Interactive effects of keystone rodents on the structure of desert grassland arthropod communities

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Certain species play particularly large roles in ecosystems, and are often referred to as keystones. However, little is known about the interactive effects of these species where they co-occur. Prairie dogs (*Cynomys* spp.) and banner-tailed kangaroo rats *Dipodomys spectabilis* are commonly considered keystone species of grassland ecosystems, creating a mosaic of unique habitats on the landscape through ecosystem engineering and herbivory. We examined the separate and interactive effects of these species on the structure of grassland arthropod communities. We conducted a cross-site study at two locations in the northern Chihuahuan Desert, and evaluated the impacts of these rodents on ground-dwelling arthropod and grasshopper communities in areas where prairie dogs and kangaroo rats co-occurred compared to areas where each rodent species occurred alone. Our results demonstrate that prairie dogs (*C. gunnisoni* and *C. ludovicianus*) and banner-tailed kangaroo rats had keystone-level impacts on arthropod communities both separately and interactively. Their burrow systems provided important habitats for multiple trophic and taxonomic groups of arthropods, and increased overall arthropod abundance and species richness. Many arthropods also were attracted to the aboveground habitats around the mounds and across the landscapes where the rodents occurred. Detritivores, predators, ants, grasshoppers, and rare rodent burrow inhabitants were especially associated with prairie dog and kangaroo rat activity. The impacts of prairie dogs and kangaroo rats were unique, and the habitats they created supported different assemblages of arthropods. Where both rodent species co-occurred, there was greater heterogeneity and arthropod diversity on the landscape. Our results suggest that the interaction of multiple keystones, especially those with engineering roles, results in unique and more diverse communities in time and space.

A fundamental goal of ecology is to understand the underlying mechanisms that regulate community structure and biodiversity. In many ecosystems, certain species play a central role in the organization of communities, creating networks of strong interactions with other species. These species are often referred to as keystones, and are defined by having distinctive and disproportionately large impacts on community structure and ecosystem function relative to their abundance (Power et al. 1996). Such species can affect ecosystems through a variety of processes, from top-down effects through the consumption of prey to bottom-up effects through ecosystem engineering (Jones et al. 1994, Power et al. 1996). Although keystone species co-occur in many systems, their interactive effects have received

little attention. Given the central role these species play in ecosystems, their combined effects may have important consequences for community structure and biodiversity.

In this paper, we evaluate the separate and interactive effects of prairie dogs (*Cynomys gunnisoni* and *C. ludovicianus*) and banner-tail kangaroo rats *Dipodomys spectabilis* on desert grassland arthropod communities. Prairie dogs (*Cynomys* spp.) and banner-tailed kangaroo rats are often considered keystone species and ecosystem engineers of grasslands (Valone et al. 1995, Kotliar 2000, Davidson and Lightfoot 2006, and see citations in Kotliar et al. 2006), although the keystone status of prairie dogs is based largely on black-tailed prairie dog *C. ludovicianus* research (Stapp 1998). By grazing grass

and building mounts, prairie dogs maintain a low mat of forbs and grazing-tolerant grasses around their mounds and within their colonies (Whicker and Detling 1988, Davidson 2005). In contrast, banner-tailed kangaroo rats alter the composition of grassland vegetation by selectively harvesting large seeds, and building large, widely dispersed mounds that provide resource-rich patches on the landscape (Brown and Heske 1990). Yet, most of the research evaluating the roles of these rodents has been conducted in areas where they occur alone. Areas where their geographic distributions overlap in the northern Chihuahuan Desert provide a unique opportunity to study the interactive effects of these species.

Little is known about the individual effects of these rodents on arthropods, and nothing is known about their potential interactive effects on arthropod communities. Studies of prairie dog and kangaroo rat impacts on arthropods have been limited both in geographic coverage and the taxa involved (Wilcomb 1954, O'Meilia et al. 1982, Davidson et al. 1984, Hawkins and Nicoletto 1992, Valone et al. 1994, Schooley et al. 2000, Kretzer and Cully 2001, Russell and Detling 2003, Bangert and Slobodchikoff 2006). Given that arthropods represent diverse trophic groups, play important roles in ecosystem processes, and comprise much of the biodiversity in grassland ecosystems (Crawford 1981, Whitford et al. 1995), it is important to understand the key drivers that organize the structure of these communities. Most desert grassland arthropods are habitat and food resource specialists (Whitford et al. 1995), and so are likely to be responsive to the habitat modifications created by these rodents. Recently we demonstrated that prairie dogs and kangaroo rats have additive, complementary impacts on vegetation by increasing habitat heterogeneity through the construction of distinct mound types and consumption of different food resources (Davidson 2005, Davidson and Lightfoot 2006). As arthropod diversity often increases with habitat heterogeneity (Dennis et al. 1998, Joern 2005), areas where these rodents co-occur may have important consequences for local and regional arthropod biodiversity.

Our first objective was to evaluate the independent effects of Gunnison's prairie dogs C. gunnisoni, black-tailed prairie dogs, and banner-tailed kangaroo rats in structuring ground-dwelling arthropod and grasshopper communities by comparing differences in abundance, species richness, and composition between areas where the rodents were present versus absent. Our second objective was to determine if prairie dogs and kangaroo rats have interactive influences on arthropod community assemblages. We hypothesized that the co-occurrence of these rodents results in greater species richness on the landscape compared to where they occur alone, as a consequence of increased habitat

heterogeneity. Since the effects of keystones are often context-dependent (Power et al. 1996, Kotliar 2000), we conducted our research across different spatial and temporal scales in two desert grassland environments with different species of prairie dogs. Addressing these questions is important because kangaroo rats and especially prairie dogs have declined dramatically, primarily due to poisoning and habitat loss from agriculture and desertification (Waser and Ayers 2003, Proctor et al. 2006, Wagner et al. 2006). The consequences of losing these species from grassland ecosystems may have large impacts on arthropod communities, and in turn other animals and ecosystem processes.

