ROOSEVELT ELK RESPONSE TO A NEWLY AVAILABLE FORAGE PATCH

by

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ABSTRACT

According to optimal foraging theory, herbivores will use a new foraging patch intensely to become familiar with a new resource. To better understand how herbivores incorporate new habitat into their home range, I examined use by a Roosevelt elk (*Cervus elaphus roosevelti)* herd in Redwoods National and State Parks, California, that was recently given access to a nearby, new foraging patch, the cattle pasture. Cattle and predators, both of which can negatively affect elk spatial patterns, also used the cattle pasture. My study objectives were to examine monthly elk use in the cattle pasture, assess cattle and predator influence on herd use of the pasture, analyze summer and winter movement patterns to assess if forage biomass was more limited in one season, and determine if the herd was using the cattle pasture intensely to become familiar with the resources. I placed six infrared, motion sensitive cameras throughout the cattle pasture from August, 2016, to November, 2017. I followed the herd from dawn to dusk, recorded elk activity, movement (step length), and forage biomass in January, 2017 and 2018. Herd movement was also recorded in July, 2017. I found avoidance between elk and cattle and elk and predators at short temporal and small spatial scales in the cattle pasture. Step lengths were similar between summer and winter months. The herd used the cattle pasture more in January, 2018, than in January, 2017. My finding were inconsistent with optimal foraging theory.

Roosevelt Elk Response to a Newly Available Forage Patch

Introduction

Knowledge of foraging and movement patterns in large herbivores is essential for understanding life histories, population dynamics, and trophic interactions. Foraging and movement studies where animals have colonized new habitat is particularly insightful because it is an infrequent occurrence and it is necessary to understand how herbivores should respond to a new food source (Berger-Tal and Bar-David 2015). Large herbivores are often familiar with forage patches and select these patches based on forage nutrition, patch types, spatial arrangement of patches, interactions with other herbivore species, climatic factors, and exposure to lethal risks from natural and anthropogenic predation (Marion et al. 2005, Weckerly 2017). Nonetheless, optimal foraging theory suggests that when a new foraging patch becomes available, herbivores will use this patch more frequently to become familiar with its available resources (Pyke et al. 1977, Focardi et al. 1996, Forrester et al. 2015).

Herbivores encounter new foraging habitats in three ways. Animals are purposely introduced to new habitats, disperse from one home range and settle into a new home range, or the home range is expanded to include nearby habitat (Hundertmark 1998). Regardless of how animals colonize new habitat, individuals obtain access to new patches comprised of unfamiliar resources. Habitat use in a new patch is influenced by many factors including available forage biomass, cover, interspecific competition, predator activity, human activity and disturbances, and

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unfamiliarity with new forage habitat (Tufto et al. 1996, Mysterud and Ims 1998, Hernández and Laundré 2005, Bjørneraas et al. 2012).

There have been several studies examining movement and habitat use by large herbivores that were introduced (Clarke 1986, Anderson et al. 2005b, Spaggiari and de Garine-Wichatitsky 2006, Fryxell et al. 2008, Massé and Côté 2009). Large herbivore dispersal to new home ranges have also been well studied (Larter and Gates 1990, Bowman et al. 2002, Spaggiari and de Garine-Wichatitsky 2006, Tatman 2008, Ricca et al. 2014). There has been less research examining home range expansion into a new foraging habitat (Hundertmark 1998, Neil and Bump 2014). Home range can be defined as an area used by an individual or group of individuals for their daily patterns which include foraging, cover, and reproduction (Burt 1943, Craighead et al. 1973). The home range of large herbivores can be influenced by size of the animal, the size of the group or herd, the composition of habitats, lethal risks from predators and anthropogenic activities, or climatic influences such as precipitation, temperature, and wind (Kie et al. 2002, Anderson et al. 2005a, van Beest et al. 2011, Beest et al. 2013).

One reason why wildlife species possess home ranges is that familiarity with resources improves resource exploitation (Stamps 1995, Wolf et al. 2009, Forrester et al. 2015). When herbivores are introduced to a landscape, they are unfamiliar with forage availability, predator activity, and any other aspect of the new habitat. How individuals might become familiar with new habitat should involve foraging thresholds, recursive movements, forage biomass, and foraging behavior. Foraging thresholds refer to the minimal available forage biomass needed for animals to consume their nutritional

intake demands. Once familiarity with foraging thresholds have been established,

individuals may return periodically to the patch, displaying a recursive movement

pattern. Seidel and Boyce (2015) describe recursive movement through a pattern of

forage depletion, departure, and return once foraging patches recover. Recursive

movement facilitates familiarity with resource distribution and abundance. Forage

biomass, foraging speed (step length) and foraging patterns within an unfamiliar patch can

influence the amount of time spent in the new patch (Focardi et al. 1996). Ample forage

biomass, typically present in the spring or summer, should allow for a slower foraging speed,

while reduced forage biomass, typically in fall and winter, should result in faster foraging

patterns (Vivas and Saether 1987, Fryxell et al. 2008). These seasonal movement patterns are

important for understanding the amount of time animals spend foraging in habitats.

Two key factors in determining the amount of time spent foraging in a place are

habitat potential and habitat effectiveness. Habitat potential is defined as any

ecological factor that influences productivity, while habitat effectiveness is the actual

use of habitat by animals (Roloff 1998). One notable ecological factor that influences

seasonal, primary productivity, and thus habitat potential is precipitation. Disturbances

impact habitat effectiveness. Disturbances can be anthropogenic activities that alter

where herbivores forage, ruminate, and rest, or interspecific interactions with natural

predators or domestic livestock such as cattle (Stewart et al. 2002). Extensive

disturbances by predators can alter the distribution and time herbivores spend foraging

in a habitat, the landscape of fear (Laundré et al. 2001, Laundré et al. 2010). Herbivore

response to natural predators is usually one of reducing risks of attacks. Herbivores can

ameliorate risks by aggregating with other individuals and avoiding places in habitats or

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patches when they are more vulnerable to attack (Frid 1997, Frair et al. 2005).

Consequently, when herbivores avoid particular places when they are vulnerable to

attack, herbivores could still use the resources at larger spatial and temporal scales.

Interactions between cattle and elk during fall and winter could be more

noticeable as forage quality and quantity is limited (Wisdom and Thomas 1996). Elk and

cattle often display asymmetric interactions (Wallace and Krausman 1987, Yeo et al.

1993). Elk appear to avoid areas frequented by cattle but cattle do not appear to avoid

areas used by elk (Coe et al. 2005, Weckerly 2005). Cattle can displace elk in both

summer and winter (Stewart et al. 2002). Cattle have been observed (personal

observation) actively pursuing elk and chasing elk away. Wisdom and Thomas (1996)

suggest that elk will attempt to distribute themselves spatially to minimize or avoid

competition with cattle, which could limit grazing opportunities for elk.

One herd of Roosevelt elk (*Cervus elaphus roosevelti*) has resided in a meadow

complex in the Prairie Creek drainage in Northwestern California for over 20 years and

has a wide range of population dynamics including an irruption, decline, and gradual

increase (Starns et al. 2014, Weckerly 2017). This particular herd recently began

frequenting a nearby meadow, which has been managed for cattle for decades, which

still continues. This setting is ideal for examining elk response to a new forage patch in a

natural setting because the herd is habituated to human presence and can be studied

from a close distance.

An elk herd is comprised of socially bonded females ($\geq$1 year of age), juveniles (<1 yr), and sub-adult males (1 – 2 yrs) (Weckerly 2017). Non-migratory, socially bonded herds spend much of their lives together in the same group (Jenkins and Starkey 1982, Weckerly 1999). Elk herds typically occupy a home range that has little overlap with other herds in the region. Each herd tends to concentrate use in meadows, which contain the bulk of herbaceous forage, that are in a landscape dominated by forest (Weckerly 2005, Bliss and Weckerly 2016, Weckerly 2017).

