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Invasions of Exotic Plants: Implications for the Desert Tortoise, *Gopherus agassizii*, and Its Habitat in the Western Mojave Desert

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ABSTRACT: **Populations of the desert tortoise, *Gopherus agassizii*, in the western Mojave Desert of California have declined precipitously over the past few decades. Many factors may be associated with the ongoing decline, including the anthropogenically induced proliferation of exotic plants. Exotic plant invasions may negatively affect tortoises by reducing or eliminating important food plants through competition, by altering tortoise nutrition, and by altering the landscape through fire.**

The desert tortoise, *Gopherus agassizii*, is a "Threatened" species throughout approximately 30% of its geographic range (U.S. Fish and Wildlife Service [USFWS], 1994; Berry, this volume). In some portions of its range, such as the western Mojave Desert, populations have declined precipitously due to a myriad of causes, including the invasion of exotic plants.

Exotic plant species appear to have arrived in the western Mojave Desert with the early settlers in the late 1880s and early 1900s. The exotic plants came from Europe and Asia and include the annual grasses *Schismus arabicus*, *S. barbatus*, *Bromus madritensis* ssp. *rubens* and *B. tectorum*, and the forb *Erodium cicutarium* (USFWS, 1994). The exotic plants most likely spread through urban and agricultural development of desert lands as well as by roads, utility lines, livestock grazing, and other anthropogenic disturbances (e.g., see U.S. Bureau of Land Management, 1980). Since the 1960s, recreational off-road vehicle (ORV) use has been another source of land disturbances (Busack and Bury, 1974; Bury et al., 1977; Campbell, 1981, 1982; Luckenbach, 1982), and sheep grazing has continually disturbed soils and vegetation, which has contributed to the spread of exotics (Busack and Bury, 1974; Nicholson and Humphreys, 1981). Exotic species of annuals now comprise a significant portion of the ephemeral vegetation (Webb and Stielstra, 1979; Nicholson and Humphreys, 1981; Rowlands, 1990; Jennings, 1993; Brooks, 1995).

Invasions of exotic plants may pose threats to desert tortoises by competitively reducing or excluding important native forage species, compromising nutrition and health, and by contributing to the frequency and severity of fires in a region where fire was previously rare (USFWS, 1994). D'Antonio and Vitousek (1992) noted that second to changes in land use, "biological invasions have caused more extinctions than have resulted from human-caused climatic change or the changing composition of the atmosphere."

Effects of Sheep and Off-Road Vehicles on Desert Tortoise Habitat

Sheep grazing and ORVs probably have had the most pervasive impact on the western Mojave Desert since the 1960s. Both types of activities affect large areas and result in loss of vegetation and altered soil characteristics (Woodbury and Hardy, 1948; Bury et al., 1977; Berry, 1978; Webb and Stielstra, 1979; Nicholson and Humphreys, 1981; Rowlands, 1990). These disturbances further enhance invasions of exotic plants by (1) removing native vegetation, which reduces competition for water and nutrients (Bock et al., 1986; Medina, 1988); and (2) creating soil disturbances that favor exotic plants (Davidson and Fox, 1974; Webb and Stielstra, 1979; Holland and Kiel, 1989). Livestock grazing has been implicated in the alteration of vegetation and proliferation of exotic plants elsewhere in the West (e.g., Young and Evans, 1971; Mack, 1981; West, 1988; Billings, 1990; D'Antonio and Vitousek, 1992).

Exotic plant invasions can alter the frequency and intensity of fires (Van Wilgen and Richardson, 1985; MacDonald and Frame, 1988; Smith and Tunison, 1992). Not only have grass-dominated systems greatly increased risk of fire, they can also set in motion a grass/fire cycle—a phenomenon in which both grasses and fire are increased synergistically (D'Antonio and Vitousek, 1992). Overall, the disturbances and exotic plants contribute to deterioration and degradation of the desert tortoise habitat (USFWS, 1994).

Foraging Ecology of Desert Tortoises in the Western Mojave

Tortoises in the western Mojave Desert are dietary specialists and feed primarily upon succulent ephemeral vegetation (Berry, 1978; Jennings and Fontenot, 1993; Jennings, 1993; Spangenberg, 1994). Most of the preferred foods—*Astragalus didymocarpus*, *A. layneae*, *Euphorbia albomar-*

ginata, *Lotus humistratus*, *Lygodesmia exigua*, and *Mirabilis bigelovii*—are locally uncommon (Jennings, 1993). However, tortoises systematically locate these plants, which grow in characteristic areas. For example, *Astragalus layneae* and *Euphorbia albomarginata* are restricted to the margins of small washes (approx. 1 m wide), and tortoises locate them by traveling up or down the washes. Similarly, tortoises locate *Lotus humistratus*, *A. didymocarpus*, *Lygodesmia exigua*, and *Mirabilis bigelovii* by searching low gravelly/rocky hills.

