Rangeland Ecology & Management 69 (2016) 52–58

Contents lists available at ScienceDirect

Rangeland Ecology & Management

journal homepage: http://www.elsevier.com/locate/rama

Cattle as Dispersal Vectors of Invasive and Introduced Plants in a California Annual Grassland☆

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A R T I C L E I N F O

Article history:
Received 17 April 2015
Received in revised form 13 October 2015
Accepted 13 October 2015

Key words:
California rangelands
cattle grazing
endozoochory
epizoochory
invasive plants
seed dispersal

A B S T R A C T

Plant invasions are a threat to rangelands in California. Understanding how seeds of invasive plants are dispersed is critical to developing sound management plans. Domestic livestock can transport seeds long distances by ingesting and passing seeds in dung (endozoochory) or by the attachment of seeds to skin and fur (epizoochory). Our objective was to characterize the role of cattle as seed dispersers of both invasive and noninvasive species via endozoochory and epizoochory in a Sierra foothills rangeland. To quantify endozoochory, we sampled dung from two dry-season grazing periods and evaluated seed content by growing dung for 3 months in a greenhouse. To quantify epizoochory, we collected seeds directly from the fur of 40 cattle. We categorized the invasion status and functional groups of all species found and quantified landscape-scale vegetation composition in order to determine whether dispersal mode was associated with functional group, invasion status, or vegetation composition. Finally, we evaluated the potential for the noxious weed medusahead (*Taeniatherum caput-medusae* [L.] Nevski) to travel long distances on cattle fur using a detachment experiment with a model cow. We found that forbs were more likely to be dispersed by endozoochory, and invasive species were more likely to be dispersed by epizoochory. Medusahead was dispersed exclusively by epizoochory and was able to travel up to 160 m on a model cow. Our results suggest that cattle may be an important dispersal vector for both invasive and noninvasive plants.

Introduction

Seed dispersal is a critical stage in every plant's life history, and differences in dispersal mode help determine the spatial distribution of species within a community (Rousset and Gandon, 2002; Levine and Murrell, 2003; Schupp et al., 2010). Dispersal of introduced plants can promote invasion into new areas (Cain et al., 2000; Sakai et al., 2001) and can accelerate the rate of spread after establishment by increasing the average distance seeds traveled (Kot et al., 1996; Hastings et al., 2005; Nathan, 2006). Animals are particularly powerful vectors for dispersal because they can increase the distance a seed is able to disperse and its chances for germination once it is deposited (Vittoz and Engler, 2007). On rangelands, livestock and other large mammalian herbivores participate in seed dispersal (Tews et al., 2004; Bartuszevige and Endress, 2008). Successful prevention of invasion into new locations, as well as management of existing invasions, requires a better understanding of the role of livestock in seed transport (Parks et al., 2008; Hogan and Phillips, 2011).

Livestock can disperse seeds through either endozoochory (ingestion and passage of seed through the gastrointestinal tract of an animal) or epizoochory (attachment to the outside of a passing animal). While both methods permit long-distance dispersal, the two mechanisms are likely to transport different types of plants. For example, livestock are selective in their diet preferences and often prefer certain functional groups of plants over others (Rutter, 2006). Likewise, although many different species of plants may be eaten by animals, only a subset of those produce seeds that are able to survive the harsh conditions of the digestive tract (Gardener et al., 1993; Cosyns et al., 2005b; Traveset et al., 2007). Because many highly invasive species are unpalatable to cattle, this group may be under-represented in cattle dung. Furthermore, seeds can be retained in the guts of cattle for hours to days (Razanamandranto et al., 2004; Whitacre and Call, 2006) and thus

☆ Research was funded by a US Department of Agriculture (USDA) National Institute of Food and Agriculture (NIFA) grant 2012-67019-19362 in the Agriculture and Food Research Initiative (AFRI) program. JC was supported by a McNair scholarship and the Berkeley Scholars Program. PM was supported by the Swiss National Science Foundation (n°PBELP3_146538).

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http://dx.doi.org/10.1016/j.rama.2015.10.009
1550-7424/

seed composition in dung may not reflect the local vegetation composition. Similarly, seeds that are dispersed via epizoochory may also contain only a subset of the local vegetation, because seeds that attach to animals often possess morphologies such as awns or barbs that enable them to readily stick to fur or skin (Couvreur et al., 2004b; Römermann et al., 2005; Bläß et al., 2010). Epizoochorous seeds may fall immediately in the area surrounding their progenitor or become deeply lodged in the animal's hide, traveling long distances before dropping in a new location (Mouissie et al., 2005; Couvreur et al., 2008).

