

# Short-Term Effects of a Summer Wildfire on a Desert Grassland Arthropod Community in New Mexico

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**ABSTRACT** Surface-active arthropods were sampled after a lightning-caused wildfire in desert grassland habitat on the Sevilleta National Wildlife Refuge, Socorro County, NM. Pitfall traps ( $n = 32$  per treatment) were used to evaluate species-specific “activity-density” indices after the June wildfire in both burned and unburned areas. In total, 5,302 individuals were collected from 69 taxa. Herbivore activity-densities generally decreased, whereas predators often increased in the burned area; pitfall trap bias likely contributed to this latter observation. Fire caused the virtual extirpation of scaly crickets (Mogoplistidae), field crickets (Gryllidae), and camel crickets (Raphidophoridae), but recolonization began during the first postfire growing season. Several grasshoppers (Acrididae) also exhibited significant postfire declines [*Ageneotettix deorum* (Scudder), *Eritettix simplex* (Scudder), *Melanoplus bowditchi* Scudder, and *Amphitornus coloradus* (Thomas)]. Some beetles showed lower activity-density, including *Pasimachus obsoletus* LeConte (Carabidae) and *Eleodes extricatus* (Say) (Tenebrionidae). Taxa exhibiting significant postfire increases in activity-density included acridid grasshoppers (*Aulocara femoratum* (Scudder), *Hesperotettix viridis* (Thomas), *Trimerotropis pallidipennis* (Burmeis.), and *Xanthippus corallipes* Haldeman); carabid beetles (*Amblycheila picolomini* Reiche, *Cicindela punctulata* Olivier), tenebrionid beetles (*Eleodes longicollis* LeConte, *Edrotes rotundus* (Say), *Glyptasida sordida* (LeConte), *Stenomorpha consors* (Casey); the centipedes *Taiyubius harrietae* Chamberlin (Lithobiidae) and *Scolopendra polymorpha* Wood (Scolopendridae); scorpions (*Vaejovis* spp.; Vaejovidae); and sun spiders (*Eremobates* spp.; Eremobatidae). Native sand roaches (*Arenivaga erratica* Rehn, *Eremoblata subdiaphana* (Scudder); Polyphagidae) displayed no significant fire response. Overall, arthropod responses to fire in this desert grassland (with comparatively low and patchy fuel loads) were comparable to those in mesic grasslands with much higher and more continuous fuel loads.

**KEY WORDS** disturbance, fire, insect, invertebrate, succession

Fire in grassland ecosystems has substantial effects on local arthropod communities through the immediate killing of vulnerable individuals (e.g., grass-dwelling species) and alteration of habitat characteristics, including the reduction or elimination of prey, food plants, and foliage habitat structure, shifts in microclimate means and extremes, and physical substrate changes, such as the creation of soil ash layers (see reviews by Warren et al. (1987) and Swengel (2001), and references therein).

Although considerable research has focused on the impact of fire on arthropod assemblages in the North American tallgrass prairie ecosystem (Evans

1984, 1988a, 1988b; Scifres et al. 1988; Panzer 2002; Fay 2003; Joern 2004, 2005; Vogel et al. 2010) and other mesic grasslands (Gillon 1983; Porter and Redak 1996, 1997; Reed 1997; Siemann et al. 1997; Chambers and Samways 1998; Kerstyn and Stiling 1999; Blanche et al. 2001; Branson 2005; Knight and Holt 2005; Langlands et al. 2006; Nadeau et al. 2006; Nunes et al. 2006; Uys et al. 2006; Branson and Vermeire 2007; Hartley et al. 2007; Johnson et al. 2008; Uehara-Prado et al. 2010; Matsuda et al. 2011), few studies have addressed such responses in semi-arid and arid grasslands (Hansen 1986, Bock and Bock 1991, Ford 2001, Zimmer and Parmenter 1998, Ford 2007). Arid and semiarid grasslands often support smaller and more spatially patchy fuel loads than mesic grasslands, contributing to both lower soil temperatures during passing fire fronts and a greater probability of unburned patches of vegetation remaining after a fire (McPherson 1995). These attributes make fires in desert grasslands qualitatively different from those in mesic grasslands, and

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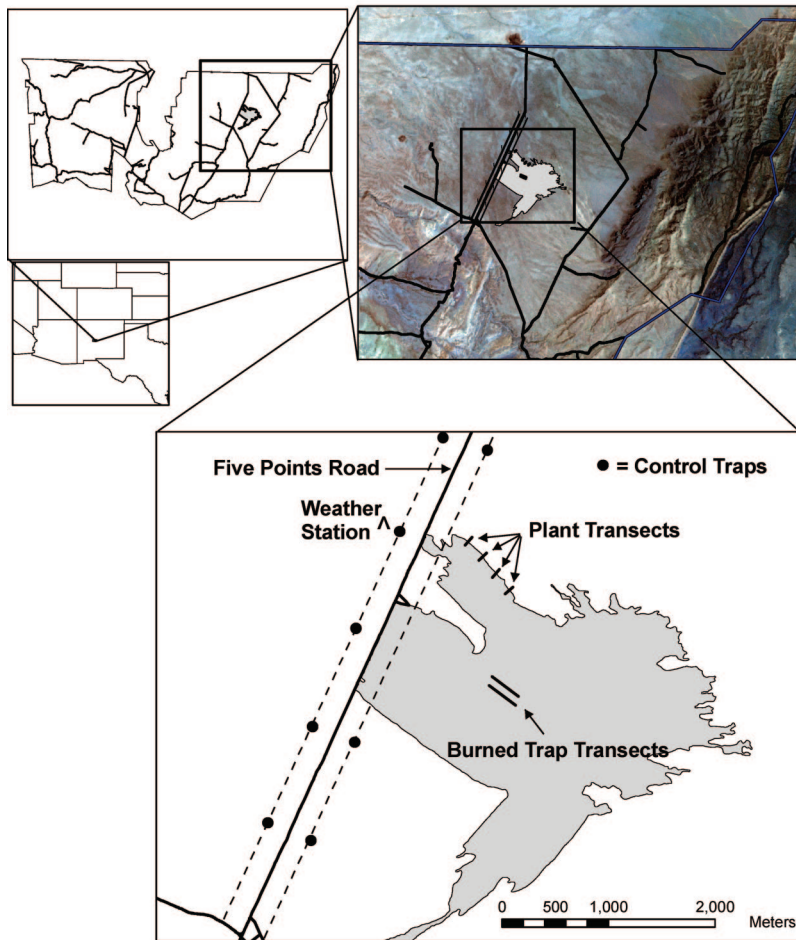
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**2001 Deep Well Fire study area on McKenzie Flats,  
Sevilleta National Wildlife Refuge, Socorro County, New Mexico**



**Fig. 1.** Maps of the study area on McKenzie Flats, Sevilleta National Wildlife Refuge, NM. Maps show the location of the Sevilleta NWR in New Mexico, the area of McKenzie Flats within the Sevilleta NWR, a LANDSAT image of McKenzie Flats with the wildfire area in gray highlight, and a schematic map showing the locations of the burned area, the two 300-m burned pitfall trap transects, the four 100-m plant transects (Table 1) crossing the wildfire boundary, the Deep Well meteorological station, and the unburned “control” pitfall trap transects across McKenzie Flats (paralleling the five Points Road). Each of the eight control pitfall trap locations had four pitfall traps spaced 20 m apart.

hence, may have less severe direct impacts on resident arthropods.

The purpose of this study was to capitalize on the serendipitous occurrence of a natural lightning-caused wildfire in a well-studied desert grassland ecosystem in central New Mexico, and record the resulting short-term (first growing season) differences in the surface-active arthropod community of burned and unburned habitat. Specifically, for each arthropod taxon, we asked if fire eliminated, reduced, increased, or had no effect on the activity-density of each taxon in the burned area relative to unburned “control” grassland. The results of these postfire observations in this desert grassland could then be compared with those from more mesic grassland fire regimes.

## Materials and Methods

**Study Area.** The study was conducted in the desert grassland habitat of the Sevilleta National Wildlife Refuge (NWR), Socorro County, NM (Fig. 1), in an area known locally as the Deep Well region of McKenzie Flats (Lat. 34° 21' 33" N, 106° 41' 26" W, Elev. 1,600 m). This area has hosted many detailed studies of the Sevilleta Long Term Ecological Research (LTER) program since 1989, and considerable background information exists on the flora, fauna, soils, and climate of the region. The site was a broad, flat grassy plain, dominated by perennial grasses (Table 1), including *Bouteloua eriopoda*, *B. gracilis*, *Pleuraphis jamesii*, *Aristida purpurea*, several species of *Sporobolus*, and a variety of forbs. Annual precipitation (1988–

**Table 1. Percentage cover of plant species, litter, and bare ground on burned and unburned line transects near Deep Well on the Sevilleta National Wildlife Refuge, NM**