Elk use of new foraging patches and the effects that disturbances have on use in an expanding home range is not well known. Examining elk response to a new foraging patch in a natural setting will increase understanding of how interspecific interactions influence habitat effectiveness for elk. From a land management perspective, examining elk habitat effectiveness will be useful to understanding how elk respond to a new foraging patch that is already grazed by cattle. My study had four objectives to examine use and disturbances in the new meadow. First, I documented monthly use of the new meadow by an elk herd. Second, I estimated whether predators, such as black bear (*Ursus americanus*) and mountain lion (*Puma concolor*) influenced elk use in different parts of the new meadow. As elk also respond to natural predators at small spatial scales, the possible influence from predators should be more apparent within parts of the new meadow rather than at the larger spatial scale of the entire, new meadow. Cattle (*Bos spp*) typically only had access to one part of the meadow and not the entire meadow because of how the meadow was fenced. I estimated whether or not cattle presence in a part of the meadow affected elk use throughout the rest of the

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meadow. Third, I measured movement patterns by the elk herd. I expected that grazing step length (distance traveled) would be shorter in summer when forage biomass should be well above the forage threshold than in winter (Schwartz and Ellis 1981, Frair et al. 2005). Because forage biomass is more limited in winter compared to summer, elk should forage closer to the foraging threshold in winter. Therefore, the fourth objective was to estimate if selection of the new meadow during winter should be higher compared to other nearby meadows as elk are attempting to become more familiar with the new resource.

Materials and Methods

Study Area

The study was conducted in Redwoods National and State Parks (Parks), along the Prairie Creek Drainage in Humboldt County, Northwest California, USA (Figure 1). Historically, the lower reach of the drainage was forest. Removing the forest and establishing meadows in the valley floor for grazing cattle began in the late 1890s (Weckerly 2017). The resulting 50 ha meadow complex, the Davison meadows, was purchased in 1991 by Save the Redwoods League and deeded to the National Park Service (Starns et al. 2014). Prior to 1991, the Davison meadows were grazed by dairy cows and elk were limited to using clear-cuts in the nearby forests. After 1991 elk colonized Davison meadows and became the Davison herd (hereafter, herd) (Weckerly 2017). The herd subsequently underwent a four stage irruption (Leopold 1943, Starns 2014, Starns et al. 2014, Starns et al. 2015). The herd displayed rapid, population

growth (stage 1), from 1991 to 1997 when the Davison meadows presumably had a surplus of forage (Weckerly 2017). The herd overshot *K* carrying capacity (stage 2) and peaked in 1997, then showed a steady population decline (stage 3) from 1997 to 2006. After the population decline, the herd appeared to be establishing a new lower K carrying capacity from 2007 to 2016, the fourth stage of an irruption (Weckerly 2017).

A 10 ha pasture, referred to as the cattle pasture, is located south of the Davison meadow complex (Figure 1). The cattle pasture has probably been grazed by cattle for over a century. In 2015 or 2016, elk were given undisturbed access to the cattle pasture when this land was purchased by Save the Redwoods League. Before 2015 elk were hazed when they were detected in the cattle pasture. The hazing ceased after 2015. Between 20 – 30 cattle (cows, calves, steers) continue to graze one part of the cattle pasture in winter (Weckerly 2017). Each part is about five ha in size.

The Davison herd is ideal for study because they are non-migratory and habituated to humans. Consequently, the herd can be observed at close distances (20-200 m) throughout the year (Weckerly 2007). Since the Davison herd is habituated to human activity, the presence of people and vehicles do not affect the use of the cattle pasture or other surrounding habitats by elk (Weckerly et al. 2001, Starns et al. 2015, Weckerly 2017).

Climate

The Prairie Creek drainage has a mild, maritime climate with daytime temperatures rarely exceeding 18° C in summer or winter (Weckerly 2007).

Precipitation in the area includes fog in summer and rain and fog in winter. Annual

precipitation is typically greater than 150 cm and occurs mostly from late autumn into

spring (Starns et al. 2015). Snow is rare. Due to the mild climate, elk do not appear to

use forested habitat to ameliorate extreme climatic conditions (Witmer and Decalesta

1983, McCorquodale et al. 1986).

Vegetation

Meadows in the region are largely comprised of perennial and annual grasses

and are surrounded by closed-canopied forests. Prevalent grasses in the drainage are

California oat grass (*Danthonia californica*), soft chess (*Bromus hordeaceus*), redtop

(*Agrostis alba*), and invasive reed canary grass (*Phalaris arundinacea)*. Common forbs

are hairy cats ear (*Hypochoeris radicata*) and narrow leaf plantain (*Plantago lancelata*)

(Harper et al. 1967, Bliss and Weckerly 2016). Invasive reed canary grass, once

established, can displace other herbaceous species (Schooler et al. 2006, Starns et al.

2015). Cattle graze reed canary grass but elk appear to graze the grass infrequently

(Marten et al. 1976, Weckerly 2017). Forest throughout the drainage mainly consist of

secondary and old-growth conifers dominated by coast redwood (*Sequoia*

sempervirens), Sitka spruce (*Picea sitchensis*), Douglas-fir (*Pseudotsuga menzeisii*), and

western hemlock (*Tsuga heterophylla*) (Harper et al. 1967, Jenkins and Starkey 1982).

Cattle and Predators

Interspecific interactions with other large herbivores include black-tailed deer

(*Odocoileus hemionus columbianus)* and cattle. Abundance of black-tailed deer is much

lower than elk in the Davison meadows and deer do not appear to displace elk (Clegg 1994, Stewart et al. 2002, Weckerly 2017). Consequently, I did not consider elk – deer interactions. Potential predators of elk in the drainage include black bear and mountain lion. Black bears appear to prey mainly on neonatal elk in late spring and early summer (Weckerly 2017). Mountain lions probably prey on all age – sex classes of elk (Toweill and Thomas 2002).

Methods

Camera data

Six infrared cameras, four Moultrie model 990i and two Moultrie model 999i, were strategically placed throughout the 10 ha cattle pasture to observe diurnal and nocturnal use of elk, cattle, black bear, and mountain lions in and near the cattle pasture (Figure 2). Cameras could detect motion up to 30 meters away. Digital photographs or 10-second-long videos taken by cameras were downloaded monthly. Camera data was collected continuously from August, 2016, to November, 2017. Hereafter, pictures refer to a photograph or video taken from a camera.

Elk, cattle, and predator use in the cattle pasture was measured by recording the number of days in each month there was one or more individuals of a species in one of more pictures taken by one or more cameras. Interactions between elk and cattle and elk and predators were measured at the scales of the camera and a 24-hour period. Whenever cattle or a predator's picture was taken at a camera, an event, I determined if elk had also been photographed within 24 hours before or after the event. Elk

avoidance to predators or cattle has been documented to occur within 24 hours (Clegg 1994, Laporte et al. 2010).

Herd Activity and Movement

Field observations of herd activity and movement throughout the Davison meadows and cattle pasture were recorded from dawn to dusk across 21 days in Januarys 2017 – 2018, and July 2017. Data collected in January included elk activity, location of the herd, and the number of females, juveniles, sub-adult males and any males in the herd. Activity was categorized as feeding, bedded, loafing (standing and ostensibly not doing anything else), and other. The category of other included running, walking, vigilance, sparing between males and any other kind of social interactions. Daily field observations were approximately 10 and 15 hours in January and July, respectively.

