ESTIMATES OF CALF SURVIVAL AND FACTORS INFLUENCING ROOSEVELT ELK MORTALITY IN NORTHWESTERN CALIFORNIA

By

Erin M. Nigon

A Thesis Presented to
The Faculty of Humboldt State University
In Partial Fulfillment of the Requirements for the Degree
Master of Science in Natural Resources: Wildlife

Committee Membership
Dr. Richard Brown, Committee Chair
Dr. Micaela Szykman Gunther, Committee Member
Dr. William Bean, Committee Member
Carrington Hilson, Committee Member
Dr. Erin Kelly, Graduate Coordinator

May 2020

ABSTRACT

ESTIMATES OF CALF SURVIVAL AND FACTORS INFLUENCING ROOSEVELT ELK MORTALITY IN NORTHWESTERN CALIFORNIA

Erin M. Nigon

Survival of juvenile ungulates is known to be highly variable, yet it is fundamental to understanding the dynamics and trends of wildlife populations. Factors influencing calf survival are poorly understood in northwestern California where Roosevelt elk (*Cervus canadensis roosevelti*) are known to exist. The objectives of this study were 1) to estimate summer and annual survival rates and determine recruitment rates for Roosevelt elk calves in the area, 2) to evaluate differences in calf survival by examining the effects of individual and population level covariates on summer and annual calf survival, 3) to identify factors influencing the timing and cause of calf mortalities, and 4) to establish a baseline of mortality factors influencing elk across all age classes. Over two seasons, this study captured and marked 58 calves and 28 cow elk in Del Norte and Humboldt counties. Calf survival was 0.67 (SE = 0.009) during the first 14 weeks of life (summer) and 0.82 (SE = 0.001) annually. Birth weight, study area, and the linear trend of time were found to be the most important covariates for summer survival, while the variable effect of time was most important for annual survival of calves. Predation was the top cause of death in calves and black bears (*Ursus americanus*) accounted for 22% of marked calf mortality. Across all age classes, human-caused mortality (roadkill, legal harvest, euthanasia, and poaching) was the most prominent for adults and yearlings. This is the first study to document calf survival and recruitment in northwestern California and provides evidence that calf survival is high but is not uniform across the area. These results will aid managers in setting appropriate harvest quotas for elk across the hunt zone and provides justification to implement targeted management that alleviates conflict.

ACKNOWLEDGEMENTS

I would like to thank my major professor, Dr. Richard Brown, for his dedication and attention to detail through all phases of this study. Thanks for constantly challenging me, supporting me, and providing quick wit in every situation. I would also like to thank Carrington Hilson for her extensive devotion to my project. Your advice, guidance, perseverance, and most of all, friendship has been invaluable to this project and my career as a biologist. I can’t thank you enough for the influence you’ve had on my future. I extend my deepest gratitude to the other members of my committee, Dr. Tim Bean and Dr. Micaela Szykman Gunther for their insightful comments and recommendations. Additionally, I would like to thank Dr. Daniel Barton for contributing to this thesis by answering many statistic-related questions and assisting me with my analysis whenever I asked.

Numerous people contributed to the success of this project in so many ways over the course of two years. Many thanks are due to my friend and colleague Emily Armstrong-Buck. I am so thankful I had you as a lab-mate, peer, and friend. I am grateful for all you have done on this study, our shared interest in disease, and your humor. Special thanks also go to Sean Ihle for all his time and effort on the project. Your friendship and good attitude in the field is something I continue to value to this day. I would also like to thank the many volunteers and technicians who dedicated many hours of time and effort in the field with me. In particular, thanks are due to K. Lopez, A. Widjaja, E. Bonnin, K. Domingo, K. Underwood, R. Carniello, H. Ziemer, K. Parker, M.

Romanucci, A. Branney, E. Aarsvold, A. Phelan-Roberts, K. Cox, S. Kanga-Livingstone, H. Sellers, A. Kowalczyk, K. Fiscus, D. Ambriz, R. Cervantes, K. Wolf, G. Culver, A. Jamal, A. Mohr, and R. Mena.

Thank you to the Redwood National and State Parks personnel for access to your lands and insight on elk in the area. Special thanks to Terry Hines and Kyle Max for the countless hours you spent helping me in the field and sharing your knowledge with me. Additional thanks go to T. King, M. Spero, B. Pero, K. Schmidt, C. Wells, S. Gayner, J. Wright, and S. Korsgren for providing extra help in a pinch.

I'd like to thank everyone with the California Department of Fish and Wildlife for supporting me on this project in so many ways. The wealth of expertise and experience many of you brought to this study was invaluable and I wouldn't have been successful without your help. In particular, I'd like to thank D. Lancaster, B. Schaefer, J. Carlson, A. Spicer, Dr. B. Munk, S. Fresz, A. Moran, M. Wells, W. Castillo, T. Pinnow, and S. Embry.

Finally, I wouldn't be here today without the support of my family and continued support of my partner. I can't thank Josh Zulliger enough for being right by my side through the long field hours and frustrations, as well as the successes and field adventures. Additionally, I wouldn't be here without the work ethic my parents instilled in me and the continued support they have provided over the years. Thank you for all the continued support as I pursue a career in wildlife biology.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

Harvested species require well informed management that accounts for how demography and population dynamics are affected by changing ecological conditions (Brodie et al. 2013). In particular, survival and mortality rates are vital for understanding how wildlife population dynamics change over time (Caughley 1966, Raithel et al. 2007). It is generally known that the interplay between a high, relatively constant, adult female survival rate and a variable juvenile survival rate shapes the dynamics of ungulate populations (Rearden et al. 2011). In Rocky Mountain elk (*Cervus canadensis nelsoni*), variation in calf survival explained 75% of the variation of population growth rates (Raithel et al. 2007). This suggests that calf survival is much more sensitive to management than adult female survival and that calf survival is the most important predictor of overall population growth (Raithel et al. 2007, Harris et al. 2008). Additional studies on ungulates have found that the annual survival of young varied dramatically compared to that of adults (O'Gara et al. 1983, Singer et al. 1997, Gaillard et al. 1998, 2000, Buuveibaatar et al. 2013). Regardless of sources of mortality or study area location, variation in juvenile survival is common across species of ungulates (O'Gara et al. 1983, Singer et al. 1997, Gaillard et al. 1998, 2000, Buuveibaatar et al. 2013).

Factors Influencing Juvenile Summer Survival

The influence of maternal condition on neonate survival has been well documented in ungulate species. In Alaskan moose (*Alces gigas*), higher rump fat in adult females was associated with higher rates of pregnancy, and those females produced young with higher birth weights than females with lower rump fat (Keech et al. 2000). Similar results have been found in caribou (*Rangifer tarandus*) in Alaska (Adams 2005), white-tailed deer (*Odocoileus virginianus*) in Michigan (Duquette et al. 2014), mule deer (*Odocoileus hemionus*) in Washington (Johnstone-Yellin et al. 2009), pronghorn (*Antilocapra americana*) in Yellowstone National Park (Barnowe-Meyer et al. 2011), and elk throughout the western United States (Thorne et al. 1976, Smith et al. 1997)

Maternal condition and care are tightly tied to the forage quality and habitat available to reproductive females (Cook et al. 2004). Habitat plays an important role in the population dynamics of ungulates and can have a cascading effect on condition, reproduction, and survival (Shallow et al. 2015). Specifically, habitat with poor forage quality and concealment cover resulted in female mule deer in poor maternal condition, with lower growth rates, and survival of young (Shallow et al. 2015). Environmental stress is known to impact female condition in several different ways including increased age of sexual maturity, decreased natality rate, and increased adult mortality, but the most profound effect is on calf production and survival (Bender et al. 2002). Therefore, habitat quality is often reflected in juvenile production and the survival of juvenile ungulates (Bender et al. 2002).

Additionally, timing of birth can be influenced by maternal condition and is thought to be an important factor in calf survival and production. In elk, peak calving season typically occurs during early June, but it varies by year and location (Toweill and Thomas 2002). Timing of birth can be delayed if ovulation or breeding are delayed due to poor nutrition or for females supporting a calf from the previous year (Mitchell and Lincoln 1973, Toweill and Trainer 2002)

Several hypotheses exist to explain why synchronized birthing occurs each spring, but this can generally be ascribed to selection pressure exerted by top-down (predation) or bottom-up (nutrition) mortality factors. Regardless of the mechanism, it is known that calves born during the peak of the season have a higher probability of survival than that of calves born very early or very late (Clutton-Brock et al. 1982). This, however, has not been found consistently across studies. In areas with harsh winter weather conditions, early birth is thought to provide the calf with more time to grow and achieve a larger body size, which is known to result in higher winter survival (Thorne et al. 1976, Cederlund et al. 1991, Singer et al. 1997, Cook et al. 2004). Whereas, in areas where mild winter weather conditions exist, it isn’t clear how timing of birth affects survival, if at all.

Female condition is often reflected in the birth weight of their young and it is well understood that birth weight is a primary factor influencing summer survival (Clutton-Brock et al. 1982, Fairbanks 1993). Females in good nutritional condition will likely produce heavier calves (Parker et al. 2009) and thus increase the survival probability of their young. Average neonate birth weights of Rocky Mountain elk (*Cervus elaphus nelsoni*) range from 14 to 18 kg (Johnson 1951, Smith et a. 1997) with calves weighing less than 11.4 kg at birth being 50% more likely to die than their heavier counterparts (Thorne et al. 1976).

To a lesser extent, sex can have some influence on calf survival as well. Many studies find that male calves are consistently born heavier than their female counterparts (Loison et al. 1999, Harris 2006, Barber-Meyer et al. 2008, White et al. 2010), which may contribute to survival based on weight. Furthermore, sex-biased survival may arise from more maternal investment in male calves (Kohlmann 1999). However, the opposite was observed in northwestern Wyoming where neonatal female survival was higher than male survival (Smith and Anderson 1998). In that study, 90% of neonatal females survived from birth to July 15th compared with 74% neonatal male survival.

The density dependent effects on population size also appear to affect calf survival. Adult females compete for forage, lose weight, conceive later, and produce calves that are born later and lighter as an elk population increases beyond some optimal size (Clutton-Brock et al. 1982, 1987). This pattern was observed in red deer (*Cervus elaphus*) where later birth dates were correlated with an increasing population size and reduced winter survival (Clutton-Brock et al. 1987). Further evidence of a density dependent effect has been noted in western Wyoming where adult females experiencing greater than normal weight loss over the winter, aborted more often, or produced lighter weight calves with lower survival (Thorne et al. 1976). Finally, similar results were found in Yellowstone National Park where winter survival of elk calves was negatively correlated with population size (Singer et al. 1997).

Factors Influencing Juvenile Annual Survival

Beyond 14 weeks of life, juvenile survival is relatively stable until winter, where survival can be influenced by stochastic environmental conditions and the nutritional condition of calves. The effects of winter severity are well understood in places where snow accumulation and extreme temperatures can persist to cause high mortality in juveniles (Toweill and Thomas 2002). In fact, the effects of starvation are often most pronounced in juveniles due to their small body size, lower energy reserves, and susceptibility to cold temperatures (Toweill and Thomas 2002). Juvenile survival in areas with mild winters, however, is not as well understood. Little information exists on winter calf survival in areas where Roosevelt elk (*Cervus canadensis roosevelti*) exist, but one study on Vancouver Island suggested that as few as 30% of juveniles survived their first year even though winter conditions were mild (Janz and Becker 1986).

Juvenile survival over the course of the first year of life is important to wildlife managers because it ends with yearlings being recruited into adult age classes. Although adult females don’t typically breed until age two or older, survival beyond one year of life is relatively stable, and thus successful recruitment at one year represents a successful addition to the breeding class of the population (Gaillard et al. 2000). Thus, the number of juveniles per the number of adult females during early spring is an accepted method of estimating population recruitment.

Major Causes of Juvenile Mortality

Calves are prone to mortality throughout the first year of life, but most juvenile mortality occurs within the first few days after birth (Guinness et al. 1978, Clutton-Brock et al. 1982, Fairbanks 1993) and can range up to 40% (Whitten et al. 1992). Survival generally increases as calves age over the course of the summer (Barber-Meyer et al. 2008, Monteith et al 2014, Quintana 2016). During the first two days, calves are particularly prone to mortality due to low birth weight or viability problems. As the summer progresses, mortality is commonly caused by predation, stochastic weather events, disease, trauma-related events, or other natural events (Toweill and Thomas 2002).

Many studies have found predation to be a major cause of mortality in elk calves during the first 6 weeks of life throughout the western United States (Singer et al. 1997, Smith and Anderson 1998, Zager et al. 2002, Raithel et al. 2007, White et al. 2010, Griffin et al. 2011). In the greater Yellowstone ecosystem, where a complete predator system exists (coyotes, *Canis latrans,* wolves, *Canis lupus,* black bears, *Ursus americanus,* grizzly bears, *Ursus arctos*, and mountain lions, *Puma concolor*), 94% of all confirmed elk calf deaths were attributed to predators and black bears were a significant source of predation despite the presence of wolves (Barber-Meyer et al. 2008). Predation has also been observed to be highest on calves with the very earliest and very latest birthdates (Jarnemo 2004), which suggests that birth timing may be important in predator-rich environments (Rutberg 1987). Some studies, however, haven’t found predation to be a major source of mortality despite high densities of black bears and coyotes being present (DeVivo et al. 2011). Variation in summer calf survival is not due to a single factor, but rather, is a result of many complex interactions, such as maternal condition, predator abundance and density, and environmental conditions (Gaillard et al. 1998, 2000, Toweill and Thomas 2002, Parker et al. 2009, Rearden et al. 2011).

Major Causes of Adult Mortality

Once elk reach one year of age, the risk of mortality becomes less and most mortality is largely attributed to human-caused activities (e.g. hunting, roadkill), malnutrition, or senescence. Adult mortality is much more density dependent than juvenile mortality, where high mortality due to hunting results in decreased mortality due to malnutrition or senescence (Caughley 1966, 1966b). Thus, two major causes of adult mortality affect elk populations: 1) those in which hunting is the major cause of death and 2) those in which debilitation (e.g. disease, parasitism, malnutrition, old age) is the major cause of death (Toweill and Thomas 2002). In either case, human influence and environmental conditions strongly influence the rate of mortality.

In areas with high human influence, many negative effects have been documented in terms of direct mortality and calving success related to hunting pressures and road densities (McCorquodale 2013). Elk respond predictably to increased hunting pressure and traffic density by becoming more mobile and expending more energy to avoid people and roads (McCorquodale 2013). In addition, increased road density has been shown to increase the probability of mortality in cow elk, to decrease the ratio of bulls to cows, and to increase hunting harvest mortality when compared to relatively roadless areas (Leptich and Zager 1991, Unsworth et al. 1993, Leptich et al. 1995)

Human disturbance has an indirect effect on elk populations as well. Calving has been shown to be negatively affected by human disturbance. In several controlled field experiments, calf mortality risk increased in elk exposed to human disturbance during the calving season compared to those that were not (Phillips and Alldredge 2000). Elk exposed to human disturbance were 22% less likely to have a calf the following summer (Phillips and Alldredge 2000).