Species	2000 (pre-fire)		2001 (post-fire)	
	Control	Burned	Control	Burned
<b>Grasses</b>				
<i>Aristida purpurea</i> Nutt.	0.6 ± 0.4	0.3 ± 0.2	0.9 ± 0.6	0.1 ± 0.1
<i>Bouteloua barbata</i> Lag.	0.0	0.0	0.0	0.1 ± 0.1
<i>Bouteloua eriopoda</i> (Torr.) Torr.	29.7 ± 6.0	29.9 ± 6.8	29.4 ± 5.7	14.2 ± 3.7
<i>Bouteloua gracilis</i> (Willd. ex Kunth) Lag. ex Griffiths	16.8 ± 4.0	23.0 ± 5.0	14.3 ± 3.5	17.2 ± 3.7
<i>Pleuraphis jamesii</i> Torr.	4.0 ± 1.8	2.4 ± 1.1	2.7 ± 1.3	1.0 ± 0.4
<i>Muhlenbergia arenicola</i> Buckley	0.0	0.2 ± 0.1	0.0	0.3 ± 0.1
<i>Panicum obtusum</i> Kunth	0.0	0.0	0.2 ± 0.2	0.0
<i>Sporobolus contractus</i> Hitchc.	0.1 ± 0.1	0.1 ± 0.1	0.0	0.2 ± 0.1
<i>Sporobolus cryptandrus</i> (Torr.) A. Gray	0.3 ± 0.2	1.5 ± 0.5	0.9 ± 0.3	1.4 ± 0.4
<i>Sporobolus flexuosus</i> (Thurb. ex Vasey) Rydb.	0.6 ± 0.3	1.3 ± 0.7	0.2 ± 0.1	0.1 ± 0.1
Total grass:	52.1 ± 12.8	58.7 ± 14.5	48.6 ± 11.7	34.6 ± 8.7
<b>Forbs</b>				
<i>Astragalus missouriensis</i> Nutt.	0.0	0.0	0.1 ± 0.1	0.0
<i>Chamaesyce albomarginata</i> (Torr. & A. Gray) Small	0.0	0.0	0.2 ± 0.1	0.6 ± 0.4
<i>Chaetopappa ericoides</i> (Torr.) G.L. Nelson	0.0	0.0	0.1 ± 0.1	0.0
<i>Chamaesyce glyptosperma</i> (Engelm.) Small	0.0	0.0	0.1 ± 0.1	0.2 ± 0.1
<i>Chamaesyce lata</i> (Engelm.) Small	0.0	0.0	0.0	0.1 ± 0.1
<i>Chamaesyce serrula</i> (Engelm.) Wott & Standl.	0.0	0.0	0.0	0.4 ± 0.2
<i>Chamaesyce serpyllifolia</i> (Pers.) Small	0.0	0.0	0.0	0.4 ± 0.3
<i>Cryptantha crassisejala</i> (Torr. & A. Gray) Greene	0.0	0.0	0.2 ± 0.1	0.2 ± 0.1
<i>Cymopterus montanus</i> Nutt. ex Torr. & A. Gray	0.0	0.0	0.1 ± 0.1	0.0
<i>Dalea jamesii</i> (Torr.) Torr. & A. Gray	0.0	0.0	0.0	0.1 ± 0.1
<i>Dalea nana</i> Torr. ex A. Gray	0.0	0.0	0.0	0.1 ± 0.1
<i>Descurainia obtusa</i> (Greene) O.E. Schulz	0.0	0.0	0.0	0.1 ± 0.1
<i>Hoffmannseggia glauca</i> (Ortega) Eifert	0.0	0.0	0.1 ± 0.1	0.1 ± 0.1
<i>Ipomoea costellata</i> Torr.	0.0	0.0	0.1 ± 0.1	0.1 ± 0.1
<i>Kallstroemia parviflora</i> J.B.S. Norton	0.0	0.0	0.0	1.2 ± 0.5
<i>Machaeranthera pinnatifida</i> (Hook.) Shinners	0.0	0.0	0.1 ± 0.1	0.0
<i>Mentzelia laciniata</i> (Rydb.) J. Darl.	0.0	0.0	0.1 ± 0.1	0.0
<i>Oenothera cespitosa</i> Nutt.	0.0	0.0	0.1 ± 0.1	0.0
<i>Pectis angustifolia</i> Torr.	0.0	0.0	0.0	0.3 ± 0.1
<i>Plantago patagonica</i> Jacq.	0.0	0.0	0.4 ± 0.2	0.2 ± 0.1
<i>Proboscidea parviflora</i> (Woot.) Woot. & Standl.	0.0	0.0	0.0	0.1 ± 0.1
<i>Sanvitalia abertii</i> A. Gray	0.0	0.0	0.0	0.1 ± 0.1
<i>Senecio flaccidus</i> Less.	0.0	0.0	0.1 ± 0.1	0.0
<i>Solanum elaeagnifolium</i> Cav.	0.1 ± 0.1	0.1 ± 0.1	0.3 ± 0.1	0.2 ± 0.1
<i>Sphaeralcea coccinea</i> (Nutt.) Rydb.	0.0	0.0	0.0	0.1 ± 0.1
<i>Sphaeralcea hastulata</i> A. Gray	0.0	0.0	0.1 ± 0.1	0.0
<i>Sphaeralcea wrightii</i> A. Gray	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1
<i>Stephanomeria pauciflora</i> (Torr.) A. Nelson	0.0	0.0	0.2 ± 0.1	0.0
<i>Tidestromia lanuginosa</i> (Nutt.) Standl.	0.0	0.0	0.0	0.1 ± 0.1
<i>Tragia ramosa</i> Torr.	0.0	0.0	0.0	0.1 ± 0.1
Total forbs	0.2 ± 0.1	0.2 ± 0.2	2.5 ± 0.9	4.9 ± 2.4
<b>Shrubs</b>				
<i>Ephedra torreyana</i> S. Watson	0.0	0.0	0.1 ± 0.1	0.0
<i>Gutierrezia sarothrae</i> (Pursh) Britton & Rusby	0.2 ± 0.1	0.4 ± 0.2	0.3 ± 0.1	0.1 ± 0.1
Total shrubs	0.2 ± 0.1	0.4 ± 0.2	0.4 ± 0.2	0.1 ± 0.1
<b>Cacti</b>				
<i>Escobaria vivipara</i> (Nutt.) Buxbaum	0.0	0.0	0.0	0.1 ± 0.1
<i>Opuntia phaeacantha</i> Engelm.	0.0	0.2 ± 0.1	0.0	0.1 ± 0.1
Total cacti	0.0	0.2 ± 0.1	0.0	0.2 ± 0.2
Litter	22.3 ± 5.5	33.2 ± 7.3	13.5 ± 5.1	14.8 ± 5.0
Bare ground	31.1 ± 8.4	17.7 ± 6.0	39.4 ± 8.6	48.6 ± 9.9

Data collected in autumn of each year; wildfire occurred on 24 June 2001. Percentage cover on transects were sampled with 1-cm resolution; taxonomy follows USDA NRCS Plants Database (2011). Values are mean percentage cover by species from four 50-m transects ± SE.

2009) averaged 242 mm, with more than half (57%) falling during the summer monsoon season (June through September). Long-term mean daily minimum temperatures were -7.3° in January, and mean daily maximum temperatures were 33.2°C in July. Total precipitation during the months of the study (June–November 2001) was 150 mm, a value somewhat below average compared with the long-term June–Novem-

ber mean of 175 mm (Fig. 2; Sevilleta LTER, Deep Well meteorological station: <http://sev.lternet.edu>). Soils were sandy loams, classified as Berino-Dona Ana association, consisting of fine-loamy, mixed, thermic Typic Haplarids (Johnson 1988).

**Study Design and Arthropod Sampling.** In early summer 2001, as part of a Sevilleta LTER large-scale assessment of surface-active arthropod communities,

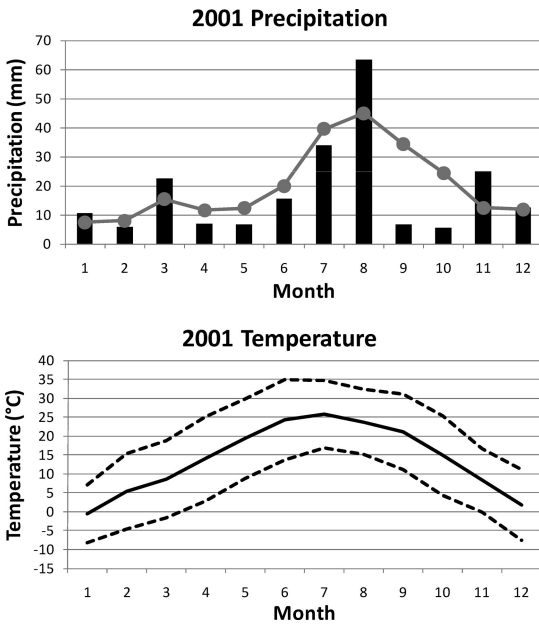


Fig. 2. Climate conditions in 2001 on McKenzie Flats, Sevilleta National Wildlife Refuge, NM. Top: Total monthly precipitation in 2001 (histograms) and long-term means (gray points with line). Bottom: Mean monthly temperature (solid line) and mean monthly maximum and minimum temperatures (dotted lines). The wildfire occurred on 24 June, 2001. Data from the Sevilleta LTER Deep Well meteorological station (<http://sev.lternet.edu/>).

a series of arthropod pitfall-trap transects were established across the McKenzie Flats study area (Fig. 1). On 24 June 2001, a late-afternoon “dry” lightning strike ignited a wildfire in the central portion of McKenzie Flats, and over the next 21 h, burned an area of 5.76 km<sup>2</sup>. On 25 June, we installed 32 additional pitfall traps in two parallel transects arbitrarily placed near the center of the burned area (>300 m from the unburned edge of the fire area). Transects were 50 m apart, and consisted of 16 pitfall traps each at 20 m intervals (300 m total transect length). Pitfall traps consisted of tin cans (8.5 cm in diameter, 13 cm deep) with plastic cup inserts filled halfway with propylene glycol. A ceramic tile (20 cm by 20 cm) elevated 2 cm on nails above the trap reduced rainfall and wind-blown ash and debris from entering the trap. Traps were open continuously through the summer and autumn, and sampled on 5 July, 20 July, 10 August, 10 September, 8 October, and 26 November 2001.

Nearby LTER pitfall traps on McKenzie Flats in similar unburned vegetation adjacent to the fire zone served as “control” pitfall traps. These traps were identical to the traps installed after the fire. The 32 traps (eight sites of four traps with 20-m spacing per site [Fig. 1]) that were closest to the actual burned area were sampled on the same schedule as the traps in the fire zone. The arthropods collected in the unburned pitfall traps preceding the 24 June fire also provided a measure of each taxon’s prefire activity-density in early summer.

Arthropods collected from the pitfall traps were preserved in 70% ethanol and transported to the laboratory for sorting, identification, and counting. Resident arthropod taxa included in the analyses were those ground-dwelling species that were reasonably sampled using pitfall traps and for which we had taxonomic expertise: Coleoptera (Carabidae, Tenebrionidae); Orthoptera (Acrididae, Gryllidae, Mogopliidae, Raphidophoridae, Tettigoniidae); Blattaria (Polyphagidae); Lithobiomorpha (Lithobiidae); Scolopendromorpha (Scolopendridae); Scorpionida (Vaejovidae); and Solifugae (Eremobatidae). Reference specimens were archived in the Arthropod Division of the Museum of Southwestern Biology, University of New Mexico, Albuquerque, NM.

**Fire Characteristics.** Lightning ignited the grassland site in late afternoon ( $\approx$ 1600 hours) on 24 June, and the wildfire burned continuously through the night. Fire suppression efforts extinguished the fire by midday on 25 June. No precipitation fell during the fire. Air temperatures during the fire ranged from 20° to 37°C, and relative humidity ranged from 14 to 54%; wind speeds averaged 3.5 m · sec<sup>-1</sup>, with gusts up to 11.5 m · sec<sup>-1</sup> (Fig. 3). Aboveground vegetation on the site was nearly completely consumed by the fire, leaving only low, charred stubble (<2 cm high; Fig. 4). Plant cover on the site, measured before the fire in autumn 2000 (see methods below), averaged 59%, with plant litter cover at 33% (Table 1). Although vegetation cover and biomass varies considerably through space and time on the Sevilleta NWR (Pennington and Collins 2007), typical grass-forb fuel loads on McKenzie Flats averaged 192 ± 52 g · m<sup>-2</sup> (mean ± 95% C.I. standing crop dry biomass, measured 1989–1992, Sevilleta LTER data). Flame lengths and rates of spread were not recorded by firefighting personnel, but during a previous prescribed experimental fire on McKenzie Flats in 1993 (under similar fuel loads and wind conditions), flame lengths ranged from 20 cm to 2 m, and exhibited rates of spread between 1.5 m · min<sup>-1</sup> and 12 m · min<sup>-1</sup> depending on local fuel load and wind gusts (Parmenter 2008).

