

Vegetation changes associated with a population irruption by Roosevelt elk

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Keywords

Herbivory, NDVI, plant traits, population regulation, remote sensing, ungulate.

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Funding Information

Funding was provided by California Department of Fish and Wildlife, National Science Foundation, Redwood National Park, Rocky Mountain Elk Foundation, Alamo Safari Club, Granite Bay Safari Club, Houston Safari Club, and Texas State University.

Received: 4 September 2014; Revised: 4 November 2014; Accepted: 5 November 2014

Ecology and Evolution 2015; 5(1): 109–120

doi: 10.1002/ece3.1327

Introduction

Free-ranging continental populations of ungulates have traditionally been understood to display a “logistic” growth curve, increasing from a small population size to a larger population size that is relatively stable near the carrying capacity (K) of the habitat. As these populations near K, density-dependent feedbacks begin to influence vital rates and movement (McCullough 1979; Clutton-Brock et al. 1985, 1987; Festa-Bianchet et al. 2003; Koos et al. 2012). Either lower recruitment, higher emigration, increased mortality or some combination of all three

Abstract

Interactions between large herbivores and their food supply are central to the study of population dynamics. We assessed temporal and spatial patterns in meadow plant biomass over a 23-year period for meadow complexes that were spatially linked to three distinct populations of Roosevelt elk (*Cervus elaphus roosevelti*) in northwestern California. Our objectives were to determine whether the plant community exhibited a tolerant or resistant response when elk population growth became irruptive. Plant biomass for the three meadow complexes inhabited by the elk populations was measured using Normalized Difference Vegetation Index (NDVI), which was derived from Landsat 5 Thematic Mapper imagery. Elk populations exhibited different patterns of growth through the time series, whereby one population underwent a complete four-stage irruptive growth pattern while the other two did not. Temporal changes in NDVI for the meadow complex used by the irruptive population suggested a decline in forage biomass during the end of the dry season and a temporal decline in spatial variation of NDVI at the peak of plant biomass in May. Conversely, no such patterns were detected in the meadow complexes inhabited by the nonirruptive populations. Our findings suggest that the meadow complex used by the irruptive elk population may have undergone changes in plant community composition favoring plants that were resistant to elk grazing.

slows the rate of increase (Ricker 1954). Subsequently, the population then fluctuates around an equilibrium with the food supply, with relatively small annual changes resulting from variation in recruitment, mortality and movement due to climatic conditions (Coulson et al. 2000; Eberhardt 2002; Bonenfant et al. 2009).

Another pattern of population growth in ungulates, irruption, has been well documented in numerous populations of large ungulates inhabiting oceanic islands (Scheffer 1951; Klein 1968; Caughley 1970; Leader-Williams 1980; Ricca et al. 2014). The model of population irruption described by Riney (1964) and Caughley

(1970) has four stages. Stage 1 is the movement of animals into new habitat with a surplus of forage. This surplus of forage fuels exponential population growth. In stage 2, the population overshoots or exhausts the surplus food supply. Stage 3 is characterized by population decline after the overshoot. In stage 4, the population re-equilibrates with a more limited food supply at a lower K .

Oceanic islands may provide ideal conditions for irruptive dynamics in large ungulates. The introduced animals have access to a supply of forage that probably has not evolved in the presence of ungulate herbivory and therefore often lacks immediate mechanisms for tolerance or resistance to ungulate herbivory (Milchunas *et al.* 1988; Augustine and McNaughton 1998; Strauss and Agrawal 1999; Nuñez-Farfán *et al.* 2007). At high latitudes, most of the documented irruptions on oceanic islands occur when large accumulations of snow and ice render forage unavailable during portions of the winter and spring (Hansen *et al.* 2011; Stien *et al.* 2012). Animals often cannot escape forage limitations by movement because oceans reduce or eliminate movement among islands (Ricca *et al.* 2012). Recruitment of young is high in the initial stage of irruption due to the availability of forage with a high plane of nutrition and absence of predators (McCullough 1979). Furthermore, the absence of predators results in lower adult mortality in stage 1 (Leader-Williams 1980; Gaillard *et al.* 2000; Mysterud *et al.* 2001).

In contrast to island settings, irruptive population dynamics according to the Riney-Caughley model have been documented in continental settings less often (Leopold *et al.* 1943; Larter *et al.* 2000; White *et al.* 2007; Starns *et al.* 2014). There are probably several reasons why irruptive dynamics have not often been reported in continental populations of large herbivores. Continental systems often have predator populations which exert some level of top-down influence on herbivore populations (Hairston *et al.* 1960; Johnson *et al.* 2013). Due to long generation times of large ungulates, few studies contain a time series of population data that is long enough to assess irruptive dynamics (Forsyth and Caley 2006). Furthermore, many continental settings allow for immigration and emigration to occur with few geographical barriers. These systems also have plants that evolved for at least centuries to the presence of large herbivores and therefore have developed mechanisms for either tolerance or resistance to herbivory (McNaughton 1984; Milchunas *et al.* 1988; Smith 1998; Mysterud 2006). However, large herbivores occupying habitat islands might exert strong pressure on forage resources because large expanses of surrounding nonforage habitat impose spatial constraints somewhat like those experienced by ungulates on oceanic islands.

