0
Boopedon flaviventris	0	0	2
Cibolacris parviceps	3	0	0
Eritettix simplex	1	0	0
Horesidotes cinereus	1	1	1
Mermiria bivittata	0	0	1
Mermiria texana	4	8	4
Opeia obscura	0	2	2
Paropomala pallida	1	17	2
Procorypha snowi	8	14	0
Psoloessa texana	25	8	0
Rhammatocereus viatorius	2	0	0
Syrbula montezuma	1	26	3
Barytettix humphryesii	0	7	1
Conalcea huachucana	6	22	13
Hesperotettix viridis	5	17	0
Melanoplus desultorius	12	46	22
Melanoplus flavidus	1	0	1
Melanoplus franciscanus	0	2	1
Melanoplus lakinus	0	0	1
Melanoplus pictus	1	0	0
Melanoplus sanguinipes	107	22	3
Phoetaliotes nebrascensis	0	17	4
Arphia conspersa	17	3	0
Arphia pseudonietana	0	0	1
Conozoa carinata	9	1	3
Lactista azteca	1	1	0
Lactista gibbosus	0	1	0
Leprus wheeleri	0	3	0
Mesostegma plattei	1	6	0
Tomonotus ferruginosus	2	3	0
Trimerotropis cyaneipennis	6	9	6
Trimerotropis inconspicua	1	0	0
Trimerotropis modesta	14	64	15
Trimerotropis pallidipennis	210	20	48
Xanthippus corallipes	2	1	0
Phrynotettix tshivavensis	0	0	2
total	481	366	144

Table C4. Species abundance by collecting period. The rows show the total numbers of adult grasshoppers of each species collected across all 61 focal sites in each collecting period.

Estimated Total Species Richness

range/habitat	2'nd-order Jackknife	rarefaction: abundance	rarefaction: incidence
Chiricahuas	25	21 (20 - 26)	22 (20 - 32)
Huachucas	30	25 (22 - 37)	26 (22 - 40)
Pinal	35	22 (18 - 32)	36 (18 - 77)
Pinaleño	30	26 (23 - 39)	27 (23 - 40)
Santa Catalina	28	19 (16 - 34)	25 (16 - 44)
Santa Rita	30	26 (22 - 37)	26 (22 - 44)
grassland	44	45 (25 - 77)	50 (25 - 84)
oak	37	35 (31 - 48)	34 (31 - 44)
pine-oak	37	54 (22 - 96)	41 (22 - 75)
coniferous	22	20 (14 - 30)	25 (14 - 44)
disturbed	11	11 (7 - 22)	10 (7 - 17)
total	48	45 (41 - 58)	44 (41 - 65)

Table C5. Estimated total species richness of grasshoppers by mountain range and habitat, along with 95% confidence intervals for the two rarefaction-based estimates.

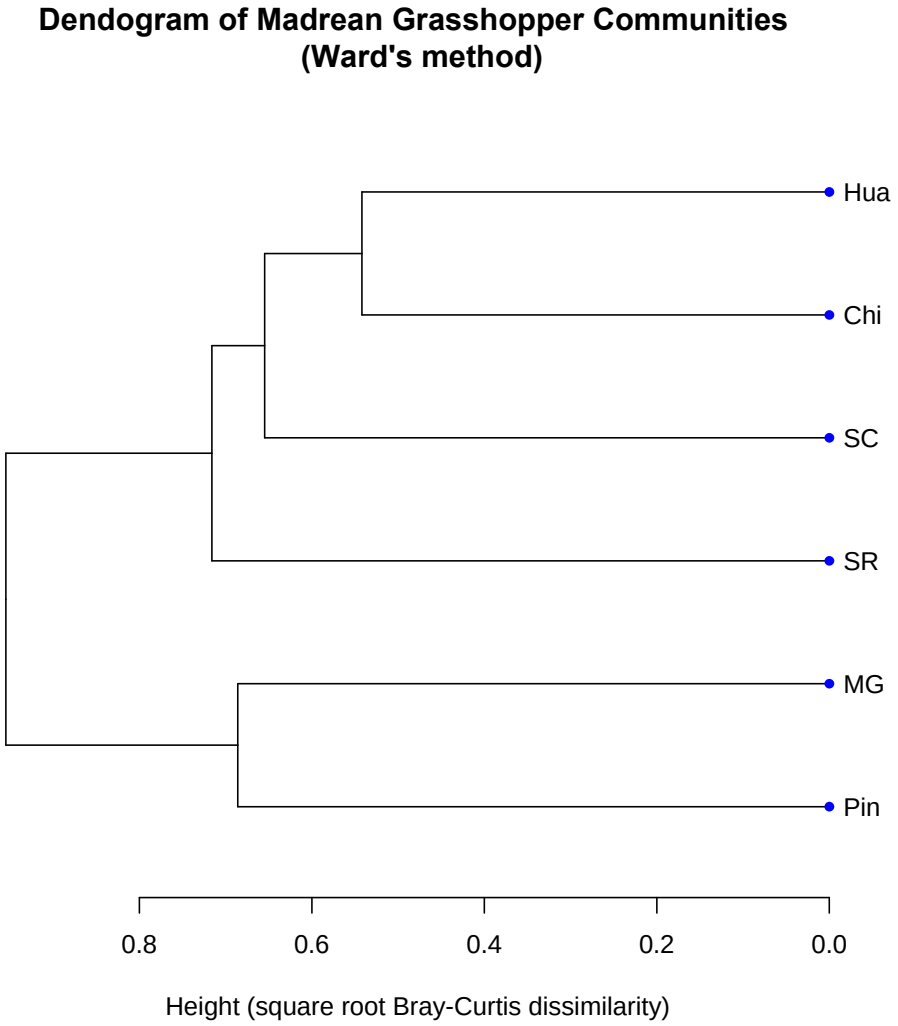


Figure C1. Hierarchical cluster analysis of the aggregated grasshopper assemblage data showing the relationships between the grasshopper assemblages in different mountain ranges. Mountain ranges: Hua - Huachuca; Chi - Chiricahua; Pin - Pinal; MG - Pinaleño (Mt. Graham); SC - Santa Catalina; SR - Santa Rita.

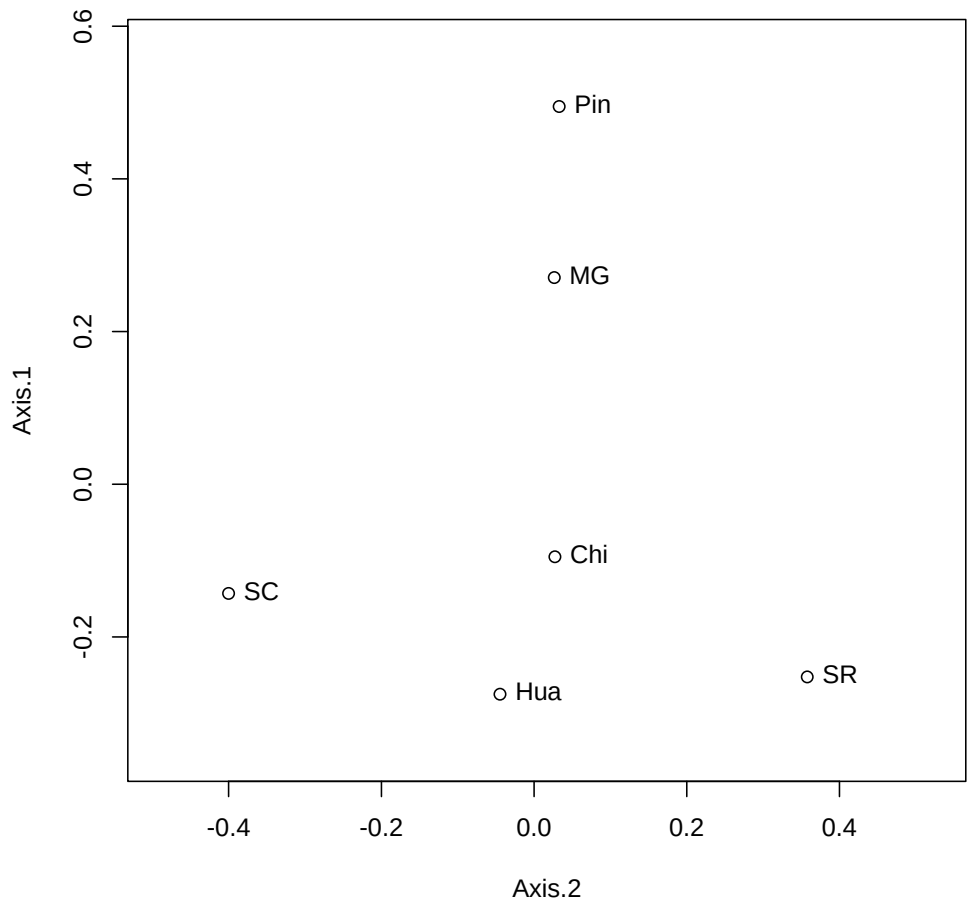


Figure C2. Principal coordinates analysis of the aggregated grasshopper assemblage data showing the relationships between the grasshopper assemblages in different mountain ranges. Mountain ranges: Hua - Huachuca; Chi - Chiricahua; Pin - Pinal; MG - Pinaleño (Mt. Graham); SC - Santa Catalina; SR - Santa Rita.

variable	adj. R^2 (cum.)	ΔR^2	F	p	axis 1 loading	axis 2 loading
latitude	0.082	0.082	6.252	0.0001		
elevation	0.138	0.056	4.800	0.0001		
% juniper	0.168	0.030	3.062	0.0003		
longitude	0.192	0.024	2.636	0.0017		
% mesquite	0.207	0.015	2.029	0.0137		

Table C6. Variance explained and statistical significance of the explanatory variables retained by forward variable selection during transformation-based redundancy analysis (tb-RDA) of the grasshopper community data.

axis	Var	% Var	F	p
RDA 1	0.0770	13.24	6.252	0.0001
RDA 2	0.0350	6.02	4.800	0.0003
RDA 3	0.0267	4.59	3.062	0.0012
RDA 4	0.0167	2.87	2.636	0.0364
RDA 5	0.0057	0.98	2.029	0.7528

Table C7. Variance explained and statistical significance of the five RDA axes obtained through transformation-based redundancy analysis (tb-RDA) of the grasshopper community data.

