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Potential Spread of Cheatgrass and Other Invasive Species by Feral Horses in Western Colorado☆

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ABSTRACT

The invasive grass cheatgrass (*Bromus tectorum* L.) presents major challenges for land management and habitat conservation in the western United States. Feral horses *(Equus ferus caballus)* have become overabundant in some areas of the West and can impact fragile semiarid ecosystems. Amid ongoing efforts to control cheatgrass in the Great Basin, we conducted a study to determine if feral horses contribute to the spread of cheatgrass through distribution via their feces. We collected feral horse fecal samples from Little Book Cliffs Herd Management Area in western Colorado in 2014. Fecal samples were dried, and 20 from each of 3 collection sessions were cultivated to examine germination success. Six species germinated from 18 samples (30%; mostly one plant per sample where germination occurred), including cheatgrass from 8% of samples. In a separate study we examined the diet of this same horse population using fecal plant DNA barcoding. Plant species that germinated were rare in the diet and germinated from fewer samples than expected relative to their detection in the diet. Our results suggest that feral horses could be contributing to cheatgrass propagation. Native ungulates and domestic cattle also have this potential. Although management of all large ungulates is necessary to mitigate cheatgrass spread, control of feral horse numbers is particularly necessary.

Introduction

The National Research Council recommended evaluating the potential contribution of feral horses *(Equus ferus caballus)* to the spread of cheatgrass (*Bromus tectorum* L.; NRC, 2013), as this plant has significantly modified grazing lands in the western United States (Anderson and Inouye, 2001). The Bureau of Land Management (BLM) in the US Department of Interior administers 247.3 million acres (100.1 million ha) of public land, including management of the feral horses that inhabit 31.7 million acres (12.8 million ha) of those lands in 177 herd management areas (HMAs) distributed among 10 western states. Understanding the ecosystem effects of feral horses is important for wildlife conservation and habitat management as ungulates are a potential vector for dispersal of invasive species (Bartuszevige and Endress, 2008) and because HMAs overlap with priority wildlife habitat management areas (e.g., for greater sage-grouse) and public lands affected by cheatgrass invasion.

Cheatgrass was introduced to North America more than 100 yr ago (Stewart and Hull, 1949; Mack, 1981) and in recent decades has been recognized as a critical threat to ecosystem and habitat management across the western United States (Mack, 1981; Mealor et al., 2013; Chambers et al., 2014a; Coates et al., 2016). The magnitude of the problem is highlighted by widespread distribution across sagebrush ecosystems, including vast areas of the Great Basin (Trowbridge et al., 2013; Schmelzer et al., 2014; Boyte et al. 2016) and Wyoming Basin (Mealor et al., 2013; Manier et al., 2014), with potential for additional expansion in the future (e.g., Bradley, 2009; Friggens et al., 2012). The spread of invasive species such as cheatgrass is driven by a combination of factors, including facilitation by human activities and land uses, and interactions with natural processes such as climate and fire (Stewart and Hull, 1949; Mack, 1981; Bradford et al. 2006; Mealor et al., 2013; Svejcar et al. 2017). Propagule pressure, a seed source in the case of cheatgrass and other annuals, and condition of the ecosystem and its ability to resist invasion are two critical biological factors affecting invasions (Davies and Johnson 2011), both of which may be affected by feral horses.

The spread and proliferation of cheatgrass is affected by several environmental factors. It is well suited to both shrub and grassland habitats ranging from 500 to 6 000 f. above sea level (150 − 1 800 m; Skinner et al., 2008) and areas with mean annual precipitation from 6

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to 22 in (15 − 55 cm); thus it is adaptable to a wide range of semiarid and mesic habitat types. Cheatgrass is a winter annual, germinating late in the growing season and producing roots and a leaf rosette that persist through the winter. In spring it initiates growth rapidly with warming temperatures and produces seeds in 5 − 6 wk (Stewart and Hull, 1949). However, recent research has confirmed plastic phenology of some populations whereby plants in xeric environments complete flowering a week before mesic populations initiate flowering (Dyer et al 2012). Cheatgrass also has a strong positive response to fire and is highly flammable, leading to short-fire return intervals that reduce the vigor of perennial grasses, remove shrubs, and result in increasing dominance of cheatgrass over time (Stewart and Hull, 1949; Balch et al., 2013; Mealor et al., 2013; Chambers et al., 2014b). Although cheatgrass may be grazed by livestock and wildlife while green, this represents a short portion of the year; thus, the optimal forage period is quite narrow temporally (Stewart and Hull, 1949; Mealor et al., 2013).