In northwestern California, calf survival and cause-specific mortality of Roosevelt elk haven't been fully studied. Many recent studies have documented the basic parameters of elk demographics that are easily observed in Redwood National and State Parks (Harper et al. 1997, Weckerly 1999, Wengert 2000, Julian et al. 2013, Weckerly et al. 2013, Redwood National and State Parks 2015, 2016) but data are limited, constrained to a relatively small spatial scale, and based on unmarked animals (C. K. Hilson, California Department of Fish and Wildlife [CDFW], pers. comm.). Data from these studies indicated that elk in certain groups may have higher calf to cow ratios compared to other areas of their geographic range (Weckerly 1999, Weckerly et al. 2013), but large areas of suitable habitat remain unoccupied and exact estimates of survival are unknown (C. K. Hilson, CDFW, unpublished data).

Factors influencing mortality are difficult to study, and little is known about the causes of mortality in northwestern California (Harper et al. 1997, Starns et al. 2014). One study in Boyes Prairie (Humboldt County, California) reported malnutrition and poaching to be the major sources of mortality for adult elk, but death from predation was unknown (Harper et al. 1967). Another study found that environmental variation had no significant effect on elk recruitment in Redwood National Park, suggesting that the mild Mediterranean environment of northwestern California is rarely a direct cause of mortality (Starns et al. 2014).

Despite these observations, it is known that elk in other parts of the western United States experience higher predation risks and nutritional stresses during the calving season (Smith and Anderson 1997, Zager et al. 2002, Barber-Meyer et al. 2008, Griffin et al. 2011, Eacker et al. 2016). Black bears have been found to predominately prey on calves in other parts of North America (Harris 2006, Barber-Meyer et al. 2008, Quintana 2016), but this had previously been unstudied in northwestern California. There was evidence that black bear densities in the area are high, as a previous study in Hoopa, California has demonstrated (Matthews et al. 2008). Black bear densities were estimated at 1.33 bears/km^2, which was thought to be high due to the effect of timber management on habitat and food-resource availability for that area (Matthews et al. 2008). Furthermore, statewide estimates of black bear populations have increased since 1982, and northern California provides some of the better bear habitat in the state (Garcia and Raymond 2018, California Department of Fish and Wildlife 1998).

Finally, a preliminary report identified U.S. Highway 101, a major highway running north and south through Del Norte and Humboldt counties, as an area with significant hotspots for vehicle-wildlife collisions (Shilling 2016). Specifically, 2-3 incidents occur per year at certain road segments around Orick, Crescent City, and Smith River, California (Shilling et al. 2018). These data, however, are limited to traffic incidents that are reported and fail to provide exact counts of vehicle collisions with elk. It is known that elk home ranges overlap major highways in Humboldt and Del Norte counties (C. K. Hilson, CDFW, unpublished data), but it isn’t clear if this represents a significant source of mortality.

Prior to this study, elk population dynamics in northwestern California were poorly understood. Populations were anecdotally thought to be increasing, but exact estimates of recruitment, calf survival, or major causes of mortality had never been fully studied. Furthermore, the increased human-wildlife conflict suggested populations might be growing and prompted the need for data to adequately manage elk. Additionally, this study presented an opportunity to study how mild winter conditions impact calf survival.

The main objective of this study was to estimate calf survival rates and determine the relative causes, timing, and factors that may affect calf survival and recruitment. Specifically, this 2-year study aimed 1) to estimate summer and annual survival rates and determine recruitment rates for Roosevelt elk calves in the area, 2) to evaluate differences in calf survival by examining the effects of individual and population level covariates on summer and annual calf survival, 3) to identify factors influencing the timing and cause of calf mortalities, and 4) to establish a baseline of mortality factors influencing elk across all age classes.

Due to the mild Mediterranean climate characteristics of northwestern California, calf survival and recruitment rates were expected to be high. I also expected calves with higher birth weight and early birthdates to have a higher probability of survival than calves with lower birth weight and later birthdates. Finally, due to high densities of predators and roads in this study area, I predicted predation and death due to human influences (i.e. roadkill, harvest, etc.) to be the major causes of mortality.

STUDY AREA

This study was conducted in two areas in Del Norte and Humboldt counties. The two areas are denoted as Del Norte and Humboldt for the purposes of this thesis (Figure 1). The Del Norte study area is bounded to the north by the Oregon border (124°7'57.397"W 41°59'46.799"N), extends as far east as the Six Rivers National Forest boundary (124°3'8.629"W 41°56'34.258"N), and extends south to the southern boundary of Del Norte Coast Redwoods State Park (123°59'41.63"W 41°38'33.097"N). The Humboldt area begins at the north boundary of the Humboldt county line (124°0'31.121"W 41°28'11.244"N), extends to the eastern boundary of private timber company property (123°46'45.013"W 41°11'52.221"N), and ranges south to Highway 299 (123°56'40.007"W 40°53'0.231"N). The Pacific Ocean borders the western edge of both Del Norte and Humboldt study areas (Figure 1).

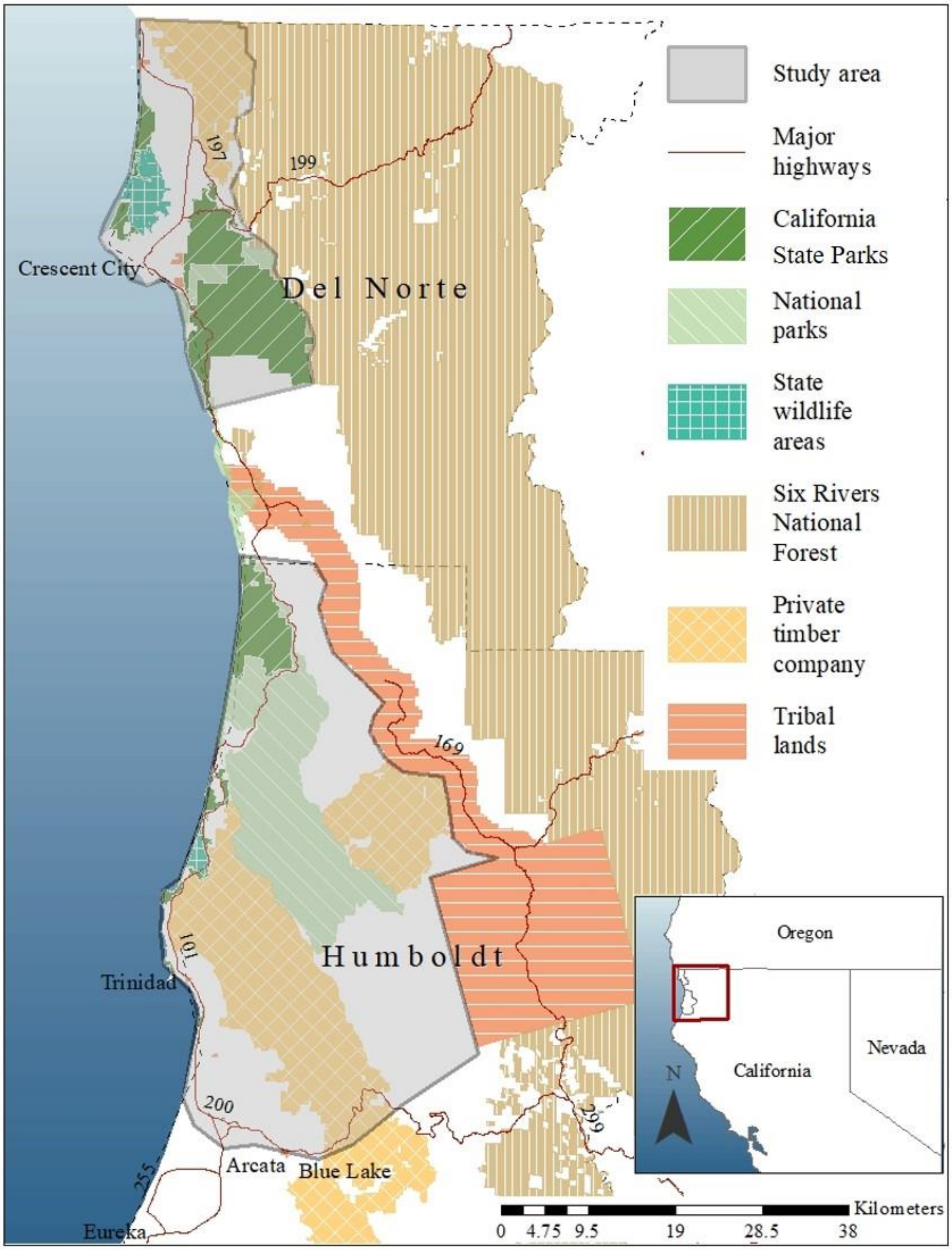

Figure 1. Study areas of Roosevelt elk (*C. canadensis roosevelti*) calf recruitment study and major land ownership in Humboldt and Del Norte counties, CA, USA, 2017-2018.

These areas encompass ranges where several groups of elk have been observed historically and recently recorded with road surveys (C. K. Hilson, California Department of Fish and Wildlife, unpublished data). Fourteen distinct groups of elk were identified and marked in these study areas and I defined a group of elk as animals that stayed separate from other known groups of elk throughout the entire 2-year study. One large group of elk (Bald Hills) exists in the Humboldt study area and mainly inhabits the Bald Hills area of Redwood National Park (RNP); another large group of elk (Tolowa) exists in and around Tolowa Dunes State Park (TDSP) in the Del Norte study area; and the rest are smaller groups that exist throughout both study areas within 30 km of the coast.

The Bald Hills group exists in open, grasslands and coastal oak woodlands dominated by tanoak (*Notholithocarpus densiflorus*), California black oak (*Quercus kelloggii*), California oat grass (*Danthonia californica*), and Idaho fescue (*Festuca idahoensis*) (Munz and Keck 1950, Ford and Hayes 2007). Land in this area is largely owned by RNP, which manages the land to provide public enjoyment, scientific study, and to preserve coastal redwood forests, streams, prairies, and woodlands (Redwood National and State Parks 2000). Adjacent land is primarily owned by a large private timber company and other private landowners.

The Tolowa group exists in coastal dune habitat that contains open beach, nearshore dunes, dune swales, and forested backdunes (Barbour et al. 2007). The forested backdunes are dominated by Sitka spruce (*Picea sitchensis*) and shore pine (*Pinus contorta contorta*) (Barbour et al. 2007). The meadows of TDSP contain native and non-native grasses (family *Poaceae*), sedges (*Carex sp.*), and rushes (*Juncus sp.*). This area is managed by California State Parks, while the agricultural fields bordering TDSP are privately owned and managed for beef and dairy cattle (Barbour et al. 2007).

All the other groups of elk in both study areas exist in coastal coniferous rainforests dominated by coast redwoods (*Sequoia sempervirens*), Douglas-fir (*Pseudotsuga menziesii*), and Sitka spruce (*Picea sitchensis)* (Waring and Franklin 1979, Harper et al. 1997, Ford and Hayes 2007). Major understory species include sword ferns (*Polystichum munitum*), lady ferns (*Athyrium felix-femina*), *Rubus* spp. and a mixture of grasses and forbs. Major property ownership in the study areas includes large dairy operations, tribal entities, private timber companies, residential properties, Redwood National Park, and California State Parks.

Elevation in the study areas ranges from sea level to approximately 700 m in the Bald Hills area. The climate of the area is characterized by mild, dry summers and cool, wet winters (Waring and Franklin 1979, Harper et al. 1997, Weckerly and Ricca 2000). Annual precipitation in the area averages 168 cm (National Oceanic and Atmospheric Administration, 2018). Snow is not common, with winter temperatures rarely dropping below freezing, but does occur in some parts of the study area at higher elevations (Harper et al. 1997, Weckerly and Ricca 2000). Average temperatures in the area range from 6.5° C in the winter to 14.7° C in the summer (National Oceanic and Atmospheric Administration, 2018).

Potential predators and scavengers in the area include mountain lions, black bears, coyotes, bobcats (*Lynx rufus*), golden eagles (*Aquila chrysaetos*), bald eagles (*Haliaeetus leucocephalus*), turkey vultures (*Cathartes aura*), and domestic dogs (*Canis lupus* *familiaris*) (Howell et al. 2002). Additionally, many groups of elk exist in close proximity to U.S. Highway 101, U.S. Highway 299, and Bald Hills Road, which represented an important source of mortality.

Elk are managed to provide quality viewing and hunting experiences by the California Department of Fish and Wildlife (CDFW). Hunting for elk currently occurs through CDFW's public drawing, the Private Lands Management (PLM) program, tribal harvest, cooperative elk hunting, and the Shared Habitat Alliance for Recreational Enhancement (SHARE) program (California Department of Fish and Wildlife, 2018). The SHARE program allows for elk harvest on private lands through fee-based access while the PLM program encourages landowners to protect wildlife habitat through incentives like extended hunt seasons. Both programs promote access to private land for increases hunting opportunities, while the public draw allows for hunting on certain public lands (California Department of Fish and Wildlife, 2018). In addition, illegal hunting is known to occur throughout both study areas (J. Hobbs, CDFW, pers. comm.).

Human use of the area is mixed and varies with property ownership (Weckerly and Ricca 2000). Outdoor recreation, hunting, fishing, dairy operations, general agriculture, and timber harvest are some of the major human activities.

MATERIALS AND METHODS

Marking, Monitoring, and Mortality Investigations

Capture

For the purposes of this study, animals less than 1 year of age were defined as calves or juveniles, while elk older than one year were considered adults. I further defined yearlings for the mortality portion of my study as animals aged 1-2 years old. As part of a parallel study of Roosevelt elk in northwestern California with CDFW, 28 cow elk were darted using a Pneu-Dart compression rifle (Pneu-Dart Inc., Williamsport, PA) and 2 mL Pneu-dart disposable darts containing butorphanol tartrate (0.20 mg/kg), azaperone tartrate, (0.07 mg/kg) and metatomidine HCl (0.08 mg/kg) (BAM). Each female was fitted with a global positioning system (GPS) collar (Iridium Track M TRD, Lotek Wireless, Inc., Newmarket, Ontario, Canada) and a vaginal implant transmitter (VIT; VIT-P, Lotek Wireless, Inc., Newmarket, Ontario, Canada) after pregnancy was confirmed by ultrasound. The following spring, I used GPS clustered points from collared females, VIT birth alerts, and observations of solitary cows to search for and capture calves.