tb-RDA: Species Loadings and Correlations

Species	r	p	axis 1 loading	axis 2 loading
Acantherus pictus	0.066	0.119	-0.029	0.010
Achurum sumichrasti	0.106	0.043	-0.127	-0.057
Ageneotettix deorum	0.330	**0.001**	-0.074	-0.112
Amblytropidia mysteca	0.257	**0.001**	-0.178	-0.070
Amphitornus coloradus	0.260	**0.001**	-0.131	-0.160
Boopedon flaviventris	0.066	0.119	-0.029	0.010
Cibolacris parviceps	0.006	0.886	0.024	-0.047
Eritettix simplex	0.048	0.201	-0.010	-0.032
Horesidotes cinereus	0.085	0.056	-0.019	-0.008
Mermiria bivittata	0.044	0.209	-0.015	0.001
Mermiria texana	0.174	**0.002**	-0.060	-0.173
Opeia obscura	0.058	0.156	-0.048	0.020
Paropomala pallida	0.158	**0.007**	-0.045	-0.166
Procorypha snowi	0.144	**0.013**	-0.170	0.060
Psoloessa texana	0.197	**0.004**	-0.089	-0.102
Rhammatocereus viatorius	0.015	0.702	-0.013	0.012
Syrbula montezuma	0.371	**0.001**	-0.210	-0.071
Barytettix humphryesii	0.199	**0.008**	-0.085	-0.017
Conalcea huachucana	0.006	0.845	0.021	-0.004
Hesperotettix viridis	0.337	**0.001**	0.017	-0.167
Melanoplus desultorius/aridus	0.017	0.610	0.002	0.015
Melanoplus flavidus	0.204	**0.001**	0.007	-0.036
Melanoplus franciscanus	0.079	0.090	0.027	-0.003
Melanoplus lakinus	0.044	0.209	-0.015	0.001
Melanoplus pictus	0.024	0.574	0.023	-0.012
Melanoplus sanguinipes	0.710	**0.001**	0.608	-0.085
Phoetaliotes nebrascensis	0.054	0.191	-0.100	-0.013
Arphia conspersa	0.003	0.919	-0.031	-0.043
Arphia pseudonietana	0.026	0.518	-0.013	0.009
Conozoa carinata	0.041	0.307	0.061	0.016
Lactista azteca	0.004	0.939	-0.005	-0.005
Lactista gibbosus	0.038	0.408	0.015	0.005
Leprus wheeleri	0.014	0.712	-0.025	-0.005
Mesostegma plattei	0.084	0.079	-0.015	-0.067
Tomonotus ferruginosus	0.012	0.727	-0.042	-0.014
Trimerotropis cyaneipennis	0.044	0.289	0.034	0.082
Trimerotropis inconspicua	0.019	0.724	0.008	0.011
Trimerotropis modesta	0.458	**0.001**	0.369	0.175
Trimerotropis pallidipennis	0.787	**0.001**	-0.257	0.378
Xanthippus corallipes	0.069	0.106	0.022	-0.020
Phrynotettix tshivavensis	0.142	**0.009**	0.035	0.001

Table C8. Environmental correlations, p-values and scores for individual species in the best-fitting RDA model. Species with statistically significant ($p < 0.01$) fits to the explanatory variables are highlighted in bold.

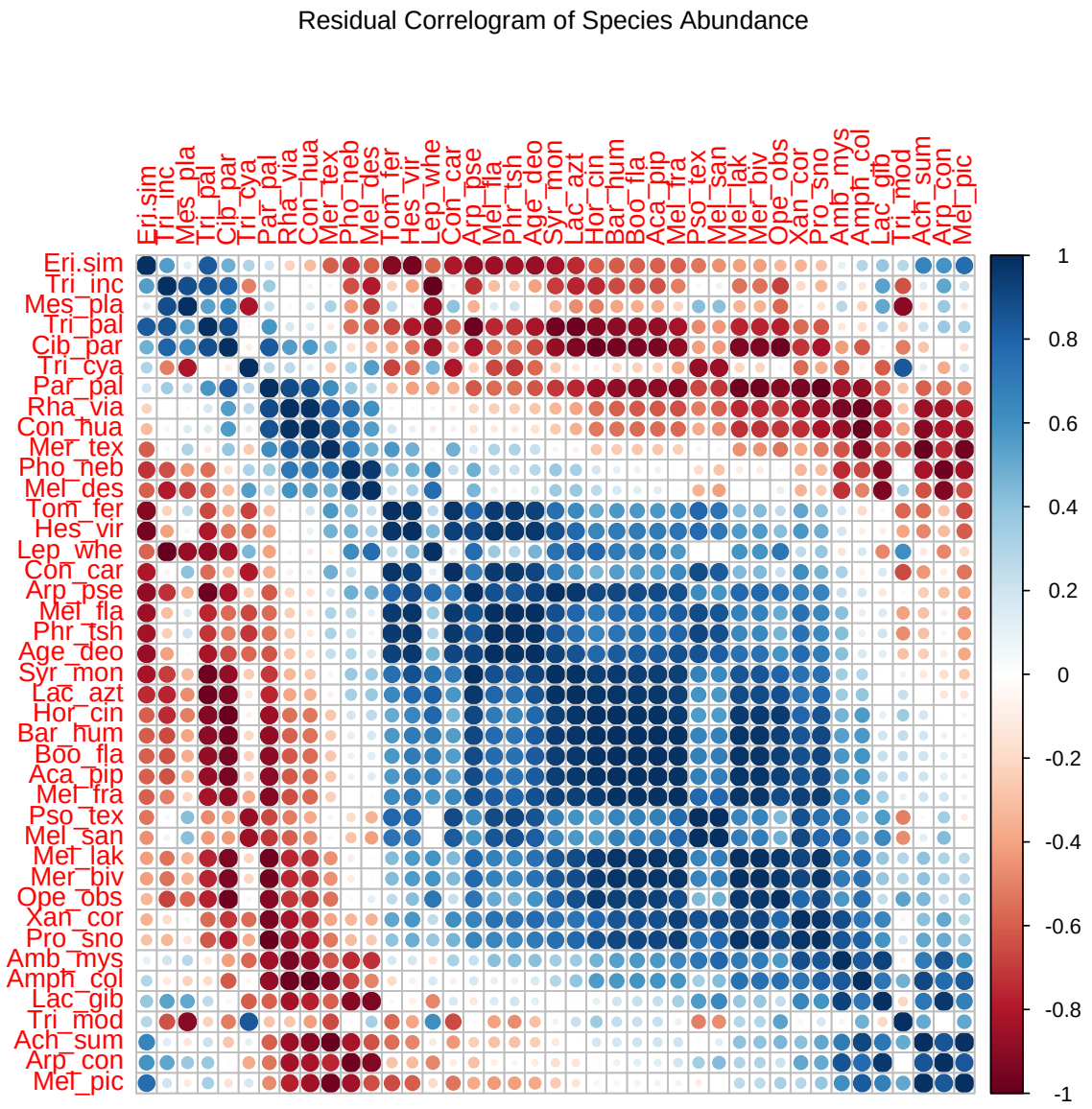


Figure C3. Heat map showing the residual correlations between species remaining after tb-RDA of the grasshopper community data.

Redundancy Analyses: Subfamilies (Adults and Juveniles)

variable	adj. R^2	ΔR^2	F	p	axis 1 loading	axis 2 loading
elevation	0.198	0.198	15.770	0.0001	0.972	-0.062
latitude	0.257	0.059	5.741	0.0004	0.206	0.879
% juniper	0.283	0.025	3.155	0.0156	-0.376	0.375

Table C9. Variance explained and statistical significance of the explanatory variables retained by forward variable selection during transformation-based redundancy analysis (tb-RDA) of the grasshopper community data.

axis	Var	% Var	F	p
RDA 1	0.0691	22.22	18.610	0.0001
RDA 2	0.0247	7.94	6.650	0.0008
RDA 3	0.0056	1.80	1.520	0.1865

Table C10. Variance explained and statistical significance of the five RDA axes obtained through transformation-based redundancy analysis (tb-RDA) of the grasshopper community data.

subfamily	stage	count	r	p	axis 1 loading	axis 2 loading
Gomphocerinae	nymphs	97	0.521	0.001	-0.437	-0.097
	adults	228	0.731	0.001	-0.595	-0.064
Melanoplinae	nymphs	195	0.607	0.001	-0.323	0.239
	adults	313	0.774	0.001	0.388	0.344
Oedipodinae	nymphs	23	0.142	0.012	0.190	0.010
	adults	448	0.906	0.001	0.352	-0.393

Table C11. Environmental correlations, p-values and scores for subfamilies/stages in the best-fitting RDA model.

Adult Sex Ratios

Species	N_{fem}	N_{male}	θ_{fem}	95% C.I.	p
Acantherus piperatus	2	0	1.00	0.16, 1.00	0.50
Achurum sumichrasti	12	9	0.57	0.34, 0.78	0.66
Ageneotettix deorum	6	10	0.38	0.15, 0.65	0.45
Amblytropidia mysteca	9	8	0.53	0.28, 0.77	1.00
Amphitornus coloradus	16	18	0.47	0.29, 0.65	0.86
Boopedon flaviventris	1	1	0.50	0.01, 0.99	1.00
Cibolacris parviceps	2	1	0.67	0.09, 0.99	1.00
Eritettix simplex	1	0	1.00	0.02, 1.00	1.00
Horesidotes cinereus	2	1	0.67	0.09, 0.99	1.00
Mermiria bivittata	0	1	0.00	0.00, 0.98	1.00
Mermiria texana	5	13	0.28	0.10, 0.53	0.10
Opeia obscura	2	2	0.50	0.07, 0.93	1.00
Paropomala pallida	3	18	**0.10**	0.03, 0.35	**0.001**
Procorypha snowi	14	8	0.64	0.41, 0.83	0.29
Psoloessa texana	23	10	0.70	0.51, 0.84	0.04
Rhammatocereus viatorius	2	0	1.00	0.16, 1.00	0.50
Syrbula montezuma	11	19	0.37	0.20, 0.56	0.20
Barytettix humphryesii	6	2	0.75	0.35, 0.97	0.29
Conalcea huachucana	21	20	0.51	0.35, 0.67	1.00
Hesperotettix viridis	13	11	0.54	0.33, 0.74	0.84
Melanoplus desultorius	40	40	0.50	0.39, 0.61	1.00
Melanoplus flavidus	0	2	0.00	0.00, 0.84	0.50
Melanoplus franciscanus	2	1	0.67	0.09, 0.99	1.00
Melanoplus lakinus	1	0	1.00	0.02, 1.00	1.00
Melanoplus pictus	0	1	0.00	0.00, 0.98	1.00
Melanoplus sanguinipes	54	78	0.41	0.32, 0.50	0.04
Phoetaliotes nebrascensis	12	9	0.57	0.34, 0.78	0.66
Arphia conspersa	12	8	0.60	0.36, 0.81	0.50
Arphia pseudonietana	0	1	0.00	0.00, 0.98	1.00
Conozoa carinata	7	6	0.54	0.25, 0.81	1.00
Lactista azteca	1	1	0.50	0.01, 0.99	1.00
Lactista gibbosus	0	1	0.00	0.00, 0.98	1.00
Leprus wheeleri	1	2	0.33	0.01, 0.91	1.00
Mesostegma plattei	2	5	0.29	0.04, 0.71	0.45
Tomonotus ferruginosus	1	4	0.20	0.01, 0.72	0.38
Trimerotropis cyaneipennis	6	15	0.29	0.11, 0.52	0.08
Trimerotropis inconspicua	0	1	0.00	0.00, 0.98	1.00
Trimerotropis modesta	34	59	**0.37**	0.27, 0.47	**0.01**
Trimerotropis pallidipennis	144	134	0.52	0.46, 0.58	0.59
Xanthippus corallipes	3	0	1.00	0.29, 1.00	0.25
Phrynotettix tshivavensis	1	1	0.50	0.01, 0.99	1.00
total	472	519	0.48	0.44, 0.51	0.14

Table C12. Sex ratios in adult grasshoppers. N_{fem}, N_{male}, numbers of females and males of each species collected at the focal sites; θ_{fem}, observed proportion of adult females; 95% confidence interval for θ_{fem}; p, probability of data under the null hypothesis that $\theta_{fem} = 0.5$. Species with a statistically significant ($p < 0.01$) sex ratio bias are highlighted in bold font.