Herbivory influence on vegetation dynamics is well documented (Dyer 1975; McNaughton 1979; Milchunas

et al. 1988; Frank *et al.* 1994; Hobbs 1996) and depends on evolutionary grazing history, herbivore density and grazing intensity, and characteristics of the plant community (Georgiadis *et al.* 1989; Milchunas and Lauenroth 1993). McNaughton (1979) reported an increase in net above-ground primary productivity (NAPP) as a result of extreme herbivory (>80% NAPP removed) by migrating wildebeest (*Connochaetes taurinus*), which prompted new vegetative growth and facilitated later use of the grazed areas by Thomson's gazelles (*Eudorcas thomsonii*). Such studies were seminal to the development of the grazing optimization hypothesis, which predicts NAPP will be stimulated by various levels of herbivory up to an optimum level and that NAPP will decrease when grazing exceeds the optimum level (McNaughton 1979). Grazing optimization can be promoted by increased community dominance of herbivory-tolerant functional plant types with low C:N ratios such as graminoids. Highly labile litter produced by these plants combined with large inputs of herbivore nitrogenous waste from large numbers of herbivores facilitated higher soil nutrient cycling and fertility that further stimulates NAPP (Hobbs 1996; Singer and Schoenecker 2003; Bardgett and Wardle 2010).

Numerous studies have evaluated the grazing optimization hypothesis. Several glasshouse and potted plant experiments supported the grazing optimization hypothesis in a laboratory setting (Detling *et al.* 1979; McNaughton 1983; Georgiadis *et al.* 1989). Also, field experiments of grazing, defecation, and urination reported vegetation growth similar to or in excess of ungrazed sites (Hik and Jefferies 1990; Fahnestock and Detling 1999; Leriche *et al.* 2003). Moreover, findings supportive of the grazing optimization hypothesis have been reported in observational field studies (Williamson *et al.* 1989; Frank and McNaughton 1993). Despite evidence supporting the grazing optimization hypothesis, its utility in some ecosystems has been heavily debated (DeAngelis and Huston 1993; Frank and McNaughton 1993; Painter and Belsky 1993; Patten 1993). Indeed, it was found that only 17% of 236 studies that investigated grazing optimization reported increased NAPP in response to herbivory (Milchunas and Lauenroth 1993).

Spatial and temporal patterns of ungulate herbivory have also been linked to contrasting changes in plant community composition (Stewart *et al.* 2006, 2009; Brathen *et al.* 2007). Such changes can be directly related to levels of soil fertility, plant community tolerance or resistance to herbivory, and grazing strategy. For example, grazing tolerant plant species preferred by ungulates remain dominant in systems that are exploited for short durations by migratory herds, whereas systems grazed continuously by nonmigratory ungulates can shift towards being dominated by nonpreferred plants resistant to

grazing (Hobbs 1996; Augustine and McNaughton 1998). From these aforementioned examples, it is clear that grazing optimization is a highly context-dependent process.

The normalized difference vegetation index (NDVI) has become widely used in ecological studies with advances in remote sensing technology and free access to the data [reviewed by Kerr and Ostrovsky (2003) and Pettorelli *et al.* (2011)]. Normalized difference vegetation index measures the ratio of near infrared to red light reflected by vegetation and correlates well with NAPP (Kerr and Ostrovsky 2003; Pettorelli *et al.* 2005) and plant biomass (Muñoz *et al.* 2010). Grazing effects from large herbivores have also been detected from NDVI (Yang *et al.* 2012; Newton *et al.* 2014).

Our purpose in this study was to assess the response of NDVI to the influence of three continental populations of Roosevelt elk (*Cervus elaphus roosevelti*, Fig. 1) that were largely restricted to meadow complexes surrounded by redwood forest (*Sequoia sempervirens*). One of these populations appears to have undergone the four stages of irruption (Starns *et al.* 2014). Using NDVI as a proxy of plant biomass, we assessed whether the elk irruption would result in NDVI patterns indicating a plant community tolerant or resistant to elk herbivory. If plants are tolerant to an elk irruption then a decline in plant biomass (indicated by a decline in NDVI) should occur across the time series. Selective grazing is associated with a decline in tolerant plants, which are replaced by plant species that are resistant to grazing (Myserud 2006). Plant traits that change from tolerant to resistant should result in less spatial variation in NDVI across the time of the population irruption (Adler *et al.* 2001).

Materials and Methods

Study areas

Elk survey data were collected from three distinct sites Davison Meadows and Boyes Meadow, in the Prairie



Figure 1. Roosevelt elk in Davison Meadows, Redwood National and State Parks, California.

