

INFLUENCE OF A POPULATION IRRUPTION BY
ROOSEVELT ELK ON A VEGETATION INDEX

by

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ABSTRACT

Understanding the factors that influence population growth is central to the study of any species. Large herbivores can influence their food supplies through herbivory. Over 23 years just before and throughout an irruption by a Roosevelt elk population I assessed temporal and spatial patterns of the Normalized Difference Vegetation Index (NDVI). My objectives were to determine if elk herbivory was associated with NDVI and whether the plant community foraged by the irruptive population was tolerant or resistant to elk grazing. Using Landsat 5 Thematic Mapper imagery, I obtained estimates of NDVI for three areas of Redwood National and State Parks, each inhabited by distinct populations of Roosevelt elk. Each population exhibited a different pattern of growth through the time series of the study. One population underwent the irruptive growth pattern while the other two populations did not. Using piece wise regression, I detected temporal changes in NDVI for the area used by the irruptive population that suggested a decline in forage biomass during the end of the dry season but I detected no decline in NDVI at the peak of the growing season. My findings suggest that the area used by the irruptive elk population may have undergone changes in plant community composition favoring plants that were resistant to elk grazing.

CHAPTER I

Influence of a Population Irruption by Roosevelt Elk on a Vegetation Index

Introduction

Understanding the factors that influence population growth is central to the study of any species. Population growth can be simplified and understood as the sum of four parameters: recruitment of young, adult mortality, immigration, and emigration. For populations of large ungulates, two very different patterns of population growth result from changes in the values of these parameters. 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 recruitment and adult mortality (Clutton-Brock et al. 1987; Clutton-Brock et al. 1985; Festa-Bianchet et al. 2003; Koons 2012). Lower recruitment and higher emigration and adult mortality slow the rate of increase, and the population then fluctuates around an equilibrium with the food supply (Ricker 1954), with relatively small annual changes resulting from variation in recruitment, mortality and movement due to climatic conditions (Bonenfant 2009; Coulson et al. 2000; Eberhardt 2002).

Another predominant pattern of population growth in ungulates, irruption, has been well-documented in numerous populations of large ungulates inhabiting islands (Caughley 1970; Klein 1968; Leader-Williams 1980; Ricca 2013; Riney 1964; Scheffer 1951). The model of population irruption developed by Riney (1964) and Caughley (1970) has four stages: stage 1 is the movement of animals into new habitat with an overabundance (relative to population size) of forage. This excess supply of forage fuels exponential population growth. In stage 2, the

population overshoots or exhausts the food supply. Stage 3 is characterized by population decline after the overshoot. In stage 4, the population re-equilibrates with the food supply at a lower size and a lower carrying capacity.

Insular settings may provide ideal conditions for irruptive dynamics in large ungulates. Immigration and emigration are greatly reduced or eliminated by barriers to dispersal (e.g. oceans). The introduced animals have access to a supply of forage that probably has not evolved in the presence of ungulate herbivory, and therefore lacks mechanisms for tolerance or resistance to ungulate herbivory (Augustine and McNaughton 1998; Milchunas et al. 1988; Smith 1998). Recruitment of young is greatly increased in the initial stage of irruption due to a high plane of nutrition and absence of predators (McCullough 1979). Moreover, in the case of long-lived species, the absence of predators results in lower adult mortality, with possible drivers of adult mortality primarily restricted to starvation, infection, and senescence (Gaillard et al. 2000; Leader-Williams 1980; Mysterud 2001). Additionally, most of the documented insular irruptions have occurred at high latitudes where large accumulations of snow and ice can render forage unavailable during portions of the year (Hansen et al. 2011; Stien et al. 2012).

Irruptive population dynamics have been documented in continental settings less often (*Odocoileus hemionus*: Leopold et al. 1943; *Antilocapra americana*: White et al. 2007; *Cervus elaphus roosevelti*: Starns et al. *in review*). There are probably several reasons why irruptive dynamics have not often been reported in continental populations of large herbivores. Due to long generation times of large ungulates, few studies contain long enough time series of population data to assess irruptive dynamics (Forsyth and Caley 2006). Continental systems often have predator populations which exert some level of top-down control to the herbivore population (Johnson 2013). Furthermore, continental settings allow for immigration and

emigration to occur without geographical barriers. These systems also have plants that evolved over centuries in the presence of large herbivores, and therefore have developed mechanisms for either tolerance or resistance to herbivory (McNaughton 1984; Milchunas et al. 1988; Mysterud 2006; Smith 1998).

Plants which exhibit tolerance to herbivory are capable of persisting in the presence of ungulate grazing by compensating for loss of plant tissue (Anderson and Briske 1995; Augustine and McNaughton 1998; McNaughton 1984). Tolerance to herbivory may be characterized by low growth forms and protected basal meristems (Augustine and McNaughton 1998; Coughenour 1985; McNaughton 1984; Strauss and Agrawal 1999). Plants resistant to herbivory have evolved traits which limit or completely deter grazing. Mechanisms for resistance to herbivory include spines, low nutritional value (Augustine and McNaughton 1998), and the production of toxic compounds (de Mazancourt and Loreau 2000; McNaughton 1985).

Herbivory influence on vegetation dynamics is well documented (Dyer 1975); (Frank et al. 1994; Hobbs 1996; McNaughton 1979; Milchunas et al. 1988). The vegetative response to herbivory, as well as the degree to which herbivory impacts vegetation dynamics, is variable 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 (1976, 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 (*Eudorcus thomsonii*). These 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).

Numerous studies have evaluated the grazing optimization hypothesis. Several greenhouse and potted plant experiments supported the grazing optimization hypothesis in a laboratory setting (Detling et al. 1979; Georgiadis et al. 1989; McNaughton 1983). Also, field simulations of ungulate grazing, defecation, and urination reported vegetation growth similar to or in excess of ungrazed sites (Fahnestock and Detling 1999; Leriche et al. 2003). Moreover, findings supportive of the grazing optimization hypothesis have been reported in observational field studies (Frank and McNaughton 1993; Williamson et al. 1989). Despite evidence supporting the grazing optimization hypothesis, its utility in some ecosystems has been heavily debated (DeAngelis and Huston 1993; 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).

