Issues and Perspectives

Enhancing and Restoring Habitat for the Desert Tortoise

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Abstract

Habitat has changed unfavorably during the past 150 y for the desert tortoise *Gopherus agassizii,* a federally threatened species with declining populations in the Mojave Desert and western Sonoran Desert. To support recovery efforts, we synthesized published information on relationships of desert tortoises with three habitat features (cover sites, forage, and soil) and candidate management practices for improving these features for tortoises. In addition to their role in soil health and facilitating recruitment of annual forage plants, shrubs are used by desert tortoises for cover and as sites for burrows. Outplanting greenhouse-grown seedlings, protected from herbivory, has successfully restored (>50% survival) a variety of shrubs on disturbed desert soils. Additionally, salvaging and reapplying topsoil using effective techniques is among the more ecologically beneficial ways to initiate plant recovery after severe disturbance. Through differences in biochemical composition and digestibility, some plant species provide better-quality forage than others. Desert tortoises selectively forage on particular annual and herbaceous perennial species (e.g., legumes), and forage selection shifts during the year as different plants grow or mature. Nonnative grasses provide low-quality forage and contribute fuel to spreading wildfires, which damage or kill shrubs that tortoises use for cover. Maintaining a diverse "menu" of native annual forbs and decreasing nonnative grasses are priorities for restoring most desert tortoise habitats. Reducing herbivory by nonnative animals, carefully timing herbicide applications, and strategically augmenting annual forage plants via seeding show promise for improving tortoise forage quality. Roads, another disturbance, negatively affect habitat in numerous ways (e.g., compacting soil, altering hydrology). Techniques such as recontouring road berms to reestablish drainage patterns, vertical mulching ("planting" dead plant material), and creating barriers to prevent trespasses can assist natural recovery on decommissioned backcountry roads. Most habitat enhancement efforts to date have focused on only one factor at a time (e.g., providing fencing) and have not included proactive restoration activities (e.g., planting native species on disturbed soils). A research and management priority in recovering desert tortoise habitats is implementing an integrated set of restorative habitat enhancements (e.g., reducing nonnative plants, improving forage quality, augmenting native perennial plants, and ameliorating altered hydrology) and monitoring short- and long-term indicators of habitat condition and the responses of desert tortoises to habitat restoration.

Keywords: annual plants; burrow; disturbance; forage; grazing; restoration; revegetation

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Introduction

Habitat of the desert tortoise *Gopherus agassizii* in the Mojave and bordering western Sonoran Desert in the southwestern United States has changed during the past 150 y. Beginning in earnest during the mid-1800s, thousands of nonnative animals (mainly cattle, sheep, horses, and burros) were moved through or kept in the region to support mining, ranching, and other human activities (Love 1916; Hohman and Ohmart 1978; Lovich and Bainbridge 1999). Numerous trails and roads, such as the Old Spanish Trail and the Mojave Road, originated or expanded from the 1800s through the 1900s (Keith et al. 2008). For example, within 6,000 km^2 of the central Mojave Desert, a road network of 605 km in 1885 expanded to 3,700 km by 1994 (Vogel and Hughson 2009). By the late 1800s, nonnative plant species were introduced that ubiquitously altered the composition of plant communities (Brooks and Esque 2002). In an inventory conducted from 2009 to 2011, at least one nonnative plant species inhabited 82% of 1,662 sites within 25,000 km^2 of national parks in the Mojave Desert (Abella et al. 2015c). In designated critical habitat for the desert tortoise in the western Mojave Desert, nonnative annual plants comprised 6% of the flora and 66% of the biomass in a wet year, and 27% of the flora and 91% of the biomass in a dry year (Brooks and Berry 2006). Large spreading wildfires, not known to have been common historically owing to sparse and discontinuous fuel, are now correlated with proximity to roads and annual plant productivity dominated by nonnative fuels (Brooks and Matchett 2006). Between 1992 and 2011, >5% of a 30,000-km^2 portion of the Mojave Desert burned in 1,700 lightning- and human-ignited fires (Hegeman et al. 2014). Many other land-clearing disturbances—such as agricultural fields, historical town sites, contemporary urban developments, energy transmission corridors, solar and wind energy facilities, and military training sites—have removed, altered, and fragmented habitat (Nichols and Bierman 2001; Webb et al. 2009a; Hernandez et al. 2014). Even where sources of disturbance have ceased (such as terminated livestock allotments, abandoned agricultural fields, closed roads), the legacies of altered hydrology, soil, and vegetation can continue for decades to centuries (Carpenter et al. 1986; Abella 2010; Berry et al. 2015, 2016).

The population of the desert tortoise in the Mojave and western Sonoran Desert was federally listed as threatened under the U.S. Endangered Species Act of 1973 (ESA 1973, as amended) in 1990 because of population declines, habitat alteration, and habitat loss (USFWS 1990). Population declines have continued in four of five recovery areas range-wide; the estimated decline was 32% for desert tortoises of breeding size between 2004 and 2014 in all recovery areas (USFWS 2015). Four of the five recovery areas experienced declines ranging from 27% to 67%; only one recovery area showed an increase in desert tortoise numbers.

The declines are serious for several reasons. First, studies at individual sites suggest that the recent 10-y decline continues a longer term trend (Peterson 1994; Berry and Medica 1995; Berry et al. 2006, 2014b; Medica et al. 2012). Populations of 75–140 desert tortoises/km^2 in the 1970s had decreased to $\leq$15/km^2 by 2011–2012 (Berry et al. 2014b; Lovich et al. 2014). Second, the desert tortoise is long-lived ($\geq$50 y), and persistence of adults at low densities may temporarily mask population declines at some sites (Berry et al. 2013). Third, densities of breeding adults in four of the five recovery areas with declining populations are precipitously low, ranging from only 1.5 to 15.3 tortoises/km^2 (USFWS 2015), and recruitment is poor (Berry et al. 2014b). Fourth, factors such as habitat loss and fragmentation, noted at the time of the 1990 listing, have not been curtailed and instead are expanding (Averill-Murray et al. 2013).

The Revised Recovery Plan for the desert tortoise emphasized habitat conservation, enhancement, and restoration as priority recovery actions (USFWS 2011). Habitat restoration was highly ranked, among 25 candidate recovery actions, for potential to enhance desert tortoise populations (Darst et al. 2013). This high ranking was because fundamental desert tortoise needs—food, water, and cover sites—hinge on what the habitat provides (Esque et al. 2014). Moreover, other threats perceived to limit populations, such as disease (Jacobson et al. 2014) and predation by common ravens *Corvus corax,* may also relate to habitat condition (Kristan and Boarman 2007; Averill-Murray et al. 2012). Poor forage quality and contamination of soil and food plants by mercury and arsenic, for example, are thought to increase vulnerability of desert tortoises to disease (Seltzer and Berry 2005; Chaffee and Berry 2006; Jacobson et al. 2014).

Although potential may be high for habitat management to increase the health and size of desert tortoise populations, many habitat improvement techniques are untested for their effectiveness as recovery actions for the desert tortoise. Literature has accumulated on topics such as vegetation restoration in the Mojave Desert, but this research has had diverse goals not necessarily focused on the tortoise (e.g., Wallace et al. 1980; Abella and Newton 2009; Scoles-Sciulla et al. 2014). Meanwhile, some studies have linked desert tortoise biology with habitat features, such as forage composition (Oftedal et al. 2002; Jennings and Berry 2015). The USFWS (2011) recommended integrating these types of habitat features with techniques for restoring and enhancing favorable habitat conditions, which could be followed by monitoring short- and long-term indicators of habitat condition and tortoise responses to habitat restoration.

A broad approach for enhancing habitat is essential for desert tortoise recovery (Averill-Murray et al. 2012). Elements of such an approach include conservation of specific favorable conditions and restoration of desired features designed to improve habitat in the context of contemporary and near-future environments. For example, restoring habitat on decommissioned roads to re-establish hydrological connectivity is feasible where old, previously disrupted stream channels are discernable (Nichols and Bierman 2001). In contrast, 150 y of grazing by nonnative animals and invasion by nonnative plants complicates our understanding of predisturbance forage