The rangelands of California support large numbers of livestock and are also some of the most heavily invaded grasslands in the world (Seabloom et al., 2006), making them an ideal system in which to evaluate the role of livestock in the dispersal of exotic and invasive plants. California rangelands provide 80% of the forage for the state's $3.05 billion cattle industry (Biswell, 1956; Bartolome, 1987; D'Antonio et al., 2002; California Department of Food and Agriculture, 2014) and are vital to the state's economy. Today, almost all of California's varied grasslands are dominated by exotic, annual grasses and forbs of Eurasian origin (Baker, 1989; Bartolome et al., 2007). A massive invasion of exotic flora began with the arrival of Spanish missionaries in 1769 (Biswell, 1956; Bartolome, 1987); in the centuries following, these invaders spread throughout the state, greatly reducing the cover and abundance of native plants. Many species from this initial wave of invasion are now so ubiquitous and integral to the structure and function of California's modern grasslands they are considered "naturalized." Some of these invaders, like slender wild oat (*Avena barbata* Pott ex Link) and long-beaked stork bill (*Erodium botrys* Cav. Bertol), were intentionally introduced by the missionaries as forage for livestock, but the vast majority were weeds in their country of origin and dispersed throughout California inadvertently as seeds in packing material or on the livestock (Baker, 1989).

Today, California faces new invasions and range expansions from non-native species like medusahead (*Taeniatherum caput-medusae* [L.] Nevski) (Young, 1992; Meimberg et al., 2010). Unlike the forage species introduced by the Spanish missionaries, medusahead (among others) is considered a problematic invasive because it threatens both the biodiversity of ecosystems in California annual grasslands and elsewhere in the intermountain west (Davies et al., 2008) and the economic interests of California's agriculture industry (Duncan et al., 2004). Highly invasive species are defined as detrimental to public health, agriculture, recreation, wildlife, or property (Sheley et al., 1999). Medusahead is not palatable to livestock during the reproductive stage of its life cycle (Swenson et al., 1964; Young, 1992; Hamilton et al., 2015) and is therefore unlikely to be dispersed via endozoochory. However, the seeds contain barbed awns that may enable dispersal via epizoochory. Although management recommendations for medusahead assume epizoochory is possible (Davies, 2008), neither its dispersal mode nor the potential for long-distance dispersal on cattle has been evaluated. Evaluating dispersal distances for seeds traveling on animal vectors is a key to predicting the rate of spread of invasive species (Kot et al., 1996; Cain et al., 2000; Clark 2001; Hastings et al., 2005) and can enable managers to anticipate and prevent introduction of medusahead into pastures that remain uninvaded.

Considering the economic consequences for California's rangelands, it is critical that we understand the role of livestock as vectors for dispersal of plants and, in particular, of highly invasive species. To further this goal, we examined the role of beef cattle as seed dispersers in a Sierra Nevada foothills grassland that is currently in the initial stages of invasion from several invasive plants. Our study focused on four main questions: 1) Which species are being dispersed through epizoochory and/or endozoochory? 2) Are species' abundance on the landscape, invasion status, functional group, and seed morphology correlated with either epizoochorous or endozoochorous dispersal? 3) Are cattle acting as dispersal vectors for invasive plants and, if so, through which dispersal method? and 4) How far can we expect the seeds of the important noxious weed medusahead to disperse? In addition to providing valuable information in the role of the livestock as seed dispersers in California rangelands, we hope to provide explicit advice on limiting spread of medusahead at the seed dispersal stage.

Methods

Study Area

This study took place at the University of California Sierra Foothill Research and Extension Center (SFREC), approximately 30 km east of Marysville, Yuba County, California (39°15′N, 0121°17′W). The climate is Mediterranean with hot, dry summers; cool, moist winters; and precipitation confined between October and May. Mean annual precipitation is 71 cm, and the mean annual temperature is 15°C. The SFREC ranges in elevation from 210 m to 580 m. Our study was conducted in two adjacent grazed pastures of approximately 10 ha each. Both of these pastures are grasslands interspersed with oak trees and bordered by a creek with a small riparian zone. The grassland habitat is dominated by naturalized exotic grasses and forbs such as slender wild oat (*Avena barbata* Pott ex Link), soft brome *(Bromus hordeaceus)*, and several species of clover *(Trifolium)*. The tree species are mainly blue oak (*Quercus douglasii* Hook. and Arn.) and valley oak (*Quercus lobata* Née). The riparian zone contains many species of rush, sedge, and forb not found in the rest of the grassland.