Creek drainage, and the Bald Hills Meadows in the lower Redwood Creek drainage (Fig. 2). We primarily selected Boyes Meadow and Bald Hills Meadows because there were no elk population irruptions, as there was in the Davison Meadows, between 1989 and 2011. Another reason for selection was that female elk in Boyes and Davison Meadows displayed strong meadow tenacity (Starns *et al.* 2014). Rarely (observed <1% of time) did the female elk population (defined below) from Boyes Meadow use Davison Meadows, and the Davison females were never observed in the Boyes Meadow (Julian *et al.* 2013). The female population inhabiting the Bald Hills were geographically separated from Boyes and Davison Meadows to the extent that it was unlikely females from these meadows used the Bald Hills or vice versa. Furthermore, the population dynamics of elk in Boyes Meadows and Bald Hills Meadows were very different (see Results). Consequently, to more robustly evaluate the influence of elk herbivory on NDVI during an irruption, temporal patterns in NDVI values in Davison Meadows were compared to NDVI values in Boyes Meadows and the Bald Hills Meadows across the same time period.

All sites are in Redwood National and State Parks in northern Humboldt County, California (Fig. 2). The Prairie Creek drainage encompasses about 100 km² and flows into Redwood Creek. Elevation ranges from near sea level in Davison Meadows to about 1050 m at the highest peak of the Bald Hills. Forest in the Prairie Creek drainage consists mainly of second-growth and old-growth redwood–conifer forests dominated by coast redwood, Sitka spruce (*Picea sitchensis*), Douglas-fir (*Pseudotsuga menziesii*), and western hemlock (*Tsuga heterophylla*). Small meadows (13–51 ha in size) are dispersed throughout the forest. Bald Hills forest consists of a mix of evergreens such as Douglas-fir, with a large component of hardwoods: tanoak (*Lithocarpus densiflorus*), madrone (*Arbutus menziesii*), big-leaf maple (*Acer macrophyllum*), California bay (*Umbellularia californica*), and red alder (*Alnus rubra*). Meadows in the Bald Hills are situated near one another and total about 1000 ha. Meadow vegetation at all sites is a mix of perennial and annual grasses such as California oat grass (*Danthonia californica*), red-top (*Agrostis alba*) and soft chess (*Bromus hordeaceus*). Common forbs are hairy cat's ear (*Hypochoeris radicata*) and narrow-leaved plantain (*Plantago lanceolata*) (Harper 1962; Weckerly *et al.* 2001). Since 1997, there has been an apparent increase in reed canary grass (*Phalaris arundinacea*) in the Davison Meadows.

Regional climate is maritime with mild, dry summers and rainy winters. Coastal fog occurs throughout the year, but is more frequent in summer. Mean minimum and maximum temperatures in the Prairie Creek drainage during winter are approximately 2°C and 10°C,

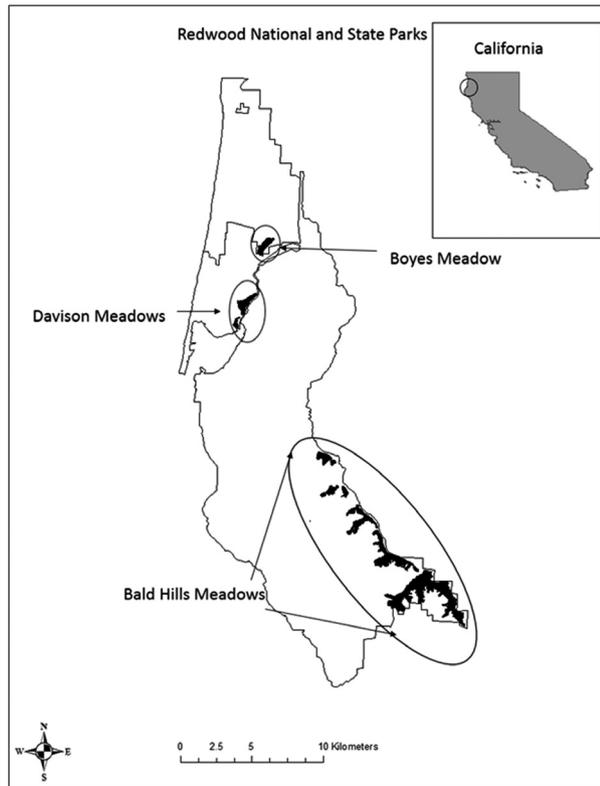


Figure 2. Map of Redwood National and State Parks, California, showing all three study sites. Northern 1/3 portion of area outlined is Prairie Creek Redwood State Park. Remainder of outlined area in Redwood National Park.

respectively, with mean temperatures in summer ranging from 10 to 20°C (Veirs 1987). Annual precipitation is usually greater than 150 cm, with rainfall mostly occurring from autumn to early spring. Snowfall in Boyes and Davison Meadows is rare, and daytime winter temperatures prohibit snow accumulation. The Bald Hills, however, receives snow more frequently and accumulations of 20–40 cm may persist for 1–2 weeks. About 35 km inland, Bald Hills temperatures are more extreme than those found in Boyes and Davison Meadows, with mean summer minimum and maximum temperatures ranging from 20 to 26°C, respectively. Mean minimum and maximum winter temperatures range from 0 to 10°C, respectively.