Calves were captured by hand, physically restrained, and blindfolded during processing. Capture and handling protocols were reviewed and approved by a CDFW veterinarian and by the Institutional Animal Care and Use Committee for Humboldt State University (15\16.W.96-A, approved 12/21/2016). I attempted to minimize stress, scent transfer, and risk of abandonment by limiting handling time to less than 10 minutes and using disposable gloves while handling calves.

I recorded sex, right hind-leg length, girth, body length, overall body condition, incisor eruption pattern, navel diameter and condition, hoof hardness and raggedness, hairline to hoof indentation length, and assessed stability and stature similar to other studies (Johnson 1951, Sarns et al. 1996). Each calf was also weighed using a hanging weigh scale and weigh bag. Estimated age at capture was determined by using these morphological measurements, along with the known birth dates from calves captured via VIT, to model age using a variable selection bootstrap method (J. Berg, University of Alberta, unpublished data).

I regressed calf capture weight on estimated age at capture and used the estimated regression coefficients by sex to predict birth weight (Smith et al. 1997). Birth date was estimated by subtracting the estimated age in days from the capture date. Birth dates were formatted using standardized Julian days across capture years and the deviation from the median birth date was calculated by subtracting the estimated birth date from the median birth date of both capture years (Smith et al. 1997).

Calf tags

Each calf was marked with a uniquely numbered 22g ear-tag VHF transmitter (TW5, Lotek Wireless, Inc., Newmarket, Ontario, Canada) designed to transmit a radio signal from the capture date until 15-May the following year. The pulse rate on the tags changed to provide a “mortality signal” if it remained motionless for >6 hours.

Monitoring the signal allowed me to determine weekly survival without visualizing the animal.

Radio telemetry

For the first 6 weeks after capture, radio transmitter frequencies of ear-tagged calves were monitored daily from the ground with a portable receiver (Model R-1000, Communications Specialist, Inc., Orange, CA) and a hand-held three-element Yagi antenna (Model 13906, Advanced Telemetry Systems, Isanti, MN), or an omni directional vehicle-mounted antenna (Model RA-5A, Telonics, Inc., Mesa, AZ). Calves were monitored 2-3 times per week thereafter until the following May. Opportunistic composition counts of elk groups were recorded any time animals could be located visually.

Calf status (dead, alive, or unknown fate) was determined whenever calves were monitored and signals were geo-referenced with a GPS handheld device (Model Rino 750, Garmin Ltd., Olathe, KS). An unknown fate was determined when a calf could no longer be monitored due to failure of the VHF, the animal losing the tag, or failure to locate the tag due to logistical issues in the field. Tag failures or losses were determined by investigating the site and finding no carcass or evidence of mortality.

Mortality investigations

When a mortality signal was detected, I attempted to investigate the site within 24 hours to conduct a field necropsy, collect samples, and document the mortality with photographs. In addition, mortality investigations were conducted for collared cows and opportunistically-found animals reported within 1-2 days of death. Each mortality site was searched for signs of predation, which could include tracks, carnivore scat and/or hair samples, or signs of struggle (O’Gara et al. 1983, Smith and Anderson 1998). Each carcass was examined for puncture wounds by canines, bite marks, claw marks, chewed bones, broken bones, or other patterns suggesting carnivore killing bites or consumption. In addition to this, major tissues and long bone midsections were collected from the carcass to test for other sources of mortality when available; carnivore hair, swabs of bite marks, or scat samples were used for predator identification, tissue samples were used to clinically diagnose disease and/or confirm other sources of mortality, and bone midsections were used to assess the nutritional condition of emaciated or starving animals (Cheatum 1949, Husseman et al. 2003, Braun 2005).

A proximate cause of death was determined based on the collective evidence of a mortality investigation. Causes of death were combined into categories as follows: predation, nutritional, natural-disease, natural-trauma, human-related, or unknown. Predation was classified as the cause of death when hemorrhaging was present, or scat or swab samples confirmed identification of predators. Swabs, hair, or scat from predators were collected at the mortality sites when available, and carnivore species were identified using DNA by sending samples to the California Department of Fish and Wildlife, Wildlife Forensics Laboratory, Sacramento, California. Nutritional issues such as malnutrition was determined to be cause of death when no sign of predation, nearly empty or empty stomachs, gelatinous and red femur marrow, absent kidney fat, and no abnormalities associated with disease was observed. Natural-disease was concluded as the proximate cause of death when histopathologic results confirmed presence of abnormalities associated with disease. All calves were classified as live, dead, or censored on 15 May the year following capture.

Survival, Recruitment, and Mortality Analysis

Summer calf survival

Most mortalities of calves occur during the first several weeks of life (Barber-Meyer et al. 2008, White et al. 2010). Therefore, summer survival (the first 14 weeks) was modeled to identify how time and covariates that would influence calf survival through summer. I developed a set of variables that I predicted would influence summer calf survival including the variable effect of time, the linear trend of time, year, study area, sex, estimated birth weight, and deviation from median birth date. Calves were censored from the summer survival analysis when transmitters failed prior to 14 weeks of age. The R (R Development Core Team 2018) package RMark (Laake 2013) was used to construct and compare known-fate models in program MARK (White and Burnham 1999, Cooch and White 2016).

Models were developed in two stages. First, models were built without covariates to assess the effect of time on survival. During summer, calves experience and transition through different life stages: concealment, inexperienced runners, and nursery group members (Barber-Meyer et al. 2008). Stage 1 of the analysis compared models that considered these different, time-varying models. For example, during the first two weeks of life calves may be relatively immobile, progress to being more mobile but not agile during the third and fourth weeks of life, and finally advance to being able to keep up with adults after five weeks of age (Table 1, Model 9). The top time-varying model from stage 1 was used during the second stage of this analysis (Monteith et al. 2014, Quintana 2016).

Table 1. A priori known-fate models developed to determine whether summer survival (first 14 weeks) varied with time for Roosevelt elk (*C. canadensis roosevelti*) calves captured during 2017-2018 in Del Norte and Humboldt counties, California, USA. The number of estimable parameters is represented by K.

	Model	K	Description
1.	$S_{(.)}$	2	Null model
2.	$S_{(time)}$	14	Survival varies each week for 14 weeks
3.	$S_{(LT)}$	2	Survival has a linear trend over time
4.	$S_{(1,2,3,4,5\text{-}14wk)}$	6	Survival varies during weeks 1,2,3,4 and is constant weeks 5-14
5.	$S_{(1,2,3,4\text{-}14wk)}$	5	Survival varies during weeks 1,2,3 and is constant weeks 4-14
6.	$S_{(1\text{-}3,4,5\text{-}14wk)}$	4	Survival is constant weeks 1-3, varies week 4, and constant 5-14
7.	$S_{(1\text{-}4,5\text{-}14wk)}$	3	Survival is constant weeks 1-4, and constant weeks 5-14
8.	$S_{(1\text{-}3,4\text{-}14wk)}$	3	Survival is constant weeks 1-3, and constant weeks 4-14
9.	$S_{(1\text{-}2,3\text{-}4,5\text{-}14wk)}$	4	Survival is constant weeks 1-2, 3-4, and 5-14

For the second stage of this analysis, the top model from stage 1 was used. The covariates of sex, year, study area, estimated birth weight, and deviation from median birth date were used to evaluate the effect of individual covariates on survival (Table 2). Covariates considered variables that included an additive effect (year + birth weight) or an interactive effect (year * birth weight) (Table 2). An additional model relating the linear trend of time, study area, and deviation from median birth date was included post hoc (Table 2; model 15). Combinations of predictor variables with a correlation coefficient > 0.6 were excluded from the models.

Table 2. A priori known-fate models used to determine if Roosevelt elk (*C. canadensis roosevelti*) summer calf survival (first 14 weeks) was influenced by sex, birth weight (weight), birth date (MBD), linear trend of time (LT), study area (SA), or sampling year (2017/2018, 2018/2019) in Del Norte and Humboldt counties, California, USA. The number of estimable parameters is represented by K.

	Model	K	Description
1.	$S_{(.)}$	1	Null model
2.	$S_{(sex)}$	5	Survival differs between sexes
3.	$S_{(weight)}$	5	Survival is influenced by birth weight
4.	$S_{(year)}$	5	Survival differs between sampling years
5.	$S_{(MBD)}$	2	Survival is influenced by birth date
6.	$S_{(SA)}$	2	Survival differs between the Humboldt and Del Norte study area
7.	$S_{(LT)}$	2	Survival is influenced by the linear trend of time
8.	$S_{(LT +sex)}$	3	Survival is influenced by linear trend of time and differs by sex
9.	$S_{(LT +year)}$	3	Survival is influenced by linear trend of time and differs by year
10.	$S_{(sex*weight)}$	4	Survival is influenced by sex which varies with birth weight
11.	$S_{(year + MBD)}$	3	Survival is influenced by sampling year and birth date
12.	$S_{(year + weight)}$	3	Survival is influenced by sampling year and birth weight
13.	$S_{(year*weight)}$	4	Survival is influenced by sampling year which varies with birth weight
14.	$S_{(LT + SA + weight)}$	4	Survival is influenced by linear trend of time, birth weight and differs by study area
15.	$S_{(LT + SA + MBD)}$	4	Survival is influenced by linear trend of time, birth date and differs by study area
16.	$S_{(LT + SA)}$	3	Survival is influenced by linear trend of time and differs by study area
17.	$S_{(LT + weight)}$	3	Survival is influenced by linear trend of time and birth weight
18.	$S_{(LT +MBD)}$	3	Survival is influenced by linear trend of time and birth date
19.	$S_{(weight + MBD)}$	3	Survival is influenced by birth weight and birth date

Annual calf survival

During this study, tag failures, restricted access to private property, and mountainous terrain prevented the data for annual calf survival from meeting all the assumptions of a known-fate model. Specifically, these data failed to meet the assumption that detection probability (p) was always equal to 1 and that all fates (dead or alive) were known (White and Garrott 1990). Therefore, I used the flexibility of multistate models as described in Devineau et al. (2014) to estimate annual survival. For this portion of my analysis, I combined weekly intervals into 12 monthly intervals and estimated survival for each month, season, and the entire year.

Three parameters are provided by multistate models: the probability of transition (ψ), survival (S), and the probability of detection (p). Additionally, three states were used to model the known fate data in a multistate framework (Devineau et al. 2014). A calf could be detected as alive (state A), be detected as newly dead (state D), or be detected as dead (state d) (Devineau et al. 2014). Newly dead individuals were defined as found dead in the same monthly interval that an individual died with the exact time interval of death known, while dead individuals died at least one-month previous and the exact time interval of death was not known. (Devineau et al. 2014). The latter dead state (d) was generally unobservable, but an animal in the newly dead state automatically transitioned to the dead state in the next time interval (Devineau et al. 2014).

Since modeling death as a state leads to modeling mortality as a transition state, the transition from alive to newly dead in these models is constrained to equal 1.

Therefore, this equation, $\psi^{AA} + \psi^{AD} = 1$, can be rearranged to estimate the monthly probability of survival ($\hat{\psi}^{AA}$) (Devineau et al. 2014).

I developed these models in two steps: first I evaluated whether detection probability differed significantly between sampling year, study area, or state (alive, newly dead, or dead) (Table 3). These models were compared using Akaike's Information Criterion corrected for small sample size (AIC_c) and I used the top model in this set to specify a second set of models to test biological hypotheses (Table 4).

Table 3. A priori multistate models used to determine if the probability of Roosevelt elk (*C. canadensis roosevelti*) calf detection (p) differed by sampling year (2017/2018, 2018/2019), study area (SA), or state (dead or alive) in Humboldt and Del Norte counties, California, USA. Number of estimable parameters is represented by K.

	Model	K	Description
1.	ψ(.)p(.)	3	Null model
2.	ψ (.)p(state)	4	Survival is constant, detection probability varies by state
3.	ψ (.)p(year)	4	Survival is constant, detection probability varies by year
4.	ψ (.)p(SA)	4	Survival is constant, detection probability varies by study area

Table 4. Multistate models used to estimate annual survival of Roosevelt elk (*C. canadensis roosevelti*) calves captured in northwestern California in 2017 and 2018. The transition probability (Ψ) from alive to dead (A to D) was used to estimate survival and examine the effects of sex, sampling year (2017/2018, 2018/2019), study area (SA), birth weight (weight), deviation from median birth date (MBD), average monthly precipitation in mm (precip), minimum monthly temperature in C^{o} (temp), the variable effect of time, the linear trend of time (LT), and the null model.

	Model	K	Description
1.	Ψ(.)p(year)	4	Null model
2.	Ψ(sex)p(year)	5	Mortality transition varies by sex
3.	Ψ(weight)p(year)	5	Mortality transition varies by birth weight
4.	Ψ(precip)p(year)	5	Mortality transition varies by the monthly mean precipitation
5.	Ψ(temp)p(year)	5	Mortality transition varies by monthly minimum temperature
6.	Ψ(time)p(year)	15	Mortality transition varies by month
7.	Ψ(LT)p(year)	5	Mortality transition varies by linear trend of time
8.	Ψ(year)p(year)	5	Mortality transition varies by year
9.	Ψ(SA)p(year)	5	Mortality transition varies by study area
10.	Ψ(MBD)p(year)	4	Mortality transition varies by birth date
11.	Ψ(weight+temp)p(year)	6	Mortality transition varies by weight and monthly minimum temperature
12.	Ψ(weight+sex)p(year)	6	Mortality transition varies by weight and sex
13.	Ψ(weight+time)p(year)	16	Mortality transition varies by weight and time

In the second set of models, survival was examined by looking at the mortality transition probability $(1 - \psi^{AD})$ with the individual covariates of year, sex, study area, deviation from median birth date, and birth weight (Table 4). I included the effect of time (time) as it varied over 12 months and the linear trend of time, where survival estimates are constrained to follow a linear trend over 12 months (Table 4). I also considered the effect of environmental variables on annual survival by including average monthly precipitation and monthly minimum temperature (Table 4). I extracted values of precipitation and temperature for each group of elk by using data from spatial climate models (PRISM Climate Group, Oregon State University, www.prism.oregonstate.edu, accessed 30 April 2019). I used the mean monthly estimates of precipitation (mm of rain) and minimum temperature (^{o}C) from GPS points at the center of each group's location. To properly compare covariates, I standardized all continuous covariates by subtracting their means and dividing by their standard deviations.

For both the summer and annual survival analysis, Akaike's Information Criterion corrected for small sample sizes (AIC_c) was used to compare and select the top models (Burnham and Anderson 1999). When Δ AIC_c was less than 2 and multiple models had similar AIC_C weights, I model averaged results to account for model uncertainty. The derived overall survival estimate for summer (14 weeks) and annual (12 months) was calculated by taking the product of the cumulative probability across all sampling intervals (e.g. weeks for summer estimates and months for yearly estimates) from the top model when there was no model uncertainty or from the model-averaged results (Cooch and White 2016). The Delta method was used to calculate the standard error for each overall survival estimate (Cooch and White 2016).