Epizoochory

To determine which species were being dispersed via epizoochory, we herded cattle through an adjacent pasture invaded by medusahead, as well as other common weedy species. All cattle were deliberately herded through a dense patch of medusahead because we were particularly interested in whether cattle transport seeds of this noxious weed via epizoochory. Thus while many other species were also present, results should be interpreted within the context of the study design: The results may under-represent species other than medusahead. Similarly, results may only be representative of medusahead dispersal in pastures with large patches of medusahead. Cattle were then placed in a livestock corral chute 100 m from the pasture and inspected for seeds. Three observers collected seeds from each cattle during a 10-minute search using a fine comb, tweezers, and a cattle shredder brush. We inspected cattle in groups of 10 on 2 sampling days in early June and 2 days in early July of 2014 for a total of 40 cattle.

To quantify the species composition of the vegetation available for epizoochorous dispersal, we established seven 100-m transects at two locations within the pasture (including through the medusahead patch). The starting point for each of the first transects was selected randomly with subsequent transects placed 20 m apart, parallel to the first and to the slope of the hill. We estimated the percent cover of dominant vegetation using ocular estimates with trained and calibrated observers within 50 cm × 50 cm quadrats every 10 m along each transect. Percent cover was only recorded for the 10 most abundant species and averaged across all quadrats to estimate the average percent cover of each species across the entire pasture. These 10 species were medusahead, slender wild oat Italian ryegrass (*Lolium perenne* L. ssp. *multiflorum* Lam. Husnot), ripgut brome (*Bromus diandrus* Roth), compact brome (*Bromus madritensis* L.), soft brome, bulbous canarygrass (*Phalaris aquatica* L.), barbed goatgrass (*Aegilops triuncialis* L.), longbeak stork's bill, and rose clover (*Trifolium hirtum* All.). All other species were recorded collectively and comprised an average of 15.6% percent of the meadow's total cover. Any species found during the cattle brushing that did not have a calculated species average was assigned a mean percent cover of 1%. Each species was assigned to a functional group (forb or grass), invasion status, and seed-morphology category. A species' invasion status (native, limited invasive, moderately invasive, or highly invasive) was determined using categories established by the California Invasive Plant Council Inventory (Cal-IPC Inventory).

Categories reflect the level of ecological impact, and other factors, including the economic impact or difficulty of management, are not included. Species known to be of non-native origin that did not appear in the Cal-IPC Inventory were categorized as "exotic." Seed morphology was quantified using the US Department of Agriculture plant species database (USDA plants database) and was broken into two categories: those possessing epizoochorous attachment mechanisms (barbs, hooks, or other attachment morphologies) versus those without any obvious attachment device.

Endozoochory

To identify which species were being dispersed by cattle via endozoochory, we examined dung-germinating seed content (Malo et al. 1995; Dai, 2000; Cosyns et al., 2005a). We collected dung patties from 45 plots distributed across five blocks (9 plots per block) in a single pasture. We randomly collected a single dung patty from each 20 × 20 m plot in late October 2013, after the grazing season was complete, but before the onset of the rainy season. Dung was deposited during two 3-week periods of grazing (in June and in early October) by a herd of 48 cattle. Dung patties were dried at 30°C for 1 week, a temperature regularly experienced during summer in the Sierra foothills and thus unlikely to affect germination. After the patties were dried, we weighed and divided each patty in half. One half of each sample was soaked overnight in a Ziploc bag with six times its mass in water. The other halves were stored in the laboratory in the case of needing to repeat the experiment. The next day, samples were kneaded to produce a "slurry" mixture intended to encourage the maximum germination of seeds. This treatment simulates the long-term decomposition of cattle dung and not necessarily the germination potential of a single season since dung often dries and hardens under field conditions, slowing decomposition and seed release (Dai, 2000). All dung samples were placed on a bed of standard potting soil in trays in a greenhouse and watered as needed. We identified and removed seedlings twice per week for 12 weeks.

To quantify species composition in the pasture from which dung patties were collected, each plot was surveyed by a team of three to four trained observers during a timed search of 5 minutes. Observers recorded both the presence and percent cover of all plant species within each plot. We then calculated the average percent cover for each species, which served as a proxy for its relative abundance across the landscape. Each of the identified species was also assigned a functional group, invasion status, and seed morphology category with the same protocol used for the epizoochory assessment.

Medusahead Dispersal

To measure the average dispersal distance of a medusahead seed, we constructed a model cow using a cattle-hide rug (Ikea) wrapped around a PVC pipe (1.2 m long, 0.5 m diameter). The model cow was designed to represent a cow's belly, a body part likely to acquire seeds because of its long hairs and frequent contact with grassland vegetation. We attached 40 seeds to the model cow and walked it along a 100-m transect in a pasture dominated by slender wild oat where medusahead was absent. The model cow was walked at a height of 50 cm, stopping to count the number of remaining seeds every meter for the first 10 m and every 10 m thereafter. If seeds remained attached at the end of the 100 m, we walked the model cow back along the transect, stopping to inspect it every 20 m until all the seeds had dropped. All sampling was conducted in May of 2013, and the experiment was repeated 20 times.

