EFFECTS OF DESERT WILDFIRES ON DESERT TORTOISE (*GOPHERUS AGASSIZII*) AND OTHER SMALL VERTEBRATES

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ABSTRACT—We report the results of standardized surveys to determine the effects of wildfires on desert tortoises (*Gopherus agassizii*) and their habitats in the northeastern Mojave Desert and northeastern Sonoran Desert. Portions of 6 burned areas (118 to 1,750 ha) were examined for signs of mortality of vertebrates. Direct effects of fire in desert habitats included animal mortality and loss of vegetation cover. A range of 0 to 7 tortoises was encountered during surveys, and live tortoises were found on all transects. In addition to desert tortoises, only small (<1 kg) mammals and reptiles (11 taxa) were found dead on the study areas. We hypothesize that indirect effects of fire on desert habitats might result in changes in the composition of diets and loss of vegetation cover, resulting in an increase in predation and loss of protection from temperature extremes. These changes in habitat also might cause changes in vertebrate communities in burned areas.

RESUMEN—Reportamos los resultados de muestreos uniformes para determinar los efectos de incendios del monte en las tortugas del desierto (*Gopherus agassizii*) y sus hábitats en el noreste del Desierto Mojave y noreste del Desierto Sonorense. Porciones de 6 áreas quemadas (de 118 a 1,750 ha) fueron inspeccionadas por signos de mortandad de vertebrados. Efectos directos del fuego en hábitats del desierto incluyeron mortalidad animal y pérdida de cobertura vegetal. Un rango de 0 a 7 tortugas muertas fue encontrado durante los muestreos y se encontraron tortugas vivas en todos los transectos. Además de tortugas del desierto, solamente mamíferos pequeños (<1 kg) y reptiles (11 taxa) se encontraron muertos en las áreas quemadas. Proponemos que los efectos indirectos del fuego en hábitats del desierto pueden resultar en cambios en la composición de la dieta de habitantes y pérdida de la cobertura vegetal, resultando en un aumento de depredadores y la pérdida de protección contra temperaturas extremas. Estos cambios en hábitat también pueden causar cambios en las comunidades de vertebrados en las áreas quemadas.

The invasion of alien grasses (Búrquez and Quintana, 1994; Brooks, 1998; Esque and Schwalbe, 2002), in conjunction with high winter precipitation from 1991 through 1993 (National Oceanic and Atmospheric Administration, 1998), resulted in abundant fine fuel loads sufficient to carry fire in desert vegetation types that are not adapted to high fire frequency (McLaughlin and Bowers, 1982; Billings, 1990; McAuliffe, 1995; Van Devender et al., 1997; Esque and Schwalbe, 2002). Prior to the spread of alien grasses, fires occurring in desertscrub vegetation burned in a mosaic pattern with the natural patchy distribution of plants and open space, and fires soon burned out for lack of fuel (McLaughlin and Bowers, 1982). Dry lightning storms in May through early July are the natural ignition source, but human population growth in the southwestern United States has provided additional ignition sources (Swetnam and Baisan, 1996; Swantek et al., 1999). As a result, the combined effects of population growth and the introduction of alien grasses have increased fire frequencies in deserts (Rogers, 1986; Schmid and Rogers, 1988; Brooks, 1998).

TABLE 1—Post-fire (burned) areas surveyed for wildlife casualties from 1987 through 1993. Rock Peak and Skyline fires occurred in Santan Mountains, Pinal County; Pusch Ridge fire was on southern slopes of Santa Catalina Mountains, Pima County; and Mother's Day fire was on eastern slope of Rincon Mountains, Saguaro National Park, Pima County. Mill Creek fire was 2 km NE of St. George, Washington County; Bulldog fire was on western slope of Beaver Dam Mountains.

Name of fire	Date of fire	Date of survey	Area burned (ha)	Area surveyed (ha)	Hours surveyed
Sonoran Desert, Arizona					
Pusch Ridge	20 September 1987	20 September 1987	1,750	15	41
Skyline	6 June 1992	18 June 1992	202	40	24
Rock Peak	20 April 1993	27 April 1993	118	35	8
Mother's Day	10 May 1994	17 June 1994	340	340	132
Mojave Desert, Utah					
Mill Creek	20 June 1993	20 June 1993	895	41	46
Bulldog	2 August 1993	4 August 1993	1,079	23	11

Fire effects on small animals can be highly variable, leading some to conclude that such disturbances are of little concern (Ford et al., 1999), while others conclude that, under certain circumstances, fires can be important to small animal populations (Simons, 1989; Simons, 1991). These discrepancies should be considered in light of variable fire conditions and specific responses of plants and animals (Lyon et al., 2000). Fires have direct and indirect effects on wildlife populations (Lyon et al., 1978; Wright and Bailey, 1982; Huff and Kapler Smith, 2000; Lyon et al., 2000). Animal mortalities are caused directly by contact with flames, exposure to lethal high temperatures (Smith et al., 2001), and smoke inhalation (Howard et al., 1959). Indirect effects of fire include habitat changes, such as altered nutrient availability and quality, loss of cover from predators, and loss of thermal refugia (Lyon et al., 1978; Whysong and Heisler, 1978; Price and Wasser, 1984; Mushinsky and Gibson, 1991; Friend, 1993; Sutherland and Dickman, 1999), and might result in faunal community shifts (changes in relative abundances or species additions and deletions) or changes in behavior (Smith et al., 2001).