**Vegetation Sampling.** The response of the site vegetation to the wildfire also was measured before and after the fire. Four line-intercept transects of 100 m each had been established on McKenzie Flats in 1995 and sampled annually before the 2001 fire as part of the Sevilleta LTER project. These transects crossed an area of unburned grassland and entered an area that had been burned in another lightning fire in 1995. The fire of 24 June 2001 burned right up to the boundary of this old fire zone, but, due possibly to a slightly reduced fuel load (Table 1), did not burn into it; this effectively created eight transects, with four 50-m transects in the burned area and four 50-m transects in the unburned area. These transects provided preburn plant cover values in autumn 2000, and were then resampled after the fire in 2001 to determine the degree of postfire vegetation regrowth during the study period.

**Statistical Analyses.** The overarching hypothesis tested in this study addressed the impact of fire on the

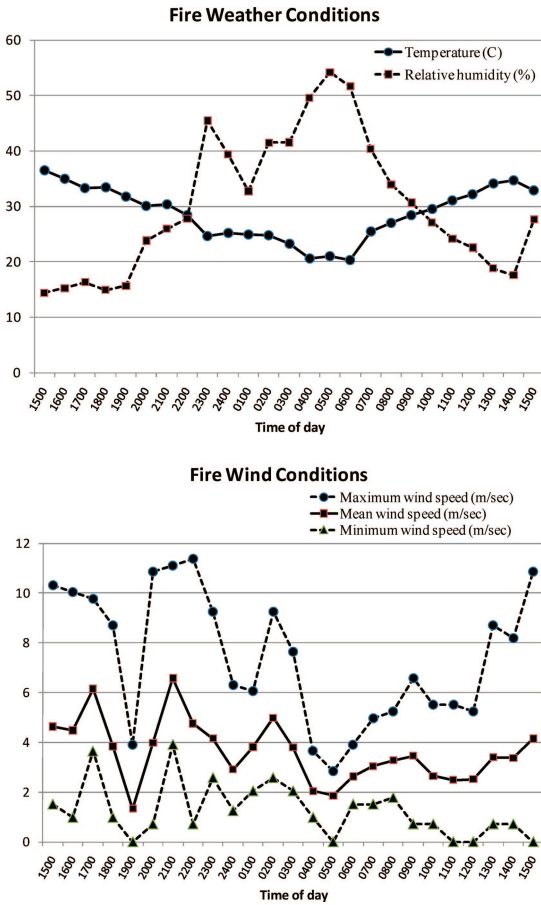


Fig. 3. Meteorological conditions during the wildfire on McKenzie Flats, Sevilleta National Wildlife Refuge, NM. The fire was ignited by a lightning strike at ≈1600 hours on 24 June, 2001, and was extinguished by wild-land firefighters by early afternoon the next day. No precipitation was recorded until late afternoon on 25 June. Data from the Sevilleta LTER Deep Well meteorological station (<http://sev.lternet.edu/>).

population activity-density responses of the resident arthropod species. As there was only a single lightning-caused wildfire, the wildfire “treatment” per se was not replicated (note that prescribed fires, which can be replicated, may partially remedy this issue, but prescribed fires are generally conducted under lower wind-speed conditions and higher humidity, resulting in less severe ecological effects). Rather, our sampling effort was directed toward assessing species-specific trap-captures across the central region of the burned area (reducing edge effects), and comparing the mean numbers of individuals captured per trap to those from traps in comparable adjacent unburned grassland. As such, individual pitfall traps were treated as experimental units (replicates) within the burned and unburned areas. Traps were spaced sufficiently far apart (minimum of 20 m) to ensure statistical independence (i.e., captures by one trap would have no measurable effect on the captures of an adjacent trap), and both the unburned and burned areas had nearly identical



Fig. 4. Photographs of study area on McKenzie Flats. Top: Study area before the fire. Middle: Postfire view of site on 25 June 2001. Bottom: Study area on 9 October 2001.

vegetation, soils, slope, aspect, and elevation (Fig. 1; Table 1). We also considered the “selection” of the burned area for the “fire treatment” as a random event, resulting from the initial lightning strike and meteorological conditions (wind speed and direction) at the time. Thus, while the wildfire treatment and site effects could not technically be statistically separated, there was sufficient habitat uniformity across the study area to justifiably interpret the observed postfire inter-site differences in trap captures as being caused by the wildfire.

In addition, pitfall traps have inherent sampling biases that warrant conservative interpretations of capture data (reviewed in Parmenter et al. 1989), particularly with respect to statistical analyses of the numbers of individuals captured per trap. In this study, the primary bias within taxa was assumed to be the influence of the fire on physical habitat characteristics, specifically the removal of nearly all aboveground

plant biomass and litter, and the resultant impact on movements of surface-active arthropods. Given the considerably more open postfire habitat, arthropod movements (distances traveled per unit time) would presumably increase because of the reduction of physical obstacles that would impede movement (Crist et al. 1992, Wiens et al. 1993). In fact, previous measurements of tenebrionid beetle movements in burned and unburned grassland habitat on the Sevilleta NWR showed that movement distances per unit time nearly tripled in burned grassland habitat compared with unburned grassland (H. Fox and R. Parmenter, Sevilleta LTER unpublished data, 1993). As such, greater numbers of captures in our pitfall traps could indicate an increase in individual movements rather than density. Therefore, in our analyses, we have adopted the "activity-density" approach used by other researchers (Halsall and Wratten 1988) that incorporates, but does not distinguish between, both movement activity and abundance per unit area (density).

Statistical tests of the mean number of individuals per trap by sample period among habitats (burned versus unburned) of each taxon were conducted using Repeated Measures Analysis of Variance (RMANOVA). Bonferoni LSDs tests (with protected  $P$  values) were employed to identify specific instances of significant differences in trap captures by sample period. Statistical significance for differences in mean arthropod counts between burned and unburned areas over time was defined as  $P \leq 0.05$ .

## Results

**Vegetation.** In 2000, before the fire, the burned area supported eight species of grasses (58.7% total cover) and a variety of forbs, shrubs and cacti; at the end of the 2001 postfire growing season, grass cover was reduced to 34.6%, and forb cover increased from 0.2% to 4.9% cover postfire (Table 1). The major grass species suffering reduced cover was black grama (*Bouteloua eriopoda*), which declined from 29.9% to 14.2%. Litter cover also was reduced by the fire (33.2% to 14.8%), and bare ground increased from 17.7% to 48.6% (Table 1). Vegetation on the unburned transects showed no change in grass cover between years, but an increase in forb cover (and species richness); litter and bare ground exhibited smaller, but similar, changes as those observed on the burned transects (Table 1). Thus, in 2001, the vegetation on the burned area partially recovered during the first postfire growing season, achieving  $\approx 40\%$  plant cover (compared with  $\approx 51\%$  on the unburned site) and having  $\approx 10\%$  more bare ground (Table 1).

**Arthropods.** During the study, we collected 5,302 individuals of 69 taxa (Table 2). These taxa included native sand roaches (Blattaria, two species), ground beetles (Carabidae, 16 species), darkling beetles (Tenebrionidae, 15 species), grasshoppers (Acrididae, 27 species), field crickets (Gryllidae, one species), scaly crickets (Mogoplistidae, one species), camel crickets (Rhaphidophoridae, one species), katydids (Tettigoniidae, two species), stone centipedes

(Lithobiidae, one species), desert centipedes (Scolopendridae, one species), scorpions (Vaejovidae, one genus), and sun spiders (Eremobatidae, one genus).

Arthropod species richness was higher in the burned area than the unburned area, both in total taxa collected (60 species in burned versus 50 in unburned areas; Table 2) and in the overall mean number of species per trap per sample period (6.03 species in burned area versus 4.96 species in unburned area;  $F = 13.12$ ,  $df = 1,62$ ,  $P = 0.0006$ ). Significantly higher mean species richness values per trap were observed only in the midsummer samples from 10 August (8.7 burned versus 6.0 unburned species per trap) and 10 September (12.1 versus 9.1 species per trap); mean species richness values during other sample periods (early summer and autumn) were not significantly different between burned and unburned areas. Overall, 14 taxa showed significantly greater activity-densities in the burned area, while nine taxa exhibited significantly reduced activity-densities in the burned area compared with the unburned area (Table 2).

Some taxa exhibited near-extirpation from the site as a result of the wildfire. First and foremost of these taxa were crickets (Fig. 5; Table 2). Captures of the field cricket (*Gryllus integer*) were significantly lower on the burned plots ( $F = 8.80$ ,  $df = 1,62$ ,  $P = 0.004$ ), with only a single specimen being captured in the burned area in late summer. The scaly cricket (*Cy-cloptilum comprehendens*) also showed highly significant reductions in captures ( $F = 28.90$ ,  $df = 1,62$ ,  $P < 0.00001$ ). The camel cricket (*Ceuthophilus pallidus*) exhibited similar significant losses after the fire ( $F = 34.60$ ,  $df = 1,62$ ,  $P < 0.00001$ ). All three of these taxa were represented by very few individuals on the burned site, with most of the individuals being collected in late summer during the monsoon season (August–September) when vegetation was recovering and adult cricket activity levels were increasing.

Some grasshopper species (Acrididae) also displayed significant reductions in captures on the burned site compared with the unburned grassland. These grasshopper species included *Ageneotettix deorum* ( $F = 12.13$ ,  $df = 1,62$ ,  $P = 0.0009$ ), *Eritettix simplex* ( $F = 7.26$ ,  $df = 1,62$ ,  $P = 0.009$ ), *Melanoplus bowditchi* ( $F = 10.89$ ,  $df = 1,62$ ,  $P = 0.0016$ ), and *Amphitornus coloradus* ( $F = 9.77$ ,  $df = 1,62$ ,  $P = 0.0027$ ) (Fig. 6; Table 2). As with the cricket taxa, most postfire individuals were captured in late summer through autumn as they became adults and were more active.

In contrast, other species of grasshoppers exhibited highly significant increases in numbers of captures on the burned site during the summer and autumn after the fire (Fig. 7; Table 2). These species included *Aulocara femoratum* ( $F = 9.15$ ,  $df = 1,62$ ,  $P = 0.0036$ ), *Hesperotettix viridis* ( $F = 11.33$ ,  $df = 1,62$ ,  $P = 0.0013$ ), *Trimerotropis pallidipennis* ( $F = 59.70$ ,  $df = 1,62$ ,  $P < 0.00001$ ), and *Xanthippus corallipes* ( $F = 37.50$ ,  $df = 1,62$ ,  $P < 0.00001$ ).