Recruitment

Traditionally, managers conduct aerial surveys to monitor trends in ungulate populations and to estimate calf recruitment (Rabe et al. 2002). In northwestern California, this survey technique is unfeasible due to dense vegetation and steep terrain. Therefore, road surveys were conducted by CDFW personnel starting in 2016 (C. K. Hilson, CDFW, unpublished data). These surveys were conducted over the entire study area where groups of elk with at least one marked cow or calf existed and elk were classified as adult males (branched antlers), spikes (unbranched antlers), adult females, or calves. For this portion of the study, adults included elk that were > 1 year while calves encompassed animals less than 1 year old.

Recruitment was estimated with these data by documenting calf to cow age ratios: the index of calf recruitment is represented as a ratio of the number of calves per 100 adult females. The road surveys were conducted throughout the year, but I limited data for this study to surveys conducted during late winter and early spring when calves were 9 to 11 months old and likely to be recruited into the population. The estimate of recruitment was used in conjunction with the equation developed by Hatter and Bergerud (1991) to estimate population growth rate of elk. The recruitment-mortality method (R/M equation) can retroactively estimate population growth rate (λ), mortality (M) or survival (S), and recruitment (R) for a given year when 2 of the 3 parameters are known (Hatter and Bergerud 1991).

Equation 1

$$\lambda = \frac{(1-\mathrm{M})}{(1-\mathrm{R})} = \frac{\mathrm{S}}{(1-\mathrm{R})}$$

This model is designed to use adult female survival estimates obtained from radio marked animals and recruitment estimates from age ratio data collected at the end of a biological year (Hatter and Bergerud 1991). Therefore, I used calf to cow ratios and annual survival of adult females to estimate lambda (λ) of elk in this study areas.

Adult female survival rates $S_a(t)$ for 2017 and 2018 were estimated using the known-fate models in Program MARK (White and Burnham 1999). I estimated age ratios, X, by taking the number of calves, n_j, per adult female, n_{af}, observed at the end of the biological year from the road survey data. To avoid overestimates of recruitment, X was divided by 2 to account for a 50:50 sex ratio of calves as described by Hatter and Bergerud (1991). A 2-sample z test was used to compare recruitment between years (Kanji 2006).

Mortality

Because calves are exposed to many factors influencing mortality during the first year of life and risk varies over time, mortality risk was evaluated over time with a cumulative incidence function (CIF). Cumulative incidence functions are used for time-to-event data where an individual is exposed to two or more causes of mortality, but the eventual mortality can be attributed to only one cause. In this case, for example, the occurrence of one event (predation mortality) hinders the occurrence of any other event (non-predation mortality) (Gray 1988, Scrucca et al. 2007). Calves were stratified into three categories (early, peak, and late) based upon the 33% and 66% quantiles of birth date. I estimated CIFs for early, peak, and late-born calves at biologically meaningful time intervals: 2 weeks, summer (14 weeks), and annual (52 weeks). The R (R Development Core Team 2018) package cmprsk (Gray 2019) was used to estimate CIFs and evaluate competing risks.

RESULTS

Cow Captures, Vaginal Implant Transmitters, and Calf Captures

During 2017 and 2018, 28 adult female elk were captured via free range darting from 14 distinct groups and 21 VITs were inserted during the two winter capture seasons (2017 = 18, 2018 = 3). A large proportion of VITs either deployed properly (0.38, *n* = 8) or never gave an alert prior to, during, or after calving (0.38, *n* = 8). The rest of the VITs failed prior to calving season (0.24, *n* = 5). The VIT birth alerts during calving season ranged from 11 May to 11 June 2017. No birth alerts were detected in 2018 during the calving season.

Twenty-one calves (10M, 11F) were caught between 20 May and 19 June 2017, and 37 calves (19M, 18F) were caught between 20 May and 25 June 2018. Handling times varied from 5 to 20 minutes with a mean time of 12.62 minutes. During both years, similar numbers of each sex were caught, with 29 males and 29 females being captured overall (Table 5). More calves were caught in the Humboldt study area (*n* = 40) than in the Del Norte study area (*n* =18) (Table 5). Most calves were captured opportunistically (45 out of 58) by searching the study area for lone cows. The rest were caught by using GPS clustered points from collared cows (0.10, *n* = 6) or by birth alerts from VITs (0.12, *n* = 7). Not every birth alert resulted in a calf capture, however, because property access limited the success of one.

Table 5. Roosevelt elk (*C. canadensis roosevelti*) calves captured during 2017 and 2018 in northwestern California, USA. Data are presented by year, number of calves captured by study area, number of calves censored at the end of one year, median birth date, and mean birth weight (kg).

	2017	2018	Overall
Number of calves captured			
Humboldt	12 (3M[a], 9F[b])	28 (17M, 11F)	40 (20M, 20F)
Del Norte	9 (7M, 2F)	9 (2M, 7F)	18 (9M, 9F)
Number calves censored[c]	8	7	15
Median birth date	27 May	29 May	29 May
Mean birth weight (SE)	17.22 (0.78)	18.64 (0.60)	18.13 (0.48)

[a] Males

[b] Females

[c] Calves were censored because their fates could not be determined due to tag loss/failure or limited property access.

I estimated birth weights for 57 calves and used the mean birth weight by sex ($\bar{x}$ = 16.67 kg) for one female calf that did not have weight measured at capture (Table 5). The mean estimated birth weight was 18.13 kg and was significantly different by sex (males = 19.58 kg, females = 16.67 kg, $F_{1,58}$ = 10.825, P = 0.0017), but was not significantly different by study area (Humboldt = 17.99 kg, Del Norte = 18.42 kg, $F_{1,58}$ = 0.200, P = 0.656) or year (2017 = 17.22 kg, 2018 = 18.64 kg, $F_{1,58}$ = 2.368, P = 0.129). In addition, male calves had higher growth rates than females (Figure 2), but there was no significant influence of the interaction of sex and age at capture in my prediction model of growth rate (β = 0.002, SE = 1.43, P = 0.99).

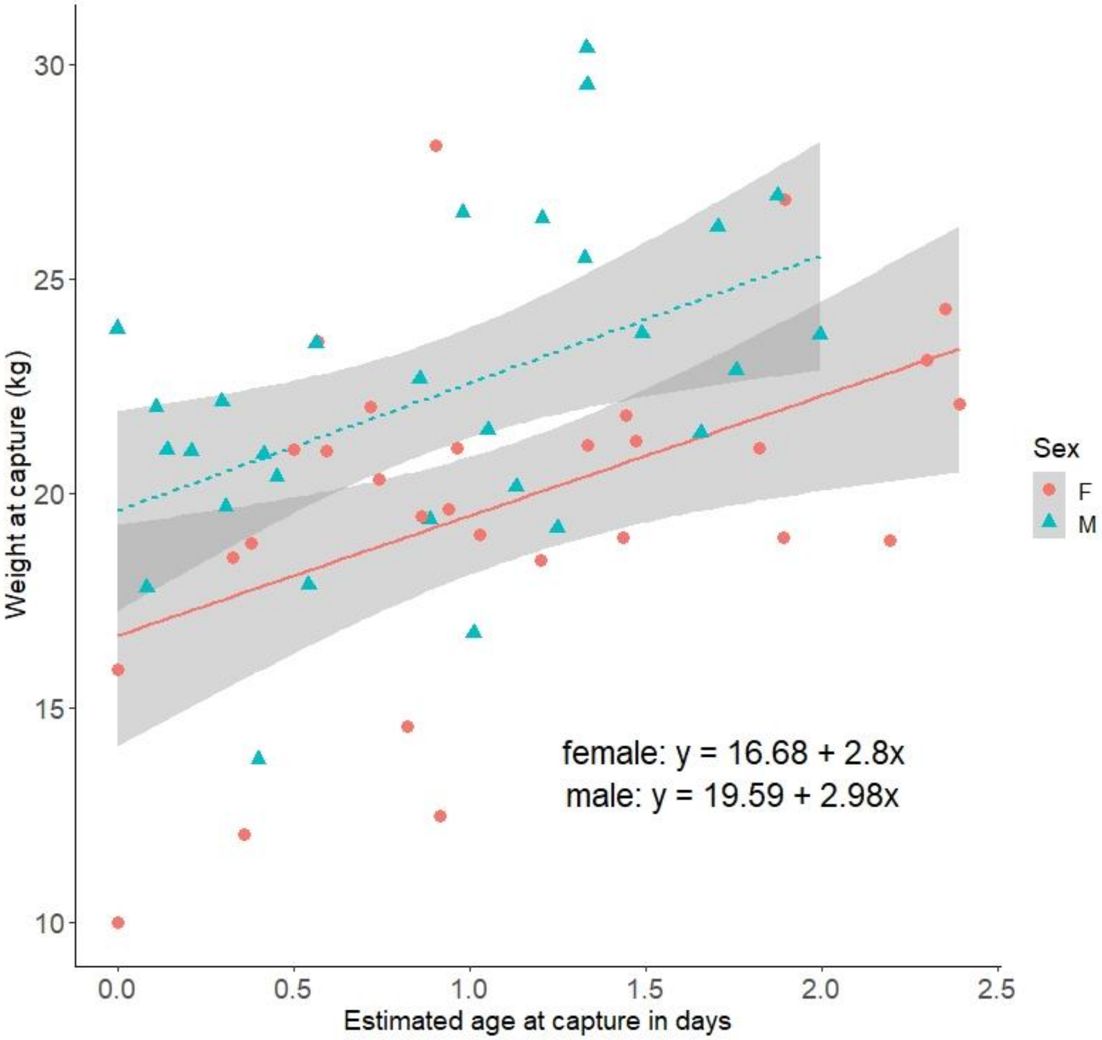

Figure 2. Weight at capture (kg) as a function of estimated age at capture (days) regressed by sex in Roosevelt elk (*C. canadensis roosevelti*) calves captured in 2017 and 2018 in Humboldt and Del Norte counties, California, USA.

Calves were captured at a mean age of one (SD = 0.09) day (range: 0-2.39) and age at capture was estimated using morphological measurements (J. E. Berg, University of Alberta, unpublished data). Estimated age at capture did not vary significantly by sex, year, or study area and no significant influence of any interaction among these variables was found. Estimated birth dates ranged from 19 May to 23 June (median = 29 May). In a 3-way ANOVA explaining standardized Julian birth dates, there were no significant interactions among sex, year, or study area. The estimate of birth date did not vary by sex ($F_{1,58} = 0.74$, $P = 0.39$) or year, ($F_{1,58} = 0.46$, $P = 0.50$) but did vary significantly by study area ($F_{1,58} = 5.99$, $P = 0.02$). Mean birth dates were significantly earlier in the Humboldt study area (28 May) than in the Del Norte study area (3 June).

Survival, Recruitment, and Mortality

Summer survival

The proportion of calves that survived during the first 14 weeks of life was far greater in the Del Norte study area (1.00, 17 out of 17) than in the Humboldt study area (0.66, 25 out of 38). Thirteen calves died within the first 14 weeks and 3 calves were censored due to tag loss or failure prior to 14 weeks of age. In order to prevent the estimates of summer survival from being biased high, I removed the censored calves from my dataset (White and Burnham 1999).

To explain weekly calf survival through 14 weeks of age, I first compared different time-dependent models without covariates. The top ranked model suggested that there was a linear trend in survival over time and survival linearly increased over time. Survival was lowest during week 1 (0.87, SE = 0.049) and increased asymptotically until week 14 (0.99, SE = 0.001).

There was some model uncertainly as all top four models had delta AIC_c values less than 2 and similar AIC_c weights (Table 6). Therefore, I used model averaged results to estimate summer survival. The model averaged estimate suggested that summer survival started at 0.89 during week 1 (SE = 0.048), increased from 0.90 in week 2 (SE = 0.041) to 0.95 in week 4 (SE = 0.027), then increased slightly from week 5 (0.99, SE = 0.012) to week 14 (0.99, SE = 0.004) (Figure 3). The cumulative probability of summer survival over all 14 weeks from the model averaged results was 0.67 (SE = 0.009).

Table 6. Model selection of Roosevelt elk (*C. canadensis roosevelti*) calf summer (first 14 weeks) survival probabilities as a function of time varying by different weeks, the full time-varying model (time), the linear trend of time (LT), and the null model (.) for calves captured in Humboldt and Del Norte counties, California, USA during 2017 and 2018. K is the number of estimable parameters.

Model	K	AIC_c	ΔAIC_c	AIC_c Weights	Deviance
1. $S_{(LT)}$	2	106.19	0.00	0.32	9.26
2. $S_{(1-2,3-4,5-14wk)}$	4	107.17	0.98	0.20	6.18
3. $S_{(1-3,4-14wk)}$	3	107.38	1.19	0.18	8.42
4. $S_{(1-4,5-14wk)}$	3	107.96	1.77	0.13	9.00
5. $S_{(1-3,4,5-14wk)}$	4	109.00	2.80	0.08	8.01
6. $S_{(1,2,3,4-14wk)}$	5	109.40	3.21	0.06	6.38
7. $S_{(1,2,3,4,5-14wk)}$	6	111.03	4.84	0.03	5.96
8. $S_{(time)}$	14	121.68	15.49	0.00	0.00
9. $S_{(.)}$	2	127.74	21.55	0.00	30.80

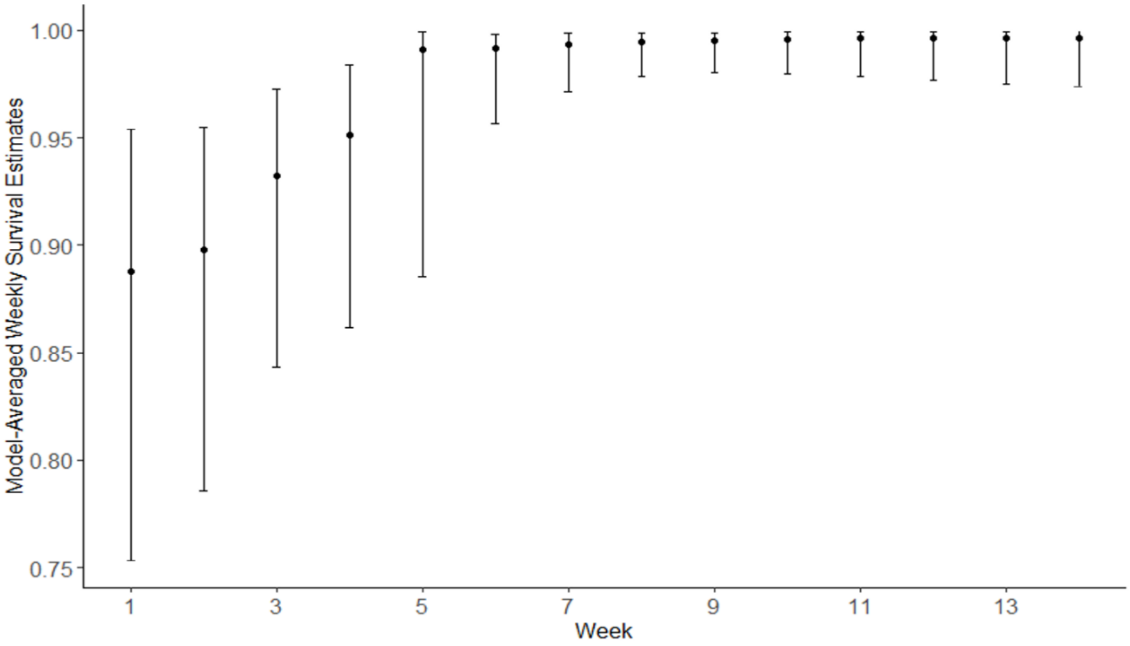

Figure 3. Model averaged weekly estimates of summer survival (first 14 weeks) and 95% confidence intervals for Roosevelt elk (*C. canadensis roosevelti*) calves captured in Humboldt and Del Norte counties, California, USA during 2017-2018.