History

Davison Meadows (50 ha) are in the lower end of the Prairie Creek drainage and include two meadows (38 and 13 ha) separated by a 0.5 km band of riparian habitat. Before purchase by the park service in 1991, the meadows were privately owned and had probably been grazed by cattle since their creation in 1890. Elk became apparent in

Davison Meadows shortly after the park service took ownership in 1991 (F. W. Weckerly, pers. obs.).

Boyes Meadow was 51 ha in area. Although it is unknown when Boyes Meadow was established, it was used for hay and cattle production during the late 1800s. In 1933 Boyes meadow was purchased by a nonprofit organization, deeded to the state of California, and converted to a state park (Bentley 1958). Dasmann (1964) reported a Roosevelt elk population irruption in the Prairie Creek Redwood State Park, which encompasses Boyes meadow, between 1937 and 1960. Between the late-1970s and when our population counts began in 1997, the elk population using Boyes Meadow probably numbered between 30 and 50 elk (Mandel and Kitchen 1976).

Bald Hills Meadows include a number of meadows situated near one another along a southwest facing ridge of Redwood Creek. Bald Hills became part of the park in 1977–1978. Before that time it was privately owned and grazed by livestock (Mandel and Kitchen 1979). In the Bald Hills, elk were reported to be sparse in the 1950s and 1970s (Harn 1958; Mandel and Kitchen 1976). In 1987, Grenier *et al.* (1990) counted 60 elk.

Elk data

Population surveys of the Boyes, Davison, and Bald Hills Meadows have been conducted during January–February between 1997 and 2014. Vehicle surveys along a predetermined route through Boyes and Davison Meadows began at dawn and lasted for 1.75 h (Weckerly *et al.* 2004). Upon encountering elk, observers stopped to count the number of individuals and document any natural features (i.e., antler morphology or scars) that could be used to track individuals across the season. As a result of tourist activity, elk along the survey route have become habituated to people and slow-moving vehicles. Ten surveys of Boyes and Davison Meadows were performed each year, except in 1998 and 1999 when only five surveys were performed. Because the Davison Meadows were the site of the irruption and therefore the primary population of interest, we estimated population abundance for Davison Meadows, using Bowden's mark-resight estimator to account for imperfect detection (Weckerly 1996, 2007). In the Boyes Meadow, we used the highest count in each year for two reasons. (1) Early in the time series, the population was almost entirely female (with juveniles and subadults) (Weckerly *et al.* 2004). These females had high sighting probabilities (≥ 0.9), which meant that across 5–10 surveys it was likely that the highest count reflected abundance (Weckerly 2007). (2) After 2010, we sighted only males in Boyes Meadow and there were too few males (see Results) to estimate sighting probabilities.

Surveys in the Bald Hills have also been performed ten times per year during 1997 and from 2002 to 2014. The Bald Hills surveys were conducted by driving along roads in the Bald Hills, with observers exiting the vehicle to observe areas not visible from the vehicle. Although males were present in the Bald Hills, it was more difficult to obtain accurate counts of males. As such, count data from only the female segment (females, juveniles, and subadults) of the Bald Hills population were used as an index of abundance.

NDVI

Landsat 5 Thematic Mapper images were downloaded from the USGS EarthExplorer system (<http://earthexplorer.usgs.gov>). Because the park service took ownership of Davison Meadows in 1991, we obtained images between January 1989 and November 2011. Due to satellite failure in November 2011, images during 2012–2013 were unavailable. Notably, these images have a 30 m² spatial resolution (pixel size), which is necessary to exclude the canopy of the surrounding redwood forest when calculating NDVI of the meadows. Landsat 5 passed over the study area at 16 day intervals, resulting in approximately 200 images across the time series that were free of cloud cover. Some images contained cloud cover over only one or two of the study sites; in this situation, the site(s) covered by clouds were not used for analysis. For each useable image, brightness values were converted to top-of-atmospheric reflectance values following the methods of Chander *et al.* (2009), which were then converted to NDVI. These conversions were carried out using ERDAS Imagine 2013 (Intergraph Corporation 2013). Using ArcGIS 10.0 (ESRI 2011), meadows were extracted from the images to restrict NDVI estimates within meadow boundaries. Pixels with NDVI values less than 0.1 were reclassified as no data because these pixels represent snow, water, or bare ground. Hence, we only used NDVI values from pixels that had visible vegetation. For months where two images were available, the average of the NDVI values was used.

Climatic variables

Temperature and precipitation might influence NDVI values (Paruelo and Lauenroth 1998; Richard and Poccarr 1998; Wang *et al.* 2001; Hao *et al.* 2012). Climatic data (monthly precipitation, mean monthly temperatures) were measured in Boyes Meadow (Station # 046498) by the National Oceanic and Atmospheric Administration (NOAA). The Bald Hills Meadows were located at a higher elevation than the other two sites. Therefore, the Bald Hills Meadows likely had more extreme

temperatures than the other two sites in any month within a year. However, the fluctuations across years in climatic conditions should be similar.