The remaining 20 species of grasshoppers listed in Table 2 displayed no significant differences in mean capture numbers (e.g., *Psoloessa delicatula* and *P. texana*) or were not collected in sufficiently large

**Table 2.** List of arthropod species and total numbers of individuals captured in pitfall traps on unburned and burned areas during June–Nov., 2001, on McKenzie Flats, Sevilleta National Wildlife Refuge, New Mexico

Taxon	Order	Family	Species	Number collected			P value
				Unburned	Burned	Total	
Blattaria		Polyphagidae	<i>Arenivaga erratica</i> Rehn	30	44	74	
			<i>Eremoblatta subdiaphana</i> (Scudder)	4	11	15	
Coleoptera		Carabidae	<i>Amara littoralis</i> Mannerheim	0	1	1	
			<i>Amblycheila picolomini</i> Reiche	0	28	28	****
			<i>Bembidion rapidum</i> LeConte	0	1	1	
			<i>Calasoma peregrinator</i> Guerin-Men.	0	2	2	
			<i>Cicindela hornii</i> Schaupp	1	15	16	
			<i>Cicindela lemniscata</i> LeConte	6	13	19	
			<i>Cicindela pulchra</i> Say	0	1	1	
			<i>Cicindela punctulata</i> Olivier	2	19	21	***
			<i>Cratacanthus dubius</i> (Beauvois) Dejean	0	7	7	
			<i>Discoderus impotens</i> LeConte	0	2	2	
			<i>Euryderus grossus</i> Say	1	0	1	
			<i>Harpalus tadorcus</i> Ball	1	0	1	
			<i>Pasimachus californicus</i> Chaudoir	1	0	1	
			<i>Pasimachus obsoletus</i> LeConte	438	154	592	****
			<i>Pisoma setosum</i> LeConte	0	1	1	
			<i>Selenophorus aeneopiceus</i> Casey	1	0	1	
		Tenebrionidae	<i>Araeoschizus decipiens</i> Horn	169	172	341	
			<i>Edrotes rotundus</i> (Say)	9	32	41	*
			<i>Eleodes carbonarius</i> (Say)	39	58	97	
			<i>Eleodes extricatus</i> (Say)	48	7	55	*
			<i>Eleodes gracilis</i> LeConte	61	97	158	
			<i>Eleodes hispilabris</i> LeConte	0	2	2	
			<i>Eleodes longicollis</i> LeConte	42	194	236	****
			<i>Eleodes tricosatus</i> (Say)	5	2	7	
			<i>Embaphion planum</i> Horn	0	1	1	
			<i>Eusattus reticulatus</i> (Say)	0	3	3	
			<i>Glyptasida sordida</i> (LeConte)	14	56	70	***
			<i>Gonasida elata inferna</i> Casey	0	5	5	
			<i>Melanastus</i> sp.	101	86	187	
			<i>Metaponium cribriceps</i> Casey	9	4	13	
			<i>Stenomorpha consors</i> (Casey)	6	29	35	**
Orthoptera		Acrididae	Acrididae nymph	3	39	42	
			<i>Ageneotettix deorum</i> (Scudder)	63	10	73	***
			<i>Amphitornus coloradus</i> (Thomas)	56	14	70	**
			<i>Aulocara elliotti</i> (Thomas)	1	3	4	
			<i>Aulocara femoratum</i> (Scudder)	56	141	197	**
			<i>Aulocara nymph</i>	9	11	20	
			<i>Conozoa texana</i> (Bruner)	0	1	1	
			<i>Cordillacris crenulata</i> (Bruner)	0	4	4	
			<i>Cordillacris occipitalis</i> (Thomas)	16	4	20	
			<i>Dactyloptum bicolor</i> (Thomas)	2	4	6	
			<i>Eritettix simplex</i> (Scudder)	16	0	16	**
			<i>Hadrotettix trifasciata</i> (Say)	8	7	15	
			<i>Hesperotettix viridis</i> (Thomas)	0	45	45	**
			<i>Melanoplus arizonae</i> Scudder	8	14	22	
			<i>Melanoplus bowditchi</i> Scudder	31	2	33	**
			<i>Melanoplus foedus</i> (Scudder)	1	0	1	
			<i>Melanoplus lakinus</i> (Scudder)	0	2	2	
			<i>Melanoplus occidentalis</i> (Thomas)	3	1	4	
			<i>Metator pardalinus</i> (Saussure)	1	2	3	
			<i>Opeia obscura</i> (Thomas)	2	0	2	
			<i>Paropomala pallida</i> Bruner	3	1	4	
			<i>Psoloessa delicatula</i> (Scudder) + <i>P. texana</i> Scudder	85	53	138	
			<i>Syrbula montezuma</i> (Saussure)	11	0	11	
			<i>Trachyrhachis kiowa</i> (Thomas)	0	1	1	
			<i>Trimerotropis californica</i> Bruner	0	2	2	
			<i>Trimerotropis melanoptera</i> McNeill	1	11	12	
			<i>Trimerotropis pallidipennis</i> (Burmeis.)	3	105	108	****
			<i>Tropidolophus formosus</i> (Say)	3	1	4	
			<i>Xanthippus corallipes</i> Haldeman	4	51	55	****
		Gryllidae	<i>Gryllus integer</i> Scudder	22	1	23	**
		Mogoplistidae	<i>Cycloptilum comprehensens</i> Hebard	1,181	33	1214	****
		Rhaphidophoridae	<i>Ceuthophilus pallidus</i> (Thomas)	259	21	280	****
		Tettigoniidae	<i>Eremopedes bilineatus</i> (Thomas)	7	1	8	
			<i>Eremopedes scuderi</i> Cockerell	1	0	1	
Lithobiomorpha		Lithobiidae	<i>Taiyubius harrietae</i> Chamberlin	44	210	254	****

Continued on next page

Table 2. Continued

Taxon	Order	Family	Species	Number collected			
				Unburned	Burned	Total	P value
Scolopendromorpha		Scolopendridae	<i>Scolopendra polymorpha</i> Wood	0	10	10	**
Scorpionida		Vaejovidae	<i>Vaejovis</i> spp. <sup>a</sup>	96	211	307	***
Solifugae		Eremobatidae	<i>Eremobates</i> spp. <sup>b</sup>	82	173	255	***
Total individuals				3,111	2,191	5,302	
Total taxa <sup>c</sup>				50	60	69	

Significant differences between burned and unburned areas tested with Repeated Measures ANOVA (see text for details): \* =  $P < 0.05$ ; \*\* =  $P < 0.01$ ; \*\*\* =  $P < 0.001$ ; \*\*\*\* =  $P < 0.0001$ . See Lightfoot et al. (2008) for additional arthropod species in the Sevilleta NWR.

<sup>a</sup> The most common species on the Sevilleta NWR site is *Vaejovis coahuilae* Williams, with some *V. russelli* Williams.

<sup>b</sup> Sevilleta NWR species include *Eremobates bajadae* Muma & Brookhart, *E. nodularis* Muma, *E. pallipes* (Say), *E. similis* Muma, and *E. simoni* Muma.

<sup>c</sup> Total taxa numbers do not include unidentified Acrididae nymphs or *Aulocara* nymphs.

samples for analysis. In total, 23 species of grasshoppers were observed on the burned site, with 21 species collected from the unburned grassland. Four grass-

hopper species in the unburned grassland were not found in the burned area, but two of these were extremely rare and represented by only three specimens (*Melanoplus foedus* and *Opeia obscura*); 11 specimens of *Syrbula montezuma* were collected in the unburned area and none in the burned site (Table 2). Six species were captured only in the burned area, but five of these species were observed only in very low numbers (Table 2); the exception (discussed above; Fig. 7) was *Hesperotettix viridis*, which was common in the postfire burned environment but absent in samples from the unburned grassland.

Darkling beetles (Tenebrionidae) also exhibited a variety of responses to the fire (Fig. 8). One species, *Eleodes extricatus*, had significantly fewer captures in the burned area ( $F = 5.15$ ,  $df = 1,62$ ,  $P < 0.0267$ ), whereas other species were captured more frequently on the burned site. These latter taxa included *E. longicollis* ( $F = 38.58$ ,  $df = 1,62$ ,  $P < 0.00001$ ), *E. rotundus* ( $F = 5.67$ ,  $df = 1,62$ ,  $P < 0.0204$ ), *Glyptasida sordida* ( $F = 15.43$ ,  $df = 1,62$ ,  $P = 0.0002$ ), and *Stenomorpha consors* ( $F = 9.64$ ,  $df = 1,62$ ,  $P < 0.0029$ ). Another darkling beetle, *E. carbonarius*, displayed a temporally variable treatment effect, with fewer individuals captured on the burn site through the summer, but greater numbers in the burned area in mid-September through November (Treatment  $\times$  Time Interaction  $F = 9.07$ ,  $df = 5,297$ ,  $P < 0.00001$ ) (Fig. 8). Other darkling beetle species with suitable sample sizes showed no significant differences between fire treatments (*Araeoschizus decipiens*, *E. gracilis*, and *Melanastus* sp.). Overall, all fifteen darkling beetle species observed during the study were collected on the burned site, whereas only eleven species were captured in the unburned grassland (Table 2).

Of the 16 species of ground beetles (Carabidae) collected during the study, three species produced sufficient samples for statistical analysis. *Pasimachus obsoletus* was the most abundant on both burned and unburned sites, but captures were significantly lower on the burned site ( $F = 18.24$ ,  $df = 1,62$ ,  $P = 0.0001$ ) (Fig. 9). Two ground beetle species exhibited significantly higher captures on the burned sites. *Amblycheila picolominii* ( $F = 20.89$ ,  $df = 1,62$ ,  $P < 0.00001$ ) was found exclusively in the burned grassland (Table 2), and the tiger beetle (a type of ground beetle),

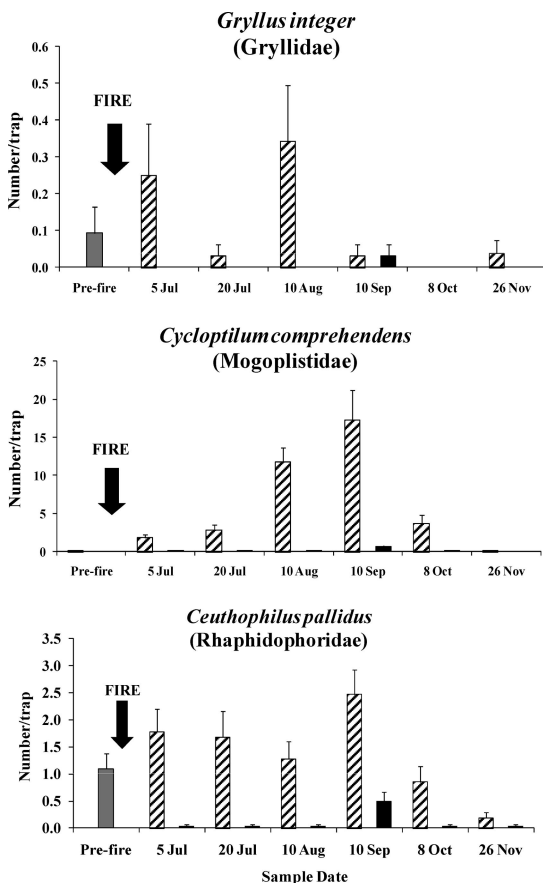


Fig. 5. Numbers of crickets captured per pitfall trap in burned (solid black histograms) and unburned sites (diagonally-striped histograms) in the desert grassland of New Mexico: (top) field cricket (*Gryllus integer*); (center) scaly cricket (*Cycloptilum comprehendens*); (bottom) camel cricket (*Ceuthophilus pallidus*). Histograms represent means and standard errors of 32 traps. Prefire data values (gray histograms) derived from unburned control traps. All cricket species showed significantly lower captures in burn site traps (see text).