APPENDIX D

SUPPLEMENTARY MATERIAL FOR CHAPTER 4

Means and Standard Deviations of Morphometric Traits

Species	sex	n	total length mm	body length mm	body height mm	body width mm	pronotum length mm	tegmen length mm	tegmen width mm
Schistocerca	f	0							
nitens	m	1	46.0	31.0	8.0	7.0	8.0	39.0	5.0
Acantherus	f	2	24.5 ± 3.5	24.5 ± 3.5	5.0 ± 0.7	4.8 ± 1.1	3.6 ± 0.2	14.2 ± 1.1	2.4 ± 0.2
piperatus	m	0							
Achurum	f	12	43.4 ± 1.4	38.8 ± 0.9	4.5 ± 0.5	3.6 ± 0.5	5.7 ± 0.4	30.7 ± 1.4	2.8 ± 0.6
sumichrasti	m	9	35.3 ± 1.0	30.2 ± 1.2	3.5 ± 0.4	2.9 ± 0.6	4.3 ± 0.2	25.4 ± 1.0	2.3 ± 0.4
Ageneotettix	f	7	19.3 ± 2.1	18.7 ± 1.7	4.9 ± 0.4	4.4 ± 0.6	3.4 ± 0.4	11.4 ± 2.7	2.2 ± 0.4
deorum	m	13	15.2 ± 0.8	15.2 ± 0.8	4.0 ± 0.0	3.7 ± 0.4	2.8 ± 0.2	8.7 ± 1.7	1.8 ± 0.3
Amblytropidia	f	8	31.2 ± 1.0	30.4 ± 1.7	6.9 ± 0.4	5.9 ± 0.4	5.2 ± 0.2	22.8 ± 0.8	3.8 ± 0.4
mysteca	m	9	23.9 ± 1.0	21.8 ± 0.8	5.1 ± 0.3	4.3 ± 0.4	4.1 ± 0.2	17.6 ± 0.7	2.8 ± 0.3
Amphitornus	f	16	25.9 ± 1.3	25.1 ± 1.0	5.7 ± 0.5	5.0 ± 0.4	4.3 ± 0.4	18.1 ± 1.3	3.1 ± 0.4
coloradus	m	19	21.7 ± 1.8	20.4 ± 1.8	4.7 ± 0.5	4.0 ± 0.4	3.5 ± 0.5	15.3 ± 1.5	2.9 ± 0.4
Boopedon	f	1	24.0	24.0	7.0	6.0	5.3	6.0	3.0
flaviventris	m	1	20.0	20.0	5.0	4.5	4.0	4.5	3.0
Cibolacris	f	2	29.5 ± 0.7	27.0 ± 1.4	6.5 ± 0.7	8.0 ± 0.0	5.1 ± 0.2	23.5 ± 0.7	4.0 ± 0.0
parviceps	m	1	20.0	17.0	4.0	6.0	5.0	16.0	2.5
Horesidotes	f	3	22.2 ± 3.8	20.0 ± 3.5	4.3 ± 0.6	4.0 ± 1.0	3.7 ± 0.6	15.8 ± 3.4	2.2 ± 0.1
cinereus	m	0							
Memiria	f	0							
bivittata	m	1	27.0	27.0	4.5	4.0	4.0	18.0	3.0
Mermiria	f	5	43.0 ± 2.3	41.4 ± 2.1	7.6 ± 0.6	6.6 ± 0.9	6.5 ± 0.4	31.7 ± 2.2	4.8 ± 0.3
texana	m	13	29.6 ± 3.1	26.3 ± 3.1	4.8 ± 0.5	4.2 ± 0.4	4.3 ± 0.4	22.3 ± 1.7	3.6 ± 0.4
Opeia	f	2	25.5 ± 3.5	25.5 ± 3.5	5.8 ± 0.4	5.0 ± 1.4	4.8 ± 1.1	12.0 ± 2.8	2.6 ± 0.5
obscura	m	2	18.0 ± 1.4	18.0 ± 1.4	4.0 ± 0.0	3.5 ± 0.7	3.5 ± 0.7	10.0 ± 0.7	2.0 ± 0.0
Paropomala	f	3	31.0 ± 1.7	31.0 ± 1.7	4.5 ± 0.5	3.8 ± 0.3	5.0 ± 0.3	20.7 ± 1.4	2.5 ± 0.5
pallida	m	19	21.4 ± 1.0	21.4 ± 1.0	2.9 ± 0.2	2.3 ± 0.2	3.1 ± 0.2	14.3 ± 0.8	2.0 ± 0.2
Procorypha	f	6	47.5 ± 1.6	47.5 ± 1.6	4.0 ± 0.0	3.1 ± 0.2	5.2 ± 0.7	9.1 ± 0.2	1.9 ± 0.2
snowi	m	8	36.2 ± 5.3	36.2 ± 5.3	2.9 ± 0.2	2.4 ± 0.4	3.7 ± 0.6	8.4 ± 0.5	1.4 ± 0.3
Psoloessa	f	1	22.0	20.0	6.0	5.0	4.3	17.0	2.5
delicatula	m	0							

Means and Standard Deviations of Morphometric Traits

Species	sex	n	total length mm	body length mm	body height mm	body width mm	pronotum length mm	tegmen length mm	tegmen width mm
Psoloessa texana	f	30	21.7 ± 0.9	19.5 ± 1.5	5.1 ± 0.3	4.7 ± 0.5	3.7 ± 0.2	16.3 ± 0.7	2.4 ± 0.7
	m	14	17.0 ± 0.5	14.4 ± 0.7	3.9 ± 0.3	3.5 ± 0.4	2.8 ± 0.3	12.8 ± 0.4	1.9 ± 0.2
Rhammatocereus viatorius	f	2	42.0 ± 0.0	35.5 ± 0.7	9.0 ± 1.4	7.5 ± 0.7	7.0 ± 0.0	32.5 ± 0.7	5.5 ± 0.7
	m	1	34.0	29.0	7.0	6.0	5.5	27.0	4.5
Syrbula montezuma	f	11	33.5 ± 2.9	33.5 ± 2.9	7.1 ± 0.7	6.2 ± 1.4	5.4 ± 0.4	23.0 ± 1.4	3.7 ± 0.3
	m	19	24.8 ± 1.0	23.6 ± 1.1	5.3 ± 0.4	4.4 ± 0.5	3.9 ± 0.1	18.0 ± 0.8	3.4 ± 0.4
Barytettix humphreysii	f	6	29.0 ± 2.0	29.0 ± 2.0	8.0 ± 0.0	7.1 ± 0.5	6.3 ± 0.2	4.8 ± 0.5	2.0 ± 0.5
	m	4	22.2 ± 1.3	22.2 ± 1.3	5.8 ± 0.5	5.0 ± 0.0	4.8 ± 0.4	3.8 ± 0.3	1.9 ± 0.2
Conalcea huachucana	f	22	25.8 ± 2.1	25.8 ± 2.1	6.8 ± 1.1	6.3 ± 0.8	5.2 ± 0.5	4.5 ± 0.4	1.9 ± 0.3
	m	16	21.6 ± 2.2	21.6 ± 2.2	5.7 ± 0.7	5.3 ± 0.7	4.7 ± 0.5	3.9 ± 0.5	1.8 ± 0.3
Hesperotettix viridis	f	13	22.7 ± 2.4	22.5 ± 2.5	5.3 ± 0.5	4.9 ± 0.8	5.0 ± 0.5	15.8 ± 1.4	2.3 ± 0.4
	m	11	18.2 ± 1.1	17.5 ± 1.4	4.0 ±0.0	3.5 ± 0.4	3.9 ± 0.2	13.1 ± 0.9	1.7 ± 0.3
Melanoplus desultorius	f	40	23.0 ± 2.6	23.0 ± 2.6	5.6 ± 0.5	5.0 ± 0.7	4.7 ± 0.8	3.9 ± 0.5	3.9 ± 0.5
	m	42	17.9 ± 1.5	17.9 ± 1.5	4.1 ± 0.3	3.6 ± 0.4	4.0 ± 0.4	3.3 ± 0.4	1.9 ± 0.3
Melanoplus flavidus	f	0							
	m	2	24.5 ± 0.7	20.5 ± 0.7	5.0 ± 0.0	4.0 ± 0.0	4.6 ± 0.6	19.0 ± 0.0	2.2 ± 0.4
Melanoplus franciscanus	f	2	32.0 ± 1.4	32.0 ± 1.4	7.5 ± 0.7	7.0 ± 0.0	5.5 ± 0.7	7.5 ± 0.7	4.2 ± 0.4
	m	1	25.0	25.0	6.0	5.0	5.0	7.0	4.0
Melanoplus lakinus	f	1	18.0	18.0	7.0	7.0	3.8	4.0	4.0
	m	0							
Melanoplus pictus	f	0							
	m	1	28.0	22.0	6.0	5.0	5.0	21.5	3.0
Melanoplus sanguinipes	f	56	28.2 ± 2.1	25.2 ± 2.2	6.6 ± 0.6	6.0 ± 0.7	5.1 ± 0.5	21.5 ± 1.8	3.2 ± 0.4
	m	80	27.8 ± 1.8	24.3 ± 1.9	6.2 ± 0.6	5.3 ± 0.6	5.0 ± 0.4	21.2 ± 1.4	3.3 ± 0.2
Phoetaliotes nebracensis	f	12	25.4 ± 2.2	25.4 ± 2.2	6.0 ± 0.5	5.5 ± 0.5	5.4 ± 0.5	5.0 ± 0.9	3.2 ± 0.3
	m	8	19.1 ± 1.6	19.1 ± 1.6	4.6 ± 0.2	4.1 ± 0.2	4.2 ± 0.2	3.9 ± 0.5	2.2 ± 0.4
Arphia conspersa	f	12	33.7 ± 1.9	29.3 ± 2.4	7.8 ± 0.9	7.1 ± 0.8	6.1 ± 0.6	26.0 ± 1.4	4.9 ± 0.3
	m	7	26.4 ± 1.5	20.0 ± 1.0	5.7 ± 0.8	5.0 ± 0.6	4.6 ± 0.4	20.3 ± 1.6	3.9 ± 0.5
Arphia pseudonietana	f	0							
	m	1	34.0	26.0	8.0	6.0	6.2	26.5	6.0

