EFFECTS OF FIRE AND PRECIPITATION ON SMALL MAMMAL POPULATIONS AND COMMUNITIES

A Thesis

by

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ABSTRACT

Effects of Fire and Precipitation on Small Mammal
Populations and Communities
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Fire and precipitation drive vegetation structure and composition; changes in vegetation will in turn influence distribution and abundance of small mammals. Precipitation also can interact with fire, aiding in recovery, whereas drought may amplify immediate fire effects and prolong recovery. I examined existing literature to reveal patterns on how both precipitation and fire can influence small mammal populations and communities. I also examined the effects of a wildfire that occurred in March 2008 at the Chaparral Wildlife Management Area in South Texas; precipitation varied greatly before and after fire. To examine individual and interactive effects of fire and precipitation, I established 15 1-ha plots that burned at varying intensities and sampled vegetation and small mammals in March–April and October–November, 2009–2010. Fire affected presence and abundance of small mammals based on habitat and dietary requirements, and precipitation altered fire effects for certain species. Examining interactive effects of disturbances provides a more comprehensive understanding for land managers; compounded effects are likely to become increasingly common with invasion of nonnative species and changes in climate and land-use.

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CHAPTER I: EFFECTS OF FIRE ON SMALL MAMMAL COMMUNITIES IN ARID AND SEMI-ARID REGIONS

ABSTRACT

Fire, whether natural or prescribed, can alter vegetation structure and composition drastically. Changes in the vegetation community have implications for fauna, such as small mammals; presence and abundance of small mammal species are determined largely by vegetation structure and composition. I examined peer-reviewed literature to reveal general patterns on how fire affects populations and communities of small mammals. The effects of fire vary by species based on habitat and dietary requirements of the small mammals present, and can be altered further with nonnative grasses, varying land uses, and other compounding variables. Fire and grazing, at low intensities, can increase diversity in vegetation and small mammal communities. More intense fires can reduce vegetation heterogeneity and promote nonnative grasses, resulting in decreased species richness of small mammals. Drought can increase the risk of high-intensity fire and increase recovery time of vegetation and small mammal communities. By applying fire with varying intensities and return intervals, while considering potential confounding factors such as grazing pressure and presence of nonnative grass, land managers can maximize diversity in small mammal and vegetation communities.

INTRODUCTION

Fire is a natural and integral process in many ecosystems, including arid and semi-arid grasslands. Historically, fire stimulated reproduction in vegetation, increased productivity of grass and forb species, maintained processes such as nutrient cycling, and limited the encroachment of shrubs in fire-adapted communities (Brockway et al. 2002, White et al. 2006). Suppression of fire in these systems over the last century has resulted in reduced reproduction of fire-dependent plant species and accumulation of fuels that can support large-scale, high-intensity fires (Parsons and DeBenedetti 1979). These changes to the fire regime may be outside the natural range of variability, which can reduce heterogeneity in vegetation structure and composition and alter the effects of fire on plants and animals.

Small mammals have diverse species-specific habitat requirements and depend heavily on vegetation for cover from predators and for food resources. Fire-induced changes in vegetation structure and composition will largely influence species presence and abundance (Rosenzweig and Winakur 1969, Fox 1990). Because small mammals have short gestation periods and can reproduce multiple times throughout the year (Nowak 1999), populations can respond quickly to changes resulting from fire, making them an ideal subjects for studying fire effects.

METHODS

I systematically searched databases of peer-reviewed scientific journals related to wildlife ecology for references pertaining to the effects of fire, both prescribed fire and wildfire, on small mammal communities. I specifically sought studies that examined fire effects in arid and semi-arid grasslands. This search produced 52 references, most directly related to fire effects on small mammals, but some provided relevant information about general fire effects on vegetation, and small mammal responses to changes in vegetation from fire surrogates (e.g., thinning) or other disturbance (Table 1.1, pg. 20). I categorized results from these studies into 4 main topics related to fire and small mammals: direct effects, indirect effects, persistence of fire effects, and factors that interact with fire (e.g., nonnative grasses and precipitation).

Wildfires typically occur in the warm-season and prescribed burning is generally done in the cool-season, when fire behavior is more predictable. Both types of fire generally have similar effects on small mammals, differing mainly in magnitude and persistence (Bock and Bock 1978); the effects of fire on vegetation and reduction in cover are of greater magnitude and longer duration with wildfire (Bock and Bock 1978, Brockway et al. 2002). As such, I did not differentiate among studies based on the source of the fire, but do discuss some differences in effects based on fire intensity.

DIRECT EFFECTS OF FIRE ON SMALL MAMMALS

Fire does not seem to have major direct effects on small mammal populations. Early researchers speculated that small mammals were subject to high rates of direct mortality from fire (Chew et al. 1959, Cook 1959); however, further research found that direct mortality generally is quite low (Beck and Vogl 1972, Crowner and Barrett 1979, Hedlund and Rickard 1981). Most small mammals are able to evade fire by utilizing refuges such as tunnels, rocks, and moist vegetation (Ford et al. 1999). Because soil does not conduct heat from fire, burrowing small mammals are able to survive high-intensity fires below ground, especially if burrows have multiple openings to provide adequate ventilation (Geluso et al. 1986). Species that dwell in above-ground nests made of flammable woody debris, such as woodrats (*Neotoma* spp.), may be more susceptible to direct mortality from fire, as they are less likely to leave their middens, even when fire is nearby (Simons 1991).

INDIRECT EFFECTS OF FIRE ON SMALL MAMMALS

Indirect effects of fire, such as changes in vegetation structure and composition, generally have a much more substantial impact on small mammals than direct effects. Indirect effects of fire on small mammal presence and abundance vary greatly in relation to habitat requirements; species-specific changes in abundance have been studied extensively (Table 1.1, pg. 20). For species that prefer thick or woody vegetation, such as the white-footed mouse (*Peromyscus leucopus*), cotton rats (*Sigmodon* spp.), and wood rats (*Neotoma* spp.), presence and abundance may decline after fire due to reduced vegetation cover (Ahlgren 1966, Krefting and Ahlgren 1974, Roberts et al. 2008, Litt and Steidl 2011). For species of small mammals that prefer more open habitat characteristics, such as pocket mice (*Perognathus* spp.), ground squirrels (*Spermophilus* spp.), and kangaroo rats (*Dipodomys* spp.), reductions in cover following fire initially may promote population growth (Krefting and Ahlgren 1974, Bock and Bock 1978, Greenberg et al. 2006, Litt and Steidl 2011).

Fire also can indirectly affect small mammal presence and abundance by altering food resources. Fire can increase the variety and abundance of certain food resources, such as native grasses, forbs, and insects (Daubenmire 1968, Hulbert 1969, Potts et al. 2003), potentially resulting in increased abundance of granivorous, herbivorous, and insectivorous small mammals. Fire may reduce other food resources, such as fruits from trees and shrubs (Keeley 1977), which can lead to reduced presence and abundance of frugivorous and omnivorous small mammals. Reduction in litter after fire may also make movement and locating seeds easier, resulting in reduced foraging effort (Greenberg et al. 2006).

Although some species of small mammals are less abundant after fire, overall diversity in the small mammal and vegetation communities can increase. Heterogeneity in vegetation structure and composition creates a diverse range of conditions that can meet habitat requirements for a greater number of small mammal species (Masters 1993, Carey and Wilson 2001). Patchy burns can increase heterogeneity in vegetation cover and create a mosaic across the landscape (Fuhlendorf et al. 2006, Roberts et al. 2008). Conversely, high-intensity fires can burn more completely, leading to more homogeneous vegetation structure (Ojeda 1989, Letnic et al. 2005). Short return intervals will promote early successional species and longer return intervals will promote mid- or late-successional species; applying multiple fires with different return intervals will create heterogeneity in vegetation structure and composition (Beck and Vogl 1972). Maintaining vegetation heterogeneity should be a management goal to support diverse small mammal communities.

Few studies have examined variation in survival, movement, or reproduction of small mammals after fire (Table 1.1, pg. 20). Survival of small mammals could decrease after fire because predation risk may increase where cover of vegetation or debris has been reduced or removed (Crowner and Barrett 1979); however, of the few studies that examined survival, only 1 observed fire effects, where survival of *Neotoma albigula* decreased following fire (Simons 1991). Other studies that examined survival failed to detect differences between burned and unburned sites (Christian 1977, Zwolak and Foresman 2008). Long-range movements of small mammals have not been observed immediately following fire (2 weeks to 6 months—Christian 1977, Banks et al. 2011). The lack of long distance dispersal suggests that individuals can persist on burned sites or only need to move short distances between unburned or lightly burned patches, and long-range dispersal is not needed to recolonize burned areas. Reproductive activity of small mammals could potentially change following fire, as reproduction is associated with available food resources (Beatly 1969) and fire can increase food resources for small mammals (Daubenmire 1968, Hulbert 1969, Potts et al. 2003); however, of the few studies that examined reproduction, none detected fire effects (Christian 1977, Zwolak and Foresman 2008). Additional research on how fire affects survival, movement, and reproduction of small mammals could provide a more complete understanding of the mechanisms driving post-fire abundance, presence, and recovery of small mammal populations.

PERSISTENCE OF FIRE EFFECTS

Although food resources are important drivers of small mammal abundance and reproduction, small mammal species respond strongly to vegetation structural characteristics (Thompson 1982, Briani et al. 2003, Monamy and Fox 2010). Composition of the small mammal community generally follows a predictable pattern of recovery after fire, ordered according to species-specific habitat requirements (Thompson 1982, Briani et al. 2003, Monamy and Fox 2010). Initially after fire or other disturbance (e.g., thinning or mowing), the small mammal community will be dominated by species that inhabit early-successional conditions (e.g., low vegetation cover and density, high amounts of bare ground), and composition and dominance change as vegetation recovers (Fox 1982, Fox et al. 2003). For example, *Pseudomys gracilacaudatus* (an early seral species) and *Rattus lutreolus* (a late seral species) both inhabit coastal heathland in Australia, but have different preferred thresholds for vegetation density (Fox and Fox

2000, Monamy and Fox 2010). Following manual removal of vegetation cover, *P. gracilacaudatus* recolonized the site first, when vegetation density provided 12% visual obstruction in the 20 to 50-cm vertical stratum. *R. lutreolus* recolonized when vegetation had recovered sufficiently to create 35% visual obstruction.

In a unique examination of small mammal responses to changing vegetation density, Thompson (1982) used small cardboard shelters to artificially increase shrub density in the Mojave Desert. The cardboard shelters mimicked vegetation structure, but lacked the clustered food resources that would normally occur below real shrubs (e.g., fallen fruit from the shrubs, insects). Despite the change in vegetation structure being artificial, Thompson (1982) still observed a shift in species composition towards late seral stage species. Creation or recovery of specific structural characteristics is integral in determining composition of the small mammal community following a disturbance such as fire.