Ungulates are a potential vector for dispersal of invasive species (Bartuszevige and Endress, 2008), as they can disperse plant species by consuming them in one area and depositing them in another via feces, as well as by transferring seeds in their pelage (Albert et al., 2015). Horses, cattle *(Bos taurus),* and cervids can all excrete viable seeds in their feces (Cosyns et al., 2005; Bartuszevige and Endress, 2008). The effect of endozoochory (consumption of seeds) varies among plant species, depending on whether seeds can survive mastication, ingestion, and digestion and whether they are consumed at all (Malo and Suárez, 1996). In one study 5 − 22% of seeds fed to a horse were recovered from the feces, and of these 2 − 64% subsequently germinated (Harmon and Keim, 1934). Another study reported germination from 13% to 90% of seeds fed to horses (St John-Sweeting and Morris, 1990) and found smaller and harder seeds had higher survival after passing through the digestive tract.

On western public lands mule deer *(Odocoileus hemionus)* and elk *(Cervus elaphus)* tend to be nomadic or migratory across the landscape, and cattle are moved on and off the range seasonally. Yet feral horses are present in the same HMA year-round, imparting a different impact than other ungulates. Depending on the digestibility of forage and species of plant, it takes 18 − 48 hr for consumed seeds to be excreted by horses (Van Dyk and Neser, 2000). The highest transmission rate is 2 − 3 d after ingestion, and some seeds were excreted up to 10 d after consumption (St John-Sweeting and Morris, 1990). In 2 d a feral horse can travel many miles from where it consumed vegetation, having the potential to disseminate seeds across the landscape.

In studies examining semiferal horses in Europe, fecal seed content correlated positively with plant species abundance in the field and in the diet, with 21 − 27% of plant species found in the area germinating from horse fecal samples (Cosyns et al., 2005; Cosyns and Hoffmann, 2005). To understand what is likely to germinate from feces, it is important to know what an animal has consumed. Plant DNA barcoding is an emerging alternative to microhistology for diet analyses (Valentini et al., 2009). A previous study by King and Schoenecker (2019) indicated that plant DNA barcoding might be more accurate than microhistology at representing diet in horse feces. Building on these analyses, we conducted a germination study to determine viability of seeds in horse fecal samples and evaluate potential contribution of feral horses to the spread of invasive species, particularly cheatgrass. Specifically, we determined which plant species survived ingestion and germinated from horse fecal samples, as well as how the proportion of these species related to the diet of horses from the same study area.

Methods

Study Area

We collected feral horse fecal samples in the Little Book Cliffs Herd Management Area (HMA), near Grand Junction, Colorado (UTM 12 722588, 4342571) in spring (May), summer (August), and fall (October) of 2014. The area is semiarid with a mean precipitation of 2.3 cm (± 2.16 standard deviation [SD]) and a mean temperature of 9.6°C (± 8.5°C SD) over the previous 10 yr (RAWSWestern Regional Climate Center, n.d). Precipitation averaged 4.4 cm/mo during the study period, mostly in August and September (King et al., 2018; King and Schoenecker, 2019). The landscape consists of mesa tops dissected by deep canyons, with water sources located throughout the upland area in tanks provided for the horses.