Means and Standard Deviations of Morphometric Traits

Species	sex	n	total length mm	body length mm	body height mm	body width mm	pronotum length mm	tegmen length mm	tegmen width mm
Conozoa carinata	f	5	30.2 ± 0.8	23.8 ± 1.8	6.6 ± 0.5	5.8 ± 0.4	5.4 ± 0.4	24.5 ± 0.7	4.0 ± 0.0
	m	5	23.5 ± 1.0	18.4 ± 0.9	4.7 ± 0.4	4.2 ± 0.4	4.1 ± 0.2	19.1 ± 0.5	3.0 ± 0.0
Lactista azteca	f	2	25.5 ± 0.7	23.0 ± 1.4	6.5 ± 0.7	6.0 ± 0.0	4.8 ± 0.4	20.5 ± 0.7	3.6 ± 0.5
	m	0							
Lactista gibbosus	f	0							
	m	1	31.0	25.0	7.0	6.0	4.5	20.0	5.5
Leprus wheeleri	f	1	43.0	40.0	11.0	10.0	9.2	34.0	7.0
	m	2	35.0 ± 1.4	27.5 ± 2.1	7.5 ± 0.7	7.0 ± 0.0	6.6 ± 0.5	27.0 ± 0.0	5.0 ±0.0
Mesostegma plattei	f	2	34.0 ± 0.0	27.0 ± 1.4	7.0 ± 0.0	7.0 ± 0.0	5.2 ± 0.4	26.0 ± 0.0	4.2 ± 0.4
	m	6	27.0 ± 2.3	20.5 ± 1.6	5.5 ± 0.5	4.9 ± 0.5	4.0 ± 0.2	21.3 ± 1.8	3.8 ± 0.5
Tomonotus ferruginosus	f	2	39.5 ± 0.7	34.5 ± 2.1	10.5 ± 0.7	9.5 ± 0.7	9.8 ± 1.1	31.0 ± 0.0	5.2 ± 0.4
	m	4	29.5 ± 1.3	23.2 ± 1.3	6.5 ± 0.6	6.2 ± 0.5	6.8 ± 1.0	22.6 ± 1.1	4.2 ± 0.3
Tomonotus mexicanus	f	0							
	m	1	28.0	21.0	6.0	6.0	6.0	22.0	4.0
Trimerotropis cyaneipennis	f	5	35.8 ± 1.1	29.6 ± 2.3	7.7 ± 0.4	7.0 ± 0.0	5.6 ± 0.6	28.0 ± 1.8	5.7 ± 0.4
	m	15	30.0 ± 1.0	23.3 ± 1.3	5.9 ± 0.4	5.2 ± 0.4	4.7 ± 0.3	24.0 ± 0.9	4.4 ± 0.4
Trimerotropis inconspicua	f	0							
	m	1	33.0	23.0	6.0	6.0	4.8	22.0	5.0
Trimerotropis modesta	f	33	32.7 ± 3.0	27.4 ± 1.8	7.6 ± 0.5	7.0 ± 0.6	5.7 ± 0.5	25.9 ± 2.6	4.7 ± 0.5
	m	60	27.5 ± 2.4	21.3 ± 1.8	5.9 ± 0.5	5.1 ± 0.5	4.5 ± 0.4	21.9 ± 2.1	4.1 ± 0.4
Trimerotropis pallidipennis	f	152	40.9 ± 3.5	31.5 ± 2.8	8.0 ± 0.7	7.0 ± 0.7	6.1 ± 0.6	33.7 ± 3.2	5.6 ± 0.5
	m	147	34.0 ± 2.4	26.2 ± 2.2	6.6 ± 0.5	5.6 ± 0.6	5.0 ± 0.4	28.0 ± 2.2	4.8 ± 0.4
Xanthippus corralipes	f	5	47.4 ± 9.2	43.4 ± 7.6	12.0 ± 1.9	12.4 ± 2.3	10.3 ± 1.2	35.7 ± 8.8	7.0 ± 1.7
	m	1	29.0	22.0	7.0	7.0	5.5	22.0	3.5
Phrynotettix tshivavensis	f	1	40.0	40.0	10.0	16.0	16.0	7.5	4.0
	m	1	24.0	24.0	6.0	8.0	9.0	5.0	3.0

Means and Standard Deviations of Morphometric Traits

Species	sex	n	head height mm	head width mm	antenna length mm	tibia length mm	femur length mm
Schistocerca	f	0					
nitens	m	1	7.0	6.0	13.0	19.0	21.0
Acantherus	f	2	6.5 ± 0.0	3.5 ± 0.7	8.8 ± 0.2	11.0 ± 1.4	12.5 ± 0.7
piperatus	m	0					
Achurum	f	12	11.2 ± 0.5	3.2 ± 0.3	11.8 ± 0.9	12.8 ± 0.5	15.3 ± 0.5
sumichrasti	m	9	8.7 ± 0.7	2.4 ± 0.3	10.6 ± 0.7	10.4 ± 0.7	12.2 ± 0.6
Ageneotettix	f	7	6.1 ± 0.8	3.7 ± 0.3	7.5 ± 0.8	9.5 ± 1.0	11.6 ± 1.0
deorum	m	13	5.1 ± 0.4	3.0 ± 0.2	7.5 ± 0.6	7.8 ± 0.6	9.7 ± 0.5
Amblytropidia	f	8	8.4 ± 0.5	4.8 ± 0.3	6.4 ± 0.5	14.9 ± 0.6	17.6 ± 0.5
mysteca	m	9	6.7 ± 0.4	3.5 ± 0.2	6.1 ± 0.7	11.6 ± 0.5	13.5 ± 0.5
Amphitornus	f	16	7.9 ± 0.6	3.9 ± 0.3	7.1 ± 0.7	11.4 ± 0.8	13.7 ± 0.9
coloradus	m	19	6.4 ± 0.5	3.1 ± 0.2	7.6 ± 0.8	9.5 ± 0.5	11.7 ± 0.7
Boopedon	f	1	8.5	5.5	11.0	14.0	15.5
flaviventris	m	1	6.0	3.5	13.0	11.0	12.0
Cibolacris	f	2	6.2 ± 0.4	4.8 ± 0.4	8.0 ± 0.0	11.5 ± 0.7	14.0 ± 1.4
parviceps	m	1	4.5	3.5	6.0	8.0	9.0
Horesidotes	f	3	6.3 ± 1.0	3.0 ± 0.5	6.3 ± 0.6	10.0 ± 1.7	12.0 ± 1.7
cinereus	m	0					
Memiria	f	0					
bivittata	m	1	7.0	3.0	11.0	15.0	15.0
Mermiria	f	5	10.9 ± 0.5	4.9 ± 0.2	16.6 ± 0.5	20.4 ± 1.5	22.1 ± 1.5
texana	m	13	7.4 ± 0.5	3.0 ± 0.4	14.0 ± 1.0	13.7 ± 1.0	15.1 ± 1.2
Opeia	f	2	7.8 ± 1.8	4.0 ± 0.7	7.2 ± 1.1	11.5 ± 0.7	14.0 ± 1.4
obscura	m	2	5.8 ± 0.4	2.8 ± 0.4	8.0 ± 1.4	8.5 ± 0.7	10.3 ± 0.4
Paropomala	f	3	8.7 ± 0.3	3.3 ± 0.6	11.3 ± 1.2	12.7 ± 0.6	13.8 ± 0.8
pallida	m	19	5.7 ± 0.3	2.0 ± 0.1	9.4 ± 0.6	8.7 ± 0.5	9.8 ± 0.5
Procorypha	f	6	10.6 ± 0.7	2.9 ± 0.2	17.8 ± 1.2	15.9 ± 1.0	17.1 ± 1.1
snowi	m	8	8.1 ± 0.7	2.0 ± 0.0	17.3 ± 1.0	13.5 ± 0.8	14.3 ± 0.8
Psoloessa	f	1	5.5	3.2	5.0	11.5	14.0
delicatula	m	0					

Means and Standard Deviations of Morphometric Traits

Species	sex	n	head height mm	head width mm	antenna length mm	tibia length mm	femur length mm
Psoloessa texana	f	30	5.8 ± 0.4	3.6 ± 0.3	6.1 ± 0.4	10.2 ± 0.5	12.1 ± 0.5
	m	14	4.6 ± 0.4	2.7 ± 0.3	5.6 ± 0.7	7.8 ± 0.4	9.3 ± 0.5
Rhammatocereus viatorius	f	2	10.0 ± 1.4	5.5 ± 0.7	10.0 ± 0.0	20.0 ± 0.0	23.5 ± 0.7
	m	1	8.0	5.0	9.0		20.0
Syrbula montezuma	f	11	9.8 ± 0.8	4.3 ± 0.4	8.8 ± 0.8	17.8 ± 1.2	19.5 ± 1.1
	m	19	6.9 ± 0.2	3.0 ± 0.2	8.7 ± 0.7	12.5 ± 0.6	13.8 ± 0.6
Barytettix humphreysii	f	6	8.7 ± 0.5	5.3 ± 0.3	10.9 ± 0.5	13.5 ± 0.4	15.8 ± 0.4
	m	4	6.9 ± 0.2	4.1 ± 0.2	10.2 ± 0.5	10.4 ± 0.8	12.2 ± 0.5
Conalcea huachucana	f	22	7.1 ± 0.7	4.5 ± 0.3	8.8 ± 0.9	11.3 ± 1.0	13.1 ± 0.9
	m	16	6.5 ± 0.6	4.1 ± 0.4	9.0 ± 0.9	10.0 ± 0.9	11.8 ± 1.0
Hesperotettix viridis	f	13	5.7 ± 0.4	3.6 ± 0.2	6.7 ± 0.7	10.8 ± 0.9	12.2 ± 1.0
	m	11	4.6 ± 0.3	3.1 ± 0.2	8.0 ± 1.7	8.5 ± 0.6	9.6 ± 0.5
Melanoplus desultorius	f	40	5.8 ± 0.6	3.8 ± 0.4	7.7 ± 1.0	10.4 ± 1.1	11.9 ± 1.2
	m	42	4.9 ± 0.3	3.3 ± 0.3	8.5 ± 0.8	8.5 ± 0.6	10.0 ± 0.7
Melanoplus flavidus	f	0					
	m	2	5.0 ± 0.0	3.5 ± 0.0	9.8 ± 0.4	9.5 ± 0.7	11.5 ± 0.7
Melanoplus franciscanus	f	2	12.0 ± 0.7	7.5 ± 0.7	9.5 ± 0.7	12.0 ± 0.0	14.0 ± 0.0
	m	1	7.0	4.0	10.0	10.0	12.0
Melanoplus lakinus	f	1	5.0	3.5	6.0	9.0	10.0
	m	0					
Melanoplus pictus	f	0					
	m	1	5.0	4.0	10.0	11.0	13.0
Melanoplus sanguinipes	f	56	6.8 ± 0.6	4.1 ± 0.5	8.3 ± 0.8	11.6 ± 0.9	13.9 ± 1.1
	m	80	6.5 ± 0.5	4.0 ± 0.4	9.5 ± 0.9	10.8 ± 0.8	13.1 ± 0.9
Phoetaliotes nebracensis	f	12	6.3 ± 0.4	4.4 ± 0.3	8.4 ± 1.2	11.5 ± 0.8	13.2 ± 0.8
	m	8	5.2 ± 0.3	3.7 ± 0.3	9.2 ± 1.1	9.2 ± 0.5	10.8 ± 0.8
Arphia conspersa	f	12	8.3 ± 0.9	5.2 ± 0.5	8.5 ± 1.0	12.8 ± 0.9	15.2 ± 1.1
	m	7	6.1 ± 0.4	3.7 ± 0.3	7.6 ± 0.5	9.9 ± 0.4	11.7 ± 0.5
Arphia pseudonietana	f	0					
	m	1	7.5	4.5	9.5	12.0	14.0