Analyses

We initially viewed scatterplots of the data to assess the form of relationships. From these observations, we determined that relationships were either linear, nonlinear or could be fit with piecewise regression. We used the “segmented” package in R to summarize piecewise changes in abundance estimates or counts across the time series from 1997 to 2013 (Muggeo 2008; R_Core_Team 2013). To assess whether monthly NDVI or coefficient of variation (CV) of NDVI in May varied among sites, we analyzed multiple regressions. Models allowed regressions between year and the response variable to vary among meadows in intercepts and slopes. We estimated piecewise regression models to determine whether the relationship between year and NDVI for the Davison Meadows differed from the other two meadows. The CV of NDVI was the standard deviation of NDVI values divided by the monthly mean NDVI and was used to estimate spatial variation in plant biomass (Adler *et al.* 2001). Simple linear regression was used to estimate possible relationships in monthly precipitation and mean temperature to NDVI as these two climatic variables can influence NDVI.

Results

Elk population dynamics

Across the time series of population data (1997–2013), population dynamics of the nonirruptive Bald Hills and Boyes populations were dissimilar in shape (Fig. 3). The Bald Hills population grew between 1997 and 2006 and then stabilized thereafter (piecewise regression: $r^2 = 0.91$, $P < 0.001$, $df = 10$), whereas the Boyes population steadily declined from 1997 to 2006 and then stabilized until the end of the time series in 2013 ($r^2 = 0.95$, $P < 0.001$, $df = 13$). The dynamics of the irruptive Davison population was similar in shape to the Boyes population from 1997 to 2013. The Davison population steadily declined from 1997 to 2006 and then stabilized until at least 2013 ($r^2 = 0.89$, $P < 0.001$, $df = 13$). As elk were first granted unhindered access to Davison Meadows in 1991, the population appeared to grow rapidly until 1997.

NDVI

Due to low numbers of usable images for some months, only the months of May and September were used for NDVI analysis at each site (Fig. 4). These two months

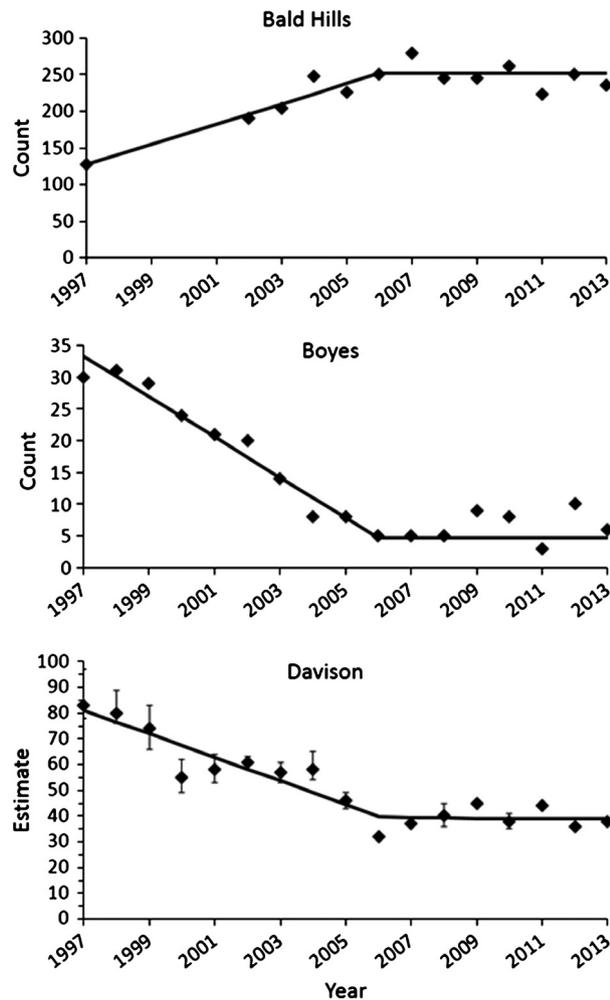


Figure 3. Roosevelt elk (*Cervus elaphus roosevelti*) population trends observed at each study site. Count data were used for Boyes Meadow and Bald Hills Meadows, while abundance was estimated for Davison Meadows using Bowden's estimator. Regression lines summarize temporal patterns detected using piece wise regression. Note that the scale of the Y axes differs among sites.

were among those with the highest number of usable images. Moreover, these months likely had significance in regards to elk forage. At all three sites, NDVI values were low from September to January, peaked in May and June and then declined. The higher NDVI values in May suggest the peak of the growing season and the lower NDVI values in September indicate the peak of the dry season.