Casualty counts can be used to quantify mortality of small terrestrial vertebrates after wildfires (Chew et al., 1959; Bigham et al., 1964; Simons, 1989). Wildlife mortality due to fire has been reported for a number of terrestrial habitat types in North America, including forest (Kipp, 1931; Cook, 1959; Simon et al., 1998), prairie (Erwin and Stasiak, 1979; Scott, 1996), woodland (Howard et al., 1959; Bigham et al., 1964; Smith et al., 2001) and chaparral (Chew et al., 1959; Lawrence, 1966; Schwilk and Keeley, 1998), but we are aware of only 1 such paper for desertscrub (Simons, 1989) and 1 previous anecdote of desert tortoise mortality due to fire (Woodbury and Hardy, 1948); however, widespread fires are new to desertscrub habitats (Humphrey, 1974). In this paper we provide additional results of surveys designed to detect wildlife mortality associated with desert fires, emphasizing effects on the desert tortoise (*Gopherus agassizii*), and we speculate on the indirect effects of fire that could change habitats and influence animal communities in the Sonoran and Mojave deserts.

We systematically searched for fire-killed or injured desert tortoises, post-fire tortoise activity, and other wildlife mortality on 6 sites burned by wildfires. Four of the burned areas were in the Arizona Upland Subdivision of the northeastern Sonoran Desert of Arizona (Turner and Brown, 1982): the Rock Peak and Skyline fires in the Santan Mountains of Pinal County, the Pusch Ridge fire on the southern slopes of the Santa Catalina Mountains, Pima County, and the Mother's Day fire on the eastern flank of the Rincon Mountains in Saguaro National Park, Pima County. The 2 burned areas surveyed in the northeastern Mojave Desert (Turner, 1982) of Washington County, Utah were the Mill Creek and Bulldog fires. The 6 burned areas ranged in size from 118 to 1,750 ha (Table 1).

Individual observers walked on 10-m wide belt transects and were spaced consecutively, walking at the same rate to provide 100% coverage (Table 1). Transects were established 1 to 60 days after fires. Between 15 and 340 ha were surveyed on the burned sites. Wildlife mortalities were examined to determine cause of death. For example, carcasses still bearing bodily fluids, yet charred by fire, were assumed to be indicative of an animal that sustained lethal injuries during the fire.

In the arid Southwest, precipitation fell in excess of long-term averages due to the El Niño cycle of 1992–1994. Average winter precipitation between 1948 and 1995 at Sky Harbor Airport, Phoenix, Arizona (near Rock Peak and Santan fires) was 109.9 mm (9.3 *SE*). From 1992 through 1994, winter precipitation was 323.1, 127.3, and 182.4 mm, respectively, with a mean of 211.1 mm, which is >10 *SE* above the long-term mean (National Oceanographic and Atmospheric Administration, 1998). At Tucson, Arizona (Mother's Day Fires), the long-term average is 125.6 mm (9.0 *SE*) for 1931 through 1997, and winter precipitation values for 1992 through 1994 were 319.0, 115.1, and 217.2 mm, respectively. Similar climate trends were observed at the St. George, Utah (Mill Creek Fire) and Littlefield, Arizona (Bulldog Fire) sites in the Mojave Desert, but incomplete data sets were reported from National Oceanographic and Atmospheric Administration (1998) field stations. Above average precipitation appears to have greatly increased annual plant production and buildup of fine fuels, particularly alien annual grasses (pers. observ.), such as red brome (*Bromus madritensis* = *B. rubens*). Fires at the Mojave Desert sites not only destroyed plant tissues to ground level but also root crowns in some cases. Flame lengths during the Mojave Desert fires exceeded 3 m when *Yucca brevifolia* was burning, indicating high fire intensity.

Desert tortoise carcasses were found in the open, under thick vegetation, or in shallow shelter sites. Zero to 7 dead tortoises were found on transects in burned areas (Table 2). Signs of activity on transects suggested that more tortoises survived the fires than were located during our surveys. The Pusch Ridge Fire had the greatest density of tortoise mortalities per hectare (Table 1). However, due to the patchy distribution of desert tortoise populations, caution should be used when extrapolating these results to larger areas. The Pusch Ridge Fire was also the only fire to occur in the fall (September), coinciding with the period of greatest tortoise activity in Sonoran Desert populations (Vaughan, 1984; Germano et al., 1994; Martin, 1995).