Herd location was determined by taking Universal Transverse Mercator (UTM) coordinates from where I observed the herd and measuring distance and taking a compass bearing to the center of the herd. I used a handheld global positioning system (GPS) unit to take UTM coordinates of my location. I used a rangefinder to measure distance to the herd to the nearest meter. Herd location and activity of every elk in the herd was recorded every five minutes from dawn to dusk in January. From the activity data, I calculated elk foraging hours as the sum of the number of hours that elk in the herd foraged during daylight hours.

Similar to January observations, I followed the herd from dawn to dusk in July, however, I only recorded herd location every 15 minutes without collecting detailed activity data. At 15 minute intervals, activity of the herd was noted as greater than 50 percent of the herd was up and foraging or bedded. Vegetation in meadows in July often exceeded 1.5 meters and prevented observations of every elk in the herd. I measured step length from the movement data collected every 15 minutes in January and July as well. Step length was the straight line distance traveled every 15 minutes. Step length was calculated for diel movement patterns across the three months at periods of time when at least 50 percent of herd members were standing up and feeding.

Forage Biomass

Forage biomass was measured in January 2017 and 2018. Biomass was not measured in summer because maximum food intake by individuals in 24 hours was probably much less than the amount of available forage biomass (Wickstrom et al. 1984, Starns et al. 2015). Biomass was estimated in 330, 0.25 m^2 plots placed throughout the sectors in Davison meadows and cattle pasture (Figure 1). In the 0.25 m^2 plots, percent coverage of palatable grasses and forbs were estimated using Daubenmire cover classes (Daubenmire 1968). I also measured the height of grasses and forbs at eight equidistant locations in the plots (Daubenmire 1968). I then estimated biomass from cover class and height measurements using the predictive equations described by Weckerly (2017).

Analyses

Elk, cattle, and bear use was measured through pictures collected monthly by the six trail cameras. Mountain lions were not considered in the analysis because there simply were not enough pictures of mountain lions across the 16 months (see Results). For each species and camera, use was estimated as number of days with pictures divided by number of days in the month. Mean use, and 95% confidence intervals, from the six cameras was estimated from 100 bootstrapped pseudo samples for each species in each month.

Overlap in use between elk and cattle and elk and black bear was measured at the temporal scale of 24 hours and the spatial scale of a camera detection. I noted the day and time there were pictures of each of the three species at a camera. Within 24 hours before and after the time we noted cattle or black bear, I determined if there were also elk pictures. When overlap occurred in two consecutive days (no case of three or more consecutive days) overlap was two days, not one day. Across months I recorded the days of the month when elk were photographed by each camera. I then measured overlap, 24 hour periods (hereafter days), when both elk and cattle or elk and black bear were photographed at a camera. Observed overlap was then calculated as the number of overlap days divided by number of days with elk pictures. I then generated the same proportion from randomly generated data (random overlap) which had the same number of days with elk, cattle, or black bear pictures. I randomly generated 1000 iterations to estimate the mean proportion and 95 percent confidence intervals (2.5th and 97.5th percentiles of the 1000 proportions). If elk were avoiding

cattle or black bear, I expected that the observed overlap would be less than the

confidence intervals of random overlap.

I analyzed step lengths considering diel (morning, midday, and evening) periods

across months (January and July, 2017, January, 2018). The morning period was from

dawn to two hours later, mid-day was from 1200 to 1400, and the afternoon period was

from dusk to two hours before dusk. I considered diel periods because elk movement

might be greatest near dawn and dusk (Forester et al. 2007). I estimated a linear mixed

effects model using sector as the random factor with an intercepts random effect.

Reference categories were evening and July, 2017. Fixed factors were diel period,

month, and the interaction between diel period and month. Because step length was

not normally distributed, I bootstrapped parameter estimates from 1000

pseudosamples. Resampling occurred at the level of the observation.

I tested for possible selection of the cattle pasture by the herd from regressions

estimated between forage biomass and elk foraging hours (hereafter elk hours) in the

Davison meadows sectors and cattle pasture in Januarys, 2017 and 2018. If the herd

selected the cattle pasture, then elk hours would be above the 95 percent confidence

envelope of the regression. Forage biomass was the kilograms of dried forage biomass

per hectare multiplied by the hectares in the sector. I estimated a linear mixed effects

model where the reference category was January 2017 and parameter estimates were

biomass, year (January 2018), and the interaction between biomass and year. Sector

was the random factor with an intercepts random effect. We also estimated the

marginal and conditional r^2 (Nakagawa and Schielzeth 2013). The marginal r^2 was the

proportion of variation in the response variable accounted by the fixed predictors. The

conditional r^2 was the proportion of variation in the response variable accounted for by

both fixed predictors and the random effect. All analyses were conducted in program R

(R Core Team 2013).

Results

Picture Data

Six trail cameras were deployed continuously from August, 2016, to November,

2017, for a total of 16 months or 487 days. Throughout this time, the number of days

elk, cattle, black bear, and mountain lion were observed in pictures were 162, 79, 87,

and 9, respectively. Due to the meager number of days mountain lions were observed

in pictures, they were not considered in further analyses. Pictures of elk were recorded

in all months except August, 2016 (Figure 3). Cattle were present in the cattle pasture

from December, 2016, to March, 2017. Cattle were not observed during other months

as the lessee removed them from the cattle pasture. Pictures of black bears were

recorded in months barring November, 2016, to January, 2017 (Figure 3). Presumably,

black bears were not observed during those three months because of winter torpor.

Between August, 2016, and March, 2017, elk use in the cattle pasture fluctuated

from 0.0 to 0.20 of the days in a month (Figure 3). Elk use then increased and peaked in

June, 2017, at 0.32. Thereafter to the end of the study in November, 2017, use steadily

declined to 0.09. Many months had confidence intervals that overlapped indicating no

significant, monthly differences in elk use. Nevertheless, the month of highest use,

June, had a lower confidence bound (0.20) that was higher than the upper confidence bounds of August, September, and November in 2016, and January, March, April, October, and November in 2017. Those months appeared to have lower elk use than June. Across all months, the general pattern of elk use increased from the beginning of the study in August, 2016, peaked in June, 2017, and then declined thereafter.

In August, 2016, black bear use in the cattle pasture was 0.12 of the days in August and then declined to 0.01 in October, 2016. (Figure 3). Black bear use began again in February, 2017, and gradually increased until it peaked in August, 2017, at 0.11. Use of the cattle pasture by black bear then declined to a low of 0.05 in November, 2017. Cattle use began in December, 2016, and concluded in March, 2017.

Overlaps of elk with black bear and cattle were estimated by pooling data across months when there were pictures of both elk and one of the species because of meager data. There was 11 days of overlap for elk and black bear and one day of overlap between elk and cattle. There were 253 days of elk pictures when estimating overlap with bear and 90 days of overlap for estimating overlap with cattle. The observed overlaps of elk and bear and elk and cattle were greater than the 95% confidence intervals of random overlaps (Table 1). Elk appeared to avoid both black bear and cattle at the scales of a camera and within 24 hours.

Herd Movement

There were 299 step lengths in January, 2017 (116, 68, 115; morning, midday, and evening, respectively), 291 in July, 2017, (113, 66, 112) and 311 in January, 2018

(112, 76, 123). I detected no differences in step lengths across diel periods or months

(Table 2). Distance traveled in 15 minutes by the herd was similar at different times of

the day and across months.