Ungulates can also alter their ecosystems via changes in grazing patterns and the nitrogen (N) cycle (Hobbs 1996). Ungulates consume N in plant tissue, and return it to the soil through urination and defecation. Urinary N is available for use by plants and soil microbes soon after excretion, and because ungulate feces have a higher nitrogen: carbon ratio than senescent plant litter, feces are more rapidly decomposed than plant litter (Hobbs 1996). Thus, in areas where ungulates excrete large quantities of feces and urine, soil nutrient levels can be higher than in ungrazed areas, dependent on site-specific soil properties (Ruess and McNaughton 1987). Moreover, ungulates have the capacity to redistribute N from foraging to bedding sites in systems with separate foraging and bedding areas (Schoenecker et al. 2004).

Spatial and temporal patterns of ungulate herbivory have also been linked to contrasting changes in plant community composition (Brathen et al. 2007; Stewart et al. 2009; Stewart et al. 2006). Such changes are directly related to the degree and types of herbivory to which plant communities are exposed and result from the degree of selectivity displayed by grazing herbivores (Augustine and McNaughton 1998; Milchunas et al. 1988). 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 non-migratory ungulates can shift towards being dominated by non-preferred plants resistant to grazing (Augustine and McNaughton 1998; Hobbs 1996). Bråthen et al. (2007) reported a decrease in species richness in an area grazed by reindeer, but Denyer et al. (Denyer 2010) reported an increase in species richness in areas grazed by sheep. Likewise, Stewart et al. (2009) reported an increase in plant species richness and NAPP due to low levels of elk (*C. elaphus*) herbivory.

My purpose in this study was to assess the influence of an irruptive, continental Roosevelt elk population on NDVI. This population appears to have undergone the four stages of irruption (Starns et al. *in review*). Using NDVI as an index of NAPP, I tested three hypotheses: 1) Elk herbivory through an irruptive growth curve would be detected by changes in NDVI; 2) Elk irruption would result in lower NDVI in Davison Meadows at the conclusion of the growing season, indicating a plant community tolerant to herbivory; 3) No change in NDVI in Davison Meadows at the end of the growing season would indicate a plant community resistant to herbivory.

Methods

Study Areas

Elk survey data was collected from three distinct sites: Davison Meadows and Boyes Meadow, in the Prairie Creek drainage, and the Bald Hills Meadows in the lower Redwood Creek drainage. All sites are in Redwood National and State Parks in northern Humboldt County, California (Fig. 1). 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 (*Sequoia sempervirens*), Sitka spruce (*Picea sitchensis*), Douglas-fir (*Pseudotsuga menzeisii*), 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 the 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*), redtop (*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 2001). Since 1997, there has been an apparent increase in reed canary grass (*Phalaris arundinacea*) in the Davison meadows.

Climate in the study area 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, respectively, with mean temperatures in summer ranging from 10° C 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° C to 26° C, respectively. Mean minimum and maximum winter temperatures range from 0° C to 10° C, respectively.

Study Site Selection

We 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. 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.

History

Davison Meadows (51 ha), are in the lower end of the Prairie Creek drainage and include two meadows (38 ha and 13 ha) separated by a 0.5 km band of riparian habitat. Before purchase by the parks in 1991, the meadows were privately owned and had probably been grazed by cattle

since their creation in 1890. Elk became ubiquitous in Davison meadows shortly after 1991 (F.W. Weckerly, pers. comm.).

Boyes Meadow was also 51 ha in area. Although it is unknown when Boyes Meadow was established, it was reportedly used for hay and cattle production during the late 1800s. In 1933 Boyes meadow was purchased by the Save the Redwoods League, 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.

Bald Hills Meadows include a number of meadows situated near one another along a south-west facing ridge of Redwood Creek. Bald Hills became part of the park in 1977-78. Before that time it was privately owned and grazed by livestock (Mandel and Kitchen 1979). Elk were reported in the area in the 1950's (Harn 1958), but no population numbers were presented.

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 pre-determined route through Boyes and Davison meadows began at dawn and lasted for 1.75 hours (Weckerly et al. 2004). Upon encountering elk, observers stopped to view and count the animals. 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; Weckerly 2007). In the Boyes Meadow we used the highest count in each year for two reasons. Early in the time series the population was almost entirely female (Weckerly et al. 2004). These females had high sighting probabilities (≥ 0.9) which meant that across 5 to 10 surveys it was likely that the highest count reflected abundance. 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 2002-2014. 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 sub-adults) of the Bald Hills population was used as an index of abundance.

NDVI

Prior to widespread availability of remotely sensed imagery and technology capable of processing such imagery, researchers often used precipitation records and water use of plants as a proxy of NAPP when actual biomass measurements were unavailable (Barboza 2008; Lauenroth 1979; Sala et al. 1988; Webb et al. 1978). While precipitation is known to be positively correlated to NAPP (Schloss et al. 1999; Sinclair 1975), spatial variability of precipitation may lead to errors in the estimate of NAPP at small spatial scales. NDVI, a measure of the ratio of near infrared to red light reflected by vegetation, correlates well with NAPP (Barboza 2008; Pettorelli et al. 2005; Tucker and Sellers 1986), plant biomass (Muñoz et al.) and species richness (Levin et al. 2007).

The NDVI has become widely used in ecological studies with recent advances in remote sensing technology and free access to the data (reviewed by (Kerr and Ostrovsky 2003), also by (Pettorelli et al. 2011). Prediction and assessment of ungulate migration patterns have been made using NDVI (Bischof et al. 2012; Boone et al. 2006; Hebblewhite et al. 2008; Mueller et al. 2008). Pettorelli et al. (Pettorelli et al. 2009) reported that primary productivity measured via NDVI correlated positively with densities of 13 African ungulate species. Also, NDVI has predicted plant species richness and biomass, peak fecal N, and ungulate recruitment (Boelman et al. 2003; Hamel et al. 2009; Levin et al. 2007; Pettorelli et al. 2006; Riedel et al. 2005; Ryan et al. 2012).