The length of time needed for vegetation and small mammals to return to pre-fire levels can vary greatly based on the specific ecosystem, fire intensity, and factors affecting the recovery of vegetation. Ecosystems that lack a prominent shrub or tree component, such as semi-arid grasslands, can mature quickly and small mammal populations may return to pre-fire levels in less than 2 years (Litt and Steidl 2011); however, some sagebrush ecosystems, and therefore sagebrush obligates, may require more than a century to recover from fire (Baker 2006). Persistence of fire effects can be extended if the fire is high-intensity (Ford and Johnson 2006). Rainfall following fire will greatly aid in recovery, especially if the rainfall occurs during the growing season.

Small mammals will respond quickly to changes in vegetation following growing season precipitation, as their gestation period is only 3 to 6 weeks (Nowak 1999).

FIRE AND CONFOUNDING EFFECTS

Various environmental conditions and land-use practices can interact with fire to create compounded effects on vegetation and small mammal communities. Previous research has focused on how precipitation, grazing, and nonnative grasses can alter fire effects. Examining these interactions can provide a more comprehensive understanding of how vegetation and small mammals will respond to and recover from fire under a variety of conditions, as fire is seldom the sole influence in an arid or semi-arid ecosystem.

Precipitation can alter the magnitude and duration of fire effects on vegetation and animals, such that fire may function in less predictable ways. Desiccated or dead vegetation resulting from drought provides a highly-combustible fuel source that can support high-intensity wildfire (Hessl et al. 2004), which can increase recovery time (Ford and Johnson 2006) and potentially reduce vegetation heterogeneity and small mammal species richness (Ojeda 1989, Letnic et al. 2005). If drought conditions occur following fire, vegetation recovery may be limited and fire effects may persist for extended periods (Frazer and Davis 1988). In arid regions where vegetation is typically sparse, rainfall can increase fuel loads that can carry an extensive wildfire (Letnic et al. 2005). Rainfall following fire can reduce recovery time of both floral and faunal communities by stimulating vegetation growth (Yarnell et al. 2007).

Grazing can also interact with fire by reducing fuel loads, thereby reducing the risk of high-intensity fire. Fire and grazing together can increase richness of the vegetation community by reducing litter and altering vegetation structure (Noy-Meir 1995), which should support a greater diversity of small mammals. Yarnell et al. (2007) explored interactions of fire, grazing, and precipitation, and found that small mammal diversity was greatest in areas that were burned and grazed at a low intensity, when precipitation values were above average.

Nonnative grasses are a major concern in arid and semi-arid ecosystems (Anable et al. 1992, Knapp 1996). Fire can make a site more susceptible to initial invasion or promote further invasion by nonnative grasses by reducing canopy cover and increasing light and nutrient availability (Hobbs and Huenneke 1992, D'Antonio et al. 1993). Nonnative grasses can recover more rapidly than some native grasses, increasing nonnative grass cover and susceptibility to fire (D'Antonio and Vitousek 1992), potentially creating a grass-fire positive feedback cycle. Following fire in shrub-steppe communities in Idaho, burned sites became near monocultures of cheatgrass (*Bromus tectorum*) and species richness and abundance of all small mammal species declined (Gano and Rickard 1982, Groves and Steenhof 1988; Table 1.1, pg. 20), suggesting that this feedback cycle can have negative consequences for small mammal communities.

Nonnative grasses also can alter fire regimes by increasing fuel load and continuity, resulting in increased fire intensity, size, and frequency (D'Antonio and Vitousek 1992, Brooks et al. 2004). Large, continuous high-intensity fires can reduce vegetation heterogeneity, which can reduce small mammal species richness (Ojeda 1989, Letnic et al. 2005). Such changes in the fire regime can result in more complete combustion, create relatively homogenous vegetation structure across the landscape, and increase the recovery time of floral and faunal communities, modifying the effects of fire as a disturbance (Steidl and Litt 2009).

The interaction of fire and nonnative grasses can create novel effects on small mammal populations and communities, modifying the magnitude, persistence, and direction of responses. For example, Litt and Steidl (2011) observed more marked decreases in presence and abundance of certain species of small mammals following fire in grasslands dominated by nonnative grass compared to sites dominated by native grasses. Litt and Steidl (2011) also observed a change in the persistence and direction of response to fire in *Chaetodipus hispidus* and *Perognathus flavus* along a gradient of nonnative grass dominance. Further exploration of these complex interactions will provide a comprehensive understanding of how combinations of factors will influence small mammal communities, as land managers frequently deal with multiple management issues, such as drought and nonnative grass invasion.

CONCLUSIONS

Fire affects small mammal species differently, according to their dietary and habitat requirements. Although some species may decline in abundance, overall species richness may increase with increased heterogeneity in vegetation structure and composition created by fire. High-intensity fires can reduce vegetation heterogeneity, but heterogeneity can be created by applying small prescribed fires at varying intensities and return-intervals and maintaining unburned refugia to maximize diversity in the small mammal community.

Although fire and small mammals have been well-studied, some gaps in our understanding remain. Additional research on the effects of fire on the survival, movement, and reproduction of small mammals is warranted, as very few studies have examined these response variables extensively (Table 1.1, pg. 20). Further exploration of interactions is critical in ameliorating our understanding of compounded effects of fire and other factors on small mammal and vegetation communities. Land managers increasingly will face multiple challenges resulting from changes in climate patterns, such as persistent drought (Aigu Dai and Trenberth 2004) and increased invasion by nonnative plants (Dukes and Mooney 1999); our ability to predict the effects of multiple confounding factors will define the future success of natural resource managers.

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TABLE 1.1—Summary of literature examining the effects of fire or fire surrogates on small mammals.

Reference	Fire/Surrogate	Species	Abundance	Other response variables
Ahlgren 1966	Prescribed fire, warm season	*Clethrionomys gapperi*	–[a]	
		Peromyscus maniculatus	+[b]	
Banks et al. 2011	Wildfire, warm season	*Antechinus agilis*	–	
		Rattus fuscipes	–	
Beck and Vogl 1972	Prescribed fire, intervals of ~1, 4, and 8 years	*Clethrionomys gapperi*	–	
		Peromyscus leucopus	–	
		P. maniculatus	+	
		Spermophilus tridecemlineatus	+	
Bock and Bock 1978	Wildfires, warm and cool seasons	*Chaetodipus hispidus*	+	
		Dipodomys merriami	+	
		Peromyscus spp.	No Δ[c]	
		Sigmodon hispidus	–	
Carey and Wilson 2001	Thinning as a fire surrogate to promote vegetation heterogeneity	*Clethrionomys gapperi*	No Δ	
		Microtus oregoni	+	
		Neurotrichus gibbsii	No Δ	
		Peromyscus keeni	No Δ	
		P. maniculatus	+	
		Sorex monticolus	No Δ	
		S. trowbridgii	No Δ	
		S. vagrans	+	

TABLE 1.1 CONTINUED

Reference	Fire/Surrogate	Species	Abundance	Other response variables
Chew et al. 1959	Wildfire, warm season	*Neotoma fuscipes*		Direct mortality observed
		Sylvilagus auduboni		
		Peromyscus sp.		
		Microtus sp.		
		Mus musculus		
Christian 1977	Wildfire, warm season	*Desmodillus auricularis*	–	No Δ in survival, reproduction, or movement
		Gerbillurus paeba	–	No Δ in survival, reproduction, or movement
		Rhabdomys, pumilio	–	No Δ in survival, reproduction, or movement
Cook 1959	Wildfire, cool season	*Reithrodontomys megalotis*	+	
		Microtus californicus	No Δ	
Converse et al. 2006a	Thinning and wildfire, warm season	*Peromyscus maniculatus,*	+	
		Tamias cinereicollis,	+	
		Tamias minimus	+	
Crowner and Barrett 1978	Prescribed fire, warm season	*Microtus pennsylvanicus*	–	
			–	
		Mus musculus	–	
		Peromyscus maniculatus		

TABLE 1.1 CONTINUED

Reference	Fire/Surrogate	Species	Abundance	Other response variables
Fala 1975	Prescribed fire, warm season	*Clethrionomys gapperi*	–	
		Microtus pennsylvanicus	–	
		Peromyscus maniculatus	+	
Geluso et al. 1986	Prescribed fire, warm season	*Microtus pennsylvanicus*		Tracked during fire; no direct morality
Greenberg et al. 2006	Thinning and prescribed fire, cool season	*Peromyscus leucopus*	+	
Groves and Steenhof 1988	Wildfire, warm season	*Peromyscus maniculatus*	–	
		Spermophilus townsendii	–	
Hedlund and Rickard 1981	Wildfire, warm season	*Perognathus parvus*	+	
		Spermophilus townsendii	+	
Letnic et al. 2005	Wildfire, warm season	*Dasycercus cristicauda*	No Δ	– Species richness
		Ningaui ridei	No Δ	
		Notomys alexis	No Δ	
		Pseudomys desertor	–	
		P. hermannsburgensis	No Δ	
		Sminthopsis youngson	No Δ	

TABLE 1.1 CONTINUED

Reference	Fire/Surrogate	Species	Abundance	Other response variables
Litt and Steidl 2011	Prescribed fire, warm and cool season	*Baiomys taylori*	–	– Species richness
		Chaetodipus hispidus	No Δ	
		C. penicillatus	–	
		Dipodomys merriami	+	
		Onychomys leucogaster	No Δ	
		Perognathus flavus	No Δ	
		Reithrodontomys fulvescens	–	
		Sigmodon arizonae	–	
		S. ochrognathus	–	
Magnusson et al. 2010	Multiple wildfires, timing varied	*Necromys lasiurus*	+	
Masters 1993	Multiple prescribed fires, unknown timing			+ Species richness
Ojeda 1989	Wildfire, warm season	*Akodon molinae*	No Δ	– Species richness
		Calomys musculinus	–	
		Eligmodontia typus	+	
		Graomys griseoglavus	–	
		Marmosa pusilla	No Δ	
Roberts et al. 2008	Multiple wildfires, timing varied	*Neotamias spp.*	+	
		Peromyscus boylii	No Δ	
		P. maniculatus	–	
		Spermophilus beecheyi	+	

TABLE 1.1 CONTINUED

Reference	Fire/Surrogate	Species	Abundance	Other response variables
Simons 1991	Prescribed fire, warm season	*Dipodomys merriami*	+	
		Chaetodipus baileyi	–	
		Neotoma albigula	–	– Survival
		Perognathus amplus	–	
Steidl and Litt 2009	Prescribed fire, warm season	*Dipodomys merriami*	+	
		Onychomys leucogaster	+	
		Sigmodon arizonae	–	
Yarnell et al. 2007	Prescribed fires, cool season, 4-5 year intervals	*Mus indutus*	+	+ Species richness
		Saccostomus campestris	+	
		Steatomys pratensis	–	
Zwolak and Foresman 2008	Wildfire, warm season	*Peromyscus maniculatus*	+	No Δ in survival, reproduction, or movement

[a] Decrease.
[b] Increase.
[c] No change.