Pasture Selection

The herd was followed for 13 days in each January totaling 130.25 hours in

January, 2017, and 127.25 hours in January, 2018. To adjust for the differing number of

hours the herd was followed in each January I divided elk hours by total observation

hours. Forage biomass in sectors ranged from 513 – 4594 kg (mean = 1808, s = 1353)

across the two years (Figure 4). Herd size was 52 in 2017 and 62 in 2018. Elk hours in

sectors ranged from 6.9 – 106.2 (51.7, 31.8) in 2017 and 23.0 – 159.9 (82.2 – 50.8) in

2018. The linear mixed effect model indicated a positive relationship between forage

biomass and adjusted elk hours, yet there were no differences between years in the

relationship (Table 3). One regression was sufficient to summarize the relationship

between forage biomass and adjusted elk hours for both years of data. The fixed

predictors in the model summarized the relationship reasonably well (r^2_m = 0.63) but

there was virtually no heterogeneity due to sector (r^2_c = 0.63). Across both years there

were 10 sectors that were within the 95 percent confidence envelope, four that were

above the confidence envelope (selection) and four below the confidence envelope.

The cattle pasture was selected in 2018 but not in 2017.

Discussion

The novel aspect of this study was examining how large, wild herbivores expand their home range to include a new foraging patch when disturbances from interspecific interactions were also present and examined. Few studies have looked into what affects home range expansion (Gates and Larter 1990). According to optimal foraging theory, a herbivore should select a new patch more frequently to become familiar with the new resources (Pyke et al. 1977, Brown 1988). The Davison herd was given undisturbed access to the cattle pasture in 2016 and used the pasture throughout the time of my study. Because the Davison herd was using the cattle pasture I predicted that the herd would use the cattle pasture more frequently than available forage biomass. Yet, in January, 2017, and January, 2018, I found that this was not the case. Selection was greater in 2018 than in 2017, opposite of what I expected. There are four possible explanations for the unexpected finding. One, the Davison herd was already familiar with the resources in the cattle pasture by the time my study began in January, 2017. Two, elk did not require increased use to familiarize themselves with the new resource. Three, elk avoided cattle and black bear, and, four, there were differences between years in forage biomass and herd abundance that effected elk selection.

The foraging patterns of the Davison herd early in my study were not consistent with the prediction from optimal foraging theory (Macarthur and Pianka 1966, Pyke et al. 1977, Belovsky 1986, Focardi et al. 1996). I might have started measuring elk use after the herd had been using and became familiar with the cattle pasture. It is possible that elk began using the cattle pasture the year before I began my study. The cattle

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pasture actually became available to elk in late autumn, 2015, whereas collection of camera data did not begin until August, 2016.

The second possibility was that the Davison herd might not have needed substantial time to familiarize themselves with the cattle pasture. The cattle pasture was less than 0.5 km from meadows that the Davison herd has used for over 20 years (Weckerly 2017). Consequently, the herd probably did not have to become familiar with an entirely new set of forage plants and differing seasonal phenology of forage biomass. Over a time scale of months, the herd probably perceived that access was unhindered and began integrating the use of the cattle pasture into the use of the meadows that the herd already used.

It is unlikely that the third possibility can explain why my findings are not consistent with optimal foraging theory. My results are consistent with the claim of Stewart et al. (2002), cattle will compete with elk and can displace them. Elk probably avoided areas with cattle because of competition for resources and physical disturbances from cattle while foraging. Yet, cattle did not use the entire cattle pasture in both Januarys so it is unlikely that the Davison herd would have avoided the cattle pasture because of cattle. Black bear also do not seem to be a likely candidate for why elk did not select the cattle pasture in January, 2017 (Fryxell and Sinclair 1988, Brown 1999). In January, bear activity appeared to be low in the cattle pasture. If black bears were prompting elk to avoid the entire cattle pasture, it seems more likely to occur in summer when neonatal elk are most vulnerable to predation (Yarkovich et al. 2011). Yet, my findings from the overlap analysis indicate that elk did not avoid the entire

cattle pasture, just parts of the cattle pasture that had been used by black bear within 24 hours. Elk appeared to be able to mitigate risks from bears by not occupying particular parts of the cattle pasture when those places were occupied by bears.

The last possible explanation for why the herd seemed to select the cattle pasture differently than expected is forage biomass differences between years considering herd size. Herd abundance was 52 in January, 2017, and 62 the following January whereas forage biomass in the cattle pasture decreased 19 percent between January, 2017 (2096 kg) and January, 2018 (1708). Perhaps the herd were using the cattle pasture similar to 2017 but with a larger herd and more limited forage, the result was selection. Yet, this explanation does not seem applicable because a similar scenario was not observed in other sectors. For example, in the south Davison sector forage biomass was about 13 percent greater in 2018 than 2017 but south Davison was selected in 2018 and avoided in 2017. Selection of sectors by the herd seemed to be affected by more than forage biomass. Other possibilities are that there were subtle differences in forage nutrition between sectors that also influenced herd use or the decreased or increased use of some sectors influenced the use of other sectors.

The possible selection of the cattle pasture should be more apparent in January then in July because of reduced forage biomass (Starns et al. 2015). In turn, step length in July should be shorter than in January because elk do not have to travel far to encounter plentiful forage. Previous studies have shown that herbivores had shorter movements when forage biomass was plentiful, whereas, when forage biomass was reduced, movement lengthened (White and Trudell 1980, Turner et al. 1993, Gross et al.

1995, de Knegt et al. 2007). I measured step length from the distance moved every 15 minutes from the center of the herd. Step length, however, can differ among individuals within the herd which might or might not affect the location of the center of the herd. To more accurately estimate step length, individuals in the herd and not the herd as a whole should be measured.

Elk response to cattle and black bear might also influence step lengths in January and July. In July, black bear were active but much less so in January. One way that elk respond to disturbances from predators is to increase step lengths (Cole et al. 1997). In July step length might have been less if black bear were absent on the landscape. Cattle were present in the cattle pasture in January but not July. In July, but not January, the Davison herd had access to the entire cattle pasture. Step lengths might then have been shortened in July and lengthened in January. The net effect of the timing of the presence of bears and cattle might have obscured straightforward influences of forage biomass on step length.

Also to be considered is step length relative to the difference in forage biomass that is likely between January and July (Starns et al. 2015). Compared to January, forage biomass in July is probably more abundant by an order of magnitude or more. Because forage biomass was not directly measured in July, due in part to its abundance, I was not able to directly include forage abundance in my analysis. It is plausible that if I had included forage biomasses in January and July, I would have found that relative step length was less in July than January.

The lack of difference between January and July step lengths does not appear to be due to variation in steps lengths across different times of the day. Movements do vary across different times of the day and night (Kie et al. 2005). Forester et al. (2007) found that elk tended to have their longest movement patterns during crepuscular hours when elk tend to forage more often, a pattern I did not detect. For the Davison herd, movement appears to be greater during daylight hours than at nighttime in January (Weckerly 2017). Perhaps the herd was more sedentary in the evening which resulted in constant movement throughout the day.

Between 2016 and 2018 the Davison herds' abundance increased from 51 to 62 individuals. The abundance in 2018 was the highest documented in the 22 year long time series. Starns et al. (2014) and Weckerly (2017) state that there is a two year lag in juvenile recruitment and population growth. This could be because of the timing of food resources to parturition and mating considering when population surveys are conducted. The recruitment of young in the Davison herd (juvenile: female ratio = 0.40, unpublished data) in 2018 was also the third highest in the time series. The abundance and recruitment observed in 2018 indicated that there was considerable forage two years previously in 2016. Perhaps the addition of the cattle pasture to the home range of the Davison herd in 2016 contributed to the food supply. Also, if the cattle pasture provided an increase in forage then the response of the Davison herd to the new forage patch occurred at a time scale of months. The quick integration of the cattle pasture into home range of the Davison herd appeared to be immediate and the availability of the new forage source appeared to impact herd demography. The spatial addition of

the cattle pasture to the Davison herd's home range occurred despite the potential for

negative interactions with cattle and black bear. This study shows how familiarity with

resources in the home range of herds of large herbivores allows individuals to exploit

forage while mitigating negative encounters with interspecific competitors and

predators.