The U.S. Geological Survey (USGS) EarthExplorer land monitoring program has several qualities that enhance the utility of NDVI for vegetation monitoring and assessment. First, the satellite imaging system (Landsat) used to assess NDVI has been in place since 1972, allowing researchers to construct long-term data sets. Second, Landsat imagery covers the entire surface of the earth. This enables researchers to obtain NDVI values of any terrestrial surface. Third, Landsat images are available at a resolution of up to 30 m², making it possible to detect vegetation changes across small land areas. Furthermore, traditional methods of assessing NAPP have been reported to overestimate NAPP (Biondini et al. 1991; Sala et al. 1988), whereas NDVI estimates are derived via precisely calibrated mathematical calculations (Chander et al. 2009).

Landsat 5 Thematic Mapper (TM) satellite images with a 30 m² spatial resolution (pixel size) were obtained from the USGS EarthExplorer system (<http://earthexplorer.usgs.gov>). Because the park took ownership of Davison meadows in 1991, I obtained images between January, 1989, and November, 2011. Due to satellite failure in November 2011, images during 2012-2013 were unavailable. Resolution of 30 m² is necessary for estimating NDVI of the

meadows while excluding the canopy of the surrounding redwood forest. Images of the study area were taken at 16 day intervals. Approximately 200 images were free of cloud cover for each study site. 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, bands one through five and band seven were “stacked” using ERDAS Imagine 2013 (Intergraph 2013). After stacking the bands, brightness values were converted to Top-of-Atmospheric (TOA) reflectance values following the methods of Chander et al. (2009). Reflectance values were then converted to NDVI values within ERDAS Imagine 2013 (Corporation 2013). I used ArcGIS 10.0 (ESRI 2011) to delineate the various meadows from the bordering redwood forests and the ArcToolbox function “extract by mask” to restrict NDVI estimates within meadow boundaries. Pixels with NDVI values less than 0.1 were re-classified as “null” because they represent snow, water, or bare ground. Hence, NDVI measurements were taken on pixels that only had vegetation. The mean NDVI value was calculated for each image for each of the study areas. For months where two images were available, the average of the means was recorded.

Climatic Variables

Temperature and precipitation might influence NDVI values (Hao et al. 2012; Paruelo and Lauenroth 1998; Richard and Pocard 1998; Wang et al. 2001). Climatic data (monthly precipitation, mean monthly temperatures) was measured in Boyes Meadow (Station # 046498) by the National Oceanic and Atmospheric Administration (NOAA). Although the Bald Hills Meadows were located at a higher elevation than the two sites, it was reasoned that weather patterns across years would be similar between all sites. Bald Hills Meadows likely had more extreme temperatures than the other two sites in any month within a year, but the fluctuations across years in climatic conditions should be similar.

Analyses

I used the ‘segmented’ package in R to summarize changes in abundance estimates or counts across the time series from 1997 to 2011 (Muggeo 2008; Team 2013). Piece wise regression was also used to summarize changes in NDVI across years for each study site. If no significant changes were detected with segmented regression, a linear regression was estimated to assess temporal trends in population sizes and NDVI. I also used linear regression to estimate temporal trends in monthly precipitation and mean temperature that might have influenced NDVI between 1989 and 2011.

Results

Elk Population Dynamics

When my study began in 1997, an estimated population of 82 individuals were using Davison Meadows. The population then decreased to a low of 32 in 2006. Since 2006, the population has ranged from 37 to 45 individuals. The piece wise regression detected a decline in population size between 1997 and 2006 with a stabilized population thereafter ($r^2 = 0.89$, $P < 0.001$, $df = 13$; Fig. 2).

In 1997 and 1998 there were about 30 to 31 elk in Boyes Meadow (Fig. 2). Thereafter, the counts steadily declined to 5 in January 2006. Since 2006, counts have fluctuated between 4 and 10. Piece wise regression detected a decline and stabilization of the time series ($r^2 = 0.95$, $P < 0.001$, $df = 13$). Only groups comprised of adult males were observed during surveys performed between 2011 and 2014 whereas from 1997 to 2010 the counts were mostly comprised of females, juveniles and sub-adult males.

The Bald Hills surveys began with 128 females, juveniles and sub-adult males counted in 1997. By 2003 the counts had increased to 190, and peaked at 279 in 2007 (Fig. 2). During the 2014 survey, 240 females, juveniles, and sub-adult males were counted in Bald Hills. The piece wise regression indicated that the Bald Hills population exhibited a trend of increasing population size between 1997 and 2006 which stabilized after 2006 ($r^2 = 0.91$, $P < 0.001$, $df = 10$).

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. 3). These two months were among those with the highest number of usable images through the time series of the study. Moreover, these months likely had significance in regards to elk forage. Across months 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 end of the growing season and the lower NDVI values in September indicate the ending of the dry season.

For the Davison Meadows I failed to detect a temporal trend from 1989 to 2011 in May NDVI values (Fig. 4, $r^2 = 0.16$, $P = 0.109$, $df = 15$). However, in September, piece wise regression indicated a decline in NDVI from 1989 to 1992 followed thereafter by stationary NDVI values ($r^2 = 0.37$, $P = 0.489$, $df = 13$). In contrast, September NDVI values for Boyes Meadow ($r^2 = 0.003$, $P = 0.857$, $df = 15$) and the Bald Hills Meadows ($r^2 < 0.01$, $P = 0.936$, $df = 18$) indicated no trend in NDVI values (Fig. 5).