Statistical Analysis

We constructed multiple linear regression models for both our endozoochory and epizoochory data to examine whether a species' abundance, invasion status, functional group, and seed morphology are related to its dispersal method. Seed data were log-transformed to satisfy the assumptions of multiple linear regression. For both models, we began by using all four explanatory variables and then eliminated extraneous variables that did not significantly change the model's results ($p < 0.05$). Model selection was conducted in a backwards stepwise function using likelihood ratio tests to compare model fit. Residuals and quantile plots were used to evaluate the fit of final models. To determine which dispersal method contributes more to the spread of noxious invasive species, we compared the percentage of seeds in dung and on cattle that belonged to the highly invasive and the moderately invasive categories using a student's *t*-test. All statistics were conducted using R version 3.1.1 (R Development Core Team, 2015).

Results

A total of 1 342 seedlings from 30 species were counted and identified in dung patties and 4 108 seeds from 19 species were found on the live cattle (Table 1). The three most abundant species in dung patties were rose clover, dovefoot geranium (*Geranium molle* L.), and toad rush (*Juncus buffonius* L.), and they comprised 72.7% of the total dung seedlings. The three most abundant species found on live cattle were bulbous canarygrass, mouse barley (*Hordeum murinum* L.), and Italian ryegrass, and they comprised 89.8% of the total cattle seeds; however, the species composition of the seeds changed radically between our first and second sampling dates (Table 2).

Moderately invasive species made up a significantly higher percentage of the total seeds dispersed through epizoochory (mean = 93.2% ± 10.4 SD) than through endozoochory (mean = 57.3 % ± 21.1 SD) (two-sided *t*-test, df = 66.19, $p < 0.0001$). Similarly, highly invasive species made up a significantly higher percentage of the total seeds dispersed through epizoochory (mean = 2.3% ± 6.7 SD) than through endozoochory (mean = 0%, two-sided *t*-test, df = 39, $p = 0.032$).

Epizoochory

Functional group, invasion status, and abundance all significantly affected the likelihood of seed transport via epizoochory (F = 15.64, df = 232, $p < 0.0001$, $r^2 = 0.27$, Fig. 1). Although functional group was significant in the model as a whole ($p < 0.0001$), there was no significant difference between the number of forb seeds (mean = 4.4 ± 8.2 SD) and grass seeds (mean = 97.8 ± 115.1 SD) per cattle ($p = 0.06$). There were significantly more seeds from moderately invasive species (mean = 98.13 ± 115 SD) than any other invasion status ($p < 0.001$, see Fig. 1). Moderately invasive species also had the highest species richness with 36.8% of the total species found on cattle. Native species comprised 21.1%, exotics 15.8%, and limited and highly invasives 10.5% (Fig. 2). Abundance on the landscape was correlated slightly negatively with the number of seeds per cattle ($p < 0.01$).

Endozoochory

Functional group and invasion status were the only parameters in our endozoochory model that significantly influenced the number of seedlings in dung (F = 32.98, DF = 210, $p < 0.0001$, $r^2 = 0.37$). Forbs were the most diverse group (63% of the total species number) by comparison with grasses (27%), and the mean number of forb seedlings per dung patty (mean = 27.13 ± 19.91 SD) significantly exceeded the number of grass seedlings (mean = 0.88 ± 4.8 SD, $p < 0.0001$, Fig. 2).

Significantly more seedlings from moderately invasive species were found in dung compared with exotics or natives ($p < 0.05$, see Fig. 2). Moderately invasive species contributed the most seedlings per dung patty (mean = 15.26 ± 11.1 SD) followed by exotics (mean = 6.64 ± 5.5 SD), natives (mean = 5.91 ± 15.5 SD), and limited invasives (mean = 0.20 ± 2.6 SD). No seedlings from any highly invasive species were found. Interestingly, despite high abundance of seeds in dung, moderately invasive species were represented by only a few species

Table 1
Comparison of seedlings per dung patty with seeds per cattle. Epizoochory data are average values calculated across two time periods collected in June and July of 2014. Endozochoory values are average seed numbers per species from 45 dung patties collected in October 2013. Both dung and live cattle data were taken from adjacent pastures with similar species composition