At the Rock Peak Fire, 1 dead adult tortoise was found in the open and was severely charred on the posterior. This tortoise was 1 m from a cover site and was thought to have been forced from the cover site into the flames (T. J. Hughes, pers. observ.). A second recently killed, juvenile tortoise was found in a cave shelter site and was being consumed by ants. After the Bulldog Fire, a dead tortoise was found under a charred creosote bush. Four of the 5 tortoise carcasses found in the Pusch Ridge Fire were in the open, while the fifth was found under a shallow rock overhang. All of the carcasses found after the Mother's Day Fire were either in the open or in a location where vegetation had been entirely incinerated.

Fifteen live tortoises were seen at the 6 study sites (Table 2). Other signs of post-burn activity by tortoises included fresh digging, feces, and tracks, indicating that there were living tortoises other than those observed along transects. However, in most cases surveys were not conducted on these plots to determine relative or total densities. After the Mother's Day Fire adult population density was estimated at 45 tortoises per km^2 (14 to 115 95% CI, 25 adult tortoises actually registered; E. Wirt and P. Holm, pers. comm.). Extrapolating from the 1995 population survey, we estimate that approximately 11% of this adult population in the area of the fire died.

Other wildlife mortalities we observed included 3 mammal species, 5 lizard species, and 2 snake species (Table 2). Aside from tortoises, only small animals (<1 kg body mass) were found dead on the surveys. Additionally, live small animals were found on burned areas during surveys (Table 2). The only large animals seen on the burned areas were javelinas (*Dicotyles tajacu*), which are not present at the Mojave Desert sites. Birds and larger mammals probably were not found due to their greater vagility and ability to escape the fires.

Size and intensity of fire will influence effects on animals. Likewise, topography and micro sites that trap animals or provide protection from fire and predators (Whelan, 1995)

TABLE 2—Results of post-fire wildlife surveys on burned areas in Sonoran and Mojave deserts of Arizona and Utah. Numbers represent live/dead individuals. When abundance was not quantified, + denotes common species and ++ denotes greater abundance. Asterisk (*) denotes number of carcasses attributed directly to fire. Rock Peak and Skyline fires occurred in Santan Mountains, Pinal County; Pusch Ridge fire was on southern slopes of Santa Catalina Mountains, Pima County; and Mother's Day fire was on eastern slope of Rincon Mountains, Saguaro National Park, Pima County. Mill Creek fire was 2 km NE of St. George, Washington County; Bulldog fire was on western slope of Beaver Dam Mountains.

	Sonoran Desert				Mojave Desert	
	Rock Peak	Skyline	Pusch Ridge	Mother's Day	Bulldog	Mill Creek
Reptilia						
Callisaurus draconoides	0/0	0/0	0/0	0/0	0/0	1/0
Cnemidophorous	+/0	+/0	0/0	46/0	1/0	16/3
Crotalus atrox	1/0	0/0	0/0	0/0	0/0	0/0
Crotalus molossus	1/0	0/0	0/0	4/0	0/0	0/0
Crotalus tigris	1/1	0/0	0/1	3/0	0/0	0/0
Crotalus viridis	0/0	0/0	0/0	0/0	0/0	2/0
Crotophytus collaris	0/0	0/0	0/0	3/0	0/0	0/0
Gambelia wislizenii	0/0	0/0	0/0	3/0	0/0	8/0
Gopherus agassizii	1/2	1/0	1/7	6/7 [5*]	1/1	5/0
Heloderma suspectum	0/0	0/0	0/0	2/0	0/0	0/0
Phrynosoma platyrhinos	0/0	0/0	0/0	1/0	0/0	8/1
Pituophis melanoleucus	0/0	0/0	0/1	2/0	0/0	0/0
Sauromalus obesus	0/1	1/0	0/0	0/0	0/0	0/0
Sceloporus	0/0	0/0	0/0	3/0	0/0	1/3
Uta stansburiana	++/0	+/0	0/0	4/0	0/0	22/3
Mammalia						
Ammospermophilus leucurus	5/0	1/0	0/0	4/0	2/0	3/0
Dicotyles tajacu	12/0	6/0	0/0	1/0	0/0	0/0
Dipodomys	0/0	0/0	0/0	0/0	1/0	0/0
Lepus californicus	0/0	0/0	0/1	0/0	0/0	3/0
Neotoma	0/0	0/0	0/1	0/0	0/0	3/0
Perognathus	0/0	0/0	0/0	0/0	0/0	1/2
Spermophilus variegatus	1/0	0/0	0/0	0/0	0/0	0/0
Sylvilagus auduboni	10/0	0/0	0/0	35/0	3/0	0/0

