

DRIVERS OF A TEMPORAL CHANGE IN THE ADULT SEX RATIO OF A
POPULATION OF ROOSEVELT ELK (*CERVUS ELAPHUS ROOSEVELTI*)

by

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LIST OF ABBREVIATIONS

Abbreviation	Description
ASR	Adult sex ratio
FSH	Female-substitution hypothesis

ABSTRACT

Ecological processes driving female-biased adult sex ratios (ASR, males:female) in ungulate populations have been addressed theoretically but empirical study is lacking. The female-substitution hypothesis asserts that a female-biased ASR reflects an overall fitness benefit to females and also males competitive in access to reproductive females. The hypothesis predicts that as female abundance increases females should acquire forage in a given area in lieu of males, thereby resulting in a declining ASR via scramble competition. My study examined a population of Roosevelt elk (*Cervus elaphus roosevelti*) inhabiting the Redwood National and State Parks, California. I sought to discern which of two potential ecological mechanisms could explain the female-biased ASR. The first mechanism was that increasing female abundance associated with a decline in forage abundance led to the passive displacement of males into the study periphery, and the second was that a decline in ASR was precipitated by a lack of males in the area. Systematic population surveys across 24-years were done by driving along a predetermined route within meadow complexes to estimate abundance and ASR, and in nearby areas to assess male abundance. Forage biomass was estimated from vegetation height and cover measurements in quarter-m² plots randomly placed in meadows inhabited by elk. My multiple regression model detected an inverse relationship between abundance and ASR indicating it was density dependent. Males were in the study periphery when female abundance increased, and male abundance declined in the study area. A generalized least squares model indicated declining food supplies across years

when female abundance increased. My empirical findings were consistent with the female-substitution hypothesis.

I. DRIVERS OF A TEMPORAL CHANGE IN THE ADULT SEX RATIO OF A POPULATION OF ROOSEVELT ELK (*CERVUS ELAPHUS ROOSEVELTI*)

Introduction

Populations of polygynous ungulates often display uneven adult sex ratios with a lower abundance of males than females (Clutton-Brock et al. 1997, Berger and Gompper 1999, Coulson et al. 2004, Weaver and Weckerly 2011). The adult sex ratio (ASR; males:female), also called the tertiary ratio, reflects the proportion of males in a population that are sexually mature relative to sexually mature females. An inverse density-dependent relationship exists between abundance and ASR that is probably due to life history differences between the sexes. To my knowledge, there are few hypotheses put forward to explain uneven sex ratios other than males having shorter lifespans than females (Clutton-Brock et al. 1982, Toigo and Gaillard 2003, Clutton-Brock and Isvaran 2007, Lemaitre et al. 2020). Rarer still are empirical studies supporting or refuting any model that predicts ASR patterns in mammals (Coulson et al. 2004).

Understanding patterns of ASR in mammal populations is important for understanding population ecology and informing the decisions of wildlife managers. This can be particularly important for polygynous ungulates for several reasons: (1) there may be a shared driver resulting in a common ASR pattern seen across populations, and (2) males are often the sex discriminately hunted or poached. Therefore, it is important to know how changes in ASR with abundance might affect population dynamics.

McCullough (1999) formulated the female-substitution hypothesis (FSH) by describing the evolutionary and ecological drivers of a density-dependent relationship

between abundance and ASR. This hypothesis predicts that as abundance increases and food resources become limiting, females should compete for and obtain prime forage habitat over males through more efficient foraging (McCullough 1999). Thus, intraspecific scramble competition functions as an ecological driver resulting in the passive displacement of males into suboptimal forage areas (Weckerly 1998). Female fecundity and survival of mothers and offspring is associated with resource acquisition (Clutton-Brock et al. 1982, 1987, Weckerly 1998). As a result, females should be motivated to be familiar with food resources thereby increasing their efficiency in forage acquisition and outcompeting males (Wolf et al. 2009, Riotte-Lambert et al. 2015, Merkle et al. 2017). Accordingly, mothers that give birth to female offspring can improve individual fitness if that offspring effectively displaces, or substitutes for, a male in forage habitat (McCullough 1999).

The female-substitution hypothesis asserts a simultaneous fitness benefit for polygynous males that are competitive in male – male interactions for access to females (McCullough 1999). Unlike females, male fecundity and survival is dictated by attempts to secure as many copulations as possible with estrous females (Clutton-Brock et al. 1982, Owen-Smith 1993, Toïgo and Gaillard 2003). If there are more females in forage habitat, competitive males should have high reproductive success (Clutton-Brock et al. 1997, McCullough 1999).

The purpose of this study was to assess if temporal changes in the adult sex ratio of a population of Roosevelt elk (*Cervus elaphus roosevelti*) followed patterns consistent with the female-substitution hypothesis. Patterns consistent with FSH would be (1) an inverse relationship between population abundance and ASR because of (2) forage

depletion from female foraging. Forage depletion from female foraging was labeled a ‘forage-enabled mechanism’. It also possible that an inverse abundance associated ASR might be due to too few males and high population abundance, what I call a ‘sparse-male mechanism’. Therefore, there were two objectives to this study. One, determine if there was an inverse abundance associated relationship with ASR. Two, test the ‘forage-enabled’ and ‘sparse-male’ mechanisms.

Materials and Methods

Ethics Statement

Prior to the initiation of the study, it was realized that no animals would be handled or approached to interfere with or disrupt animal activity. Nonetheless, all animal research was reviewed and approved by the Texas State University Institutional Animal Care and Use Committee (IACUC).

Study Area

My 24 year-long study was conducted in the lower reach of the Prairie Creek Drainage (41°24’N, 124°02’W) of the Redwood National and State Parks, Humboldt County, California, USA (Figure 1). The climate of this region is maritime with mild dry summers and rainy, wet winters. Precipitation in this area is often greater than 150 cm annually, with the majority of precipitation (approximately 90%) occurring between October and May (Starns et al. 2014, 2015). Weather patterns typically include coastal fog throughout the year and steady rainfall in winter. Snow and ice are uncommon. During winter, the minimum and maximum average annual temperatures are 2 and 10 °C. During summer, the average annual temperatures range from 10 to 20 °C.

The study population inhabited two meadow complexes that are approximately 3 km apart: the Davison and Boyes meadows (Peterson and Weckerly 2017). These two meadow complexes are near sea level and the terrain is predominately flat. The size of meadows within this drainage area range from 13 to 51 ha (Weaver and Weckerly 2011). The study area is surrounded by both old-growth and second-growth coastal redwood (*Sequoia sempervirens*) conifer forests. Common conifer species in this area include Douglas fir (*Pseudotsuga menziesii*), Sitka spruce (*Picea sitchensis*), and western hemlock (*Tsuga heterophylla*) (Weckerly 1998, Weckerly 2007). Other parts of the study area contain riparian or riparian-meadow habitat mostly comprised of red alder (*Alnus rubra*) (Weaver and Weckerly 2011).