CHAPTER II: EFFECTS OF PRECIPITATION ON SMALL MAMMAL COMMUNITIES IN ARID AND SEMI-ARID REGIONS

ABSTRACT

Precipitation influences vegetation cover heavily. In general, precipitation increases primary production, which in turn increases food resources for small mammals and creates cover that provides protection from predators; however, the magnitude of these effects depends on the ecosystem and timing of rainfall. I reviewed 31 references from peer-reviewed scientific journals to reveal patterns and better understand the effects of precipitation on small mammal communities and their habitats, focusing mainly on arid and semi-arid systems. In arid and semi-arid landscapes that receive little rainfall, precipitation can have marked effects on vegetation, leading to irruptions of small mammal populations. Natural climatic patterns, such as El Niño Southern Oscillations, can create extreme and atypical precipitation events that can have negative effects on small mammals, such as mortality from flooding. Examining extreme precipitation events can improve our ability to understand and predict potential effects of changing weather patterns associated with climate change on small mammal communities.

INTRODUCTION

Precipitation is an important driver of both the structure and composition of vegetation communities. Vegetation characteristics, in turn, largely influence the abundance and composition of small mammal communities (Rosenzweig and Winakur 1969, Rosenzweig 1973, Krefting and Ahlgren 1974). In general, increased precipitation results in increased plant productivity that provides additional food resources and cover for small mammals and other fauna. Increased abundance and diversity of forage will lead to higher reproductive activity and success (Beatley 1969) and subsequent increases in population size (Ernest et al. 2000, Thibault et al. 2010).

Despite some general patterns, the effects of precipitation on vegetation and small mammals can vary greatly across temporal, spatial, and environmental gradients. Temporal variation in precipitation has been studied most often, including the effects of drought and El Niño Southern Oscillation (ENSO). Few studies have examined variation in precipitation effects across geographical and environmental gradients, comparing changes in small mammal abundance and diversity across multiple ecosystems or ecoregions. I examined existing literature (31 references directly related to precipitation effects on small mammals, as well as other supporting studies) to reveal general patterns and identify factors that contribute to variation in precipitation effects on small mammal communities and populations in arid and semi-arid regions.

PRECIPITATION EFFECTS ON SMALL MAMMAL POPULATIONS AND COMMUNITIES

Abundance.—Minimal rainfall is needed to maintain vegetation in arid and semi-arid regions, as these vegetation communities are adapted to drought and low annual precipitation. When precipitation events do occur, they generally lead to subsequent increases in small mammal abundance (Brown 1973, Windberg 1998, Lima et al. 1999b), resulting from the food, water, and cover created. This bottom-up relationship is well-documented in arid and semi-arid regions (Rosenzweig and Winakur 1969, Rosenzweig 1973, Brown 1975, Brown et al. 1979); however, the relationship between rainfall and abundance of small mammals may be more complex.

Brown and Ernest (2002) argued that because many of the studies examining the effects of precipitation on small mammal abundance were short-term, these studies provide a simplified perspective. After examining a 22-year dataset, the authors found no significant relationship between precipitation and small mammal abundance. They postulated that other factors such as herbivory, timing and amount of rainfall, predation, disease, and extreme weather events can influence the response of vegetation and small mammals to precipitation, making the relationship difficult to predict over longer time periods. For example, high density of larger, more mobile species, such as ungulates, may reduce food resources and indirectly reduce small mammal abundance (Keesing 1998), potentially negating the benefits of precipitation. Timing of rainfall could alter the magnitude of precipitation effects, as precipitation during the non-growing season has little or no effect on vegetation cover or small mammal abundance (Ernest et al. 2000, Bradley et al. 2006). Extreme temperature or precipitation events, predation, and parasitism/disease can negatively influence small mammal populations (Sinclair et al. 1990, Jackson et al. 2001, Elliot and Root 2006, Lemaître et al. 2009), possibly reducing benefits of rainfall. Over longer periods of time, these factors may singularly or interactively influence precipitation effects on small mammal populations. Results from most studies support bottom-up effects of precipitation (Brown 1973, Windberg 1998, Lima et al. 1999b), but these interactions could provide explanations when small mammal abundance does not increase systematically with precipitation. Although I did not find any long-term studies that examined interactive effects of precipitation and other biotic and abiotic factors on small mammal abundance, future studies that consider such compounded disturbances over longer time frames could be useful to predict outcomes of changes in climate patterns.

Species Richness.—Changes in distribution and abundance of habitat for small mammals resulting from precipitation also can affect species richness. Increases in vegetation cover after rainfall potentially can create diverse habitat conditions and abundant food resources, which may support more species (Milstead et al. 2007). Species richness of granivorous small mammals increases across a gradient of precipitation in the Sonoran, Colorado, Mojave, and Great Basin Deserts in the southwestern United States (Brown 1973). Increased annual rainfall yields higher abundance and diversity of seed-producing plants, a pattern that is associated with increased dietary specialization and diversity of granivorous small mammals. Seeds are the primary food source in desert ecosystems; as such, small mammal species vary in body size and may specialize on certain sizes of seeds to reduce interspecific competition and exploit available food resources more efficiently (Brown 1973, 1975, M'Closkey 1976).

Conversely, some large-bodied species of desert rodents are able to monopolize available resources, which can lead to increased reproduction of the dominant rodent species, limited resource availability for other species, and reduction in species richness or evenness of small mammal communities (Orland and Kelt 2007). Because granivorous small mammals inhabiting the driest areas are less specialized and multiple species are competing for the same resources, these communities may be more likely to be dominated by a single species following rainfall, resulting in reduced species richness. Population irruptions of a dominant species could be a concern for threatened or endangered species of small mammals, such as the Stephens' kangaroo rat (*Dipodomys stephensi),* which has been negatively affected by fragmentation (Kelt et al. 2008).

Effects of precipitation on species richness also can vary depending on the ecosystem examined. Species richness of omnivorous, insectivorous, and herbivorous small mammals typically increases across a precipitation gradient from deserts to grasslands (range of 88 to 1,158 mm/year) in the southwestern to south-central United States, whereas species richness of granivorous small mammals decreases (Reed et al. 2006). Abundant and diverse resources associated with increased rainfall can provide food and habitat for a myriad of species with varying dietary requirements. Decreases in species richness of granivorous small mammals across the desert-grassland continuum is most likely due to increased litter depth and homogeneity in vegetation structure, which can impede movement, increase foraging effort, and limit the number of available niches (Reed et al. 2006). Species richness of granivores also may be nonlinear, increasing with precipitation and food resources up to some threshold of litter depth or cover, and decreasing beyond that threshold (Reed et al. 2006).

Lag Time Following Precipitation.—Small mammal populations require time to respond to increases in cover and food resources created by rainfall. Over time, body condition of small mammals will improve and reproductive activity can increase (Field 1975). Gestation time can vary from 3 to 6 weeks (Nowak 1999) and weaning time can vary from 3 to 5 weeks (Nowak 1999), depending on the species of small mammal; these time periods also must be incorporated into determinations of lag time. As a result, increases in abundance often are observed within 3 to 6 months following precipitation, but may take up to 1 year depending on timing of rainfall (Ernest et al. 2000, Bradley et al. 2006).

In arid and semi-arid ecosystems, total rainfall in the previous 1 to 2 growing or non-growing seasons provides the best predictor of how quickly small mammal populations will respond to precipitation events (Ernest et al. 2000). Because rainfall during the growing season will stimulate food resources during times of peak reproductive activity in small mammal populations, warm-season rainfall typically results in a shorter lag time with larger increases in small mammal abundance (Ernest et al. 2000, Bradley et al. 2006). Diet also influences lag time; folivores and granivores typically respond to precipitation from the previous growing or non-growing season, regardless of which season the rainfall occurred (Thibault et al. 2010). In contrast, insectivores respond to precipitation that fell during the previous year, because of the additional lag time required for arthropods to respond to increased primary production (Kaspari et al. 2000).

EXTREME PRECIPITATION EVENTS

Flooding.—Although the effects of increased precipitation on small mammal communities generally are positive, excessive precipitation can be detrimental. Heavy spring and summer rainfall can flood riparian areas, reduce cover and forage during important breeding times, and result in reduced abundance of small mammals (Elliott and Root 2006). Non-arboreal species of small mammals inhabiting riparian areas exhibit high site fidelity and may drown in floodwaters (Anderson et al. 2000). Some small mammals will move to higher ground when flooding occurs, but riparian vegetation provides refugia in highly fragmented landscapes (e.g., agricultural areas) and the absence of adjacent, upland habitat could have serious conservation implications for small mammal communities if flooding occurs.

Drought.—Drought also can play an important role as a disturbance, leading to short-term declines in abundance (Bradley et al. 2006). Drought can increase the risk of wildfire, potentially increasing the spread of nonnative vegetation (Smith et al. 2009) and reducing diversity in structure and composition of the vegetation community (D'Antonio and Vitousek 1992). Survival and reproduction of small mammals predictably decline under drought conditions because of reduced food resources and cover. Post-drought recovery can occur rapidly (Bradley et al. 2006) because most small mammals can produce large litters in a relatively short amount of time (Nowak 1999). Bradley et al. (2006) studied small mammals in south Texas thorn scrub during and after a 12-month drought (precipitation during drought, June 2001 to June 2002 = 34 cm; post-drought precipitation, July 2002 to July 2003 = 101 cm). Three months after growing-season rainfall, researchers observed a 500% increase in total abundance of all species captured. Similarly, Witecha et al. (Chapter 3) documented a 400% increase in total captures of small mammals in south Texas thorn scrub following a 16-month drought and significant growing-season rainfall (precipitation during drought, September 2008 to December 2009 = 54 cm; post-drought precipitation, January 2010 to October 2010 = 62 cm).

Influence of El Niño Southern Oscillation.—ENSO refers to the 2 stages in the quasi-periodic climatic pattern, El Niño and La Niña, which can have varying effects depending on geographic location (NOAA 2010). The El Niño phase is caused by warming surface temperatures near the equator in the Pacific Ocean. Arid and semi-arid regions of Chile and the southwestern United States receive above average precipitation in the winter during the El Niño phase; these conditions create extreme rain events that can lead to flooding and landslides. The La Niña phase is caused by cooler surface temperatures near the equator in the Pacific Ocean. Typically, La Niña conditions result in cool, dry winters, which can cause extreme drought in semi-arid Chile and arid and semi-arid southwestern United States. La Niña produces heavy rainfall in the Simpson Desert in Australia and Amazonian savannas in South America (NOAA 2010); fire probability can increase following La Niña rainfall because of increased fuel loads (Letnic et al. 2005).