Means and Standard Deviations of Morphometric Traits

Species	sex	n	head height mm	head width mm	antenna length mm	tibia length mm	femur length mm
Conozoa carinata	f	5	6.5 ± 0.5	3.7 ± 0.3	8.8 ± 0.8	11.1 ± 0.7	12.8 ± 0.8
	m	5	5.1 ± 0.2	3.0 ± 0.1	8.4 ±0.5	8.6 ± 0.5	10.3 ± 0.4
Lactista azteca	f	2	6.0 ± 0.0	4.0 ± 0.7	9.0 ± 0.0	8.5 ± 0.7	11.0 ± 0.7
	m	0					
Lactista gibbosus	f	0					
	m	1	7.0	4.0	10.0	11.0	13.0
Leprus wheeleri	f	1	11.0	7.5	12.0	17.0	19.0
	m	2	7.8 ± 0.4	5.5 ± 0.0	9.5 ± 0.7	12.0 ± 0.0	13.8 ± 0.4
Mesostegma plattei	f	2	8.5 ± 0.7	5.2 ± 0.4	11.2 ± 1.1	11.5 ± 0.7	13.5 ± 0.7
	m	6	6.3 ± 0.5	4.0 ± 0.3	11.3 ± 1.2	10.1 ± 0.5	11.5 ± 0.8
Tomonotus ferruginosus	f	2	9.5 ± 0.7	6.2 ± 0.3	11.5 ± 0.7	15.5 ± 0.7	18.5 ± 0.7
	m	4	6.8 ± 0.5	4.0 ± 0.0	10.2 ± 1.0	11.5 ± 0.6	13.5 ± 0.6
Tomonotus mexicanus	f	0					
	m	1	7.0	4.0	9.0	11.0	12.5
Trimerotropis cyaneipennis	f	5	7.1 ± 0.2	4.5 ± 0.0	11.1 ± 0.5	11.8 ± 0.4	13.6 ± 0.4
	m	15	6.4 ± 0.5	3.7 ± 0.3	10.7 ± 0.7	10.1 ± 0.5	11.9 ± 0.6
Trimerotropis inconspicua	f	0					
	m	1	7.0	4.0	12.0	11.0	13.0
Trimerotropis modesta	f	33	7.4 ± 0.5	4.4 ± 0.5	10.9 ± 1.0	11.8 ± 0.9	14.0 ± 1.2
	m	60	5.9 ± 0.5	3.6 ± 0.3	10.7 ± 0.9	9.9 ± 0.8	11.4 ± 0.9
Trimerotropis pallidipennis	f	152	8.0 ± 0.7	4.6 ± 0.4	10.7 ± 1.1	12.8 ± 1.2	15.1 ± 1.3
	m	147	6.7 ± 0.5	3.9 ± 0.4	10.3 ± 0.9	10.8 ± 0.9	12.8 ± 1.0
Xanthippus corralipes	f	5	12.0 ± 1.9	8.6 ± 2.3	13.0 ± 1.2	18.0 ± 3.3	21.5 ± 3.7
	m	1	7.0	5.0	11.0	11.0	12.0
Phrynotettix tshivavensis	f	1	10.0	7.0	13.0	16.0	17.0
	m	1	6.0	4.5	10.0	10.0	11.0

Table D1. Morphometric traits of Madrean sky island grasshopper species. Cells show the mean plus/minus the standard deviation. n is the number of individuals that were measured.

species	% Variance			
	PC1	PC2	PC3	cumulative
A. coloradus	66.8	11.0	9.7	87.5
P. texana	73.3	7.2	4.9	85.4
S. montezuma	79.2	8.9	6.7	94.8
C. huachucana	67.9	9.6	6.9	84.4
H. viridis	74.9	8.9	5.4	89.2
M. desultorius	70.5	10.4	3.8	84.7
M. sanguinipes	53.6	9.1	7.5	70.1
T. modesta	80.4	6.8	3.4	90.6
T. pallidipennis	82.0	5.8	2.6	90.3

Table D2. Percentage of variance explained individually and collectively by the first three principal components. Each species was analyzed separately, and the morphological variables were log-transformed and standardized prior to PCA.

	Amp_col	*Pso_tex*	*Syr_mon*	*Con_hua*	*Hes_vir*	*Mel_des*	*Mel_san*	*Tri_mod*	*Tri_pal*
body length	0.344	0.304	0.318	0.315	0.317	0.316	0.305	0.302	0.304
body height	0.300	0.302	0.304	0.288	0.320	0.309	0.300	0.304	0.290
body width	0.309	0.287	0.303	0.317	0.307	0.308	0.304	0.300	0.293
tegmen length	0.314	0.321	0.315	0.267	0.305	0.278	0.338	0.300	0.310
tegmen width	0.194	0.245	0.138	0.195	0.242	0.291	0.173	0.268	0.292
pronotum length	0.312	0.300	0.314	0.323	0.317	0.281	0.279	0.295	0.291
hind femur length	0.314	0.321	0.318	0.325	0.324	0.326	0.356	0.309	0.308
hind femur width	0.262	0.261	0.302	0.303	0.248	0.298	0.287	0.300	0.285
hind tibia length	0.314	0.320	0.315	0.333	0.318	0.325	0.341	0.303	0.306
head height	0.329	0.289	0.316	0.298	0.304	0.307	0.299	0.303	0.293
head width	0.297	0.307	0.309	0.314	0.282	0.271	0.244	0.283	0.272
antenna length	-0.002	0.173	0.099	0.095	-0.107	0.036	0.170	0.171	0.204

Table D3. Loadings of morphological variables on the first principal component (PC 1). Each species was analyzed separately, and the morphological variables were log-transformed and standardized prior to principal components analysis. Species codes contain the first three letters of the genus and the specific epithet.

	Amp_col	*Pso_tex*	*Syr_mon*	*Con_hua*	*Hes_vir*	*Mel_des*	*Mel_san*	*Tri_mod*	*Tri_pal*
body length	0.061	-0.007	-0.025	-0.169	0.197	-0.113	0.160	-0.124	-0.015
body height	0.058	-0.252	0.170	-0.316	-0.068	-0.278	-0.369	-0.128	-0.284
body width	-0.020	0.074	0.033	-0.219	0.011	-0.121	-0.141	-0.232	-0.218
tegmen length	0.315	-0.043	-0.001	0.247	-0.020	0.182	0.267	0.145	0.050
tegmen width	0.589	-0.073	0.561	0.173	-0.125	0.097	-0.373	0.008	0.040
pronotum length	0.034	0.097	-0.162	0.040	0.099	0.244	0.090	-0.044	-0.054
hind femur length	-0.182	-0.031	-0.126	0.003	0.082	0.006	-0.027	-0.019	0.040
hind femur width	-0.231	-0.317	0.002	0.045	0.341	0.175	0.029	-0.037	0.064
hind tibia length	-0.222	-0.020	-0.146	-0.086	0.128	-0.016	-0.131	0.050	0.043
head height	0.010	0.139	-0.077	0.058	-0.138	-0.096	0.222	0.028	-0.072
head width	-0.241	-0.112	-0.145	0.057	-0.203	-0.143	-0.270	-0.180	-0.238
antenna length	0.593	0.884	0.751	0.845	0.855	0.856	0.677	0.924	0.892

Table D4. Loadings of morphological variables on the second principal component (PC 2). Each species was analyzed separately, and the morphological variables were log-transformed and standardized prior to principal components analysis. Species codes contain the first three letters of the genus and the specific epithet.

	Amp_col	*Pso_tex*	*Syr_mon*	*Con_hua*	*Hes_vir*	*Mel_des*	*Mel_san*	*Tri_mod*	*Tri_pal*
body length	0.008	0.007	0.016	-0.131	0.003	0.127	-0.061	-0.030	0.007
body height	0.054	-0.163	0.105	0.038	-0.025	-0.023	-0.061	0.031	-0.162
body width	0.201	-0.436	-0.050	-0.045	-0.302	0.074	-0.252	-0.129	-0.228
tegmen length	0.152	0.093	-0.022	-0.356	0.291	0.545	-0.020	0.325	0.101
tegmen width	0.345	0.825	0.768	0.860	0.488	0.453	0.713	0.786	0.234
pronotum length	-0.259	0.046	-0.023	0.077	-0.002	-0.316	-0.042	-0.187	0.263
hind femur length	-0.180	-0.045	0.022	-0.111	-0.001	-0.009	-0.142	-0.017	0.116
hind femur width	-0.496	-0.229	-0.165	-0.132	-0.609	-0.070	0.009	-0.109	0.360
hind tibia length	-0.126	-0.005	-0.006	-0.015	-0.036	-0.123	-0.159	0.075	0.084
head height	0.150	-0.159	0.020	0.237	0.174	-0.088	-0.172	-0.239	0.114
head width	0.202	0.088	-0.049	-0.104	0.163	-0.570	0.329	-0.346	-0.720
antenna length	-0.624	0.011	-0.604	-0.102	0.395	-0.151	0.485	-0.168	-0.325

Table D5. Loadings of morphological variables on the third principal component (PC 3). Each species was analyzed separately, and the morphological variables were log-transformed and standardized prior to principal components analysis. Species codes contain the first three letters of the genus and the specific epithet.

sex	% Variance			
	PC 1	PC 2	PC 3	cumulative
female	64.3	15.6	7.7	87.6
male	58.4	19.8	7.4	85.6

Table D6. Percent variance explained by the first three components in principal components analyses of the log-transformed morphological data. Note that females and males were analyzed separately.

	PC 1		PC 2		PC 3	
	f	m	f	m	f	m
body length	0.300	0.293	0.340	0.339	-0.033	-0.029
body height	0.311	0.329	-0.310	-0.267	-0.027	0.038
body width	0.290	0.315	-0.368	-0.303	-0.108	-0.035
tegmen length	0.226	0.257	0.027	0.080	0.774	0.720
tegmen width	0.294	0.311	-0.163	-0.087	0.462	0.474
pronotum length	0.317	0.321	0.014	-0.089	-0.198	-0.291
hind femur length	0.311	0.319	0.244	0.237	-0.103	-0.144
hind femur width	0.263	0.255	-0.436	-0.429	-0.058	-0.052
hind tibia length	0.298	0.293	0.280	0.308	-0.181	-0.166
head height	0.283	0.273	0.372	0.340	-0.025	-0.038
head width	0.289	0.267	-0.292	-0.370	-0.294	-0.283
antenna length	0.268	0.205	0.272	0.334	-0.022	-0.186

Table D7. Loadings of the morphological variables on the first three components in principal components analyses of the log-transformed morphological data. Note that females and males were analyzed separately.

habitat	subfamily		
	Gomphocerinae	Melanoplinae	Oedipodinae
grassland	48.0	23.4	28.7
oak	36.0	17.4	46.6
pine-oak	13.0	31.9	54.7
coniferous	1.5	37.6	60.0
disturbed	0.0	89.5	8.8

Table D8. Percent composition by subfamily of adult grasshopper assemblages in each habitat. The subfamily Cyrtacanthacridinae also is not shown as it was represented by 1 individual in pine-oak forest (0.04%). Likewise, the subfamily Romaleinae is not shown as it was represented by 1 individual in coniferous habitat (0.05%) and 1 individual in disturbed habitat (1.8%).

trait	sex	subfamily			p
		Gomphocerinae	Melanoplinae	Oedipodinae	
n	f	111	145	213	
	m	123	156	247	
body length (mm)	f	28.0 ± 8.9^{a}	24.7 ± 3.0^{b}	30.8 ± 4.0^{c}	10^{-15}
	m	22.3 ± 6.0^{a}	21.5 ± 3.4^{a}	24.3 ± 3.2^{b}	10^{-12}
PC 1	f	-1.42 ± 2.80^{a}	-1.82 ± 1.90^{a}	1.95 ± 1.79^{b}	10^{-15}
	m	-2.14 ± 2.57^{a}	-0.82 ± 2.55^{b}	1.55 ± 1.51^{c}	10^{-15}
PC 2	f	1.25 ± 2.32^{a}	-0.30 ± 0.36^{b}	-0.44 ± 0.41^{c}	10^{-12}
	m	1.55 ± 2.50^{a}	-0.58 ± 0.55^{b}	-0.41 ± 0.46^{c}	10^{-15}
PC 3	f	0.20 ± 0.66^{a}	-0.81 ± 1.07^{b}	0.46 ± 0.52^{c}	10^{-15}
	m	0.40 ± 0.81^{a}	-0.98 ± 0.90^{b}	0.44 ± 0.38^{a}	10^{-15}

Table D9. Mean and standard deviation of adult body length (mm) and the first three principal components in males and females grouped by subfamily. The p-value was calculated using the Kruskal-Wallis test which assesses whether the distribution of each trait differs across subfamilies. Distinct superscripts indicate pairs of subfamilies with significantly different trait distributions according to a post-hoc Dunn test. n, sample size for each habitat category.