The Boyes meadow complex totals 70 ha of meadows and consists of the large Boyes meadows, as well as numerous small meadows north and east of Boyes meadow (Peterson and Weckerly 2017; Figure 1). The Davison meadow complex totals 51 ha of meadows and is south of the Boyes meadow complex. In both meadow complexes vegetation was primarily perennial and annual grasses with some forbs (Weckerly et al. 2001, Williamson 2020, Williamson and Weckerly, in press). Some differences in vegetation between meadow complexes include the presence of Western Bracken fern (*Pteridium aquilinum*) and California blackberry (*Vitaceae*) in Boyes, and invasion of Reed canary grass (*Phalaris arundinacea*) in some parts of the Davison meadow complex which became apparent in 2000 (Harper et al. 1967, Weckerly et al. 2001, Starns et al. 2015). Natural predators of elk are mountain lions (*Puma concolor*) and black bears (*Ursus americanus*). Deaths from vehicle collisions also contribute to mortality for this population.

History

Two main meadows (13 and 38 ha) comprise the Davison meadow complex. Elk were not present in Davison meadows prior to 1991, which is when the U.S. National Park Service acquired the privately-owned land that had once been fenced and grazed by cattle (Harn 1958, Harper et al. 1967). The Davison meadow has not been burned since acquisition by the National Park Service (Weckerly 2017). Historically, the large Boyes meadow had been used for hay and cattle production in the late 1800s. In 1933, the Boyes meadow was acquired by the California Department of Parks and Recreation after the deed was transferred from a non-profit organization (Bentley 1959). According to Mandel and Kitchen (1976) the elk population inhabiting Boyes meadow numbered somewhere between 30 and 50 elk in the early 1970s. Approximately 66% or more of Boyes meadow had been intentionally burned every 2–4 years since 1996 (Peterson and Weckerly 2017, Williamson and Weckerly, in press).

As a result of the strong social bonding of female elk, two herds comprised mostly of the same females were present. The Davison and Boyes herds which includes adult females, subadults (1 – 2 year-old) males, subadult females, and juveniles (<1 year-old) are spatially separated and partitioned meadows (Weckerly 1999). The Boyes herd declined in abundance from the low 30s in 1997 to 4 – 5 animals from 2005 to 2010. In 2010 the herd was extinct. The Davison herd was present throughout the entire time of the study. Hunting of elk in the parks is prohibited, and elk in the parks are non-migratory and habituated to people (Weckerly 1999).

Data Collection

All data was collected in January. At this time of year, the bulk of elk forage is grasses and forbs in meadows, with some browse. Elk use of habitats should be driven by resource acquisition and not complicated by reproductive events like parturition in late spring or the mating season in late summer and early autumn (Weckerly 2017).

Furthermore, juveniles and adults can be readily distinguished by body size differences and males have yet to cast antlers (Weckerly 2017). From January 1997 to 2020, population surveys were conducted from a vehicle in the Davison and Boyes meadow complexes (Weckerly 1996, Weckerly et al. 2004, Weckerly 2017) (Figure 1). Up to a month before surveys were conducted, both meadow complexes were scanned for elk with unusual features such tags, scars, marks, or antler anomalies that allowed for individual identification (Weckerly 1996, Weckerly 2007). Uniquely identified elk were considered marked elk. Each January, 10 surveys lasting 1.75 hours were initiated at daybreak, but in 1998 and 1999 there were only five surveys (Peterson and Weckerly 2017, Weckerly et al. 2004). When elk were spotted during surveys, I observed them from a vehicle or approached on foot to a distance of 20–200 m away to count, record marked elk, and classify animals to age-sex classes of female, juvenile, subadult male, and adult male. Subadult males had unbranched antlers and adult males had branched antlers. Individuals suspected of being counted repeatedly during a survey were not recorded (Weckerly 2007).

In 2016, 2017, 2019, and 2020, surveys for adult males were conducted to encompass a larger spatial survey area than the lower Prairie Creek drainage to examine the ‘sparse-male mechanism’. The peripheral survey area was approximately 3–5 km

outside the designated Davison and Boyes study areas (Figure 1). The peripheral survey areas were the lower part of the Redwood Creek and the Gold Bluff area west of Davison and Boyes meadow complexes (Figure 1). Male surveys were conducted in the same manner as the surveys done in both meadow complexes. Male surveys were also conducted on days that surveys in the Davison and Boyes meadow complexes were surveyed. Male abundance in the peripheral area was the highest count across the surveys in a year. In 2017, the Davison herd was found to have expanded south of the Davison meadow complex into cattle pasture areas containing forage. Therefore, in 2017 and 2019, the survey route was expanded to include these cattle pasture areas. In 2020, the Davison herd was found to have expanded further south into areas of North Orick. Therefore, the survey route was again expanded to include these areas.

Individuals detected during surveys were placed within two categories: adult male-only groups or female groups. The latter group is comprised of females, subadult males, and juveniles. It was not unusual for a few (<5) adult males to enter female groups for several days and then leave (Weckerly, 2020). Thus, the group was still classified as a female-group. Because juveniles of both sexes and subadult males were observed in the same groups as adult females in more than 99% of all surveys they were included in the counts of female groups (Weckerly et al. 2001, Weaver and Weckerly 2011). The Davison and Boyes herds partitioned meadows. The Boyes herd were observed in the Davison meadows <1% of all surveys, and the Davison herd was never observed in the Boyes meadows (Weckerly 2017).

Female abundance, adult male abundance, and adult sex ratio (adult males: adult females, subadults, and juveniles) of herds inhabiting both meadow complexes within the

Prairie Creek Drainage system were estimated across years in one of two ways: with Bowden's mark-resight estimator or the highest count in a year (Bowden and Kufeld 1995, Peterson and Weckerly 2017). The former method was employed when unmarked males were detected across the surveys conducted in a year. Unlike males, females had high sighting probabilities (>80%) in all surveys and thus the highest herd count was my index of abundance (Weckerly 2017). If all males that were observed across surveys were marked, then the number of marked animals was used as an estimate of male abundance for that year (Weaver and Weckerly 2011).

Population Analyses

Time-series data collected from 1997 to 2020 were used in my analyses (Figure 2). The Davison herd was the total female abundance as they were the only herd present throughout the time of my study. Also, before the Boyes herd went extinct in 2010 most males occupied the Davison meadows and not the Boyes meadows (Peterson and Weckerly 2017, Weckerly 2017). Population growth patterns were examined in three phases displayed by the Davison herd: a period of decline from 1997–2005, a period of density-dependence from 2006–2016, and a period of expansion from 2017–2020 (Figure 2). Female abundance (adult females, subadults, and juveniles) and phases of population growth were predictor variables. Adult sex ratio was my response variable. Because juvenile females could not be distinguished from adult females ASR was adult males:juvenile and adult females. I analyzed a multiple regression model to determine if a significant relationship existed between female abundance and ASR in this population. To assess if temporal autocorrelation was present, I estimated a lag one Pearson's correlation coefficient on the residuals extracted from the multiple regression (Aiken et

al. 1991). After estimating the model, I obtained bootstrapped 95% confidence intervals for estimated parameters. Estimation of my model was conducted in the R computing platform version 4.0.2.