Methods

Study sites

We established a cross-site comparative study in the northern Chihuahuan Desert. One study site was at the Sevilleta National Wildlife Refuge (SNWR) in central New Mexico, USA, 90 km south of Albuquerque, in Socorro County (NAD-27: 34°24′N, 106°36′W; 1600 m elevation). The SNWR site is typical northern Chihuahuan Desert grassland with burrograss *Scleropogon brevifolius,* sand dropseed grass *Sporobolus cryptandrus,* and black grama grass *Bouteloua eriopoda.* Domestic livestock have been absent from the SNWR since the refuge was established in 1972. Prairie dogs were exterminated prior to the establishment of the refuge, but Gunnison's prairie dogs began to recolonize our study site in 1998. The other study site was located in the Janos-Casas Grandes region (JCG) of northwestern Mexico, 75 km south of the United States-Mexico border and ca 600 km south of the SNWR (NAD-27: 30°7′N, 108°3′W; 1500 m elevation). Much of the area has been heavily grazed by cattle, and degraded from perennial desert grassland to ephemeral grassland dominated by annual grasses, needle grama *B. aristidoides,* sixweeks grama *B. barbata,* sixweeks threeawn *Aristida adscensionis,* and numerous forbs (Ceballos et al. 2005). The region supports one of the largest remaining black-tailed prairie dog colony complexes in North America (Ceballos et al. 2005).

Experimental design

Ground-dwelling arthropods and grasshoppers were sampled at two spatial scales, the local mound-scale (m) and the landscape-scale (ha) in areas with just prairie dogs (Pdog plot; JCG site only), just kangaroo rats (Krat plot), and where both species of rodents co-occurred (Pdog + Krat plot) (Appendix, Fig. S1 and S2). At the SNWR, the landscape-scale plots were

180 × 180 m. They were established on a Krat plot, a Pdog + Krat plot, and in a transitional area where both rodent species occurred (Transition plot). Statistically valid replication was not possible at the SNWR since there was only one contiguous prairie dog colony of relatively small size (ca 13 ha). At JCG, four replicate 0.25 km² blocks were established. Each block consisted of three 100 × 100 m landscape-scale plots (Pdog plot, Krat plot, and Pdog + Krat plot) for a total of 12 plots.

To evaluate arthropods associated with mound disturbance patches and rodent burrow systems, we established replicate mound-scale plots with paired "non-mound" control plots. Samples were collected from prairie dog mounds on each Pdog plot (JCG only), kangaroo rat mounds on each Krat plot, prairie dog and kangaroo rat mounds on each Pdog + Krat plot, and on paired non-mounds. Existing mounds were selected from each landscape plot in such a way as to disperse the sample mounds to the greatest extent across each plot. Paired non-mounds represented areas with minimal rodent disturbance (i.e. no rodent mound), systematically positioned 10 m from each study mound.

Ground-dwelling arthropods

We sampled ground-dwelling arthropods using two complementary methods: 1) pitfall traps and 2) nocturnal oat-bait sampling. Pitfall traps were established only at the SNWR site and not at JCG because of heavy cattle grazing in the area. On each landscape-scale plot, pitfall traps were installed using a 4 × 7 grid array (Appendix, Fig. S1). Pitfall traps also were placed next to 10 prairie dog mounds and 10 paired non-mounds on the Pdog + Krat plot and at 10 kangaroo rat mounds and 10 paired non-mounds on the Krat plot. Traps consisted of 300 ml plastic cups set in 360 ml cans, buried up to the soil surface, filled with propylene glycol, and covered with elevated ceramic tiles. To protect traps from rodent digging, pitfall traps at mound-scale plots were surrounded by wire mesh with 2.54 cm openings, large enough to allow arthropods to pass through. Traps were opened for one month in spring (May) and autumn (September), from spring 2000 through autumn 2001.

Nocturnal oat-bait sampling was conducted on mound-scale plots at both sites. Equivalent amounts of rolled oats were sprinkled around burrow entrances of each mound, and on the soil surface at each adjacent paired non-mound at sunset. Twenty-five replicate mound-scale plots were sampled at the SNWR and 40 at JCG, for each treatment type. Approximately 2 h after sunset, arthropods attracted to the oatmeal were counted and identified to species. Voucher specimens were identified in the laboratory. Sampling was

conducted for 5 separate nights at the SNWR and 3 separate nights at JCG during 2001 and 2002.

We examined species-level patterns from both the pitfall and oat-bait data for target taxa of ground-dwelling species. We combined data for multiple arthropod species from the pitfall samples to evaluate patterns in: 1) taxonomic family-level groups and 2) trophic groups (Appendix, Table S1). All arthropods were identified to species, except weevils (Curculionidae), velvet ants (Mutillidae), and spider wasps (Pompilidae) that were pooled at the family rank and not included in species-level analyses. Arthropod voucher specimens were deposited at the Division of Arthropods, Museum of Southwestern Biology (MSB), Univ. of New Mexico (UNM).