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 trends across this time period in precipitation (May: $r^2 = 0.15$, $P = 0.116$, $df = 16$; September: $r^2 < 0.01$, $P =$

0.773, $df = 16$) or mean temperature (May: $r^2 = 0.11$, $P = 0.172$, $df = 16$; September: $r^2 < 0.01$, $P = 0.866$, $df = 15$).

Discussion

I did detect a change in NDVI measurements associated with elk herbivory in Davison Meadows. In September, NDVI values in Davison Meadows decreased from 1989 to 1992 and then persisted at lower values for the remaining years. Elk had access to Davison Meadows beginning in 1991. In Boyes Meadow and Bald Hills Meadows, where elk irruptions did not occur between 1989 and 2011, no such patterns were observed. The lack of decline in NDVI from 1989 to 2011 at the end of the growing season (May) suggests that the plant community present in Davison Meadows became or were comprised of plants resistant not tolerant to elk herbivory.

Weather patterns in precipitation and temperature did not differ over the 23 years of this study. NDVI values are influenced by climatic factors such as precipitation and temperature that influence plant biomass across seasons and among years (Hao et al. 2012; Richard and Pocard 1998; Wang et al. 2001). Therefore, it is unlikely that the NDVI variation documented in this study is a consequence of climatic conditions that changed over the course of this study.

Indeed, coevolution of plants and ungulates has been investigated for more than a century (Laycock 1978). The theory of coevolution of herbivores and plants suggests that plants exposed to long periods of herbivory develop traits which provide resistance or tolerance to herbivory (Laycock 1978; Nuñez-Farfán et al. 2007; Tiffin 2000). Further support of the importance of grazing history on the evolution of plant traits has been documented in many cases of caribou (*Rangifer tarandus*) irruptions in insular settings where herbivore and plant species did not

coevolve (Klein 1968; Ouellet et al. 1993; Ricca 2013; Scheffer 1951). Lichens (*Cladonia* sp.) are a forage consumed in winter. Yet, this food source has little tolerance to caribou herbivory. Depletion of lichen stands has been correlated with population crashes (Klein 1968; Ouellet et al. 1993; Scheffer 1951).

Given the long grazing history (~ 100 years) of the Davison Meadows by cattle, the indication of a plant community not tolerant to elk herbivory is somewhat surprising. Common animal husbandry practices in the area included feeding supplemental hay to cattle during periods of food shortage (Harper 1967). Coupled with the irruptive pattern of elk population growth (Starns et al. *in review*), the lack of change in NDVI at the peak of the growing season in May suggests that the plant community in Davison Meadows has changed. This change apparently favors plants which are more resistant to elk herbivory.

The decline in September NDVI values detected in Davison Meadows suggests that elk herbivory during the initial, rapid growth phase of the elk population irruption (stage 1) decreased dry season NDVI and, presumably, dry season forage biomass. Because of the lack of rainfall during the summer, elk herbivory in Davison Meadows during the early years of the study might have decreased forage availability in summer. Reduced food availability in summer differs from other populations of elk where forage availability is highest in summer (Clutton-Brock et al. 1985; Coughenour and Singer 1996). The differences observed in NDVI among the three study sites probably resulted from differences in the grazing history of each site. Over the course of this study, the elk population in Boyes Meadow did not undergo an irruption but declined to near zero while NDVI values remained stable. Davison Meadows and Boyes Meadow, however, appear to have similar histories of elk population dynamics: both populations displayed irruptive growth during the years immediately following cessation of livestock

grazing. Boyes Meadow was converted from cattle and hay production to an elk refuge and viewing area in 1933. Dasmann (1964) reported an irruptive population growth pattern in Boyes Meadow between 1937 and 1963: the population increased from a few to 100-200 animals between 1937 and 1949, followed in 1949-1950 by a decline to 50 to 60 elk. Between 1952 and 1963, the population fluctuated between 35 and 55 (Dasmann 1964). During the winter of 1949-1950, the elk population in Boyes Meadow apparently declined precipitously (Dasmann 1964; Harn 1958). Elk in the Bald Hills Meadows probably have not undergone a population irruption.

Although I was unable to directly estimate plant community composition across the period of the study, there was an apparent increase in the presence of reed canarygrass (*Phalaris arundinacea*) in the Davison Meadows (F.W. Weckerly, personal observation, Fig. 6). Reed canarygrass is a common invader of mesic sites throughout North America (Martina and von Ende 2013). In Davison Meadows there is standing water throughout the rainy part of the year (October-April). Reed canarygrass is high in alkaloid concentrations (Hagman et al. 1975; Marten et al. 1973; Woods and Clark 1971). Alkaloid concentrations are negatively correlated with palatability in cattle and sheep (Marten et al. 1976). Also, Suring and Vohs (1979) reported avoidance of reed canarygrass by white-tailed deer (*Odocoileus virginianus*) and Larter (Larter 1994) reported similar avoidance by bison (*Bison bison athabasca*). The increase of reed canarygrass in the Davison Meadows might explain the lack of a temporal pattern in May NDVI across the time series of the study. Because NDVI is a measure of the spectral reflectance of vegetation, most grass species likely return similar values of NDVI. Moreover, pixel resolution of 30 m² is probably inadequate to detect shifts in the herbaceous community. As such, palatable forage species available to elk during the early portion of the study might have been replaced by reed canarygrass later in the study.

Shifts in plant community composition from tolerant to resistant species have been observed in association with ungulate grazing (Anderson and Briske 1995; Augustine and McNaughton 1998; Klein 1968; Leader-Williams et al. 1981; Leader-Williams et al. 1987). Focardi and Tinelli (2005) studied the effects of ungulate herbivory in a Mediterranean ecosystem and suggested that high levels of grazing would lead to a structural change of the plant community. Considering the numerous reports of herbivore-driven changes in plant community composition, similar changes in Davison Meadows is neither implausible nor surprising. It is possible that the apparent change in community composition took place as a result of differences in diet selection between cattle and elk. Hagman et al. (1975) reported that the alkaloid concentration, and therefore, the unpalatability of reed canarygrass increased with plant maturity. If reed canarygrass was present in the Davison Meadows during the period of cattle grazing, it may have been grazed heavily enough during early growth to prevent an increase in biomass within Davison Meadows.