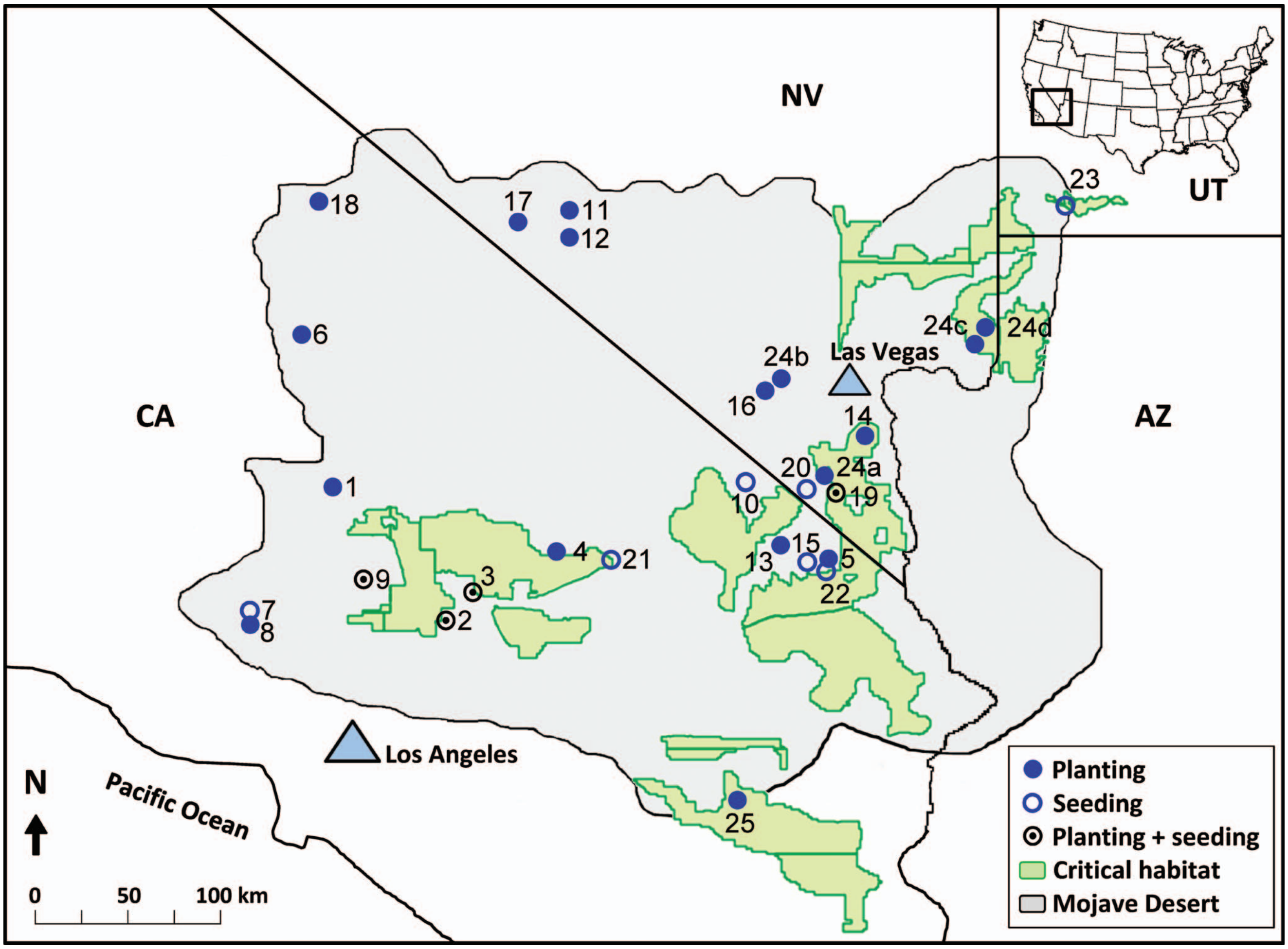

Figure 1. Distribution of critical habitat units for the desert tortoise *Gopherus agassizii* and published revegetation studies in the Mojave Desert of California, Nevada, northwestern Arizona, and Utah. The desert tortoise is distributed across much of the Mojave Desert (shown in green outline and shading). Many different maps of the boundary of the Mojave Desert are in the literature, and this map shows a combined generalization of maps in Rowlands et al. (1982), Rundel and Gibson (1996), and Webb et al. (2009b). Revegetation studies included planting nursery-grown plants and seeding. Studies numbered 1–18 correspond with 18 studies mapped in Abella and Newton (2009). Studies 19–25 are recent: 19, Abella et al. (2012b); 20, Abella et al. (2015a); 21, DeFalco et al. (2012); 22, Jones et al. (2014); 23, Ott et al. (2011); 24a–d, 4 sites in Scoles-Sciulla et al. (2014); and 25, Weigand and Rodgers (2009). Note that few of the revegetation studies are in tortoise critical habitat units. We did not find revegetation studies in the western Sonoran Desert in southeastern California that also contain a desert tortoise population.

composition, creating challenges for restoration efforts (Oldemeyer 1994). In this situation, establishing a plant composition adapted to the site and nutritionally favorable to desert tortoises may be most appropriate (Oftedal 2002; Hazard et al. 2009, 2010).

In support of recovery actions, we synthesize relationships of habitat features (vegetation and soil) with the listed Mojave and western Sonoran Desert population of the desert tortoise, and the status of knowledge for enhancing and restoring the key habitat elements of shrub cover, food, and soils. Our review has two parts: 1) requirements of the desert tortoise for shelter, food, and water; and 2) candidate practices and rationale for improving habitat condition and restoring habitats, including revegetating severe disturbances; enhancing quality of tortoise forage; removing or remediating damaged soil; salvaging topsoil; and decommissioning backcountry roads. Our focus is on habitat management practices aimed at enhancing health and growth of desert tortoise populations and for restoring damaged and deteriorated habitats within the context of past and existing recovery plans for the tortoise (USFWS 1994, 2011).

Methods

Study area

Our study area is the geographic range of the federally listed desert tortoise population, which is hot desert habitat north and west of the Colorado River. This includes most of the 124,000-km^2 Mojave Desert occupying parts of Arizona, Utah, Nevada, and California, as well as the Colorado Desert Subdivision of the western Sonoran Desert, in southeastern California (Figure 1). The study area receives much of its rainfall from November through April, during winter and spring (Rowlands et al. 1982). Annual precipitation averages 10–20 cm at low and middle elevations below 1,500 m. Topography includes mountain ranges, low hills, washes (ephemeral stream channels), and valleys. Soils include those derived from several rock types (e.g., basalt, limestone) and depositional material from erosion (Rautenstrauch and O'Farrell 1998; Berry et al. 2006; Mack et al. 2015). Geological history and soil age are key factors affecting biota, such as old surfaces of desert pavement compared with young soils in ephemeral stream channels (McDonald et al. 1995).

Dominant vegetation is desert shrubland (Rundel and Gibson 1996). Creosote bush *Larrea tridentata* and white bursage *Ambrosia dumosa* predominate across extensive low elevations, blackbrush *Coleogyne ramosissima* and succulent woodlands containing Joshua trees *Yucca brevifolia* at middle elevations from 1,300 to 1,800 m, and coniferous woodlands and forests at the higher elevations. Desert tortoises are most abundant in the low- and middle elevation creosote bush and mixed shrublands, and are sparse to absent in the higher elevation woodland and forest vegetation associations (Rautenstrauch and O'Farrell 1998; Berry et al. 2006). In years with sufficient rainfall, most annual plants in the desert shrubland germinate in winter, grow through spring, and senesce by May (Beatley 1974; Smith et al. 2014). The eastern Mojave and western Sonoran also have a component of summer annuals, stimulated by summer monsoonal storms (Jennings 2001; Wallace and Thomas 2008). Annual plants are typically most abundant below canopies of shrubs that form "fertile islands" of shaded, nutrient-enriched soil (Brooks 2009). Some annual species, however, are most abundant in interspaces between shrubs (Abella and Smith 2013). The spatial variation in the distribution of different shrub species and interspaces creates heterogeneity in the annual plant community, which may be important for diversifying the forage available to desert tortoises (Jennings and Berry 2015). The amount and timing of rainfall are also variable among years and across the landscape within a year (Hereford et al. 2006). Some years or locations have essentially no annual plants, while others support 50 species of annual plants within a single square kilometer (Brooks and Berry 2006).

Study species

The desert tortoise is distributed at elevations below 1,300 m across much of the Mojave and western Sonoran Desert, except for the Death Valley floor and other low-elevation valleys with minimal rainfall (USFWS 1994). Typical home ranges are up to 20 ha for adult females and 20–50 ha for adult males (Harless et al. 2010). Desert tortoises conduct daily and seasonal activities within these home ranges, including foraging, retreating to burrows, and reproduction. Occasionally they travel longer distances, such as 3–7 km over weeks and months, for reasons that may relate to mating, foraging, or locating new home ranges (Berry 1986). Desert tortoises spend >90% of their lives underground in burrows, thereby escaping temperature extremes, lack of moisture, and predators (Nagy and Medica 1986; Mack et al. 2015). All age classes of tortoises are active in spring during the peak spring growing season for plants. Juveniles can emerge from burrows in February and continue being active through May and June (Berry and Turner 1986), and periodically between November and February (Wilson et al. 1999). A second period of heightened activity of adults occurs during the mating season in summer and early autumn (Rostal et al. 1994). The species is primarily herbivorous (Morafka and Berry 2002; Oftedal 2002; Jennings and Berry 2015). Desert tortoises obtain moisture from succulent, green forage (Nagy et al. 1998) and drink from self-constructed catchments or puddles (Minnich 1977; Medica et al. 1980). Most desert tortoises respond to precipitation at any time of year by emerging to drink, unless they are already hydrated.

Information gathering

We focused on evaluating 1) the vegetation and soil attributes of habitat likely required by desert tortoises to survive and maintain viable populations into the foreseeable future; and 2) how these habitat features can be enhanced or restored for desert tortoises given existing habitat condition. We conducted a systematic review of information published in journal articles, book chapters, conference proceedings, and publicly available U.S. government serials (e.g., U.S. Forest Service General Technical Reports, U.S. Geological Survey Open-File Reports). We first examined review articles of the desert tortoise and disturbance and restoration in the Mojave and western Sonoran Desert (e.g., Webb and Wilshire 1983; Grover and DeFalco 1995; Abella and Newton 2009; Brooks and Lair 2009; Abella 2010). We then systematically searched the following article databases from their period of record through 2015: AGRICOLA, BioOne, GoogleScholar, JSTOR, Scopus, ScienceDirect, SpringerLink, Web of Science, and Wiley Online Library. We searched article titles, abstracts, and key words for articles containing the following terms: Mojave, Sonoran, livestock, grazing, fire, restoration, revegetation, road, right of way, corridor, desert tortoise, *Gopherus agassizii,* habitat, vegetation, forage, food, burrow, cover, perennial plant, and shrub. We also screened the 1976 to 2003 Desert Tortoise Council Proceedings for relevant papers. Nomenclature of plants follows NRCS (2016).

Relationships Between Habitat Features and Desert Tortoises

Perennial plants and protective cover

Desert tortoises predominately construct burrows in soil beneath canopies of native shrubs and under rocks; on certain sites they also use caves in cliffs or banks of ephemeral stream channels as shelters or dens (Woodbury and Hardy 1948; Burge 1978; Berry and Turner 1986; Baxter 1988; Lovich and Daniels 2000; Rautenstrauch et al. 2002; Mack et al. 2015). In three studies in natural shrubland habitat, desert tortoises constructed 72–97% of burrows beneath perennial plants (Burge 1978; Berry and Turner 1986; Baxter 1988). Furthermore, most burrows were below the largest shrubs. Burge (1978) found that the large catclaw acacia *Acacia greggii* harbored burrows at nine times that expected from its density, Mojave yucca *Yucca schidigera* seven times, and creosote bush four times. In addition to using shrubs as locations for constructing burrows, desert tortoises use shrubs as temporary resting or shelter sites during periods of activity outside burrows. In a 5-y study in the northeastern Mojave Desert, tortoises were observed beneath shrubs twice as often as in interspaces (Drake et al. 2015).

Although these studies show that desert tortoises use shrubs for protection, it is more difficult to determine how much shrub cover they need and if there are requirements for certain species and sizes of shrubs. Andersen et al. (2000), in a model of desert tortoise habitat use in the central Mojave Desert, reported that tortoises avoided areas of minimal plant cover. Berry et al. (2013) found that desert tortoise abundance was lower in areas denuded of vegetation than in adjacent undisturbed habitat. On a burned site, desert tortoises sought shelter below the skeletons of dead shrubs but frequently retreated to unburned areas with higher live perennial plant cover (Drake et al. 2015). If disturbance substantially reduces shrub density, locations for burrows and protective cover from temperature extremes and predation could limit tortoise population sizes (Andersen et al. 2000; Berry et al. 2013; Drake et al. 2015; Mack et al. 2015).