Grasshoppers

Grasshoppers were visually sampled along strip transect lines established along each gridline of the landscape-scale plots, and through each mound-scale plot (Appendix, Fig. S1 and S2). Twenty replicate mound-scale plots were sampled at the SNWR and 40 at JCG, for each treatment type. Strip transects on the landscape-scale plots measured 1 × 30 m at the SNWR and 1 × 25 m at JCG, and on the mound-scale plots they were 1 × 5 m. Grasshoppers flushed from the ground were counted and identified to species, and the substrate (i.e. plant species, bare soil) they were observed on was recorded. This is the standard method used at both the Sevilleta Long-Term Ecological Research (LTER) and Jornada Basin LTER sites, and is similar to that developed by Paftd (1982). Grasshoppers were sampled from autumn 1999 through spring 2002 at the SNWR and from spring 2001 through autumn 2002 at JCG. Note that kangaroo rat mounds and non-mounds were sampled on the SNWR Pdog + Krat plot only in autumn 2001 and spring 2002. In addition to examining individual species patterns, we also considered grasshopper life-form groups that reflect similar habitat and diet preferences as described by Uvarov (1977) and Lightfoot (1985) (Appendix, Table S2).

Statistical analyses

Data were normalized by log transformations and all analyses were performed using SAS version 8.2 (Anon. 2001). Simultaneous comparisons of total abundance and species richness among treatment plots were conducted using multivariate analysis of variance (MANOVA) tests. For the SNWR, t-tests then were used to analyze differences in abundance and richness of arthropods between the Pdog + Krat and Krat plots, and between mound types within the Pdog + Krat plot.

Paired comparisons t-tests were used to compare the paired mound and non-mound plots at the SNWR. For JCG, analysis of variance (ANOVA) tests with Bonferroni adjustments then were used for comparisons among the landscape treatments (i.e. Pdog, Krat, Pdog+Krat plots), and between prairie dog and kangaroo rat mounds within the Pdog+Krat plots. Mixed-linear models (MLM) were used to test for differences between paired mounds and non-mounds at JCG. The fixed effects for each model were the mound treatment types, blocks, and the interaction between the mound treatments and blocks. Each model included a random mound effect, which allowed for correlated responses on the paired mound and non-mound plots.

Canonical discriminant function analysis (CDFA) provided a MANOVA test for potential differences among mound and landscape-scale treatment plots based on simultaneous analysis of all ground-dwelling arthropod or grasshopper species. Rare species were not included (McCune and Grace 2002). Proc CANDISC procedure calculated the Mahalanobis distance measures (D^2) to provide a measure of difference in arthropod species composition between the treatment types, and provided F-tests and p-values of equal mean vectors, based on the D^2. Spearman-rank correlation analysis was used to test for relationships between the grasshopper life forms and the substrates where they occurred.

To determine if the co-occurrence of prairie dogs and kangaroo rats at the landscape-scale resulted in increased species richness on the greater landscape, we used PopTools (Hood 2005) to conduct Monte Carlo randomization procedures (1000 iterations) to estimate species richness for each landscape treatment and a hypothetical combined treatment, holding area constant.

Results

Ground-dwelling arthropods

Our SNWR pitfall dataset resulted in 218 target species. The oat-bait datasets resulted in 32 and 36 target species at the SNWR and JCG, respectively. Although pitfall traps only were used at the SNWR, we found similar patterns in arthropod abundance, richness, and composition across both sites. Abundance and richness of arthropods were consistently greater on mounds than non-mounds, kangaroo rat mounds than prairie dog mounds, and where the rodents co-occurred at both sites (MANOVA: oat-bait data and landscape plots p < 0.03, for all tests; mound pitfall data p > 0.05, for both tests) (Fig. 1). Mean arthropod abundance from pitfall traps was ca 25% greater on mounds than on paired non-mounds. Arthropods attracted to oat-

bait were 2–5 times more abundant on mounds than non-mounds, and similarly greater on kangaroo rat mounds than prairie dog mounds at both sites (p < 0.002, for all tests). At the landscape-scale, the Pdog+Krat plot had 12% greater abundance of arthropods than the Krat plot, based on SNWR pitfall data (t-test: DF = 54, t = −2.71, p = 0.009), and the Pdog+Krat plots at JCG had significantly greater abundance of arthropods than the Pdog plots and Krat plots based on mound oat-bait data (ANOVA: $F_{2,317} = 7.42$, p = 0.01). Pitfall data showed that, during the four sample periods, kangaroo rat and prairie dog mounds had 5–40% and 6–16%, respectively, more arthropod species than paired non-mounds. Oat-bait data showed that species richness was 2–3 times greater on the mounds than paired non-mounds at both sites (p < 0.003, for all tests). Kangaroo rat mounds also were more species-rich than prairie dog mounds at JCG (ANOVA: $F_{1,72} = 28.76$, p < 0.0001).

At the landscape-scale, richness of all species combined, and that of detritivores, ants, and beetles was higher on the Pdog+Krat plot than on the Krat plot at the SNWR (t-test: adjusted p < 0.01, for all tests). Mean arthropod species richness (S) estimated by random sampling from both landscape-scale plots at the SNWR was greater (S = 115.2 ± 0.92, 1 SE) than when richness was estimated from only the Krat plot (S = 100.2 ± 0.79, 1 SE) or the Pdog+Krat plot (S = 111 ± 0.83, 1 SE), indicating higher richness on the greater landscape. Species richness, from mound oat-bait data only, did not differ at JCG. Nevertheless, kangaroo rat mounds on the Pdog+Krat plots were more species-rich than those on the Krat plots at JCG (ANOVA: $F_{1,72} = 6.78$, p = 0.01).