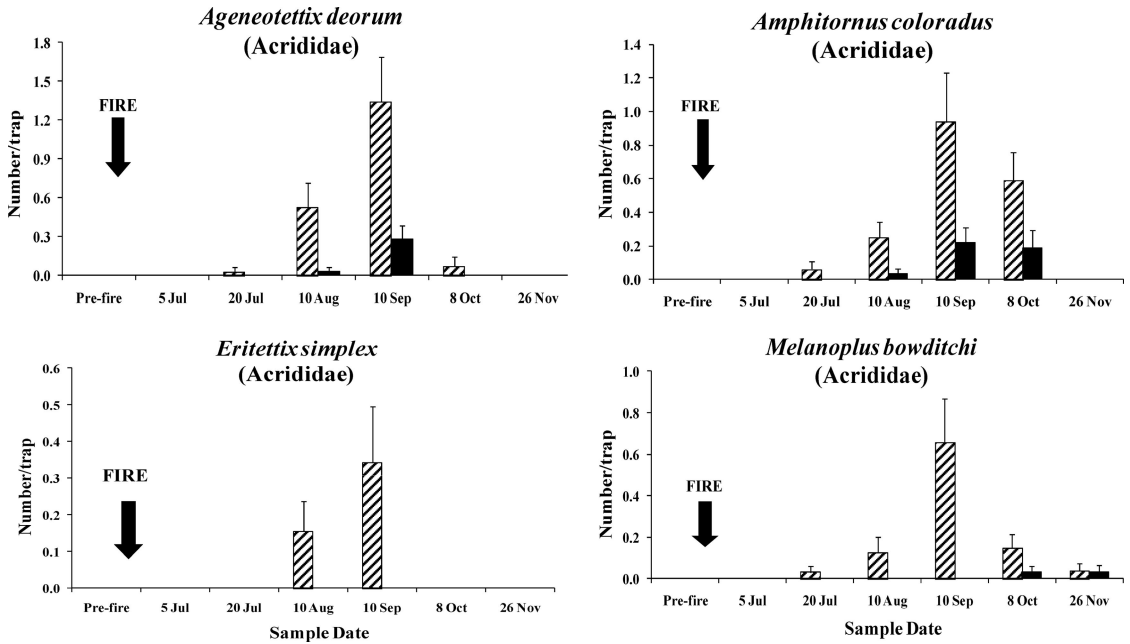


Fig. 6. Numbers of grasshoppers (Acrididae) captured per pitfall trap in burned (solid black histograms) and unburned sites (diagonally-striped histograms) in the desert grassland of New Mexico: (top, left) *Ageneotettix deorum*; (top, right) *Amphitornus coloradus*; (bottom, left) *Eritettix simplex*, (bottom, right) *Melanoplus bowditchi*. Histograms represent means and standard errors of 32 traps. All species showed significantly lower captures in burn site traps (see text).

*Cicindela punctulata* ( $F = 14.87$ ,  $df = 1,62$ ,  $P = 0.0003$ ) was significantly more common there (Fig. 9). In addition, the other tiger beetles (*C. horni*, *C. lemniscata*, and *C. pulchra*), although less commonly collected, also dem-

onstrated a tendency of being more common in the burned area (Table 2). Twelve of the 16 ground beetle species were collected from the burn site, while only eight species were collected in the unburned area.

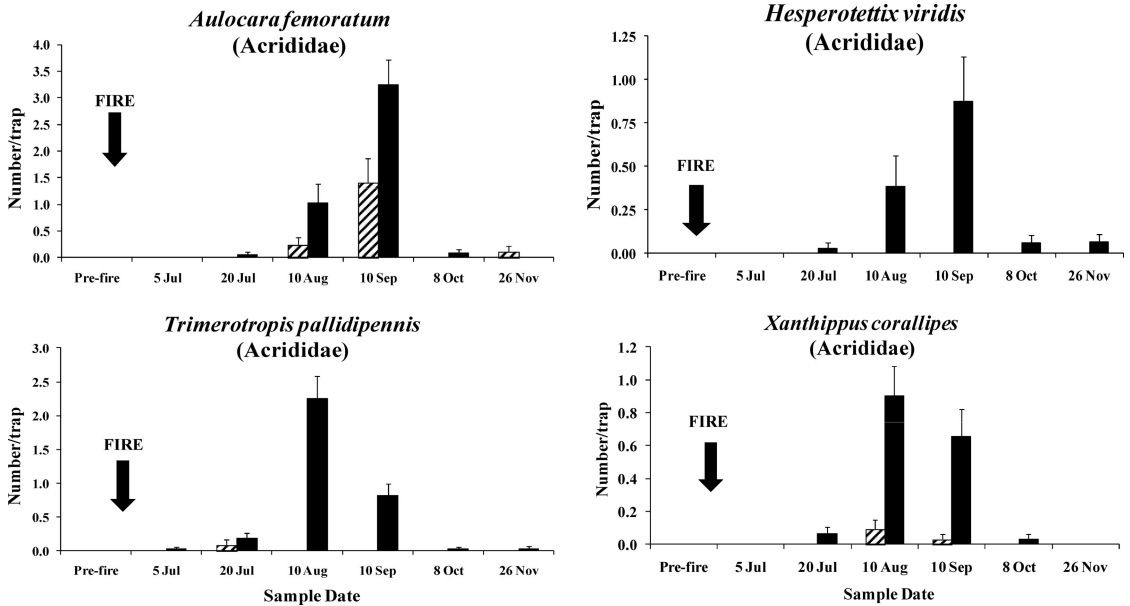


Fig. 7. Numbers of grasshoppers (Acrididae) captured per pitfall trap in burned (solid black histograms) and unburned sites (diagonally-striped histograms) in the desert grassland of New Mexico: (top, left) *Aulocara femoratum*; (top, right) *Hesperotettix viridis*; (bottom, left) *Trimerotropis pallidipennis*, (bottom, right) *Xanthippus corallipes*. Histograms represent means and standard errors of 32 traps. All species showed significantly higher captures in burn site traps (see text).

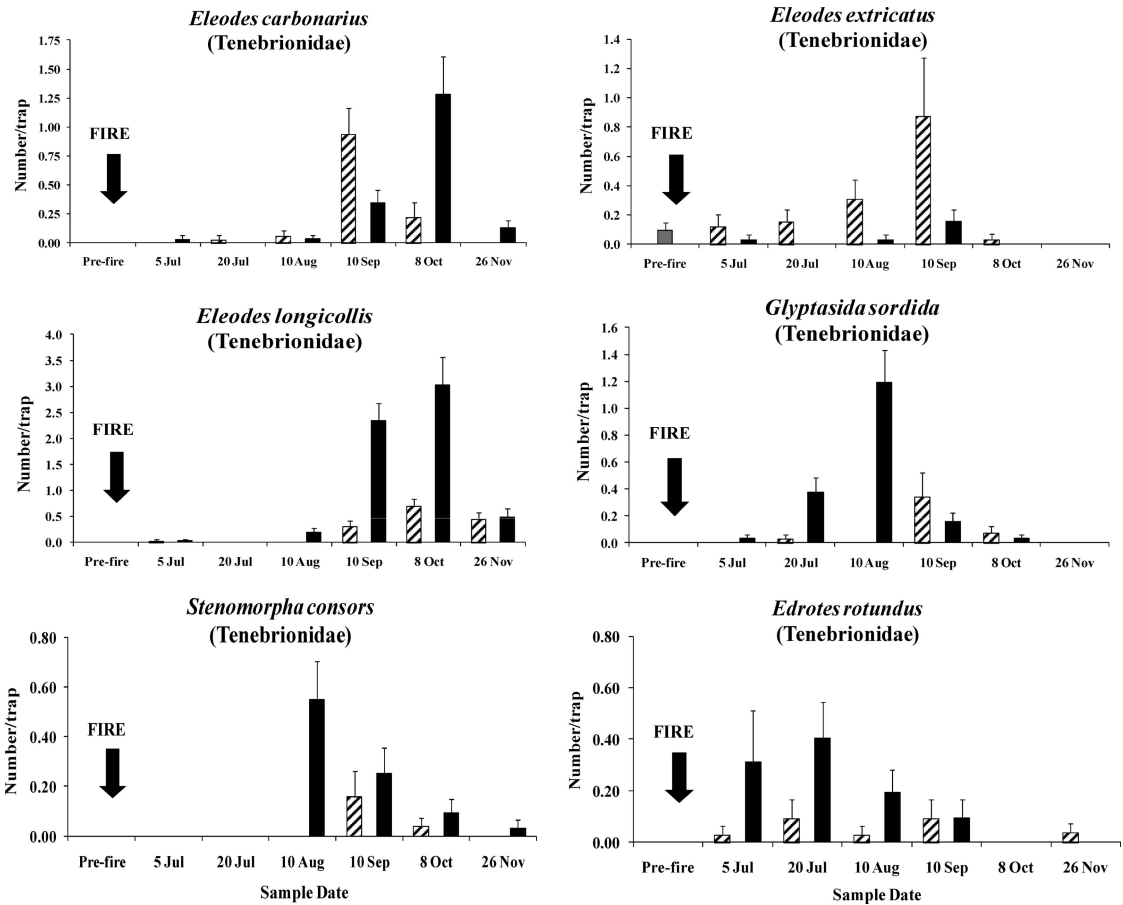


Fig. 8. Numbers of darkling beetles (Tenebrionidae) captured per pitfall trap in burned (solid black histograms) and unburned sites (diagonally-striped histograms) in the desert grassland of New Mexico: (top, left) *Eleodes carbonarius*; (top, right) *Eleodes extricatus*; (center, left) *Eleodes longicollis*; (center, right) *Glyptasida sordida*; (bottom, left) *Eleodes rotundus*; (bottom, right) *Stenomorpha consors*. Histograms represent means and standard errors of 32 traps. Prefire data values (gray histograms) derived from unburned control traps.

Two species of native sand roaches (Polyphagidae) were collected in both burned and unburned traps (Table 2). Although both species (*Arenivaga erratica* and *Eremoblata subdiaphana*) tended to be more frequently captured in the burn area, these differences were not statistically significant.

All four of the remaining arthropod taxa included in this study proved to have significantly higher captures in the burned area (Table 2). Two species of centipedes were represented, with *Taiyubius harrietae* (Lithobiidae) being the most common in both burned and unburned habitats, but captured significantly more often in the burned area ( $F = 42.11$ ,  $df = 1,62$ ,  $P < 0.00001$ ) (Fig. 10). *Scolopendra polymorpha* (Scolopendridae) was sampled exclusively in the burned area ( $F = 10.50$ ,  $df = 1,62$ ,  $P = 0.0019$ ). Scorpions (*Vaejovis* spp.) also were captured more often in the burned area ( $F = 15.19$ ,  $df = 1,62$ ,  $P = 0.0002$ ), particularly in late summer and autumn (Fig. 10). Finally, the sun spiders (or wind scorpions), *Eremobates* spp. (Eremobatidae), were common throughout the study

period on both sites, but exhibited higher captures in the burned grassland traps ( $F = 15.04$ ,  $df = 1,62$ ,  $P = 0.0003$ ) (Fig. 10).

