

GEOGRAPHIC PATTERNS OF GROUND-DWELLING ARTHROPODS ACROSS AN ECOREGIONAL TRANSITION IN THE NORTH AMERICAN SOUTHWEST

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ABSTRACT.—We examined the biogeographic patterns of ground-dwelling arthropod communities across a heterogeneous semiarid region of the Southern Rio Grande Rift Valley of New Mexico. Our 3 sites included portions of 5 ecoregions, with the middle site a transition area where all ecoregions converged. We addressed the following 3 questions: (1) Do the species assemblage patterns for ground arthropods across habitats and sites conform to recognized ecoregions? (2) Are arthropod assemblages in distinct vegetation-defined habitats within an ecoregion more similar to each other or to assemblages in similar vegetation-defined habitats in other ecoregions? (3) Is there a detectable edge effect with increased arthropod diversity in the area of converging ecoregions? We encountered 442 target arthropod species from pitfall traps operating continuously for 7 years over a series of different habitats at each of the 3 sites. We examined geographic distributions of spider and cricket/grasshopper species in detail, and they showed affinities for different ecoregions, respectively. Each habitat within a study site supported a unique overall arthropod assemblage; nevertheless, different habitats at the same site were more similar to each other than they were to similar habitats at other sites. Overall arthropod species richness was greatest in the area where all 5 ecoregions converged. Arthropod species and their geographic distributions are poorly known relative to vascular plants and vertebrate animals. Findings from this research indicate that ecoregional classification is a useful tool for understanding biogeographic patterns among arthropods.

Key words: biome transition, crickets, diversity, ecoregion, ecotone, edge effect, grasshoppers, insects, species, spiders.

Geographic distribution patterns of plant and animal species result from multiple factors, including proximity to historical and evolutionary source areas, climate, distribution and availability of environmental resources, and biotic interactions (Ricklefs and Schluter 1993, Brown and Lomolino 1998, Lomolino and Heaney 2004). Much is known about the geographic distribution and diversity patterns of vascular plants and vertebrate animals, however, relatively little is known about the geographic patterns and processes accounting for the distributions of most terrestrial invertebrates (Parmenter et al. 1995, Ricketts et al. 1999). One of the goals of our research was to provide much-needed information on the distribution and abundance patterns of terrestrial arthropods.

At the continental scale, conceptual biomes (Whittaker 1975, Ricklefs and Miller 2000), or more finely delineated ecoregions (e.g., Ricketts et al. 1999), are biogeographic areas with similar climates, landscapes, and biotic assemblages that are more similar to each other than to those in adjacent ecoregions. The association

of species with biogeographic regions includes abiotic factors (especially climate) and biotic factors such as plant-animal and predator-prey interactions (Shmida and Wilson 1985, Brown 1995). Species richness is expected to increase at ecotones (edge effect of Odum 1971, Holland et al. 1991, Risser 1993, 1995), the areas where different regional assemblages converge. The extent of species overlap depends on individual species' distributions, the number and steepness of environmental gradients, and the number of converging biogeographic regions.

The American Southwest is geologically young, with a flora and fauna that developed mostly during the Quaternary Period (Axelrod 1958, Van Devender and Spaulding 1983, Van Devender 1995). The area supports some of the most topographically (Hunt 1983) and biologically diverse semiarid temperate landscapes in the world (Brown 1982, Parmenter et al. 1995), ranging from hot, dry lowland deserts to cool, moist montane forests. Within the Southwest, several continental ecoregions (Ricketts et al. 1999) converge across the Southern Rio Grande Rift Valley that bisects New Mexico from north

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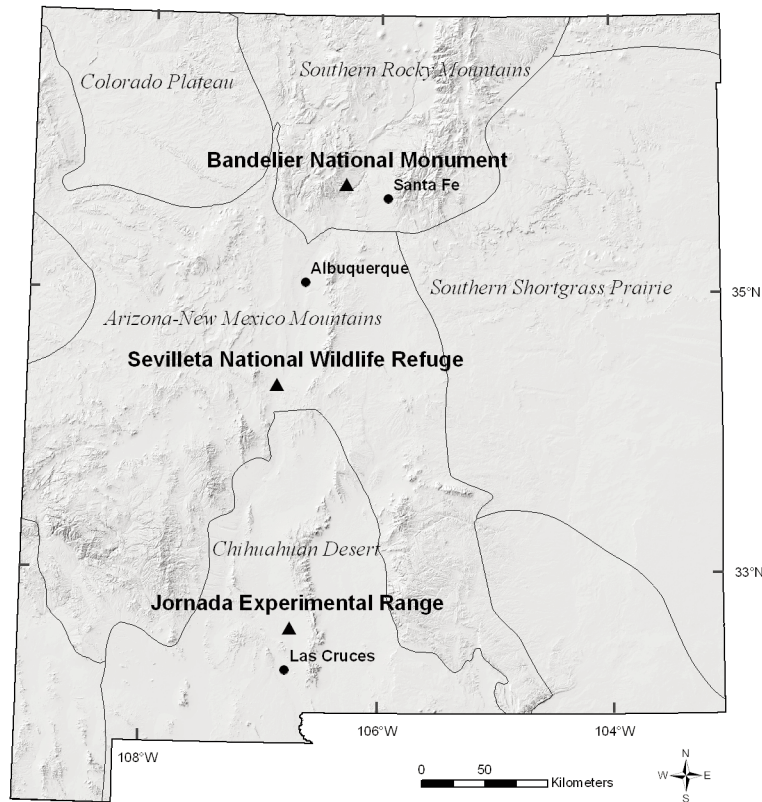


Fig. 1. Map of the study area and ecoregion boundaries.

to south (Hawley 1978): forests of the Southern Rocky Mountains (sensu current Nature Conservancy / World Wildlife Fund designation) and forests of the Arizona–New Mexico Mountains (sensu current Nature Conservancy / World Wildlife Fund designation) occupy the high elevations; and the Colorado Plateau, the Chihuahuan Desert, and the Western Short Grasslands (Southern Shortgrass Prairie, sensu current Nature Conservancy / World Wildlife Fund designation) all converge in the lowlands (Fig. 1). Additionally, the Southern Rio Grande Rift Valley spans the convergence of 3 geographically higher-ranking bioregions: eastern North America to the east, northern Mexico to the south, and western North America to the north (Ricketts et al. 1999).

The goal of this study was to assess geographic patterns of arthropod communities associated with landscapes across this area of ecoregion transitions. We focused on ground-dwelling arthropods, which have important roles in semiarid systems as detritivores, her-

bivores, and predators (Crawford 1981, Whitford 1986, Polis 1991). To better understand the biogeography of these arthropods, we addressed the following questions: (1) What are the species assemblage patterns for ground arthropods across the study sites and across within-site habitats, and do they conform to recognized ecoregions (sensu Ricketts et al. 1999)? (2) Are arthropod assemblages in distinct vegetation-defined habitats within an ecoregion more similar to each other than to assemblages in similar vegetation-defined habitats in other ecoregions? (3) Are there detectable edge effects (Odum 1971) for increased arthropod diversity in the transition area of converging ecoregions?

METHODS

Study Sites

This study was conducted at 3 sites located along the Southern Rio Grande Rift Valley in New Mexico (Fig. 1). A series of 3–4 local

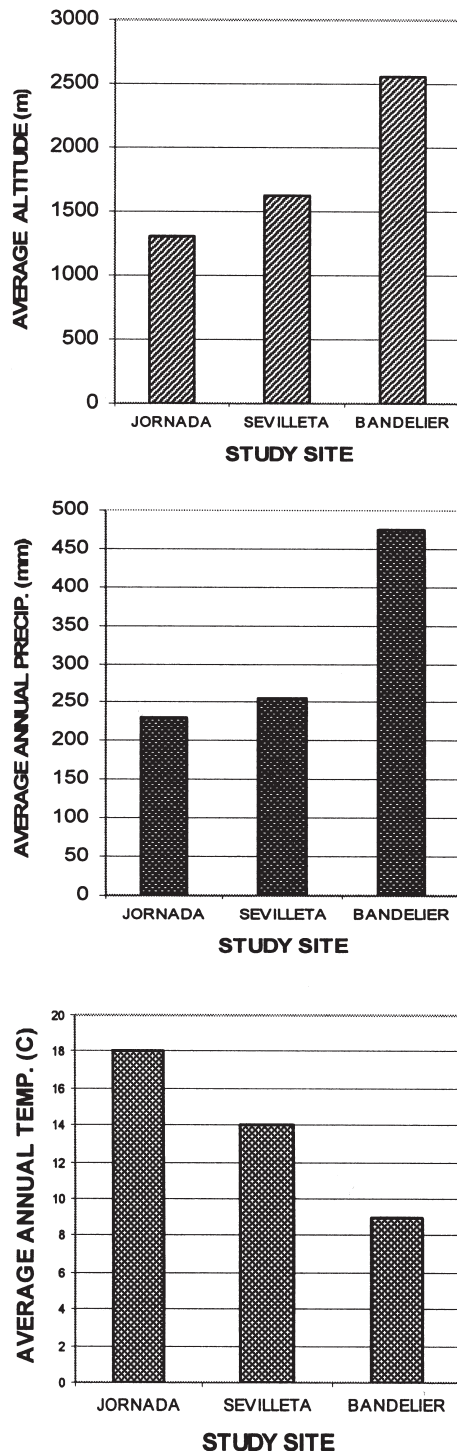


Fig. 2. Average elevations (m asl) (a), long-term average annual precipitation (b); and long-term average daily ambient temperatures (c) from each of the 3 principal study sites.