Prairie dogs and kangaroo rats provided unique habitats for arthropods, altering species composition at the mound and landscape-scales (Fig. 2 and 3). The CDFA indicated that, across both sites and sampling methods, arthropod species composition differed significantly between mounds and non-mounds, prairie dog mounds and kangaroo rat mounds, and also among the Pdog+Krat, Krat, and Pdog plots (MANOVA: p < 0.01, for all tests) (Fig. 2 and 3). The Mahalanobis distance measures based on species composition demonstrated significant distances between these plots (p < 0.008, for all tests) (Appendix, Table S3).

Certain groups of arthropods associated strongly with prairie dog and kangaroo rat mounds and the landscape where they co-occurred (Fig. 4), and species-level patterns were largely consistent across sites and methods. Detritivores associated most strongly with both mound types compared to paired non-mounds, especially darkling beetles (Tenebrionidae), spider beetles (Anobiidae), and camel crickets (Rhaphidophoridae). Predators also were generally more abundant on mounds than non-mounds, including velvet ants
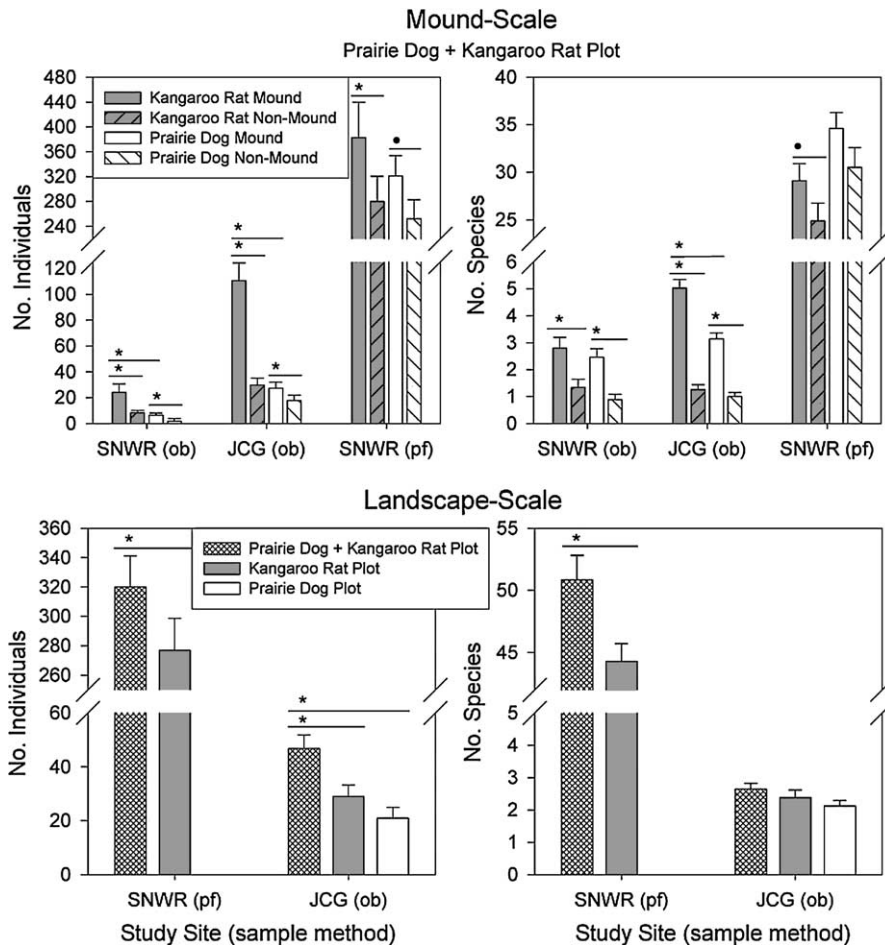
Fig. 1. Mean abundance and richness (+ SE) of ground-dwelling arthropods on the mound- and landscape-scale plots at the Sevilleta National Wildlife Refuge (SNWR) and the Janos-Casas Grandes (JCG) study sites over all years sampled. Means were calculated from oat-bait samples (ob) on a per mound basis and from pitfall (pf) samples on a per trap basis. *p < 0.05 over all sample periods, •p < 0.05 during one sample period.

(Mutillidae) and a gnaphocid ant-mimic spider, *Micaria porta*, on Gunnison's prairie dog mounds. Ants (Formicidae) showed a consistent negative association with kangaroo rat mounds at the SNWR, (paired t-test: spring 2000 n = 10, t = −3.40, p = 0.008), but a positive association with prairie dog mounds at both sites (p < 0.026, for all tests). Spider beetles, cellar spiders (Pholcidae), fire ants (*Solenopsis* spp.), and black widow spiders *Latrodectus hesperus* were more abundant in kangaroo rat mounds compared to prairie dog mounds at both sites, based on oat-bait samples (p < 0.05, for all tests). A rare rodent burrow specialist ant, *Aphaenogaster puncticeps* (MacKay and MacKay 2002), and a rare camel cricket, *C. fissicaudus* (Hubbell 1936), are reported here for the first time from prairie dog burrows. *Aphaenogaster puncticeps* associated strongly with both rodent mound types, at both sites, but *C. fissicaudus* was only found in Gunnison's prairie

dog burrows. Similar to the mounds, the landscape-scale Pdog + Krat plot at the SNWR had greater abundance of detritivores, granivores, predators, cellar spiders, darkling beetles, ants, camel crickets, and *M. porta,* but spider beetles were more common on the Krat plot.