How does availability of perennial plants to desert tortoises fluctuate through time or change after anthropogenic disturbance? Severe, multiyear droughts have corresponded with die-off events in perennial plant communities. For example, some areas may still reflect effects of brief, but severe, droughts in 1989–1991 and 2002 associated with widespread mortality of some species of perennial plants (Hereford et al. 2006). In a 1-ha permanent plot remeasured between 1984 and 2004 in Joshua Tree National Park, density of mature white bursage declined from 1,600 to 523 individuals after the 2002 drought (Miriti et al. 2007). Eastern Mojave buckwheat *Eriogonum fasciculatum* dropped from 256 to 11 individuals, and desert globemallow *Sphaeralcea ambigua* from 59 to 0 individuals. Mature shrublands of creosote bush can generally be stable, but turnover can be substantial in short-lived perennial plants within creosote bush shrubland and in postdisturbance communities dominated by short-lived perennials (Webb et al. 2003). These fluctuations could affect cover as well as forage provided by herbaceous perennials such as desert globemallow (Jennings and Berry 2015).

The amount of alteration to vegetation increases with severity of disturbance and whether root systems of perennial plants remain intact (Prose et al. 1987; Scoles-Sciulla and DeFalco 2009; Webb et al. 2009a). After destruction of aboveground plant parts by off-road vehicles or low-severity wildfires, some perennial species (e.g., creosote bush) can resprout and resemble their former height within 5 y, depending on climatic conditions (Gibson et al. 2004). After wildfires, resprout frequency has varied among species and sites from 0% to near 100% (Abella 2009). Variation in resprouting can be a key influence to cover available for tortoises in postdisturbance environments because regeneration by seed of many shrubs such as creosote bush is infrequent (Esque et al. 2003; Drake et al. 2015).

Based on 30 studies of disturbance in the Mojave Desert, cover of perennial plants can reestablish to levels of nearby undisturbed areas within an average of 80 y (Abella 2010). Estimated time required for reestablishment of perennial cover varied among studies from 24 to 335 y. This variation correlated with plant community type, disturbance type and severity, site factors (e.g., soil parent material, grazing history), and weather following a disturbance (Engel and Abella 2011).

Much of the plant cover reestablishing after disturbance, however, consisted of different species than those before disturbance. Reestablishment of perennial species composition (species present and their relative abundance) was estimated to require decades to centuries after disturbance in the Mojave and Sonoran deserts (Abella 2010). These estimates assume that future conditions (e.g., climate, competition from nonnative plants) are conducive to native plant recovery. Many examples exist of town-sites and pipeline corridors cleared decades ago that remain dominated by species differing from nearby undisturbed areas (Webb et al. 2009a). The functional attributes of fertile islands, annual plant forage, and supply of large shrubs for tortoise burrows of the persistent, postdisturbance communities are poorly understood. Generally, many of the postdisturbance colonizers (e.g., desert globemallow, cheesebush *Hymenoclea salsola,* and desert trumpets *Eriogonum inflatum*) are smaller statured than those of mature shrublands and may therefore provide less protection to tortoises (Shryock et al. 2014).

Forage plants

Diet analyses and observations of foraging indicate that desert tortoises eat dozens of plant species but are selective foragers (Coombs 1979; Henen 2002; Esque et al. 2014; Jennings and Berry 2015). Diets change seasonally with variation in timing of emergence, growth, and senescence of different species of plants in spring and summer (Jennings 2002). Furthermore, juvenile and adult tortoises have access to different-sized plants (Morafka and Berry 2002).

Three sources of evidence suggest that forage quality and quantity have associations with desert tortoise

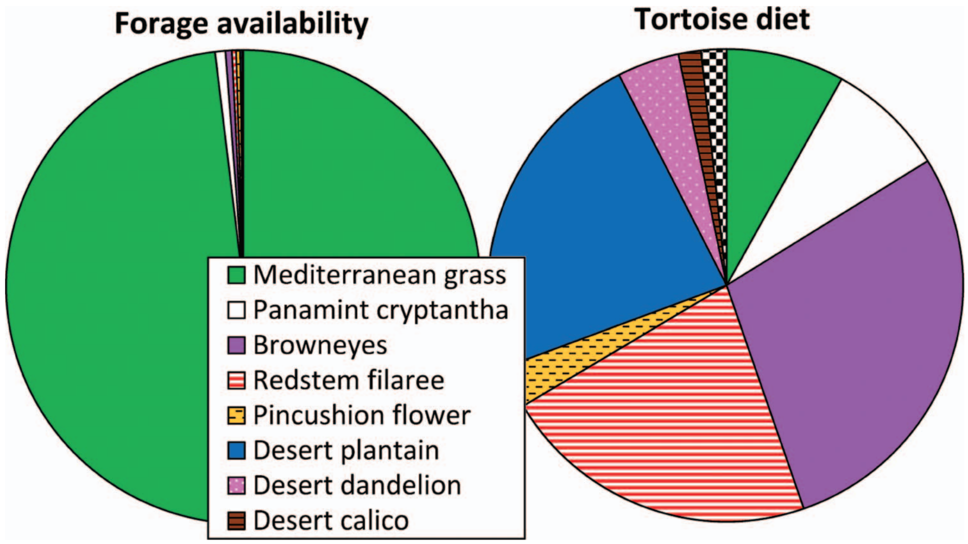

Figure 2. Availability of annual plant forage, relative to what juvenile desert tortoises *Gopherus agassizii* ate, in 1998, in an enclosure at the U.S. Army's Fort Irwin National Training Center, California. The nonnative annual Mediterranean grass dominated plant composition, but desert tortoises avoided eating them. Instead, desert tortoises preferentially ate native annual forbs, with browneyes and desert plantain constituting 52% of tortoise diets. Scientific names for species: Mediterranean grass *Schismus* spp., Panamint cryptantha *Cryptantha angustifolia,* browneyes *Camissonia claviformis,* redstem filaree *Erodium cicutarium,* pincushion flower *Chaenactis fremontii,* desert plantain *Plantago ovata,* desert dandelion *Malacothrix glabrata,* and desert calico *Loeseliastrum matthewsii*. Data from Oftedal et al. (2002).

demography: 1) links between plant productivity and health of individual tortoises, 2) experimental feeding trials, and 3) selective foraging displayed by tortoises. Between 1991 and 2011 in Joshua Tree National Park, desert tortoise survival was correlated with winter rainfall (Lovich et al. 2014). Winter rainfall in turn was correlated with biomass of native annual plants (Rao and Allen 2010) and densities of herbaceous perennial forage species such as desert globemallow (Miriti et al. 2007). At a drought-prone site in the eastern Mojave Desert, desert tortoise survival was only 33% during the 1990s (Longshore et al. 2003). High death rates corresponded with low production of annual plants and limited amounts of drinking water for tortoises in dry years (Nagy et al. 1997). In a long-term study in the northern Mojave Desert, growth of individual desert tortoises was positively correlated with annual plant production over 40 y between 1964 and 2003 (Medica et al. 2012).

Experimental feeding trials indicate that forage quality affects desert tortoise health (Barboza 1995; Nagy et al. 1998; Hazard et al. 2009, 2010). For example, Hazard et al. (2009) reported that captive, juvenile desert tortoises (0.5–1.5 y old) lost weight when fed senesced grasses low in nitrogen. In contrast, tortoises gained weight when fed the native forb desert dandelion *Malacothrix glabrata* or nonnative forb redstem filaree *Erodium cicutarium*. Similarly, in another experiment, adult desert tortoises gained weight when fed a protein- and nutrient-rich native perennial forb (desert globemallow), but lost weight when fed the nonnative grasses *Schismus* spp. (Barboza 1995). Barboza (1995) further noted the importance of a diverse "menu" of preferred food plants for long-term nutrient balances in desert tortoises.

When desert tortoises have a choice, they are selective foragers. Studies that compare what desert tortoises eat to what forage is available are rare, but two examples highlight selectivity. In a fenced enclosure in the central Mojave Desert, juvenile tortoises ate only 42 (0.02%) of the 239,000 individuals of the nonnative grasses *Schismus* spp. they encountered (Oftedal et al. 2002). In contrast, they ate 35% of 346 plants of the native forb desert plantain *Plantago ovata*. Other favored native annual forbs were desert dandelion, desert calico *Loeseliastrum matthewsii,* and browneyes *Camissonia claviformis* (Figure 2). In the particular collection of plant species analyzed, the nonfavored *Schismus* had low water and protein content, whereas the favored species were rich in water and protein (Oftedal et al. 2002).

The biochemical traits of plants thought to contribute to quality of forage for desert tortoises are similar to those for other herbivores and include water, nutrient, and fiber content and digestibility (Nagy et al. 1998; Oftedal et al. 2002; Hazard et al. 2010). Plant biochemistry fluctuates through time and across the landscape, because the chemical composition of plants varies among species, within a species during a year, and across soil types (El-Ghonemy et al. 1978; Chaffee and Berry 2006). Oftedal (2002) noted that desert tortoises are vulnerable to excess potassium, which is abundant in desert plants. Desert tortoises must excrete excess potassium to avoid toxic effects, but this requires that tortoises use water or gain sufficient nitrogen from other forage plants to excrete potassium as urates. If too much