habitats recognized on the basis of plant community classifications (Dick-Peddie 1993) were sampled within each study site, for a total of 10 habitat samples across a biogeographic transition region from the Chihuahuan Desert to the south, the Southern Rocky Mountains to the north, the Arizona–New Mexico Mountains and Colorado Plateau to the west, and the Southern Shortgrass Prairie to the east (Ricketts et al. 1999; Fig. 1). Dick-Peddie (1993) and Brown (1982) provide detailed hierarchical vegetation classifications for the floristic and environmental characteristics of this region.

The 3 study sites were associated with 3 different long-term ecological research programs: the National Science Foundation (NSF)–funded Jornada Basin Long-Term Ecological Research (LTER) program, the NSF Sevilleta LTER program, and the United States Geological Survey, Jemez Mountains Field Station. The habitats used for this study were representative of the ecoregions listed above and were the dominant environments across each of the 3 research sites.

The Chihuahuan Desert ecoregion (Ricketts et al. 1999), consisting of Chihuahuan Desert scrub and desert grassland communities (Dick-Peddie 1993) in the southern Rio Grande valley of New Mexico, was represented by 4 habitats in the Jornada Basin (JRN) in south central New Mexico: (1) mesquite (*Prosopis glandulosa*) sand dune fields, 1330 m, 32°33'0"N, 106°42'39"W (datum NAD27 for all coordinates); (2) tarbush (*Flourensia cernua*) basin floor, 1315 m, 32°37'09"N, 106°47'13"W; (3) creosotebush (*Larrea tridentata*) piedmont slopes, 1355 m, 32°40'04"N, 106°46'12"W; and (4) black grama (*Bouteloua eriopoda*) grassland, 1318 m, 32°29'22"N, 106°46'47"W.

The Sevilleta National Wildlife Refuge (SEV) in the central Rio Grande valley of New Mexico was geographically centered between the JRN to the south and Bandelier (see below) to the north. The SEV also represented a region of multiple ecoregional transitions from the north, south, east, and west. The SEV was located within the Arizona–New Mexico Mountains ecoregion, yet the lowland environments contained flora characteristic of the surrounding low-elevation Chihuahuan Desert and the Southern Shortgrass Prairie ecoregions. We sampled 3 principal habitats at the SEV: (1) creosotebush piedmont (Chihuahuan Desert ecoregion; Ricketts et al. 1999), 1615 m,

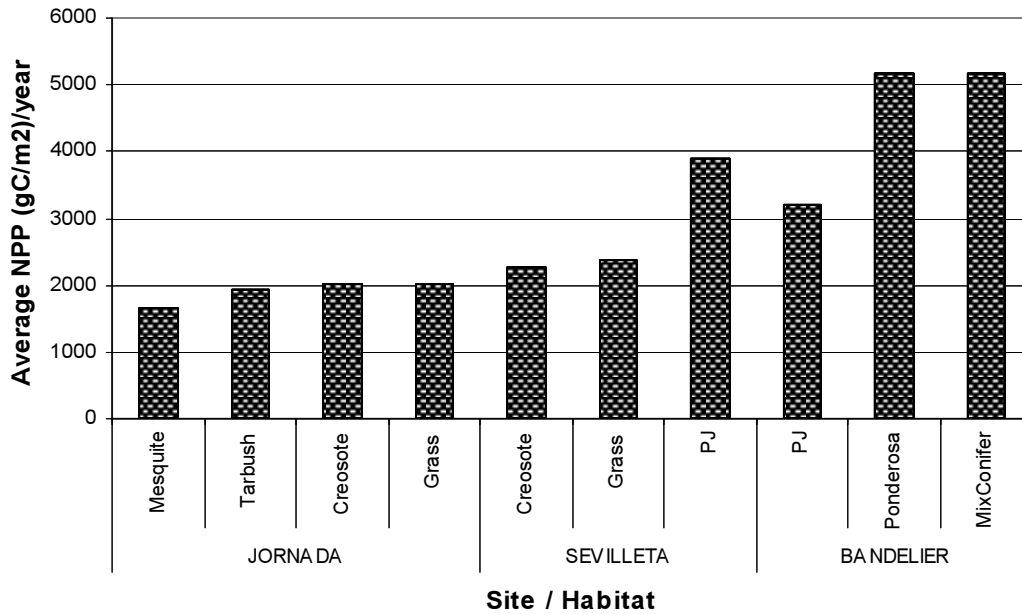


Fig. 3. Average annual net primary production among study sites and habitats estimated from MODIS remote sensing data, averaged over the years 2000–2002.

34°19'59.0"N, 106°44'9"W; (2) black grama grassland (Chihuahuan Desert ecoregion) mixed with some blue grama (*Bouteloua gracilis*; Southern Shortgrass Prairie and Colorado Plateau), 1616 m, 34°20'17.0"N, 106°43'3"W; and (3) pinyon-juniper (*Pinus edulis* and *Juniperus monosperma*, respectively) woodland (Arizona–New Mexico Mountains forest ecoregion), 1976 m, 34°22'6.3"N, 106°32'6"W.

Three habitats at Bandelier National Monument (BNM) in the Jemez Mountains at the north end of the Southern Rio Grande Rift valley represented higher-elevation ecoregions and formed an elevational gradient: (1) pinyon-juniper woodland (Arizona–New Mexico Mountains forest ecoregion), 1948 m, 35°49'47"N, 106°22'4"W, with variable densities of pinyon (*P. edulis*) and juniper trees (*J. monosperma*); (2) ponderosa pine (*Pinus ponderosa*) forest (Arizona–New Mexico Mountains forest ecoregion), 2454 m, 35°45'45"N, 106°15'52"W, with moderate to open conifer canopies; and (3) montane mixed conifer forest (*P. ponderosa*, *Pseudotsuga menziesii*, *Pinus strobiformis*, *Abies concolor*, *Populus tremuloides*; Southern Rocky Mountains forest ecoregion), 2712 m, 35°51'6"N, 106°24'41"W, with dense conifer canopy.

Elevation and long-term average precipitation increased from JRN to BNM (Fig. 2a–b),

but long-term average annual ambient temperatures decreased (Fig. 2c). We used moderate resolution imaging spectroradiometer (MODIS) remotely-sensed data (Zhao et al. 2005, Zhao and Running 2006) averaged from 2000 to 2002 to estimate aboveground plant net primary production (ANPP; a 1-km pixel centered on pitfall traps within each habitat type per site). Plant productivity at JRN was consistently lower than at SEV or BNM; estimated ANPP values were highest at BNM (Fig. 3)

Arthropods

Ground arthropods were sampled from pitfall traps (Southwood 1966, Digweed et al. 1995, Ward et al. 2001, Woodcock 2005) consisting of small plastic cups (7.5 cm top diameter × 10 cm deep, 0.25-L volume) placed inside small steel cans (7.5 cm top diameter × 10 cm deep) that were dug into the ground until the top of the can was level with the soil surface. Propylene glycol was used as the preservative, and tile covers (or local rocks at BNM where elk [*Cervus elaphus*] were attracted to artificial covers) protected the samples from weather. Replicate lines of traps (3 at JRN, 5 at SEV, and 5 at BNM) 30–50 m long were placed in each habitat type at each study site. Arthropod species richness and arthropod