might influence survival rates. Our results were consistent with other casualty counts, indicating that direct mortality of wildlife in desert fires is fairly common, but highly variable. In some instances, few to no mortalities were found (Howard et al., 1959), while many mortalities were found among several taxa in other studies (Erwin and Stasiak, 1979). After a particularly severe chaparral fire, 43 vertebrates among 6 taxa were counted in 0.7 ha (Chew et al., 1959). Extirpation (100% mortality) of entire populations in burned areas is unlikely (Howard et al., 1959). Desert tortoises from the Mojave Desert, for example, spend most of their lives underground (Nagy and Medica, 1986), where they might be protected from fire. Other species might have seasonal or daily activity periods that place them out of harms way. In contrast, animals such as woodrats (*Neotoma*), which use above ground nests made from flammable materials with little in the way of underground refugia, can suffer high losses (Chew et al., 1959; Simons, 1989).

Even though many desert tortoises in a given population might be underground and survive a particular fire during the height of the wildfire season in June and July, fires carried in habitats heavily infested with introduced grasses are likely to kill a disproportionate number of gravid female tortoises compared to males or non-reproducing females. Only females searching for sites to lay their eggs are generally active during the hot, dry period preceding the summer monsoon rains (Bailey and

Schwalbe, unpublished data; Esque and Schwalbe, unpublished data). Of the 7 tortoises found dead after the Mother's Day Fire, 4 were females (2 of which could not be reliably determined to have died by fire), 2 were subadults, and none were males (Table 2). In contrast, most healthy tortoises should be active after the monsoon rains in July and August. Of the 7 tortoises killed in the Pusch Ridge Fire (September), 2 were female, 3 were males, and 2 were of undetermined sex (Table 2).

Losses of individuals in long-lived species with low reproductive capacity, such as tortoises, leads to population-level effects (Hailey, 2000). Signs of activity along surveyed areas suggested that more tortoises survived the fires than were located during surveys. However, a loss of 11% of the adult population is a catastrophic loss for this long-lived species (United States Fish and Wildlife Service, 1994). This effect might have greater ramifications in the Sonoran Desert, where most fires occur prior to the onset of the monsoon season, when fuels are dry and females are active and laying eggs. Males are less active in the spring (Martin, 1995). The only incidence of male mortality in the Sonoran Desert was the Pusch Ridge Fire, which occurred at the end of the summer rainy season.

Locating carcasses after a fire is also dependent on the time elapsed between the fire and surveys for carcasses. This is due mainly to the presence of scavengers. Javelina, ants, and other unobserved scavengers might be attracted to burned sites. Preliminary data from studies in coastal sage scrub habitats indicate that scavenging is an important factor in the quantification of fire mortalities (R. Fisher, 1999, pers. comm.). Therefore, estimates of small animals might be severely underrepresented unless searches are conducted immediately after or during fires.

Indirect effects of fires can cause changes in wildlife populations that are considered detrimental or beneficial but vary depending on habitat requirements and vagility of each species (Mushinsky and Gibson, 1991; Pianka, 1992; Medica et al., 1993; Trainor and Woinarski, 1994; Vieira, 1999; Sutherland and Dickman, 1999; Huff and Kapler Smith, 2000). Wildfire can cause rapid and profound habitat change in desertscrub habitats (Brown and Minnich, 1986; Johnson and Miyanishi, 1995; Brooks, 1998). Many desert plants are not well adapted to large disturbances by fire (O'Leary and Minnich, 1981; McLaughlin and Bowers, 1982; Rogers, 1986), which has lead to biotic impoverishment in arid habitats (Billings, 1990). Short-term loss of vegetative cover might predispose burned regions to other long-term changes, such as soil erosion (Johansen et al., 1982; Callison et al., 1985; Greene et al., 1990), invasion by alien plant species (D'Antonio and Vitousek, 1992), shifts in annual (Humphrey, 1974; Cave and Patten, 1984; Rogers and Vint, 1987) and perennial plant community composition (McLaughlin and Bowers, 1982), or loss of habitat structure (Cave and Patten, 1984; Thomas and Goodson, 1992). If such changes affect desert tortoises, we hypothesize that Mojave Desert tortoises would be at greater risk than Sonoran Desert tortoises because of large-scale physiographic differences between the 2 deserts.

Desert tortoises and other animal populations are patchy in distribution, making accurate comparisons of burned to unburned populations difficult without experimental controls. In spite of these difficulties, tortoises are probably one of the easiest animals to detect in post-fire surveys because of their conspicuous and persistent shells. In some respects, the occurrence of fire increased the likelihood of finding animal carcasses by visual survey because of the loss of vegetative cover. We suspect that some moribund animals would have sought cover underground, been buried in ashes, or been scavenged by other animals and, therefore, been undetected during our surveys. Thus, we probably underestimated mortality.