We failed to detect differences among sites in May NDVI or a linear relationship between years and this measure of NDVI (Table 1). Fitting a piecewise regression, we detected a break in the relationship between year and September NDVI in Davison (Fig. 5). With years coded one (1989) through 23 (2011), the break in the relationship was at year five in Davison (year \pm 95% CI,

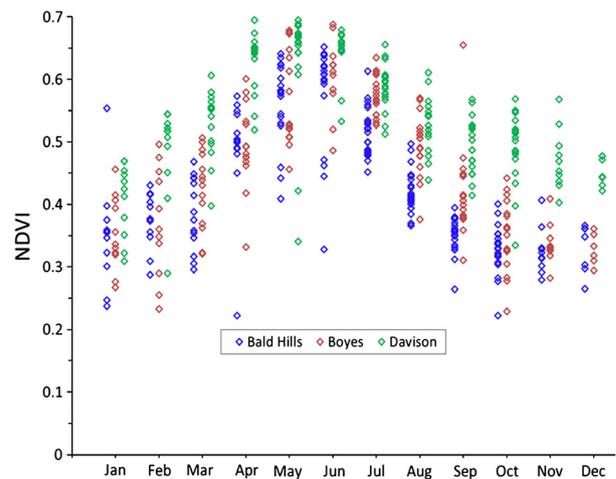


Figure 4. Monthly pattern of Normalized Difference Vegetation Index (NDVI) values from 1989 to 2011, Redwood National and State Parks, California.

5 ± 3.23) but there was no break in the relationship in Bald Hills (5 ± 39.41) or Boyes (5 ± 5.59). Also, we detected no linear relationship between year and September NDVI in Bald Hills (slope \pm 95% CI, -0.002 ± 0.039) or in Boyes (0.017 ± 0.034). However, in Davison September NDVI declined between 1989 and 1993 (slope \pm 95% CI, -0.037 ± 0.034) but remained stationary thereafter (0.002 ± 0.004). In Davidson Meadows, we also detected a decelerating decline in CV of May NDVI across 1989 to 2011 which differed from the other two sites (Fig. 6, Table 1). Furthermore, in Bald Hills and Boyes we detected no relationship between year and CV of NDVI in May.

Between 1989 and 2011, there was little to suggest that variation in mean temperature or precipitation influenced NDVI values in May or September. There were no linear relationships across this time period between precipitation and NDVI (May: $r^2 = 0.15$, $P = 0.116$, $df = 16$; September: $r^2 < 0.01$, $P = 0.773$, $df = 16$) or mean temperature and NDVI (May: $r^2 = 0.11$, $P = 0.172$, $df = 16$; September: $r^2 < 0.01$, $P = 0.866$, $df = 16$).

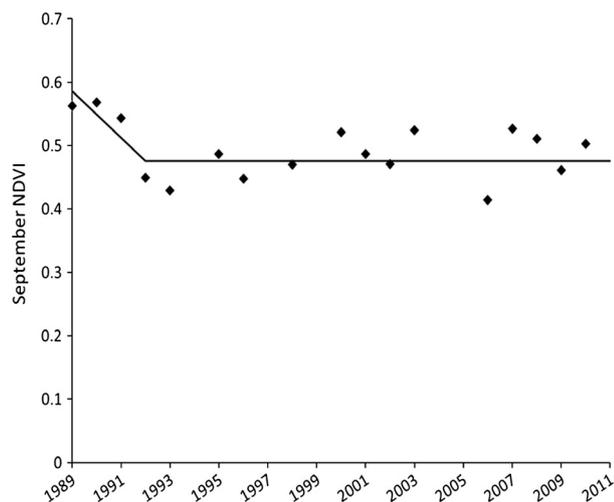
Discussion

Critical to documenting an irruption by a population of large herbivores is detecting a change in plant traits that results in a lower K at stage 4 than during the population overshoot at stage 2 (Caughley 1970). Our findings suggest that the onset of elk herbivory reduced forage biomass in Davison Meadows at the peak of the dry season and that there was a change in plant traits as the elk population grew rapidly, peaked, declined and then stabilized at an abundance that was about half of the peak

Table 1. Summaries of linear models estimating mean normalized difference vegetation index (NDVI) in May and the coefficient of variation (CV) of NDVI in May from the Bald Hills, Boyes and Davison Meadows, Redwood National and State Parks, USA.

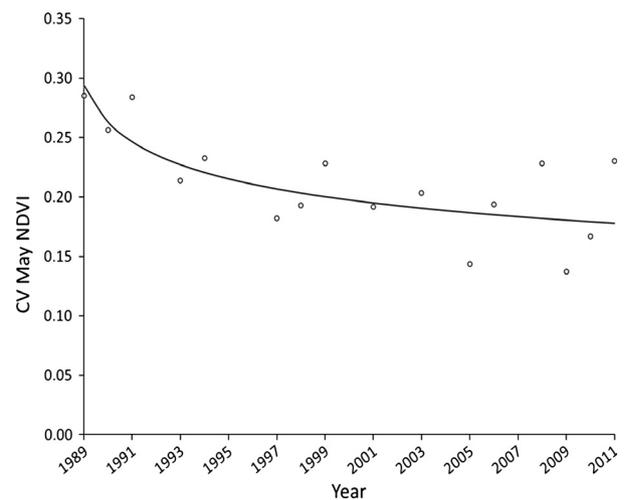
Parameter	May NDVI				CV NDVI May			
	Estimate	SE	<i>t</i>	<i>P</i>	Estimate	SE	<i>t</i>	<i>P</i>
Intercept	0.526	0.034	14.20	<0.001	0.145	0.026	5.65	<0.001
Boyes	0.036	0.054	0.67	0.509	−0.005	0.037	−0.14	0.887
Davison	0.039	0.053	0.74	0.464	0.142	0.037	3.86	<0.001
Year	0.003	0.002	1.10	0.275	−0.003	0.011	−0.25	0.801
Year:Boyes	−0.003	0.004	−0.67	0.508	0.0002	0.015	0.01	0.989
Year:Davison	0.002	0.004	0.59	0.561	−0.032	0.015	−2.07	0.045