Species	Invasion status	Functional group	*Endozoochory*		*Epizoochory*	
			Mean seedlings per dung sample (± SE)	% of total seedlings	Mean seeds per cattle (± SE)	% of total seeds
Aegilops truncialis	Highly invasive	Grass	–	–	0.13 ± 0.06	0.1
Amsinkia menziesii	Native	Forb	0.02 ± 0.02	0.07	1 ± 0.3	0.9
Avena sp.	Moderately invasive	Grass	0.1 ± 0.09	0.4	1.8 ± 0.4	1.7
Brachypodium distachyon	Exotic	Grass	0.1 ± 0.07	0.2	1.3 ± 0.3	1.3
Bromus hordeaceus	Limited invasive	Grass	–	–	1.4 ± 0.3	1.4
Capsella bursa-pastoris	Exotic	Forb	0.02 ± 0.02	0.07	–	–
Cynodon dactylon	Moderately invasive	Grass	0.5 ± 0.3	1.7	–	–
Cyperus eragrostis	Native	Forb	1.9 ± 1.8	6.3	–	–
Elymus caput-medusae	Highly invasive	Grass	–	–	0.5 ± 0.1	0.5
Epilobium ciliatum	Native	Forb	0.2 ± 0.1	0.7	–	–
Erodium sp.	Exotic	Forb	–	–	0.2 ± 0.1	0.2
Festuca perennis	Moderately invasive	Grass	0.04 ± 0.03	0.2	20.7 ± 5.9	20.2
Festuca temulenta	Exotic	Grass	0.02 ± 0.02	0.07	0.5 ± 0.2	0.5
Hordeum murinum	Moderately invasive	Grass	–	–	29.6 ± 3.7	28.79
Galium parisiense	Exotic	Forb	0.02 ± 0.02	0.1	–	–
Geranium molle	Exotic	Forb	4.2 ± 0.67	14.2	–	–
Juncus bufonius	Native	Forb	2.8 ± 0.54	9.5	0.05 ± 0.03	0.04
Madia gracilis	Native	Forb	–	–	0.3 ± 0.2	0.3
Matricaria discoidea	Exotic	Forb	0.02 ± 0.02	0.1	–	–
Medicago polymorpha	Exotic	Forb	0.02 ± 0.02	0.1	–	–
Paspalum dilitatum	Native	Grass	0.04 ± 0.03	0.2	–	–
Phalaris aquatica	Moderately invasive	Grass	–	–	42 ± 11.9	40.9
Picris echoides	Limited invasive	Forb	0.02 ± 0.02	0.1	0.03 ± 0.03	0.02
Plantago lanceolata	Limited Invasive	Forb	0.1 ± 0.1	0.5	–	–
Polypogon monspeliensis	Limited Invasive	Grass	0.04 ± 0.04	0.2	–	–
Pseudognaphalium stamineum	Native	Forb	0.4 ± 0.4	1.3	–	–
Rorippa paslustris	Native	Forb	0.5 ± 0.2	1.7	–	–
Setaria pumila	Exotic	Grass	0.04 ± 0.03	0.2	–	–
Sherardia arvensis	Exotic	Forb	0.2 ± 0.1	0.8	–	–
Silybum marianum	Exotic	Forb	–	–	0.03 ± 0.03	0.02
Stellaria media	Exotic	Forb	0.5 ± 0.2	1.7	–	–
Torilis arvensis	Moderately invasive	Forb	–	–	1.5 ± 0.6	1.4
Trifolium hirtum	Moderately invasive	Forb	14.6 ± 1.7	48.9	1.3 ± 0.4	1.3
Trifolium subterraneum	Exotic	Forb	0.8 ± 0.3	2.8	–	–
Veronica persica	Exotic	Forb	0.04 ± 0.03	0.2	–	–
Vicia villosa	Exotic	Forb	0.5 ± 0.1	1.8	–	–
Zanthium spinosum	Native	Forb	–	–	0.03 ± 0.03	0.02

(13.3% of the total number of species, see Fig. 2) while exotic species represented the most diverse group (43%), followed by natives (23.3%) and limited invasives (10.0%).

Table 2
Mean number of seeds per cattle (± SE) from epizoochory experiment for each month from two sampling points in June and July of 2013. Seeds per cattle are average estimates from 20 individuals per sampling date

Species	*June*	*July*
	Mean seeds per cattle (± SE)	Mean seeds per cattle (± SE)
Aegilops truncialis	0.2 ± 0.1	0.05 ± 0.05
Amsinkia menziesii	1.9 ± 0.6	–
Avena sp.	1.25 ± 0.3	2.25 ± 0.7
Bromus diandrus	1.6 ± 0.4	1.05 ± 0.4
Bromus hordeaceus	2.7 ± 0.4	0.15 ± 0.1
Elymus caput-medusae	0.5 ± 0.2	0.45 ± 0.1
Erodium sp.	0.25 ± 0.2	0.20 ± 0.1
Festuca perennis	38.25 ± 10.5	3.15 ± 1
Festuca temulenta	0.65 ± 0.3	0.35 ± 0.3
Hordeum murinum	42.65 ± 5.3	16.45 ± 2.9
Juncus bufonius	0.1 ± 0.1	–
Madia gracilis	0.65 ± 0.3	–
Phalaris aquatica	84.05 ± 19.9	–
Picris echioides	–	0.05 ± 0.05
Silybum marianum	0.05 ± 0.1	–
Torilis arvensis	2.8 ± 1.1	0.10 ± 0.1
Trifolium hirtum	2.05 ± 0.1	0.60 ± 0.2
Zanthium spinosum	0.05 ± 0.05	–