Vegetation Collection

From January 2005 to 2020, forage biomass was estimated in the Davison and Boyes meadow complexes. First, each meadow was divided into sectors: seven sectors were delineated in the Davison meadows and four sectors were delineated in the Boyes meadows. The sectors in the Davison meadows were grazed by the Davison herd in every year of the study (Weckerly 1998, 2017, Williamson 2020). Sector boundaries were set up to sample all parts of the meadow complexes. Next, transects were randomly placed within each sector. Along these transects 10–40 quarter-meter squared plots were spaced 10 m apart and vegetation measurements were taken in every plot (Weckerly 2017). In 2005, 550 plots were measured and in remaining years 570 plots were measured. In 2020, vegetation was measured in an additional 139 plots in an area of North Orick the Davison herd had ventured into. This area was 32.5 ha in size.

Vegetation Analysis

In each plot plant height and coverage was measured. Plants edible to elk were measured for height at eight equidistant locations to the nearest centimeter, and percent cover of grasses, forbs, and shrubs were visually assessed and recorded into Daubenmire coverage classes (Daubenmire 1968). The coverage classes were 0–5, 6–25, 26–50, 51–75, 76–95, and 96–100%. I predicted the biomass of grasses from a multiple regression model with predictors of plant height means from the eight equidistant measurements and grass cover ($r^2 = 0.84$, $F_{7,122} = 97.1$, $P < 0.001$). The biomass of edible forbs and shrubs

were predicted from forb and shrub cover ($r^2 = 0.33$, $F_{2, 93} = 24.9$, $P < 0.001$) (Peterson and Weckerly 2017). The multiple regressions were estimated from height, cover, and dried forage biomass (response variable) data collected in separate 129 quarter-meter squared plots that were measured in 2005–2007.

A generalized linear regression with temporal autocorrelation was analyzed to estimate forage biomass (kg) in both meadow complexes in each year from 2005–2020 (Pinheiro and Bates 2000). Forage biomass was summed across sectors in each meadow complex. Predictors were meadow, year, expansion, and the interaction between meadow and year. For meadow, the reference category was Boyes meadow complex. For expansion, the reference category was the years the Davison herd had not expanded its home range. An expansion predictor was considered because the grazing pressure in the seven sectors in Davison meadows might have decreased due to the range expansion. The forage biomass in Boyes meadows was included in analyses as a spatial control (Faas and Weckerly 2010). If there was a decline in forage biomass in the Davison meadows from female grazing, then I would not expect it in the Boyes meadows where the Boyes herd was small from 2005 to 2010 (4-5 animals) and nonexistent thereafter (Weckerly 2017). Estimation of my model was performed in the R computing platform version 4.0.2.

Results

Female abundance declined from 1997 to 2006 and then increased gradually to 2016 (Figure 2). When the Davison herd expanded its home range beginning in 2017 abundance of the herd continued to increase. Temporal variation in male abundance was markedly different. Male abundance was highest early in the time series and gradually

declined to about 2016. From 2017 to 2019 there was a gradual increase in male abundance but there was a dramatic increase in 2020. Adult sex ratios in the decline phase were mostly higher than ASR in the density-dependent phase (Figure 3). During the first three years of the expansion phase ASR was low but in 2020 ASR was comparable to estimates in the decline phase. Female abundance was inversely associated with ASR during the density-dependent phase, but not in the decline phase. During the expansion phase there was a positive relationship between female abundance and ASR (Table 1). I did not detect a lag one temporal autocorrelation ($r = 0.05$, $P = 0.81$)

Male surveys conducted in the study periphery in 2016, 2017, and 2019 when male abundance was low indicated that there were males in areas near the Prairie Creek drainage (Figure 4). At minimum there were between six to 16 males in the periphery. In 2020, when male abundance increased markedly, there were still males in the nearby area.

Meadow, expansion, and the interaction between meadow and year were all found to influence forage biomass (Table 2). Year and the lag one temporal autocorrelation coefficient were not influential (Table 2). Summarizing the relationships detected revealed an inverse relationship between year and forage biomass in the Davison meadow complex, but not the Boyes meadow complex (Figure 5). In 2020 when the Davison herd expanded further south, the forage abundance in this new area was very high (Figure 5).

Discussion

My findings were consistent with the female-substitution hypothesis. Temporal changes in the adult sex ratio of the Davison herd displayed an inverse relationship with

female abundance during the density-dependent phase. Associated with an increase in female abundance was a decline in forage biomass in the sectors of Davison meadows that were continuously grazed by the Davison herd from 2005 to 2020, supporting the forage-enabled mechanism. The small size of the Boyes herd (4-5 individuals) from 2005 to 2010 and the absence of a herd thereafter enabled this meadow complex to serve as a spatial control. No correlation between year and forage biomass was detected in the Boyes meadow complex indicating that the inverse correlation between year and forage biomass in the Davison meadow complex was not spurious. Also, it does not appear that the decline in ASR later in the time series was from a paucity of males. I conducted male surveys in the study periphery after 2015 and detected males in nearby areas that had the potential to use the Davison meadow complex. Thus, my findings do not support the sparse-male mechanism.

Across the time of the density-dependent phase, meadow use by the Davison herd did not contract or expand. The herd grazed different parts of this meadow complex in proportion to the availability of forage in those parts (Weckerly 2017, McGuire 2018). This forage pattern should maintain familiarity with forage abundance and distribution as well as maintain forage efficiency. As herd abundance increased, the forage pressure on all parts of the Davison meadow increased and the elk food supply became more limited. Consequently, males should have sought forage in other meadows and habitat besides the Davison meadows (Bliss and Weckerly 2016).

Contrary to the density-dependent phase, a positive relationship between female abundance and ASR was found during the expansion phase. In 2017 and 2020, the Davison herd expanded into areas south of the Davison meadow complex. This included

meadows on new public land and private land in North Orick containing abundant forage. The range expansion in North Orick included 32 ha of additional meadow grazed by the Davison herd. The reversal in ASR pattern during this phase does not contradict the predictions of the female-substitution hypothesis. Instead it provides additional support for the hypothesis by providing a real-world example of the change in population dynamics when intersexual competition is presumably lessened. Males had previously been found foraging in these areas. The inclusion of a new and abundant food source for the Davison herd would not immediately lead to the passive displacement of males via scramble competition. Therefore, we would expect the ASR to increase from an increase in number of males exploiting the new food supply. A food supply that had probably not become an established part of the home range of the Davison herd.