Years ranged from 1989 to 2011. For CV NDVI in May, year was natural log transformed. The reference meadows were Bald Hills. The adjusted r^2 for the May NDVI model was 0.14 ($F = 2.58$, $P = 0.039$, $df = 5$, 45). The adjusted r^2 for CV NDVI in May model was 0.46 ($F = 9.43$, $P < 0.001$, $df = 5$, 44). Colons denote statistical interactions.

**Figure 5.** September Normalized Difference Vegetation Index (NDVI) values for Davison Meadows from 1989 to 2011, Redwood National and State Parks, California, USA. Regression lines summarize temporal patterns of September NDVI values as detected using piecewise regression.

abundance. Plant traits in Davison Meadows evidently changed from a preponderance of plants tolerant to elk grazing to more plants that were resistant to elk foraging. We had two novel features in our study. One, we had NDVI data before the irruption and through all four stages of the population irruption, which allowed some degree of temporal control and, two, we also had some degree of spatial control because we had NDVI data on two nearby populations with different nonirruptive population dynamics during the time when the Davison population irrupted.

Association between forage offtake by elk and NDVI would have augmented our analysis of temporal changes in NDVI across 1989–2011. However, we did not have elk abundance estimates during the stage 1 (1991–1997) of

**Figure 6.** Coefficient of variation (CV) of May Normalized Difference Vegetation Index (NDVI) values for Davison Meadows from 1989 to 2011, Redwood National and State Parks, California, USA. Regression line summarizes the temporal pattern of CV of NDVI values.

the irruption in Davison Meadows nor did we have estimates of meadow use by all the elk populations at any time. To obtain robust indications of forage offtake, elk abundance and meadow use would be useful variables to estimate because density-dependent meadow selection is likely (Perez-Barberia et al. 2013). Nonetheless, cropping rates of male and female elk measured in 1994 and 2002 indicated a change in elk feeding behavior in the Prairie Creek drainage (Weckerly et al. 2001, 2004). This evidence, in conjunction with the temporal changes detected in NDVI in Davison but not Boyes or Bald Hills Meadows, suggests that changes in NDVI in Davison Meadows are associated with the irruptive, Davison population.

Because population irruptions by large herbivores are usually an unintended consequence, documentation of changes in plant traits due to the herbivore are usually

incomplete. Changes in plant traits associated with irruptive populations are most often investigated during and after the irruption at the location of the irruption. Our study design allowed us to associate the change in NDVI patterns in Davison Meadows with the elk irruption. The changes in NDVI patterns in Davison Meadows were likely a consequence of temporal changes in vegetation associated with elk grazing beginning in 1991 and continuing throughout the study.

The merits of having spatial and temporal controls for documenting changes in plant traits in the system we studied are evident when comparing findings to those from irruptive populations of caribou or reindeer (*Rangifer tarandus*) on oceanic islands. On oceanic islands at high latitudes lichens (*Cladonia*) have a low tolerance to caribou herbivory and are rapidly depleted by caribou populations in stage 1 (Leader-Williams *et al.* 1981). When lichens are depleted by caribou herbivory there often is a concomitant increase in graminoid species that are more tolerant to grazing (Ricca *et al.* 2014). The different plant forms have different plant traits, and the changes in plant communities associated with irruptive populations of caribou is ostensibly apparent. In the Davison Meadows, the presumed change in plant traits is more subtle because it likely involved shifts in species composition within a single functional type (i.e., graminoids). Presumably, either resistant grass species that were sparse in Davison Meadows in 1989 increased in abundance thereafter or new, resistant grass species colonized and increased in abundance after 1989.

Although we were unable to directly estimate plant community composition across the period of study, there was an apparent increase in reed canary grass in the Davison Meadows between 1997 and 2013 (Appendix S1). Reed canary grass is a common invader of mesic sites throughout North America (Martina and Von Ende 2013), and the Davison Meadows met this criteria as they do flood and contain standing water during the rainy season. Boyes Meadow and Bald Hills Meadows do not have standing water during the rainy season. Importantly, reed canary grass can harbor high concentrations of alkaloids (Woods and Clark 1971; Marten *et al.* 1973; Hagman *et al.* 1975). Palatability of reed canary grass to cattle and sheep can correlate negatively with alkaloid concentrations (Marten *et al.* 1976) and white-tailed deer (*Odocoileus virginianus*) and bison (*Bison bison athabasca*) appear to avoid the species all together (Suring and Vohs 1979; Larter 1994). By synthesis, it is unlikely that elk readily graze reed canary grass. An increase in grazing resistant reed canary grass in the Davison Meadows as elk were given unhindered access in 1991 is consistent with a decline in spatial variation in May NDVI (when plant biomass peaks) between 1989 and 2011. Conversely, if

there had been a change to more tolerant species in Davison Meadows then we should have detected a decline in NDVI in May and an increase in spatial variation in NDVI. An increase in spatial variation in NDVI should have resulted from uneven grazing of patches in Davison Meadows by elk, which should reflect greater spatial variation in plant biomass (Adler *et al.* 2001).