Medusahead Dispersal

The average dispersal distance of medusahead seeds on a model cow was 7.3 m with a standard error of 0.52 m and a median dispersal distance of 2 m (Fig. 3). Of the total seeds attached on each repetition, an average of 50% dropped within the first 2 m. However, the farthest traveling 5% of seeds achieved dispersal distances of 30–160 m.

Discussion

Our study demonstrates the importance of cattle as seed dispersers in California rangelands. Seeds readily dispersed via both endozoochory and epizoochory, and the two modes acted as complementary processes. Both dung and cattle fur contained high levels of species diversity, though different sets of species were associated with each dispersal mode. Invasive species were far more likely to be dispersed on animal fur than from ingestion by cattle, highlighting the importance of this method in the movement of invasive species on the landscape. Similarly, the functional composition of suites of seeds dispersed via endozoochory differed from that of epizoochory.

For example, legumes and forbs greatly outnumbered grasses in both seed abundance and species diversity in cattle dung. This result is only partially consistent with the dietary preferences of free-ranging cattle across ecosystems: A meta-analysis of cattle diet studies showed cattle demonstrate a preference for a diet of 70 ± 10% legumes, though both grass and legumes are necessary for a healthy diet (Rutter, 2006). Comparably, we found that nearly 50% of seeds in dung were from the

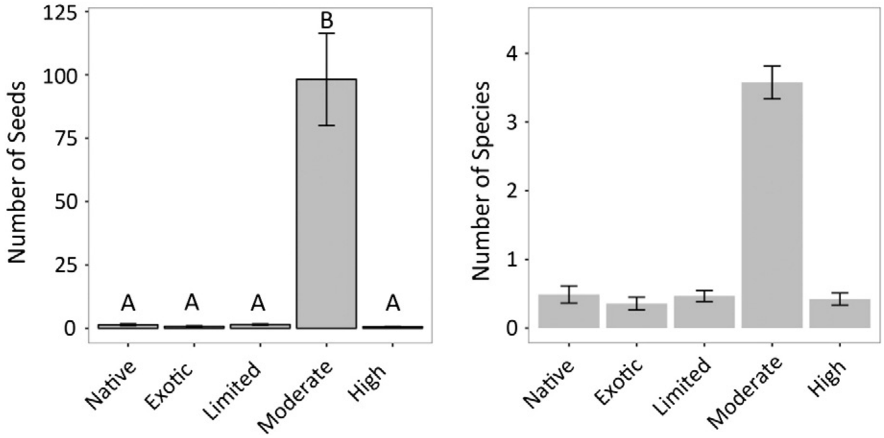

Fig. 1. Mean number of seeds (left panel) and species (right panel) per cattle from epizoochory experiment for each category of invasion ($n = 40$). Different letters represent significant differences, and error bars display 1 SE.

legume rose clover, and seeds from moderately invasive species were significantly more common as a result of the high number of seeds from this species. However, the diversity of seeds in dung was high, with seeds contributed from all categories of invasive and native species. Most previous studies regarding the impacts of endozoochoric dispersal on invasion have focused on a binary system of exotics and natives, without any distinction between the levels of potential threat from exotic species (Constible et al., 2005; Bartuszevige and Endress, 2008; Williams et al., 2008). Our study went further by investigating differences in dispersal efficacy among several types of exotic species.

The two most threatening categories of invasive species (moderately and highly invasive) were more likely to be dispersed via epizoochory than endozoochory. Moderately invasive seeds were also both more abundant and diverse on cattle fur than any other invasion category. This finding is consistent with other studies that connect large herbivores to the epizoochorous dispersal of exotic and invasive species (Constible et al., 2005; Dovrat et al., 2012). Highly invasive species, including medusahead, were not found in any of our dung samples, confirming the low palatability to grazers of many of the most highly invasive species in California (Peters et al., 1996; Hamilton et al., 2015).