Fires have become an important factor that shapes desert habitats. However, it appears that there are great differences in the way terrestrial chelonians respond to fire disturbances. Gopher tortoises (*Gopherus polyphemus*) and their habitats are considered to be fire-adapted and apparently benefit from fire disturbances (Mushinsky and Gibson, 1991). The ornate box turtle (*Terrapene ornata*) also benefits from a thermally diverse habitat maintained by periodic burning (Curtin, 1997). In contrast, the desert tortoise and its habitat are not fire-adapted, so fires might be detrimental to both individuals and populations. However, even tortoise species that inhabit fire-adapted communities, such as the fynbos (a distinctive Mediterranean-type community of plants with small, fine stems and leaves, and vegetation with a brushy appearance) in South Africa might be prone to population declines as a result of recent fires (E. Baard, pers. comm.). As wildlands become increasingly rare, the original large-scale mosaics of open habitats have been reduced to mere island habitats that are easily converted into monocultures of alien plant species, which might not provide all of the required resources for populations to survive.

With increased use of fire as a habitat management tool, it is important to ascertain the likely impacts of fire on small animal communities (Palis, 1995). The potential direct and indirect effects of fire on tortoises, other small animals, and their habitats need to be understood to assure proper fire management in desert habitats (Narog et al., 1995). We need to know more about the use of plants that provide thermal cover for tortoises and other wildlife (Main, 1981; Zimmerman et al., 1994), nurse-plants for plant re-establishment (Nobel, 1980), and plants that provide cover from predators (Burge, 1977; Berry and Turner, 1986). Wildfires sustained and spread by alien grasses, such as red brome and buffelgrass (*Pennisetum ciliare*), represent a threat to biotic diversity in the Arizona Upland of the Sonoran Desert and Mojave Desertscrub communities (Brooks, 1998; Esque et al., 2002; Esque and Schwalbe, 2002). Thus, several aspects of fire ecology in desert habitats require further attention if these diverse and unique habitats are to remain intact and sustain wildlife populations.

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Literature Cited

Berry, K. H., and F. B. Turner. 1986. Spring activities and habits of juvenile tortoises (*Gopherus agassizii*) in California. Copeia 1986:1010–1012.

Bigham, S. R., J. L. Hepworth, and R. P. Martin. 1964. A casualty count of wildlife following a fire. Proceedings of the Oklahoma Academy of Science 45:47–50.

Billings, W. D. 1990. *Bromus tectorum,* a biotic cause of ecosystem impoverishment in the Great Basin. In: Woodwell, G. W., editor. The earth in transition: patterns and processes of biotic impoverishment. Cambridge University Press, Cambridge, United Kingdom. Pp. 301–322.

Brooks, M. L. 1998. Ecology of a biological invasion: alien annual plants in the Mojave Desert. Unpublished Ph.D. dissertation, University of California, Riverside.

Brown, D. E., and R. A. Minnich. 1986. Fire and changes in creosote bush scrub of the western Sonoran Desert, California. American Midland Naturalist 116:411–422.

Burge, B. L. 1977. Movements and behavior of the desert tortoises, *Gopherus agassizii.* Unpublished M.S. thesis, University of Nevada, Las Vegas.

Búrquez, A., and M. de los Angeles Quintana. 1994. Islands of diversity: ironwood ecology and the richness of perennials in a Sonoran desert biological preserve. In: Nabhan, G. P., and J. L. Carr, editors. Ironwood: an ecological and cultural keystone of the Sonoran Desert. Conservation International Occasional Paper Number 1, Conservation International, Washington, D.C. Pp. 9–27.

Callison, J., J. D. Brotherson, and J. E. Bowns. 1985. The effects of fire on the blackbrush (*Coleogyne ramosissima*) community of southwestern Utah. Journal of Range Management 38:535–538.

Cave, G. H., and D. T. Patten. 1984. Short-term vegetation responses to fire in the Upper Sonoran Desert. Journal of Range Management 37:491–496.

Chelazzi, G., and R. Calzolai. 1985. Thermal benefits from familiarity with the environment. Oecologia 68:557–558.

Chew, R. M., B. B. Butterworth, and R. Geechman. 1959. The effects of fire on the small mammal populations of chaparral. Journal of Mammalogy 40:253.

Cook, S. F., Jr. 1959. The effects of fire on a population of small rodents. Ecology 40:102–108.

Curtin, C. G. 1997. Biophysical analysis of the impact of shifting land use on ornate box turtles, Wisconsin, USA. In: Van Abbema, J., editor. Conservation, restoration and management of tortoises and turtles: an international conference. New York Turtle and Tortoise Society and WCS Turtle Recovery Program, New York.