Table 1. Observed overlap and the 95% confidence interval from randomly generated

overlap between elk and cattle and elk and black bear. Overlap was the number of days

elk and the other species were photographed at the same camera divided by the

number of days of photographs of elk.

Species	Observed overlap	Random Overlap	
		Lower Bounds	Upper Bounds
Elk and Cattle	0.011	0.100	0.122
Elk and Black Bear	0.044	0.249	0.253

Table 2. Summary of a linear mixed effects model and bootstrapped 95% confidence

intervals of parameter estimates to test for differences in step lengths among diel

periods (morning, midday, afternoon) and months (Januarys 2017, 2018, and July 2017).

Reference categories were July, 2017, and afternoon. The conditional and marginal R^2

values were both 0.007 for this model. The colons denote interactions.

Parameter	Estimate	Lower Bounds	Upper Bounds
Intercept	67.06	53.44	82.00
Jan 2017	17.68	-4.75	43.16
Jan 2018	2.71	-15.03	22.01
Midday	22.60	-9.10	54.47
Morning	17.37	-4.50	37.24
Jan 2017:midday	-8.40	-63.71	61.55
Jan 2018:midday	-17.65	-59.09	18.89
Jan 2017:morning	-0.46	-51.21	78.53
Jan 2018:morning	-20.32	-48.30	7.40

Table 3. Summary of a linear mixed effects model estimating the relationship between forage biomass (kg) and hours the Davison herd spent foraging in the Davison meadows in January 2017 and 2018 (labeled year). The reference category was January, 2017. The conditional and marginal R^2 values were both 0.63 for this model. The colon denotes an interaction.

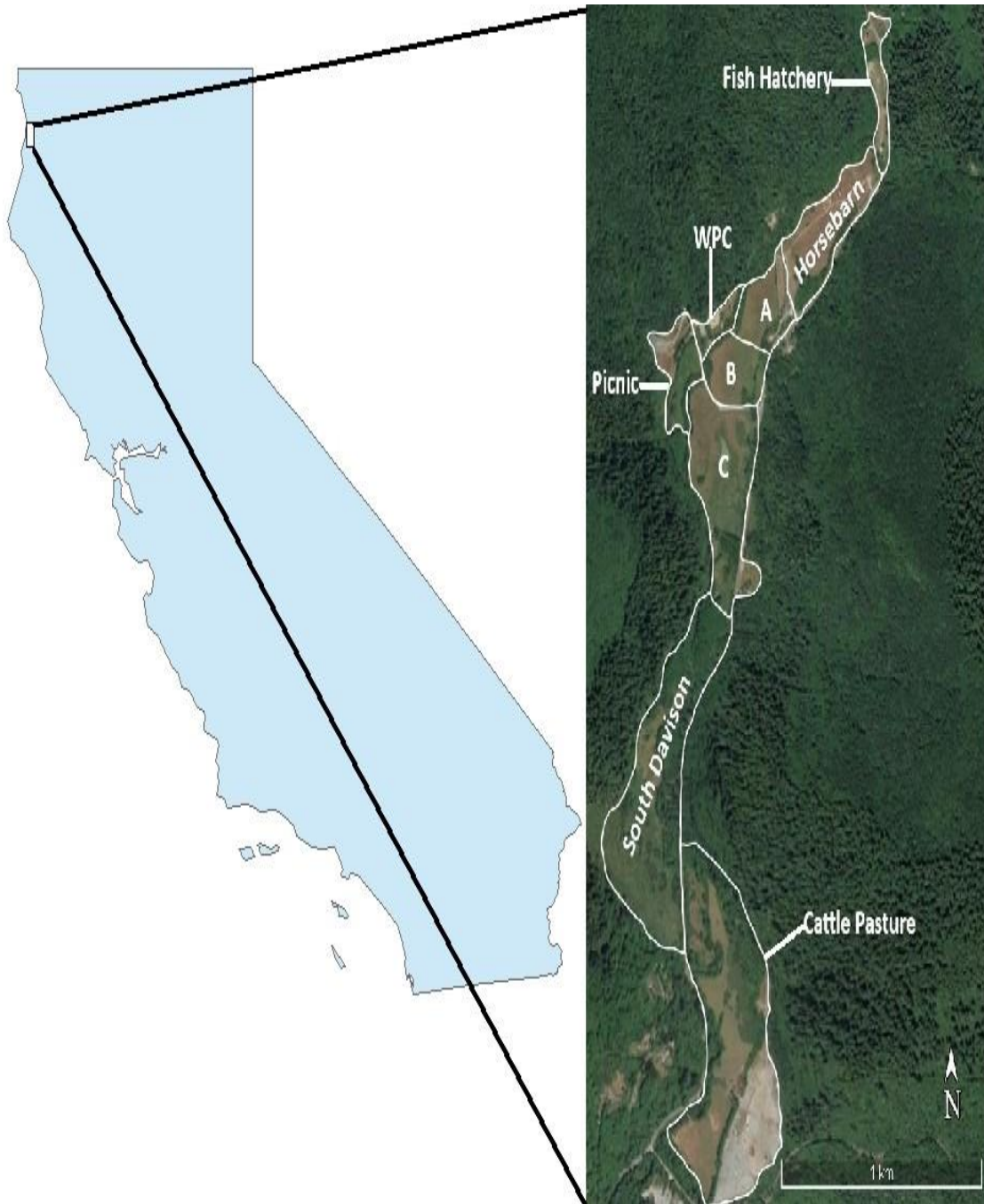| Parameter	Estimate	SE	t	df	p
Intercept	0.1061	0.126	0.84	14	0.413
Biomass	< 0.0001	< 0.001	2.28	14	0.014
Year	0.1614	0.174	0.92	14	0.370
Biomass: year	< 0.0001	< 0.001	0.49	14	0.628

Figure 1. Map of study area in the Prairie Creek Drainage of the Redwoods National and State Parks, in Humboldt County, California. Sectors in the Davison meadows and cattle pasture are also delineated.