High rainfall events associated with ENSO phases have varying effects on small mammal populations based on species-specific habitat requirements. Kelt et al. (2008) observed decline in abundance of 2 species of kangaroo rats (*Dipodomys stephensi*, a federally endangered species, and *Dipodomys simulans*) during a period of heavy El Niño rainfall in southern California. Kangaroo rats prefer open areas with sparse vegetation (Bleich 1977); rainfall may have resulted in vegetation cover that exceeded a maximum threshold. Five months after the rainy period, populations of both species recovered to pre-rainfall levels. Conversely, abundance of Darwin's leaf-eared mouse (*Phyllotis darwini*), which prefers thicker cover, increases following high levels of El Niño rainfall in semi-arid regions in Chile (Lima et al. 1999a). High rainfall from La Niña also results in increased abundance of omnivorous and herbivorous small mammals, due to increased food resources and decreased fire probability in the Simpson Desert in Australia and the Amazonian savanna in Chile (Letnic et al. 2005, Magnusson et al. 2010). In semi-arid thorn scrub in Chile, opportunistic small mammals (*Oligoryzomys longicaudatus* and *Abrothrix longipilis*) will exploit the thorn scrub under favorable conditions, but go locally extinct or emigrate to adjacent riparian and fog-forest patches in drought following El Niño (Milstead et al. 2007).

CONCLUSIONS AND FUTURE RESEARCH NEEDS

In the short-term, precipitation events generally lead to resource pulses and subsequent increases in small mammal populations following sufficient lag time. Species that prefer sparse cover will also benefit from increased food resources, however, changes in vegetation structure may not be beneficial. Over longer time periods, the relationship is less predictable because precipitation can interact with other abiotic and biotic factors, such as herbivory, predation, competition, and temperature, to alter effects on small mammal communities. Additional long-term research could help could provide insight into how such interactive effects influence small mammal communities and how those effects differ in various ecosystems and across geographic gradients.

Although most populations of small mammals recover quickly from drought or flooding rainfall, species in fragmented habitat may be more susceptible to local extirpation (Kelt et al. 2008). Habitat loss, degradation, and fragmentation continue to be major challenges for conservation. Additional information on changes in small mammal abundance following varying precipitation could be crucial for conservation and management of small mammal species that occur in highly fragmented areas or are listed as threatened or endangered.

Lastly, additional information about the influence of ENSO could provide insight into consequences of changing climate for plant and animal populations, as weather patterns associated with ENSO parallel those projected to occur with climate change. Future climate changes could create sporadic but extreme rainfall events (Christensen and Christensen 2003), followed by periods of drought due to elevated evapotranspiration rates and decreased soil moisture (Aigu Dai and Trenberth 2004). These highly variable climatic conditions could result in extreme fluctuations in populations of small mammals, as well as high-intensity, large-scale wildfires and other disturbances (Williams et al. 2010), which could severely limit small mammal populations ability to recover from such events. Additional research on extreme weather events could improve our ability to predict the future effects of climate change.

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CHAPTER III: EFFECTS OF WILDFIRE AND PRECIPITATION ON SMALL MAMMAL POPULATIONS AND COMMUNITIES

ABSTRACT

Fire and precipitation drive vegetation structure and composition; changes in vegetation will in turn influence distribution and abundance of small mammals. Precipitation also can interact with fire, aiding in recovery, whereas drought may amplify immediate effects and prolong recovery. A wildfire occurred in March 2008 at the Chaparral Wildlife Management Area in South Texas; precipitation varied greatly before and after the fire. To examine individual and interactive effects of fire and precipitation, I established 15 1-ha plots that burned at varying intensities and sampled vegetation and small mammals in March–April and October–November 2009–2010. Fire effects on presence and abundance of small mammals were related to habitat and dietary preferences; granivorous species that prefer sparse vegetation (*Chaetodipus hispidus* and *Perognathus merriami*) benefitted from fire, whereas an omnivorous species associated with woody vegetation (*Peromyscus leucopus*) preferred unburned areas. Small mammal abundance and vegetation cover tended to increase with growing season precipitation, whereas precipitation during the non-growing season had little effect on abundance. Precipitation also altered fire effects on vegetation cover and abundance of *Reithrodontomys fulvescens* and *Sigmodon hispidus*; growing season precipitation increased vegetation cover and abundance of these small mammals regardless of fire intensity, but increases were greatest on high-intensity burned plots. Examining interactive effects of disturbances provides land managers and ecologists with a more comprehensive understanding of how multiple factors influence vegetation and small

mammal communities; compounded effects are likely to become increasingly common with invasion of nonnative species and changes in climate and land-use.

INTRODUCTION

Historically, wildfires have been a natural and common disturbance in many ecosystems, stimulating vegetation growth, maintaining early successional communities and driving ecosystem processes, such as nutrient cycling (Brockway et al. 2002, White et al. 2006); however, the natural fire regime has been altered dramatically. Following extensive wildfires in 1910, the United States government instituted a highly successful campaign for wildfire suppression. Fire suppression has resulted in unnaturally high fuel loads that can lead to wildfires of increased scale and intensity, and may exceed the natural range of variation in the fire regime, modifying the effects of fire on vegetation structure and composition (Parsons and DeBenedetti 1979).

Fire-induced changes in vegetation will in turn influence the distribution and abundance of wildlife, based on species-specific dietary and habitat requirements (Rosenzweig and Winakur 1969, Fox 1990). Fire can increase abundance and diversity of food resources such as grasses, forbs, and insects (Daubenmire 1968, Hulbert 1969, Potts et al. 2003), and reduce woody cover to favor species of plants and animals that prefer early successional conditions (Krefting and Ahlgren 1974, Bock and Bock 1978, Monamy and Fox 2010). Fires that burn at varying intensities or with varying return intervals can create a heterogeneous mosaic of vegetation structure and composition, producing a wide array of conditions that can benefit multiple wildlife species (Fuhlendorf et al. 2006).

Like fire, precipitation can affect vegetation structure and composition, as well as faunal communities. Following increased precipitation, increases in plant productivity provide abundant food resources, which can improve body condition and potentially lead to increased reproductive activity (Beatly 1969) and subsequent increases in abundance (Ernest et al. 2000, Thibault et al. 2010). The relationship between precipitation and abundance is especially evident in arid and semi-arid regions, where rainfall is a limiting factor and resource pulses following drought are common (Bradley et al. 2006).

Fire and precipitation can create interactive, compounded effects on vegetation and animals. Desiccated or dead vegetation resulting from drought provides a highly-combustible fuel source that can support high-intensity wildfire (Hessl et al. 2004). If drought conditions occur following fire, vegetation recovery may be limited and fire effects on both floral and faunal communities may persist for extended periods (Frazer and Davis 1988), whereas rainfall following fire can reduce recovery time (Yarnell et al. 2007).

On March 14, 2008, an intense wildfire burned 95% of the Chaparral Wildlife Management Area (CWMA) in South Texas. The combination of low humidity and high temperatures, wind speeds, and fine fuels produced a large-scale, high-intensity fire. Following the wildfire, the area was subjected to a 16-month drought, followed by a period of above-average rainfall. The wildfire and variable precipitation provided a unique set of conditions that allowed me to quantify the simple effects of fire and precipitation on small mammal communities, as well as any interactive, compounding effects of both factors. I selected small mammals for study because they are sensitive to changes in vegetation structure and heterogeneity (Rosenzweig and Winakur 1969, Krefting and Ahlgren 1974, Fox 1990, Monamy and Fox 2010). Small mammal species can respond to and recover from disturbances rapidly, as they have a gestation period of only 3 to 6 weeks and can reproduce multiple times throughout the year (Nowak 1999). In addition, small mammals are an important food resource for predators (Hanski et al. 2001), and serve functional roles in dispersal of seeds and mychorrizal fungi (Vander Wall 2002, Maser et al. 1978) and soil disturbance, which can increase soil aeration, infiltration, and organic matter (Martin 2003).

MATERIALS AND METHODS

Study Area.—The CWMA is located in Dimmit and La Salle counties in South Texas (28°20’N, 99°25’W). The 6,151-ha CWMA is managed intensively for biodiversity and game species, such as northern bobwhites (*Colinus virginianus*), by the Texas Parks and Wildlife Department. Common management practices include prescribed burning, grazing, and mechanical removal of woody vegetation, although management activities ceased in areas adjacent to research plots for at least 1 year before and during sampling.

Vegetation at the CWMA is characteristic of mixed-brush shrublands in South Texas (McLendon 1991). The dominant woody species is honey mesquite (*Prosopis glandulosa*); other common shrubs include whitebrush (*Aloysia gratissima*), brasil (*Condalia hookeri*), granjeno (*Celtis pallida*), Texas hogplum (*Colubrina texensis*), and Texas persimmon (*Diospyros texana*). Common forbs include prickly poppy (*Argemone mexicana*), croton (*Croton* spp.), and partridge pea (*Chamaechrista fasciculata*). Common native grasses include hooded windmill grass (*Chloris cucullata*) and hairy grama (*Bouteloua hirsuta*), and common nonnative grasses include buffelgrass

(*Pennisetum ciliare*), Lehmann lovegrass (*Eragrostis lehmanniana*), and Kleberg bluestem (*Dichanthium annulatum*).

Rainfall can be extremely variable and droughts are a common occurrence in South Texas. Average rainfall at the CWMA is 60.7 cm/yr ± 20.0 *SD* (CWMA, unpublished data). Precipitation data are collected at a single rain gauge located at the CWMA headquarters, ≤7 km from the research plots.

Study Design.—Ten months after the wildfire, I established five 1-ha research plots for each of 3 different levels of fire intensity (unburned, low-intensity, and high-intensity), for a total of 15 research plots; plots were located in the West Blocker, Hogue, Rosindo, South Jay, and Mare pastures. Fire intensity was determined based on the proportion of killed or top-killed shrubs on a plot; low-intensity burned plots had <65% dead or top-killed woody vegetation, whereas high-intensity burned plots had ≥65%. All plots were ≥50 m from roads and other plots, with the exception of the westernmost unburned plot, which was only 20 m from the road because of limited space. Nonnative grass cover was low (<20%); soil types were similar for all research plots and included Dilley fine sandy loam, Duval fine sandy loam, Duval loamy fine sand, Duval very fine sandy loam, and Webb very fine sandy loam (NRCS 2011).

Vegetation Sampling.—I characterized vegetation on research plots in March and October of 2009 and 2010. The initial sampling period occurred approximately 1 year after the wildfire. I estimated aerial canopy cover (%) for native grasses, nonnative grasses, cacti, litter, woody vegetation, forbs, and bare ground within a 1-m radius of each small mammal trap. I quantified vegetation heterogeneity (i.e., patchiness) based on the coefficient of variation of total cover for all trap locations on each plot during each sampling period. I counted the number of shrubs, dead shrubs, and resprouting shrubs within a 2-m radius of each trap. I separated shrubs into 2 height classes, <1 m and ≥1 m tall, and counted a shrub with multiple stems as 1 individual. I estimated shrub density (individuals/m^2) for both height classes based on the number of shrubs (live and resprouting) at each trap location.