D'Antonio, C. M., and P. M. Vitousek. 1992. Biological invasions by exotic process, the grass/fire cycle and global change. Annual Review of Ecology and Systematics 23:63–87.

Erwin, W. J., and R. H. Stasiak. 1979. Vertebrate mortality during the burning of a reestablished prairie in Nebraska. American Midland Naturalist 101:247–249.

Esque, T. C., A. Búrquez M., C. R. Schwalbe, T. R. Van Devender, J. M. Nijhuis, and P. Anning. 2002. Fire ecology of the Sonoran desert tortoise. In: Van Devender, T. R., editor. The Sonoran desert tortoise: natural history, biology and conservation. Arizona-Sonora Desert Museum, University of Arizona Press, Tucson.

Esque, T. C., and C. R. Schwalbe. 2002. Alien annual grasses and their relationships to fire and biotic change in Sonoran Desertscrub. In: Tellman, B., editor. Invasive exotic species in the Sonoran Desert. Arizona-Sonora Desert Museum, University of Arizona Press, Tucson.

Ford, W. M., M. A. Menzel, D. W. McGill, J. Laerm, and T. S. McCay. 1999. Effects of a community restoration fire on small mammals and herpetofauna in the southern Appalachians. Forest Ecology and Management 114:233–243.

Friend, G. R. 1993. Impact of fire on small vertebrates in mallee woodlands and heathlands of temperate Australia: a review. Biological Conservation 65:99–114.

Germano, D. J., R. B. Bury, T. C. Esque, T. H. Fritts, and P. A. Medica. 1994. Range and habitats of the desert tortoise. In: Bury, R. B., and D. J. Germano, editors. Biology of North American tortoises. United States Department of the Interior, National Biological Survey, Fish and Wildlife Research Report Number 13. United States Fish and Wildlife Service, Washington, D.C. Pp. 73–84.

Greene, R. S. B., C. J. Chartres, and K. C. Hodgkinson. 1990. The effects of fire on the soil in a degraded semi-arid woodland. I. Cryptogam cover and physical micromorphological properties. Australian Journal of Soil Research 28:755–777.

Hailey, A. 2000. The effects of fire and mechanical habitat destruction on survival of the tortoise *Testudo hermanni* in northern Greece. Biological Conservation 92:321–333.

Howard, W. E., R. L. Fenner, and H. E. Childs. 1959. Wildlife survival in brush burns. Journal of Range Management 12:230–234.

Huff, M. H., and J. Kapler Smith. 2000. Fire effects on animal communities. In: Kapler Smith, J., editor. Wildland fire in ecosystems: effects of fire on fauna. General Technical Report RMRS-GTR-42, volume 1. United States Department of Agriculture-Forest Service, Rocky Mountain Research Station, Ogden, Utah. Pp. 35–42.

Humphrey, R. R. 1974. Fire in the deserts and desert grassland of North America. In: Kozlowski, T. T., and C. E. Ahlgren, editors. Fire and ecosystems. Academic Press, San Diego, California. Pp. 365–401.

Johansen, J. R., A. Javakul, and S. R. Rushforth. 1982. Effects of burning on the algal communities of a high desert soil near Wallsburg, Utah. Journal of Range Management 35:598–600.

Johnson, E. A., and K. Miyanishi. 1995. The need for consideration of fire behavior and effects in prescribed burning. Restoration Ecology 3:271–278.

Kipp, D. H. 1931. Wildlife in a fire. American Forests 37:323–325.

Lawrence, G. E. 1966. Ecology of vertebrate animals in relation to chaparral fire in the Sierra Nevada foothills. Ecology 47:278–290.

Lyon, L. J., H. S. Crawford, E. Czuhai, R. L. Fredriksen, R. F. Harlow, L. J. Metz, and H. A. Pearson. 1978. Effects of fire on fauna: a state-of-knowledge review. United States Department of Agriculture, General Technical Report WO-6. Pp. 22.

Lyon, L. J., E. S. Telfer, and D. S. Schreiner. 2000. Direct effects of fire and animal responses. In: Kapler Smith, J., editor. Wildland fire in ecosystems: effects of fire on fauna. General Technical Report RMRS-GTR-42, volume 1. United States Department of Agriculture-Forest Service, Rocky Mountain Research Station, Ogden, Utah. Pp. 51–58.

Main, A. R. 1981. Fire tolerance of heathland animals. In: Specht, R. L., editor. Heathlands and related shrublands. Ecosystems of the world, 9B. Elsevier Scientific Publishing Co., New York. Pp. 85–90.

Martin, B. E. 1995. Ecology of the desert tortoise (*Gopherus agassizii*) in a desert-grassland community in southern Arizona. Unpublished M.S. thesis, University of Arizona, Tucson.

McAuliffe, J. R. 1995. The aftermath of wildfire in the Sonoran Desert. Sonoran Quarterly 49:4–8.