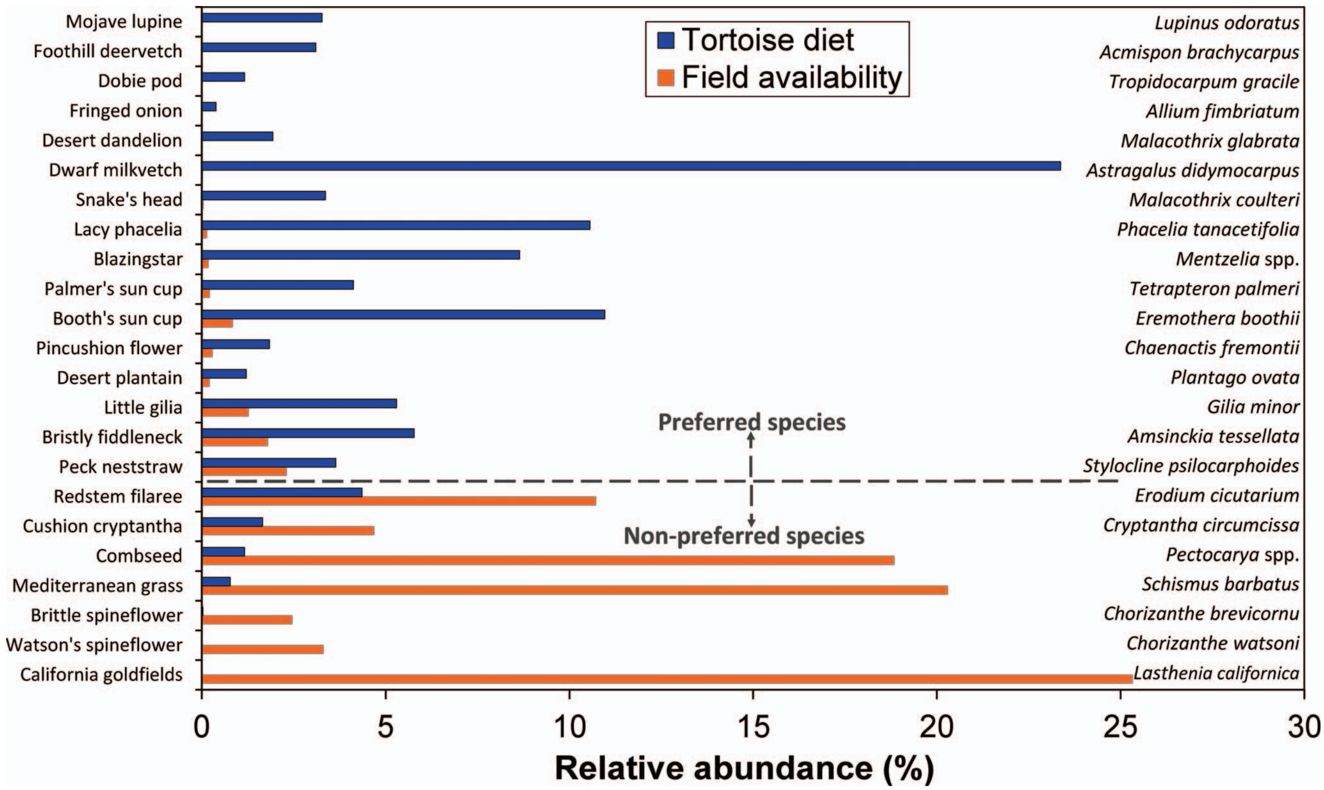

Figure 3. Comparison of availability of annual forage plants to what desert tortoises *Gopherus agassizii* ate, March and April 1992, at the Desert Tortoise Research Natural Area, California. Data from Jennings and Berry (2015).

nitrogen is required to excrete potassium, nitrogen may become limiting to tortoise growth. Oftedal et al. (2002) developed a potassium excretion potential (PEP) index that integrated potassium, water, and protein to indicate favorability of plant forage chemistry for desert tortoises to excrete potassium. Forage with high PEP was likely advantageous to tortoises compared with forage with low PEP. Plants consumed, but not preferred by tortoises (e.g., the nonnative grass *Schismus* spp.), had low PEP, whereas preferred species frequently had high PEP (e.g., plants of the Fabaceae family). Based on these biochemical traits along with field studies comparing food plant consumption to availability (Jennings and Fontenot 1992; Avery and Neibergs 1997; Oftedal et al. 2002; Jennings and Berry 2015) and feeding experiments (e.g., Barboza 1995; Hazard et al. 2009, 2010), desert tortoises favor legumes (family Fabaceae), mallows (family Malvaceae), evening primroses (family Onagraceae), and some species in the Asteraceae and Boraginaceae families. These studies further suggest that, in general, annual and herbaceous perennial forbs supply higher quality forage than nonnative annual grasses.

A study in the western Mojave Desert in southern California, at the Desert Tortoise Research Natural Area, highlighted temporal and spatial variability in tortoise foraging, which could be important to long-term tortoise behavior and nutrition balances (Jennings and Berry 2015). The authors reported seasonal variation in desert tortoise forage preferences from March to June; preferential foraging on certain herbaceous perennial forbs even though annuals were available; and that >75% of bites consumed were on a subset of 10% of the site's 80 annual and perennial species. Three herbaceous perennial forbs—desert wishbone-bush *Mirabilis laevis,* widow's milkvetch *Astragalus layneae,* and whitemargin sandmat *Chamaesyce albomarginata*—were rarely recorded in vegetation surveys but constituted significant components of desert tortoise diets. Some of the more preferred native annual forbs included Mojave lupine *Lupinus odoratus,* foothill deervetch *Acmispon brachycarpus,* dwarf milkvetch *Astragalus didymocarpus,* lacy phacelia *Phacelia tanacetifolia,* and desert dandelion (Figure 3). These favored foods were distributed unevenly within the habitat. Some favored plants were in ephemeral stream channels, and desert tortoises rarely passed by the plants without taking bites. Given how uncommon some preferred forage species are and that they also are eaten by animals other than tortoises, the possibility cannot be dismissed that availability of quality forage is a limiting factor for desert tortoise health.

Disturbance is another factor that can affect variability of annual plant forage. Effects of disturbance on annual plants appear contingent on effects to the perennial plant community and on weather conditions after disturbance, similar to temporal patterns in undisturbed desert (Abella 2010). There may be no response of annual forage plants to disturbance until a year of sufficient rainfall. Given sufficient rainfall, the cover and species richness of annual plants can attain levels found on undisturbed areas within 1–15 y after disturbance (Callison et al. 1985; Brooks and Matchett 2003; Vamstad and Rotenberry 2010). However, nonnative annual grasses—poor-quality forage for tortoises—often dominate the disturbed communities within a few years and are persistent (Callison et al. 1985; Brooks and Matchett 2003; Brooks and Berry 2006). In a study of annual plant recovery 36 y after construction of the Los Angeles Aqueduct in the western Mojave Desert, certain annual species (e.g., stiff-haired lotus *Acmispon strigosus*) known to be favored by desert tortoises had not colonized the disturbance corridor (Berry et al. 2015). These plants occurred in nearby undisturbed habitat.

Soil and topography, including the special case of roads

In addition to their effect on vegetation, soil and topography interact with desert tortoises in several ways. To create burrows, desert tortoises utilize calcic soils (caliche) in hillsides and banks of ephemeral stream channels by constructing or altering caves (Woodbury and Hardy 1948; Rautenstrauch et al. 2002; Mack et al. 2015). Burrows dug in fine sands easily collapse and do not persist (Wilson and Stager 1992). Compacted soils, including those compacted through human disturbance, are unsuitable as burrow sites because tortoises cannot dig in them. Likewise, soils contaminated with toxic wastes from mining, vehicular traffic, or other sources are unsuitable, because they can contribute to poor health of tortoises (Seltzer and Berry 2005; Jacobson et al. 2014; Kim et al. 2014). Soil type and fine-scale topography are also important for retaining rain water because tortoises drink from puddles or construct their own catchments in soil (Medica et al. 1980). Sites with slow water infiltration or depressions are likely most suitable for supplying drinking water (Henen et al. 1998).

Hazardous chemicals have been intentionally or inadvertently introduced into soils in a variety of desert tortoise habitats. In some cases, the contaminants are along roadsides from decades of vehicle traffic (e.g., leaded gasoline), and in other cases from historical mining (Chaffee and Berry 2006; Kim et al. 2014). Some contaminants are of recent origin, such as illegal dumping or drug operations. Toxic materials, whether airborne or in soil and plants, can accumulate in long-lived desert tortoises. Two examples from the western Mojave Desert illustrate potential effects. Desert tortoises ill and dying of upper respiratory disease at the Desert Tortoise Research Natural Area had 11 times the levels of mercury in their livers as did healthy tortoises from a control site (Jacobson et al. 2014). Near the Rand Mining District, elevated levels of arsenic occurred in tissues (lungs, scutes) of necropsied tortoises (Seltzer and Berry 2005). The probable sources were mining wastes and soils disturbed by mining activities and exacerbated through off-road vehicle activities. Mining wastes with mercury and arsenic from the Rand Mining District have moved tens of kilometers via transport in dust and flowing water (Chaffee and Berry 2006; Kim et al. 2012).

An important consideration in developing restoration plans is the composition of plant species existing in soil seed banks, the effects of past human activities on seed banks, and whether seed banks have been swamped by nonnative annual plants. Do adequate seeds of forage plants preferred by tortoises remain in the soil and can the seed banks support recovery of desert tortoise populations? With the arrival of settlers from the New World in the 1700s to the Southwest, native vegetation has experienced waves of impacts from human uses and the introduction of nonnative annual plants (Minnich 2008). Although we are aware of above-ground changes in cover, composition, and biomass of annual vegetation and how quickly nonnatives have become dominant (e.g., Brooks and Berry 2006; Berry et al. 2014a), we know less about the composition of soil seed banks in different desert regions and whether different types of human activities (e.g., livestock grazing, military maneuvers, off-road vehicle use) have reduced seed banks of forage plants favored by desert tortoises. Although information is limited for desert tortoise habitats, some studies illustrate effects of disturbance on soil seed banks. Brooks (1995), in a study of the benefits of protective fencing at the Desert Tortoise Research Natural Area, reported that biomass of seeds was more than twice as high inside the fence than outside. Habitat inside the fence was protected from sheep grazing and off-road vehicle use for 12–13 y. In a study in the central Mojave Desert on lands degraded by military maneuvers, DeFalco et al. (2009) found that densities of annual plant seeds in compacted soils were 33% less than on control sites. Fire temperatures during desert wildfires can alter survival of seeds (Brooks 2002) and granivores and ants can play a role in seed availability too (Suazo et al. 2013).

Roads are a special case of human alterations to soils, topography, vegetation, and wildlife not only in deserts but elsewhere (Forman et al. 2003; Brooks and Lair 2009; Vogel and Hughson 2009). Roads fragment desert tortoise habitat and can result in the deaths or losses of tortoises from collisions with vehicles, collection by visitors, and predation by predators that feed on road kills or animals crossing roads (von Seckendorff Hoff and Marlow 2002; Boarman and Sazaki 2006; Kristan and Boarman 2007; Hughson and Darby 2013; Nafus et al. 2013). The common raven is an example of a predator subsidized in part by roads and perch sites often found adjacent to roads (e.g., utility corridors; Boarman and Coe 2002). Roads, whether as highways or in the backcountry, also alter the hydrological function of desert ecosystems by changing sheet flow and water movement in drainages (Schlesinger and Jones 1984; Brooks and Lair 2009). Hydrological connectivity is often severed; instead of water flowing across soil surfaces or through multiple channels, water is diverted down the compacted surfaces of roads or through culverts into a

Table 1. Summary of authors' experience and the findings of a literature review conducted in 2015 of habitat management aims, actions, and practices for enhancing vegetation and soil habitat conditions for the desert tortoise *Gopherus agassizii* in contemporary environments of the Mojave and western Sonoran Desert. Aims are in bold. Main management actions and best practices for them are summarized below each aim.