A critique of my analysis is the inclusion of subadult females with adult females in estimating ASR. To remain consistent with females I could have included subadult males with adult males to estimate ASR. Including subadult males with adult males was unrealistic as subadult males were mostly associated with females (Weckerly 2017). Subadult males were therefore part of the female population. I included subadult females with adult females because it was difficult to distinguish the two age classes of females by body size. Nonetheless, not being able to exclude subadult females from the ASR calculation is unlikely to affect my findings as they were likely to be a small fraction relative to adult females (Weckerly 2017). An ASR excluding subadult females would likely be somewhat higher than what is reported herein. But as long as the fraction of subadult females was constant across the years of the study, the patterns I detected would not change if I had estimated ASR excluding subadult females (Appendix A).

Time series of both male and female abundances for un hunted populations of *C. elaphus* or any ruminant species are sparse. To my knowledge there are only two such studies. One long-term population study was at Point Reyes National Seashore (Cobb 2010). The findings of this study indicated an inverse relationship between female and male abundance. The other study was also a long-term study of a population of *C. elaphus* on the Isle of Rum in Scotland. Coulson and colleagues (2004) reported demographic information for this population that also mirrored the pattern found in my study population. These two populations inhabited environments quite different from my study, yet the same patterns were evident. As female abundance increased, and food supplies presumably became more limited, male abundance declined.

In seeming contradiction to my study, Conradt et al. (1999) concluded that male habitat use was not affected by scramble competition with females. Conradt et al. (1999) experimentally manipulated numbers of both sexes in populations and then examined intersexual habitat use pre- and post-removals. Their results indicated that habitat use was not affected by changes in female or male abundance, and thus concluded that indirect competition did not explain intersexual habitat use. This study, however, did not examine temporal changes in food supplies or grazing patterns in relation to forage abundance. Furthermore, the delineation of habitats might not have captured areas with the most nutritious forage (McLoughlin et al. 2006). Another consideration is the time needed to detect a response and the extent of change in female abundance. For example, if I had limited my study to the first 10 years during the decline phase I also would not have detected intersexual habitat use patterns consistent with the female-substitution hypothesis (Peterson and Weckerly 2017). It was not until the abundance of the Boyes

herd declined markedly that male habitat use began to also shift.

Understanding density-dependent relationships are crucial for insight into population regulation and stability. This has implications for both understanding population ecology and managing and conserving large herbivores. In polygynous ungulates, ASR patterns should be skewed towards females at carrying capacity (Clutton-Brock et al. 1997, Berger and Gompper 1999, Coulson et al. 2004, Weaver and Weckerly 2011). My study is useful for highlighting ASR relationships in ungulates that can be explained by factors other than differential survivorship between the sexes. In current literature, female-biased ASR is most commonly attributed to the shorter lifespan of males (Clutton-Brock et al. 1982, Toigo and Gaillard 2003, Clutton-Brock and Isvaran 2007, Lemaitre et al. 2020). This sex difference in life history is due to their greater absolute metabolic requirements, male – male competition for access to females, and risks associated with dispersing from the natal area (Clutton-Brock et al. 1997, McCullough 1999, Berger and Gompper 1999, Creel et al. 2007, Loe et al. 2009). The female-substitution hypothesis adds another dimension of competition for habitat.

Based on my study and the theoretical work done by McCullough (1999), females are the sex driving habitat-use patterns in polygynous ungulates. Understanding this dynamic is critical for wildlife managers. If changes in food supply occur managers must be aware of how changes in habitat-use may shift over time. They may be able to predict how sexual segregation in the landscape will increase if food supply dwindles, or conversely, how intersexual mixing will increase if food supply increases. Males are the sex usually hunted or poached, however, declines in their abundance will probably have no density-dependent effects on females. This understanding can allow managers to

allocate resources and time for managing the sex in different ecological scenarios to have the highest impact on the population dynamics.

My study is the first to provide empirical support for the female-substitution hypothesis. Work that not only required measuring female and male abundances but also estimating food supplies. Study of grazing patterns of the Davison herd in relation to the food supply provided more information which further supported male displacement through scramble competition from females. Nonetheless, more work is necessary to directly measure if these same mechanisms operate in other ungulate populations and possibly other polygynous mammals.

Table 1. Multiple regression model: estimates and corresponding 95% confidence intervals of correlation between abundance and adult sex ratio (ASR). The time period reference category was the density-dependent phase (DD) from 2006-2016. The Decline phase was from 1997-2005 and the Expand phase was from 2017-2020. Data was collected in the Davison Meadow complex in the Prairie Creek Drainage, Redwood National and State Parks, Humboldt County, California, USA, from 1997-2020.

Source of Variation	β_i	<i>SE</i>	95% Confidence Interval	
			Lower	Upper
Intercept	0.95	0.12	0.69	1.20
Female abundance	-0.02	0.00	-0.03	-0.01
Decline	-0.09	0.17	-0.45	0.26
Expand	-2.20	0.44	-3.13	-1.27
Female abundance:decline	0.01	0.01	0.00	0.02
Female abundance:expand	0.042	0.008	0.026	0.058

Table 2. Generalized least squares model: estimates and corresponding 95% confidence of different predictors (including a temporal autocorrelation term). Estimating forage biomass (kg) in the Boyes and Davison meadow complexes, Redwood National and State Parks, Humboldt County, California, USA, 2005-2020. Forage biomass was the sum of forage biomass across all sectors in each meadow complex. Predictors were meadow, year, expansion, and the interaction between meadow and year. For meadow, the reference category was Boyes meadow complex. For expansion, the reference category was years when the Davison herd had not expanded its home range.

Source of Variation	Estimates	95% Confidence Interval	
		Lower	Upper
Intercept	8502.75	6868.93	10136.56
Meadow	8195.81	5708.80	10682.82
Year	38.97	-148.42	226.37
Expansion	3825.57	674.52	6976.61
Meadow:year	-526.99	-873.89	-180.10
Autocorrelation	-0.40	-0.70	0.02
Residual SE	2426.30	1812.75	3247.52