There are four primary plant communities within the HMA; cheatgrass *(B. tectorum)* is found in all four types:

1. Piñon-juniper woodland: characterized by piñon pine (*Pinus edulis* Engelm.) and juniper (*Juniperus osteosperma* [Torr.] Little, and *J. monosperma* [Englem. Sarg.]) with varying amounts of herbaceous and shrub forage in the understory (West, 1988);
2. Mixed mountain shrub: a variable mixture of shrub species including Gambel oak (*Quercus gambelii* Nutt.), mountain mahogany (*Cercocarpus montanus* Raf.), snowberry (*Symphoricarpos* spp. Duham.), sumac (*Rhus trilobata* Nutt.), and big sagebrush (*Artemisia tridentata* Nutt.) with abundant grasses and a diversity of other herbaceous species (West, 1988, Landfire, 2016, p. 162);
3. Salt-desert shrub: shadscale and fourwing saltbush (*Atriplex confertifolia* [Torr. & Frem.] S. Watson and *A. canescens* [Pursh] Nutt., respectively), greasewood (*Sarcobatus vermiculatus* [Hook.] Torr.), and winterfat (*Krascheninnikovia lanata* [Pursh] A. Meeuse & Smit) predominate with sparse cover of grasses and forbs that tolerate salinity and alkalinity (West, 1988);
4. Sagebrush-grassland: typically characterized by Wyoming big sagebrush (*A. tridentata* ssp. *wyomingensis* Beetle & Young), but also basin big sage (*A. tridentata* ssp. *tridentata*), black sagebrush (*A. nova* A. Nelson), and rubber rabbitbrush (*Ericameria nauseosa* [Pall. ex Pursh] G.L. Nesom & Baird), codominant with grasses and a diverse mixture of other herbaceous species (West, 1988; Landfire, 2016).

Experimental Design and Data Collection

We subjectively divided the HMA into sampling areas using ArcGIS (version 10.30.1, ESRI) where each area could be sampled by ground observers in 1 d. Each area included sagebrush-grassland, woodland, and at least one type of shrub community and avoided areas inaccessible to horses or ground observers on foot. We developed a random sampling scheme of sampling areas to collect fecal samples for this and other studies from across the entire HMA. The order and choice of sampling areas to visit were randomized on each sampling occasion (May, August, and October), but coverage of the HMA remained consistent. To collect fecal samples we walked across a sampling area in a group of 3 − 6 people in parallel lines roughly 10 − 20 m apart, with each person covering a 3- to 4-m-wide belt transect, conducting as many sweeps as needed to cover the area. We collected samples from fecal piles that were visually assessed to be 0 − ≈6 mo old (most were estimated to be ≈ 2 − 3 mo old; King et al., 2018; King and Schoenecker, 2019). Samples were collected in a paper bag: two whole boli from the middle of a pile were placed in the same bag, using nitrile gloves or sterile tongue depressors to manipulate the fecal bolus. Paper bags containing samples were placed in large cotton bags to air dry under shelter during each sampling session. Subsequently, paper bags were placed in a drying oven at 40°C for 3 d and stored. The same methods were followed on each field sampling visit, resulting in collection of > 1 800 samples from across the HMA.

Germination Experimental Design

We used 60 samples (20 from each collection period) for the germination study. We randomly selected samples for inclusion but excluded samples that were moldy, part of a stud pile (a large dung pile marked by multiple stallions), or small, indicating they were probably deposited by a foal. We also excluded samples that had touched the ground in the field as these may have picked up seeds that were not consumed. The dried fecal samples were gently broken up by hand and planted one sample to a row in plastic trays of sterile composting soil. Each sample row was marked with a colored stake to identify it by sample name. Each tray also contained a control row ($n = 20$) consisting of sterile composting soil with no feces added. These seed trays were maintained in a greenhouse at Colorado State University (CSU) under ambient light and temperature conditions and watered daily. We conducted the germination experiment from 26 March, 2015 to 31 July, 2015, at which time there was no further evidence of germination. Plant species were identified by a CSU botanist (J. Hardin) from their leaves or seeds. We recorded the number of shoots (individual plants) and dry weight of aboveground plant material as a measure of biomass.

Proportion of Diet

To compare plant species in the diet to the proportion of germinated species, we sent 90 subsamples from the overall dataset (30 from each season) rehydrated in vials of alcohol to Jonah Ventures laboratory (https://jonahventures.com) for plant DNA barcoding analyses in order to examine horse diet. These were analyzed at the laboratory as described by King and Schoenecker, 2019). One sample did not produce enough amplifiable DNA, leaving 89 samples in the analyses. Results were presented as proportion of each sample made up by an operational taxonomic unit (OTU). Multiple OTUs of the same genus were combined for analyses. We summed the percentage of each genus OTU across all samples. Overall percentage component of the diet was formed from the sum across all samples as a percentage of the total.