McCoy, E. D., H. R. Mushinsky, and D. S. Wilson. 1994. Growth and sexual dimorphism of *Gopherus* *polyphemus* in central Florida. Herpetologica 50: 119–128.

McLaughlin, S. P., and J. E. Bowers. 1982. Effects of wildfire on a Sonoran Desert plant community. Ecology 63:246–248.

Medica, P. A., M. B. Saethre, and R. B. Hunter. 1993. Recovery of a desert community after fire in the northern Mojave. In: Fletcher, A., editor. Proceedings of the 19th Annual Desert Tortoise Council Symposium. Desert Tortoise Council, Tucson, Arizona. Pp. 68–92.

Mushinsky, H. R., and D. J. Gibson. 1991. The influence of fire periodicity on habitat structure. In: Bell, S. S., E. D. McCoy, and H. R. Mushinsky, editors. Habitat structure: the physical arrangement of objects in space. Chapman and Hall, New York. Pp. 237–256.

Nagy, K. A., and P. A. Medica. 1986. Physiological ecology of desert tortoises in southern Nevada. Herpetologica 42:73–92.

Narog G. M., A. L. Koonce, R. C. Wilson, and B. M. Corcoran. 1995. Burning in Arizona's giant cactus community. In: Weise, D. R., and R. E. Martin, technical coordinators. Proceedings of the Biswell Symposium: fire issues and solutions in urban interface and wildland ecosystems. United States Department of Agriculture-Forest Service, General Technical Report PSW-GTR-158, Walnut Creek, California. Pp. 175–176.

National Oceanic and Atmospheric Administration. 1998. http://www.ncdc.noaa.gov/pub/data/coop-precip/arizona.txt.

Nobel, P. S. 1980. Morphology, nurse plants, and minimum apical temperatures for young *Carnegiea gigantea*. Botanical Gazette 141:188–191.

O'Leary, J. F., and R. A. Minnich. 1981. Postfire recovery of creosote bush scrub vegetation in the western Colorado Desert. Madroño 28:61–66.

Palis, J. G. 1995. Post-fire herpetofauna of Morgan Ridge, Hoosier National Forest, Indiana. Bulletin of the Chicago Herpetological Society 30:167–171.

Pianka, E. 1992. Disturbance, spatial heterogeneity, and biotic diversity: fire succession and arid Australia. Research and Exploration 8:352–371.

Price, M. V., and N. M. Waser. 1984. On the relative abundance of species: postfire changes in a coastal sage scrub rodent community. Ecology 65: 1161–1169.

Rogers, G. F. 1986. Comparison of fire occurrence in desert and non-desert vegetation on Tonto National Forest, Arizona. Madroño 33:278–283.

Rogers, G. F., and M. K. Vint. 1987. Winter precipitation and fire in the Sonoran Desert. Journal of Arid Environments 13:47–52.

Schmid, M. K., and G. F. Rogers. 1988. Trends in fire occurrence in the Arizona Upland subdivision of the Sonoran Desert, 1955–1983. Southwestern Naturalist 33:437–444.

Schwilk, D. W., and J. E. Keeley. 1998. Rodent populations after a large wildfire in California chaparral and coastal sage scrub. Southwestern Naturalist 43:480–483.

Scott, N. J., Jr. 1996. Evolution and management of the North American grassland herpetofauna. In: Finch, D. M., editor. Ecosystem disturbances and wildlife conservation in western grasslands. United States Department of Agriculture-Forest Service, General Technical Report RM-GTR-285. Pp. 40–53.

Simon, N. P. P., F. E. Schwab, E. M. Baggs, and G. I. M. Cowan. 1998. Distribution of small mammals among successional and mature forest types in western Labrador. Canadian Field-Naturalist 112: 441–445.

Simons, L. H. 1989. Vertebrates killed by desert fire. Southwestern Naturalist 34:144–145.

Simons, L. H. 1991. Rodent dynamics in relation to fire in the Sonoran Desert. Journal of Mammalogy 72:519–524.

Smith, L. J., A. T. Holycross, C. W. Painter, and M. E. Douglas. 2001. Montane rattlesnakes and prescribed fire. Southwestern Naturalist 46:54–61.

Sutherland, E. F., and C. R. Dickman. 1999. Mechanisms of recovery after fire by rodents in the Australian environment: a review. Wildlife Research 26:405–419.

Swantek, P. J., W. L. Halvorson, and C. R. Schwalbe. 1999. GIS database development to analyze fire history in southern Arizona and beyond: an example from Saguaro National Park. Technical Report Number 61. United States Geological Survey-Cooperative Studies Unit, School of Renewable Natural Resources, University of Arizona, Tucson.