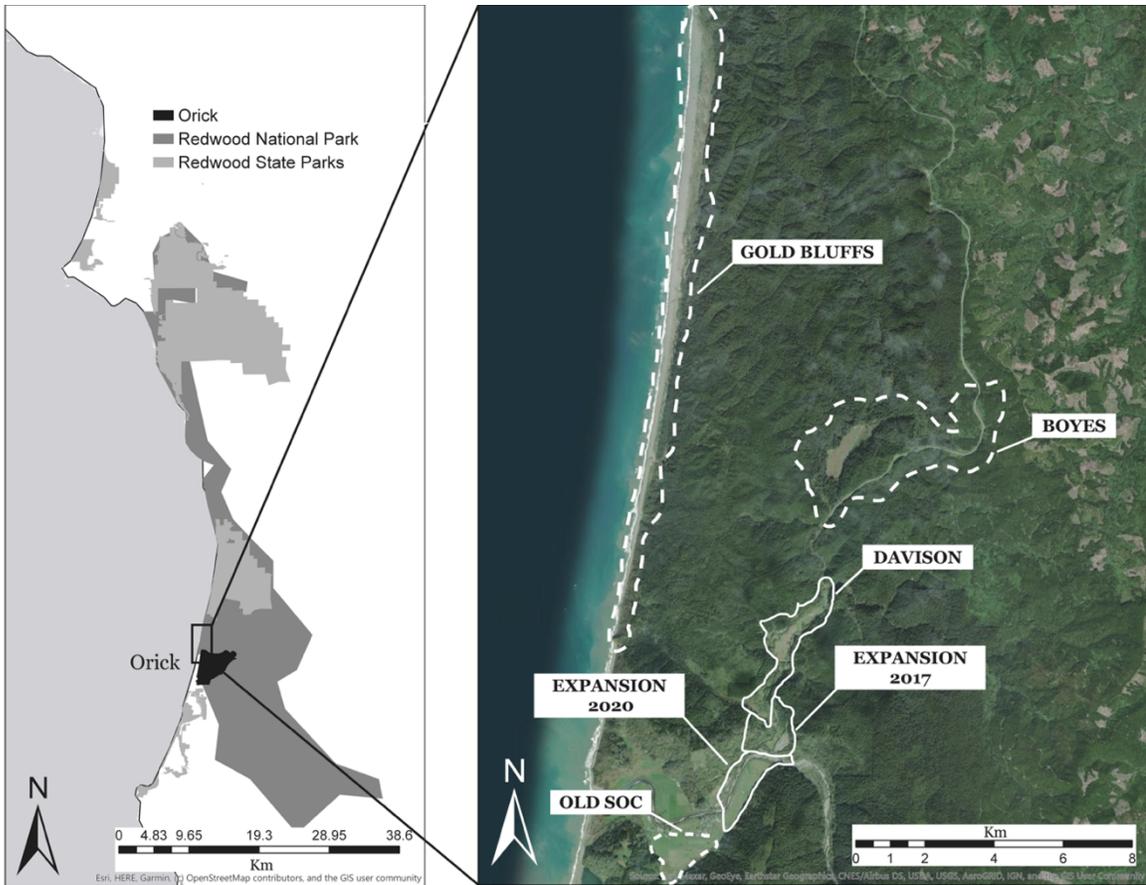


Figure 1. Map of study area within the Redwood National and State Parks, California. Left: map of California showing the location of the Redwood National and State Parks along the northwest coast. Right: aerial photograph showing the Prairie Creek drainage and the location of the Gold Bluffs, Boyes, Davison, and Old SOC meadow complexes. Also shown are solid polygons indicating areas in which the Davison herd expanded in 2017 and 2020.

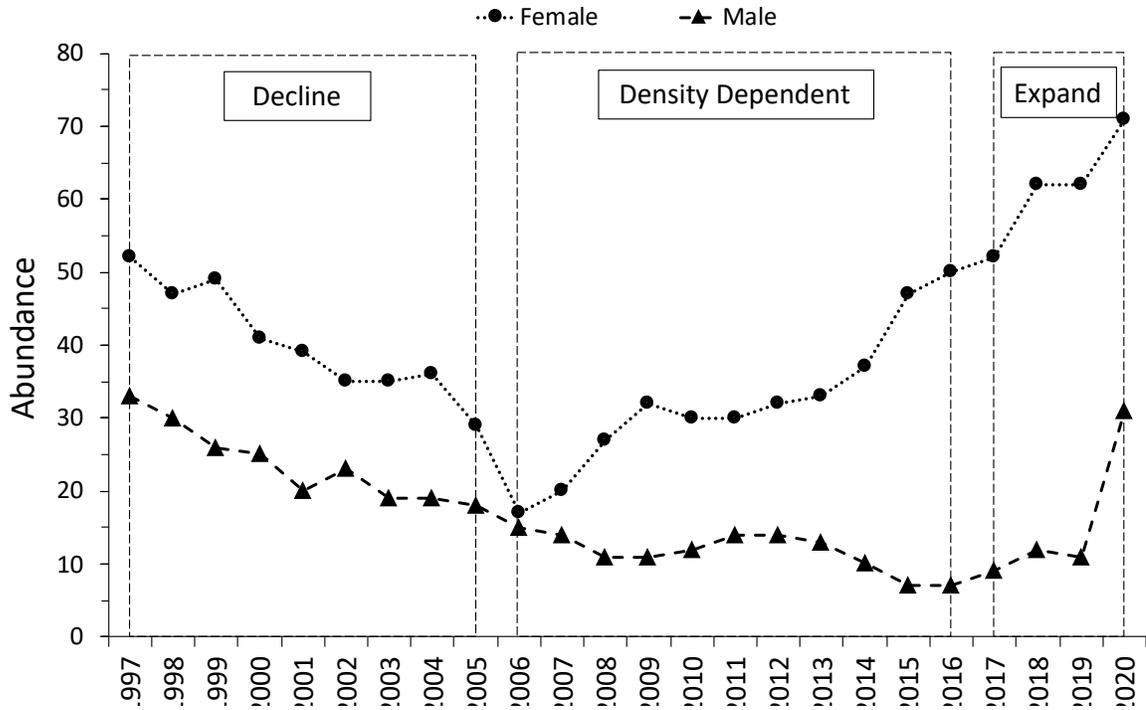


Figure 2. Graph of Davison herd abundance and adult males from 1997 to 2020. Prairie Creek Drainage, Redwood National and State Parks, Humboldt County, California, USA. Female abundance includes subadult females, subadult males, and juveniles. Also delineated are the three phases in population growth of the Davison herd.