Statistical Analyses

We explored which plant species germinated from fecal samples and described this qualitatively. We tested whether there was a difference in dry weight of germinated plants across sampling seasons with a Kruskal-Wallis test in the statistical software R (R Core Team, 2017). We used a nonparametric test due to lack of normality in our small sample size. We evaluated differences in detection of species that germinated and species in horse diets derived from plant DNA barcoding with a chi-squared test in *Microsoft Excel* using plant DNA data as an expected value.

Results

Germination of Fecal Samples

No plants germinated from controls. Of the 60 fecal samples that were cultivated in the greenhouse, 18 samples (30%) had plants germinate and survive. Fifty-five individuals representing six species germinated: desert madwort (*Alyssum desertorum* Stapf.), hedgemustard/tumblemustard (*Sisymbrium* spp.), spike dropseed (*Sporobolus cryptandrus* [Torr.] A. Gray), cheatgrass (*B. tectorum*), bluegrass (*Poa* spp.), and sixweeks fescue (*Vulpia octoflora* [Walter] Rydb.; formerly *Festuca octoflora* Walter). *Alyssum desertorum, Sisymbrium* spp., and *B. tectorum* are non-native, invasive species (native status of *Poa* spp. depends on the species). When germination occurred, there was only one species per sample, except for one instance in which two species germinated from the same sample (*A. desertorum* and *Poa* spp.). Fewer species germinated from fecal piles deposited in spring (two species) compared with summer (five species) and fall (four species). The greatest dry weight biomass was from summer fecal piles: most dry weight consisted of *A. desertorum* (46.5 g), followed by *B. tectorum* (17.9 g; Kruskal-Wallis $K = 7.1928$, $df = 2$, $P = 0.02742$; Fig. 1). *B. tectorum* made up 22% of the total dry weight and germinated from 5 (8%) of the 60 fecal samples, all collected during summer or fall (see Figs. 1 and 2).

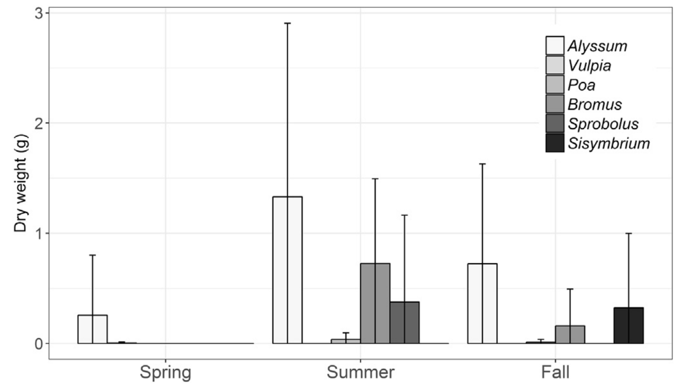

Figure 1. Mean dry weight (± 95% confidence intervals) of plant species that germinated from feral horse fecal samples collected from Little Book Cliffs Wild Horse Herd Management Area, Colorado in three different seasons in 2014.

Comparison with Diet Analyses

Results of plant DNA barcoding indicated 42 genera or plant groups made up > 20% of horse diet when summed across all samples (King and Schoenecker, 2019). Although forbs made up 19.24% of the diet, the forb species that germinated from the fecal samples were detected only in trace amounts (*Alyssum* spp. not detected *Sisymbrium* spp. = 0.01% of diet). Graminoids made up 68.76% of the diet, of which *Poa* spp. made up 14.81%. *Bromus* spp. accounted for 8.86% of the diet, although only 1.80% of that was *B. tectorum*. *Sporobolus* spp. made up a trace amount of the diet (0.05%). *Vulpia* spp. were not detected by plant DNA barcoding, although fescues (*Festuca* spp.) made up 0.10% of the diet; because *Vulpia* spp. were formerly recognized as *Festuca* spp. (USDA Plants, 2018), these data are presented together here. The grass species that germinated corresponded to grass genera that were evident in almost all samples, whereas the forbs that germinated were rare in diet analyses (see Fig. 2). All species germinated less than would be expected from their presence in fecal samples, except for *A. desertorum* ($X^2 = 270.3967$, $df = 4$, $P = < 0.0001$; see Fig. 2).