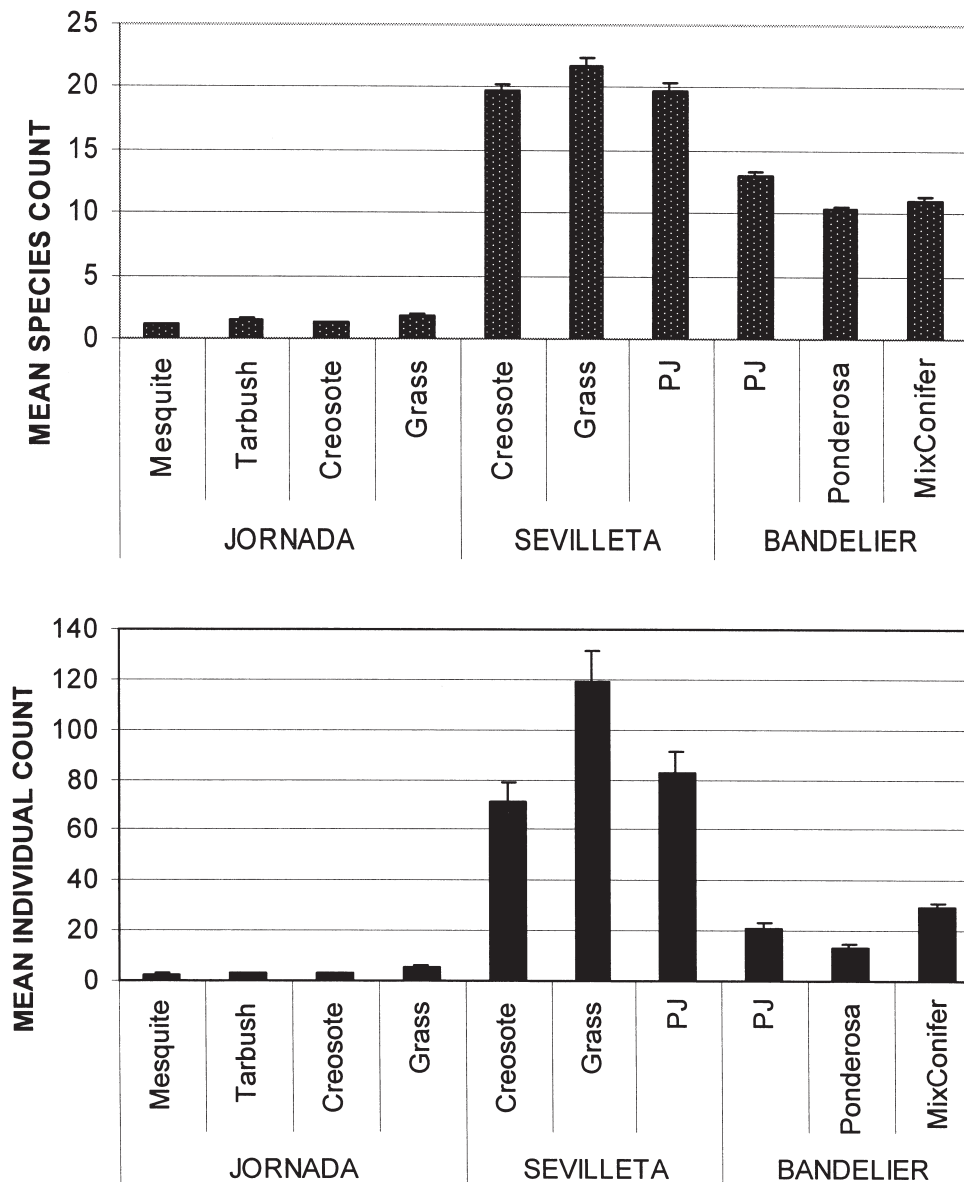


Fig. 4. Ground arthropod species richness among different habitats across the 3 principal study sites (a). Ground arthropod abundance across different habitats across the 3 principal study sites (b). Values are means per trap per replicate plot per year, with 1 standard error, over a 7-year period (1996–2002).

abundance were averaged over all traps by habitat. Trap line locations were subjectively chosen to represent a range of environments within each habitat type. Traps were left open continuously and arthropods were collected every 2 months from 1996 to 2002. Trap lines within habitats were located within 10 km of each other, and all habitat types within a study site were no more than 20 km apart.

Target taxa (i.e., taxa that we studied) included only those arthropods that are known to live primarily on the ground and that are appropriately sampled by pitfall traps (Uetz and Unzicker 1976, Thomas and Sleeper 1977, Adis 1979): spiders (4 families), bristletails (1 family), crickets (3 families), grasshoppers (2 families), true bugs (2 families), and beetles (4 families), as well as scorpions, sun spiders, centipedes, and

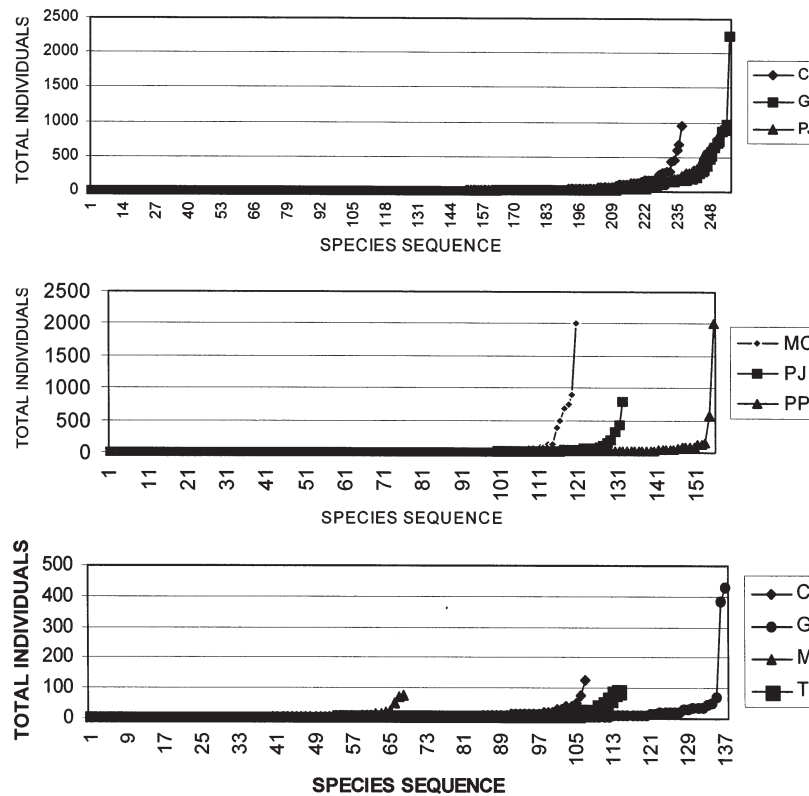


Fig. 5. Species richness and abundance curves for ground arthropods from the Sevilleta (a), Bandelier (b), and Jornada (c) habitats from 1996 to 2002.

millipedes (see Appendix 1 for scientific names of classes, orders, and families). Taxonomic classification followed Arnett (2000) for ranks from the class to the subfamily level and Poole and Gentili (2003) for genera and species. We used published distribution information to analyze patterns of grasshoppers/crickets and spiders in detail (Appendix 2). Two of us were specialists on the taxonomy, biogeography, and ecology of grasshoppers (D.C. Lightfoot) and spiders (S.L. Brantley) relative to other arthropod groups. Voucher specimens representing all target taxa were deposited in the Museum of Southwestern Biology, Division of Arthropods, University of New Mexico, Albuquerque.

Data Analysis

Multivariate and univariate data analyses were performed with PC SAS (Statistical Analysis Systems, v. 8.2; SAS Institute, Inc. 2003) software. We used nonparametric agglomerative hierarchical unweighted pair-group average cluster analysis (SAS, PROC CLUS) as a

descriptive method to examine similarities of arthropod species assemblages among and within habitats, based on Euclidean distance as a measure of the similarity of species composition between habitats and sites. Only species that were represented by 10 or more observations over the entire study period were included in that analysis, thereby emphasizing only relatively common or important taxa, not rare species that may not have been adequately sampled. We used log-transformed count data for canonical discriminant function analysis (CDFA; SAS, PROC CANDISC) to test the hypothesis of no spatial differences among site habitats based on arthropod taxa/trophic groups (i.e., the family-level ranks listed above), and to provide ordinations of habitats within sites based on arthropod composition. Large numbers of species encountered and unequal sample variances associated with various species counts (see results section, Fig. 4a–c) precluded us from using CDFA with species-level data.