Figure 2. Camera locations throughout the cattle pasture labeled by yellow markers.
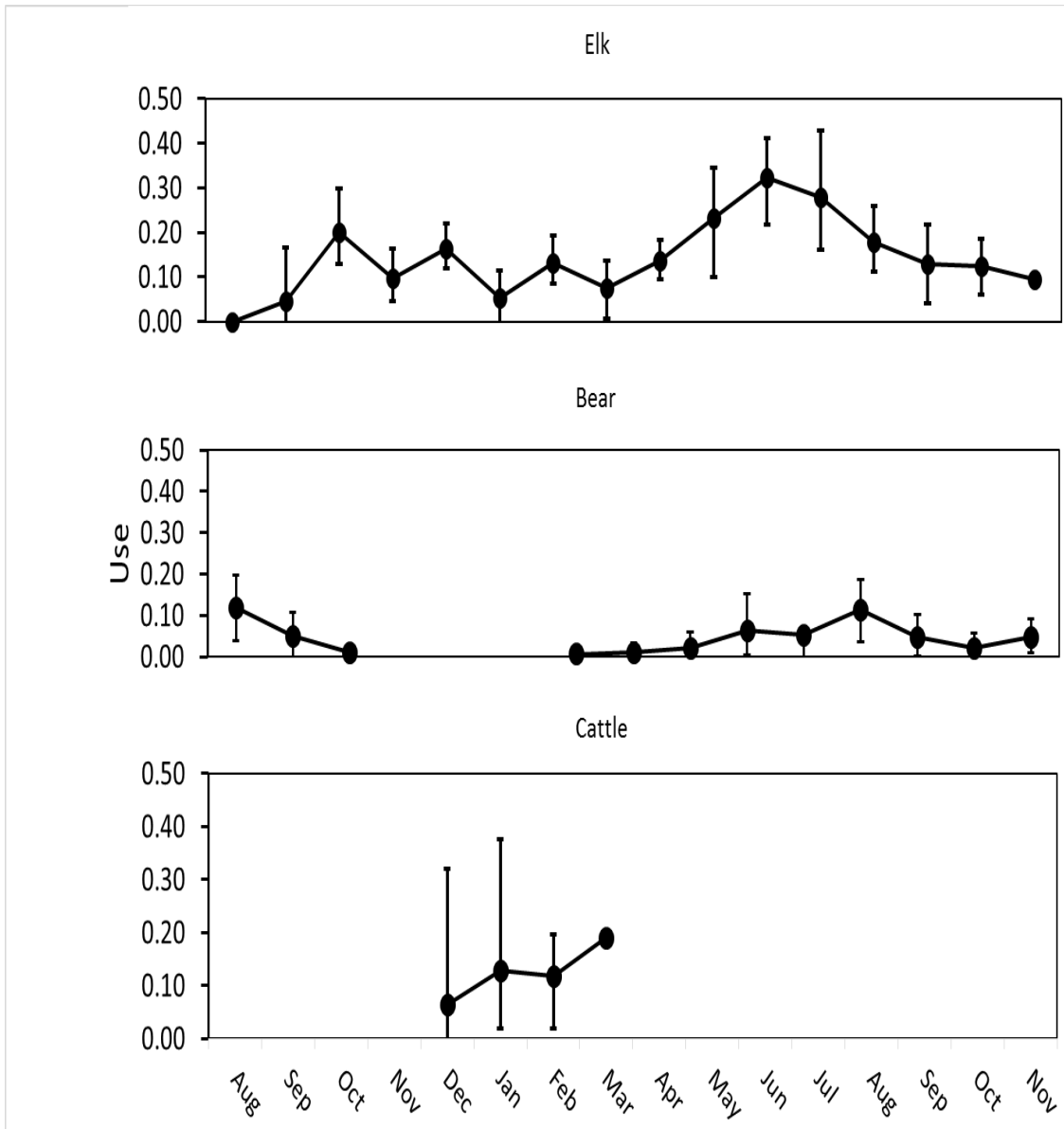
Figure 3. Elk, black bear, and cattle use in the cattle pasture from August, 2016, to

November, 2017. Cattle use ceased in March, 2017. Use was estimated as number of

days with pictures divided by number of days in the month. The error bars are 95%

confidence intervals. For elk use in November, 2017, bear use in October, 2016,

February and March 2017, and cattle use in March, 2017, the intervals were small such

that bars were not present outside the data point.
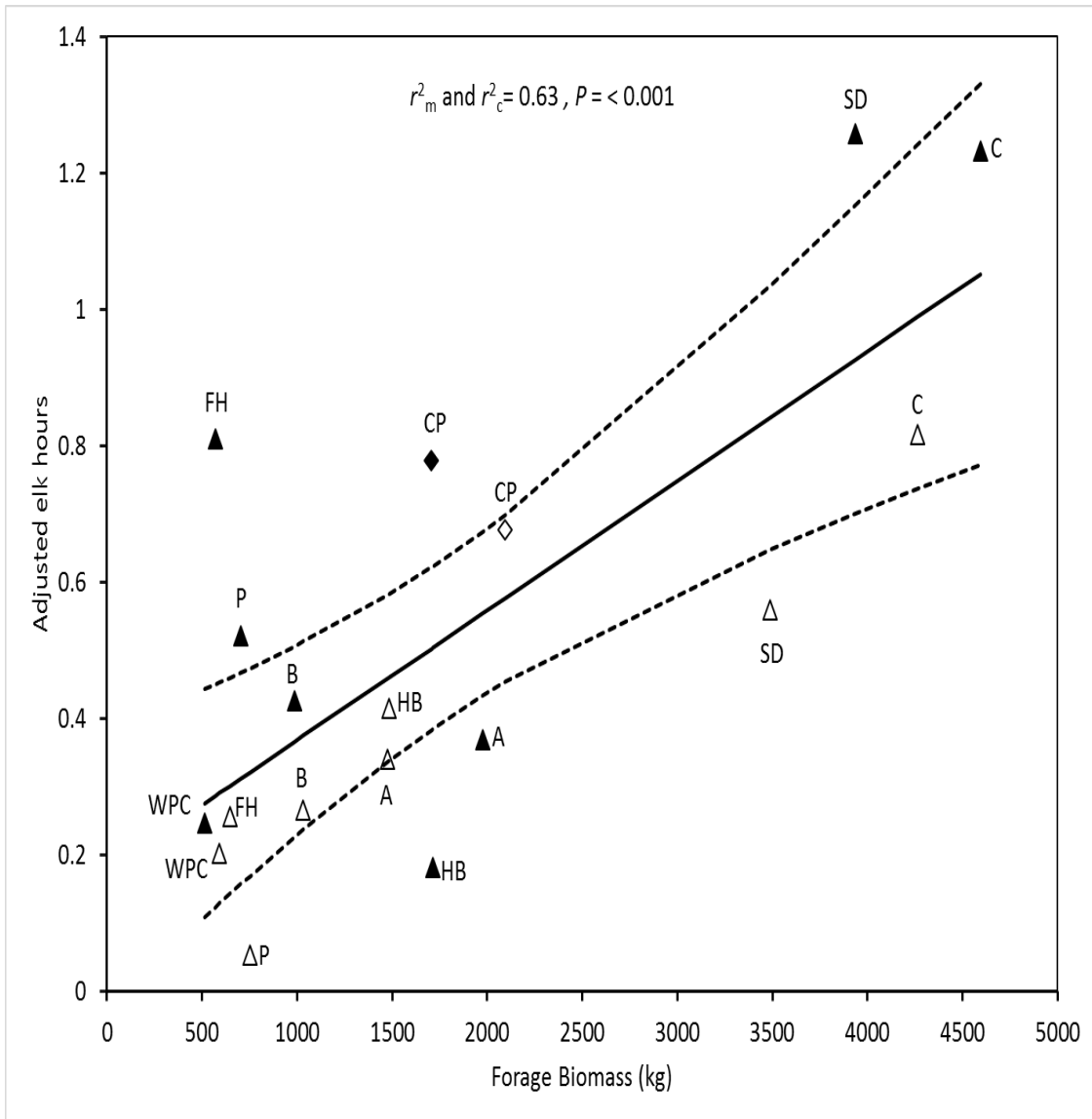
Figure 4. Linear mixed effects regression with 95% confidence intervals of available forage biomass (kg) and adjusted hours the Davison herd spent foraging in each sector during the daytime in January, 2017, (open triangles), and January, 2018 (closed triangles). Sectors are initialized as follows: cattle pasture (CP), South Davison (SD), picnic area (P), WPC, Davison A (A), Davison B (B), Davison (C), horse barn (HB), fish hatchery (FH). Adjusted elk hours were calculated by dividing elk hours by total hours the herd was observed that year.

LITERATURE CITED

Anderson, D. P., J. D. Forester, M. G. Turner, J. L. Frair, E. H. Merrill, D. Fortin, J. S. Mao, and M. S. Boyce. 2005a. Factors influencing female home range sizes in elk (*Cervus elaphus*) in North American landscapes. Landscape Ecology **20**:257-271.