Although NDVI was useful in detecting elk herbivory through an irruptive pattern of population growth, its utility was limited to detection of changes. Without quantitative vegetation monitoring data from the beginning of the study period, these changes cannot be attributed to specific aspects of plant population dynamics. Future meadow acquisition by RNSP would provide opportunities to quantitatively test the effects of Roosevelt elk herbivory on plant community composition.

APPENDIX

Figure Legend

Figure 1. 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.

Figure 2. Elk population trends observed at each study site. Count data was 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.

Figure 3. Monthly pattern of NDVI values from 1989 to 2011, Redwood National and State Parks, California.

Figure 4. May and September NDVI values for Davison Meadows from 1989 to 2011. Regression lines summarize temporal patterns of September NDVI values as detected using piece wise regression.

Figure 5. September NDVI values for Boyes Meadow and Bald Hills Meadows from 1989 to 2011, Redwood National and State Parks, California.

Figure 6. Photos showing the presence of reed canary grass in Davison Meadows in August 1996, and July 2013.

Figure 1.

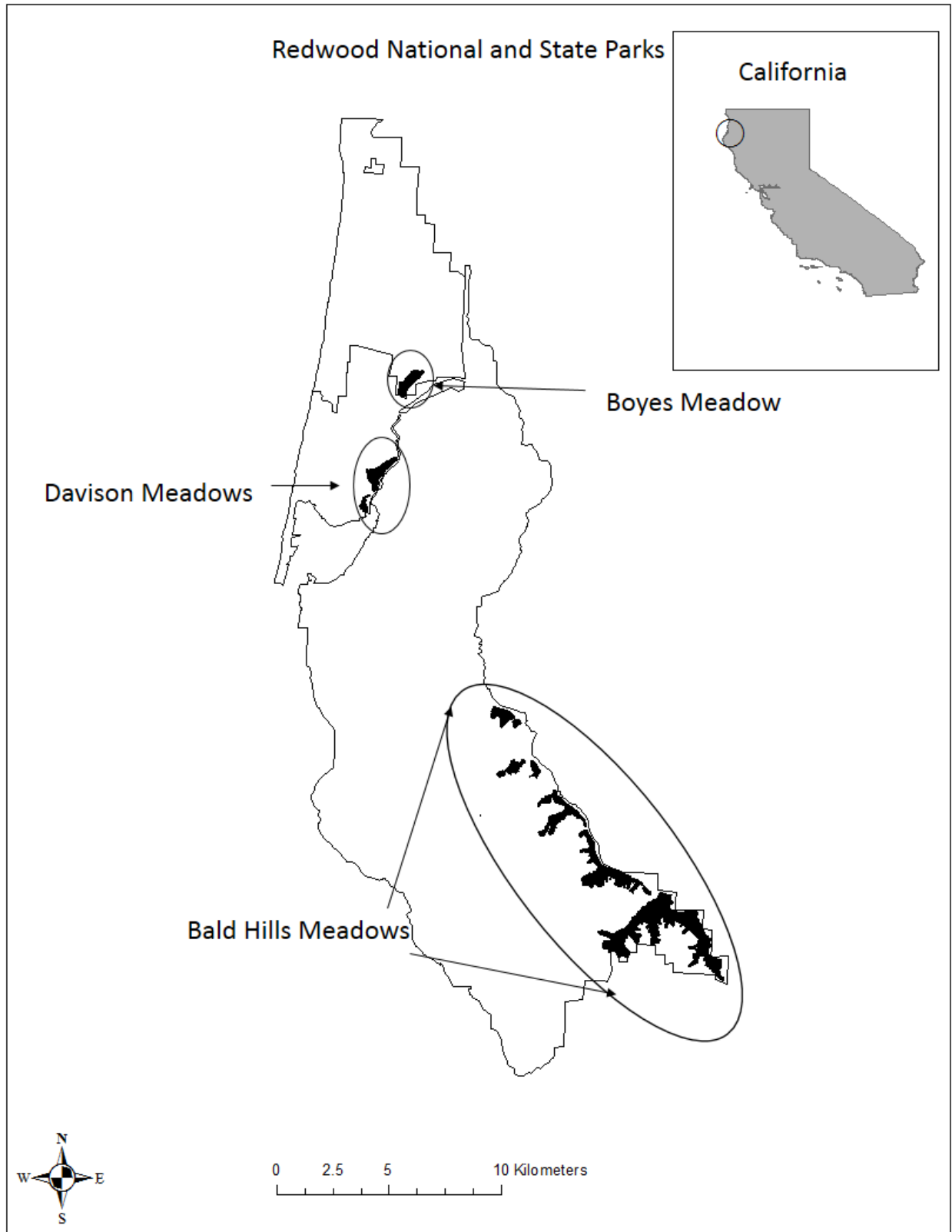


Figure 2.