Legumes and herbaceous perennials are important dietary constituents (43% and 30% of adult tortoise diets respectively, Jennings, 1993) in this region. The leguminous species (e.g., *Lotus* and *Astragalus* spp.) are probably important because of their high nutritional values, and the herbaceous perennials (e.g., *Astragalus layneae*, *Mirabilis bigelovii*, and *Euphorbia albomarginata*) may play an important role during drought years.

The temporal and spatial variation in distribution of food plants influences diet, seasonal movements, and locations and types of cover sites of the tortoises (Jennings, 1993). For example, early in spring tortoises almost exclusively use shrubs as cover sites, whereas later in spring they show strong fidelity to permanent burrows located next to "patches" (approx. 100–600 m²) of preferred food plants such as *Lotus humistratus* or *Lygodesmia exigua*.

Loss of preferred foods can have deleterious effects. Most preferred plant species are distributed in patches within the habitat, which may serve as focal points for tortoise activities (e.g., foraging and social interactions). Extirpation of these patchy resources may not only result in deprivation of preferred foods but may also disrupt or preclude social activities.

Tortoises may congregate at patches of high-value native forage plants, which also affords the opportunity for courtship and mating. In spring 1992 I observed the interactions of three tortoises at the Desert Tortoise Research Natural Area. In mid-May a large male tortoise (269 mm carapace length, 4.04 kg) was observed using an old burrow at the edge of a *Lotus* patch for the two-week period when the *Lotus* was flowering. Each day the tortoise visited the patch and fed exclusively upon *Lotus* before returning to the same burrow. Concurrently an adult female was also observed using an old burrow on the edge of the same *Lotus* patch. A week later, a subadult male (195 mm carapace length, 1.4 kg) appeared at the patch and began to feed upon *Lotus*. The larger male attacked the smaller male, which subsequently left the area. A few days later the large male mated with the female at the patch. It is possible that the large male tortoise may have used the old burrow previously and may have also previously defended the *Lotus* patch. In any case, the *Lotus* served as a setting for the observed social interactions.

Potential Effects of Exotic Annual Plants on Desert Tortoises and Their Habitats

The invasion of exotic plants in the western Mojave Desert has several adverse implications for desert tortoise populations. Recent research has revealed that desert tortoises are highly selective feeders and that they have evolved behaviors that allow them to locate rare food plants. Therefore, reduction or extirpation of the native plant species through competition with exotic plants could be detrimental to their well-being. Such an occurrence would not be unprecedented. The exotic grass *Eragrostis lehmanniana* has replaced many native Sonoran Desert plants, which has caused local declines in native bird and insect species (Bock et al., 1986; Medina, 1988). Similarly, the alien beach grass *Ammophila arenaria* has replaced several native dune plants, causing precipitous declines and extinction in some native insect species (Slobodchikoff and Doyen, 1977).

Tortoises occasionally consume exotic plants, and some have argued that tortoises could subsist on an exotic plant diet in the event their preferred native foods became unavailable. However, the negative correlation between exotic grass cover and native plant diversity or growth is well established (D'Antonio and Vitousek, 1992). If tortoises depend on a complex association of plant species for a nutritionally balanced diet, the elimination of even those food species that are consumed infrequently may negatively affect tortoises. Recent research has shown that the annual exotic grasses, *Schismus* sp., may be relatively deficient in key nutrients and may contain higher levels of metals than native plants (H. Avery, pers. comm.). High quantities of exotic plants in the habitat may compromise the health of the tortoises, thus rendering them susceptible to disease. The potential links between habitat quality, nutrition, and upper respiratory tract disease in desert tortoises have been described by Jacobson et al. (1991).

Perhaps the most significant consequence of invasions of exotic grasses in the western Mojave Desert is the increased frequency and severity of fires (USFWS, 1994). Fire was formerly a rare event in the Mojave Desert, even as recently as 30 years ago, and the native flora is not adapted to fire regimes. Thus habitat damage is often severe.

CONCLUSION

Exotic plants are now a significant component of the ephemeral vegetation in the western Mojave Desert, which has numerous implications for desert tortoises. These include competitive exclusion of food plants, altered nutrition, disturbance of social behavior, and a new-found fire hazard. Although these studies were conducted in the western Mojave Desert, they may be applicable to other desert tortoise populations as well as other tortoise species living in arid regions. Because disturbances to the habitat largely contribute

to these exotic plant invasions, it is possible that if such disturbances are halted, habitats may stabilize or improve (Brooks, 1995).

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