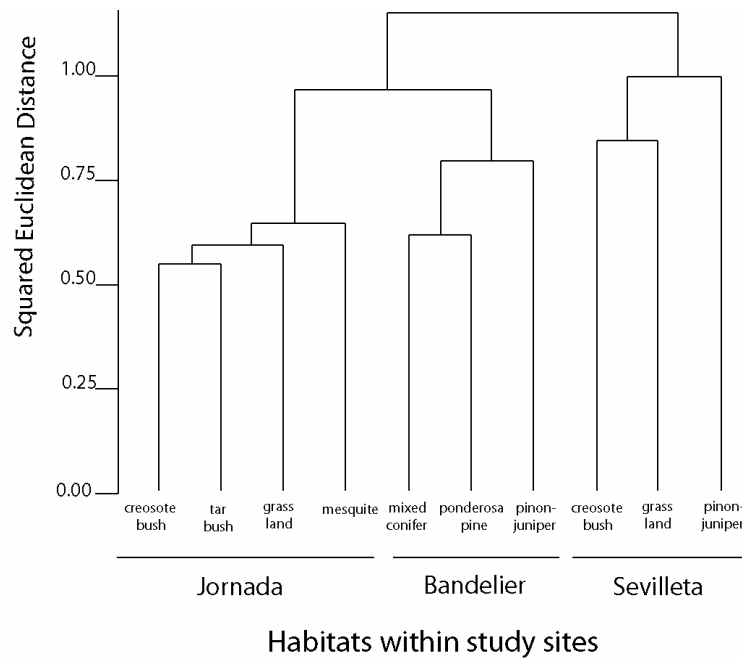


Fig. 6. Cluster analysis dendrogram of the different habitats from the 3 study sites based on ground arthropod species composition. Group average linkage method scaled by squared Euclidean distance. Habitat codes: con = mixed conifer, cre = creosotebush, gra = grassland, mes = mesquite, pj = pinyon-juniper, pon = ponderosa pine.

RESULTS

Species Diversity Patterns of Ground Arthropod Assemblages

We encountered a total of 442 target taxa across the 3 study sites over the 7-year period (Appendix 1). The greatest species richness was at SEV with 306 species, followed by BNM with 190 species and JRN with 144 species.

The greatest species richness was at the SEV black grama grassland followed by the SEV pinyon-juniper woodland and creosotebush habitats (Fig. 4a). The SEV grassland had the highest species richness and highest overall abundance of individuals (Fig. 5a). Species richness among BNM montane habitats was lowest at the high-elevation montane mixed conifer and midelevation ponderosa pine forests, and greatest at the low-elevation pinyon-juniper woodland habitat (Figs. 4a, 5b). Species richness across the 4 JRN Chihuahuan Desert habitats was greatest in the black grama grassland, followed by the tarbush, creosotebush, and mesquite sand dune habitats, respectively (Figs. 4a, 5c).

Abundance or counts of arthropod taxa followed patterns similar to those of species rich-

ness (Figs. 4b, 5). Ground arthropod counts averaged over the 7-year study period were greatest at the SEV sites, of which the black grama grassland habitat supported by far the greatest numbers of arthropods (Fig. 4b). BNM had the 2nd-greatest overall arthropod abundance, ranging from highest in the montane conifer forest, followed by the pinyon-juniper woodland and then the ponderosa pine forest. The Chihuahuan Desert habitats at JRN had the lowest overall ground arthropod counts, with greatest abundance within the black grama grassland.

Spatial Patterns of Ground Arthropod Habitat Associations

Cluster analysis of all 10 habitats from the 3 study sites based on ground arthropod species composition resulted in squared Euclidean distances >0.50 among all habitats and a distance of about 1.00 among the 3 sites (Fig. 6). The JRN creosotebush and tarbush habitats were most similar in ground arthropod species composition, followed by grassland and mesquite sand dune habitats. At BNM, montane conifer and ponderosa pine forests were more similar to each other than to the pinyon-juniper

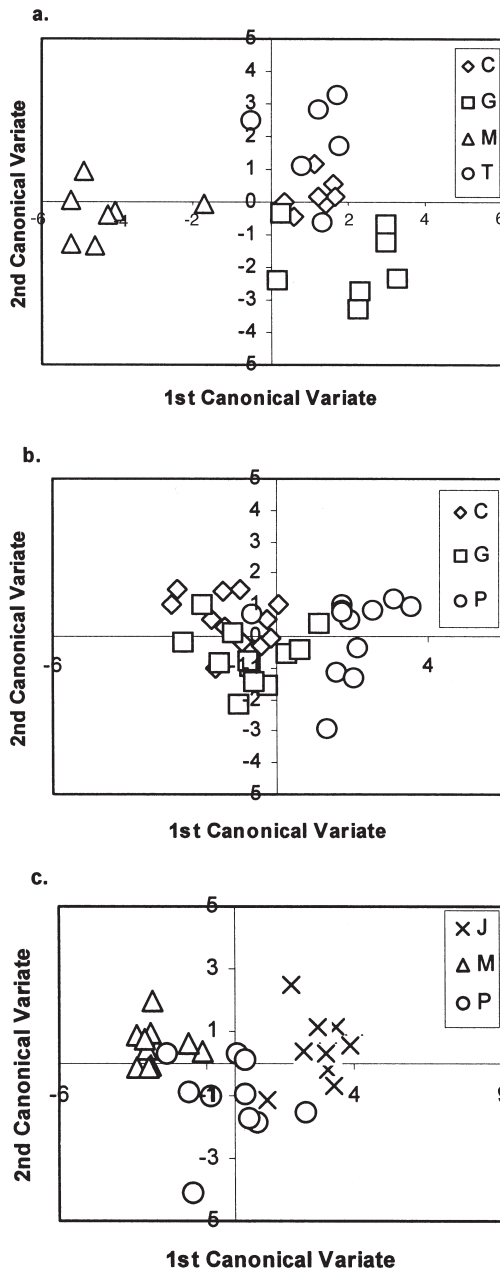


Fig. 7. Canonical discriminant function analysis ordination of Jornada (a), Sevilleta (b), and Bandelier (c) arthropod assemblages samples from the different habitats based on ground arthropod family-level composition and abundance averaged over a 6-year period. See text for explanation of canonical variates.

woodland, and at SEV, creosotebush and black grama grassland habitats were more similar to each other than to the pinyon-juniper woodland.

Arthropod species assemblages among different habitats within each of the 3 study sites were more similar to each other than to similar habitats across the 3 study sites: black grama grassland and creosotebush habitats at JRN were distinct from those at SEV, and pinyon-juniper habitat at BNM was distinct from the pinyon-juniper habitat at SEV (Fig. 6).

Canonical discriminant function analysis (CDFA) tested for differences in ground arthropod taxonomic composition (at the family level) and in abundance among the habitats. The 4 JRN Chihuahuan Desert habitats were significantly different from each other ($P < 0.0001$; Table 1, Fig. 7a). Standardized canonical coefficient scores revealed that spiders contributed most to the separation of JRN habitats, followed by millipedes, crickets, sun spiders, and bristletails. The Chihuahuan Desert, Rocky Mountain, and Western Short Grassland habitats at SEV were also significantly distinct ($P < 0.01$; Table 1, Fig. 7b). Beetles contributed most to the separation of SEV habitats, followed by grasshoppers, spiders, centipedes, and millipedes. The Rocky Mountain forest woodland habitats at BNM supported significantly distinct assemblages ($P < 0.0001$), with spiders contributing most to the separation of habitats, followed by bristletails, sun spiders, and crickets (Table 1, Fig. 7c).

Ecoregion Affinities of Selected Ground Arthropods

Two arthropod orders, crickets/grasshoppers (Orthoptera) and spiders (Araneae), were well represented in the pitfall samples by 76 and 121 species, respectively, and were used to examine ecoregion affinities in detail based on published geographic distribution information (Appendix 2). Although many species occurred in ≥ 2 ecoregions, the crickets/grasshoppers and spiders showed different patterns across the sites: orthopteran species richness was most similar between JRN and SEV, while spider species richness was most similar between SEV and BNM. Eight orthopteran species and 16 spider species were found at all 3 sites, representing 10% of the orthopterans and 16% of the spiders (Table 2).