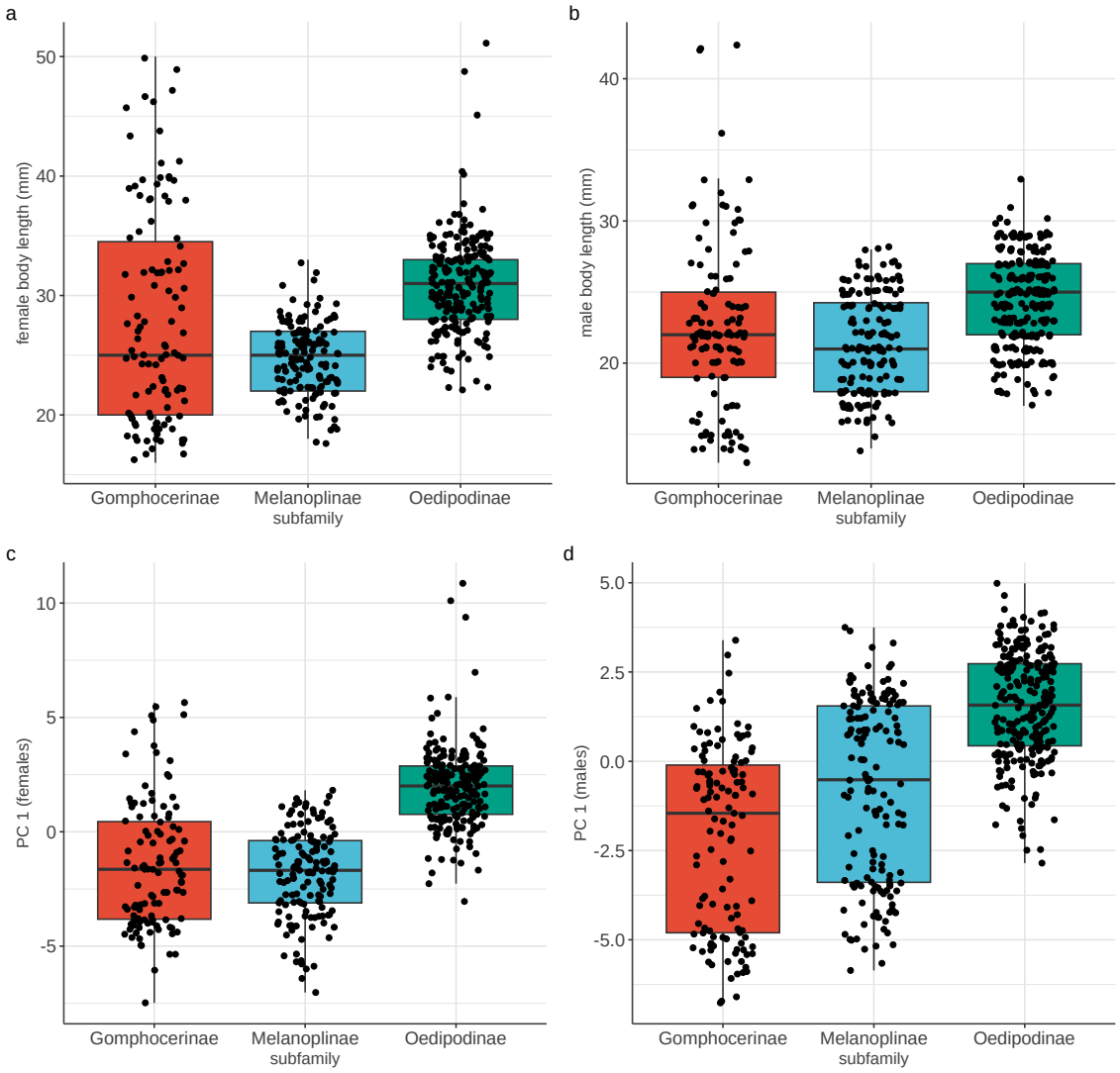


Figure D1. Boxplots illustrating the distribution of adult body length (mm) and the first principal component in females and males in the three most abundant subfamilies. Each point corresponds to an individual adult grasshopper.

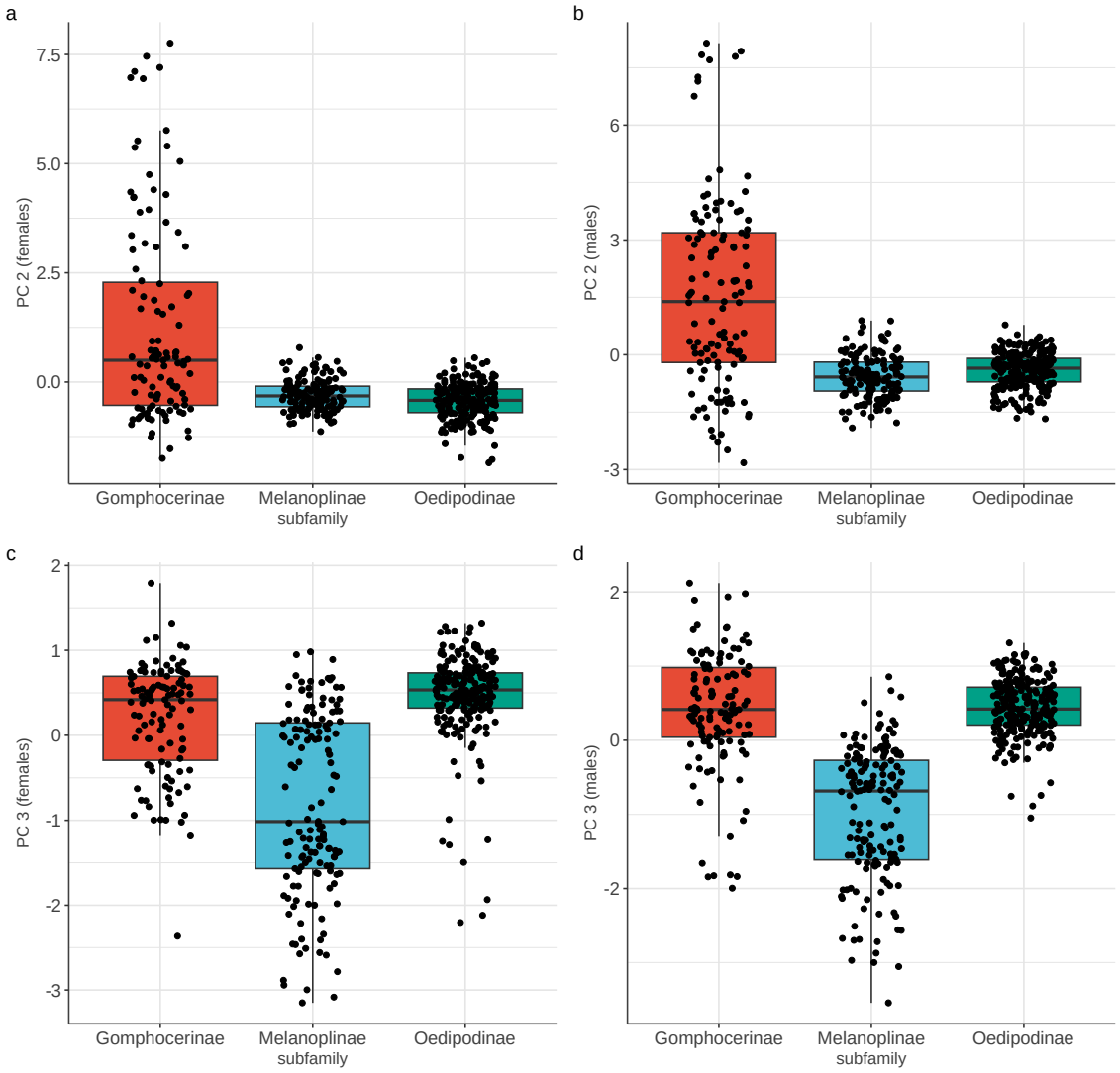


Figure D2. Boxplots illustrating the distribution of the second and third principal components in females and males in the three most abundant subfamilies. Each point corresponds to an individual adult grasshopper.

group	sex	habitat					p
		grassland	oak	pine-oak	conifer	disturbed	
all	f	27.1 ± 7.3^{a}	30.0 ± 6.8^{b}	27.9 ± 4.8^{ab}	27.8 ± 4.6^{ab}	25.7 ± 3.0^{a}	10^{-4}
Gomph	f	24.8 ± 7.9	29.7 ± 9.3	27.7 ± 7.8	29.0 ± 9.9	NA	0.09
Mel	f	24.7 ± 3.5	24.9 ± 3.3	24.0 ± 2.3	24.8 ± 3.3	25.1 ± 2.6	0.60
Oed	f	31.5 ± 3.4	31.5 ± 3.4	30.2 ± 3.2	29.9 ± 3.6	29.8 ± 2.2	0.12
all	m	21.2 ± 4.5^{a}	23.7 ± 4.2^{b}	23.0 ± 3.6^{ab}	22.8 ± 3.6^{ab}	24.4 ± 2.4^{b}	10^{-4}
Gomph	m	19.6 ± 4.4^{a}	24.7 ± 6.8^{b}	23.0 ± 2.5^{ab}	15.0^{ab}	NA	10^{-4}
Mel	m	21.2 ± 3.6^{a}	20.0 ± 2.5^{a}	20.2 ± 3.0^{a}	22.3 ± 3.9^{ab}	24.2 ± 2.2^{b}	10^{-5}
Oed	m	25.0 ± 2.9^{ab}	25.1 ± 2.6^{a}	24.5 ± 3.1^{ab}	23.1 ± 3.4^{b}	29^{ab}	0.001

Table D10. Mean and standard deviation of body length (mm) in the full assemblage and by subfamily in each habitat. The p-value was calculated using the Kruskal-Wallis test which assesses whether the distribution of each trait differs across habitats. Distinct superscripts indicate pairs of habitats with significantly different trait distributions according to a post-hoc Dunn test. Group codes: Gomph - Gomphocerinae; Mel - Melanoplinae; Oed - Oedipodinae.

group	sex	habitat					p
		grassland	oak	pine-oak	conifer	disturbed	
all	f	-0.66 ± 3.35^{a}	0.41 ± 2.90^{b}	-0.03 ± 2.39^{ab}	0.12 ± 2.50^{ab}	-0.73 ± 2.11^{ab}	0.006
Gomph	f	-2.21 ± 2.81	-1.14 ± 2.85	-1.26 ± 2.10	0.75 ± 5.84	NA	0.14
Mel	f	-1.74 ± 2.28	-1.77 ± 2.08	-2.30 ± 1.50	-1.88 ± 1.96	-1.20 ± 1.70	0.16
Oed	f	1.94 ± 3.13^{ab}	2.41 ± 1.62^{a}	1.66 ± 1.35^{ab}	1.50 ± 1.31^{b}	2.33 ± 2.15^{ab}	0.01
all	m	-1.79 ± 3.18^{a}	0.11 ± 2.49^{b}	0.40 ± 2.41^{b}	0.51 ± 2.25^{b}	1.24 ± 1.34^{b}	10^{-6}
Gomph	m	-3.67 ± 2.22^{a}	-1.23 ± 2.26^{b}	-0.03 ± 1.39^{b}	-6.72^{ab}	NA	10^{-6}
Mel	m	-0.82 ± 2.86^{ab}	-2.01 ± 1.85^{a}	-1.74 ± 2.43^{a}	-0.24 ± 2.71^{ab}	1.14 ± 1.26^{b}	10^{-5}
Oed	m	1.76 ± 1.56^{ab}	1.96 ± 1.27^{a}	1.63 ± 1.37^{ab}	0.99 ± 1.68^{b}	3.79^{ab}	0.001