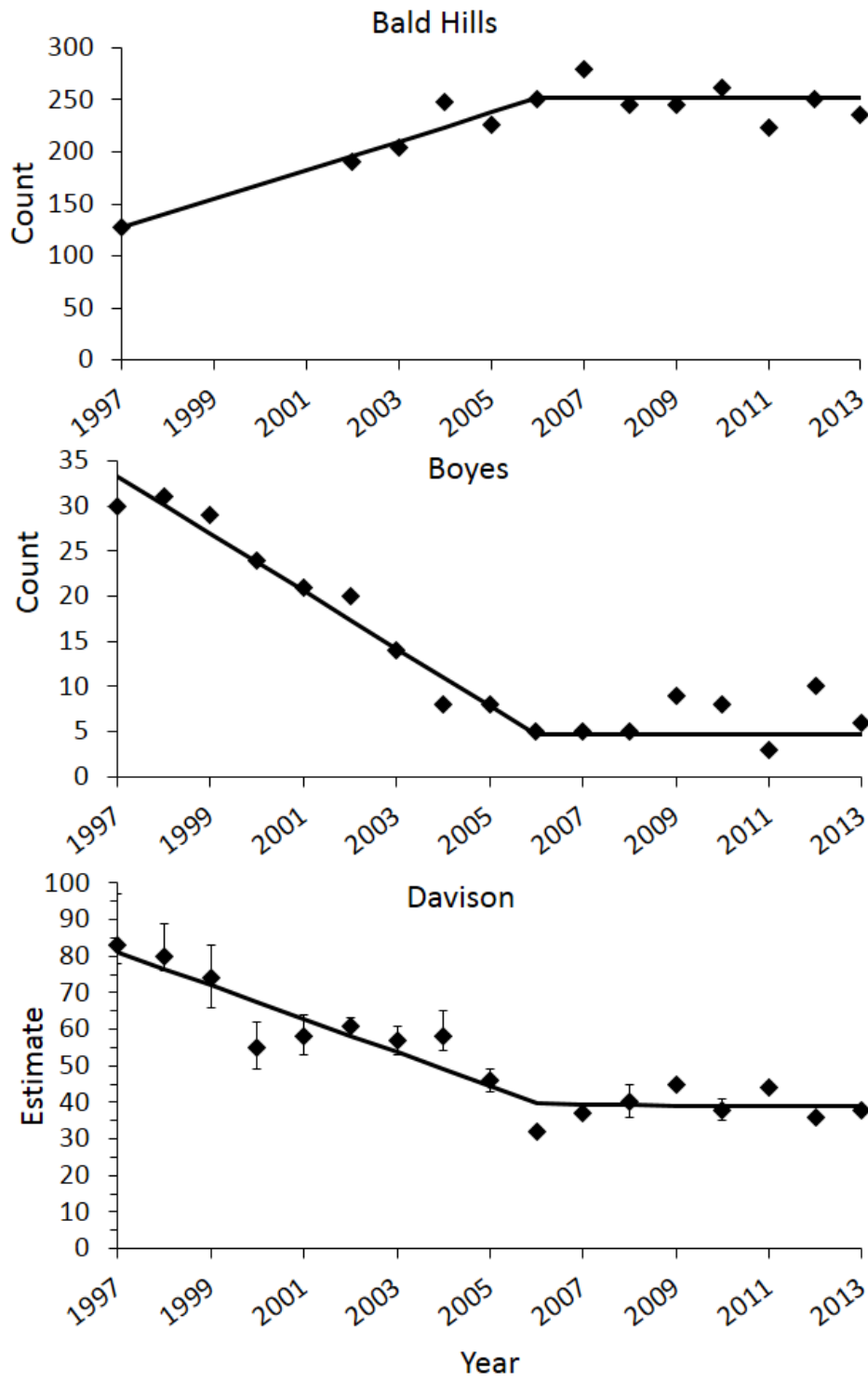


Figure 3.

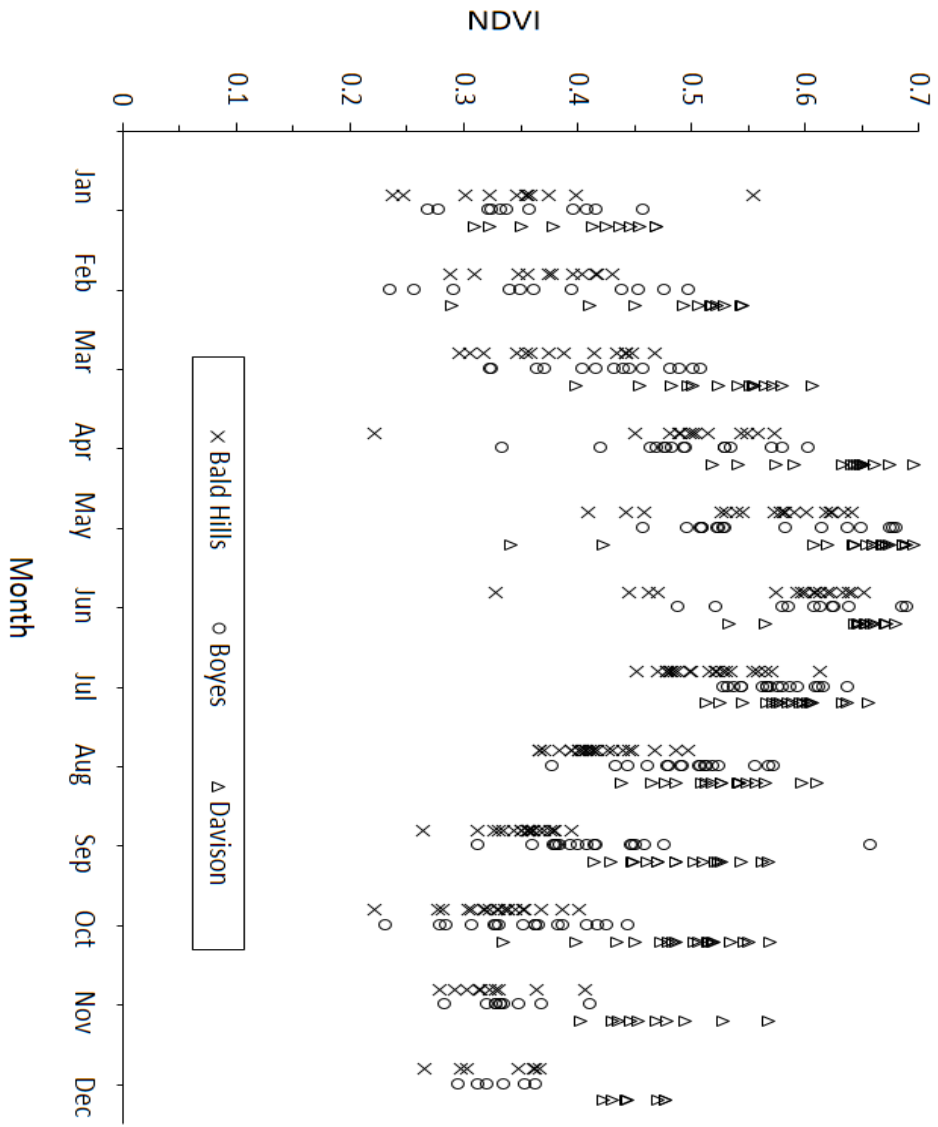


Figure 4.