Small Mammal Sampling.—I used 10 × 10 grids of Sherman live traps to sample small mammals during March and October 2009 and 2010, with traps spaced 10 m apart. I trapped small mammals in spring and fall to sample during periods of low and high population abundance, examine potential seasonal differences, and avoid trap mortalities from heat and cold stress during summer and winter. I trapped for 4-night periods in spring 2009, but increased to 5-night periods in fall 2009, spring 2010, and fall 2010 to improve recapture rates and abundance estimates. In the afternoon prior to the first day of trapping, traps were baited with a mixture of millet and sunflower seeds and checked shortly after sunrise the following morning. For the remainder of the trapping period, traps were baited after being checked in the morning and remained open throughout the day. During a given week of trapping, 3 plots (1 of each treatment) were sampled simultaneously; trapping on all plots was completed within 5 weeks, which I termed a sampling period.

All captured animals were individually double-marked with a numbered ear tag (Monel tag 1005-1, National Band and Tag Co., Newport, KY) and permanent felt-tipped markers. Species with small ears (*Chaetodipus*, *Perognathus*, *Spermophilus* spp.) were marked uniquely with ink only. I recorded standard morphological measurements (weight, length of body, tail, and hind foot), as well as trap number, species, sex, and reproductive status for each captured animal (Texas A&M University – Kingsville Institutional Animal Care and Use Committee protocol number 2008-09-16A). All individuals were released at the point of capture.

Estimation.—I quantified characteristics of small mammals at population and community scales for each plot during each sampling period; each scale provided a different perspective on the simple and interactive effects of fire and precipitation. At the population-level, I examined changes in presence, which I defined as capturing ≥1 individual of a species on a plot, and abundance by species. Presence indicated whether an area provided habitat for a given species, whereas abundance provided a potential indication of habitat quality. At the community-level, I examined changes in species richness.

I generated estimates of abundance and species richness to account for varying and imperfect detection probabilities and make more reliable inferences (Williams et al. 2002). I had sufficient captures to generate estimates of abundance for 6 species (*Chaetodipus hispidus*, *Onychomys leucogaster*, *Perognathus merriami*, *Peromyscus leucopus*, *Reithrodontomys fulvescens*, and *Sigmodon hispidus*). I generated model-averaged estimates of abundance using closed-capture Huggins models in program MARK (version 5.1, White and Burnham 1999). To improve model selection and abundance estimates, I aggregated data across years and treatments (Litt and Steidl 2010), allowed capture probability to vary by year, season, and treatment, and generated species-specific estimates of abundance for each plot during each sampling period. I generated estimates of species richness for each plot during each sampling period using the first-order jackknife estimator to account for varying detection probabilities among species (Burnham and Overton 1979).

Statistical Analyses.—I used generalized linear mixed models for all analyses and selected the appropriate distribution and link function for the response variable of interest. I examined continuous (cover classes, woody density, and heterogeneity of vegetation, abundance and richness of small mammals) and binary (presence of small mammal species) variables. To account for repeated sampling on research plots over time, I selected 1 of 4 possible covariance structures (compound symmetric, first-order autoregressive, first-order autoregressive moving average, and toeplitz) based on Akaike's information criterion values corrected for finite sample size (AIC_c) or -2 log-likelihood values (Littell et al. 2006). Continuous vegetation and small mammal variables were natural log-transformed to meet assumptions of homogeneity of variance.

I examined multiple explanatory variables to quantify the simple effects of fire intensity and precipitation, as well as interactive effects of fire intensity and precipitation, fire intensity and season, and timing of precipitation (growing or non-growing season, precipitation × season) on vegetation and small mammals (Table 3.1, pg. 69). To assess the effects of precipitation, I computed total rainfall for the 3 to 6 month window prior to each sampling period, as this is the typical response time of small mammal populations to precipitation (Ernest et al. 2000, Bradley 2006). As such, spring sampling was associated with precipitation during the previous non-growing season (September–December) and fall sampling was associated with precipitation during the previous growing season (April–July). To generate the best estimates of effects, I eliminated interaction terms if $P \geq 0.10$, but retained all single terms in the final model. To quantify differences in vegetation or small mammal characteristics based on fire intensity or season, I present least square means and confidence intervals in the text and tables. I express variation in presence as probabilities of occurrence. For all effects involving precipitation, I present back-transformed slope estimates and confidence intervals in the text to express the multiplicative percentage change in the response variable with every 1-cm increase in precipitation, and show predicted values in graphs. Where there were both fire × precipitation and precipitation × season interactions, I express the precipitation effect using fall as the reference.

RESULTS

General.—Drought occurred from September 2008–December 2009; Palmer Drought Severity Index (PDSI) ranged between 0 and -4 (NOAA 2011; Fig. 1, pg. 76). During this 16-month period, 53.9 cm of precipitation fell at the CWMA (monthly average ± *SD* = 3.37 ± 3.67 cm). In contrast, 61.5 cm of rain fell between January and October 2010 and average monthly rainfall nearly doubled (6.15 ± 5.51 cm). Rainfall began during the non-growing season and continued through the growing season with peaks in February, May, and July (Fig. 1, pg. 76). Total precipitation in the 3 to 6 month window prior to trapping was 7.2 cm for spring 2009, 12.3 cm for fall 2009, 31.6 cm for spring 2010, and 32.4 cm for fall 2010.

I captured 2,392 individual small mammals of 9 different species during 28,500 trap nights (Table 3.2, pg. 70). *P. merriami*, *S. hispidus*, *O. leucogaster,* and *C. hispidus* were the most abundant species and comprised 87% of all individuals captured (Table 3.2, pg. 70). I captured 455 unique individuals in spring 2009, 408 in fall 2009, 317 in spring 2010, and 1,212 in fall 2010. I was unable to examine changes in abundance of

Baiomys taylori, *Neotoma micropus*, or *Spermophilus mexicanus* due to very few captures, or changes in presence of *O. leucogaster* because this species was captured on every plot in every sampling period.

Fire Effects on Vegetation.—Eight of nine vegetation characteristics (total, nonnative grass, native grass, woody, and litter cover, heterogeneity, and density of shrubs <1-m and ≥1-m tall) differed with fire intensity (i.e., at least 1 term included fire intensity; Table 3.3, pg. 71); forb cover did not vary with fire intensity. Cacti cover was very low on all plots; as such, I did not examine fire-related differences. In general, unburned plots had higher litter, woody cover, and density of shrubs ≥1-m tall, low-intensity burned plots had greater native grass cover, and high-intensity burned plots had higher density of shrubs <1-m tall (Table 3.4, pg. 72). Nonnative grass cover was higher on high-intensity burned plots in the fall, but values were similar in the spring, regardless of fire intensity (Table 3.4, pg. 72; Appendix I, pg. 78). On high-intensity burned plots, density of shrubs <1-m tall decreased 0.3% (95% CI = 0.2 to 0.4) with every 1-cm increase in precipitation, whereas shrubs ≥1-m tall increased 0.2% (95% CI = 0.2 to 0.4) with precipitation, regardless of timing. I failed to detect effects of precipitation on density for either shrub class on unburned and low-intensity burned sites (Table 3.3, pg. 71). Vegetation cover was highest and least heterogeneous on unburned plots in spring (Table 3.4, pg. 72), but became more similar with increased time since fire (Appendix I, pg. 78). Vegetation cover increased with precipitation; increases in cover were greatest on burned plots (high-intensity = 1.8%, 95% CI = 1.4–2.3; low-intensity = 2.2%, 1.8–2.7; unburned = 0.8%, 0.3–1.3).

Fire Effects on Mammals.—Presence of 3 of 7 species of small mammals varied with fire intensity, and these differences were consistent regardless of precipitation (Table 3.5, pg. 73). *P. merriami* occurred on every burned plot and was slightly less likely to occur on unburned plots (probability of occurrence = 0.95, 95% CI = 0.63 to 1.00), *P. leucopus* was least likely to occur on high-intensity burned plots (high = 0.50, 0.23 to 0.77; low = 0.86, 0.53 to 0.97; unburned = 0.95, 0.59 to 1.00), and *S. hispidus* was most likely to occur on high-intensity burned plots (high = 0.83, 0.54 to 0. 95; low = 0.45, 0.21 to 0.72; unburned = 0.42, 0.19 to 0.69). Species richness averaged 5.9 species per plot (4.4 to 7.4) and varied little with fire intensity (Table 3.6, pg. 74).

Abundance of 5 of 6 species of small mammals varied with fire intensity; abundance of *O. leucogaster* did not vary with fire intensity (Table 3.6, pg. 74). The direction and magnitude of fire effects often differed with precipitation or by season (Table 3.6, pg. 74; Fig. 2, pg. 77). In general, *S. hispidus* was most abundant on high-intensity burned plots, *C. hispidus* on low-intensity burned plots, and *P. leucopus* on unburned plots; abundance generally was higher in fall (Table 3.7, pg. 75). Abundance of *P. merriami* increased on unburned plots with precipitation, whereas abundance on burned plots changed little with precipitation, regardless of intensity (high = 2.6%, 95% CI = -0.9 to 6.2; low = 3.4%, -0.2 to 7.0; unburned = 9.2%, 5.5 to 13.1; Fig. 2, pg. 77). Abundance of *S. hispidus* generally increased on burned and unburned plots with precipitation; the greatest increase in abundance occurred on high-intensity burned plots (high = 18.9%, 14.9 to 23.0%; low = 16.1%, 12.2 to 20.1; unburned = 13.2%, 9.4 to 17.1). *R. fulvescens* also had the greatest increase in abundance on high-intensity burned plots with precipitation (high = 9.8%, 6.5 to 13.1; low = 3.8%, 0.7 to 7.0; unburned = 4.7%, 1.6 to 7.9 with every 1-cm increase in precipitation; Fig. 2, pg. 77).

Precipitation Effects on Vegetation.—Precipitation or the timing of precipitation (i.e., precipitation × season) affected 8 of 9 vegetation characteristics (cover of native grasses, nonnative grasses, woody plants, litter, and forbs, heterogeneity, and <1-m and ≥1-m tall shrub density, Table 3.3, pg. 71). Native grass cover increased 5.2% (3.2 to 7.2) with each additional cm increase of precipitation during the growing season, whereas nonnative grass cover declined 2.8% (1.5 to 4.1) with precipitation in the non-growing season; cover of both grass types remained relatively unchanged with precipitation in the non-growing season (native: -2.3%, -5.4 to 0.1; nonnative: 0.8%, -0.8 to 2.5). Cover of forbs decreased 2.1% (0.4 to 3.2) with precipitation during the growing season, but increased 16.7% (14.9 to 18.3) with precipitation during the non-growing season. Woody cover increased and vegetation heterogeneity decreased with precipitation; woody cover increased more with growing season precipitation (spring = 0.4%, 0.1 to 0.7, fall = 1.0%, 0.7 to 1.3) and heterogeneity decreased more with non-growing season precipitation (spring = -3.2, -2.5 to -3.9, fall = -2.4, -1.6 to -3.1).

