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

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ABSTRACT

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

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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).