Discussion

We had low germination rates from our fecal samples, compared with studies on domestic and feral horses in more mesic habitats (Cosyns et al., 2005; Cosyns and Hoffmann, 2005; Quinn et al., 2008) and compared with the detection of these species in horse diets from the same area (King and Schoenecker, 2019). Only 6 species germinated from horse feces in our study, whereas in a European study 21 − 27% of plant species present germinated and 8 − 27 species germinated from

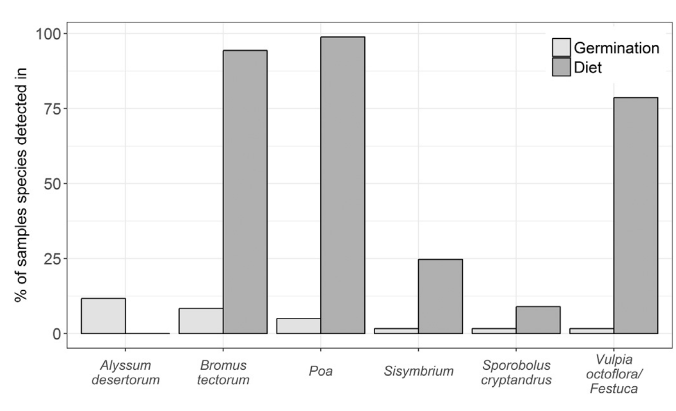

Figure 2. Difference in detection of plant species that germinated from feral horse fecal samples collected in Little Book Cliffs Wild Horse Herd Management Area, Colorado in samples collected for the germination experiment (60 samples) and those collected for plant DNA barcoding analyses (90 samples).

samples collected in California and Colorado (Cosyns et al., 2005; Cosyns and Hoffmann, 2005; Wells and Lauenroth, 2007; Quinn et al., 2008). This may be attributed to seeds being compromised when we dried our samples but may also be the result of low productivity (low number of seeds) or low gut-survival rate of forage species seeds from this semiarid area. The latter two possibilities are more likely as fecal samples were dried at approximately the maximum environmental temperature in the study area. The greatest germination rate was from samples collected later in the year, which correlates with availability of viable seeds in this ecosystem.

The low proportion of the diet made up by the species that germinated was unexpected, although the grasses were almost ubiquitous in diet samples. Plant DNA barcoding detects plant species by amplifying chloroplast trnL (Valentini et al., 2009). The relative abundance of chloroplasts is a representation of the relative protein content of that plant, rather than the biomass. Lack of, or low, detection in the diet could be due to low relative abundance of chloroplasts from these species or be indicative of low protein content. We expected to see a similar proportion of species consumed to those that germinated; other studies have found the proportion of germinating seeds correlates with local abundance (Couvreur et al., 2005). Unfortunately, we did not have data on plant species abundance in the study area.

Importantly, the diet analyses showed that horses consume cheatgrass (King and Schoenecker, 2019) and the germination experiment showed that horses can distribute viable seeds in their feces. Although germination may be reduced by digestion (Blackshaw and Rode 1991), our work shows that desert alyssum, hedgemustard, and cheatgrass seeds can remain viable after passing through the digestive tract of a horse. The principal dispersal mechanism of cheatgrass is physical attachment to the pelage of animals via small stiff hairs on the glumes and the awn attached to each lemma (Stewart and Hull, 1949; Mealor et al., 2013). Thus, although it may not be a primary mechanism of dispersal, the potential for long distance movement and introduction of cheatgrass into new habitats is additionally created by transport within the digestive system of horses. The potential for cheatgrass spread from horse feces could be across a substantial area. For example, maximum distances traveled by feral horses in Australia were 5–17.5 miles per day (Hampson et al. 2010). This maximum equates to the distance from one side to the other of an average western HMA. Plant DNA barcoding analyses indicated that cheatgrass made up only 1.8% of horse diet but was found in horse diets across all three seasons we sampled. It germinated in 8% of fecal samples, all of which were collected in August and October, but even this small amount may be sufficient to have an effect on invasive plant distributions when multiplied by many horses over a period of years. While these results have important ramifications for management, it should be noted that horses are not the only grazers on the landscape that may consume and spread invasive plant species (Bartuszevige and Endress, 2008). Further research would be worthwhile to examine the contribution of domestic livestock, wildlife species, *and* feral horses to dispersal of cheatgrass and other invasive plants in arid and semiarid landscapes, especially those that include important rangeland habitats and conservation areas.