To evaluate the effect of individual covariates on survival, I developed a set of models that included study area, sex, sampling year, estimated birth weight, and deviation from median birth date. Study area, sex, birth weight, sampling year, and deviation from birth date covariates were added to the top ranked time model from the first part of the summer survival analysis (Table 6). Ranked models of summer survival did not suggest that sampling year or sex were important to predicting summer survival (Table 7). The top ranked model included a weekly time trend and the effect of study area and estimated birth weight on summer survival (Table 7). This model had the lowest AIC_c score, had a Δ AIC_c less than 2, and carried over half the AIC_C weight. However, the second top model also had a Δ AIC_c less than 2, indicating some model uncertainty. Among all the covariates, study area was the most important covariate, along with birth weight. The model, $S_{(LT+SA+MBD)}$, including study area and birth date also ranked high, but it didn't explain these data better than the top model including birth mass (Table 7).

Table 7. Model selection table of Roosevelt elk (*C. canadensis roosevelti*) calf summer survival as a function of individual covariates including: study area (SA), estimated birth weight (weight), sex, sampling year (2017/2018, 2018/2019), deviation from median birth date (MBD), linear trend of time (LT), and the null model (.) for calves captured in Humboldt and Del Norte counties, California, USA. K is the number of estimable parameters.

	Model	K	AIC_c	ΔAIC_c	Weight	Deviance
1.	$S_{(LT + SA + weight)}$	4	96.90	0.00	0.66	88.82
2.	$S_{(LT + SA)}$	3	98.42	1.52	0.31	27.89
3.	$S_{(LT + SA + MBD)}$	4	98.97	2.07	0.19	90.89
4.	$S_{(LT + weight)}$	3	103.82	6.92	0.02	97.78
5.	$S_{(LT)}$	2	106.19	9.30	0.00	9.26
6.	$S_{(LT + sex)}$	3	107.38	10.49	0.00	101.34
7.	$S_{(LT + year)}$	3	107.48	10.59	0.00	101.44
8.	$S_{(LT + MBD)}$	3	107.82	10.93	0.00	101.78
9.	$S_{(SA)}$	2	115.60	18.70	0.00	111.58
10.	$S_{(weight)}$	2	123.35	26.46	0.00	119.33
11.	$S_{(weight + MBD)}$	3	124.09	27.19	0.00	118.04
12.	$S_{(year + weight)}$	3	124.26	27.37	0.00	118.22
13.	$S_{(weight * MBD)}$	4	125.43	28.53	0.00	117.36
14.	$S_{(.)}$	1	125.73	28.83	0.00	30.80
15.	$S_{(year * weight)}$	4	125.87	28.97	0.00	117.80
16.	$S_{(sex)}$	2	126.47	29.57	0.00	122.44
17.	$S_{(MBD)}$	2	127.17	30.28	0.00	123.15
18.	$S_{(year)}$	2	127.35	30.45	0.00	123.33
19.	$S_{(sex * weight)}$	4	127.36	30.47	0.00	119.29
20.	$S_{(year + MBD)}$	3	128.88	31.98	0.00	122.83

An effect of study area was present in the top three models (Table 7). The top model suggested that calves born in the Humboldt study area had a 0.57 (SE = 0.096) probability of surviving through summer, while estimated survival for the Del Norte study area calves was 1.00 (SE = 0.00). This model also suggested that survival increased as birth weight increased for calves captured in the Humboldt study area, but birth weight had no effect on the summer survival of calves in the Del Norte study area (Figure 4). In fact, there was no calf mortality in Del Norte during the summer.

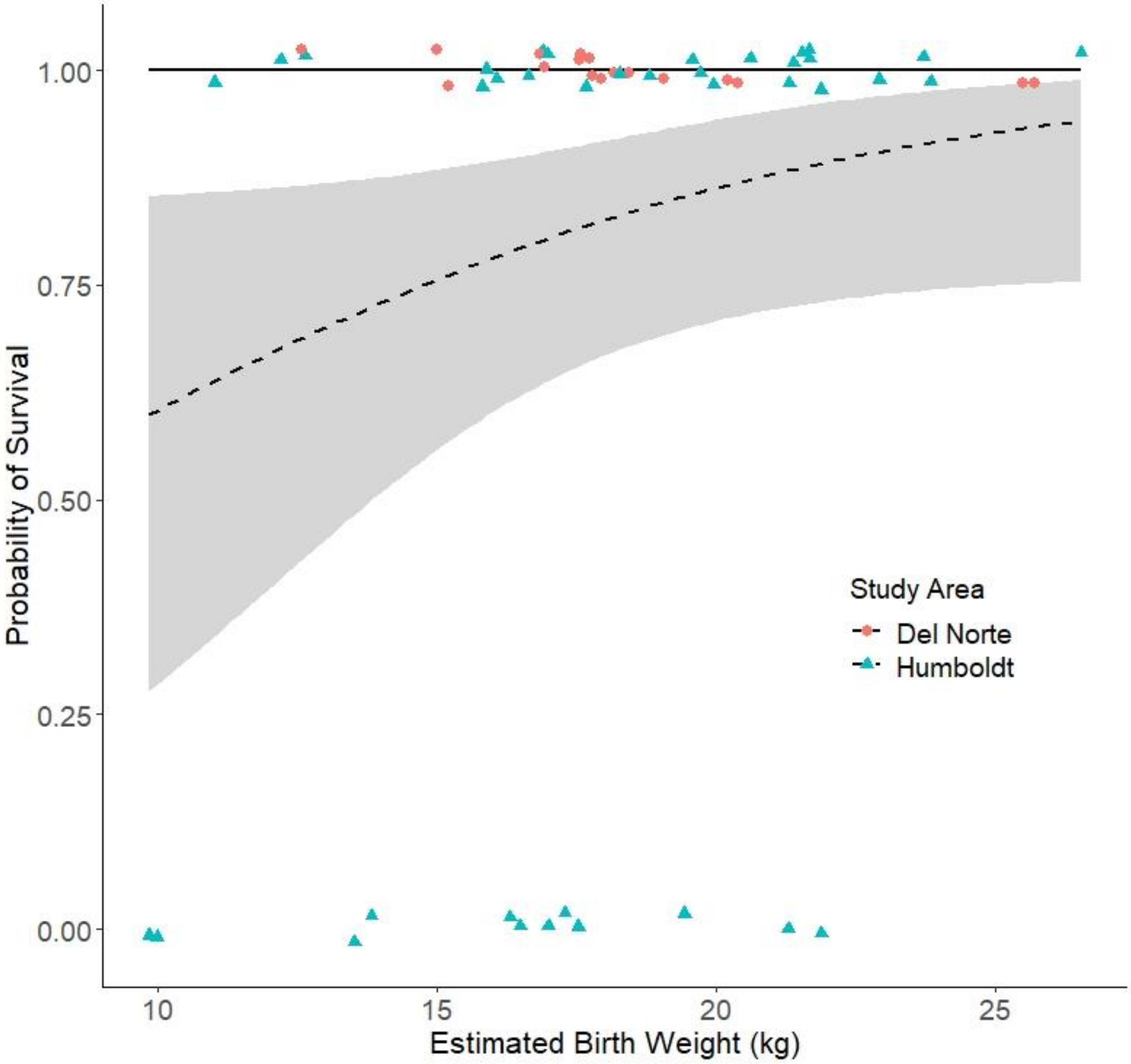

Figure 4. Logistic regression curve estimated from top model $S_{(LT+weight+SA)}$ and 95% confidence intervals, showing the relationship between estimated birth weight and summer survival in Roosevelt elk (*C. canadensis roosevelti*) calves in Humboldt (dashed line) and Del Norte (solid line) counties, California, USA, 2017-2018. The points represent each calf's fate (*n* = 55) at 14 weeks of life but are shifted slightly around zero (dead) and one (survived) for graphing visibility.

Annual survival

Forty-three percent (n = 25) of calves marked as neonates (n = 58) survived to one year of age whereas 31% (n = 18) died within their first year and 26% (n = 15) had unknown fates due to tag loss (n = 8), tag failure (n = 5), or restricted property access (n = 2). The multistate model with the lowest AIC_c score suggested that the probability of detecting calves ($\hat{\hat{p}}$) varied with year (Table 8).

Table 8. Model selection for detection probability of Roosevelt elk (*C. canadensis roosevelti*) calves marked in Humboldt and Del Norte counties, California, USA as a function of year (2017/2018, 2018/2019), study area (SA), state (alive, newly dead, or dead) and the null model (.). K is the number of estimable parameters.

	Model	K	AIC$_c$	Δ AIC$_c$	AIC$_c$ Weight	Deviance
1.	ψ (.)p(year)	3	319.03	0.00	0.65	312.97
2.	ψ (.)p(state)	4	320.83	1.78	0.27	31.41
3.	ψ (.)p(SA)	3	324.12	5.09	0.05	318.07
4.	ψ(.)p(.)	2	325.33	6.29	0.03	39.97

Calves born in 2017 had a lower detection probability (0.92, SE = 0.023) compared to calves born in 2018 (0.98, SE = 0.009). Overall, detection increased from the first sampling year to the second and detection probability was 6.5% higher in 2018 than in 2017. The second top model included the effect of state on detection probability (Table 8). Calves in the alive state had a detection probability of 0.96 (SE = 0.009), while newly dead calves were always detected (1.00, SE = 0.00). Since both top models had Δ AIC_c less than 2, there was some model uncertainty in what influences detection probability (Table 8). In my model selection tables, the effect of year had over half the AIC_c weight, but the effect of state also carried a large portion of the AIC_c weight. I averaged the models and obtained an overall detection probability of 0.93 (SE = 0.03).

Annual survival was estimated by examining the transition probability from alive to newly dead ($\hat{\psi}^{AD}$). Since $\psi^{AA} + \psi^{AD} = 1$, I rearranged this equation to estimate survival (Devineau et al. 2014). The top model suggested that survival is influenced by the varied effect of time (Table 9). This model had the lowest AIC_c score, had a Δ AIC_c less than 2, and carried over half the AIC_c weight.

Table 9. Model selection of Roosevelt elk (*C. canadensis roosevelti*) calf annual (12 months) survival probabilities (Ψ) as a function of sex, year (2017/2018, 2018/2019), birth weight (weight), study area (SA), the linear trend of time (LT), average monthly precipitation in mm (precip), monthly minimum temperature (temp), varying time (time), and the null model (.) for calves captured in Humboldt and Del Norte counties, California, USA during 2017 and 2018. K is the number of estimable parameters.

	Model	K	AIC_c	$\Delta\ \text{AIC}_c$	AIC_c Weights	Deviance
1.	$\Psi_{(\text{time})}p_{(\text{year})}$	14	299.41	0.00	0.46	270.41
2.	$\Psi_{(\text{LT})}\ p_{(\text{year})}$	4	300.47	1.06	0.27	292.38
3.	$\Psi_{(\text{weight+time})}\ p_{(\text{year})}$	15	300.54	1.12	0.26	269.39
4.	$\Psi_{(\text{SA})}\ p_{(\text{year})}$	4	309.08	9.67	0.004	300.99
5.	$\Psi_{(.)}p_{(\text{year})}$	3	319.03	19.62	0.00	312.97
6.	$\Psi_{(\text{precip})}\ p_{(\text{year})}$	4	319.04	19.63	0.00	310.95
7.	$\Psi_{(\text{weight})}\ p_{(\text{year})}$	4	319.65	20.24	0.00	311.56
8.	$\Psi_{(\text{MBD})}\ p_{(\text{year})}$	4	320.69	21.28	0.00	312.60
9.	$\Psi_{(\text{sex})}\ p_{(\text{year})}$	4	321.04	21.63	0.00	312.95
10.	$\Psi_{(\text{temp})}\ p_{(\text{year})}$	4	321.06	21.65	0.00	312.97
11.	$\Psi_{(\text{year})}\ p_{(\text{year})}$	4	321.07	21.66	0.00	312.97
12.	$\Psi_{(\text{weight+sex})}\ p_{(\text{year})}$	5	321.38	21.97	0.00	311.24
13.	$\Psi_{(\text{weight+temp})}\ p_{(\text{year})}$	5	321.69	22.28	0.00	311.55

Among all the covariates, time and birth weight were important predictors of annual survival. The third top model, $\Psi_{(\text{weight + time})}\ p_{(\text{state})}$, also included the effect of time along with the additive effect of birth weight and the second top model, $\Psi_{(\text{LT})}\ p_{(\text{state})}$, included the linear effect of time. All three top models had a ΔAIC_c less than 2 (Table 9).

The monthly estimates of survival in the top model varied from 0.89 (SE = 0.03) to 1.00 (SE = 0.00) (Figure 5a). Survival was lowest during the first month of life (May 15 – June 15) and when calves were approximately five months old (0.96, SE = 0.02) (Figure 5a). Seasonally, survival was lowest during summer (0.88, SE = 0.001) and highest the following spring (1.00, SE = 0.00) (Figure 5b). There was some model uncertainty in the results since the top three models had ΔAIC_c of less than 2 and these three models carried almost all of the AIC_c weight (Table 9). Therefore, I averaged all the models, which resulted in monthly estimates of survival that ranged from 0.90 (SE = 0.033) to 1.00 (SE =0.001) (Figure 6). The overall estimate of annual survival from the model averaged results was 0.82 (SE = 0.003).