## Discussion

Taken collectively, the observed responses by the ground-dwelling arthropod taxa in this study indicated that the wildfire primarily directly affected those species dependent on grasses for food or shelter, and many of those were showing signs of recovery by the end of the first postfire growing season. Some taxa, especially the true grass-dwelling species, such as the scaly cricket (*C. comprehensens*), were initially eliminated within the burned area by the fire, but as grasses resprouted with the monsoon rains shortly after the fire, adult individuals began to appear in the burned area, apparently dispersing from adjacent unburned grassland. Most other taxa (roaches, beetles, centipedes, scorpions, sun spiders) may have survived the actual fire, sheltered underground in the soil, beneath

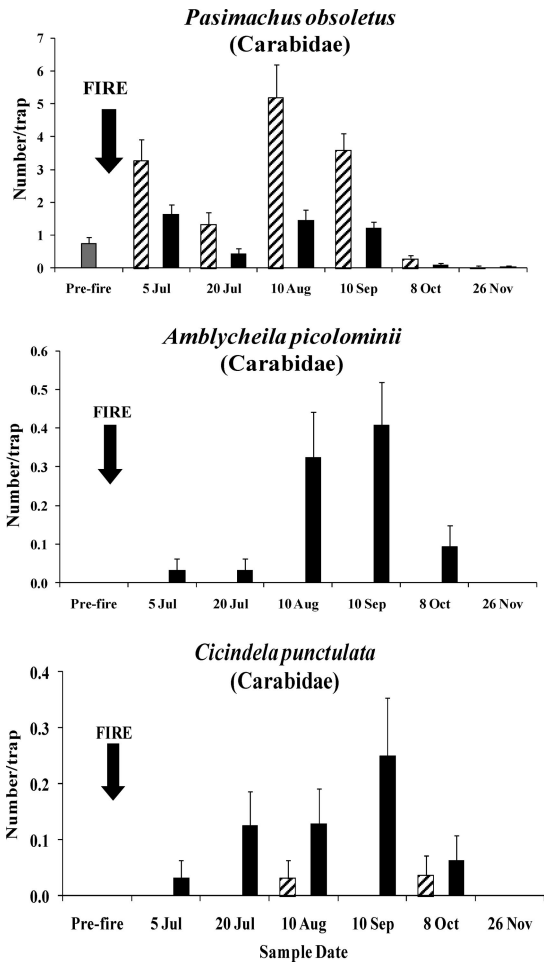


Fig. 9. Numbers of ground beetles (Carabidae) captured per pitfall trap in burned (solid black histograms) and unburned sites (diagonally-striped histograms) in the desert grassland of New Mexico: (top) *Pasimachus obsoletus*; (middle) *Amblycheila picolomini*, (bottom) *Cicindela punctulata*. Histograms represent means and standard errors of 32 traps. Prefire data values (gray histograms) derived from unburned control traps.

rocks, or in rodent burrows (Hawkins and Nicoletto 1992, Davidson and Lightfoot 2007, Duval and Whitford 2009), but also may have dispersed into the burned area from the unburned grassland. The population responses of these taxa were likely mediated through the postfire habitat conditions (e.g., food plants, prey species, and physical cover or shading). Finally, some species survived the wildfire underground as eggs or larvae, and appeared later in the summer as nymphs (e.g., Acrididae, Table 2) or newly metamorphosized adults (e.g., Coleoptera).

Reductions in the abundance or activity-density observed for some beetles and grasshoppers were likely the result of a lack of food plants and shelter, although the cause of these reductions (e.g., death of individuals or movement out of the burned area) could not be distinguished. Observed increases in

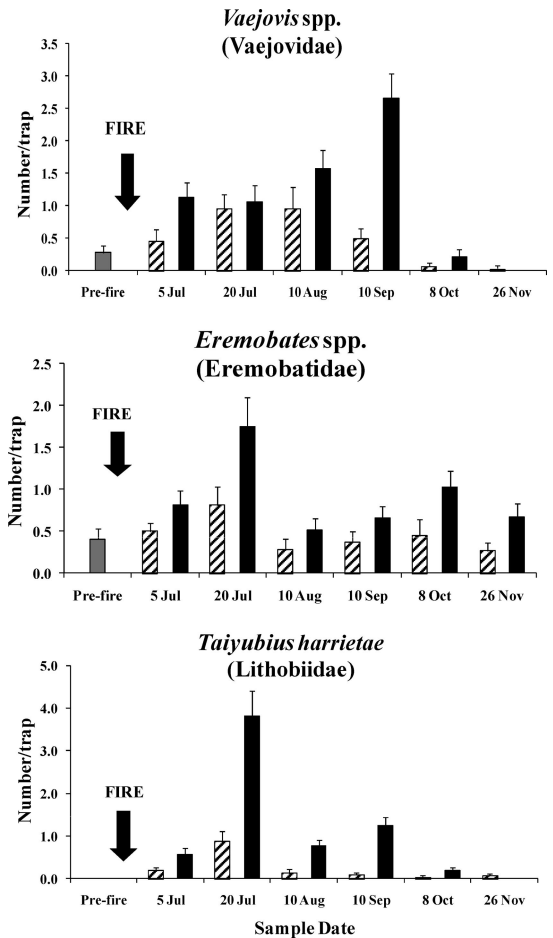


Fig. 10. Numbers of scorpions, sun spiders, and centipedes captured per pitfall trap in burned (solid black histograms) and unburned sites (diagonally-striped histograms) in the desert grassland of New Mexico: (top) *Vaejovis* spp. (Vaejovidae); (middle) *Eremobates* spp. (Eremobatidae), (bottom) *Taiyubius harrietae* (Lithobiidae). Histograms represent means and standard errors of 32 traps. Prefire data values (gray histograms) derived from unburned control traps.

many taxa, particularly predators, was likely because of positive trap bias, with higher capture rates in the burned area because of reduced physical obstacles, greater activity movements, and the attractiveness of the shaded traps during hot, daylight periods. Finally, recolonization of species from unburned areas could proceed relatively quickly, as the distance from the fire's edge to the center of the burned area was <1 km.

The overall patterns in this study are comparable to some, but not all, studies on grassland fires in other, more mesic, ecosystems. For example, a comparison of grasshopper responses to fire between tallgrass prairie (with considerably greater and more continuous fuel loads) and the desert grassland reveals substantial differences. At the Konza Tallgrass Prairie LTER site in eastern Kansas, annual aboveground net primary production (ANPP) averaged  $417 \text{ g} \cdot \text{m}^{-2}$  during 1975–

1996 (Knapp et al. 1998). In tallgrass prairie, fires (especially annual fires) promoted increased relative abundance of  $C_4$  grasses, and decreased relative abundance of forbs, woody species, and  $C_3$  grasses (as well as declines in overall plant species richness and diversity) (Hartnett and Fay 1998). Grass-feeding grasshoppers dominated tallgrass prairie sites immediately after fire, whereas grasshoppers with diets of forbs and mixed forb-grasses initially declined in the year of the fire, increasing in subsequent years as forb abundance recovered (Evans 1984, 1988a, b; Jonas and Joern 2007).

In contrast, the desert grassland of the Sevilleta NWR averaged only  $51 \text{ g} \cdot \text{m}^{-2}$  ANPP annually during 1999–2004 (Muldavin et al. 2008). With accumulated plant litter (resulting from slow decomposition processes), the total aboveground standing crop biomass value was  $192 \text{ g} \cdot \text{m}^{-2}$ , less than half of the potential fuel load of the tallgrass prairie. In the first year after fire, unlike tallgrass prairie postfire vegetation, forb percentage cover, and forb species richness increased in the Sevilleta NWR's desert grassland (Table 1). Concomitantly, forb-feeding and mixed forb-grass feeding grasshoppers (Richman et al. 1993, Lamp et al. 2007) exhibited significant increases in activity-densities; these species included *T. pallidipennis* and *X. corallipes* (Table 2; Fig. 7), along with *H. viridis* which, on the Sevilleta NWR, is almost exclusively associated with broom snakeweed (Asteraceae: *Gutierrezia sarothrae*), a small perennial sub-shrub. Similarly, grass-feeding Orthoptera showed significant declines in activity-density; these included *Ag. deorum*, *Am. coloradus*, *E. simplex*, and *C. comprehendens* (Table 2; Figs. 4 and 5). The only grass-feeding species showing a significant increase was *A. femoratum* (Fig. 7), whereas *P. delicatula* and *P. texana* (two early-summer species that feed primarily on *Bouteloua* grasses on the study site (Rominger et al. 2009) showed no significant response in activity-density; however, postfire *B. gracilis* recovered quickly (Table 1; see also Gosz and Gosz 1996, Parmenter 2008), which would have provided ample food resources for *Psoloessa* spp. Finally, *Melanoplus bowditchi*, which feeds on woody plants and shrubs (particularly winterfat (Chenopodiaceae: *Krascheninnikovia lanata* (Pursh) A. Meeuse & Smit) and broom snakeweed on the Sevilleta NWR), exhibited a highly significant decline on the burned site (Table 2).

Thus, while the general pattern observed in tallgrass prairie grasshopper assemblages of forb- and grass-feeding species tracking their plant food resources is corroborated, the differences in forb and grass abundances in the postfire desert grassland of the Sevilleta NWR functionally reversed the dominant grasshopper assemblage in favor of forb-feeding species at the expense of grass-feeding species. Bock and Bock (1991) reported a similar successional pattern for grasshoppers after a wildfire in desert grassland habitat in southern Arizona, based on higher forb:grass ratios in the recovering plant community. Vermeire et al. (2004) also found postfire reductions of *H. viridis* in sagebrush-mixed prairie in Oklahoma because of

fire and livestock grazing damage to host plants (often species of Asteraceae), and declines of *Ag. deorum* because of potential fire-induced mortality of eggs in the soil. Finally, Ford (2007) observed no significant differences in orthopteran abundances on burned and unburned shortgrass prairie in New Mexico (with a standing crop dry biomass of  $112 \text{ g} \cdot \text{m}^{-2}$  [Ford and Johnson 2006]), although there was a significantly greater number of orthopteran species on the burned plots.

Other desert grassland orthopteran species, particularly field crickets and camel crickets, suffered decreases in activity-densities after the fire, potentially because of direct fire-caused mortality and the unfavorable postfire environment. These taxa are generally nocturnal, and because this study's fire burned throughout the night, individuals caught by the fire aboveground could have perished in the passing fire front. Previous studies on fire impacts on crickets have been varied; Gillon (1983) reported high fire-induced mortality levels of crickets (Gryllidae) in African savanna, whereas Andersen and Müller (2000) found no significant fire effect on crickets in an Australian tropical savanna. Similarly, Ford (2007) observed no significant fire effects on *Gryllus* activity-density in burned and unburned shortgrass prairie in New Mexico.