Table D11. Mean and standard deviation of principal component PC1 in the full assemblage and by subfamily in each habitat. The p-value was calculated using the Kruskal-Wallis test which assesses whether the distribution of each trait differs across habitats. Distinct superscripts indicate pairs of habitats with significantly different trait distributions according to a post-hoc Dunn test. Group codes: Gomph - Gomphocerinae; Mel - Melanoplinae; Oed - Oedipodinae.

group	sex	habitat					p
		grassland	oak	pine-oak	conifer	disturbed	
all	f	0.04 ± 1.32^{ab}	0.37 ± 1.84^{a}	-0.21 ± 0.97^{ab}	-0.41 ± 0.46^{b}	-0.31 ± 0.49^{ab}	0.02
Gomph	f	0.56 ± 1.96	1.70 ± 2.53	1.00 ± 2.01	0.39 ± 1.29	NA	0.15
Mel	f	-0.19 ± 0.39	-0.26 ± 0.40	-0.41 ± 0.27	-0.36 ± 0.34	-0.19 ± 0.37	0.03
Oed	f	-0.37 ± 0.51	-0.42 ± 0.41	-0.46 ± 0.37	-0.47 ± 0.47	-1.09 ± 0.50	0.13
all	m	0.36 ± 1.84^{abe}	0.53 ± 2.14^{ae}	-0.32 ± 0.80^{bcde}	-0.55 ± 0.55^{cde}	-0.20 ± 0.54^{de}	10^{-4}
Gomph	m	0.93 ± 2.29	2.23 ± 2.81	1.25 ± 1.00	-0.41	NA	0.06
Mel	m	-0.49 ± 0.58^{ab}	-0.62 ± 0.41^{ab}	-0.82 ± 0.48^{a}	-0.55 ± 0.56^{ab}	-0.20 ± 0.55^{b}	10^{-3}
Oed	m	-0.26 ± 0.42	-0.36 ± 0.43	-0.36 ± 0.40	-0.54 ± 0.53	-0.30	0.14

Table D12. Mean and standard deviation of principal component PC2 in the full assemblage and by subfamily in each habitat. The p-value was calculated using the Kruskal-Wallis test which assesses whether the distribution of each trait differs across habitats. Distinct superscripts indicate pairs of habitats with significantly different trait distributions according to a post-hoc Dunn test. Group codes: Gomph - Gomphocerinae; Mel - Melanoplinae; Oed - Oedipodinae.

group	sex	habitat					p
		grassland	oak	pine-oak	conifer	disturbed	
all	f	0.09 ± 0.95^{a}	0.02 ± 0.96^{a}	-0.09 ± 0.95^{a}	-0.02 ± 1.04^{a}	0.08 ± 0.73^{a}	0.671
Gomph	f	0.32 ± 0.49	0.14 ± 0.75	0.22 ± 0.59	-0.10 ± 0.94	NA	0.66
Mel	f	-0.80 ± 1.08^{ab}	-1.26 ± 1.19^{a}	-1.25 ± 0.72^{a}	-0.61 ± 1.09^{ab}	0.07 ± 0.72^{b}	10^{-5}
Oed	f	0.51 ± 0.82	0.39 ± 0.54	0.51 ± 0.36	0.53 ± 0.39	0.12 ± 0.92	0.22
all	m	0.43 ± 0.78^{a}	-0.03 ± 0.99^{b}	-0.20 ± 1.00^{b}	0.02 ± 0.92^{b}	-0.36 ± 0.32^{c}	10^{-7}
Gomph	m	0.69 ± 0.70^{a}	0.15 ± 0.89^{b}	0.23 ± 0.38^{ab}	1.93^{ab}	NA	10^{-3}
Mel	m	-0.36 ± 0.83^{a}	-1.48 ± 1.01^{b}	-1.38 ± 0.80^{b}	-0.88 ± 0.81^{ab}	-0.36 ± 0.33^{a}	10^{-6}
Oed	m	0.52 ± 0.37	0.37 ± 0.40	0.41 ± 0.37	0.51 ± 0.37	-0.23	0.04

Table D13. Mean and standard deviation of principal component PC3 in the full assemblage and by subfamily in each habitat. The p-value was calculated using the Kruskal-Wallis test which assesses whether the distribution of each trait differs across habitats. Distinct superscripts indicate pairs of habitats with significantly different trait distributions according to a post-hoc Dunn test. Group codes: Gomph - Gomphocerinae; Mel - Melanoplinae; Oed - Oedipodinae.

APPENDIX E

PHOTOGRAPHS OF SELECT ORTHOPTERA

Acanthus piperatus

Figure E1. *Acantherus piperatus*, adult female collected at site SR1 in the Santa Rita Mountains on November 4, 2023.

Boopedon flaviventris

Figure E2. *Boopedon flaviventris*, adult male collected at site SR1 in the Santa Rita Mountains on November 4, 2023. All specimen records of this species are from southeastern Arizona, but observations with photos submitted on iNaturalist show that it also occurs along the Sierra Madre Occidental at least as far south as the Mexican state of Nayarit.

Arethaea sp.

Figure E3. *Arethaea* sp., adult male collected at Mount Graham on June 30, 2023. In this genus, only adult males have long wings that allow them to fly.

Figure E4. *Insara apache,* adult female collected at Mount Graham on June 30, 2023.

APPENDIX F

SUPPLEMENTARY POPULATION DATA

SUPPLEMENTARY POPULATION DATA

Description: Tables F1 through F6 provide the raw count data for the adult grasshoppers collected during our surveys of the Madrean sky islands in 2023. Each cell shows the number of adults of that species collected in the corresponding site on that date. Empty cells correspond to 0's. Data is only shown for species present on that date and only for sites that were visited on that date. However, we do include the count data for the sites that were surveyed during our first visit to each mountain range, as well as data that was collected during a preliminary visit to the Santa Catalina Mountains in May 2023. The full species names can be found in Table B1.

Counts of Adult Grasshoppers – Chiricahua Mountains

species	Chi1	Chi2	Chi3	Chi4	Chi5	Chi6	Chi7	Chi8	Chi9	Chi10	Chi11
A. sumichrasti			5		1						
A. mysteca			1	1	1						
E. simplex			1								
M. texana			3	1							
P. texana	3										
H. viridis	2										
A. conspersa				3	4						2
C. carinata						2					
T. ferruginosus						1					
T. cyaneipennis								1	2		
T. modesta										3	2
T. pallidipennis	12		4	4	5	1	1	3	6		11

Table F1.1. Count data for the Chiricahua Mountains on 2 July 2023.

species	Chi1	Chi3	Chi4	Chi5	Chi6	Chi7	Chi8	Chi9	Chi10	Chi11
A. sumichrasti		1								
A. deorum	1									
A. mysteca		2								
A. coloradus	1	2		1						
M. texana		1	2		1	2	1			
P. pallida	13									
P. texana	1						1			
S. montezuma		2	1		1		3			
C. huachucana		2	1		1	1				
M. desultorius		1			2			2	4	3
M. sanguinipes			1	1						
A. conspersa		1		1	1					
L. wheeleri			1							
M. plattei		1		1			2			
T. ferruginosus			2							
T. cyaneipennis								1		
T. modesta								3	4	9
T. pallidipennis		1		1			1	1		

Table F1.2. Count data for the Chiricahua Mountains on 6 August 2023.

Counts of Adult Grasshoppers – Chiricahua Mountains

species	Chi1	Chi3	Chi4	Chi5	Chi6	Chi7	Chi8	Chi9	Chi10	Chi11
A. deorum	1									
M. texana		1								
P. pallida	1									
C. huachucana		2					3			
M. desultorius								2		
T. cyaneipennis							1			
T. modesta								1	1	
T. pallidipennis				1					1	

Table F1.3. Count data for the Chiricahua Mountains on 8 October 2023.

Counts of Adult Grasshoppers – Huachuca Mountains

species	Hu1	Hu2	Hu3	Hu4	Hu5	Hu6	Hu7	Hu8	Hu9	Hu10	Hu11
A. sumichrasti				1	1						
A. deorum		1									
A. mysteca	1										
A. coloradus	1										
H. cinereus				1							
P. texana		2	1								
R. viatorius											1
S. montezuma				1							
C. huachucana							1				
M. desultorius							6			1	1
A. conspersa				2		1					
T. ferruginosus			1								
T. cyaneipennis											1
T. modesta											1
T. pallidipennis	6	5	10	7	6	8	3	5	6	5	4

Table F2.1. Count data for the Huachuca Mountains on 7 July 2023. Site names abbreviated to Hu for space.

species	Hua1	Hua2	Hua3	Hua4	Hua5	Hua6	Hua7	Hua8	Hua9	Hua10
A. sumichrasti			1	2	2					
A. deorum	1									
A. mysteca	1	2		2	2					
A. coloradus				1	1					
H. cinereus				1						
M. texana						1				
O. obscura			1	1						
P. pallida	1									
P. snowi		4	1	4						
S. montezuma	1			3	1	2				
B. humphreysii				2	1					
C. huachucana							1	1		7
M. desultorius			1			1	5	1		3
L. wheeleri						1				
T. ferruginosus			1							
T. cyaneipennis				1		3	1			
T. modesta			6			2				1
T. pallidipennis			2	3						

Table F2.2. Count data for the Huachuca Mountains on 11 August 2023.

Counts of Adult Grasshoppers – Huachuca Mountains

species	Hua1	Hua2	Hua3	Hua4	Hua5	Hua6	Hua7	Hua8	Hua9	Hua10
C. carinata	1									
T. pallidipennis					1					

Table F2.3. Count data for the Huachuca Mountains on 11 November 2023.

species	Pin1	Pin2	Pin3	Pin4	Pin5	Pin6	Pin7	Pin8	Pin9	Pin10	Pin11
A. deorum	1										
C. parviceps	1	2									
P. texana	2										
M. flavidus	1										
M. pictus								1			
M. sanguinipes	2					2	28	3	13	15	17
T. pallidipennis		1		2	1	2		1	1	2	2

Table F3.1. Count data for the Pinal Mountains on 17 June 2023.

species	Pin1	Pin2	Pin3	Pin4	Pin5	Pin6	Pin7	Pin8	Pin9	Pin10	Pin11
A. coloradus								2			
P. texana	2										
S. montezuma	1										
C. huachucana					1						
H. viridis	4										
M. desultorius				1		1					2
M. franciscanus										2	
M. sanguinipes										7	3
L. azteca										1	
T. modesta				5		9		1		3	
T. pallidipennis								1			

Table F3.2. Count data for the Pinal Mountains on 19 August 2023.

species	Pin1	Pin2	Pin3	Pin4	Pin5	Pin6	Pin7	Pin8	Pin9	Pin10	Pin11
A. deorum	2										
C. huachucana									2		
M. desultorius				1			1		6	2	1
M. franciscanus										1	
T. modesta						3					
P. tshivavensis										1	1

Table F3.3. Count data for the Pinal Mountains on 23 September 2023.