Most of the cricket and grasshopper species (44 species) occurred in the Chihuahuan Desert, followed by lesser numbers of species associated with the Shortgrass Prairie, Southern Rocky Mountains, Colorado Plateau, and

TABLE 1. Canonical discriminant function analysis for differences in ground arthropod taxonomic composition (family level) and abundance among the habitats within each of the 3 study sites. Habitats at Jornada were dominated by mesquite, tarbush, grass, and creosotebush; at Sevilleta by grass, creosotebush, and pinyon/juniper; and at Bandelier by pinyon/juniper, ponderosa pine, and mixed conifers.

	Jornada			Sevilleta		Bandelier	
Overall multivariate F test (prb. $> F$)	<0.0001			<0.01		<0.0001	
Discriminant variates	1	2	3	1	2	1	2
Significance (prb. $> F$)	<0.0001	0.01	0.08	0.01	0.74	<0.0001	0.01
Eigenvalue	7.2	2.1	1.2	2.0	0.23	5.9	0.21
Cumulative variance	68%	88%	100%	89%	100%	90%	100%

TABLE 2. Total numbers of cricket/grasshopper and spider species found at each and different combinations of our 3 study sites.

	Crickets and grasshoppers	Spiders
Total species sampled	76	121
Jornada only	6	10
Sevilleta only	13	35
Bandelier only	8	29
Jornada and Sevilleta	23	11
Jornada and Bandelier	0	0
Sevilleta and Bandelier	10	15
Jornada, Sevilleta, and Bandelier	10	21

Arizona–New Mexico Mountains (Table 3). The Chihuahuan Desert also contributed the greatest number of species unique to an ecoregion (7 species), followed by the Southern Rocky Mountains (6 species). None of the species encountered in this study were unique to the Southern Shortgrass Prairie or to the Colorado Plateau, and only 2 species were unique to the Arizona–New Mexico Mountains.

Spider distributions showed a stronger response to an elevation-precipitation gradient from high richness at high elevation at BNM to lowest richness at JRN. Most spider species were associated with the Arizona–New Mexico Mountains and the Colorado Plateau. Species known from the Chihuahuan Desert and/or the Southern Rocky Mountains also made up a significant part of the fauna. The Shortgrass Prairie region contributed the fewest species. Eight species were reported from only a single ecoregion, and 6 of those were collected from the SEV transition site (Table 3).

DISCUSSION

Local and Regional Community Similarity and Diversity

Results from cluster analysis (at the species level) and CDFA (at the family level) demon-

strated that different habitats within a site (JRN, SEV, or BNM) contained distinct ground arthropod assemblages (Figs. 6, 7). Although some species occurred in more than 1 habitat, abundances were not evenly distributed among them. In a similar study, Gering et al. (2003) showed that forest canopy beetles clearly formed different assemblages (with $<50\%$ similarity) among the 3 sites in each of 2 ecoregions in forests of Ohio and Indiana. The pattern was maintained for early and late seasons, even with some changes in species composition.

Because of such differences within ecoregions, some researchers may not regard ecoregions as useful delineations for studies of biogeography. Wright et al. (1998) found a poor match between vegetation cover classes and ecoregion boundaries in the American Pacific Northwest. They expected vegetation cover to incorporate information about ecoregion landforms and climate, but perhaps the varied topography of the region obscured the associations. McDonald et al. (2005) examined species turnover between pairs of adjacent ecoregions and found that similarity declined in the American Southwest, which also is topographically variable. We believe that some groups of plants and animals, and some heterogeneous regions, may not conform well to geographically defined ecoregions or portions of ecoregions. Biogeographic studies involving ecoregions also should address multiple taxa across classes and orders, and examine both species composition and richness.

The importance of regional species source areas to our study was especially clear when we examined arthropod species distributions across the 3 study sites. At this spatial scale, arthropod assemblages that shared common habitats as defined by dominant plant cover (pinyon-juniper habitat at SEV and BNM, desert grassland and creosotebush habitats at SEV and JRN) were not as similar to each other as they

TABLE 3. Numbers of cricket/grasshopper species (in bold and below the diagonal) and spider species (above the diagonal) found in this study that are known to be associated with particular ecoregions (based on literature). The numbers in parentheses are species in this study reported to be unique to a particular ecoregion.

	Chihuahuan Desert	Shortgrass prairie	Colorado Plateau	Arizona mountains	Southern Rockies
Chihuahuan Desert	64 (3) 44 (7)	44	48	56	42
Shortgrass prairie	27	46 (1) 38 (0)	37	40	34
Colorado Plateau	23	24	77 (1) 34 (0)	67	71
Arizona mountains	21	21	20	78 (2) 29 (2)	57
Southern Rockies	17	22	23	22	65 (1) 36 (6)

were to other habitats within their ecoregions (Fig. 6). In Australia, MacNally et al. (2002) found that the match between ecoregion and faunal diversity depended on the animal taxa studied. Birds and mammals matched ecoregion boundaries more closely than invertebrates and reptiles. MacNally et al. (2002) identified arthropods only to order and acknowledged that greater taxonomic resolution might have improved the strength of regional associations. However, they confirmed that very different taxa do not substitute for each other and that no ecoregion definition will apply to all taxa.

Species Distributions across the Transition Zone

The SEV ecoregion transition site did contain greater species richness and abundance than comparable areas deeper within their respective ecoregions (BNM and JRN, Fig. 4) and the SEV arthropod assemblages were distinct from the other 2 sites (Fig. 6). Evidence for the ecotone or edge effect (Odum 1971) on other ground-dwelling arthropod communities has been mixed. In Israel, Krasnov and Shenbrot (1998) found that the distributions of ground-dwelling darkling beetle (tenebrionid) species did correspond to phytogeographic regions, with increased species diversity at phytogeographic boundaries. In contrast, Bestelmeyer and Wiens (2001) found that the geographic distributions of ground-dwelling ant species did not correspond to phytogeographically defined biomes of the shortgrass steppe (= Western Short Grassland; Ricketts et al. 1999) and Chihuahuan Desert region of North America, nor did ant species diversity increase at biome boundaries. For trees, birds, and

mammals in North America, McDonald et al. (2005) found no marked increase in species turnover rates between pairs of adjacent ecoregions, based on range data and using ecoregion definitions of Ricketts et al. (1999). They did find increased turnover between ecotones that were also on biome boundaries or that followed major mountain ranges. In relation to our study, the SEV site was not only an area of ecoregional transition, it also was in the Southern Rio Grande Rift Valley, which is a transitional area for 3 continental biomes as described in the introduction section. One of our ecoregions, the Southern Rocky Mountains, does track part of a major mountain range, so some of the patterns we observed may be due to these larger geographical features and not just to ecoregions alone.

When we analyzed the ecoregion affinities of crickets and grasshoppers (Orthoptera) and spiders (Araneae) separately, we also found that not all ground arthropods reflected geographic affinities to the same degree. Orthopterans were clearly associated with particular ecoregions, and the overlap in taxa from different ecoregions, particularly Chihuahuan Desert and Western Short Grassland, did contribute to higher species diversity at SEV. Also, as herbivores, grasshoppers tend to specialize on particular plant taxa or groups (Otte and Joern 1977), which themselves tend to be part of the definition of an ecoregion.

Predatory spiders, in contrast, are less closely associated with plant species, although vegetation and substrate structure are important habitat features for them (Wise 1993). Our sites were dominated by the families Gnaphosidae and Lycosidae, both of which have numerous

species associated with mesic microhabitats (e.g., Lowrie 1973 for *Pardosa*), as shown by the greatest contribution to our diversity coming from the higher-elevation ecoregions: Colorado Plateau, Arizona–New Mexico Mountains, and Southern Rocky Mountains. The high number of species from the Chihuahuan Desert came in part from families not represented from the higher elevations and from different species within widely distributed families. Our sites also shared 58% of the spider species found in a study in shortgrass steppe in Colorado (Weeks and Holtzer 2000), in the Western Short Grasslands ecoregion, to the north of our sites. The distribution pattern for spiders in our study more closely matches a tracking of the precipitation gradient that Bestelmeyer and Wiens (2001) found in ants. Nevertheless, 6 of the 8 spider species that we sampled that were unique to an ecoregion (as reported in the literature) were from SEV, indicating that biogeographical transitional sites do contribute to regional biodiversity of spiders.