Precipitation Effects on Mammals.—I failed to detect variation in species richness of small mammals with precipitation (Table 3.6, pg. 74), however, presence of 4 of 7 species of small mammals did change (Table 3.5, pg. 73). Presence of *C. hispidus* increased 6.1% (95% CI = 0 to 12.7) and *P. merriami* increased 31.2% (6.6 to 61.4) with every 1-cm increase in precipitation, regardless of timing. Presence of *R. fulvescens* increased 18.8% (6.2 to 32.8) and *S. mexicanus* increased 6.7% (-2.2 to 16.2) with growing season precipitation, but changed little with precipitation during the non-growing season (*R. fulvescens*: -4.5%, -10.1 to 2.5; *S. mexicanus:* -5.1%, -14.4 to 5.2; Table 3.7, pg. 75).

Abundance of all 6 species of small mammals varied based on the timing of precipitation (i.e., precipitation × season interaction); abundance increased with precipitation during the growing season (Table 3.5, pg. 73). For each additional cm of rainfall during the growing season, abundance of *C. hispidus* increased 3.7% (95% CI = 1.7 to 5.8), *O. leucogaster* increased 3.4% (1.6 to 5.2), and *P. leucopus* increased 3.6% (1.0 to 6.2). With increased precipitation during the non-growing season, abundance remained relatively stable (*C. hispidus* -0.9%, -2.4 to 0.6; *Onychomys leucogaster* -0.6%, -2.5 to 0.9; *P. leucopus* -1.2%, -3.2 to 0.8). Abundance of *R. fulvescens*, *S. hispidus*, and *P. merriami* depended on fire intensity, precipitation, and season (Table 3.6, pg. 74).

DISCUSSION

Vegetation structural characteristics are important determinants of habitat for small mammals (Rosenzweig and Winakur 1969, Yarnell et al. 2007, Monamy and Fox 2010). As such, changes in vegetation structure resulting from fire and precipitation largely will dictate small mammal presence, abundance, and species richness. Fire and drought both can reduce vegetation cover and thus, may create similar effects for certain species of small mammals. Species that prefer areas with woody cover, such as *P. leucopus*, may respond negatively to reduced vegetation following fire (Fox et al. 2003, Briani et al. 2004, Schmidly 2004), but likely benefit from vegetation growth following increased precipitation; *P. leucopus* was most abundant on unburned plots and abundance increased with precipitation during the growing season. Species of small mammals that prefer more sparsely vegetated areas, such as species of pocket mice, may increase in presence or abundance in response to reduced vegetation cover from fire or drought (Ahlgren 1966, Rosenzweig 1973). *P. merriami* and *C. hispidus* typically occur in relatively open areas (Schmidly 2004); fire and drought may have reduced cover sufficiently, as abundance of both species were highest on burned plots. *S. hispidus* has somewhat different habitat requirements than the pocket mice, preferring a canopy of overhanging bunchgrasses (Schmidly 2004), and typically responds negatively to fire (Bock and Bock 1978, Kaufman et al. 1990). Increased abundance of *S. hispidus* on high-intensity burned plots could be due to increased nonnative grass cover, which can provide the overhanging canopy this species prefers (Guthery et al. 1979). Also, *S. hispidus* may have benefited from fire-caused tree death and associated increases in woody debris, which provides a quality nesting substrate (Loeb 1999). *O. leucogaster* did not vary in abundance with fire intensity; this species commonly occurs in both grassland and shrubland (Schmidly 2004), and as such, may tolerate a wide range of habitat conditions.

Fire may create a diverse mosaic of vegetation structural conditions across the landscape due to variation in fuel loads, weather conditions, and topography (Turner et al. 1994); in grasslands, high-intensity fires generally burn relatively evenly, whereas low-intensity fires tend to burn in patches. The resulting heterogeneity in vegetation structure provides a diverse range of conditions that can meet habitat requirements for a variety of small mammal species (Fox and Fox 2000, Carey and Wilson 2001) and potentially can lead to increased species richness after fire (Roberts et al. 2008). Twelve to nineteen months after the fire, vegetation structure was more heterogeneous on plots that burned at low intensity. Despite the initial difference in vegetation heterogeneity, species richness of small mammals remained relatively constant, regardless of fire intensity. Because species richness is a coarse measure of community-level changes, this lack of variation could reflect both increases and decreases in presence and abundance of some species of small mammals with fire or drought, or shifts in dominance because certain species were better able to compete for resources (Briani et al. 2004, Orland and Kelt 2007). Little variation in species richness with fire also could be a product of relatively low diversity in this small mammal community, as 4 species comprised 87% of individuals.

Diversity and abundance of food resources are also important determinants of habitat quality for small mammals. In addition to reducing woody cover, fire also likely reduced some food resources, such as fruits from trees and shrubs (Ahlgren 1966, Krefting and Ahlgren 1974, Fox et al. 2003, Roberts et al. 2008); both factors likely contributed to reduced abundance of *P. leucopus* on burned plots. Conversely, fire likely increased the variety and abundance of native grasses and other food resources that may benefit granivorous species of small mammals such as *C. hispidus* and *P. merriami* (Krefting and Ahlgren 1974, Bock and Bock 1978, Litt and Steidl 2011). In addition, reduced litter cover after fire may make movement and locating seeds easier, resulting in decreased foraging effort (Greenberg et al. 2006). Vegetation growth following fire also often results in increased abundance of arthropods (Potts et al. 2003), which in turn, could potentially increase abundance of insectivores, such as *O. leucogaster*. Food resources may have been readily available to *O. leucogaster* across the landscape, as I did not detect changes in abundance of this species with fire intensity. In addition, drought may have masked the effects of fire; drought conditions occurred for much of the 2-year period after the wildfire, resulting in reduced abundance of small mammals when fire effects would have been most evident.

Timing of precipitation is integral to determine recovery time of vegetation and small mammal communities; precipitation during the growing season will have a more significant effect on vegetation growth after fire than rainfall during the non-growing season (Cable 1975). Total cover, vegetation heterogeneity, and litter differed with fire intensity 1 year post-fire. Vegetation characteristics became more similar among treatments within 2 years after the fire, suggesting at least a partial recovery of vegetation despite the potential that drought extended the duration of fire effects (Frazer and Davis 1988). Forbs increased with non-growing season precipitation, likely due to the dominance of cool-season forbs, such as prickly poppy.

Effects of timing of rainfall on vegetation will in turn influence presence and abundance of small mammals (Ernest et al. 2000, Bradley et al. 2006). Vegetation will respond quickly to rainfall during the growing season, stimulating production of cover and food resources during periods of peak breeding activity. The rapid response of vegetation to growing season precipitation allows small mammals to reproduce and populations to recover more quickly from disturbances such as fire or drought than with non-growing season precipitation (Ernest et al. 2000, Bradley et al. 2006). For many of the species of small mammals I captured, presence and abundance increased with precipitation during the growing season, but remained relatively unchanged with precipitation during the non-growing season.

Increased abundance of certain species of small mammals following precipitation during the growing season may change composition and competitive dynamics in the small mammal community and could even result in reduced species richness (Orland and Kelt 2007). Dominant species can increase in abundance with increased food resources following precipitation, and can out-compete other species resulting in reduced species richness. Precipitation was 31.6 cm in the 3 to 6-month window prior to sampling in spring 2010; during this sampling period, I captured only 317 individuals. Precipitation increased little in the 3 to 6-month window prior to sampling in fall 2010 (32.4 cm), but I captured 1,212 individuals – nearly a 4-fold increase. *Sigmodon hispidus* contributed greatly to this increase in abundance; *S. hispidus* comprised only 2% of the individuals captured in spring 2010, but 38% in fall 2010. Abundance of *S. hispidus* increased most on high-intensity burned plots, where species richness was lower, which may indicate that this species was able to out-compete other species for resources on high-intensity burned plots. Understanding what factors structure interspecific competitive relationships may be important if a threatened or endangered species is present, as an increase in a numerically and/or socially dominant species could deplete resources, leading to decreased abundance of other species.

Fire and precipitation may interact, resulting in changes in the magnitude and persistence of fire effects on vegetation and small mammals (Yarnell et al. 2007). Insufficient precipitation can reduce primary productivity and extend the persistence of fire effects (Frazer and Davis 1988), whereas ample rainfall can stimulate vegetation growth and promote a quick recovery of both vegetation and small mammal communities (Yarnell et al. 2007). Precipitation increased vegetation cover overall, but increases were greatest on burned plots, as vegetation growth may have been stimulated by fire and reduced litter, and further promoted by increased precipitation. Abundance of *R.*

fulvescens and *S. hispidus* also increased with growing season precipitation regardless of fire intensity, with the greatest increases on high-intensity burned plots, likely due to the increase in food resources.

Although the simple effects of fire and drought have been relatively well-studied for a diversity of organisms (Cook 1959, Letnic et al. 2005, Bradley et al. 2006, Litt and Steidl 2011), compounded disturbances create novel conditions for flora and fauna, as effects are often multiplicative and hard to predict, especially over the long-term (Paine et al. 1998, Litt and Steidl 2011). Understanding how multiple factors alter population structure and community composition will be especially important given predicted changes in global climate patterns, such as change in timing and amount of rainfall (Christensen and Christensen 2003) and severity and duration of drought (Aigu Dai and Trenberth 2004), as well as concomitant changes in distributions of nonnative species, disturbance regimes, and land-use patterns. Compounded, interactive disturbances create unique challenges for management, conservation, and research; however, the need to make decisions in the face of uncertainty is likely to be increasingly common (Paine et al. 1998). Exploring complex interactions between disturbances and environmental conditions could improve our ability to predict outcomes and ensure conservation of diversity and ecosystem function.

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TABLE 3.1—Model terms and descriptions for analyses on effects of fire and precipitation on vegetation and small mammals, 2009-2010, Chaparral WMA, Texas, USA.

Model term	Effect
Fire	Fire intensity (high, low, or unburned)
Season	Spring and fall
Precipitation	Precipitation during 3-6 month window prior to sampling
Fire × season	Fire intensity effects differ by season
Fire × precipitation	Fire intensity effects differ based on precipitation
Season × precipitation	Precipitation effects differ by season

TABLE 3.2—Species of small mammals and percent of 2,392 total individuals captured during 28,500 trap nights, 2009-2010, Chaparral WMA, Texas, USA.

Scientific name	Common name	% of total individuals
Baiomys taylori	Northern pygmy mouse	0.08
Chaetodipus hispidus	Hispid pocket mouse	15.06
Neotoma micropus	Southern plains woodrat	0.25
Onychomys leucogaster	Northern grasshopper mouse	15.31
Perognathus merriami	Merriam's pocket mouse	32.87
Peromyscus leucopus	White-footed mouse	9.16
Reithrodontomys fulvescens	Fulvous harvest mouse	2.84
Sigmodon hispidus	Hispid cotton rat	23.76
Spermophilus mexicanus	Mexican ground squirrel	0.67

TABLE 3.3—Factors affecting vegetation cover classes, heterogeneity, and woody density based on generalized linear mixed models, 2009-2010, Chaparral WMA, Texas, USA. I removed interactions from models when *P* > 0.10.