Anderson, D. P., M. G. Turner, J. D. Forester, J. Zhu, M. S. Boyce, H. Beyer, and L. Stowell. 2005b. Scale-dependent summer resource selection by reintroduced elk in Wisconsin, USA. Journal of Wildlife Management **69**:298-310.

Beest, F. M. v., E. Vander Wal, A. V. Stronen, and R. K. Brook. 2013. Factors driving variation in movement rate and seasonality of sympatric ungulates. Journal of Mammology **94**:691-701.

Belovsky, G. E. 1986. Optimal foraging and community structure: implications for a guild of generalist grassland herbivores. Oecologia **70**:35-52.

Berger-Tal, O., and S. Bar-David. 2015. Recursive movement patterns: review and synthesis across species. Ecosphere **6**.

Bjørneraas, K., I. Herfindal, E. J. Solberg, B. E. Saether, B. v. Moorter, and C. M. Rolandsen. 2012. Habitat quality influences population distribution, individual space use and functional responses in habitat selection by a large herbivore. Oceologica **168**:231-243.

Bliss, L. M., and F. W. Weckerly. 2016. Habitat use by male and female Roosevelt elk in northwestern California. California Fish and Game **102**:8-16.

Bowman, J., J. A. G. Jaeger, and L. Fahrig. 2002. Dispersal distance of mammals is proportional to home range size. Ecology **83**:2049-2055.

Brown, J. S. 1988. Patch Use as an Indicator of Habitat Preference, Predation Risk, and

Competition. Behavioral Ecology and Sociobiology **22**:37-47.

Brown, J. S. 1999. Vigilance, patch use and habitat selection: Foraging under predation

risk. Evolutionary Ecology Research **1**:49-71.

Burt, W. H. 1943. Territoriality and home range concepts as applied to mammals.

Journal of Mammalogy **24**:346-352.

Clarke, C. M. H. 1986. Chamois movements and habitat use in the Avoca River area,

Canterbury, New Zealand. New Zealand Journal of Zoology **13**:175-198.

Clegg, K. 1994. Density and Feeding Habits of Elk and Deer in Relation to Livestock

Disturbance. Utah State University, All Graduate Theses and Dissertations.

Coe, P. K., B. K. Johnson, K. M. Stewart, and J. G. Kie. 2005. Spatial and temporal

interactions of Elk, Mule Deer, and Cattle. Pages 150-158 *in* M. J. Wisdom, editor.

Wildlife and Natural Resources Conference. The Starkey Project: a synthesis of

long-term studies of elk and mule deer.

Cole, E. K., M. D. Pope, and R. G. Anthony. 1997. Effects of road management on

movement and survival of Roosevelt elk. Journal of Wildlife Management

61:1115-1126.

Craighead, J., F. Craighead, R. Ruff, and B. O'Gara. 1973. Home ranges and activity

patterns of nonmigratory elk of the Madison Drainage herd as determined by

biotelemetry. Wildlife Monographs **33**:3-50.

Daubenmire, R. F. 1968. Plant communities: a textbook of plant synecology. Harper &

Row, New York, New York, USA.

de Knegt, H. J., G. M. Hengeveld, F. van Langevelde, W. F. de Boer, and K. P. Kirkman. 2007. Patch density determines movement patterns and foraging efficiency of large herbivores. Behavior Ecology **18**:1065-1072.

Focardi, S., P. Marcellini, and P. Montanaro. 1996. Do ungulates exhibit a food density threshold? A field study of optimal foraging and movement patterns. Journal of Animal Ecology **65**:606-620.

Forester, J. D., A. R. Ives, M. G. Turner, D. P. Anderson, D. Fortin, H. L. Beyer, D. W. Smith, and M. S. Boyce. 2007. State-space models link elk movement patterns to landscape characteristics in Yellowstone National Park. Ecological Monographs **77**:285-299.

Forrester, T. D., D. S. Casady, and H. U. Wittmer. 2015. Home sweet home: Fitness consequences of site familiarity in female black-tailed deer. Behavioral Ecology and Sociobiology **69**:603-612.

Frair, J. L., E. H. Merrill, D. R. Visscher, D. Fortin, H. L. Beyer, and J. M. Morales. 2005. Scales of movement by elk (*Cervus elaphus*) in response to heterogeneity in forage resources and predation risk. Landscape Ecology **20**:273-287.

Frid, A. 1997. Vigilance by female Dall's sheep: Interactions between predation risk factors. Animal Behaviour **53**:799-808.

Fryxell, J. M., M. Hazell, L. Borger, B. D. Dalziel, D. T. Haydon, J. M. Morales, T. McIntosh, and R. C. Rosatte. 2008. Multiple movement modes by large herbivores at multiple spatiotemporal scales. Proc Natl Acad Sci U S A **105**:19114-19119.

Fryxell, J. M., and A. R. Sinclair. 1988. Causes and consequences of migration by large herbivores. Trends Ecol Evol **3**:237-241.

Gates, C. C., and N. C. Larter. 1990. Growth and Dispersal of an Erupting Large Herbivore Population in Northern Canada - the Mackenzie Wood Bison (*Bison bison athabascae*). Arctic **43**:231-238.

Gross, J. E., C. Zank, N. T. Hobbs, and D. E. Spalinger. 1995. Movement Rules for Herbivores in Spatially Heterogeneous Environments - Responses to Small-Scale Pattern. Landscape Ecology **10**:209-217.

Harper, J. A., J. H. Harn, W. W. Bentley, and C. F. Yocom. 1967. The status and ecology of Roosevelt elk in California. Wildlife Monographs **16**.

Hernández, L., and J. W. Laundré. 2005. Foraging in the 'landscape of fear' and its implications for habitat use and diet quality of elk *Cervus elaphus* and bison *Bison bison*. Wildlife Biology **11**:215-220.

Hundertmark, K. 1998. Home range, dispersal and migration. Pages 303-335 *in* A. W. Franzmann, C. C. Schwartz, and R. E. McCabe, editors. Ecology and management of the North American moose, University press of Northern Colorado, Boulder.

Jenkins, K. J., and E. E. Starkey. 1982. Social-Organization of Roosevelt Elk in an Old-Growth Forest. Journal of Mammalogy **63**:331-334.

Kie, J. G., A. A. Ager, and R. T. Bowyer. 2005. Landscape-level movements of North American elk (*Cervus elaphus*): effects of habitat patch structure and topography. Landscape Ecology **20**:289-300.

Kie, J. G., R. T. Bowyer, M. C. Nicholson, B. B. Boroski, and E. R. Loft. 2002. Landscape heterogeneity at differing scales: Effects on spatial distribution of mule deer. Ecology **83**:530-544.

Laporte, I., T. B. Muhly, J. A. Pitt, M. Alexander, and M. Musiani. 2010. Effects of wolves on elk and cattle behaviors: implications for livestock production and wolf conservation. PLoS ONE **5**:e11954.

Larter, N. C., and C. C. Gates. 1990. Home ranges of Wood Bison in an expanding population. Journal of Mammalogy **71**:604-607.

Laundré, J. W., L. Hernández, and K. B. Altendorf. 2001. Wolves, elk, and bison: reestablishing the "landscape of fear" in Yellowstone National Park, U.S.A. Canadian Journal of Zoology **79**:1401-1409.

Laundré, J. W., L. Hernández, and W. J. Ripple. 2010. The Landscape of Fear: Ecological Implications of Being Afraid The Open Ecology Journal **3**:1-7.

Leopold, A. 1943. Deer irruptions. Wisconsin Conservation Bulletin **8**:3-11.