Counts of Adult Grasshoppers – Pinaleño Mountains

species	MG1	MG2	MG3	MG4	MG5	MG6	MG7	MG8	MG9	MG10	MG11	MG12	MG13	MG14	MG15
A. sumichrasti					1										
A. deorum		2													
A. mysteca		1													
A. coloradus	2														
M. texana			2												
P. pallida	1														
P. texana		1		4											1
H. viridis	3			2											
M. desultorius					1										
M. sanguinipes	2	2								1		1	2	2	10
A. conspersa						1									
C. carinata										1		2	1		
M. plattei				1											
T. cyaneipennis							1								
T. modesta					3								3	1	
T. pallidipennis				1	1		2				1	3		2	10
X. corallipes	1														

Table F4.1. Count data for the Pinaleño Mountains on 1 July 2023.

Counts of Adult Grasshoppers – Pinaleño Mountains

species	MG1	MG2	MG3	MG4	MG5	MG7	MG10	MG12	MG13	MG14	MG15
A. sumichrasti						1					
A. deorum		1	1	1							
A. coloradus	1		1			3					
M. texana			1								
P. pallida	1	1	1								
P. texana	1			1							
S. montezuma		1									
B. humphreysii			1								
C. huachucana						1					
H. viridis	6	3	6								
M. desultorius		1	1								
M. franciscanus											
M. sanguinipes	2	2					1			1	3
C. carinata									1		
L. gibbosus											1
M. plattei				2							
T. modesta			1		3	1			2	3	3
T. pallidipennis	1	2									
X. corallipes	1										

Table F4.2. Count data for the Pinaleño Mountains on 5 August 2023.

Counts of Adult Grasshoppers – Pinaleño Mountains

species	MG1	MG2	MG3	MG4	MG5	MG7	MG10	MG12	MG13	MG14	MG15
A. deorum		1		1							
H. cinereus			1								
M. texana		3									
P. pallida	1										
S. montezuma			1		1						
B. humphreysii		1									
C. huachucana				1				1		2	
M. desultorius		4	1								
M. flavidus	1										
M. sanguinipes											2
C. carinata							1				
T. cyaneipennis					1	1					2
T. modesta					1			1		4	2
T. pallidipennis							1			1	3
X. corallipes				1							

Table F4.3. Count data for the Pinaleño Mountains on 7 October 2023.

Counts of Adult Grasshoppers – Santa Catalina Mountains

species	SC1	SC2	SC3	SC5	SC6	SC7	SC10	SC11	SC13
S. nitens						1			
M. sanguinipes		1				3		1	
T. ferruginosus		1							
T. pallidipennis					4				
X. corallipes		1						1	1

Table F5.1. Count data for the Santa Catalina Mountains on 20 May 2023. *Note:* This was an exploratory visit to the Santa Catalina Mountains and these counts were not included in the data used for ecological analysis.

species	SC1	SC2	SC3	SC4	SC5	SC6	SC7	SC8	SC9	SC10	SC11	SC12	SC13
A. sumichrasti			2										
P. texana		3	1										
R. viatorius		1											
M. sanguinipes							1	2			3		1
A. conspersa							1						
C. carinata					1								
T. inconspicua								1					
T. modesta											1		
T. pallidipennis	1	4	7		3	4	8	10	6	8	2	3	2
X. corallipes											1		

Table F5.2. Count data for the Santa Catalina Mountains on 24 June 2023.

species	SC1	SC2	SC3	SC5	SC7	SC8	SC9	SC10	SC11	SC13
S. montezuma				1						
C. huachucana									1	
M. desultorius				2						
M. sanguinipes			1							
T. cyaneipennis						1	1			
T. modesta					1		6	1	1	
T. pallidipennis		1	3							

Table F5.3. Count data for the Santa Catalina Mountains on 30 August 2023.

species	SC1	SC2	SC3	SC5	SC7	SC8	SC9	SC10	SC11	SC13
P. pallida		1								
C. huachucana							1			
M. sanguinipes									1	
P. nebrascensis		2								
C. carinata		1								
T. modesta					1		1			
T. pallidipennis	4	4	2		3	3	1		1	1

Table F5.4. Count data for the Santa Catalina Mountains on 14 October 2023.

Counts of Adult Grasshoppers – Santa Rita Mountains

species	SR1	SR2	SR3	SR4	SR5	SR6	SR7	SR8	SR9
A. sumichrasti	1					2			
A. mysteca	1					1			
A. coloradus	1			2		3	1		4
P. snowi	8								
P. texana	1	2		1			2		1
C. huachucana								4	1
M. desultorius								2	1
A. conspersa								1	
L. azteca		1							
T. cyaneipennis									1
T. pallidipennis			3	2	1	3	1	1	8

Table F6.1. Count data for the Santa Rita Mountains on 15 August 2023.

species	SR1	SR2	SR3	SR4	SR5	SR6	SR7	SR8	SR9
A. deorum	1								
A. mysteca	1								
A. coloradus							2		4
P. snowi	2			2			1		
S. montezuma	1	2		1		1	2		2
B. humphreysii	1	1		1					
C. huachucana						2		1	2
H. viridis									
M. desultorius									15
P. nebrascensis				1		2		14	
L. wheeleri									1
T. cyaneipennis									1
T. pallidipennis		1	1						1

Table F6.2. Count data for the Santa Rita Mountains on 9 September 2023.

Counts of Adult Grasshoppers – Santa Rita Mountains

species	SR1	SR2	SR3	SR4	SR5	SR6	SR7	SR8	SR9
A. piperatus	2			1					
A. deorum				1					
B. flaviventris	1			1					
M. bivittata	1								
O. obscura	1								1
S. montezuma						1			
C. huachucana									1
M. lakinus	1								
M. desultorius				2		2			
P. nebrascensis		1		1					
T. pallidipennis	2	2	2	8		5	1		

Table F6.3. Count data for the Santa Rita Mountains on 4 November 2023.

Orthoptera Counts and Species Richness by Site

site	elev (m)	# individuals				# species			
		2 July	6 Aug	8 Oct	total	2 July	6 Aug	8 Oct	total
Chi 1	1425	15	16	2	33	3	4	2	6
Chi 2	1536	0			0	0			0
Chi 3	1669	13	13	3	29	6	10	2	11
Chi 4	1765	9	8	0	17	5	6	0	10
Chi 5	1862	11	5	1	17	5	5	1	8
Chi 6	1948	4	6	0	10	4	5	0	5
Chi 7	2013	1	3	0	4	3	3	0	4
Chi 8	2246	4	8	4	16	3	5	2	7
Chi 9	2359	8	7	3	18	2	4	2	4
Chi 10	2514	3	8	2	13	1	2	2	3
Chi 11	2567	12	12	0	24	3	2	1	4
total		80	86	15	181	12	18	8	20

Table F7.1. Number of adults and species per site in the Chiricahua Mountains.

site	elev (m)	# individuals				# species			
		7 July	11 Aug	11 Nov	total	7 July	11 Aug	11 Nov	total
Hua 1	1465	8	4	1	14	3	5	1	8
Hua 2	1578	8	6	0	14	3	3	0	5
Hua 3	1640	12	13	0	25	3	7	1	8
Hua 4	1742	12	20	0	32	6	10	1	11
Hua 5	1827	7	7	1	15	2	5	1	6
Hua 6	1994	9	10	0	19	2	6	0	8
Hua 7	2060	10	7	0	17	3	3	0	4
Hua 8	2157	5	2	0	7	1	2	0	3
Hua 9	2258	6	0	0	6	1	0	0	1
Hua 10	2322	13	12	0	25	3	3	0	5
Hua11	2457	9			8	6			6
total		90	81	2	173	15	18	2	22

Table F7.2. Number of adults and species per site in the Huachuca Mountains.

Orthoptera Counts and Species Richness by Site

site	elev (m)	# individuals				# species			
		17 June	19 Aug	23 Sept	total	17 June	19 Aug	23 Sept	total
Pin 1	1332	9	7	2	18	8	3	1	9
Pin 2	1433	3	0	0	3	2	0	0	2
Pin 3	1543	0	0	0	0	1	0	0	1
Pin 4	1664	2	6	1	9	2	2	1	3
Pin 5	1747	1	1	0	2	2	1	0	2
Pin 6	1805	4	10	3	17	2	2	1	4
Pin 7	2989	28	0	1	29	2	1	2	3
Pin 8	2101	5	4	1	10	4	3	1	6
Pin 9	2180	14	0	8	22	2	0	2	4
Pin 10	2301	17	13	4	34	3	4	3	8
Pin 11	2373	19	5	2	26	2	2	1	4
total		102	46	22	170	8	11	7	18

Table F7.3. Number of adults and species per site in the Pinal Mountains.

site	elev (m)	# individuals				# species			
		1 July	5 Aug	7 Oct	total	1 July	5 Aug	7 Oct	total
MG 1	1362	19	13	2	34	5	6	2	8
MG 2	1454	6	8	9	23	5	6	4	10
MG 3	1565	2	10	3	15	3	8	3	10
MG 4	1660	8	10	3	21	15	4	3	7
MG 5	1786	6	3	3	12	4	1	4	6
MG 6	1844	1			1	1			1
MG 7	1969	3	6	1	10	3	4	1	7
MG 8	2005	0			0	0			0
MG 9	2176	1			1	1			1
MG 10	2254	2	2	2	6	2	3	2	5
MG 11	2359	1			1	1			1
MG12	2482	6	1	1	8	3	0	2	5
MG13	2590	6	3	0	9	3	2	0	4
MG14	2690	6	7	5	18	4	3	3	6
MG15	2770	23	7	9	39	4	3	4	7
total		90	70	38	198	17	18	14	23

Table F7.4. Number of adults and species per site in the Pinaleño Mountains (Mt. Graham).

Orthoptera Counts and Species Richness by Site

site	elev (m)	# individuals				# species			
		24 June	30 Aug	14 Oct	total	24 June	30 Aug	14 Oct	total
SC 1	1327	1	0	4	5	3	2	1	4
SC 2	1466	8	1	8	17	4	2	4	9
SC 3	1564	10	4	2	16	4	2	1	4
SC 4	1680	1			1	1			1
SC 5	1776	4	3	0	7	3	2	0	4
SC 6	1913	4			4	1			1
SC 7	2181	10	1	4	15	3	1	2	4
SC 8	2270	13	1	3	17	3	1	1	4
SC 9	2375	6	7	3	16	1	2	3	4
SC 10	2430	8	0	0	8	1	2	0	3
SC 11	2567	7	2	2	11	4	3	2	5
SC 12	2665	3			3	1			1
SC 13	2743	3	0	1	4	2	0	1	2
total		78	19	27	124	10	8	7	16

Table F7.5. Number of adults and species per site in the Santa Catalina Mountains.

site	elev (m)	# individuals				# species			
		7 July	11 Aug	11 Nov	total	7 July	11 Aug	11 Nov	total
SR 1	1348	12	6	7	25	6	5	6	15
SR 2	1429	3	4	3	10	2	3	2	6
SR 3	1568	3	1	2	6	1	2	1	2
SR 4	1632	5	5	15	25	4	4	7	12
SR 5	1746	1	0	0	1	1	0	0	1
SR 6	1874	9	8	5	22	6	3	3	9
SR 7	1948	4	5	1	10	4	3	1	5
SR 8	2054	8	15	0	23	4	2	0	5
SR 9	2159	16	26	2	44	6	7	2	9
total		61	70	35	166	11	12	11	22

Table F7.6. Number of adults and species per site in the Santa Rita Mountains.