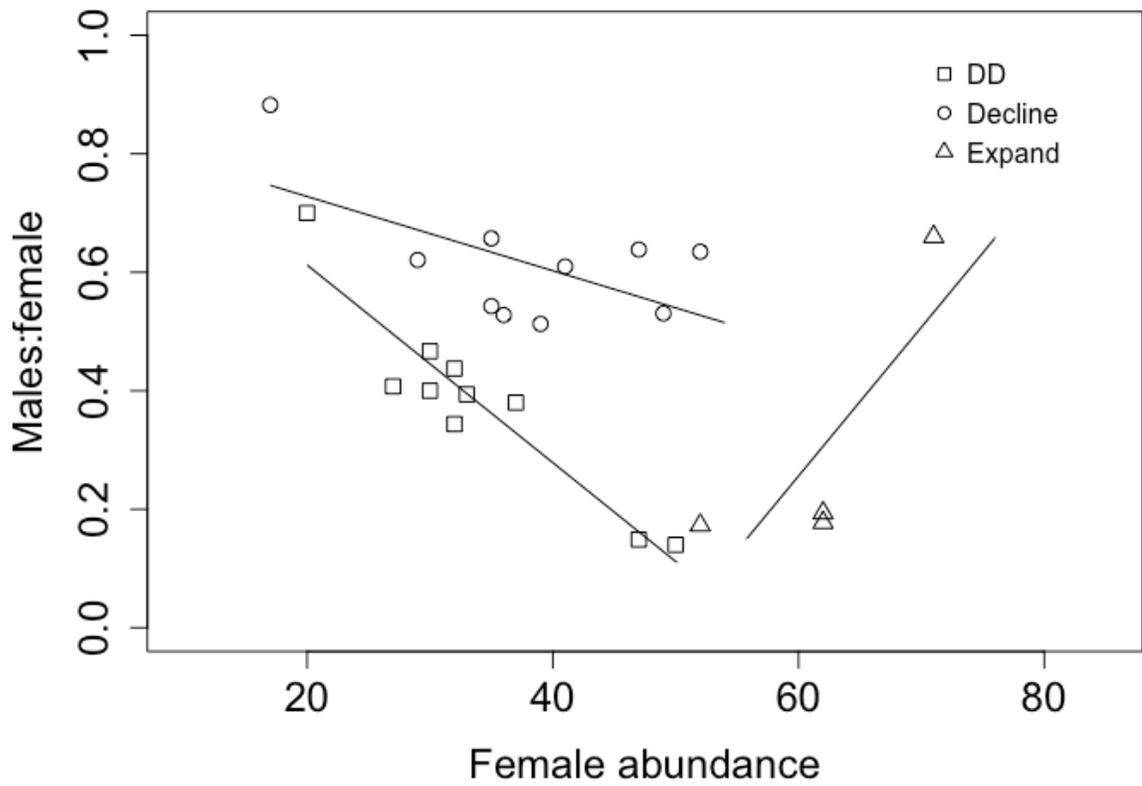


Figure 3. Scatterplot with regressions fit to abundance and adult sex ratio during the three growth phases between 1997 and 2020. Data from the density-dependent phase (DD, 2006-2016) is squares, circles from the decline phase (1997-2005), and triangles for the expansion phase (2017-2020).

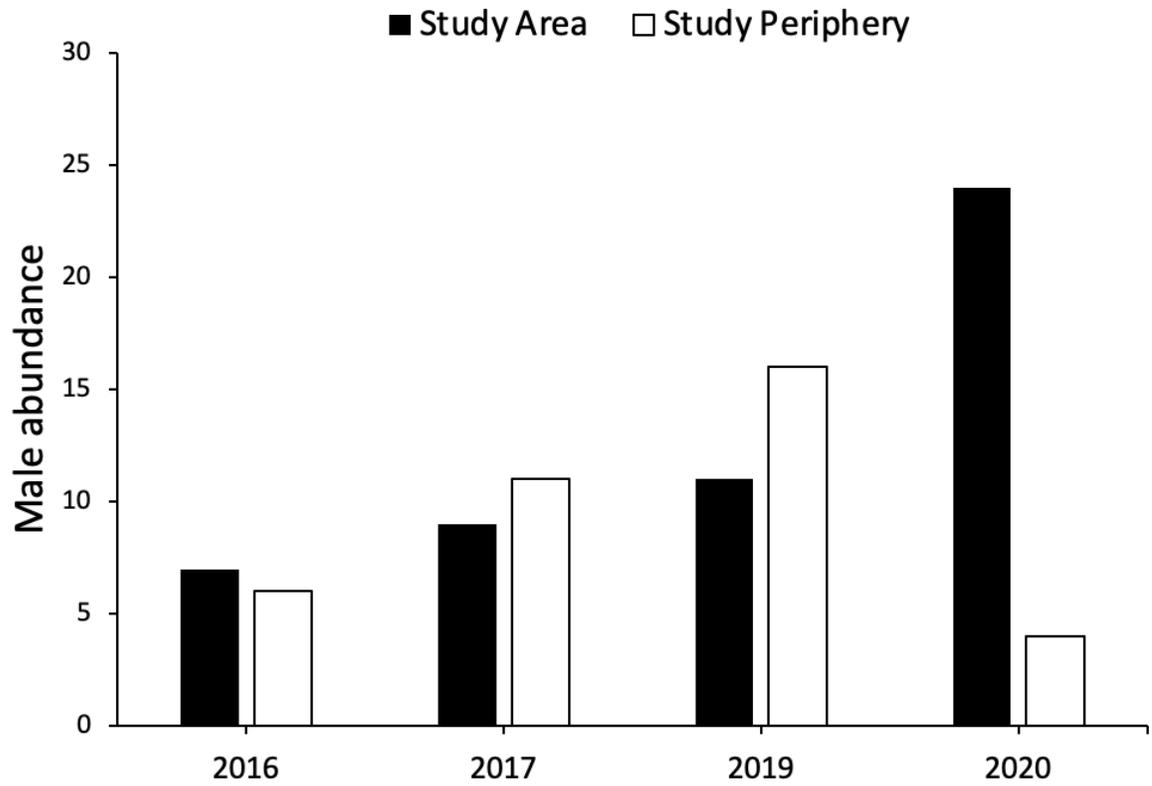


Figure 4. Graph of male abundance in study area and highest count of males in peripheral areas in four years between 2016 and 2020. Data was collected in the Davison and Boyes meadow complexes (study area) and surrounding or peripheral areas in the Prairie Creek Drainage, Redwood National and State Parks, Humboldt County, California, USA.