It is possible that changes in plant traits in Davison Meadows were affected by differences in diet selection between cattle and elk. Hagman *et al.* (1975) reported that the alkaloid concentration of reed canary grass increased with plant maturity and that mature reed canary grass was unpalatable to cattle. If reed canary grass was present in the Davison Meadows during the period of cattle grazing, it might have been grazed heavily enough during early growth to retard its prevalence (Brummer and Moore 2000). When cattle were removed in 1991, elk grazing pressure on reed canary grass was probably light. The reduced herbivory by elk allowed reed canary grass to establish in many parts of Davison Meadows. Once reed canary grass becomes established, it is adept at displacing other herbaceous species at mesic sites because of the plasticity of its clonal architecture (Green and Galatowitsch 2002; Martina and Von Ende 2013). During the elk population decline and stabilization at lower abundance an even lighter grazing pressure by elk might have further facilitated the spread of reed canary grass.

The rapid growth or stage 1 of a population irruption is driven by surplus food (Forsyth and Caley 2006). Once the surplus food is consumed by an abundant population, the irrupting population declines and there are fewer plants in the food supply that are as nutritious to large herbivores as what was there during stage 1. At peak population size, the Davison population was abundant as its density (number \cdot ha⁻¹ of meadows⁻¹) of female, juvenile, and subadult males [1.02, Starns *et al.* (2014)] was greater than in the largest population sizes we documented in Boyes (0.61) or Bald Hills populations (0.28). The alterations to the food supply precipitated by large mammal herbivory also affects ecosystem processes which can have long-term consequences to plant communities (Klein 1968; Coomes *et al.* 2003). In our system, the surplus food appeared to be graminoid species tolerant to elk herbivory. Owing to elk forage selection, the abundance of these species declined during stage 1, exhausting the surplus food supply. After stage 1, the surplus food appeared to be replaced by reed canary grass, which is presumed to be resistant to elk herbivory. Consistent with our finding that there has been a change in food supply due to change in plant traits associated with the elk irruption is a re-equilibration in density-dependent recruitment during stage 4 (Starns *et al.* 2014).

Populations of Roosevelt elk in Redwood National and State Parks are nonmigratory (Harper et al. 1967). A sedentary, abundant population of elk can exert substantial grazing pressure that defoliates forage plants and reduces above-ground primary productivity (Stewart et al. 2006). In our study, the decline in NDVI at the peak of the dry season indicated substantial grazing pressure from elk. The extent of herbivory by the abundant population exceeds the level prompting overcompensation in plant growth (Georgiadis et al. 1989; Stewart et al. 2006). The year round herbivory by a sedentary elk population should create conditions conducive for invasion by less palatable or resistant plant species (Augustine and McNaughton 1998). Our findings are consistent with Augustine and McNaughton's (1998) model. There is, however, an alternative model. The transition from tolerant to more resistant plants might have a role for cattle. When cattle were removed from Davison Meadows, resistant species to elk during the young growth stage were released from intense grazing pressure from cattle. The release of resistant species from cattle grazing then resulted in the transition of plant traits across the elk population irruption because elk do not graze the resistant plants to a substantial degree at any plant growth stage.

A feature common to colonizing populations of large herbivores that irrupt is the absence of herbivory by large mammals before the irrupting species arrived. The changes that take place in plant communities are often associated with the lack of prior exposure to large mammal herbivory. Some or many of the plants in the food supply do not possess traits that allow them to tolerate or resist herbivory. To the contrary, our findings suggest that colonizing populations of large mammals can also irrupt while exploiting plant communities exposed previously to large mammal herbivory.

Acknowledgments

We thank the many students and local biologists that assisted with field work over the years: R. Keleher, J. Hunt, D. Lancaster, M. Longoria, R. Luna, K. McFarland, M. O'Dell, K. Richardson, S. Robinson, S. Shelton, G. Street, and D. Wolcott. In particular, we are grateful to Redwood National and State Parks for their assistance and logistical support. Funding was provided by California Department of Fish and Wildlife, National Science Foundation, Redwood National Park, Rocky Mountain Elk Foundation, Alamo Safari Club, Granite Bay Safari Club, Houston Safari Club, and Texas State University. P. Van Mantgem provided helpful comments on previous manuscript drafts. Use of product names does not imply endorsement by the U. S. Government.

Conflict of Interest

None declared.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Photographs of similar views showing the presence of reed canary grass in Davison Meadows in August, 1996, and July, 2013. The vertical arrows are pointing to the same telephone pole in both photographs.