Swetnam, T. W., and C. H. Baisan. 1996. Fire histories of montane forests in the Madrean borderlands. In: Ffolliott, P. R., L. F. DeBano, M. B. Baker, G. J. Gottfried, G. Solis-Garza, C. B. Edminster, D. G. Neary, L. S. Allen, and R. H. Hamre, technical coordinators. Effects of fire on Madrean province ecosystems—a symposium proceedings. General Technical Report RM-GTR-289, United States Department of Agriculture-Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado. Pp. 15–36.

Thomas, P. A., and P. Goodson. 1992. Conservation of succulents in desert grasslands managed by fire. Biological Conservation 60:91–100.

Trainor, C. R., and J. C. Z. Woinarski. 1994. Responses of lizards to three experimental fires in the savanna forests of Kakadu National Park. Wildlife Research 21:131–148.

Turner, R. M. 1982. Mohave Desertscrub. Desert Plants 4:157–179.

TURNER, R. M., AND D. E. BROWN. 1982. Sonoran Desertscrub. Desert Plants 4:181–222.

UNITED STATES FISH AND WILDLIFE SERVICE. 1994. Desert tortoise (Mojave population) recovery plan. United States Fish and Wildlife Service, Portland, Oregon.

VAN DEVENDER, T. R., R. S. FELGER, AND A. BÚRQUEZ M. 1997. Exotic plants in the Sonoran Desert region, Arizona and Sonora. In: Kelly, M., and E. Wagner, editors. Proceedings California Exotic Pest Plant Council Symposium 3:10–15.

VAUGHAN, S. L. 1984. Home range and habitat use of the desert tortoise (*Gopherus agassizii*) in the Picacho Mountains, Pinal County, Arizona. Unpublished M.S. thesis. Arizona State University, Tempe.

VIEIRA, E. M. 1999. Small mammal communities and fire in the Brazilian Cerrado. Journal of Zoology 249:75–81.

WHELAN, R. J. 1995. The ecology of fire. Cambridge Studies in Ecology, Cambridge University Press, New York.

WHYSONG, G. L., AND M. H. HEISLER. 1978. Nitrogen levels of soil and vegetation in the Upper Sonoran Desert as affected by fire. Proceedings of the First International Rangeland Congress, Society of Range Management, Denver, Colorado. Pp. 697–699.

WOODBURY, A. M., AND R. HARDY. 1948. Studies of the desert tortoise, *Gopherus agassizii*. Ecological Monographs 18:145–200.

WRIGHT, H. A., AND A. W. BAILEY. 1982. Fire ecology: United States and Canada. John Wiley and Sons, New York.

ZIMMERMAN, L. C., M. P. O'CONNOR, S. J. BULOVA, J. R. SPOTILA, S. J. KEMP, AND C. J. SALICE. 1994. Thermal ecology of desert tortoises in the eastern Mojave Desert: seasonal patterns of operative and body temperatures, and microhabitat utilization. Herpetological Monograph 7:45–59.

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NATURAL HISTORY OF THE TEXAS HORNED LIZARD, *PHRYNOSOMA CORNUTUM* (PHRYNOSOMATIDAE), IN SOUTHEASTERN COLORADO

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ABSTRACT—Colorado Division of Wildlife currently considers the Texas horned lizard a species of special concern. From May 1995 to October 1997, Texas horned lizards were captured or collected during the active season from 6 counties in Colorado to document abundance and distribution of the species. We captured or collected 290 Texas horned lizards (170 alive and 120 dead on road). In Colorado, average snout-vent length (SVL) for adult males was not significantly different from females; the largest male and female lizards measured 84.9 mm SVL and 90.4 mm SVL, respectively. The sex ratio of adult males to adult females is 1M:1.4F. Results of distribution and habitat analysis indicated that the Texas horned lizard in Colorado is locally common in arid shortgrass and sandsage prairie lacking ground litter. Activity of the Texas horned lizard in Colorado is diurnal in spring and fall and bimodal (almost crepuscular) in the summer. Texas horned lizards in Colorado apparently breed in May and June, and hatchlings emerge in late August to mid-September. Mortality due to vehicle traffic seems high, but because the Texas horned lizard occurs in remote areas, the Colorado population in general seems to be relatively stable.

RESUMEN—La división de vida silvestre del estado de Colorado denomina el lagarto *Phrynosoma cornutum* como una de las especies en riesgo en el estado. De mayo de 1995 a octubre de 1997, se documentaron capturas y colectas del lagarto *P. cornutum* durante la época de actividad para determinar su abundancia y distribución en seis condados del estado de Colorado. Capturamos o colectamos 290 lagartos (170 vivos y 120 muertos en la carretera). En Colorado, el promedio longitudinal hocico-cloaca (LHC) para adultos macho no fue significativamente diferente que el de las hembras; el macho y la hembra más largos midieron 84.9 mm LHC y 90.4 mm LHC,