	Fire		Season		Precipitation		Fire × season		Fire × precipitation		Precipitation × season	
	F	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Total cover	17.78	0.0003	4.06	0.0505	149.41	<0.0001	2.62	0.0856	10.03	0.0003		
Nonnative grasses	0.40	0.6803	3.81	0.0747	2.71	0.1075	7.27	0.0086			18.99	<0.0001
Native grasses	10.37	0.0024	12.94	0.0008	8.45	0.0058					35.68	<0.0001
Woody plants	8.89	0.0043	0.10	0.7548	9.43	0.0037					9.80	0.0032
Litter	8.56	0.0049	46.54	<0.0001	21.89	<0.0001	2.96	0.0640	4.74	0.0066	45.85	<0.0001
Forbs	1.10	0.3639	191.70	<0.0001	460.67	<0.0001					241.08	<0.0001
Heterogeneity	4.38	0.0373	1.24	0.2719	94.62	<0.0001	5.45	0.0080			3.12	0.0848
Shrub density, <1 m	15.88	0.0004	0.66	0.4314	41.59	<0.0001	11.03	0.0019	10.79	0.0002	4.45	0.0415
Shrub density, ≥1 m	10.48	0.0023	2.81	0.1193	9.75	0.0034	12.10	0.0013	7.61	0.0016		

TABLE 3.4—Least square means (above) and 95% confidence intervals (below) for vegetation variables (% cover by category, heterogeneity, and woody density) affected by fire intensity, based on generalized linear mixed models, 2009-2010, Chaparral WMA, Texas, USA. When I detected a fire intensity × season interaction, I provide means for each season separately.

	Season	Unburned	Low-intensity	High-intensity
Total cover	Spring	74.03	61.56	66.52
		69.12 to 78.94	56.65 to 66.47	61.60 to 71.43
	Fall	64.52	57.39	66.65
		59.61 to 69.43	52.48 to 62.30	61.74 to 71.57
Nonnative grasses	Spring	6.87	5.45	6.48
		2.14 to 11.59	0.73 to 10.18	1.76 to 11.20
	Fall	6.96	7.62	14.94
		2.24 to 11.69	2.90 to 12.35	10.22 to 19.67
Native grasses		4.14	14.86	10.38
		0.29 to 7.99	11.01 to 18.70	6.53 to 14.23
Woody plants		25.71	14.81	18.10
		21.75 to 29.66	10.86 to 18.76	14.14 to 22.05
Litter	Spring	18.45	6.79	10.73
		15.00 to 21.91	3.34 to 10.24	7.28 to 14.18
	Fall	17.41	5.51	6.50
		13.96 to 20.86	2.06 to 8.97	3.05 to 9.96
Heterogeneity	Spring	18.47	27.75	25.13
		13.41 to 23.54	22.70 to 32.82	20.07 to 30.19
	Fall	30.48	34.72	26.95
		25.42 to 34.55	29.65 to 39.79	21.88 to 32.02
Shrub density,	Spring	0.07	0.07	0.17
<1 m		0.03 to 0.11	0.03 to 0.11	0.13 to 0.22
	Fall	0.08	0.06	0.14
		0.04 to 0.12	0.02 to 0.10	0.10 to 0.18
Shrub density,	Spring	0.11	0.05	0.06
≥1 m		0.08 to 0.13	0.03 to 0.07	0.04 to 0.09
	Fall	0.10	0.05	0.08
		0.08 to 0.13	0.03 to 0.07	0.06 to 0.10

TABLE 3.5—Factors affecting presence of small mammal species based on generalized linear mixed models, 2009-2010, Chaparral WMA, Texas, USA. I removed interactions from models when $P > 0.10$. I did not detect any fire × season or fire × precipitation interactions.

	Fire		Season		Precipitation		Precipitation × season	
	F	*P*	*F*	*P*	*F*	*P*	*F*	*P*
C. hispidus	2.46	0.1276	1.46	0.2467	3.91	0.0545		
N. micropus	0.48	0.6318	0.10	0.7583	2.00	0.1644		
P. merriami	5.30	0.0225	2.98	0.1063	6.98	0.0115		
P. leucopus	3.51	0.0632	1.25	0.2821	0.00	0.9540		
R. fulvescens	0.63	0.5484	14.22	0.0005	9.63	0.0034	14.54	0.0004
S. hispidus	3.05	0.0851	4.33	0.0562	1.42	0.2391		
S. mexicanus	0.68	0.5251	0.65	0.4243	2.30	0.1370	3.08	0.0868

TABLE 3.6—Factors affecting abundance and species richness of small mammals based on generalized linear mixed models, 2009-2010, Chaparral WMA, Texas, USA. I removed interactions from models when $P > 0.10$.

	Fire		Season		Precipitation		Fire × season		Fire × precipitation		Precipitation × season	
	F	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Species richness	0.21	0.8096	5.87	0.0295	0.29	0.5928						
C. hispidus	1.42	0.2795	0.13	0.7281	4.26	0.0456	3.11	0.0818			14.44	0.0005
O. leucogaster	0.04	0.9642	1.86	0.1938	5.09	0.0293					13.88	0.0006
P. leucopus	15.52	0.0005	0.60	0.4440	0.69	0.4117			5.89	0.0057	5.77	0.0211
P. merriami	7.97	0.0063	11.53	0.0053	2.06	0.1586	4.21	0.0413			8.94	0.0048
R. fulvescens	2.51	0.1226	23.89	<0.0001	1.45	0.2352			6.13	0.0048	23.50	<0.0001
S. hispidus	0.18	0.8375	115.10	<0.0001	26.71	<0.0001	3.97	0.0470	2.87	0.0689	216.63	<0.0001

TABLE 3.7—Least square means (above) and 95% confidence intervals (below) for abundance of small mammal species by fire intensity and sampling period, based on generalized linear mixed models, 2009-2010, Chaparral WMA, Texas, USA.

	Season	Unburned	Low-intensity	High-intensity
C. hispidus	Spring	2.66	5.43	3.31
		-0.24 to 5.56	2.53 to 8.33	0.41 to 6.21
	Fall	12.62	12.99	10.33
		9.73 to 15.54	10.09 to 15.90	7.42 to 13.23
P. leucopus	Spring	10.46	3.38	3.19
		7.50 to 13.43	0.41 to 6.34	0.22 to 6.14
	Fall	7.38	5.24	0.96
		4.42 to 10.35	2.28 to 8.21	-2.00 to 3.93
S. hispidus	Spring	3.19	2.53	6.71
		-9.73 to 16.12	-10.40 to 15.45	-6.21 to 19.64
	Fall	4.93	20.25	49.99
		-8.02 to 17.88	7.30 to 33.20	37.03 to 62.94

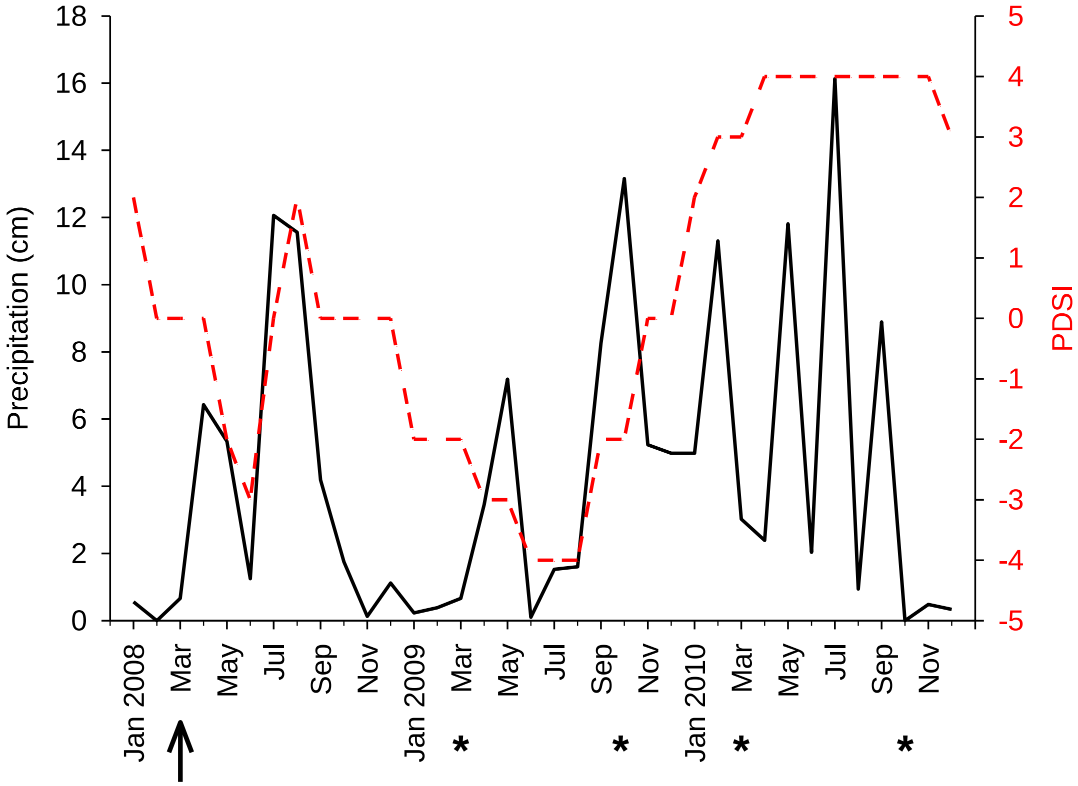

FIG. 1.—Total monthly rainfall (left axis, solid black) and Palmer Drought Severity Index (PDSI, right axis, dashed red), 2008-2010, CWMA, Texas, USA. The wildfire occurred in March 2008 (arrow); sampling occurred in March and October 2009 and 2010 (asterisks).