Grasshoppers

A total of 35 and 28 grasshopper species were recorded at the SNWR and JCG study sites, respectively. At the landscape-scale, the Krat plot and Pdog + Krat plot differed significantly in species richness and abundance at the SNWR (MANOVA: $F_{2,45} = 47.09$, p < 0.0001), with the Krat plot having greater grasshopper abundance (t-test: DF = 46, t = 6.08, p < 0.0001), but not richness, than the Pdog + Krat plot. At JCG, there were no significant differences in abundance or richness.
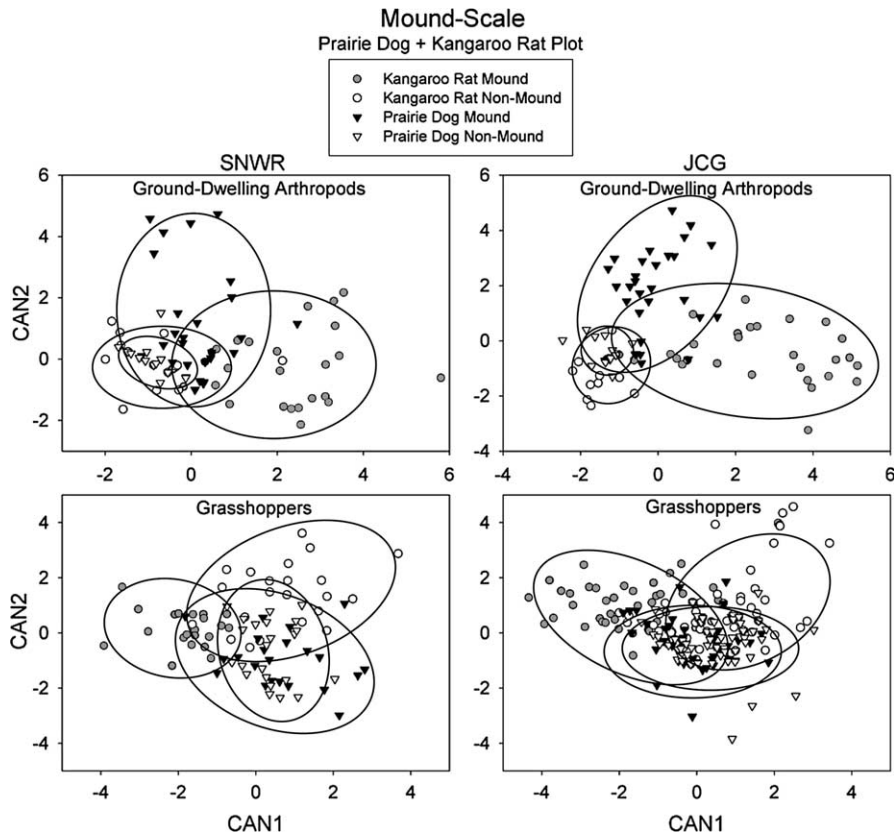
Fig. 2. Ordination of canonical variates for ground-dwelling arthropods on mound-scale plots at the SNWR (MANOVA: $F_{48,235} = 2.64$, p < 0.0001) and JCG (MANOVA: $F_{81,371} = 4.33$, p < 0.0001), and for grasshoppers on mound-scale plots at the SNWR (MANOVA: $F_{66,402} = 3.83$, p < 0.0001) and JCG (MANOVA: $F_{57,174} = 2.64$, p < 0.0001). Ordinations are based on differences in ground-dwelling arthropod species composition (from oat-bait data) and grasshopper species composition among plots. Note that mound-scale plots shown here are from the prairie dog + kangaroo rat plots, which are plotted in Fig. 3. Ellipses represent 95% confidence intervals for each group.

However, at both sites, Monte Carlo randomization tests indicated that species richness on the hypothetical combined plot was consistently greater than on the individual landscape treatments, indicating that the presence of both rodents on the greater landscape increased overall grasshopper species richness at this greater landscape-scale (mean ± 1SE SNWR: both plots S = 27.4 ± 0.23, Pdog + Krat plot S = 25.5 ± 0.16, Krat plot S = 25.7 ± 0.17; JCG: all plots S = 21.8 ± 0.52, Pdog + Krat plots S = 18.6 ± 0.48, Krat plots S = 18.5 ± 0.50, Pdog plots S = 18.5 ± 0.57). At the mound scale, mean grasshopper abundance and species richness differed significantly between mounds and non-mounds at both study sites, in all but one case (MANOVA: p < 0.002, for all tests), typically being greater off mounds than on. However, abundance was almost two times greater on kangaroo rat mounds compared to non-mounds at JCG (MLM: p < 0.0001, for both tests).

Grasshopper community composition also differed among treatments at the mound and landscape scales

(Fig. 2 and 3). The CDFA demonstrated that grasshopper species composition differed significantly between the mounds and non-mounds, prairie dog mounds and kangaroo rat mounds, and also among the Pdog + Krat, Krat, and Pdog plots across both sites (MANOVA: p < 0.0001, for all tests) (Fig. 2 and 3). The Mahalanobis distance measures demonstrated significant distances between these treatments based on species composition (p < 0.002, for all comparisons), with the exception of prairie dog mounds and paired non-mounds on the Pdog + Krat plots (during autumn 2001–spring 2002, only) (Appendix, Table S3).