Neither endozoochorous nor epizoochorous dispersal was positively related to local vegetation composition, reflecting the selective nature of these dispersal modes. Numerous studies have shown that endozoochory can have important impacts on spatial vegetation patterns. For example, Malo and Suarez (1995) found that dung patties in

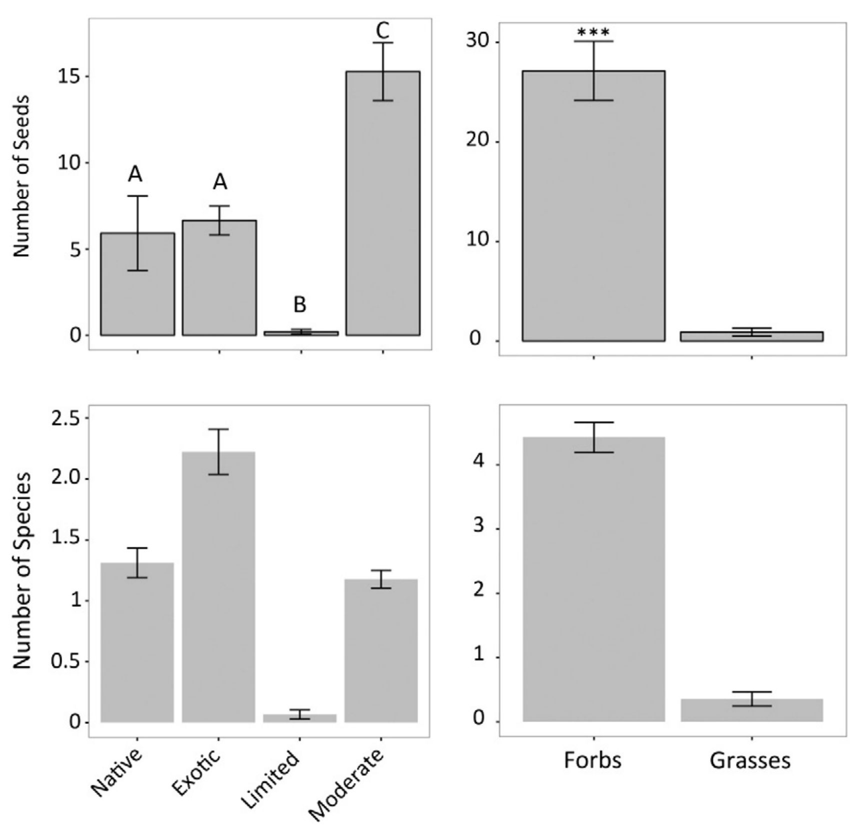

Fig. 2. Mean number of seeds (top panel) and species (bottom panel) per dung patty from endozoochory experiment for each invasion status (left panel) and each functional group (right panel, $n = 45$ each). Different letters (top left panel) and asterisk (*, top right panel) represent significant differences (*** $p < 0.001$) and error bars display 1 SE.

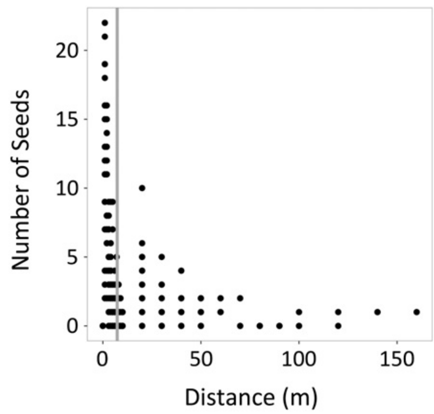

Fig. 3. Number of medusahead seeds dispersed for each recorded distance (m). Gray line indicates the mean dispersal distance (mean = 7.3, SE = 0.52).

a Mediterranean cattle pasture were dominated by species that had passed through a cattle's digestive system and germination of endozoochorous seeds in cattle dung helped maintain that pasture's diversity by increasing the frequencies of those species beyond what would be expected if cattle had not been present. Similarly, Cosyns et al. (2005a) found that cattle and horses increased grassland diversity in a Scottish coastal grassland by transporting species from a less preferred grazing habitat to a more preferred one. They further hypothesized that this directional movement of seed dispersal makes preferred grazing areas more vulnerable to invasion. Long-distance endozoochorous dispersal events also likely played a role in the arrival and diffusion of exotic European plants in California rangelands (Hogan and Phillips, 2011).

Surprisingly, we found that abundance of plants at the landscape scale was negatively correlated with the number of seeds dispersed via epizoochory. This result may reflect the presence of seeds retained from a previous pasture. Before herding through the epizoochory pasture, cattle were grazed in the endozoochory pasture, which may explain the presence of mouse barley seeds (the second biggest epizoochorous contributor), a species that makes up no more than 1% of the epizoochory pasture but nearly 7% of the endozoochorous pasture. The timing of our study likely also explains the pattern of epizoochorous seeds. Our first epizoochory sampling in June, designed to correspond with the dispersal period for medusahead seeds, occurred after seeds of many common early flowering species had dropped, including slender wild oat and soft brome (Chiariello, 1989). Large differences between the first and second sampling date are also evident. For example, bulbous canarygrass, the most common species in June, was absent by the July sampling period. Seed transport by epizoochory was also unrelated to seed attachment morphology, which was the primary mechanism we expected to predict attachment. While many studies have found that barb or hook appendages increase the likelihood of attachment to and retention in animal fur (Römermann et al., 2005; Bläß et al., 2010; Bullock et al., 2011), other studies have established that these structures are not necessary for a species to participate in epizoochory (Couvreur et al., 2004a, 2005; Rosas et al., 2008). However, while these structures may not be necessary, the barbed appendages on medusahead appeared to help the seeds remain embedded in cattle fur and may be important in helping carry seeds long distances.