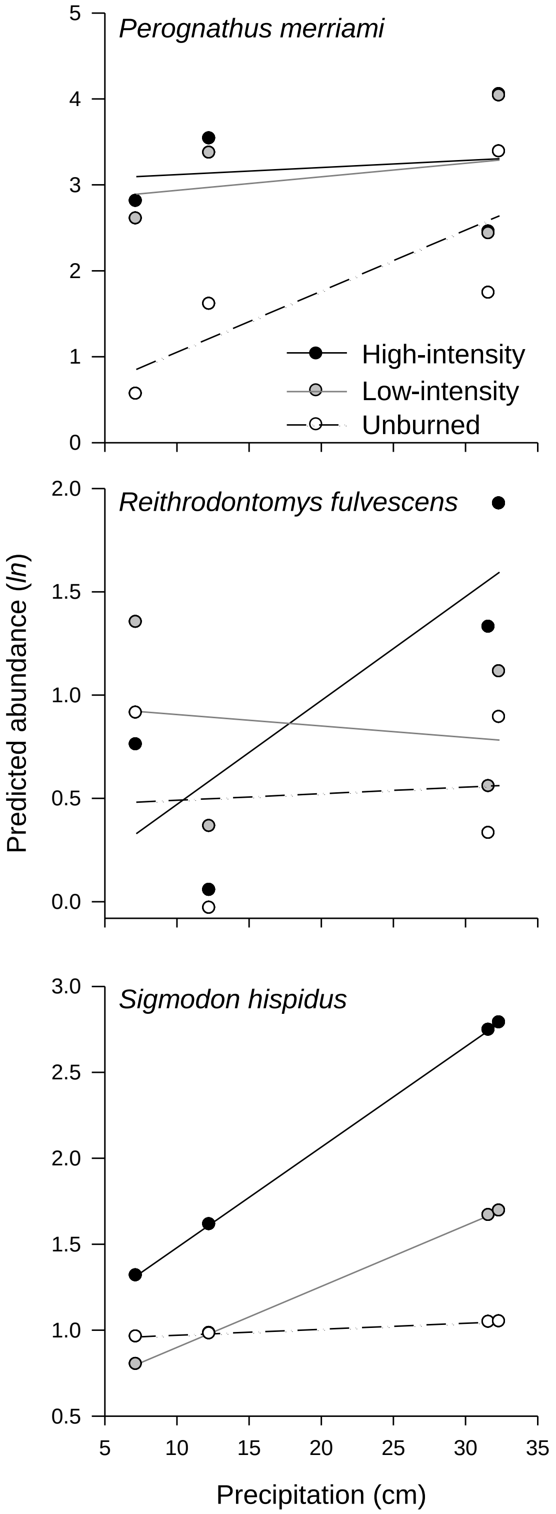

FIG. 2.—Changes in the effects of fire intensity on abundance of small mammals with varying precipitation (fire × precipitation), 2009–2010, CWMA, Texas, USA.

APPENDIX I.—Means (above) and 95% confidence intervals (below) for vegetation characteristics (% cover by category, heterogeneity, and live woody stems/m^2) by fire intensity and sampling period, 2009-2010, Chaparral WMA, Texas, USA.

	Season	Unburned	Low	High
Total cover	Spring 2009	67.4	43.0	49.7
		63.0 to 71.8	33.5 to 52.5	39.2 to 60.3
	Fall	57.7	47.7	57.5
		50.1 to 65.3	39.1 to 56.3	46.6 to 68.3
	Spring 2010	78.9	76.4	79.9
		75.8 to 82.1	71.3 to 81.5	74.9 to 84.8
	Fall	73.1	70.8	79.2
		59.8 to 86.3	62.3 to 79.2	75.8 to 82.7
Nonnative grasses	Spring 2009	10.7	7.1	8.7
		3.4 to 18.0	4.1 to 10.1	1.2 to 16.2
	Fall	7.5	6.1	14.4
		2.3 to 12.6	2.2 to 10.1	-1.8 to 30.5
	Spring 2010	4.2	3.8	4.8
		0.2 to 8.2	1.2 to 6.4	-0.8 to 10.4
	Fall	6.2	9.5	15.9
		0.9 to 11.6	3.3 to 15.7	4.2 to 27.6
Native grasses	Spring 2009	3.4	15.1	8.2
		-1.9 to 8.6	8.6 to 21.6	2.0 to 14.4
	Fall	2.3	11.0	6.4
		-1.0 to 5.5	5.1 to 16.9	1.0 to 11.8
	Spring 2010	0.7	9.2	4.7
		-0.1 to 1.4	4.7 to 13.6	0.2 to 9.3
	Fall	10.3	24.2	22.2
		-2.2 to 22.8	13.2 to 35.1	3.3 to 41.1
Woody cover	Spring 2009	21.9	12.6	16.0
		17.3 to 26.6	9.7 to 15.6	10.1 to 21.9
	Fall	24.7	14.5	17.6
		21.9 to 27.4	10.9 to 18.0	10.6 to 24.6
	Spring 2010	25.9	13.9	17.2
		19.2 to 32.6	9.1 to 18.8	9.6 to 24.9
	Fall	30.3	18.2	21.5
		24.8 to 35.8	14.8 to 21.7	14.8 to 28.2
Litter	Spring 2009	29.9	7.4	16.8
		25.9 to 33.9	5.2 to 9.6	12.0 to 21.6
	Fall	15.7	2.9	2.5
		10.1 to 21.3	2.3 to 3.5	0.5 to 4.5
	Spring 2010	8.5	7.7	5.5
		1.6 to 15.5	1.9 to 13.8	0.6 to 10.4

	Fall	18.5	10.9	11.2
		8.8 to 28.1	4.3 to 17.5	5.9 to 16.5
Forb	Spring 2009	0	0	0
	Fall	6.5	12.7	16.5
		2.2 to 10.9	1.9 to 23.6	6.8 to 26.2
	Spring 2010	38.7	41.2	47.5
		26.2 to 51.3	27.9 to 54.6	40.5 to 54.5
	Fall	7.0	7.3	8.4
		0 to 13.9	-0.6 to 15.3	-1.3 to 18.1
Bare ground	Spring 2009	32.6	57.0	50.3
		28.2 to 37.0	47.5 to 66.5	39.7 to 60.8
	Fall	42.3	52.3	42.5
		34.7 to 49.9	43.7 to 60.9	31.7 to 53.4
	Spring 2010	21.1	23.6	20.1
		17.9 to 24.2	18.5 to 28.7	15.2 to 25.1
	Fall	27.0	29.2	20.8
		13.7 to 40.2	20.8 to 37.7	17.3 to 24.2
Heterogeneity	Spring 2009	25.5	42.5	37.0
		20.1 to 30.8	29.0 to 55.9	26.7 to 47.3
	Fall	35.0	41.7	33.6
		25.3 to 44.6	27.8 to 55.5	25.8 to 41.4
	Spring 2010	13.5	15.6	15.8
		8.4 to 18.7	11.2 to 20.0	10.8 to 20.8
	Fall	24.8	25.0	18.1
		16.9 to 32.6	15.9 to 34.1	13.2 to 23.0
Shrub density, <1 m tall	Spring 2009	0.08	0.08	0.25
		0.04 to 0.12	0.06 to 0.10	0.16 to 0.34
	Fall	0.10	0.09	0.19
		0.06 to 0.14	0.06 to 0.11	0.14 to 0.24
	Spring 2010	0.07	0.07	0.14
		0.02 to 0.12	0.05 to 0.10	0.10 to 0.18
	Fall	0.07	0.05	0.10
		0.02 to 0.12	0.03 to 0.06	0.06 to 0.14
Shrub density, ≥1 m tall	Spring 2009	0.14	0.06	0.06
		0.11 to 0.16	0.05 to 0.07	0.04 to 0.08
	Fall	0.12	0.05	0.09
		0.10 to 0.15	0.04 to 0.06	0.06 to 0.11
	Spring 2010	0.10	0.04	0.08
		0.07 to 0.14	0.03 to 0.04	0.04 to 0.11
	Fall	0.09	0.04	0.09
		0.05 to 0.13	0.04 to 0.05	0.05 to 0.13

APPENDIX II.—Means (above) and 95% confidence intervals (below) for species abundance and richness by fire intensity and sampling period, 2009-2010, Chaparral WMA, Texas, USA.

	Season	Unburned	Low	High
Species richness	Spring 2009	5.8	5.6	4.8
		3.3 to 8.3	3.0 to 8.2	3.2 to 6.4
	Fall	5.6	6.4	6.4
		3.3 to 7.9	5.3 to 7.5	3.8 to 9.0
	Spring 2010	4.6	5.2	6.0
		2.3 to 6.9	3.2 to 7.2	5.1 to 6.9
	Fall	7.4	7.0	5.8
		6.7 to 8.1	5.5 to 8.5	4.8 to 6.8
C. hispidus	Spring 2009	3.0	7.3	4.0
		-0.9 to 7.0	4.3 to 10.3	0.6 to 7.3
	Fall	7.8	6.4	9.8
		4.1 to 11.6	2.4 to 10.3	3.4 to 16.2
	Spring 2010	2.4	3.3	3.5
		0.6 to 4.1	1.4 to 5.2	0.8 to 6.2
	Fall	18.9	20.7	12.4
		11.4 to 26.3	13.6 to 27.9	6.4 to 18.4
O. leucogaster	Spring 2009	7.0	5.8	9.2
		2.4 to 11.6	1.9 to 9.7	4.4 to 14.0
	Fall	8.8	8.0	8.8
		2.1 to 15.6	3.7 to 12.3	1.6 to 16.1
	Spring 2010	4.6	5.6	7.2
		1.1 to 8.2	3.9 to 7.4	1.4 to 13.0
	Fall	18.5	19.3	15.1
		13.5 to 23.5	1.7 to 36.7	2.0 to 28.2
P. merriami	Spring 2009	0.4	18.3	28.2
		-0.8 to 1.6	-4.8 to 41.5	7.2 to 49.1
	Fall	11.0	31.0	30.2
		-2.7 to 24.6	13.8 to 48.3	-0.6 to 61.1
	Spring 2010	5.3	13.8	13.3
		0.6 to 9.9	0.9 to 26.6	1.2 to 25.5
	Fall	34.7	66.6	61.0
		-0.2 to 69.6	14.5 to 118.8	40.6 to 81.5
P. leucopus	Spring 2009	14.3	3.3	3.5
		7.1 to 21.4	0 to 6.6	0.5 to 6.6
	Fall	4.3	2.3	0.7
		1.5 to 7.0	0 to 4.6	-1.2 to 2.5
	Spring 2010	7.0	3.7	3.1
		-0.2 to 14.2	0.5 to 6.9	0.2 to 6.0

	Fall	11.2	9.0	2.0
		2.8 to 19.6	6.2 to 11.6	-3.5 to 7.5
R. fulvescens	Spring 2009	1.5	3.8	1.9
		-0.5 to 3.5	0.9 to 6.7	-1.0 to 4.8
	Fall	0.3	0.3	0
		-0.6 to 1.2	-0.6 to 1.2	
	Spring 2010	0.4	2.5	3.6
		-0.6 to 1.4	-2.4 to 7.4	-0.9 to 8.1
	Fall	2.1	2.5	7.5
		-0.3 to 4.4	-0.9 to 5.8	1.9 to 13.1
S. hispidus	Spring 2009	7.9	5.9	9.3
		-0.6 to 16.4	-0.1 to 11.8	-3.2 to 21.8
	Fall	0.3	0.9	2.9
		-0.6 to 1.2	-0.8 to 2.7	0.3 to 5.5
	Spring 2010	0	0	4.0
				-1.9 to 10.0
	Fall	13.4	46.7	110.2
		3.3 to 23.6	10.4 to 82.9	63.1 to 157.3

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