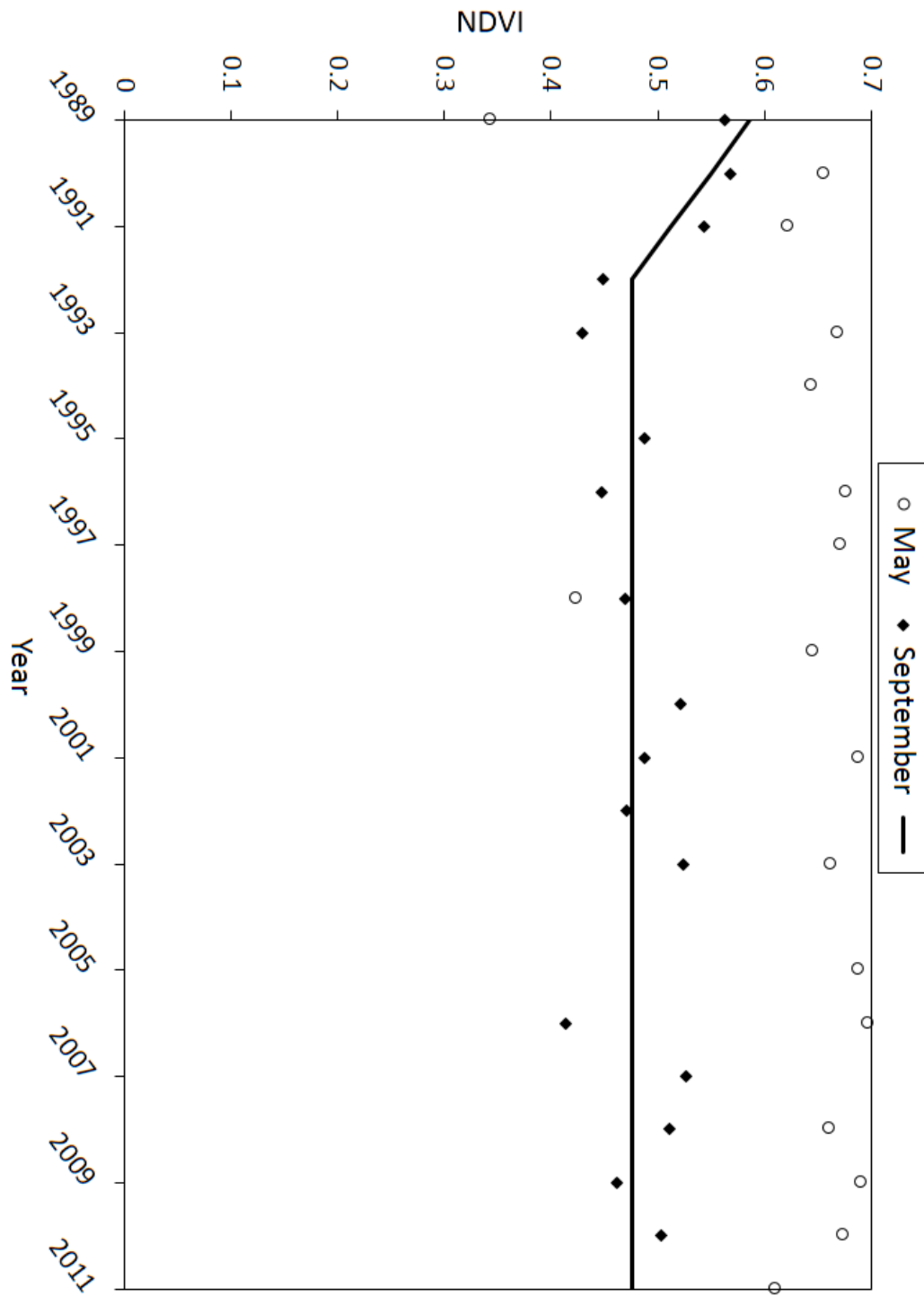


Figure 5.