Implications

Across the Great Basin, detrimental effects of cheatgrass through shortened intervals between fires and conversion of native grass and sagebrush habitats to cheatgrass dominance create considerable management challenges (Knapp, 1996; Cox and Anderson, 2009). Feral horse herds roam across sagebrush and grassland habitats, including priority habitats in and around wild horse and burro HMAs in the western United States that are also challenged by cheatgrass invasion. We have demonstrated that feral horses consume cheatgrass and excrete viable seeds, confirming their potential to contribute to cheatgrass range expansion and distribution within these important rangeland ecosystems. Whereas horses can directly contribute to the propagation of cheatgrass through their feces, they may also be contributing to its persistence through the effects of overgrazing (Knapp, 1996; Davies et al., 2014). More than half of the on-range feral horse population on public lands is found in Nevada, and the population continues to grow. Together with climate change and frequent fires, overgrazing and other land uses can stress arid and semiarid ecosystems, making them less resilient to invasive species (Chambers et al., 2007; Chambers and Wisdom, 2009; Chambers et al., 2014a, 2014b). While livestock are moved seasonally on the range, horses are present in HMAs year round. Where horses are at high densities, this can lead to degradation of the rangeland, decreasing ecosystem resistance. Managing cheatgrass therefore requires management of all grazers on public lands, including better control of feral horse numbers.

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References

Albert, A., Auffret, A.G., Cosyns, E., Cousins, S.A.O., D'hondt, B., Eichberg, C., Eycott, A.E., Heinken, T., Hoffmann, M., Jaroszewicz, B., Malo, J.E., Mårell, A., Mouissie, M., Pakeman, R.J., Picard, M., Plue, J., Poschlod, P., Provoost, S., Schulze, K.A., Baltzinger, C., 2015. Seed dispersal by ungulates as an ecological filter: a trait-based meta-analysis. Oikos 124, 1109–1120.

Anderson, J.E., Inouye, R.S., 2001. Landscape-scale changes in plant species abundance and biodiversity of a sagebrush steppe over 45 years. Ecology Monographs 71, 531–556.

Balch, J.K., Bradley, B.A., D'Antonio, C.M., Gomez-Dans, J., 2013. Introduced annual grass increases regional fire activity across the arid western USA (1980-2009). Global Change Biology 19 (1), 173–183.

Bartuszevige, A.M., Endress, B.A., 2008. Do ungulates facilitate native and exotic plant spread? Seed dispersal by cattle, elk and deer in northeastern Oregon. Journal of Arid Environments 72, 904–913.

Blackshaw, R.E., Rode, L.M., 1991. Effect of Ensiling and Rumen Digestion by Cattle on Weed Seed Viability. Weed Science 39, 104–108.

Bradford, J.B., Lauenroth, W.K., 2006. Controls over invasion of *Bromus tectorum*: The importance of climate, soil, disturbance and seed availability. Journal of Vegetation Science 17, 693–704.

Bradley, B.A., 2009. Regional analysis of the impacts of climate change on cheatgrass invasion shows potential risk and opportunity. Global Change Biology 15, 196–208.

Chambers, J.C., Bradley, B.A., Brown, C.S., D'Antonio, C., Germino, M.J., Grace, J.B., Hardegree, S.P., Miller, R.F., Pyke, D.A., 2014b. Resilience to stress and disturbance, and resistance to *Bromus tectorum* L. invasion in cold desert shrublands of western North America. Ecosystems 17, 360–375.

Chambers, J.C., Miller, R.F., Board, D.I., Pyke, D.A., Roundy, B.A., Grace, J.B., Schupp, E.W., Tausch, R.J., 2014a. Resilience and resistance of sagebrush ecosystems: Implications for state and transition models. Rangeland Ecology & Management 67 (5), 440–454.