Aims, actions, and best practices
Restore or augment perennial plants as cover or forage
Action 1: Outplanting
Carefully select species
Use good planting stock
Perform effective plant care
Action 2: Seeding
Make controllable factors favorable
Match seed treatments to species
Develop backup plans for seeding failures
Improve forage quality and quantity
Action 1: Reduce nonnative plants
Focus on comprehensively treating damaging, widespread invaders
Detect and remove new invaders early
Implement preventive measures from invasive plant science
Action 2: Manage herbivory by nonnative animals on tortoise forage plants
Monitor changes in habitats after reducing nonnative animals
Strategically deploy exclosures
Action 3: Augment native forage plants
Experimentally test forage augmentation strategies
Compare forage augmentation with other candidate actions
Restore or conserve soil health
Action 1: Salvage topsoil if large soil disturbances are planned
Carefully plan salvage operations
Carefully store soil to maximize biotic retention
Action 2: Evaluate and remediate soil potentially toxic to tortoises
Assess potential for toxic soils
Avoid or remediate toxic soils before conducting other habitat activities
Action 3: Decommission certain backcountry roads
Ameliorate topographic and soil surface alterations
Limit postrestoration vehicle incursions

few channels (Hereford 2009). This can affect the productivity of plants downstream, which is an important consideration for the desert tortoise because plants growing in small washes are important food sources (Jennings and Berry 2015).

Roads have long been implicated in contributing to the invasion and spread of nonnative plants (Frenkel 1977). Brooks and Berry (2006), in a study of nonnative annual plants in desert tortoise critical habitat, reported that density of dirt roads was correlated with abundance of nonnatives. A paved highway appeared to be the source of the invasion of another noxious, nonnative species, Sahara mustard *Brassica tournefortii* in at least one valley within desert tortoise critical habitat in the western Sonoran Desert (Berry et al. 2014a). The highway intersected a major wash, and Sahara mustard likely further spread into the desert from that source. Roads are not always correlated with the distribution of nonnative plants, especially for invasive plants already occupying most of the landscape, but they are probable entry points (Craig et al. 2010).

Habitat Management Aims, Actions, and Practices

Using the systematic literature review and our experiences, we organized actions and best practices aimed at conserving and enhancing three key elements of desert tortoise habitats: cover sites, forage, and soil (Table 1). Elements of a comprehensive, systematic approach to employing these best practices would include conducting site assessments to evaluate probable factors limiting habitat quality to guide the aims of management actions; identifying the most feasible actions with the greatest chance of success for enhancing habitat quality; and monitoring outcomes of actions to inform future projects. In the sections below, we discuss the three broad aims (improving cover, forage quality, and soil health), management actions for accomplishing each aim, and best practices for implementing each action.

Restore or augment perennial plants as cover or forage

Restoring or augmenting abundance and diversity of perennial plants can enhance protective cover and forage (in the case of herbaceous perennials) for desert tortoises. Planting nursery-grown perennials (outplanting) and seeding are the two main methods for revegetating severely disturbed soil (Bainbridge 2007). In the Mojave Desert, outplanting is more reliable than seeding for establishing perennial plants any given year (Abella et al. 2012b). Outplanting has achieved a relatively long-term ($\geq$2 y) survival of $\geq$50% for a variety of perennial species when using good planting stock and proper plant care (Abella and Newton 2009; Weigand and Rodgers 2009; Scoles-Sciulla et al. 2014). For establishing perennial plants, we discuss the actions of

Table 2. Summary of the best-performing perennial species outplanted as nursery-grown plants at revegetation sites in ≥3 studies reported in the literature in the Mojave Desert (Figure 1). Survival was monitored for ≥1 y after outplanting during studies published between 1978 and 2014. The species in the table are medium- to large-sized shrubs that provide cover or burrow sites to desert tortoises *Gopherus agassizii*.

Common name	Scientific name	Total no. of studies	No. of studies with ≥50% survival[a]
White bursage	*Ambrosia dumosa*	10	5
Fourwing saltbush	*Atriplex canescens*	5	4
Nevada jointfir	*Ephedra nevadensis*	3	3
Creosote bush	*Larrea tridentata*	8	5
Anderson thornscrub	*Lycium andersonii*	3	2

[a] In at least one treatment, with treatments including irrigation, fencing to deter herbivory, and others. Data synthesized from Abella and Newton (2009), Abella et al. (2012b), Scoles-Sciulla et al. (2014), and Weigand and Rodgers (2009).

outplanting and seeding, and three best practices for each.

Action 1: Outplanting. Because of cost and logistical challenges, outplanting can be criticized for being unable to cover as much area as seeding. However, no matter how large an area is seeded, the area revegetated is still zero if no seeded species become established, a situation not uncommon (Bainbridge 2007). Furthermore, >50% of surviving outplants have flowered and produced seed within 3 y in some projects, potentially expanding the area revegetated (Abella et al. 2012b). Given that outplanted shrubs can rapidly grow to heights of 40–50 cm within 3 y—reestablishing shaded microsites important to natural plant recruitment—it is possible that outplanting can also stimulate natural plant establishment. Therefore, a management goal using outplanting could be strategically establishing patches of native plants for stimulating recovery within the larger landscape. There are three main best practices well-supported in the literature for increasing success of outplanting: carefully select species, use good planting stock, and perform effective plant care.

1) *Carefully select species*. Species selection is critical to outplanting success because survival and ecological functions of perennial plants differ among species. Also, treatments required for plants to survive vary among species and can affect project costs and logistics. Of 45 native perennial species outplanted in the Mojave Desert, 64% have achieved ≥50% survival in at least one study (Abella and Newton 2009; Abella et al. 2012b; Scoles-Sciulla et al. 2014). Examples of the best-performing species outplanted in three or more studies are in Table 2, including shrubs beneath which desert tortoises construct burrows (Burge 1978; Berry and Turner 1986; Baxter 1988). Generally, large shrubs (e.g., creosote bush) have performed well in outplanting, forbs have performed moderately well, and grasses have struggled. Lowered overall survival in a project may be worth the benefit of diversifying plantings, by including species that do not necessarily survive at high rates but that provide important functions. Even some difficult-to-establish forbs and grasses can still achieve 10–25% survival. In an example of different functions provided by species, some native perennial species (e.g., desert globemallow) exist that can competitively reduce nonnative annuals, or at least become established on sites infested by nonnative annuals (Abella et al. 2011, 2012a). In an example of how species selection affects treatments required, planted cacti have not needed irrigation; whereas, irrigation has doubled survival of white bursage, desert globemallow, and other species (Abella et al. 2015b). The ability of cacti to become established without treatments could be important, because Medica et al. (1982) found that cacti formed >50% of tortoise diets in a dry year. Examining outplanting success and treatments required for little-studied genera, such as *Mirabilis,* that provide important herbaceous perennial forage (Jennings and Berry 2015) could increase the number of tortoise forage species available for outplanting.
2) *Use good planting stock*. Good planting stock can underpin the success of entire projects and requires advance planning. Preparing outplants typically entails ≥6–12 mo of care in nurseries to grow root systems sufficient to provide the best chance of survival in the field (Bainbridge 2007). Plants that are unhealthy leaving the greenhouse often have reduced chance of field survival.
3) *Perform effective plant care.* Treatments to enhance survival after planting at restoration sites are essential for most species. Protection from grazing by small mammals and larger herbivores can be even more important than irrigation (Scoles-Sciulla et al. 2014). It is not uncommon for outplants without protection from grazing to be all or mostly gone from restoration sites within days. An unprotected planting of 100 individuals was killed by animals in <4 h (S.R. Abella, unpublished data). This undesirable herbivory may result from outplants being nutrient-enriched from their nursery propagation (Bainbridge 2007). Enclosing plants in cages or shelters can deter herbivory and increase survival and growth (Figure 4).

Irrigation has enhanced survival in certain studies, potentially making it worth the added cost (Wallace et al. 1980). Species can respond differently to the type of irrigation. For instance, watering by hand improved survival of desert globemallow, whereas a slow-release irrigation gel did not (Abella et al. 2015b). Survival of white bursage increased with both irrigation types. It is also noteworthy that plantings on sites receiving salvaged topsoil had twice the survival of plantings on nontopsoil areas, possibly because organic matter in the salvaged topsoil retained water for gradual extraction by plants (Abella et al. 2015b).

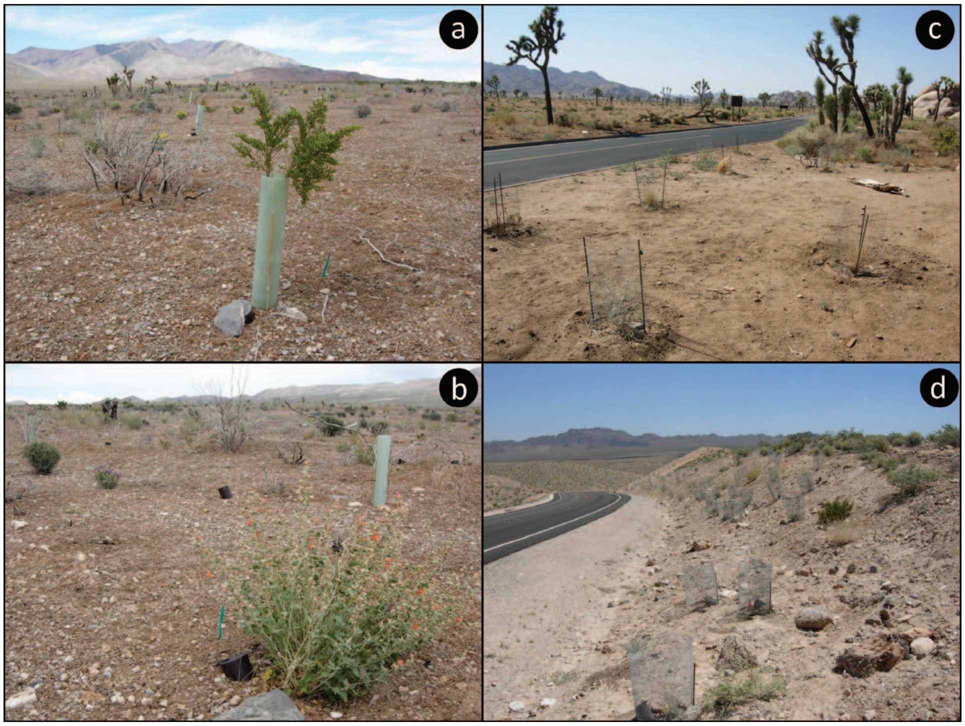

Figure 4. Examples of outplanting and care of perennial plants to revegetate disturbed habitat in the Mojave Desert. The left photos are on the 2005 Goodsprings Fire, southern Nevada, and show **(a)** an outplanted creosote bush *Larrea tridentata* protected by a shelter in the foreground, and **(b)** an outplanted desert globemallow *Sphaeralcea ambigua,* affixed with DriWater as a slow-release irrigation. Wire cages protect outplants from herbivory in roadside revegetation in **(c)** Joshua Tree National Park, California, in 2008, and **(d)** Lake Mead National Recreation Area, Nevada, in 2011. Photos by S.R. Abella.