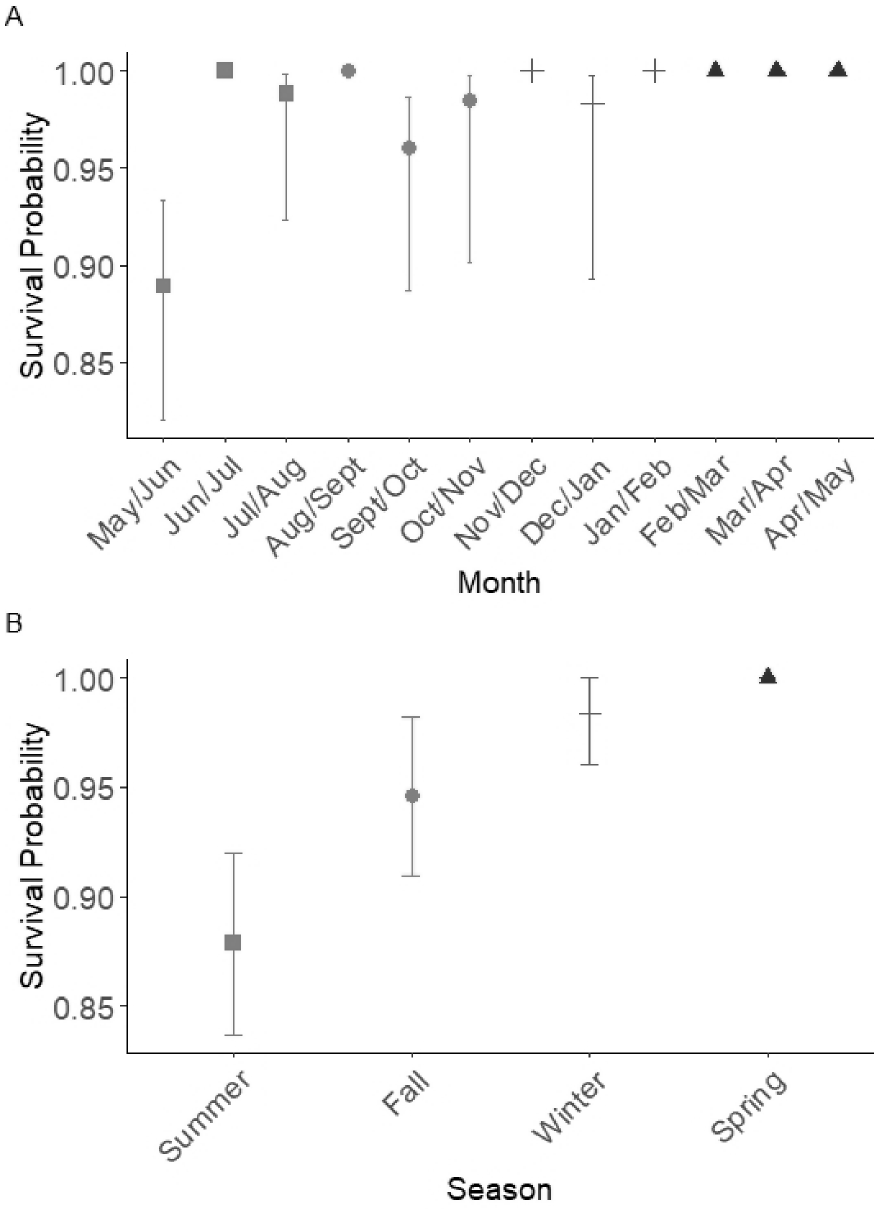

Figure 5. Monthly estimates (A) and seasonal estimates (B) of survival with 95% confidence intervals for Roosevelt elk (*C. canadensis roosevelti*) calves captured in Humboldt and Del Norte counties, California, USA during 2017-2018. Estimates were obtained from the top multistate model $\Psi_{(time)}p_{(year)}$, where survival (Ψ) varies by time and detection probability (p) varies by year (2017/2018, 2018/2019). The point shapes represent how the 12 monthly intervals (A) are split into seasons (B).

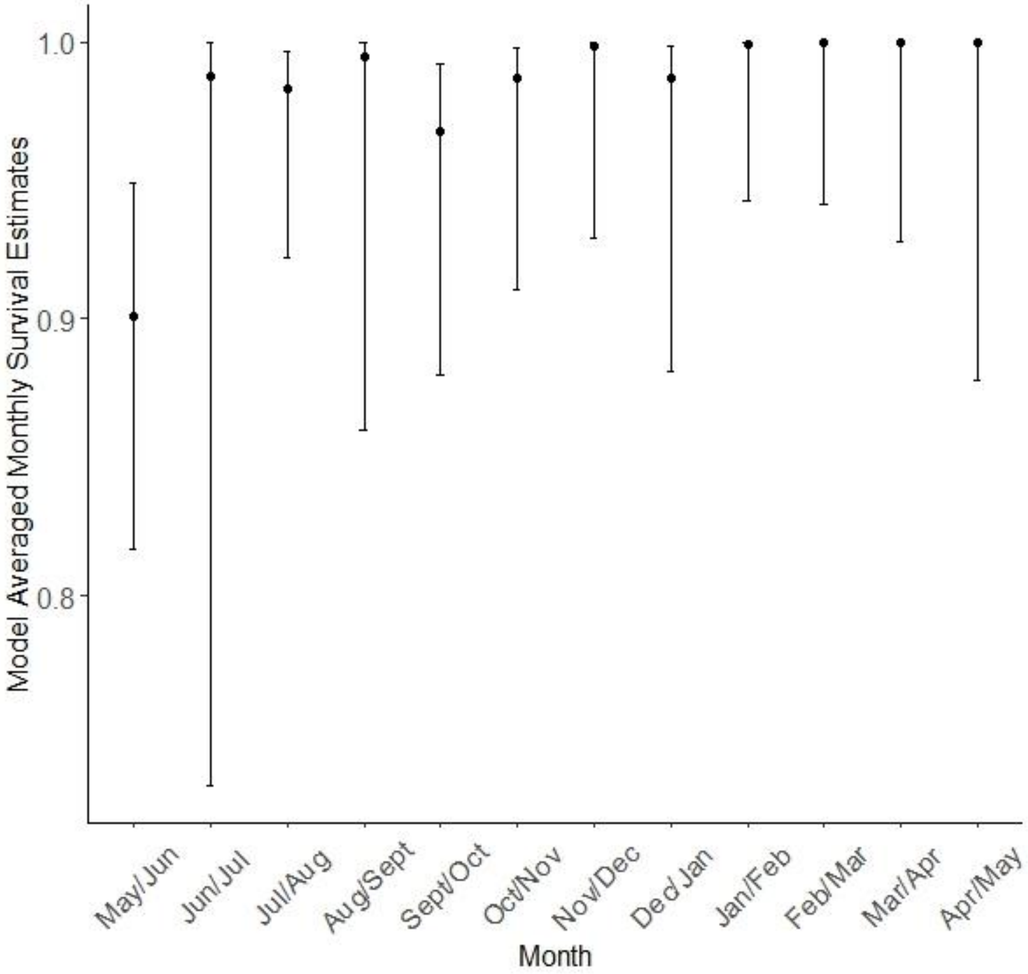

Figure 6. Model averaged monthly estimates of annual survival for Roosevelt elk (*C. canadensis roosevelti*) calves captured 2017-2018 in Humboldt and Del Norte counties, California, USA.

Recruitment

Over two years, 66 road surveys were conducted on 11 distinct groups during late winter and early spring. The maximum count of calves and cows from these surveys was used to estimate recruitment during that sampling year. Average recruitment of calves into adult populations ranged from 22.3 calves per 100 cows in sampling year 2018/2019 to 26.9 calves per 100 cows in 2017/2018 (Table 10), but was not significantly different between sampling years ($P = 0.305$).

Twenty-eight adult females were marked from 24 January 2017 to 26 February 2018. Five mortalities occurred over the course of 2 years and 4 animals were censored from the known-fate analysis due to collar failure. Annual adult female survival ranged from 0.857 (SE = 0.08) to 1.00 (SE = 0.00) over the course of 2 years. I model averaged the results to get an annual adult female survival of 0.92 (SE = 0.03, $n = 24$) and used this estimate to obtain estimates of λ (Table 10).

Table 10. Annual recruitment rates (calves per 100 cows) of Roosevelt elk (*C. canadensis roosevelti*) in Del Norte and Humboldt counties, California, USA. Calf to cow ratios were calculated from road surveys conducted in late winter during the sampling year. Lambda was calculated using the equation described by Hatter and Bergerud (1991).

Year	n[a]	Calf to cow ratio (SE)	$\hat{\lambda}$
2017/2018	410	26.9 (0.002)	1.06
2018/2019	482	22.3 (0.001)	1.04

[a] The total number of cows and calves counted during road surveys conducted during February, March, and April of the sampling year.

Mortality

The primary factor influencing mortality of calves was predation (*n* = 10). Most predation was due to black bears (*n* = 4), followed by unknown predation (*n* = 3), mountain lion, (*n* = 2) and coyote (*n* = 1) (Table 11). Additionally, more predation occurred during summer (first 14 weeks) than during any other period in the first year of life. Black bears killed calves with a mean age of 36 days (SE = 38.10), while mountain lions preyed on calves at a mean age of 173 days (SE = 58.70). The one case of coyote predation occurred when the calf was 14 days old and calves killed by unknown predators died at a mean age of 94 days (SE = 68.50) (Figure 7).

Table 11. Total number by fate of Roosevelt elk (*C. canadensis roosevelti*) calves marked as neonates in 2017-2018 in Humboldt and Del Norte counties, California, USA. Number includes the total during each sampling year (birth - 30 April each year), the total occurring during summer overall (first 14 weeks of life), and the overall total.

Fate	2017	2018	Summer	Overall
Mortality[a]	6	12	13	18
Predation	5	5	6	10
Black bear	2	2	4	4
Mountain lion	1	1	0	2
Coyote	1	0	1	1
Unknown predator	1	2	1	3
Nutritional	0	4	4	4
Natural-disease	1	0	0	1
Natural-trauma	0	1	1	1
Human-related	0	0	0	0
Unknown	0	2	2	2
Survived	7	18	42	25
Censored[b]	8	7	3	15
Total Uncensored Sample[c]	13	30	55	43

[a] The presumed cause of mortality based on mortality site investigations, present predator DNA, gross necropsy findings, or histological results from tissue samples.

[b] Calves were censored because their fates could not be determined due to tag loss or failure or restricted property access.

[c] Only includes the sum of mortality, unknown, and survived fates.

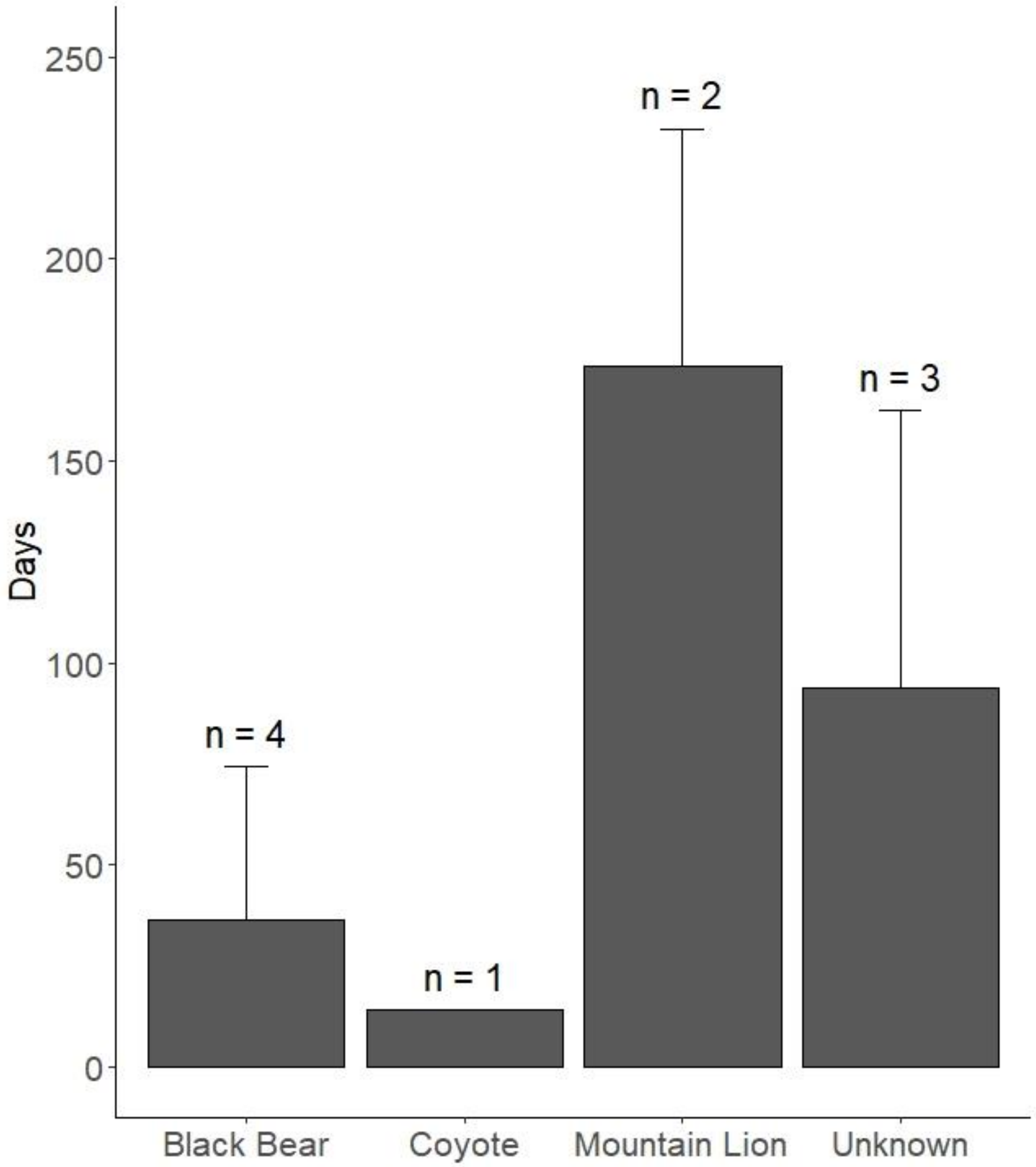

Figure 7. Mean age in days at death of radio-tagged Roosevelt elk (*C. canadensis roosevelti*) calves killed by various predators. Calves were captured in Del Norte and Humboldt counties, California, USA during 2017-2018.

The second most common cause of mortality was nutritional (*n* = 4). This included malnutrition (*n* = 3) and one case where histology results noted meconium aspiration syndrome as a “nonspecific change indicating fetal distress” (L. Woods, California Animal Health and Food Safety Laboratory, unpublished data). Calves that died from nutritional factors were a mean age of 5 days (SE = 2.94). Other factors influencing mortality included natural-disease (specifically *Leptospirosis*, *n* =1) and natural-trauma (specifically drowning, *n* = 1) (Table 11).