Chambers, J.C., Roundy, B.A., Blank, R.R., Meyer, S.E., Whittaker, A., 2007. What makes Great Basin sagebrush ecosystems invasible by *Bromus tectorum?* Ecological Monographs 77 (1), 117–145.

Chambers, J.C., Wisdom, M.J., 2009. Priority research and management issues for the imperiled Great Basin of the western United States. Restoration Ecology 17, 707–714.

Coates, P.S., Ricca, M.A., Prochazka, B.G., Brooks, M.L., Doherty, K.E., Kroger, T., Blomberg, E. J., Hagen, C.A., Casazza, M.L., 2016. Wildfire, climate, and invasive grass interactions negatively impact an indicator species by reshaping sagebrush ecosystems. Proceedings of the National Academy of Sciences of the United States of America 113 (45), 12745–12750.

Cosyns, E., Claerbout, S., Lamoot, I., Hoffmann, M., 2005. Endozoochorous seed dispersal by cattle and horse in a spatially heterogeneous landscape. Plant Ecology 178, 149–162.

Cosyns, E., Hoffmann, M., 2005. Horse dung germinable seed content in relation to plant species abundance, diet composition and seed characteristics. Basic Applied Ecology 6, 11–24.

Couvreur, M., Cosyns, E., Hermy, M., Hoffmann, M., 2005. Complementarity of epi- and endozoochory of plant seeds by free ranging donkeys. Ecography 28, 37–48.

Cox, R.D., Anderson, V.J., 2009. Increasing native diversity of cheatgrass-dominated rangeland through assisted succession. Journal of Range Management 57, 203–210.

Davies, K.W., Johnson, D.D., 2011. Are we "missing the boat" on preventing the spread of invasive plants in rangelands? Invasive Plant Science Management 4, 166–172.

Davies, K.W., Collins, G., Boyd, C.S., 2014. Effects of feral free-roaming horses on semi-arid rangeland ecosystems: an example from the sagebrush steppe. Ecosphere 5 (10), 127.

Dyer, A.R., Hardison, J.L., Rice, K.J., 2012. Phenology constrains opportunistic growth response in *Bromus tectorum* L. Plant Ecology 213, 103–112.

Friggens, M.M., Warwell, M.V., Chambers, J.C., Kitchen, S.G., 2012. Modeling and predicting vegetation response of western USA grasslands, shrublands and deserts to climate change. In: Finch, D.M. (Ed.), Climate change in grasslands, shrublands, and deserts of the interior American West: a review and needs assessment. USDA Forest Service, Rocky Mountain Research Station, General Technical Report, RMRS-GTR-285, Washington, DC, USA, pp. 1–20.

Hampson, B.A., De laat, M.A., Mills, P.C., Pollitt, C.C, 2010. Distances travelled by feral horses in outback Australia. Equine Veterinary Journal 42, 582–586.

Harmon, G.W., Keim, F.D., 1934. The percentage and viability of weed seeds recovered in the feces of farm animals and their longevity when buried in manure. Agronomy Journal 26, 762.

King, S.R.B., Schoenecker, K.A., 2019. Comparison of methods to examine diet of feral horses from non-invasively collected fecal samples. Rangeland Ecology and Management. In Press. https://doi.org/10.1016/j.rama.2019.02.005.

King, S.R.B., Schoenecker, K.A., Fike, J.A., Oyler-McCance, S.J., 2018. Long-term persistence of horse fecal DNA in the environment makes equids particularly good candidates for noninvasive sampling. Ecology and Evolution 8, 4053–4064.

Knapp, P.A., 1996. Cheatgrass (*Bromus tectorum* L) dominance in the Great Basin Desert. Global Environmental Change 6, 37–52.

Landfire, 2016. Landfire/GAP Land Cover Map Unit Descriptions. Available at:. US Department of Agriculture, Forest Service, US Department of Interiorwww.landfire.gov/evt.php, Accessed date: 13 August 2018.

Mack, R.N., 1981. Invasion of *Bromus tectorum* L into western North America: an ecological chronicle. Agro-Ecosystems 7, 145–165.