Other treatments to enhance survival of outplants have not been extensively studied or are not necessarily recommended. Many desert species have relationships with mycorrhizae (Titus et al. 2002), but it is unclear how limiting mycorrhizae are after disturbance. Fertilizing plants in the field has not been recommended because it has not increased survival (Scoles-Sciulla et al. 2014), and augmenting soil fertility raises concerns about nonnative plant growth (Rao et al. 2010). Although nonnative annuals can compete with perennial plants (Rodríguez-Buriticá and Miriti 2009), treating nonnative plants with herbicide did not increase survival of perennial outplants in one study (Scoles-Sciulla et al. 2014).

Action 2: Seeding. Although seeding is risky during any year, it has enhanced establishment of native perennials in some projects. Short-term successes were reported in the 1970s, which was a wet decade, but it was frequently unclear how persistent seedlings were after 1–2-y, short-term studies (Abella and Newton 2009). More recently, some seeded plant establishment occurred during a 14-y monitoring period on a mine restoration site in the northeastern Mojave Desert, but the extent to which seeding improved upon natural plant establishment was uncertain (Ott et al. 2011). Another recent project resulted in no plant establishment over 3 y, despite protecting seeds from mammalian granivory and providing irrigation (Abella et al. 2012b). We emphasize three best practices for seeding in contemporary environments: make controllable factors favorable, match seed treatments to species, and have backup plans for seeding failures.

1) *Make controllable factors favorable.* Managers cannot control the weather and may also have little flexibility for attempting to time seeding with years of favorable weather because of logistical challenges, difficulty of obtaining seed, and deterioration of stored seed. Managers can control, to some extent, the quality and species of seed used, the locations for seeding, and conditions of sites receiving seed. A synthesis published in the 1970s of the phenological timing of perennial species for seed collection, seed storage procedures, and germination requirements is still among the most comprehensive reviews for optimizing seed germination in the Mojave Desert (Kay et al. 1977). Ideally, both viability and germination assays should be performed on seed lots prior to seeding. In some seeding failures, it was unclear whether seeds placed in the field were even viable (Abella and Newton 2009).

   Owing to the usual limitation of availability of native plant seed and to the potential influence of seed source on project outcomes, the question of whether to use locally collected seed (and if so, how local) is commonly raised for desert restoration projects. This issue is unresolved and the subject of ongoing research, because combined genetics and plant performance analyses are required to determine how successful particular seed sources are in different present and anticipated future environments. Given extensive evidence for local adaptation of plants, the current consensus is that seeds for restoration projects should be collected as locally as possible, unless there are specific reasons to expect that genotypes from elsewhere or other environmental site types will perform better (Johnson et al. 2010). In an example of site-type adaptation in the Mojave Desert, Shryock et al. (2015) identified genetic differentiation in desert globemallow populations along environmental gradients of water stress and temperature seasonality.

Certain sites may be more amenable to seeding than others, and conducting preliminary trials across sites is a good strategy for identifying potentially favorable locations for seeding projects (Grantz et al. 1998). If soils are degraded (e.g., erosion-affected soils), ameliorating site conditions should occur before attempting seeding. For example, roughening soil surfaces or using tackifiers to enhance soil and seed retention has potential for building soil seed banks and promoting plant establishment (DeFalco et al. 2012).

2) *Match seed treatments to species.* An important decision is whether to pretreat seeds, such as applying germination stimulants or protective coatings, because these treatments can increase project costs while sometimes being counterproductive. In a short-term project (4 mo) in the Mojave Desert, seeding bare seed resulted in 22% seedling emergence of blackbrush, whereas only 5% emergence occurred from pelletized seed (Jones et al. 2014). Seeding pelletized seed of three shrubs facilitated short-term seedling establishment (within 1 y) in another study, but the seedlings died by the second year (Abella et al. 2015a). Desert seeding projects should include preliminary assays to identify whether seed treatments are beneficial. Moreover, managers could consider "hedging bets," such as by pretreating or pelletizing a portion of seed and not treating the rest of seed.

Similarly, several options exist for treating seeds after they have been seeded on field sites or timing seeding to coincide with optimal conditions. However, effectiveness of these variations has been mixed. Irrigation has increased short-term seedling establishment in some studies but not in others, regardless of natural rainfall (Winkel et al. 1995; Grantz et al. 1998). Soil surface treatments, such as applying mulches, may only be applicable to localized areas (e.g., compacted soils) and have not consistently improved seeding success (Grantz et al. 1998). Abundant seed can be moved around or off site by mammals and invertebrates within days to weeks after seeding (DeFalco et al. 2012). Seed movement by animals does not preclude seedling establishment if some seeds escape predation and are deposited in microsites favorable for germination. Loss of seed has, however, resulted in suggestions to 1) minimize time that seeds reside on the ground before conditions conducive to germination occur, or 2) time seeding to correspond with nonpeak activity of granivores (Suazo et al. 2013). To minimize the time that dormant seeds are exposed to predation, seeds of some species can be pretreated to speed germination (Ostler et al. 2003). Although still no guarantee of success, if seeding can be timed to correspond with wet years and reduce time to germination, it may facilitate at least short-term plant establishment (Grantz et al. 1998; Ott et al. 2011).

3) *Have backup plans for seeding failures.* Even when best known practices for seeding are implemented, seeding may not be successful because of granivory, lack of germination cues, dry weather, or other factors (Bainbridge 2007). As a result, a precautionary approach would include pairing seeding with other actions for enhancing plant cover. For example, combining seeding with outplanting warrants consideration. This approach was already successful for one postburn restoration project: seeding failed completely, but outplanting successfully produced patches of perennial plants that generated their own seed within 3 y (Abella et al. 2012b).

Improve forage quality and quantity

Composition of the annual plant community across the range of the desert tortoise has changed drastically over the past century, with a major increase in nonnative species (Brooks and Esque 2002; Brooks and Berry 2006; Averill-Murray et al. 2012). Nonnative annual grasses are some of the chief increasers and, unfortunately for tortoises, these grasses provide lower quality forage than many native forbs (Oftedal et al. 2002; Medica and Eckert 2007; Hazard et al. 2009; Jennings and Berry 2015). Returning the annual plant community to primarily natives could improve forage for desert tortoises while also reducing chance of nonnative-grass-fueled fires that kill shrubs used by tortoises for cover. Additionally, protecting shrubs from fires maintains fertile islands as locations for recruitment of a diverse native annual plant community (Abella and Smith 2013) potentially important for balanced nutrition of desert tortoises. We evaluated three main actions for favorably changing forage quality and quantity provided to tortoises by the annual plant community: 1) reduce nonnative plants, 2) manage herbivory by nonnative animals on tortoise forage plants, and 3) augment native forage plants.

Action 1: Reduce nonnative plants. There are two priorities for decreasing potential impacts of nonnative plants: reducing abundance of nonnative plants already dominant across the geographic range of the desert tortoise; and limiting the establishment of new nonnative plants. Three main best practices are suggested for reducing nonnative plants in desert tortoise habitat: focus on comprehensively treating damaging, widespread invaders; detect and remove new invaders early; and implement preventive measures from invasive plant science.

1) *Focus on comprehensively treating damaging, widespread invaders*. Treatment of nonnative annual grasses is strongly supported from our synthesis because of their undesirability as desert tortoise forage and their potential to facilitate fire disturbance across large areas, in turn, creating opportunities for invasion by other nonnative plants (Brooks and Esque 2002). Other widespread invaders in desert tortoise habitat are the nonnative annual forbs redstem filaree and Sahara mustard. Although redstem filaree provides some forage value (Hazard et al. 2010), a concern with this species is that it forms monocultures that may exclude a diversity of native annuals nutritionally important to tortoises (Steers and Allen 2010; Jennings and Berry 2015). Sahara mustard has invaded desert tortoise critical habitats and often forms dense stands (Berry et al. 2014a). Sahara mustard is not a good food plant and contains oxalates, which are likely harmful to tortoise health (Jacobson et al. 2009). Nonnative grasses are the top priority for control at this time, followed by Sahara mustard, redstem filaree, and other invaders that form low-diversity stands or provide poor forage.

   When nonnative annuals are reduced, native annuals have generally responded positively. For example, Brooks (2000) found that thinning *Schismus* via cutting doubled density of native annuals in a wet year. Some of the increasing natives were bristly fiddleneck *Amsinckia tessellata* and other species that Jennings and Berry (2015) identified as forage favored by desert tortoises. Native annuals also remained green 2 wk later in spring on *Schismus*-thinned plots, which could allow tortoises to forage longer (Brooks 2000).

   Carefully timed herbicide applications have reduced nonnative plants while increasing native annuals. On a burned site in the western Mojave Desert, Steers and Allen (2010) found that applying the postemergent herbicide Fusilade early in the growing season reduced nonnative grasses as well as the forb redstem filaree. Species richness and cover of native annuals were up to three times greater in treated compared with untreated areas. Glyphosate and some other herbicides were effective in reducing or eliminating germination of Sahara mustard (Abella et al. 2013). Effects of herbicide on the desert tortoise are unclear, but early timed herbicide applications—to exploit the accelerated phenology of nonnative compared with native species (Marushia et al. 2010)—could generally occur when tortoises are inactive (Esque et al. 2014). For example, Steers and Allen (2010) applied herbicide in January. Adult tortoises remain in underground burrows until at least mid-February in some years (Burge 1977; Rautenstrauch et al. 1998), although juveniles may be active from November through February when local temperatures are warm (Wilson et al. 1999). The California Invasive Plant Council (2015) published best-management practices to reduce nontarget effects of herbicides to animals while controlling nonnative plants damaging to wildlife populations, which may be useful in desert tortoise habitats. Potential negatives of nonnative plant treatments must be balanced against the positives of curtailing deterioration of tortoise habitats by nonnative plants.