Differences in species composition between the mound-scale and landscape-scale plots were due primarily to responses of different grasshopper life-form groups (Fig. 4). Spearman correlation showed that the different grasshopper life-form groups were positively correlated with their preferred micro-habitats or substrates (Appendix, Table S2 and S4). Graminicoles
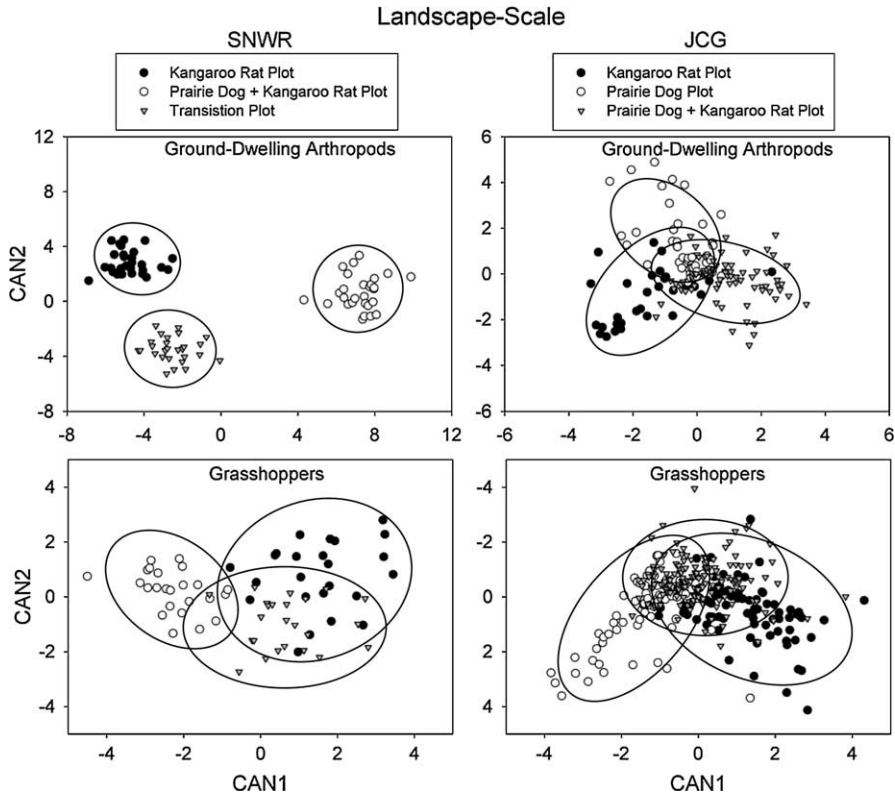
Fig. 3. Ordination of canonical variates showing differences in species composition of ground-dwelling arthropods on landscape-scale plots at the SNWR (MANOVA: $F_{142,22} = 2.23$, $p = 0.015$) and JCG (MANOVA: $F_{66,558} = 2.09$, $p < 0.0001$), and for grasshoppers at the landscape-scale at the SNWR (MANOVA: $F_{52,88} = 287$, $p < 0.0001$) and JCG (MANOVA: $F_{48,588} = 6.89$, $p < 0.0001$). Ordinations of ground-dwelling arthropods at the SNWR are based on pitfall and grasshopper data from the landscape-scale plots, and at JCG are based on mound-scale oat-bait and grasshopper data. Ellipses represent 95% confidence intervals for each group.

associated with dense grass cover, graminiterricoles with open, patchy grass cover, herbicoles mostly with forbs, and terricoles primarily with bare soil. Herbicoles were consistently more abundant on kangaroo rat mounds compared to paired non-mounds and prairie dog mounds ($p < 0.04$, for all tests). At the SNWR, graminicoles were associated with non-mounds compared to kangaroo rat mounds on the Krat plot, especially during the spring (paired t-test: $n = 20$, $t = -3.16$, $p = 0.005$), and terricoles were less abundant on kangaroo rat mounds than on prairie dog mounds (t-test: $DF = 38$, $t = 3.51$, $p = 0.001$), but were more abundant on kangaroo rat mounds than paired non-mounds on the Krat plot (paired t-test: $n = 20$, $t = 4.59$, $p = 0.0002$). Graminiterricoles were more abundant on prairie dog mounds compared to paired non-mounds (paired t-test: $n = 20$, $t = 2.59$, $p = 0.02$) and kangaroo rat mounds (t-test: $DF = 38$, $t = -3.70$, $p = 0.007$), but were more common on non-mounds than prairie dog mounds at JCG (MLM: $p < 0.02$, for both tests). The strongest landscape-scale patterns in grass-hopper trophic groups were seen at the SNWR, with no significant differences among the landscape plots at JCG. Graminicoles were more abundant on the Krat plot than the Pdog+Krat plot (t-test: $DF = 46$, $t = 6.8$, $p < 0.0001$), and herbicoles and terricoles were more abundant on the Pdog+Krat plot compared to the Krat plot at the SNWR (t-test: herbicoles $DF = 46$, $t = 6.13$, $p < 0.0001$; terricoles $DF = 46$, $t = -2.54$, $p = 0.01$).