Malo, J.E., Suárez, F., 1996. New insights into pasture diversity: the consequences of seed dispersal in herbivore dung. Biodiversity Letters 3, 54–57.

Manier, D.J., Aldridge, C.L., O'Donnell, M., Schell, S.J., 2014. Human infrastructure and invasive plant occurrence across rangelands of southwestern Wyoming, USA. Journal of Rangeland Management 67 (2), 160–172.

Mealor, B.A., Mealor, R.D., Kelley, W.K., Bergman, D.L., Burnett, S.A., Decker, T.W., Fowers, B., Herget, M.E., Noseworthy, C.E., Richards, J.L., Brown, C.S., Beck, K.G., Fernandez-Gimenez, M., 2013. Cheatgrass management handbook. Managing an invasive annual grass in the Rocky Mountain region, Rocky Mountain Cheatgrass Management Project. University of Wyoming and Colorado State University, Laramie, WY, and Fort Collins, CO, USA, 136 pp.

National Research Council, 2013. Using science to improve the BLM wild horse and burro program: a way forward. The National Academies Press, Washington, DC, USA.

Quinn, L.D., Kolipinski, M., Coelho, V.R., Davis, B., Vianney, J.-M., Batjargal, O., Alas, M., Ghosh, S., Lauren, D., 2008. Germination of invasive plant seeds after digestion by horses in california germination of invasive plant seeds after digestion by horses in California. Natural Areas Journal 28, 356–362.

R Core Team, 2017. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

RAWS Western Regional Climate Center https://wrcc.dri.edu/cgi-bin/rawMAIN.pl?coCPNR, Accessed date: 14 December 2018.

St John-Sweeting, R.S., Morris, K.A., 1990. Seed transmission through the digestive tract of the horse. Proceedings of the 9th Australian Weeds Conference, pp. 137–139.

Schmelzer, L., Perryman, B., Bruce, B., Schultz, B., McAdoo, K., McCuin, G., Swanson, S., Wilker, J., Conley, K., 2014. Case Study: reducing cheatgrass (*Bromus tectorum* L.) fuel loads using fall cattle grazing. Professional Animal Science 30, 270–278.

Skinner, M., Ogle, D.G., St. John, L., Briggs, J., Neese, E., 2008. Plant guide: cheatgrass, *Bromus tectorum* L. US Department of Agriculture, Natural Resources Conservation Service, National Plant Data Center, Washington, DC, USA Available at:. plants.usda.gov/plantguide/pdf/pg_brte.pdf, Accessed date: 9 August 2018.

Stewart, G., Hull, A.C., 1949. Cheatgrass (*Bromus tectorum* L.)—an ecologic intruder in southern Idaho. Ecology 30 (1), 58–74.

Svejcar, T., Boyd, C., Davies, K., Hamerlynck, E., Svejcar, L., 2017. Challenges and limitations to native species restoration in the Great Basin, USA. Plant Ecology 218, 81–94.

Trowbridge, W., Albright, T., Ferguson, S., Li, J., Perryman, B., Nowak, R.S., 2013. Explaining patterns of species dominance in the shrub steppe systems of the Junggar Basin (China) and Great Basin (USA). Journal of Arid Land 5, 415–427.

US Department of Agriculture [USDA], 2018. Plants database. Available at:. Natural Resources Conservation Serviceplants.usda.gov, Accessed date: 1 August 2018.

Valentini, A., Pompanon, F., Taberlet, P., 2009. DNA barcoding for ecologists. Trends in Ecology and Evolution 24, 110–117.

Van Dyk, E., Neser, S., 2000. The spread of weeds into sensitive areas by seeds in horse faeces. Journal of South African Veterinary Association 71, 173–174.

Wells, F.H., Lauenroth, W.K., 2007. The potential for horses to disperse alien plants along recreational trails. Rangeland Ecology & Management 60, 574–577.

West, N.E., 1988. Intermountain deserts, shrub steppes, and woodlands. In: Barbour, M.G., Billings, W.G. (Eds.), North American terrestrial vegetation. Cambridge University Press, New York, NY, USA, pp. 209–—230.