Ground beetle responses to fire on our study site varied by species, with more species being collected in burned grasslands (12) than unburned (8), but with the numerically dominant species, *P. obsoletus*, exhibiting a greatly reduced activity-density on the burned site (Table 2). This flightless species is nocturnal, and feeds predominantly on caterpillars (Larochelle and Larivière 2003); the night-time fire may have killed some *P. obsoletus* outright, and the fire would have virtually eliminated caterpillars from the burned grasslands, thereby further reducing the surviving individuals through a lack of prey resources. In contrast, *Amblycheila picolomini*, another flightless, nocturnal species that preys on grasshoppers, crickets, and other invertebrates, appeared to have survived the fire and thrived in the postfire environment. Other tiger beetles (*Cicindela*) increased in capture frequency in the burned grassland; these species are strong fliers and visual pursuit hunters, preferring open, sparsely-vegetated habitats (Pearson and Vogler 2001). Comparable increases in activity-density by *Cicindela* spp. have been documented in New Mexican Rio Grande "bosque" (riparian cottonwood) forests after wildfire, during which large areas of bare ground were created for these visual predators (Bess et al. 2002).

Previous studies on ground beetle responses to fires have shown a range of fire-related impacts. Australian tropical savanna fire had no significant effect on surface-active beetles, including ground beetles (Andersen and Müller 2000). Ford (2007) also found no significant changes in abundances of ground beetles, but higher species richness, in New Mexico shortgrass prairie postfire environments. Similarly, Cook and Holt (2006) observed no significant changes in ground beetle trap captures in the first season after fire in

tallgrass prairie in Kansas. In Hungarian forest-steppe, Samu et al. (2010) reported increased ground beetle captures but similar species richness in burned areas 2.5 yr after fire; species inhabiting the burned area were strong fliers and tended to be more granivorous, whereas the species in unburned areas were more brachypterous and predatory.

The activity-densities of darkling beetles generally increased after the fire; only one species (*E. extricatus*) showed a significant decline (Table 2; Fig. 8). Adult darkling beetles may have survived the fire in rodent burrows and other belowground shelters, although some may have died if caught aboveground by the fire at night. In addition, darkling beetle larvae, developing from eggs laid the previous year and feeding underground on plant roots, could have survived the fire in their subterranean habitat to emerge later in the summer; this would be reflected in high rates of capture. However, high capture frequencies may have been because of trap bias. Darkling beetles are generally nocturnal and crepuscular, seeking shade or belowground refugia to avoid the heat of the day (Parmenter et al. 1989a, 1989b). As such, the increased number of captures in the burned area may have reflected an increase in shade-seeking behavior as individuals moved under the pitfall trap covers, rather than an actual increase in population size. Increased captures of darkling beetles also were observed by Blanche et al. (2001) after a fire in an Australian savanna woodland; this response was attributed to darkling beetles being highly adapted to the xeric environment created by the fire. In northeastern New Mexico, Ford (2007) recorded no significant differences in numbers of darkling beetles captured on burned and unburned plots after experimental fires in shortgrass prairie. However, extreme drought and high temperatures have been shown to reduce activity-density of *E. extricatus* in semiarid grasslands (Deslippe et al. 2001), and the reduced numbers of this species collected in the burned area during this study may indicate an actual population decline in the hot, shadeless habitat of the postfire environment.

Pitfall trap bias may also have contributed to the increased number of captures of centipedes, scorpions, and sun spiders (Table 2; Fig. 10). These species also are nocturnal, ambulatory predators that seek belowground shelter (animal burrows and soil crevices) during the daylight hours; hence, the shaded traps were likely attractive sites. However, in view of their consistently greater numbers in the burned area throughout the summer and autumn, it was likely that these taxa survived the fire and were thriving in the postfire environment of the desert grassland. Similar results have been reported for centipedes from Mediterranean postfire environments (Sgardelis et al. 1995, Trucchi et al. 2009). In contrast, centipedes in tallgrass prairie were substantially reduced after fire (Rice 1932, Seastedt 1984).

Although not quantified in this study, it was apparent that ants (Hymenoptera: Formicidae) were little affected by the wildfire and the postfire environmental changes; visual observations of harvester ant col-

onies within the burned area indicated all colonies were active after the fire, and ants of many species were common in the pitfall trap samples. A previous study in desert grassland of the Sevilleta NWR showed that a desert seed-harvester ant (*Pogonomyrmex rugosus*) exhibited only minimal responses to fire (Zimmer and Parmenter 1998), and this result appeared to be corroborated on our study site. In addition, the fire burned most aboveground portions of the desert shrubs scattered across the study site (e.g., *Larrea tridentata* (DC.) Coville (Zygophyllaceae), *Atriplex canescens* (Pursh) Nutt. (Chenopodiaceae); see Fig. 4), and arthropod populations inhabiting these shrubs would have been destroyed (Sanchez and Parmenter 2002); recovery of these assemblages would take several years, depending on the species-specific recovery rates of stump-sprouting shrubs (Parmenter 2008).

In summary, the summer-season wildfire appeared to have only a moderate, short-term impact on the ground-dwelling arthropod assemblage of this desert grassland site. Most species examined exhibited no significant postfire difference in activity-density, while some species showed increases in trap captures; some of the observed increases were likely sampling artifacts from using pitfall traps. While a few grass-dwelling species were reduced in activity-density, or perhaps extirpated temporarily, recolonization and recovery were beginning to occur during the first growing season. Herbivorous species tracked the postfire changes in vegetation (e.g., forb:grass ratios, reduction of woody species), and predator species appeared to respond to changes in habitat structure and prey species availability. Recovery and regrowth of resident plant species on this site varies from 1 to 10 plus yr (Parmenter 2008), so multiple growing seasons may be required before the arthropod assemblage is fully restored to prefire composition and abundances.

Incorporating these results into the broader literature of fire effects on grassland arthropods, it is apparent that fire impacts on desert grassland arthropods are comparable to those arthropods in more mesic grasslands with higher fuel quantities and more homogeneous fuel distributions. As noted in previous studies, species-specific natural history attributes contribute to explanations for the observed arthropod responses across grassland ecosystems in terms of survivorship, reproduction, and recolonization movements (Warren et al. 1987, Swengel 2001). However, wildfires are notoriously variable in fire behavior and ecological impact, occurring across a range of spatial scales, during different seasons, under a wide range of meteorological conditions, and driven by differing fuel loads, fuel types, and fuel distributions. The specifics of these antecedent and concurrent conditions will ultimately determine the ecological impact on any given arthropod species, and most grassland arthropod species appear to be well-adapted to surviving or recovering quickly from natural wildfires. However, some species clearly suffer large short-term reductions in activity-density during and after wildfire, and longer-term studies on arthropod assemblages in desert grassland will be required to identify more subtle

changes in community structure and processes, particularly with respect to the impacts of antecedent climatic and vegetation conditions, fire intensity, fire return intervals, and seasonal effects (Chambers and Samways 1998, Blanche et al. 2001).

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### References Cited

- Andersen, A. N., and W. J. Müller. 2000. Arthropod responses to experimental fire regimes in an Australian tropical savannah: ordinal-level analysis. *Austral Ecol.* 25: 199–209.
- Bess, E. C., R. R. Parmenter, S. McCoy, and M. C. Molles. 2002. Responses of a riparian forest-floor arthropod community to wildfire in the Middle Rio Grande Valley, New Mexico. *Environ. Entomol.* 31: 774–784.
- Blanche, K. R., A. N. Andersen, and J. A. Ludwig. 2001. Rainfall-contingent detection of fire impacts: responses of beetles to experimental fire regimes. *Ecol. Appl.* 11: 86–96.
- Bock, C. E., and J. H. Bock. 1991. Response of grasshoppers (Orthoptera, Acrididae) to wildfire in a southeastern Arizona grassland. *Am. Midl. Nat.* 125: 162–167.
- Branson, D. H. 2005. Effects of fire on grasshopper assemblages in a northern mixed-grass prairie. *Environ. Entomol.* 34: 1109–1113.
- Branson, D. H., and L. T. Vermeire. 2007. Grasshopper egg mortality mediated by oviposition tactics and fire intensity. *Ecol. Entomol.* 32: 128–134.
- Chambers, B. Q., and M. J. Samways. 1998. Grasshopper response to a 40-year experimental burning and mowing regime, with recommendations for invertebrate conservation management. *Biodivers. Conserv.* 8: 985–1012.
- Cook, W. M., and R. D. Holt. 2006. Fire frequency and mosaic burning effects on a tallgrass prairie ground beetle assemblage. *Biodivers. Conserv.* 15: 2301–2323.
- Crist, T. O., D. S. Guertin, J. A. Wiens, and B. T. Milne. 1992. Animal movement in heterogeneous landscapes: an experiment with *Eleodes* beetles in shortgrass prairie. *Funct. Ecol.* 6: 536–544.
- Davidson, A. D., and D. C. Lightfoot. 2007. Interactive effects of keystone rodents on the structure of desert grassland arthropod communities. *Ecography* 30: 515–525.
- Deslippe, R. J., J. R. Salazar, and Y.-J. Guo. 2001. A darkling beetle population in West Texas during the 1997–1998 El Niño. *J. Arid Environ.* 49: 711–721.
- Duval, B. D., and W. G. Whitford. 2009. Camel spider (Solifugae) use of prairie dog colonies. *West. N. Am. Nat.* 69: 272–276.
- Evans, E. W. 1984. Fire as a natural disturbance to grasshopper assemblages of tallgrass prairie. *Oikos* 43: 9–16.
- Evans, E. W. 1988a. Grasshopper (Insecta: Orthoptera: Acrididae) assemblages of tallgrass prairie: Influences of fire frequency, topography and vegetation. *Can. J. Zool.* 66: 1495–1501.
- Evans, E. W. 1988b. Community dynamics of prairie grasshoppers subjected to periodic fire: predictable trajectories or random walks in time? *Oikos* 52: 283–292.
- Fay, P. A. 2003. Insect diversity in two burned and grazed grasslands. *Environ. Entomol.* 32: 1099–1104.
- Ford, P. L. 2001. Biodiversity and fire in shortgrass steppe, pp. 884–885. *In* Proceedings, Grassl. ecosystems: an outlook into the 21<sup>st</sup> Century. The XIX International Grassl. Congress, São Pedro, São Paulo, Brazil.
- Ford, P. L. 2007. Shared community patterns following experimental fire in a semiarid grassland, 9 pp. *In* Proceedings of the 4<sup>th</sup> International Wildland Fire Conference, May 13–17, 2007, Seville, Spain.
- Ford, P. L., and G. V. Johnson. 2006. Effects of dormant- vs. growing-season fire in shortgrass steppe: biological soil crust and perennial grass responses. *J. Arid Environ.* 67: 1–14.
- Gillon, D. 1983. The fire problem in tropical savannas, pp. 617–641. *In* F. Boulière (ed.), *Ecosystems of the World 13: Tropical Savannas*. Elsevier, Amsterdam, Holland.
- Gosz, R. J., and J. R. Gosz. 1996. Species interactions on the biome transition zone in New Mexico: response of blue grama (*Bouteloua gracilis*) and black grama (*Bouteloua eriopoda*) to fire and herbivory. *J. Arid Environ.* 34: 101–114.
- Halsall, N. B., and S. D. Wratten. 1988. The efficiency of pitfall trapping for polyphagous predatory Carabidae. *Ecol. Entomol.* 29: 293–299.
- Hansen, J. D. 1986. Comparison of insects from burned and unburned areas after a range fire. *Great Basin Nat.* 46: 721–727.
- Hartley, M. K., W. E. Rogers, and E. Siemann. 2007. Responses of prairie arthropod communities to fire and fertilizer: balancing plant and arthropod conservation. *Am. Midl. Nat.* 157: 92–105.
- Hartnett, D. C., and P. A. Fay. 1988. Plant populations. Patterns and Processes, pp. 81–100. *In*: A. K., Knapp, J. M. Briggs, D. C. Hartnett and S. L. Collins (eds.), *Grassl. Dynamics*. Long-Term Ecological Research in Tallgrass Prairie. Oxford University Press, New York.
- Hawkins, L. K., and P. F. Nicoletto. 1992. Kangaroo rat burrows structure the spatial organization of ground-dwelling animals in a semiarid grassland. *J. Arid Environ.* 23: 199–208.
- Joern, A. 2004. Variation in grasshopper (Acrididae) densities in response to fire frequency and bison grazing in tallgrass prairie. *Environ. Entomol.* 33: 1617–1625.
- Joern, A. 2005. Disturbance by fire frequency and bison grazing modulate grasshopper assemblages in tallgrass prairie. *Ecology* 86: 861–873.
- Johnson, S. D., K. C. Horn, A. M. Savage, S. Windhager, M. T. Simmons, and J. A. Rudgers. 2008. Timing of prescribed burns affects abundance and composition of arthropods in the Texas hill country. *Southwest. Nat.* 53: 137–145.
- Johnson, W. R. 1988. Soil survey of Socorro County Area, New Mexico. U.S. Dep. Agric., Soil Conservation Service, Albuquerque, NM.
- Jonas, J. L., and A. Joern. 2007. Grasshopper (Orthoptera: Acrididae) communities respond to fire, bison grazing