2) *Detect and remove new invaders early*. A central tenet of invasive species science is that the early detection and removal of new invaders is cheaper and more effective than managing established infestations (Davis 2009). Surveying for incipient populations of nonnative plants along roadsides is a best practice, because roads can be entry points for nonnative plants (Brooks 2009; Berry et al. 2014a). An early detection program surveyed 3,300 km of roads between 2009 and 2011 in the eastern Mojave Desert, including in desert tortoise habitat, and removed >37,000 nonnative plants (Abella et al. 2009). Prioritizing surveys in wet years may enhance detection of species and maximize benefit from limited resources for surveys and treatments. Roads should be incorporated into broader landscape strategies for nonnative plant management because many firmly established nonnative plants are not, or at least are no longer, distributed only along roadsides (Craig et al. 2010). Thus, restricting surveys only to roadsides may provide a misleading impression of the distribution of nonnative plants, because desert washes, old disturbances, and areas of seemingly undisturbed desert should also be part of detection programs. Washes in particular facilitate the spread of Sahara mustard (Berry et al. 2014a).

3) *Implement preventive measures from invasive plant science*. A concern is that desert tortoise habitats have already been invaded by several species of nonnative plants and the potential exists for transport of new invasive plants by ongoing or proposed human activities, such as renewable energy development near, or adjacent to, critical habitats (Hernandez et al. 2014). It is prudent to view desert tortoise habitats as susceptible to new invaders in the future, in addition to ongoing expansion of incipient populations of species such as Sahara mustard not yet as widespread as nonnative grasses (Berry et al. 2014a). Many best-management practices developed in invasive plant science are applicable to help forestall further invasion of desert tortoise habitats by nonnative plants (Abella 2014). For example, Lake Mead National Recreation Area, including tortoise habitat in the eastern Mojave Desert, recently developed a nonnative plant management plan detailing practices such

as cleaning vehicles to remove seeds (National Park Service 2010). Desert tortoise recovery areas may benefit from the development of similar long-term, nonnative plant management plans.

Action 2: Manage herbivory by nonnative animals on tortoise forage plants. In addition to potential for nonnative animals to affect perennial plant cover and soil in desert tortoise habitats (Webb and Stielstra 1979; Brooks et al. 2006), there may be similarity in forage consumed by nonnative animals and desert tortoises, which is important for understanding contemporary vegetation condition. Early studies comparing food habits of desert tortoises with domestic livestock and feral burros were frequently based on analysis of scats (e.g., Hansen and Martin 1973; Hansen et al. 1976; Coombs 1979; Medica et al. 1982). These studies indicated similarities in diets among tortoises, cattle, and feral burros, with overlap mainly in the grass component. This component is the one most accurately characterized by scat analysis because fibrous material from grasses is less digestible than forbs and passes through the gastrointestinal tract in greater bulk (e.g., Barboza 1995). To more thoroughly characterize diet similarity, scientists began making direct observations of tortoises foraging and counted bites consumed (Jennings and Fontenot 1992; Jennings 2002; Oftedal 2002; Oftedal et al. 2002; Jennings and Berry 2015). Through these studies, it became apparent that forbs were the major and important part of desert tortoise diets. Native forbs were also heavily utilized by nonnative animals. In seven studies across the Mojave Desert, the native annual desert plantain comprised the greatest percentage (11%) of feral burro diets (Abella 2008). Based on bite counts of juvenile desert tortoises, this forb also formed 23% of tortoise diets in the central Mojave Desert (Oftedal et al. 2002). Other forbs preferred by tortoises in at least one study (Jennings and Berry 2015), such as desert wishbone-bush, are also eaten by burros (Abella 2008). Bite counts in the Ivanpah Valley during the 1990s revealed that both cattle and tortoises consumed native annual forbs such as desert dandelion (Avery and Neibergs 1997). Similarly, domestic sheep utilized desert dandelion in a western Mojave Desert allotment (Nicholson and Humphreys 1981).

On landscapes where enhancing forage conditions for desert tortoises is a goal, a conservative approach is ensuring that tortoises do not have to alter their preferred foraging activities because nonnative animals are present (Oldemeyer 1994). This consideration partly led to the first recovery plan for the desert tortoise recommending that grazing of domestic livestock and feral horses and burros be prohibited in Desert Wildlife Management Areas, which generally became designated tortoise critical habitat units (USFWS 1994). By 2009, livestock grazing had been eliminated from 53% of 13,000 km^2 of allotments in tortoise critical habitat (USFWS 2011). Decommissioning livestock allotments remains ongoing in certain areas, though some decommissioned allotments still contain abundant feral horses and burros (Ostermann-Kelm et al. 2009). We suggest two main best practices for nonnative animals in desert tortoise habitat within the context of forage and recovery plan directives for allotment decommissioning: monitor changes in habitats after reducing nonnative animals and strategically deploy exclosures.

1) *Monitor changes in habitats after reducing nonnative animals.* Little monitoring or research has been conducted during the past 20 y to identify transitions within plant communities of desert tortoise habitats following allotment decommissioning or to compare with areas still containing livestock or feral animals. Before/after or grazed/ungrazed comparisons deserve more attention to understand if or when preferred forage plants recover or whether additional actions are needed. It should also be considered that many desert tortoise habitats were grazed by livestock and feral animals for more than a century, which could leave legacies persistent long after the animals are removed (McKnight 1958; Beever 2013; Abella 2015). A possible legacy warranting evaluation is the long-term depletion of soil seed banks of native annual and herbaceous perennial plants preferred by desert tortoises (Minnich 2008). The possibility cannot presently be dismissed that forage plants favored by tortoises remain "missing," or at low abundance, even within areas now protected from herbivory by nonnative animals. Two management implications of this uncertainty are that 1) restoration seed mixtures in priority tortoise habitats could liberally include preferred forage plants, regardless of the prerestoration presence or absence of these plants at contemporary restoration sites (while still ensuring matching species to sites where they are adapted to grow); and 2) monitoring changes in forage composition and foraging activities by tortoises after removing nonnative animals remains an important best practice that should be employed more frequently than it has been.
2) *Strategically deploy exclosures.* When high densities of nonnative animals persist within desert tortoise habitats, strategically excluding the animals from certain areas may benefit vegetation conditions for tortoises. During 3 y in the northwestern Mojave Desert, native perennial grasses were 3–9 times denser inside exclosures compared with areas outside and open to feral burros (Abella 2008). After the Desert Tortoise Research Natural Area had been fenced for 12 y (excluding large herbivores and other disturbances), perennial plant cover was twice as high inside the fence compared with outside (Brooks 1995). Furthermore, the amount and quality of annual plant forage was greater inside the fence (Figure 5).

Action 3: Augment native forage plants. Most efforts aimed at improving forage conditions for the desert tortoise are indirect, such as removing nonnative plants

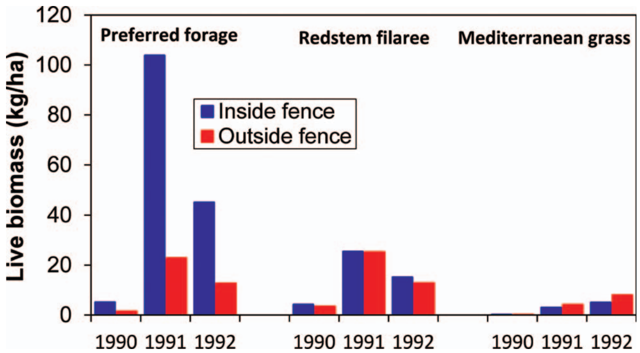

Figure 5. Comparison of the abundance of native annual and herbaceous perennial plants preferred by desert tortoises (preferred forage) with the nonnative redstem filaree *Erodium cicutarium* and Mediterranean grass *Schismus barbatus* inside and outside of fences, among 3 y, in the Desert Tortoise Research Natural Area, California. Data from Brooks (1995).

or livestock, under the assumption that forage plants will then increase naturally. Actively increasing forage plants is another option, but because research is limited to one study that showed potential (Abella et al. 2015a), the best current strategies are implementing further research and adaptive management trials. We suggest two practices: experimentally test forage augmentation strategies, and compare forage augmentation with other candidate actions.

1) *Experimentally test forage augmentation strategies.* A study at the desert tortoise Large-Scale Translocation Site in southern Nevada illustrated that actively augmenting abundance of a native annual forb—desert plantain—preferred by tortoises was feasible when effective treatments were identified (Abella et al. 2015a). Seeding bare seed without protective fencing resulted in minimal plant establishment. However, fencing and using pelletized seed produced six times the density of desert plantain relative to unseeded, unfenced controls. The seeding was followed by 2 y of average rainfall, and the one-time seeding augmented abundance of desert plantain for both years. The study showed that 0.25-ha patches of augmented forage could be established across the landscape, but it also showed that an iterative process was essential for identifying successful treatment combinations.
2) *Compare forage augmentation with other candidate actions.* The costs and benefits of actively augmenting forage remain unclear compared with other candidate actions such as treating nonnative plants or installing exclosures. For example, simply erecting fencing doubled the abundance of desert plantain in the study by Abella et al. (2015a). Yet to be tested is how fencing plus treating nonnative plants compares with the fencing plus seeding treatment. Identifying the cost- and ecological-effectiveness of a range of strategies for enhancing tortoise forage quality should be a priority.

Restore or conserve soil health

Different types of anthropogenic disturbances vary in their immediate and longer term effects on soil and vegetation. On certain soil types, such as desert pavements, even single passes of off-road vehicles leave visible scars of altered soil properties for decades (Adams et al. 1982; Belnap and Warren 2002). On nonpavement soils, several studies involving experimentally driving vehicles over soil have shown increased soil compaction, reduced water infiltration, and increased erosion compared with areas without off-road vehicles (e.g., Eckert et al. 1979; Adams et al. 1982; Webb 1982). Wildfires also can influence soil, with variable effects on different properties such as pH and total and available nutrient contents (Allen et al. 2011). Fires can increase concentrations of soil organic carbon and total nitrogen, likely by partly converting plant material to soil organic matter (Abella and Engel 2013). Elevated soil-nutrient status is not necessarily good for native ecosystems if nonnative plants usurp the additional resources (Allen et al. 2011). Wildfires also can change the structure of fertile islands, by reducing their size and killing the seeds they store (Esque et al. 2010). Severe soil disturbances—those that clear the surface layer of soil through blading or other means—can remove nutrients, biological soil crusts, and soil seed banks (Nishita and Haug 1973; Belnap and Warren 2002; Williams et al. 2013). Guo et al. (1998) reported that 97% of the viable soil seed bank was in the upper 2 cm of soil at a northern Mojave Desert site. By removing upper soil layers, land-clearing disturbances also reduce available rooting depth, which can decrease the size and productivity of perennial plants, affecting cover for desert tortoises (Bedford et al. 2009). In addition to best practices discussed in earlier sections for restoring native plant cover and reducing nonnative plant fuels to protect soils, the literature has emphasized three main actions for conserving or restoring soil health in desert tortoise habitats: 1) salvage topsoil if large soil disturbances are planned, 2) evaluate and remediate soil potentially toxic to tortoises, and 3) decommission certain backcountry roads for habitat enhancement.