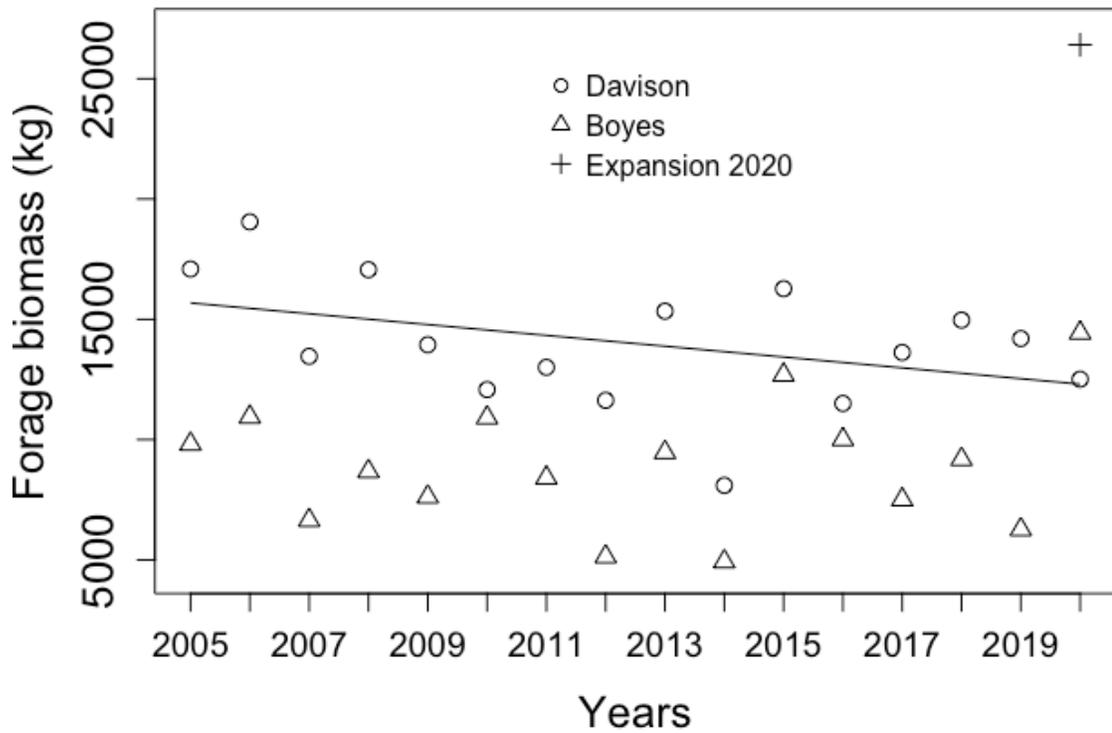


Figure 5. Scatterplot of linear regressions summarizing forage biomass in Boyes and Davison meadow complexes, 2005-2020. Redwood National and State Parks, Humboldt County, California. In 2020, a data point represented with a crosshair shows the total forage biomass available to the Davison herd as a result of their expansion into a 32 ha pasture in North Orick. There was no year trend detected in the Boyes meadow complex. Line reflects significant relationship between year and forage biomass in the Davison meadow complex.

APPENDIX SECTION

APPENDIX A

Subadult females can be estimated from the number of juveniles in year t minus the number of subadult males in year $t - 1$ (Weckerly 2017). This estimate of number of subadult females requires that the Davison herd be the natal herd of subadult males and that survival rates of juveniles did not differ between females and males. Using this estimate, number of subadult females ranged from 1 to 12 (Table A1) and the estimates of aASR (adult sex ratio adjusted for adults only) averaged 0.10 higher (range: 0.0006 – 0.32). Analyzing aASR as the response variable indicated the same patterns as ASR (Table A2). I conclude that although ASR estimates would likely change by excluding subadult females, the relationships between female abundance and ASR would be similar.

Table A1. Number of females (subadult and adults) and estimates of subadult and adult females in the Davison herd, 1997 – 2020. Also reported is the ASR (adult males:subadult and adult females) and aASR (adult males:estimated adult females) in each year.

Year	Females	Subadult females	Adult females	ASR	aASR
1997	35	7	28	0.63	0.79
1998	34	6	28	0.64	0.79
1999	36	6	30	0.53	0.63
2000	30	6	24	0.61	0.75
2001	26	3	23	0.51	0.57
2002	27	7	20	0.66	0.90
2003	26	3	23	0.54	0.61
2004	26	1	25	0.53	0.56
2005	22	3	19	0.62	0.74
2006	14	4	10	0.88	1.20
2007	14	1	13	0.70	0.80
2008	15	3	12	0.41	0.50
2009	18	4	14	0.34	0.43
2010	21	5	16	0.40	0.50
2011	18	1	17	0.47	0.47
2012	24	6	18	0.44	0.61
2013	27	7	20	0.39	0.55
2014	26	3	23	0.38	0.43

Table A1 (Cont.)

2015	30	4	26	0.15	0.19
2016	35	8	8	0.14	0.18
0.2017	38	6	6	0.17	0.19
2018	40	4	4	0.19	0.22
2019	41	12	12	0.18	0.24
2020	47	8	8	0.66	0.79

Table A2. Multiple regression model: estimates and corresponding 95% confidence intervals of correlation between abundance and adjusted adult sex ratio (aASR). The time period reference category was the density-dependent phase (DD) from 2006-2016. The Decline phase was from 1997-2005 and the Expand phase was from 2017-2020. Data was collected in the Davison Meadow complex in the Prairie Creek Drainage, Redwood National and State Parks, Humboldt County, California, USA, from 1997-2020.

Source of Variation	β_i	<i>SE</i>	95% Confidence Interval	
			Lower	Upper
Intercept	1.08	0.18	0.67	1.22
Female abundance	-0.02	0.005	-0.02	-0.005
Decline	0.06	0.25	-0.82	0.57
Expand	-2.65	0.67	-4.84	0.94
Female abundance:decline	0.008	0.007	0.00	0.03
Female abundance:expand	0.049	0.011	0.018	0.083

LITERATURE CITED

- BEIER, P., AND D. MCCULLOUGH. (1990). Factors influencing white-tailed deer activity patterns and habitat use. *Wildlife Monographs*, **109**:3-51.
- AIKEN, L. S., WEST, S.G. AND R. R. RENO. (1991). Multiple regression: Testing and interpreting interactions. Sage.
- BENTLEY, W. W. (1959). The range relationships of Roosevelt elk, *Cervus canadensis roosevelti* (Merriam), at Prairie Creek Redwoods State Park, Humboldt County, California, in 1958 (Unpublished master's thesis). Humboldt State University, Arcata, CA.
- BERGER, J., AND M. E. GOMPPER. (1999). Sex ratios in extant ungulates: products of contemporary predation or past life histories? *Journal of Mammalogy*, **80**:1084-1113.
- CLUTTON-BROCK, T. H., F. E. GUINNESS, AND S. D. ALBON. (1982). Red deer: behavior and ecology of two sexes. Chicago, IL: University of Chicago Press.
- CLUTTON-BROCK, T. H., G. R. IASON, AND F. E. GUINNESS. (1987). Sexual segregation and density-related changes in habitat use in male and female Red deer (*Cervus elaphus*). *Journal of Zoology*, **211**:275-289.
- CLUTTON-BROCK, T. H., AND K. ISVARAN. (2007). Sex differences in ageing in natural populations of vertebrates. *Proceedings of the Royal Society Biological Sciences Series B*, **274**:3097-3104.
- CLUTTON-BROCK, T. H., K. E. ROSE, AND F. E. GUINNESS. (1997). Density-related changes in sexual selection in red deer. *Proceedings of the Royal Society Biological Sciences Series B*, **264**:1509-1516.