Results from our study did not fully support other likely alternative biogeographic hypotheses—namely, energy or productivity gradients—that would explain our patterns. The energy hypothesis (Hawkins et al. 2003) predicts increasing species diversity with increasing ambient temperature, precipitation, and evapotranspiration, and support for this hypothesis has been found in some arthropod groups (beetles—Kerr and Packer 1999; butterflies—Kerr 2001, Hawkins and Porter 2003). The productivity hypothesis (O'Brien 1998, Whittaker et al. 2003) predicts increasing species richness along with increasing ecosystem productivity, usually measured as plant net primary production (NPP). Temperature and precipitation in the desert Southwest tend to be negatively correlated across elevation gradients (Whittaker and Niering 1975, Brown 1982), often forcing a trade-off between preferred temperature and moisture conditions for arthropods (which are ectothermic animals). Waide et al. (1999) found no consistent relationship between productivity and species diversity for invertebrates within or between communities, or over spatial scales ranging from local (<20 km) to regional (200–4000 km).

Our findings that species composition and richness patterns were consistent with predictions based on ecoregions and edge effects and that these patterns were present among

organisms as taxonomically diverse as arthropods in a region as physiographically diverse as the American Southwest indicate that recognition of large-scale biogeographic regions or provinces does have merit. Even though individual species distributions probably are relatively independent from each other, large geographic areas with similar climates and landscapes may support recognizable assemblages of ecologically similar ground arthropod species, as we found. Spatial patterns of terrestrial arthropod communities continue to be poorly understood compared to those of vascular plants and vertebrates. Our findings indicate that consideration of larger geographic source regions, such as ecoregions, may help elucidate patterns of arthropod community species composition and diversity at the local scale.

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APPENDIX 1. List of target arthropod species included in this study and their occurrence by site. BNM = Banderli National Monument, SEV = Sevilleta Long-Term Ecological Research areas, JRN = Jornada Basin Long-Term Ecological Research areas.

Taxon	BNM	SEV	JRN
Class Chilopoda – centipedes			
Order Geophilomorpha			
Family Diagonothodontidae			
<i>Strigamia chionophila</i>	16		
Order Lithobiomorpha			
Family Lithobiidae			
<i>Anobius centurio</i>	1		
<i>Lithobius forficatus</i>			4
<i>Nadabius holzingeri</i>	9		
<i>Nadabius mesenchinus</i>	47		
<i>Nadabius pullus</i>	12		
<i>Paitobius juvenis</i>	2		
<i>Pokabius bilabiatus</i>	3		
<i>Taiubius harrietae</i>	2	2	
Order Scolopendromorpha			
Family Scolopendriidae			
<i>Scolopendra polymorpha</i>	1	53	3
Class Diplopoda – millipedes			
Order Parajulida			
Family Parajulidae			
<i>Oriulus medianus</i>	259		
parajulid sp.		14	
Order Polydesmida			
Family Polydesmidae			
<i>Utadesmus hoffi</i>	2		
Order Spirostreptida			
Family Spirostreptidae			
<i>Orthoporus ornatus</i>		7	8
Class Arachnida			
Order Araneae – spiders			
Family Agelenidae			
<i>Agelenopsis</i> sp.			1
<i>A. longistylus</i>		12	
<i>Agelenopsis utahensis</i>	2	2	
<i>Hololena hola</i>	39	17	
<i>Novalena lutzi</i>	5		
agelenid immatures	6	33	
Family Anyphaenidae			
<i>Anyphaena dixiana</i>		16	
<i>A. hespar</i>	13		
<i>A. marginalis</i>	2		
<i>A. pacifica</i>	2		
<i>Hibana incursa</i>		3	
anyphaenid immatures	26	38	
Family Clubionidae			
<i>Clubiona</i> sp.		53	
clubionid immatures		25	
Family Corinnidae			
<i>Castianeira</i> sp. 1	3		
<i>Castianeira</i> sp. 2			19
<i>Castianeria</i> sp. 3		3	
<i>C. occidentalis</i>		71	
<i>Meriola decepta</i>		2	
corinnid immatures		3	
Family Dictynidae			
<i>Cicurina deserticola</i>	1		
<i>C. robustus</i>	31		
<i>Cicurina</i> spp.	72	98	9
<i>C. varians</i>	11		3

APPENDIX 1. Continued.

Taxon	BNM	SEV	JRN
<i>Dictyna</i> sp. 1			5
<i>Dictyna</i> sp. 2		11	
dictynid immatures		4	
Family Filistatidae			
<i>Filistatinella</i> sp.		14	
<i>Kukulcania hibernalis</i>		3	
Family Gnaphosidae			
<i>Callilepis chisos</i>		3	
<i>C. mumai</i>	6	16	2
<i>Cesonia sincera</i>		36	6
<i>Drassodes gosiutus</i>	2	30	20
<i>Dd. neglectus</i>	6	1	
<i>Dd. saccatus</i>	2	53	
<i>Drassyllus antonito</i>		1	
<i>Dr. conformans</i>		8	
<i>Dr. dromeus</i>	8	34	
<i>Dr. insularis</i> group		1	
<i>Dr. lamprus</i>		3	
<i>Dr. lepidus</i>		1	1
<i>Dr. mexicanus</i>		6	
<i>Dr. mormonus</i>		7	
<i>Dr. mumai</i>		42	1
<i>Dr. orgilis</i>	1	2	
<i>Gnaphosa clara</i>	1	2	3
<i>G. muscorum</i>	92		
<i>Halpodrassus bicornis</i>	2		
<i>Ha. chamberlini</i>	14	133	21
<i>Ha. dixianus</i>	8		
<i>Ha. eunis</i>	3		
<i>Ha. signifer</i>	17		
<i>Herpyllus bubulcus</i>	1	25	23
<i>He. cockerelli</i>	5		
<i>He. excelsus</i>		1	
<i>He. hesperolus</i>	1	34	
<i>He. propinquus</i>		2	
<i>Micaria aenea</i>	3		
<i>M. gosiuta</i>		4	
<i>M. imperiosa</i>		10	
<i>M. longipes</i>			17
<i>M. porta</i>		1	4
<i>M. pulicaria</i>	4		
<i>M. nr. triangulosa</i>			1
<i>Nodocion utus</i>		1	
<i>Orodrassus coloradensis</i>	8		
<i>Zelotes anglo</i>	2	24	6
<i>Z. fratris</i>	23		
<i>Z. lasalamus</i>	7	22	1
<i>Z. puritanus</i>	12		
<i>Z. tuobus</i>	21	80	11
gnaphosid immatures	90	1599	7
Family Linyphiidae			
combined species	88	107	2
<i>Pityohyphantes</i> sp.	14		
Family Lycosidae			
<i>Alopecosa kochi</i>	130	112	
<i>Geolycosa rafaelana</i>		4	1
<i>Hogna carolinensis</i>	1	35	2
<i>H. frondicola</i>	6	2	
<i>Pardosa montanensis</i>	23		
<i>P. orophila</i>	5	177	
<i>P. uncata</i>	503		
<i>P. xerophila</i>	12		
<i>P. yavapa</i>	101		

APPENDIX I. Continued.

Taxon	BNM	SEV	JRN
<i>Schizocosa chiricahua</i>		12	
<i>S. mccooki</i>	60	39	8
<i>S. mimula</i>	2	1	
<i>Trochosa terricola</i>	11	2	
<i>Varacosa gosiuta</i>	34	17	2
lycosid immatures	193		2
Family Liocranidae			
<i>Neoanagraphis chamberlini</i>		3	1
Family Mimetidae			
<i>Mimetus hesperus</i>		8	2
Family Miturgidae			
<i>Cheiracanthium inclusum</i>			2
<i>Syspira</i> sp.			17
Family Oxyopidae			
<i>Oxyopes lynx</i>		6	
<i>O. salticus</i>		2	
<i>O. tridens</i>			27
Family Philodromidae			
<i>Apollophanes texanus</i>		10	31
<i>Ebo</i> sp.	3		
<i>Ebo parabolis</i>		22	24
<i>Philodromus infuscatus</i>	1		
<i>P. keyserlingi</i>		3	
<i>Thanatus coloradensis</i>	1	51	10
<i>Tibellus duttoni</i>		8	
Family Salticidae			
<i>Habronattus clypeatus</i>		55	
<i>H. conjunctus</i>	1	1	
<i>H. geronimoi</i>		9	14
<i>Metacurba taeniola</i>			2
<i>Pellenes limatus</i>		1	
<i>Phidippus</i> spp.	5	6	5
<i>Platycryptus arizonensis</i>		14	
<i>Sassacus</i> sp.			12
salticid immatures	8	110	
Family Sicariidae			
<i>Loxosceles apachea</i>		4	2
Family Theridiidae			
<i>Euryopes scriptipes</i>	17	8	6
<i>Latrodectus hesperus</i>	22	35	8
<i>Steatoda</i> sp.		1	
<i>S. fulva</i>	2	7	11
<i>S. hespera</i>	5		
theridiid immatures	7		1
Family Thomisidae			
<i>Bassaniana versicolor</i>		2	
<i>Misumenops</i> sp.		1	
<i>Xysticus apachecus</i>		9	
<i>X. cunctator</i>	6	6	1
<i>X. facetus</i>	1	24	3
<i>X. gosiutus</i>	1		
<i>X. gulosus</i>	2	10	
<i>X. lassanus</i>	1	77	9
<i>X. locuples</i>	6	11	
<i>X. luctuosus</i>	9		
<i>X. montanensis</i>	19		
<i>X. orizaba</i>		7	
thomisid immatures	13	168	22
Order Solifugae – solifugids, sun spiders			
Family Eremobatidae			
<i>Eremobates</i> sp.	232	253	129
Order Opiliones – harvestmen			
Family Sclerosomatidae			

APPENDIX I. Continued.