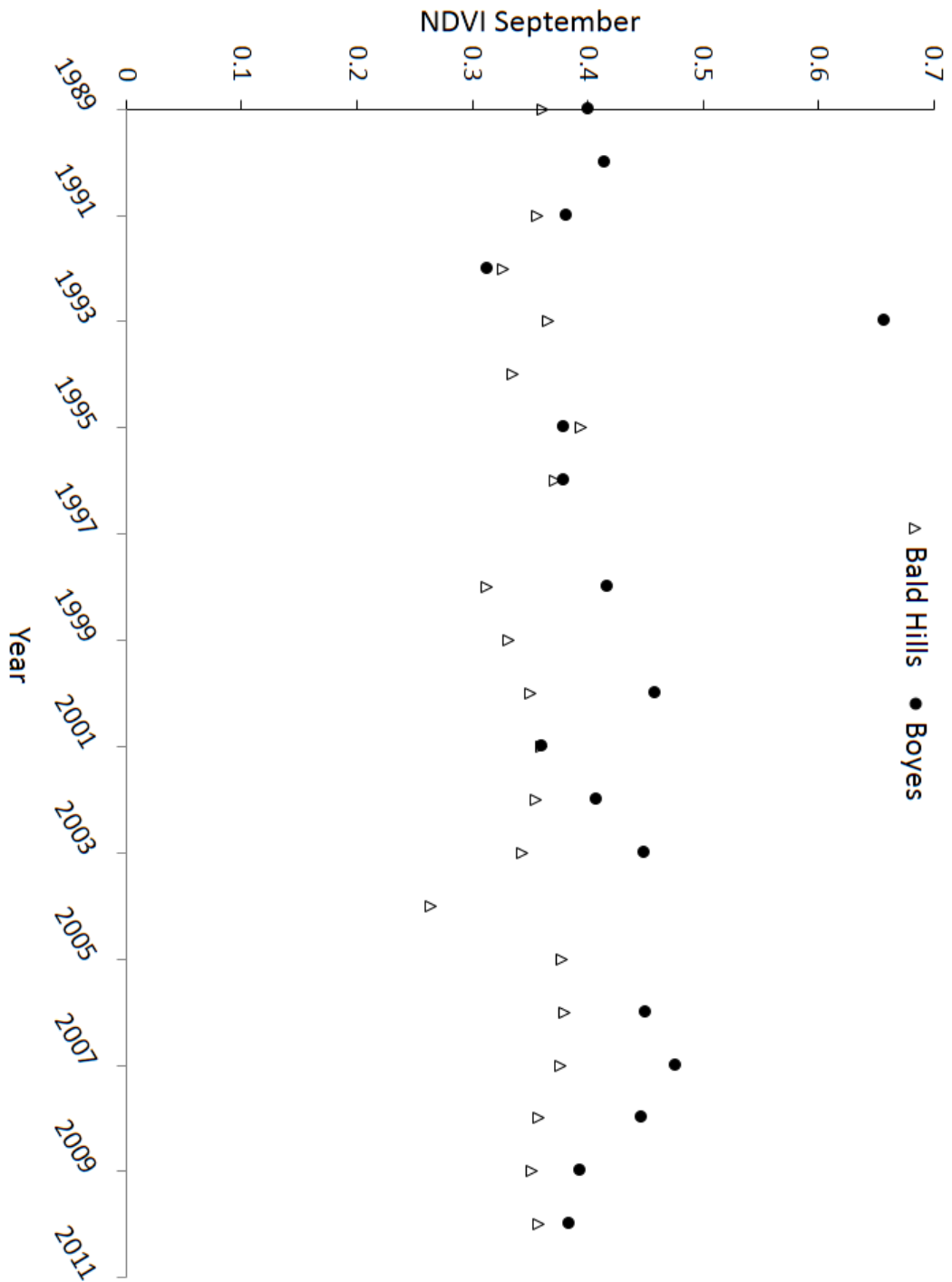
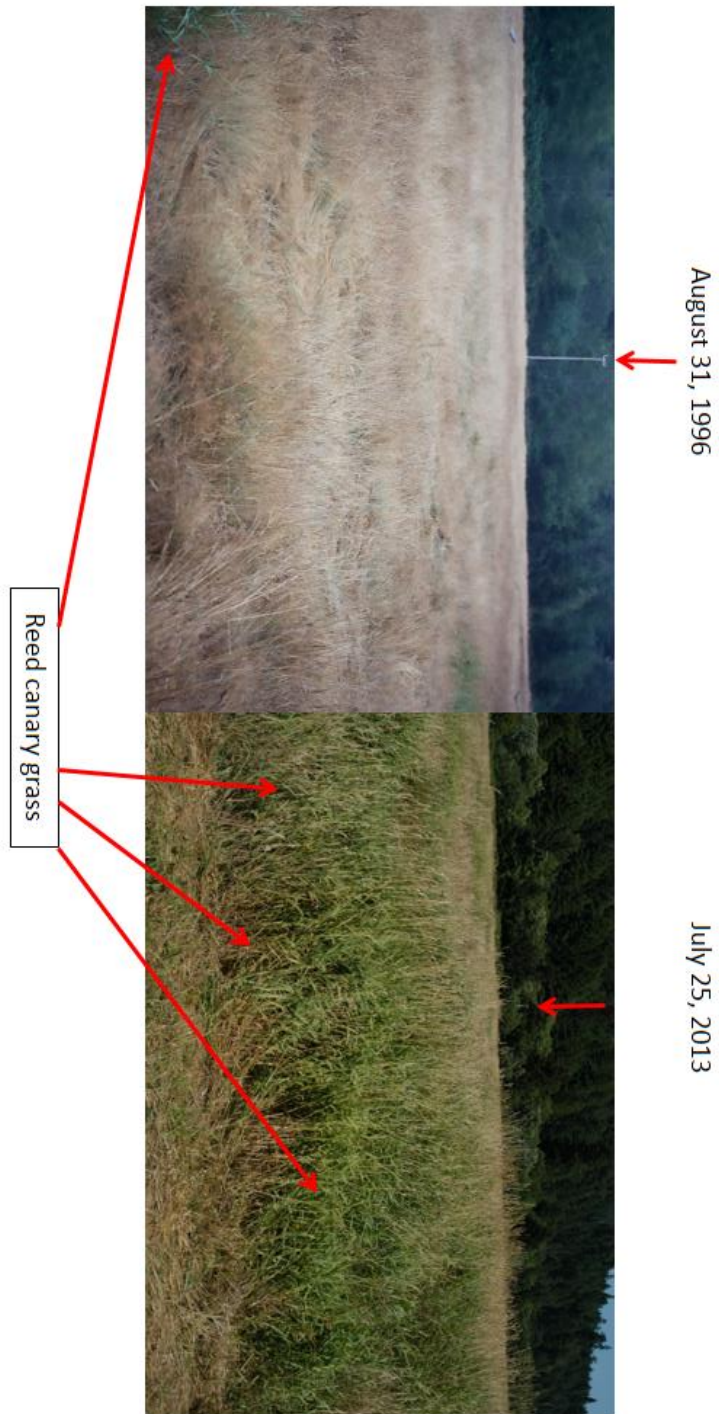


Fig. 6



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