- COBB, M. A. (2010). Spatial ecology and population dynamics of tule elk (*Cervus elaphus nannodes*) at Point Reyes National Seashore, California. [Doctoral Dissertation, UC Berkeley.]. *UC Berkeley Electronic Theses and Dissertations*:1-202.
- CONRADT, L., T. H. CLUTTON-BROCK, AND D. THOMSON. (1999). Habitat segregation in ungulates: are males forced into suboptimal foraging habitats through indirect competition by females? *Oecologia*, **119**:367-377.
- CORREA, L. A., B. ZAPATA, H. SAMANIEGO, AND M. SOTO-GAMBOA. (2013). Social structure in a family group of Guanaco (*Lama guanicoe*, Ungulate): is female hierarchy based on 'prior attributes' or 'social dynamics'? *Behavioural Processes*, **98**:92-97.
- COULSON, T., F. GUINNESS, P. JOSEPHINE, AND T. H. CLUTTON-BROCK. (2004). The demographic consequences of releasing a population of red deer from culling. *Ecology*, **85**:411-422.
- CREEL, S., D. CHRISTIANSON, S. LILEY, AND J. A. WINNIE, JR. (2007). Predation risk affects reproductive physiology and demography of elk. *Science*, **315**:960.
- DAUBENMIRE, R. F. (1968). Plant communities: a textbook of plant synecology. New York: Harper & Row.
- FAAS, C. J., AND F. W. WECKERLY. (2010). Habitat interference by axis deer on white-tailed deer. *Journal of Wildlife Management*, **74**:698-706.
- HARN, J. H. (1958). The Roosevelt elk, *Cervus canadensis roosevelti* (Merriam), at Prairie Creek Redwoods State Park, Humboldt County, California (Unpublished master's thesis). Humboldt State University, Arcata, CA.

- HARPER, J. A., J. H. HARN, W. W. BENTLEY, AND C. F. YOCOM. (1967). The status and ecology of the Roosevelt elk in California. *Wildlife Monographs*, **16**:1-49.
- JULIAN, A. E., K. SCHMIDT, AND F. W. WECKERLY. (2013). Group size dynamics of female Roosevelt elk in Redwood National and State Parks, California. *California Fish and Game*, **99**:49-54.
- LEMAITRE, J. F., V. RONGET, M. TIDIÈRE, D. ALLAINE, V. BERGER, A. COHAS, . . . J. M. GAILLARD. (2020). Sex differences in adult lifespan and aging rates of mortality across wild mammals. *Proceedings of the National Academy of Sciences of the United States of America*, **117**:8546-8553.
- LOE, L. E., A. MYSTERUD, V. VEIBERG, AND R. LANGVATN. (2009). Negative density-dependent emigration of males in an increasing red deer population. *Proceedings of the Royal Society B*, **276**:2581-2587.
- MAIN, M. B. (2008). Reconciling competing ecological explanations for sexual segregation in ungulates. *Ecology*, **89**:693-704.
- MANDEL, R. D., AND D. W. KITCHEN. (1979). The ecology of Roosevelt elk in and around Redwood National Park. Humboldt State University, Arcata, CA.
- MCCULLOUGH, D. R. (1999). Density dependence and life-history strategies of ungulates. *Journal of Mammalogy*, **80**:1130-1146.
- MCCULLOUGH, D. R., D. H. HIRTH, AND S. J. NEWHOUSE. (1989). Resource partitioning between sexes in white-tailed deer. *Journal of Wildlife Management*, **53**:277-283.
- MCGUIRE, A. S. (2018). Roosevelt elk response to a newly available forage patch [Master's thesis, Texas State University].

- McLOUGHLIN, P. D., M. S. BOYCE, T. COULSON, AND T. CLUTTON-BROCK. (2006). Lifetime reproductive success and density-dependent, multi-variable resource selection. *Proceedings of the Royal Society B*, **273**:1449-1454.
- MERKLE, J. A., J. R. POTTS, AND D. FORTIN. (2017). Energy benefits and emergent space use patterns of an empirically parameterized model of memory-based patch selection. *Oikos*, **126**.
- MOLVAR, E. M., AND R. T. BOWYER. (1994). Costs and benefits of group living in a recently social ungulate: the Alaskan moose. *Journal of Mammalogy*, **75**:621-630.
- OWEN-SMITH, N. (1993). Comparative mortality rates of male and female kudu- the costs of sexual size dimorphism. *Journal of Animal Ecology*, **62**:428-440.
- PEREZ-BARBERIA, F. J., I. J. GORDON, AND M. PAGEL. (2002). The origins of sexual dimorphism in body size in ungulates. *Evolution*, **56**:1276-1285.
- PETERSON, L. M., AND F. W. WECKERLY. (2017). Male group size, female distribution and changes in sexual segregation by Roosevelt elk. *PLoS ONE*, **12**:1-15.
- PETERSON, L. M., AND F. W. WECKERLY. (2018). Social behavior and changes in foraging behavior in a gregarious ungulate. *Journal of Mammalogy*, **99**:1422-1429.
- PINHEIRO, J. C., AND D. M. BATES. (2000). Linear mixed effects models. *Mixed Effects Models in S and S-Plus*. Springer Verlag: New York.
- RIOTTE-LAMBERT, L., S. BENHAMOU, AND S. CHAMAILLE-JAMMES. (2015). How memory-based movement leads to nonterritorial spatial segregation. *American Naturalist*, **185**:E103-116.

- RUCKSTUHL, K. E., AND P. NEUHAUS. (2002). Sexual segregation in ungulates: a comparative test of three hypotheses. *Biological Reviews*, **77**:77-96.
- SHELDON, B. C., AND S. A. WEST. (2004). Maternal dominance, maternal condition, and offspring sex ratio in ungulate mammals. *American Naturalist*, **163**:40-54.
- 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. *Ecology and Evolution*, **5**:109-120.
- TOIGO, C., AND J. M. GAILLARD. (2003). Causes of sex-biased adult survival in ungulates: sexual size dimorphism, mating tactic or environment harshness? *Oikos*, **101**:376-384.
- TRIVERS, R. L., AND D. E. WILLARD. (1973). Natural selection of parental ability to vary the sex ratio of offspring. *Science*, **179**:90-92.
- WEAVER, S. P., AND F. W. WECKERLY. (2011). Sex ratio estimates of Roosevelt elk using counts and Bowden's estimator. *California Fish and Game*, **97**:130-137.
- WECKERLY, F. W. (1998). Sexual segregation and competition in Roosevelt elk. *Northwestern Naturalist*, **79**:113-118.
- . (1999). Social bonding and aggression in female Roosevelt elk. *Canadian Journal of Zoology*, **77**:1379-1384.
- WECKERLY, F. W. (2001). Are large male Roosevelt elk less social because of aggression? *Journal of Mammalogy*, **82**:414-421.

- 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. (2020). Frequency and density associated grouping patterns of male Roosevelt elk. *Frontiers in Ecology and Evolution*, **8**: 1-9.
- WECKERLY, F. W., K. MCFARLAND, M. RICCA, AND K. MEYER. (2004). Roosevelt elk density and social segregation- foraging behavior and females avoiding larger groups of males. *American Midland Naturalist*, **152**:386-399.
- 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.
- WILLIAMSON, L. H. (2020). Food supply early in the plant growing season: influences from elk abundance and precipitation [Master's thesis, Texas State University].
- WILLIAMSON, L. H., AND F. W. WECKERLY. (2019). Elk forage response to prescribed fire in Boyes meadow, Prairie Creek Redwoods State Park, California. *California Fish and Game*:1-16.
- 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.