Taxon	BNM	SEV	JRN
<i>Eurybunus brunneus</i>	6		
sclerosomatid sp.		15	
<i>Togwoteeus biceps</i>	271		
<i>Trachyrhinus marmoratus</i>	624		
Family Triaenonychidae			
<i>Sclerobunus robustus</i>	14		
Order Scorpiones – scorpions			
Family Vaejovidae			
<i>Vaejovis coahuilae</i>		523	138
<i>V. russelli</i>		2	1
Order Uropygi – vinegaroons			
Family Thelyphoridae			
<i>Mastigoproctus giganteus</i>		14	
Class Insecta			
Order Archaeognatha – bristletails			
Family Meinertellidae			
<i>Machilinus aurantiacus</i>	788	1199	
<i>Praemachilellus rentzi</i>			545
Family Machilidae			
<i>Mesomachilis</i> sp.			3
Order Dictyoptera – cockroaches, mantises			
Family Blattellidae			
<i>Parcoblatta desertae</i>			21
Family Polyphagidae			
<i>Arenivaga erratica</i>		54	65
<i>Eremoblatta subdiaphana</i>		6	13
Family Mantidae			
<i>Litaneutria minor</i>		6	2
<i>Yersiniops solitaria</i>		3	
Order Orthoptera – grasshoppers, katydids, crickets			
Family Acrididae			
<i>Acantherus piperatus</i>		35	58
<i>Aeoloplides elegans</i>			1
<i>Ageneotettix deorum</i>		48	6
<i>Amphitornus coloradus</i>		16	2
<i>Arphia conspersa</i>	22	410	2
<i>A. pseudonietana</i>	5	54	6
<i>Aulocara femoratum</i>		444	1
<i>Barytettix humphreysi</i>		9	
<i>Boottettix argentatus</i>		280	23
<i>Camnula pellucida</i>	1		
<i>Campylacantha olivacea</i>			13
<i>Chorthippus curtispennis</i>	16		
<i>Cibolacris parviceps</i>		98	42
<i>Clematodes larreae</i>			7
<i>Cordillacris crenulata</i>		1	
<i>C. occipitalis</i>		23	2
<i>Dactylotum bicolor</i>		29	1
<i>Eritettix simplex</i>	6	57	13
<i>Heliaula rufa</i>		19	
<i>Hesperotettix viridis</i>	1	2	2
<i>Hippopedon capito</i>		3	1
<i>L. wheeleri</i>		6	
<i>Ligurotettix planum</i>			9
<i>Melanoplus aridus</i>	6	2	5
<i>M. arizonae</i>		53	
<i>M. bowditchi</i>		56	3
<i>M. femur-nigrum</i>	3		
<i>M. gladstoni</i>	3	26	
<i>M. lakinus</i>		10	2
<i>M. occidentalis</i>	3		
<i>M. packardi</i>		1	
<i>M. splendidus</i>	3	3	

APPENDIX I. Continued.

Taxon	BNM	SEV	JRN
<i>Mestobregma plattei</i>		21	
<i>Opeia obscura</i>		18	3
<i>Paropomala pallida</i>		15	4
<i>Phlebotroma quadrimaculatum</i>		3	
<i>Phoetaliotes nebracensis</i>		2	
<i>Psoloessa delicatula</i>		227	3
<i>P. texana</i>	37	700	8
<i>Spharagemon equale</i>		2	
<i>Syrbula admirabilis</i>		7	
<i>S. montezuma</i>		53	
<i>Trachyrhachys kiowa</i>		9	1
<i>Trimerotropis californica</i>		8	4
<i>T. cincta</i>	6	2	
<i>T. modesta</i>	3		
<i>T. pallidipennis</i>	67	940	86
<i>T. pistrinaria</i>		12	
<i>T. suffusa</i>	16		
<i>Tropidolophus formosus</i>		9	5
<i>Xanthippus corallipes</i>	4	54	6
acridid immatures	55	642	19
Family Gryllidae			
<i>Gryllus</i> sp. 1 undescribed		428	613
<i>Gryllus pennsylvanicus</i>		314	
<i>G. personatus</i>		439	
<i>Gryllus</i> sp. 2 undescribed	113		
<i>Oecanthus californicus</i>	14	12	
gryllid immatures		733	5
Family Mogoplistidae			
<i>Cycloptilium comprehendens</i>	26	2634	37
<i>Hoplosphyrum boreale</i>		363	
Family Rhaphidophoridae			
<i>Ammobaenetes phrixocnemoides</i>			30
<i>Ceuthophilus lamellipes</i>		5	
<i>C. pallidus</i>	195	155	
<i>C. utahensis</i>	4111	38	
<i>C. variegatus</i>			53
<i>Daihiniodes hastiferum</i>		919	7
<i>Styracosceles neomexicana</i>	3		
rhaphidophorid immatures		922	
Family Stenopelmatidae			
<i>Stenopelmatus fuscus</i>	153	130	
<i>Stenopelmatus</i> sp. 1 undescribed		9	
Family Tettigoniidae			
<i>Arethaea gracilipes</i>	2	33	9
<i>Capnobotes fuliginosus</i>		1	1
<i>Dichopetala brevihastata</i>			5
<i>Eremopedes balli</i>	1	27	
<i>E. bilineata</i>		14	
<i>E. scudderi</i>		237	34
<i>Insara elegans</i>		9	37
<i>Insara juniperi</i>	3	7	
tettigoniid immatures		41	1
Order Hemiptera – true bugs			
Family Aradidae			
<i>Aradus lugubris</i>	9		
Family Cydnidae			
cydnid sp.		1884	
<i>Dallasiellus discrepans</i>	6	1197	6
Family Lygaeidae			
<i>Emblethis vicarius</i>	33	310	40
<i>Geocoris</i> sp.		5	
lygaeid sp. 2	1		
lygaeid sp. 28		2	

APPENDIX I. Continued.

Taxon	BNM	SEV	JRN
<i>Lygaeus kalmi</i>		43	5
<i>Melacoryphus lateralis</i>			2
<i>Ozophora</i> sp.		172	
<i>Prytanus</i> sp.		2	
<i>Sphragisticus</i> sp.		1	
Family Miridae			
<i>Eustictus</i> sp.		560	
Order Coleoptera – beetles			
Family Anobiidae			
anobiid sp.			23
<i>Niptus ventriculus</i>			1
Family Carabidae			
<i>Amara</i> sp.	1		
<i>A. apachensis</i>		5	
<i>A. discors</i>		8	
<i>A. erratica</i>		4	
<i>A. nr. idahoana</i>		20	
<i>A. rubrica</i>		30	
<i>Calosoma obsoletus</i>		2	
<i>C. peregrinator</i>		12	
<i>Carabus taedatus</i>	787		
<i>Cicindela lemniscata</i>		4	2
<i>C. pulchra</i>		13	
<i>C. punctulata</i>		28	
<i>Cymindis arizonensis</i>	1	49	
<i>C. cribricollis</i>	2		
<i>C. punctigera</i>	9	110	11
<i>Dyschirius</i> sp.	2		
<i>D. globulosa</i>		5	
<i>Euryderus grossus</i>		10	2
<i>Harpalus amputatus</i>		12	
<i>H. katiae</i>		1	
<i>H. pennsylvanicus</i>		1	2
<i>H. tadorcus</i>		149	
<i>Helluomorphoides ferruginea</i>		1	
<i>He. latitarsus</i>		1	4
<i>Lebia viridis</i>		21	
<i>Notiophilus novemstriatus</i>	19		
<i>Pasimachus californicus</i>		56	53
<i>P. elongatus/obsoletus</i>		1693	15
<i>Poecilus lucublandus</i>		1	
<i>Pterostichus adstrictus</i>	1019		
<i>Rhadine dissectus</i>		2	
<i>Rhadine</i> sp. 3		1	
<i>R. umbra</i> group	24		
<i>Scaphinotus snowi</i>	2		
<i>Scarites subterraneus</i>		5	
<i>Tachys</i> sp.	1		
Family Cryptophagidae			
cryptophagid sp. 1	14	116	
<i>Cryptophagus dentatus</i>	19		11
<i>C. fumidulus</i>		1	
<i>C. stromus</i>		9	
<i>Myrmedophila americanus</i>	1		
Family Curculionidae			
<i>Apion</i> sp.		1	
<i>Cimbocera buchanani</i>		31	
<i>C. conspersa</i>		2	10
<i>Cleonidius poricollis</i>		1	
<i>Crocidema</i> sp.		4	
curculionid sp.	1		
<i>Gerstaeckeria lecontei</i>		17	
<i>G. turbida</i>		1	

APPENDIX I. Continued.