Discussion

Our results demonstrate that the activities of Gunnison's prairie dogs, black-tailed prairie dogs, and kangaroo rats had keystone-level effects on arthropod communities through large changes in species richness, composition, and abundance, at both small and large spatial scales. Further, the effects we found were generally consistent across both species of prairie dogs, suggesting that they have similar ecological effects on arthropod communities. Impressively, even within a
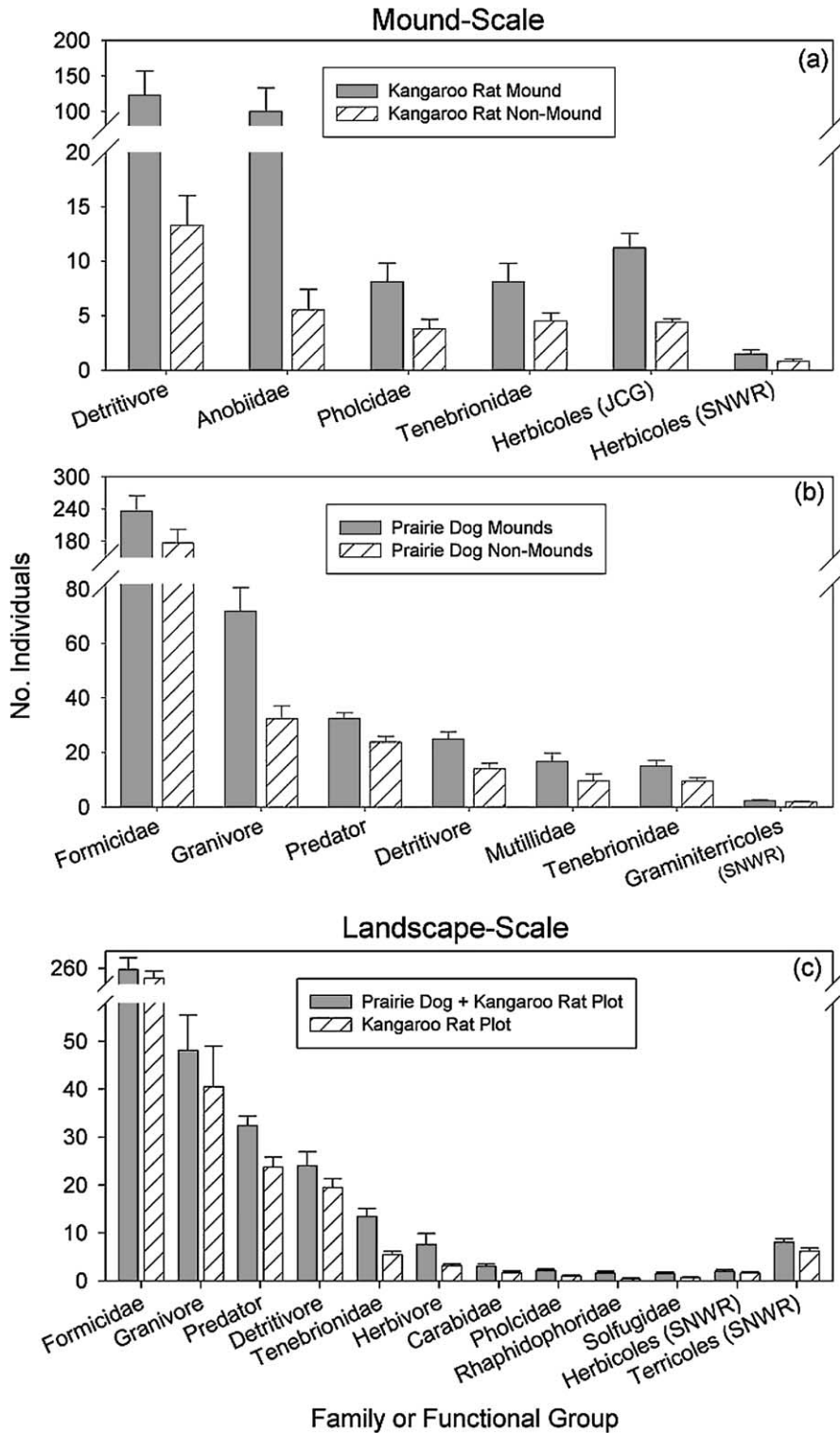
Fig. 4. Mean abundance (+SE) of ground-dwelling arthropod family and trophic groups (per pitfall trap) at the SNWR and grasshopper life-form groups (per 5 m^2 at mound-scale, 30 m^2 and 25 m^2 at SNWR and JCG landscape-scales, respectively) that significantly associated (p < 0.05) with (a) kangaroo rat mounds, (b) prairie dog mounds, and (c) the prairie dog + kangaroo rat plot during one or more sample periods.

distance of 10 m, the difference in ground-dwelling arthropod abundance and richness was up to 5-fold greater on mounds than on off-mound areas (Fig. 1). Especially interesting was our finding that the co-occurrence of prairie dogs and kangaroo rats resulted in a unique combination of habitats for both ground-dwelling arthropods and grasshoppers, increasing biodiversity on the landscape.