The number of mortality events also differed by study area. Calves born in the Humboldt study area were more likely to die across all categories when compared to calves born in the Del Norte study area. In fact, very little mortality was detected in the Del Norte study area. No calves marked in Del Norte County died during the first 14 weeks of life and only one calf died at 215 days old due to mountain lion predation. Calves marked in the Humboldt study area were a mean age of 43 days old (SE = 59.27) at the time of death and predation was the major cause of death. Due to small sample sizes, I could not statistically compare age at death with cause of death while appropriately accounting for main effects and interactions of capture age, capture year, sex, birth date, and study area.

Mortality risk was highest during the first 2 weeks of life (Figure 8). Fifty-five percent of all marked calf mortalities occurred during this time (10 out of 18) with 30% of those due to predation (3 out of 10) and 40% of those due to nutrition/metabolic (4 out of 10). Calves born early in the season had the highest risk of mortality and were most likely to die of predation by bears (0.22, SE = 0.10, *n* = 4) while calves born late in the season had the lowest risk of mortality as all late-born calves survived to one year of age.

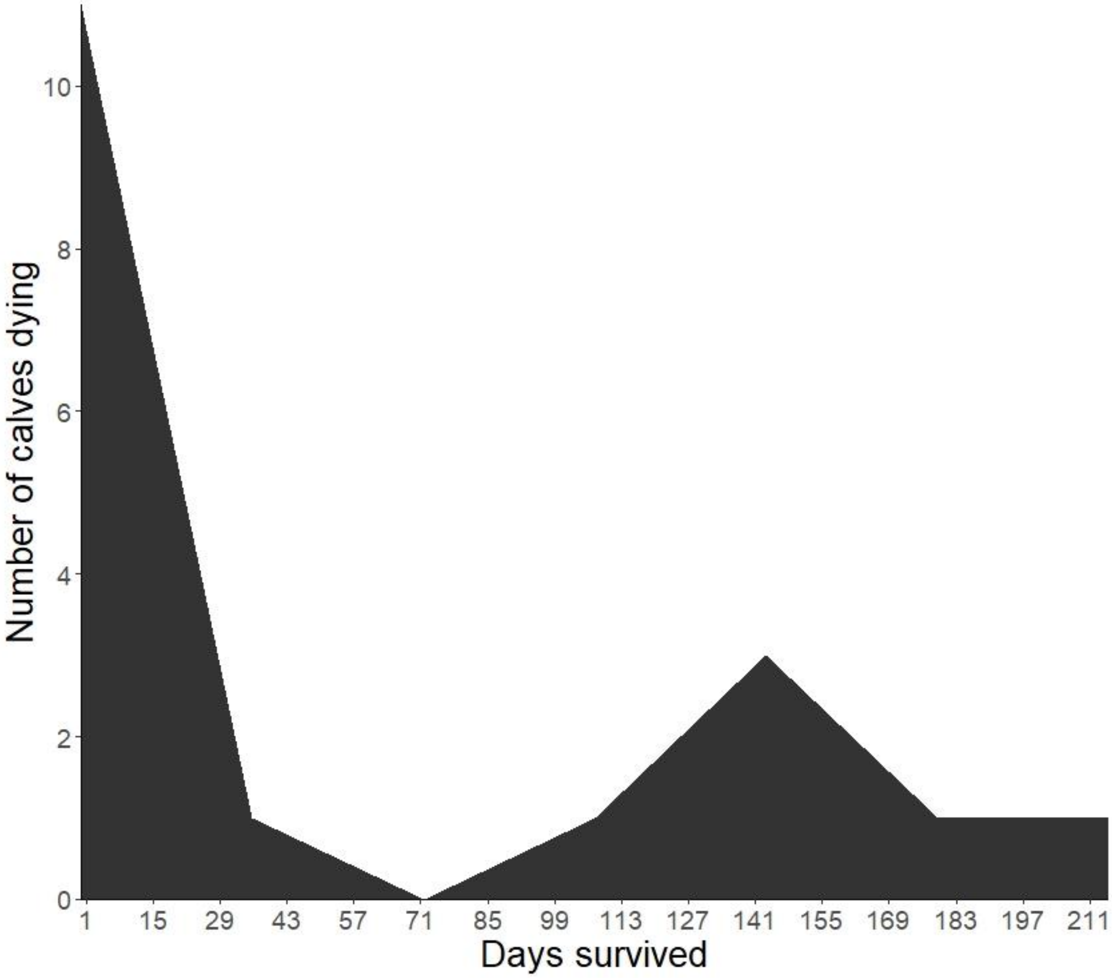

Figure 8. Number of Roosevelt elk (*C. canadensis roosevelti*) calf mortalities occurring from birth through 215 days (n = 18). Calves were marked as neonates in Del Norte and Humboldt counties, California, USA during 2017-2018.

I further investigated mortality risks by evaluating predation versus non-predation mortality events using cumulative incidence functions. Overall, non-predation events (0.12, SE = 0.001) were more likely to occur during summer (first 14 weeks) over predation events (0.10, SE = 0.002) for all calves.(Table 12; Figure 9). As calves increased in age, the mortality risk changed and predation events (0.18, SE = 0.003) were more likely to occur over non-predation events (0.14, SE = 0.002) (Table 12; Figure 9).

Table 12. The number of calves and estimated marginal probability (CIF) of predation and non-predation mortality at 2 weeks, 14 weeks (summer), and 52 weeks (annual) with the 95% confidence intervals in parentheses (lower, upper) for 18 confirmed Roosevelt elk (*C. canadensis roosevelti*) calf mortalities by birth date category (early, peak) and overall in Humboldt and Del Norte counties, California, USA. CIFs for late-born calves were not included because no mortality was detected in that group.

Mortality Event	Number of early-born	Early-born CIF	Number of peak-born	Peak-born CIF	Number overall	Overall CIF
Two weeks						
Predation	2	0.06 (0.01, 0.19)	1	0.05 (0.00, 0.20)	3	0.05 (0.01, 0.13)
Non-predation	3	0.10 (0.02, 0.23)	4	0.19 (0.06, 0.38)	7	0.12 (0.05, 0.22)
Summer						
Predation	3	0.16 (0.06, 0.31)	0	0.05 (0.00, 0.20)	3	0.10 (0.04, 0.20)
Non-predation	0	0.10 (0.02, 0.23)	0	0.19 (0.06, 0.38)	0	0.12 (0.05, 0.22)
Annual						
Predation	1	0.20 (0.08, 0.35)	3	0.21 (0.06, 0.39)	4	0.18 (0.09, 0.28)
Non-predation	0	0.10 (0.02, 0.23)	1	0.24 (0.08, 0.44)	1	0.14 (0.06, 0.24)

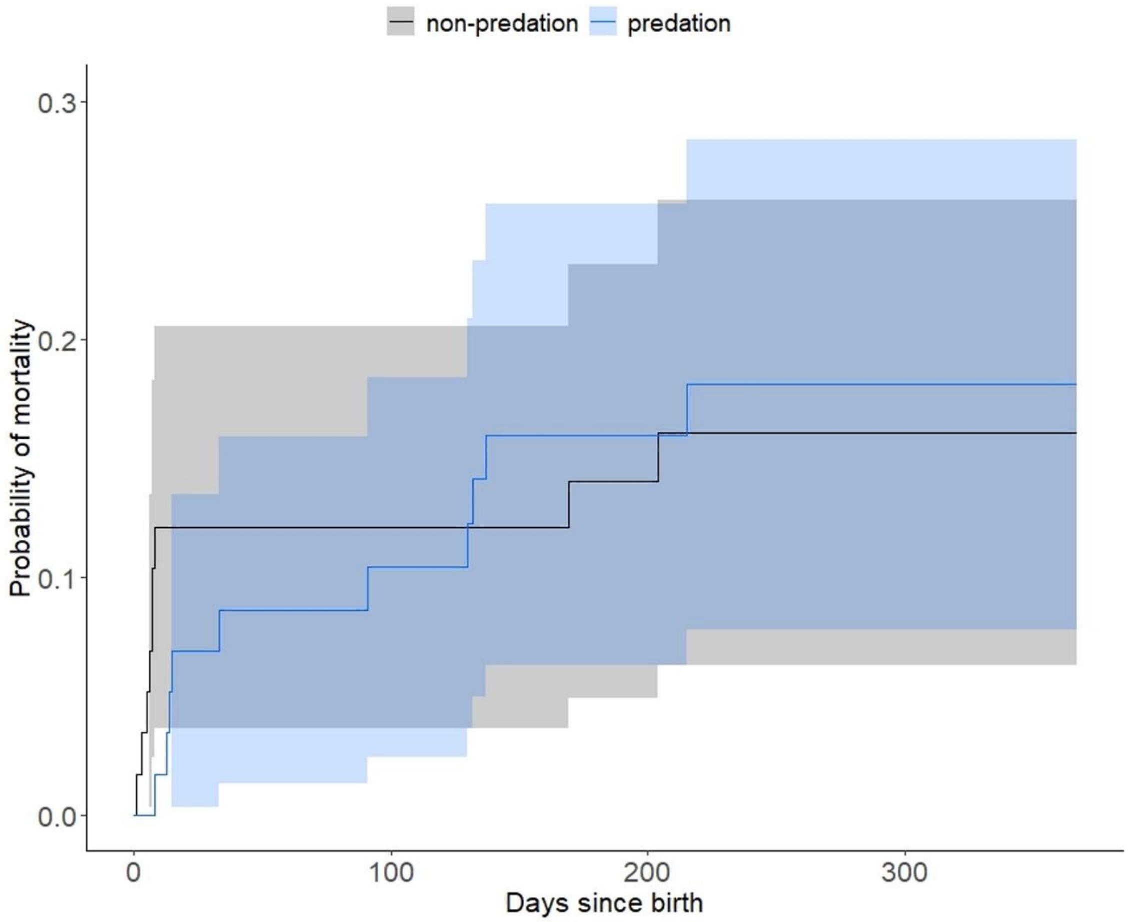

Figure 9. Cumulative incidence for predation and non-predation mortality events over age in days for Roosevelt elk (*C. canadensis roosevelti*) calves in Humboldt and Del Norte counties, California, USA, marked during 2017-2018.

Next, I evaluated mortality risk of calves categorized by birth date (early, peak or late). Mortality risk differed over time between predation and non-predation events of calves born during the early, peak, or late portion of the calving season (Figure 10). Non-predation events were more likely to occur immediately following birth for both early-born (0.10, SE = 0.003) and peak-born calves (0.19, SE = 0.008; Table 12). This changed, however, by 14 weeks of life. At that time, early-born calves were more likely to die of predation (0.16, SE = 0.067), while peak-born calves were more likely to die from non-predation (0.19, SE = 0.880) events (Table 12).

Annually, early born calves were at a higher risk for predation events from 2 weeks on, but this trend was not the same for peak-born calves (Figure 10). Mortality risk was lowest for late-born calves, as no mortality was detected for calves in this group (Figure 10). The difference in age at mortality between early-born, peak-born, and late-born calves was not statistically significant for predation (χ^2 = 1.29, df = 2, P = 0.524) or non-predation (χ^2 = 3.00, df = 2, P = 0.222) events.

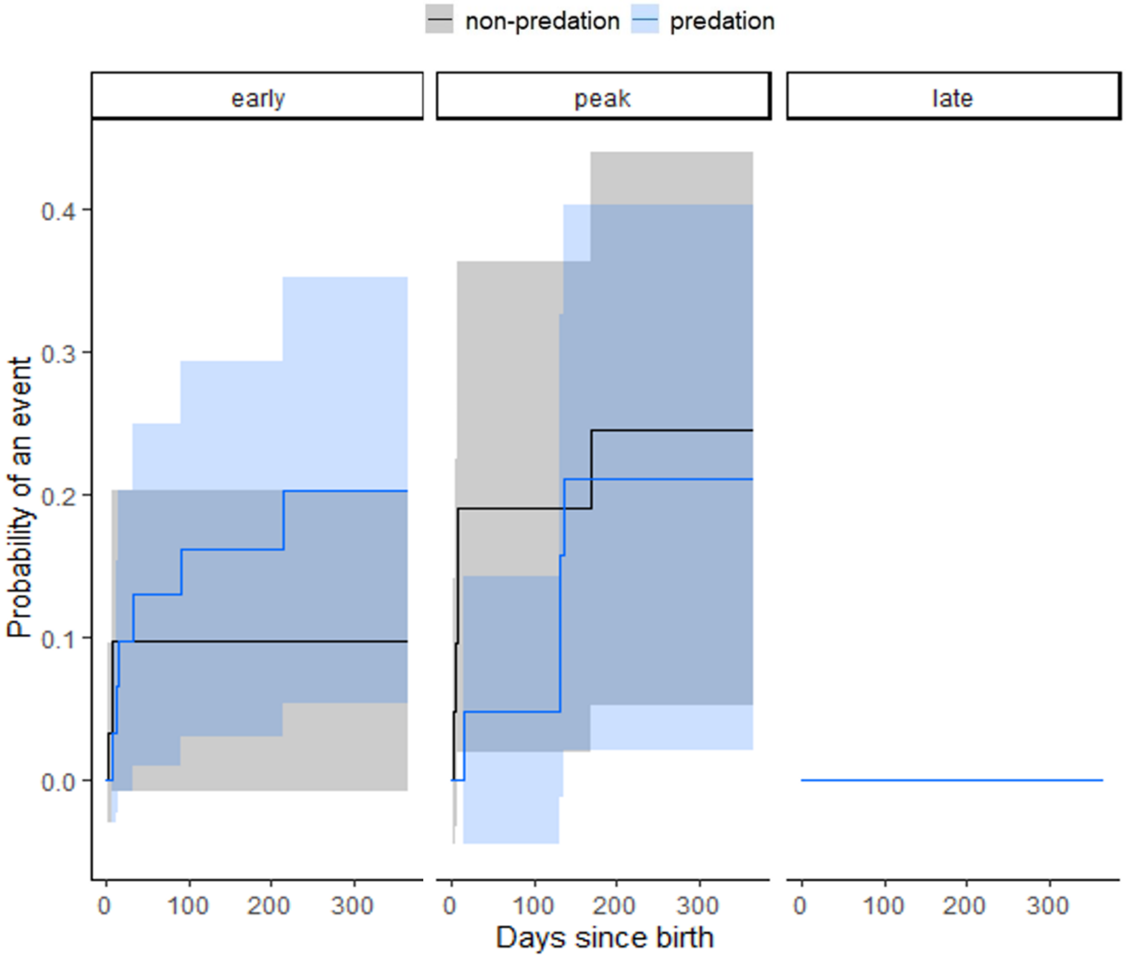

Figure 10. Cumulative risk over time of predation versus non-predation events for Roosevelt elk (*C. canadensis roosevelti*) calves born early (early), during the peak (peak), or late (late) in the calving season. Calves were captured and marked with radio ear tags during 2017 and 2018 in Del Norte and Humboldt counties, California, USA.