Action 1: Salvage topsoil if large soil disturbances are planned. Soil formation is in constant flux, with some desert soils requiring millions of years to develop (McDonald et al. 1995). Topsoil salvage is among the most cost-effective strategies for initiating recovery on severe disturbances (Allen 1995). Salvaging and reapplying topsoil can accelerate plant colonization after disturbance because topsoil contains much of the soil organic matter, biological soil crust organisms (cyanobacteria, algae, lichens, and mosses), soil microbiota, and seed bank (Wallace et al. 1980). For example, survival of perennial plant species doubled when planted on Mojave Desert sites receiving topsoil, which was a benefit nearly equal to irrigating plants (Abella et al. 2015b). We emphasize two critical practices for effective topsoil salvage: carefully plan salvage operations, and carefully store soil to maximize biotic retention.

1) *Carefully plan salvage operations*. Several studies of salvaging desert soils have highlighted the importance of proper salvage procedures to avoid negating the benefits of salvage (e.g., Ghose 2001; Scoles-Sciulla and DeFalco 2009; Abella et al. 2015b). Present knowledge suggests that ideal salvage procedures for Mojave Desert soils include: 1) avoiding areas infested by nonnative plants or soil contaminants; 2) consistently salvaging the upper 5–10 cm; and 3) timing salvage to occur in summer from June through September (and later into autumn if it is a dry year) to capture winter annual seeds dispersed the previous spring, but before seedlings emerge in autumn–winter. Owing to concentration of live material in the upper 5–10 cm of desert soils, salvaging this depth as consistently as possible is important to avoid "diluting" the biota-rich layer with subsoil. For example, Scoles-Sciulla and DeFalco (2009) found that germinable seed density was reduced by 86% for the upper 4 cm of soil (the most important for seedling emergence) when salvaging the upper 30 cm of soil. Further research could examine benefits of strategically salvaging "fertile island" soil below the canopy driplines of shrubs to increase efficiency of nutrient and seed capture, thereby reducing space required to store soil (Abella et al. 2015b). Salvaging some interspace soil would also be wise to ensure capture of seeds of annual plants primarily growing in the open (Guo et al. 1998).
2) *Carefully store soil to maximize biotic retention*. Topsoil should be stored as briefly as possible before reapplication. Ideally, soil should not be stored at all and immediately applied to a recipient site. Practical constraints typically result in some storage being required, and this unavoidably creates some loss of biotic components. If soils must be stored, storage time ideally would not exceed 6–12 mo (Ghose 2001; Scoles-Sciulla and DeFalco 2009). For long storage durations, treatments could be used to potentially extend longevity of biotic components. Some possible treatments may include transplanting vegetation (such as native cactus pads) on top of the piles to potentially enhance longevity of soil microorganisms. These types of treatments have not been tested extensively and should be considered experimental. Also, the height of stockpiles should be as short as possible, preferably not $>$45–60 cm tall, because the deeper the pile, the more likely biotic components will be lost. If storage space limitations require deeper piles, consider periodically turning the soil. Stored soil should be protected, such as via tackifier, from wind erosion or other damage.

Action 2: Evaluate and remediate soil potentially toxic to tortoises. Toxic materials are a potentially insidious threat to desert tortoises because the presence of toxicants may not be superficially obvious and they can accumulate in the bodies of long-lived tortoises (Seltzer and Berry 2005; Jacobson et al. 2014; Kim et al. 2014). We suggest two main practices for reducing potential effects of toxicants to desert tortoises: assess potential for toxic soils, and avoid or remediate toxic soils before conducting other habitat activities.

1) *Assess potential for toxic soils*. A first step is identifying known or suspected areas with contaminants within, or adjacent to, desert tortoise critical habitats and protected areas (Chaffee and Berry 2006). For example, synthesizing records of past mining activities or identifying mine sites through remote sensing or field reconnaissance can help delineate potential locations contaminated by mining. Vectors for transport of mine wastes, such as prevailing winds or desert washes, should be evaluated (Kim et al. 2012, 2014). Other potential sources of contaminants, such as old industrial sites and associated downwind areas, should also be assessed. Ideally, soil sampling and laboratory analysis for typical contaminants, (e.g., arsenic and mercury) would be conducted to characterize areas of known or suspected contamination (Chaffee and Berry 2006).
2) *Avoid or remediate toxic soils before conducting other habitat activities*. If potential problem areas are identified, habitat enhancement actions that could draw desert tortoises to problem areas should be avoided or conducted elsewhere. Furthermore, strategies such as sealing old mines or limiting off-road vehicle use to avoid generating dust and transporting contaminants could be paramount before implementing other habitat improvements (Kim et al. 2014).

Action 3: Decommission certain backcountry roads for habitat enhancement. Strategically decommissioning and revegetating a portion of the extensive backcountry dirt road network can increase soil and plant community health (Brooks and Lair 2009). Best practices previously discussed for establishing perennial plants can also be applicable to revegetating decommissioned roads, along with practices for managing nonnative plants that can be transported along roads. Even in cases where roads have no apparent effect on adjoining vegetation, the area of the road represents a nonvegetated surface that removes an area of potential desert tortoise forage. One road 50 km long and 10 m wide, for example, occupies 50 ha of land, which is equivalent to a large home range of an adult desert tortoise (Harless et al. 2010). Practices for augmenting forage quality and quantity may be appropriate on decommissioned roads because these are already severely disturbed environments that could potentially be converted to special areas of desert tortoise forage. In addition, several studies have highlighted two main best practices for decommissioning backcountry roads: ameliorate topographic and soil surface alterations, and limit postrestoration vehicle incursions.

1) *Ameliorate topographic and soil surface alterations*. After road decommissioning, a key objective is restoring surface water flow by reconnecting severed

drainages (e.g., ephemeral stream channels) and roughening compacted road surfaces to improve water retention (Schlesinger and Jones 1984; Nichols and Bierman 2001). Recontouring road berms can be critical to restore natural water flow, whereas treatments such as ripping and constructing check dams can increase soil roughness and water infiltration (Bainbridge 2007). More work is required to understand effectiveness of mulching because the type of mulch can affect soil water and potentially erosion. For example, Walker and Powell (2001) found that straw mulch reduced soil water, likely via absorption, on a decommissioned road in the central Mojave Desert. Likewise, Caldwell et al. (2006) cautioned that additional research be directed toward developing ripping techniques for reducing soil compaction, to avoid undesirable effects like raising salts from subsoils into the rooting zone.

2) *Limit postrestoration vehicle incursions.* Another priority for road decommissioning is limiting subsequent vehicle trespasses through proper signage, traffic barriers, and camouflage (Bainbridge 2007). Investing in barriers and revegetation at road entry points can efficiently use limited resources by reducing trespasses that undermine other restoration efforts (Weigand and Rodgers 2009). Raking out vehicle tracks, applying stains for color blending, and installing live and dead plant material (vertical mulching) can blend decommissioned roads into the landscape (Bainbridge 2007; Smith et al. 2012). As DeFalco and Scoles-Sciulla (2011) noted, it is good practice to systematically document damage from unauthorized trespasses, because monetary value can be assigned to damaged public resources in court cases.

Conclusion

Changes in desert tortoise habitat during the past 150 y, including grazing by nonnative animals, invasion of nonnative plants, wildfires, proliferation of roads, urban and agricultural development, and other land-clearing disturbances, have affected habitat quantity and quality (USFWS 1994; Lovich and Bainbridge 1999; Brooks and Lair 2009; Berry et al. 2013, 2014b). Degradation of desert tortoise habitat includes lowered availability of large perennial plants as cover sites, reduced forage quality, and greater area harmful to tortoises (e.g., contaminated soil). Habitat management tools—such as actively revegetating disturbed soil and reducing nonnative plants—have potential to partly ameliorate habitat degradation. What has not been evaluated, however, is whether actively restoring habitat increases health or population sizes of desert tortoises. Short-term indicators that could provide insight into responses of desert tortoises to improved habitat may include enhanced growth or fecundity of individual tortoises, reduced evidence of mortality, or construction of new burrows by tortoises.

This review reinforces recommendations in the desert tortoise recovery plans (USFWS 1994, 2011) to implement a comprehensive suite of habitat enhancements. To date, no examples of this approach exist for the desert tortoise. Individual habitat management activities have not been related to the desert tortoise (e.g., vegetation restoration, treating nonnative plants) or have been mainly conducted in isolation as the only habitat management activity (Averill-Murray et al. 2012). To expand on the positives of individual actions such as fencing (e.g., Brooks 1995; Berry et al. 2014b), a next step is identifying priority locations to implement coordinated, integrated actions for recovery of habitat. Such actions could include mitigating roads, revegetating disturbances, enhancing forage quality, and reducing nonnative plants. It is important to ensure that these actions are not undermined by factors such as toxic soils. Sufficient science exists, including that summarized here, to identify candidate actions for implementing comprehensive habitat-enhancement trials. Improving habitat is already known to benefit other components of desert ecosystems (e.g., perennial plant communities), so implementing habitat enhancement measures is a conservative, low-risk strategy with high potential for assisting desert tortoise recovery.

Supplemental Material

Please note: The *Journal of Fish and Wildlife Management* is not responsible for the content or functionality of any supplemental material. Queries should be directed to the corresponding author for the article.

Reference S1. Abella SR. 2014. Effectiveness of exotic plant treatments on National Park Service lands in the United States. Invasive Plant Science and Management 7:147–163.

Found at doi: 10.3996/052015-JFWM-046.S1; also available at http://www.bioone.org/doi/abs/10.1614/IPSM-D-13-00058.1 (209 KB PDF).

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