We found that medusahead was dispersed readily by epizoochory and that this dispersal could result in dispersal distances that are substantially farther than transport by gravity. A recent study evaluating the dispersal of medusahead by wind and gravity found that most seeds travel less than 0.5 m from an invasion front (Davies, 2008). Unsurprisingly, we show that seeds can travel many times farther when attached to cattle; the average seed disperses a distance of 7.3 m, with some seeds remaining attached for up to 160 m when attached to a model cow. This corroborates a number of previous studies that show seeds disperse farther via epizoochory than by gravity alone (Couvreur et al., 2004a; Mouissie et al., 2005; Couvreur et al., 2008). A substantial body of theoretical work has demonstrated that rates of spread of an invasion front are most strongly influenced by small numbers of seeds that travel the longest distances (Kot et al., 1996; Higgins and Richardson, 1999; Cain et al., 2000; Neubert et al., 2000; Clark et al., 2001; Neubert and Lewis, 2004; Caplat et al., 2012). These comparatively rare long-distance transport events can increase the likelihood of establishment of nascent satellite populations and can accelerate rates of spread outward from a population center (Neubert et al., 2000; Clark et al., 2001; Neubert and Lewis, 2004; reviewed in Hastings et al., 2005). It is therefore possible that the presence of livestock on California rangelands has enabled rapid spread of medusahead in the past. Although we have shown that dispersal of medusahead by livestock is possible, our study does not give us information on how this dispersal will ultimately affect the invasion of medusahead, since many other factors unrelated to dispersal can also influence whether an invasion succeeds or fails (reviewed in Sakai et al., 2001). In addition, our experimental results do not allow us to determine how livestock grazing has influenced the historic spread of medusahead across California. Quantifying how livestock have affected the spread of medusahead would require large-scale observational data linking patterns of livestock to historical spread, coupled with experimental introduction of landscapes with and without grazing that can then be followed over time. In addition, livestock are most likely not the sole disperser of medusahead. For example, one other study found greater medusahead densities along unimproved roads compared with trails and random transects, highlighting a potential role for dispersal by vehicles (Davies et al., 2013). In spite of these caveats, we found evidence that livestock could be an important vector for dispersal of medusahead, and this potential should be considered when managing livestock grazing around pastures where medusahead could be introduced.

Another caveat of our study is that it is restricted to a single grassland type and time period. Evaluating community-wide patterns of seed dispersal is necessarily limited by the local species pool (Levine and Murrell, 2003) and the temporal period of sampling (Carnicer et al., 2009; Yang et al., 2013). In our study, the timing of epizoochory sampling likely missed some of the most common forage grasses including *Avena* spp. and soft brome, both of which are common in our epizoochory pasture. Likewise, dung collection after two grazing periods during the dry season probably missed some seeds that might have been present if grazing had been conducted early in the growing season. However, despite these caveats, our study was conducted in pastures and during periods that include many of the species of concern for California rangelands and have therefore some generalizability to other locations and times within California. Medusahead is also present in other states, including large parts of the intermountain west (Davies and Svejcar, 2008). In these locations, the suites of species dispersed are likely to be different, but the role of livestock as dispersers of medusahead could be similar (Nafus and Davies, 2014), depending on the timing of livestock grazing.

Management Implications

Land managers should be aware of the potential for livestock to transport seeds by both endozoochory and epizoochory. The presence of highly invasive species in cattle fur suggests that rangeland managers should focus their resources on preventing spread via epizoochory. Medusahead dispersal could be reduced by limiting grazing of invaded pastures during the period when viable seeds can be dispersed (Nafus and Davies, 2014). Another method would be to pen cattle in a corral for 1 or 2 days to allow shallowly attached seeds to fall off the fur before moving cattle to another pasture. These management practices might not be feasible or economically viable at large spatial scales but could be valuable for preventing invasion of individual pastures that land managers would particularly like to protect.

Acknowledgements

We thank Dustin Flavell, Nikolas Schweitzer, and the staff at SFREC who provided valuable assistance in the field. We thank members of the Suding laboratory for their help with field work and discussions about the manuscript and experiment.

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