Taxon	BNM	SEV	JRN
<i>Hypera postica</i>		1	
<i>Minyomerus languidus</i>		8	3
<i>Notiodes limatulus</i>		8	
<i>Ophryastes</i> sp.			7
<i>O. dunnianus</i>		1	
<i>O. globularis</i>		45	
<i>O. latirostris</i>		1	
<i>O. sulcatus</i>		3	3
<i>O. vittatus</i>		1	2
<i>Pandeleiteius dentipes</i>		3	
<i>Rhypodillus brevicollis</i>		1	
<i>Sapotes longipilis</i>		37	
<i>S. puncticollis</i>		5	
<i>Scyphophorus acupunctatus</i>		2	
<i>Sitona hispidulus</i>		1	
<i>Smicronyx</i> sp.			1
<i>Sphenophorus</i> sp.	1		
<i>Yuccaborus frontalis</i>		5	
Family Elateridae			
<i>Aeolus mellillus</i>		2	
<i>Agrypnus rectangularis</i>	50		6
<i>Cardiophorus</i> sp.		89	
<i>Conoderus athoides</i>		27	5
<i>Ctenicara carbo</i>		4	
<i>C. pudica</i>	3		
<i>Glyphonyx</i> sp.	1		
<i>Heteroderes sordidus</i>		2	
<i>Horistonotus simplex</i>		19	
<i>Lanelater schotti</i>	9	1816	121
<i>Limontus lanei</i>	7		
<i>Melanotus similis</i>		1	
<i>Neotrichophorus arizonensis</i>		2	7
Family Endomychidae			
<i>Aphorista</i> sp.	1		
Family Erotylidae			
<i>Cypherotylus californicus</i>	3		
Family Histeridae			
<i>Hister abbreviatus</i>	9		32
<i>Iliotona cacti</i>		5	1
<i>Saprinus</i> sp.	1		
<i>S. discoidalis</i>		34	
<i>S. pennsylvanicus</i>		5	
<i>Xerosaprinus</i> sp. 1			1
<i>Xerosaprinus</i> sp. 2		399	
Family Lathridiidae			
<i>Corticaria rudis</i>	8		
Family Leiodidae			
<i>Catops basilarus</i>	1		
<i>Ptomaphagus texanus</i>	14	1	16
Family Nitidulidae			
<i>Carpophilus</i> sp.	2		
<i>C. humeralis</i>	67		
<i>C. lugubris</i>	45	2	69
<i>C. pallidipennis</i>	26		
<i>C. sayi</i>			3
<i>Epuraea adumbrata</i>	4		
<i>Phenolia grossa</i>	15		
<i>Thalycra keltoni</i>	7		
Family Ptiliidae			
<i>Acrotrichus</i> sp.	83		
Family Salpingidae			
<i>Elacatis umbrosus</i>	2		
Family Scarabaeidae			

APPENDIX I. Continued.

Taxon	BNM	SEV	JRN
<i>Anatropis verticalis</i>			152
<i>Aphodius</i> sp. 1		4	
<i>Aphodius</i> sp. 2			1
<i>Aphodius</i> sp. 3		1	
<i>Boreocanthon ebenus</i>			2
<i>B. probus</i>		1	
<i>Canthon puncticollis</i>			5
<i>Cremastocheilus planatus</i>		2	
<i>Diplotaxis</i> sp. 1	17		
<i>Diplotaxis</i> sp. 2		32	
<i>Diplotaxis</i> sp. 3		114	
<i>D. carbonata</i>	1		18
<i>D. knausi</i>			19
<i>D. subangulata</i>	6	25	9
<i>Euphoria inla</i>	127	37	3
<i>Hoplia laticollis</i>		1	
<i>Onthophagus</i> sp.		1	
<i>O. hecate</i>			5
<i>Paracotalpa puncticollis</i>			13
<i>Phyllophaga</i> sp.	5		
<i>P. vetula</i>	3	14	
<i>P. wickhami</i>		160	
scarabaeid sp. 46		16	
scarabaeid sp. 51		1	
scarabaeid sp. 57		4	
scarabaeid sp. 60		1	
Family Staphylinidae			
aleocharine spp.	1265	6	
<i>Carphacis nepigonensis</i>	4		
<i>Dexiogygia</i> sp.	11		
<i>Hapalaraea cacti</i>			2
<i>Lordithon arizonensis</i>	46		
omaliine sp. 1	1	11	
<i>Ocypus ater</i>		3	
<i>Oxytelus</i> sp.	2		
<i>Parothius</i> sp.	2		
<i>Philolonthus</i> sp.	1		
<i>Pseudopsis callosa</i>	3		
<i>Quedius desertus</i>	1	4	
staphylinine sp. 1	1		
staphylinine sp. 2	1		
<i>Tachyporus jocusus</i>	55		
Family Tenebrionidae			
<i>Anepsius</i> sp.		221	
<i>Araeoschizus decipiens</i>		194	39
<i>Argoporis rufipes</i>		50	6
<i>Blapstinus fortis</i>	1	1	
<i>B. pinalis</i>		61	4
<i>Conibius uniformis</i>			15
<i>Edrotes leechi</i>		5	
<i>Ed. rotundus</i>		23	
<i>Eleodes carbonarius</i>		6	
<i>E. caudiferus</i>		48	4
<i>E. debilis</i>	1		
<i>E. extricatus</i>	594	1193	8
<i>E. fusiformis</i>		9	
<i>E. gracilis</i>		369	4
<i>E. hispilabris</i>		15	125
<i>E. hoppingi</i>	80		
<i>E. longicollis</i>	8	1410	39
<i>E. nigrinus</i>	99		
<i>E. obscurus</i>	339		
<i>E. obsoletus</i>		92	5

APPENDIX I. Continued.

Taxon	BNM	SEV	JRN
<i>E. pimelioides</i>	8		
<i>E. sponsus</i>		33	
<i>E. tenuipes</i>		94	
<i>E. tricostatus</i>		17	
<i>Embaphion contusum</i>	31	1	1
<i>Em. glabrum</i>			3
<i>Em. planum</i>		10	
<i>Eupsophulus castaneus</i>			3
<i>Eusattus reticulatus</i>		3	3
<i>Glyptasida sordida</i>		16	2
<i>Gonasida elata</i>		6	
<i>Helops callosa</i>		8	
<i>Lobometopon fusiformis</i>		12	
<i>Megasida oblitterata</i>		32	
<i>M. tenuicollis</i>		173	32
<i>Melanastus</i> sp. 1		345	

APPENDIX I. Continued.

Taxon	BNM	SEV	JRN
<i>Me. coarcticollis</i>			3
<i>Metopoloba pruinosa</i>			9
<i>Metaponium</i> sp. 1	12		
<i>Mt. cribriceps</i>	1	1	183
<i>Mt. implicans</i>	1		
<i>Neobaphion planipennis</i>		24	
<i>Stenomorpha consors</i>		5	
<i>S. convexicollis</i>		16	9
<i>S. obovata</i>		29	
<i>S. rimata</i>		1	
<i>S. severa</i>		7	
<i>Steriphanus convexus</i>	30	540	
<i>Telabis histricus</i>		1	
<i>Trimytilis pruinosa</i>		28	22
<i>Troglderis costatus</i>		3	

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