By providing key habitat with a high concentration of resources, prairie dog and kangaroo rat burrows enhanced populations and species richness of multiple trophic and taxonomic groups of surface-active arthropods, as well as obligate burrow specialists. The strong association of detritivores (especially spider beetles, darkling beetles, and camel crickets) with the burrows was probably due to both increased organic material and favorable microclimates in the rodent burrow systems (Hawkins and Nicoletto 1992, Bangert and Slobodchikoff 2006). The rare ant, *A. punctaticeps,* which nests in the burrow systems (MacKay and MacKay 2002), along with other ant species, utilized the burrows to obtain food resources as demonstrated by foraging trails that we frequently observed. The entrance holes of mounds also served as important habitat structure for webs of cellar and black-widow spiders. Other predator populations also were enhanced around the mounds and on the landscape where burrow density was highest (Davidson 2005), likely due to some combination of greater diversity and abundance of arthropod prey and better protection from their own predators. In addition, the burrow systems are known to attract many other invertebrate groups such as insect larvae, nematodes, and microarthropods (Wilcomb 1954, Seastedt et al. 1986)

Despite broad similarities in the arthropod taxa associated with both prairie dog and kangaroo rat burrows, a more detailed examination showed that the different burrow systems provided unique habitats and attracted different assemblages of arthropod species. Differences in size, shape, depth, complexity, and soil texture between the burrow systems provide different environments (Kay and Whitford 1978). Kangaroo rat mounds typically are 3−6 m in diameter, honeycombed by a network of shallow tunnels that extend ca 1 m deep (Best 1988), whereas prairie dog mounds are 2−3 m in diameter with a single tunnel that often extends 2−3 m deep and 5−10 m long (Hoogland 2006). Ground-dwelling arthropods tended to be more abundant and diverse at kangaroo rat mounds than prairie dog mounds, which may have been due to the greater architectural complexity and mound surface area. The longer and deeper prairie dog burrows probably provided moister, cooler, and more constant microclimates for species such as camel crickets. Arthropods also were likely attracted to the different food resources available in the two burrow types. Although nest material and feces are common in both burrow systems, kangaroo rats actively store seeds and other plant material, whereas prairie dogs only occasionally bring food into their burrows (Wilcomb 1954, Best 1988). Spider beetles, which are common in mammal nests, were especially abundant in kangaroo rat burrows perhaps because of the availability of seed caches (White 1983). Additionally, our SNWR pitfall trap data indicates that although kangaroo rat burrows supported greater numbers of ground-dwelling arthropods per mound, higher densities of Gunnison's prairie dog burrows on the landscape (Davidson 2005) resulted in greater numbers of ground-dwelling arthropods at the landscape-scale.

Prairie dogs and kangaroo rats also played important roles in structuring arthropod communities by altering the aboveground environment. Elsewhere, we showed that on these same study plots prairie dogs and kangaroo rats significantly altered vegetation composition and structure around their mounds and at the landscape-scale (Davidson 2005, Davidson and Lightfoot 2006). These modifications likely explain many of the patterns we found in arthropod community composition and abundance. For example, overall ant abundance was greater where Gunnison's prairie dogs and kangaroo rats co-occurred, perhaps by facilitating the establishment of annual plants that provide important seed resources (Davidson et al. 1984, Davidson 2005). Although some species of ants are known to associate with kangaroo rat mounds (Schooley et al. 2000), and did so in this study, greater numbers of ants, especially harvester ants, occurred at Gunnison's prairie dog mounds. The reason for this is unclear, since both species increased forbs around their mounds (Davidson 2005). Our results suggest competition between kangaroo rats and ants for available seed resources (Valone et al. 1994). Considering that prairie dog mounds are more numerous on the landscape, they also may provide more food resources and, therefore, support higher densities of ants and other species that associate with ants such as the ant-mimic spiders.

The associations of grasshopper species with the different habitats created by prairie dogs and kangaroo rats were consistent with their known associations with particular microhabitat types (Uvarov 1977, Lightfoot 1985). For example, terricoles associated with bare soil on rodent mounds, herbicoles associated with high forb cover on kangaroo rat mounds, graminterricoles with sparse, grazed perennial grasses around prairie dog mounds, and graminicoles with tall, dense grasses away from rodent mounds. These results are consistent with known effects of grazers and disturbance on grasshoppers, and the general effects of black-tailed prairie dogs on grasshoppers in mixed-grass prairie (Jepson-Innes and Bock 1988, Russell and Detling 2003). However, while the plant-grasshopper-rodent

relationships were pronounced at the SNWR, they appeared to have been somewhat disrupted at JCG by the intensive cattle grazing that had desertified much of the landscape from a perennial grassland to annual grassland. JCG also lacked an entire functional group of graminicole grasshoppers, apparently due to the lack of perennial grass on which they live (Uvarov 1977). Domestic livestock grazing is known to alter grasshopper species compositions (Pfadt 1982, Jepson-Innes and Bock 1988, Quinn and Walgenbach 1990). The combined disturbance effects of livestock, prairie dogs, and kangaroo rats resulted in a landscape dominated by bare soil and annual plants, a different outcome from the effects of rodents alone at the SNWR. Nevertheless, at both sites, the different mounds and landscape plots where the rodents occurred provided unique habitats for different assemblages of grasshoppers.

Our results demonstrate that prairie dogs and kangaroo rats had complementary, additive effects on grassland arthropod communities. The distinct species assemblages of arthropods at the mound and landscape scales resulted in greater heterogeneity and species richness where prairie dogs and kangaroo rats co-occurred. These results are consistent with growing evidence from other research, demonstrating the importance of ecosystem engineering and multiple disturbance types in promoting landscape heterogeneity and biodiversity (Joern 2005, Wright et al. 2006). Based on our results, we suggest that co-existing keystones in other systems, especially those that play engineering roles, also may have important interactive effects that drive community organization leading to increased biodiversity.

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