- and weather in North American tallgrass prairie: a long-term study. *Oecologia* 153: 699–711.
- Kerstyn, A., and P. Stiling. 1999. The effects of burn frequency on the density of some grasshoppers and leaf miners in a Florida sandhill community. *Fla. Entomol.* 82: 499–505.
- Knapp, A. K., J. M. Briggs, J. M. Blair, and C. L. Turner. 1998. Patterns and controls of aboveground net primary production in tallgrass prairie, pp. 193–221. In A. K. Knapp, J. M. Briggs, D. C. Hartnett, and S. L. Collins (eds.), *Grassl. Dynamics. Long-Term Ecological Research in Tallgrass Prairie*. Oxford University Press, New York.
- Knight, T. M., and R. D. Holt. 2005. Fire generates spatial gradients in herbivory: an example from a Florida sandhill ecosystem. *Ecology* 86: 587–593.
- Lamp, W. O., R. C. Berberet, L. G. Higley, and C. R. Baird. 2007. Handbook of forage and rangeland insects. Entomological Society of America, Lanham, MD.
- Langlands, P. R., K.E.C. Grennan, and D. J. Pearson. 2006. Spiders, spinifex, rainfall and fire: long-term changes in an arid spider assemblage. *J. Arid Environ.* 67: 36–59.
- Larochelle, A., and M.-C. Larivière. 2003. A natural history of the ground-beetles (Coleoptera: Carabidae) of America north of Mexico. Pensoft, Sofia, Bulgaria.
- Lightfoot, D. C., S. L. Brantley, and C. D. Allen. 2008. Geographic patterns of ground-dwelling arthropods across an ecoregional transition in the North American Southwest. *West. N. Am. Nat.* 68: 83–102.
- Matsuda, T., G. Turschak, C. Brehme, C. Rochester, M. Mitrovich, and R. Fisher. 2011. Effects of large-scale wildfires on ground foraging ants (Hymenoptera: Formicidae) in southern California. *Environ. Entomol.* 40: 204–216.
- McPherson, G. R. 1995. The role of fire in the desert grassland, pp. 130–151. In M. P. McClaran and T. R. Van Devender (eds.), *The Desert Grassl.* University of Arizona Press, Tucson, AZ.
- Muldavin, E. H., D. I. Moore, S. L. Collins, K. R. Wetherill, and D. C. Lightfoot. 2008. Aboveground net primary production dynamics in a northern Chihuahuan Desert ecosystem. *Oecologia* 155: 123–132.
- Nadeau, L., P. E. Cushing, and B. C. Kondratieff. 2006. Effects of fire disturbance on grasshopper (Orthoptera: Acrididae) assemblages of the Comanche National Grasslands, Colorado. *J. Kans. Entomol. Soc.* 79: 2–12.
- [NRCS] USDA. 2011. The PLANTS Database National Plant Data Center, Baton Rouge, LA. (<http://plants.usda.gov>).
- Nunes, L., I. Silva, M. Pite, F. Rego, S. Leather, and A. Serrano. 2006. Carabid (Coleoptera) community changes following prescribed burning and the potential use of carabids as indicators species to evaluate the effects of fire management in Mediterranean regions. *Silva Lusit.* 14: 85–100.
- Panzer, R. 2002. Compatibility of prescribed burning with the conservation of insects in small, isolated prairie reserves. *Conserv. Biol.* 16: 1296–1307.
- Parmenter, R. R., J. A. MacMahon, and D. R. Anderson. 1989. Animal density estimation using a trapping web design: field validation experiments. *Ecology* 70: 169–179.
- Parmenter, R. R., C. A. Parmenter, and C. D. Cheney. 1989a. Factors influencing microhabitat partitioning in arid-land darkling beetles (Tenebrionidae): temperature and water conservation. *J. Arid Environ.* 17: 57–67.
- Parmenter, R. R., C. A. Parmenter, and C. D. Cheney. 1989b. Factors influencing microhabitat partitioning among co-existing species of arid-land darkling beetles (Tenebrionidae): behavioral responses to vegetation architecture. *Southwest. Nat.* 34: 319–329.
- Parmenter, R. R. 2008. Long-term effects of a summer fire on desert grassland plant demographics in New Mexico. *Rangeland Ecol. Manag.* 61: 156–168.
- Pearson, D. L., and A. P. Vogler. 2001. Tiger beetles. The evolution, ecology, and diversity of the cicindelids. Comstock Publishing Associates, Ithaca, New York.
- Pennington, D. D., and S. L. Collins. 2007. Response of an aridland ecosystem to interannual climate variability and prolonged drought. *Landsc. Ecol.* 22: 897–910.
- Porter, E. E., and R. A. Redak. 1996. Short-term recovery of the grasshopper communities (Orthoptera: Acrididae) of a California native grassland after prescribed burning. *Environ. Entomol.* 25: 987–992.
- Porter, E. E., and R. A. Redak. 1997. Diet of migratory grasshopper (Orthoptera: Acrididae) in a California native grassland and the effect of prescribed spring burning. *Environ. Entomol.* 26: 234–240.
- Reed, C. C. 1997. Responses of prairie insects and other arthropods to prescription burns. *Nat. Area. J.* 17: 380–385.
- Rice, L. A. 1932. The effect of fire on the prairie animal communities. *Ecology* 13: 392–401.
- Richman, D. B., D. C. Lightfoot, C. A. Sutherland, and D. J. Ferguson. 1993. A manual of the grasshoppers of New Mexico. Orthoptera: Acrididae and Romaleidae. Handbook No. 7. New Mexico State University Cooperative Extension Service, Las Cruces, NM.
- Rominger, A. J., T.E.X. Miller, and S. L. Collins. 2009. Relative contributions of neutral and niche-based processes to the structure of a desert grassland grasshopper community. *Oecologia* 161: 791–800.
- Samu, F., F. Kádár, G. Ónodi, M. Kertész, A. Szirányi, É. Szita, K. Fetykó, D. Neidert, E. Botos, and V. Altbáker. 2010. Differential ecological responses of two generalist arthropod groups, spiders and carabid beetles (Araneae, Carabidae), to the effects of wildfire. *Community Ecol.* 11: 129–139.
- Sanchez, B. C., and R. R. Parmenter. 2002. Patterns of shrub-dwelling arthropod diversity across a desert shrubland-grassland ecotone: a test of island biogeographic theory. *J. Arid Environ.* 50: 247–265.
- Seifres, C. J., T. W. Oldham, P. D. Teel, and D. L. Drawe. 1988. Gulf Coast tick (*Amblyomma maculatum*) populations and responses to burning of coastal prairie habitats. *Southwest. Nat.* 33: 55–64.
- Seastedt, T. R. 1984. Belowground macroarthropods of annually burned and unburned tallgrass prairie. *Am. Midl. Nat.* 111: 405–408.
- Sgardelis, S. P., J. D. Pantis, M. D. Argyropoulou, and G. P. Stamou. 1995. Effects of fire on soil macroinvertebrates in a Mediterranean phryganic ecosystem. *Int. J. Wildland Fire* 5: 113–121.
- Siemann, E., J. Haarstad, and D. Tilman. 1997. Short-term and long-term effects of burning on oak savanna arthropods. *Am. Midl. Nat.* 137: 349–361.
- Swengel, A. B. 2001. A literature review of insect responses to fire, compared to other conservation managements of open habitat. *Biodivers. Conserv.* 10: 1141–1169.
- Trucchi, E., M. Pitzalis, M. Zapparoli, and M. A. Bologna. 2009. Short-term effects of canopy and surface fire on centipede (Chilopoda) communities in a seminatural Mediterranean forest. *Entomol. Fenn.* 20: 129–138.
- Uehara-Prado, M., A. de M. Bello, J. de O. Fernandes, A. J. Santos, I. A. Silva, and M. V. Cianciaruso. 2010. Abundance of epigeic arthropods in a Brazilian savanna under different fire frequencies. *Zoologia* 27: 718–724.
- [USDA] U.S. Department of Agriculture NRCS. 2011. The PLANTS Database. National Plant Data Center, Baton Rouge, LA. ([plants.usda.gov](http://plants.usda.gov)).

- Uys, C., M. Hamer, and R. Slotow. 2006. Effect of burn area on invertebrate recolonization in grasslands in the Drakensberg, South Africa. *Afr. Zool.* 41: 51–65.
- Vermeire, L. T., R. B. Mitchell, S. D. Fuhlendorf, and D. B. Wester. 2004. Selective control of rangeland grasshoppers with prescribed fire. *J. Range Manage.* 57: 29–33.
- Vogel, J. A., R. R. Koford, and D. M. Debinski. 2010. Direct and indirect responses of tallgrass prairie butterflies to prescribed burning. *J. Insect Conserv.* 6: 663–677.
- Warren, S. D., C. J. Scifres, and P. D. Teel. 1987. Response of grassland arthropods to burning: a review. *Agric. Ecosyst. Environ.* 19: 105–130.
- Wiens, J. A., T. O. Crist, and B. T. Milne. 1993. On quantifying insect movements. *Environ. Entomol.* 22: 709–715.
- Zimmer, K., and R. R. Parmenter. 1998. Harvester ants and fire in a desert grassland: ecological responses of *Pogonomyrmex rugosus* (Hymenoptera: Formicidae) to experimental wildfires in central New Mexico. *Environ. Entomol.* 27: 282–287.

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