Macarthur, R. H., and E. R. Pianka. 1966. On Optimal Use of a Patchy Environment. American Naturalist **100**:603-+.

Marion, G., D. L. Swain, and M. R. Hutchings. 2005. Understanding foraging behaviour in spatially heterogeneous environments. J Theor Biol **232**:127-142.

Marten, G. C., R. M. Jordan, and A. W. Hovin. 1976. Biological Significance of Reed Canarygrass Alkaloids and Associated Palatability Variation to Grazing Sheep and Cattle. Agronomy Journal **68**:909-914.

Massé, A., and S. D. Côté. 2009. Habitat Selection of a Large Herbivore at High Density

and Without Predation: Trade-Off Between Forage and Cover? Journal of

Mammalogy **90**:961-970.

McCorquodale, S. M., K. J. Raedeke, and R. D. Taber. 1986. Elk Habitat Use Patterns in

the Shrub-Steppe of Washington. Journal of Wildlife Management **50**:664-669.

Mysterud, A., and R. A. Ims. 1998. Functional Responses In Habitat Use: Availability

Influences Relative Use In Trade-Off Situations. Ecology **79**:1435-1441.

Nakagawa, S., and H. Schielzeth. 2013. A general and simple method for obtaining R2

from generalized linear mixed-effects models. Methods in Ecology and Evolution

4:133-142.

Neil, S. T. O., and J. K. Bump. 2014. Modeling habitat potential for elk expansion in

Michigan, USA. Wildlife Biology in Practice **10**:111- 131.

Pyke, G. H., H. R. Pulliam, and E. L. Charnov. 1977. Optimal foraging: A selective review

of theory and tests. The Quarterly Review of Biology **52**:137-154.

R Core Team. 2013. R: A language and environment for statistical computing R

Foundation for Statistical Computing, Vienna, Austria.

Ricca, M. A., D. H. Van Vuren, F. W. Weckerly, J. C. Williams, and A. K. Miles. 2014.

Irruptive dynamics of introduced caribou on Adak Island, Alaska: an evaluation of

Riney-Caughley model predictions. Ecosphere **5**.

Roloff, G. J. 1998. Habitat potential model for Rocky Mountain elk. Pages 158-175 *in* J. J.

C. deVos, editor. Proceedings of the 1997 deer-elk workshop.

Schooler, S. S., P. B. McEvoy, and E. M. Coombs. 2006. Negative per capita effects of purple loosestrife and reed canary grass on plant diversity of wetland communities. Diversity and Distributions **12**:351-363.

Schwartz, C. C., and J. E. Ellis. 1981. Feeding Ecology and Niche Separation in Some Native and Domestic Ungulates on the Shortgrass Prairie. Journal of Applied Ecology **18**:343-353.

Seidel, D. P., and M. S. Boyce. 2015. Patch-use dynamics by a large herbivore. Mov Ecol **3**:7.

Spaggiari, J., and M. de Garine-Wichatitsky. 2006. Home range and habitat use of introduced rusa deer (*Cervus timorensis russa*) in a mosaic of savannah and native sclerophyll forest of New Caledonia. New Zealand Journal of Zoology **33**:175-183.

Stamps, J. 1995. Motor learning and the value of familiar space. American Naturalist **146**:41-58.

Starns, H. D. 2014. Influences of a Population Irruption by Roosevelt Elk on a Vegetation Index. Texas State University.

Starns, H. D., M. A. Ricca, A. Duarte, and F. W. Weckerly. 2014. Climatic and density influences on recruitment in an irruptive population of Roosevelt elk. Journal of Mammalogy **95**:925-932.

Starns, H. D., F. W. Weckerly, M. A. Ricca, and A. Duarte. 2015. Vegetation changes associated with a population irruption by Roosevelt elk. Ecol Evol **5**:109-120.

Stewart, K. M., R. T. Bowyer, J. G. Kie, N. J. Cimon, and B. K. Johnson. 2002.

Temporospatial distributions of elk, mule deer, and cattle: Resource partitioning

and competitive displacement. Journal of Mammalogy **83**:229-244.

Tatman, N. M. 2008. Ecology and Management of the North American Moose. Journal of

Wildlife Management **72**:1877-1878.

Toweill, D. E., and J. W. Thomas. 2002. North American elk ecology and management.

Smithsonian Institution Press: Washington and London.

Tufto, J., R. Andersen, and J. D. C. Linnell. 1996. Habitat use and ecological correlates of

home range size in a small cervid: The roe deer. Journal of Animal Ecology

65:715-724.

Turner, M. G., Y. G. Wu, W. H. Romme, and L. L. Wallace. 1993. A Landscape Simulation-

Model of Winter Foraging by Large Ungulates. Ecological Modelling **69**:163-184.

van Beest, F. M., I. M. Rivrud, L. E. Loe, J. M. Milner, and A. Mysterud. 2011. What

determines variation in home range size across spatiotemporal scales in a large

browsing herbivore? J Anim Ecol **80**:771-785.

Vivas, H. J., and B. E. Saether. 1987. Interactions between a Generalist Herbivore, the

Moose *Alces alces*, and Its Food Resources - an Experimental-Study of Winter

Foraging Behavior in Relation to Browse Availability. Journal of Animal Ecology

56:509-520.

Wallace, M. C., and P. R. Krausman. 1987. Elk, mule deer, and cattle habitats in central

Arizona. Journal of Range Management **40**:80-83.

Weckerly, F. W. 1999. Social bonding and aggression in female Roosevelt elk. Canadian

    Journal of Zoology-Revue Canadienne De Zoologie **77**:1379-1384.

Weckerly, F. W. 2005. Grass and supplemental patch selection in a population of

    Roosevelt elk. Journal of Mammalogy **86**:630-638.

Weckerly, F. W. 2007. Constant proportionality in the female segment of a Roosevelt elk

    population. Journal of Wildlife Management **71**:773-777.

Weckerly, F. W. 2017. Population ecology of Roosevelt elk: Conservation and

    management in Redwood National and State Parks. University of Nevada Press,

    Reno, Nevada.

Weckerly, F. W., M. A. Ricca, and K. P. Meyer. 2001. Sexual segregation in Roosevelt elk:

    Cropping rates and aggression in mixed-sex groups. Journal of Mammalogy

    82:825-835.

White, R. G., and J. Trudell. 1980. Habitat Preference and Forage Consumption by

    Reindeer and Caribou near Atkasook, Alaska. Arctic and Alpine Research **12**:511-

    529.

Wickstrom, M. L., C. T. Robbins, T. A. Hanley, D. E. Spalinger, and S. M. Parish. 1984.

    Food-Intake and Foraging Energetics of Elk and Mule Deer. Journal of Wildlife

    Management **48**:1285-1301.

Wisdom, M. J., and J. W. Thomas. 1996. Management of wildlife on rangelands- Elk.

Witmer, G. W., and D. S. Decalesta. 1983. Habitat Use by Female Roosevelt Elk in the

    Oregon Coast Range. Journal of Wildlife Management **47**:933-939.

Wolf, M., J. Frair, E. Merrill, and P. Turchin. 2009. The attraction of the known: the
importance of spatial familiarity in habitat selection in wapiti *Cervus elaphus*.
Ecography **32**:401-410.

Yarkovich, J., J. D. Clark, and J. L. Murrow. 2011. Effects of Black Bear Relocation on Elk
Calf Recruitment at Great Smoky Mountains National Park. Journal of Wildlife
Management **75**:1145-1154.

Yeo, J. J., J. M. Peek, W. T. Wittinger, and C. T. Kvale. 1993. Influence of rest-rotation
cattle grazing on mule deer and elk habitat use in east-central Idaho. Journal of
Range Management **46**:245-250.