In addition to investigating mortalities from calves marked as neonates (*n* = 18), this study investigated mortalities from tagged adults (*n* = 7) and opportunistic mortalities from all age classes (*n* = 25) to assess factors influencing mortality across all age classes. Collectively, predation was the highest cause of mortality affecting 26% of elk (13 out of 50), but only affected calves (Figure 11). The next highest mortality factor was human-caused mortality, which contributed to yearling (*n* = 2) and adult mortality (*n* = 11) (Figure 11). Human-caused mortality specifically included roadkill (*n* = 7), legal harvest (*n* = 4), euthanasia due to fence entanglement (*n* = 1), and poaching (*n* = 1). Other factors of mortality included nutritional, which affected 10% of calves (*n* = 5) and natural-disease affecting 2% of calves (*n* = 1) and 4% of adults (pneumonia, *n* = 2).

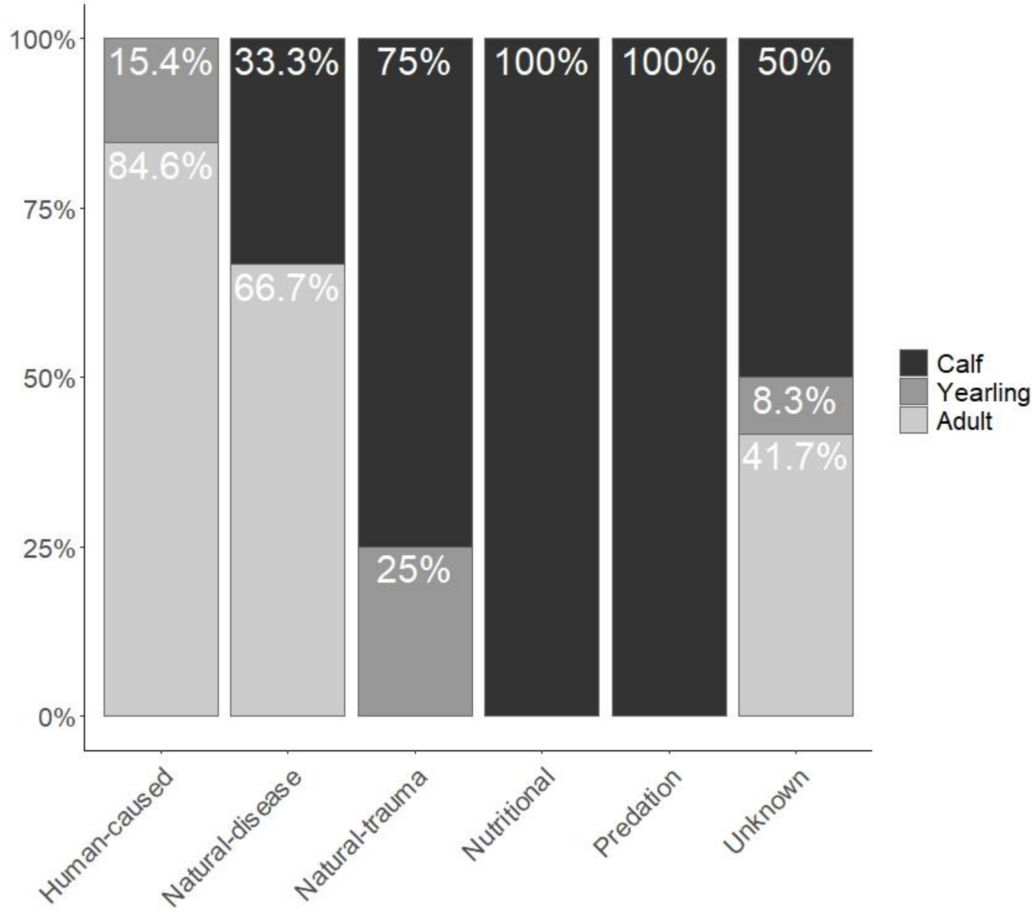

Figure 11. Proportion of Roosevelt elk (*C. canadensis roosevelti*) mortality caused by major factors of mortality and age class (tagged and opportunistic, n = 50) investigated from December 2016 to May 2019 in Humboldt and Del Norte counties, California, USA.

DISCUSSION

The results of this study confirm that calf elk survival in Humboldt and Del Norte counties is relatively high and replicated other work where summer survival varied during the first few weeks of life (Barber-Meyer et al. 2008, Quintana 2016). As expected, I found that birth weight influenced summer survival, calf mortality was primarily due to predation, and adult mortality was primarily due to human-caused events. Results also indicated that birth date had an influence on calf survival but differed from what I predicted as late born calves appeared to have an advantage and there was a difference in survival and birth dates between the two study areas. Additionally, this study detected a higher percentage of mortalities due to nutritional issues than other studies (Singer et al. 1997, Raithel 2005, Harris 2006, Barber-Meyer et al. 2008, Lehman 2015, Quintana 2016).

Similar to other studies, summer survival was lowest during weeks 1 and 2, before gradually increasing over the course of summer (Barber-Meyer et al. 2008, Quintana 2016). This result suggested that calves in northwestern California are particularly vulnerable during the first few weeks of life. The overall estimate of summer survival (66%) in this study was also comparable to most studies in North America (Singer et al. 1997, Smith and Anderson 1998, Raithel et al. 2005, Harris 2006, Zager, White, and Pauley 2007) (Table 13). This suggested that summer survival for elk in northwestern California is at an appropriate level.

Annual survival in northwestern California, however, varied from other survival studies. This study estimated a much higher annual calf survival (82%) than other studies and represented an upward trend from summer estimates, which contrasted greatly with other studies (Singer et al. 1997, Smith and Anderson 1998, Raithel et al. 2005, Harris 2006, Zager, White, and Pauley 2007, Barber-Meyer et al. 2008, Lehman et al. 2015, Quintana et al. 2016) (Table 13). Additionally, little winter mortality was observed and the estimates of lambda from age ratios indicated the population was growing.

Table 13. Comparisons of calf survival and causes of mortality in elk across the western United States. Summer and annual calf survival estimates were reported in percentages, when available, along with the primary and secondary cause of death with their respective percentage for each study.

Study area	Summer survival	Annual survival	Primary mortality (%)	Secondary mortality (%)	Reference
Northern Yellowstone	0.29	0.22	grizzly bear (0.38)	malnutrition (0.05)	Barber-Meyer et al. 2008
Northern Yellowstone	0.65	0.43	starvation (0.25)	Grizzly bear and coyote (0.17)	Singer et al. 1997
West-central Montana	0.74	0.58	black bear (0.10)	malnutrition/disease (0.08)	Raithel 2005
Northwestern Wyoming	0.86	0.58	-	-	Smith and Anderson 1998
West central Montana	0.79	-	black bear (0.27)	malnutrition (0.17)	Harris 2006
Southwestern South Dakota	0.25-0.41	0.07-0.27	mountain lion (0.63)	other (0.05)	Lehman et al. 2015
Northern New Mexico	0.52	0.33-0.47	black bear (0.39)	unknown (0.09)	Quintana et al. 2016
West central Montana	0.55	-	unknown (0.26)	mountain lion (0.20)	Eacker et al. 2015
North central Idaho	0.30 - 0.64	0.25 - 0.36	black bear (0.39)	mountain lion (0.39)	Zager, White, and Pauley 2007

Summer survival can vary considerably across years as young ungulate survival is sensitive to habitat conditions and environmental factors (White et al. 2010, Harris 2006, Lehman 2015). Other studies have shown that summer survival varied considerably between years (26% - 65%, White et al. 2010, 36% - 91%, Harris 2006, 25% - 41%, Lehman 2015). In contrast, this study did not show an effect of year on summer survival. This was evident in the fact that the covariate of year consistently ranked low in the candidate set of models and carried no weight in predicting summer survival (Table 7). Additionally, summer survival was relatively similar between years in this study; the estimated overall summer survival for 2017 was 0.74 (SE = 0.11) and 0.61 for 2018 (SE = 0.10).

Environmental conditions and sampling year had little importance in annual survival as well. Precipitation and minimum temperature were not important variables for predicting annual survival, and models with the covariate of year ranked very low in the candidate set of annual survival models (Table 9). This suggests that there wasn’t much variation between the two years of this study and that environmental conditions did not appear to impact juvenile survival.

However, there is evidence that mild, Mediterranean environmental conditions do have an impact on juvenile survival of ungulates in other areas. Roe deer (*Caperolus caprelus*) exhibited a low probability of summer survival (33%), which was influenced by total spring rainfall along with birth weight and a linear time trend in northern Italy (Raganella-Pelliccioni et al. 2006). The impact of spring rainfall isn’t clearly understood in this area. It was not explicitly examined, and this study only includes two years of data, limiting my understanding of how environmental conditions impact calf survival.

Conversely, this study replicated an effect of time, birth weight and birth date on survival similar to other studies (Raganella-Pelliccioni et al. 2006, Barber-Meyer et al. 2008, Quintana 2016). The results found here showed that summer survival was influenced by birth weight, study area, and the linear trend of time. Furthermore, annual survival indicated that time was an important factor in a calf surviving to one year of age. Regardless of season, this study indicated that survival always increased with time and calves were most at risk of mortality during summer. Other studies have noted a substantial increase in calf mortality during the winter (Singer et al. 1997, Eacker et al. 2016), but this study failed to replicate those results and winter survival was relatively high at 0.98 (SE = 0.0002).

Birth weight is known to be an important factor influencing survival and is influenced by maternal condition, environmental conditions, and forage quality. I predicted that birth weight would impact survival and found evidence of this with both summer and annual survival. Similar to other studies, I found that larger calves had a higher probability of survival regardless of sex, sampling year, or birth date (Singer et al. 1997, Smith et al. 2006, White et al. 2010). This trend, however, did not hold true across both study areas. Larger calves in the Humboldt study area were more likely to survive the first 14 weeks of life, whereas all calves in the Del Norte study area survived regardless of birth weight.

Although birth weight is commonly cited to influence survival, other studies have found no relationship between birth weight and survival (Adams et al. 1995, Smith and Andersen 1998). For example, no correlation was found between birth weight and survival in Wyoming elk, but mean cohort birth weight as a function of environmental conditions was correlated positively with survival (Smith and Andersen 1998). The results of this study indicated that birth weight was most important during summer and had little influence during the rest of the calves' first year. Birth weight didn't appear to be important in predicting annual survival and the effect of time was the most important predictor of survival beyond the summer period.

Predation has been cited as a top cause of mortality for ungulate populations across the United States (Raithel et al. 2005, Harris 2006, Barber-Meyer et al. 2008, Quintana 2016) (Table 13). This study produced similar results, with predation accounting for 55% of mortality of marked calves, but differed from other studies that found predation to be higher than what was found in this study area (95% Barber et al. 2008, 66% Harris 2006, 68% Smith and Anderson 1998, 75% Singer et al. 1997). In addition, black bears were found to be the number one predator responsible for calf predation in Humboldt and Del Norte counties, which agrees with some other studies (Singer et al. 1997, Raithel 2005, Harris 2006, Zager, White, and Pauley 2007, White et al. 2010, Quintana 2016) (Table 13). This study found black bear predation to be 22%, which is within in the range of bear predation found in other studies (Smith and Anderson 1998, Singer et al. 1997, Zager, White, and Pauley 2007, Barber et al. 2008). Finally, most mortality of calves occurred soon after birth in this study area, which is similar to other studies (Raithel 2005, Barber-Meyer et al. 2008, White et al. 2010, Griffin et al. 2011).

Other predators included mountain lions and coyotes, accounting for a total of 16% of known mortalities in marked calves. This study found that mountain lions killed older calves rather than neonates, as reported for other ungulates (Barber-Meyer et al. 2008, White et al. 2010, Monteith et al. 2014, Quintana 2016). However, this study may have underestimated mountain lion kills because tag loss/failure limited the sample size of marked calves by late fall during both sampling years.

In contrast, summer mortality caused by nutritional issues was much higher in this study (22%) when compared to places such as Montana (Raithel 2005), South Dakota (Lehman 2015), and New Mexico (Quintana 2016). My analysis of mortality risk further emphasized this trend, with non-predation events being higher during the first 14 weeks of life than predation events. The difference in nutritional issues in this study compared to others may be due to difficulties in assessing malnutrition. Estimates of malnutrition range from 0-17% and other studies may often underestimate malnutrition and attribute some of those mortalities to predation instead (Raithel 2005, Harris 2006, Barber-Meyer et al. 2008). My study may have suffered from similar problems since some investigations were hindered by a lack of intact carcasses. Despite this, a similar percentage of malnutrition (17%) was found in my marked calves as another study (Harris 2006). Malnutrition of calves is a result of many different factors such as maternal care, forage availability to the cow prior to parturition, and age of the cow at first breeding (Toweill and Thomas 2002) and my results might simply suggest an enhanced ability to document malnutrition mortalities due to elk being in close proximity to people throughout most of the study areas. However, this study also detected selenium and copper deficiencies in 45% of cases that were sent in for toxicology (n = 20), regardless of death or age class.

Selenium is needed for proper reproductive performance and immune function in ungulates (Flueck et al. 2012). Selenium deficiency is particularly problematic for neonates as it causes nutritional muscular dystrophy, which can result in muscle stiffness, respiratory distress, or sudden death (Flueck et al. 2012). Additionally, higher predation may result for wild ungulate neonates that are deficient in one of these micronutrients (Hnilicka et al. 2004). Northwestern California is known to be deficient for these trace minerals, but it is unclear how this impacted elk survival in this study. Future research could examine if and how this plays a role, but my estimates of calf survival suggest this doesn’t have a current negative impact on populations.

This study also indicated that survival differed between study areas. Specifically, little mortality was observed in calves captured in the Del Norte study area compared to the Humboldt study area. The reason for this difference remains unclear, but differences in land features and the distribution of marked calves may explain some of this. A majority of the calves marked in the Del Norte study area (61%) spend time on or near Tolowa Dunes State Park, which is bordered by the ocean to the west and agricultural land to the east. This area is highly impacted by human activity which may have an influence on survival in several ways.

First, proximity to humans may provide better forage opportunities for elk. It has been suggested that humans influence available vegetation, and this strengthens the bottom-up effects for species such as elk (Muhly et al. 2013). Specifically, it was found that humans positively contributed to the forage biomass through crop production and by modifying forest-land to pastureland (Muhly et al. 2013). Access to high quality forage is important to maternal condition and has been positively correlated with higher birth weight and higher calf survival (Thorne et al. 1976, Clutton-Brock et al. 1982, Fairbanks 1993, Smith et al. 1997, Keech et al. 2000). Although birth weight was not significantly different between study areas, 17 out of 40 calves born in the Humboldt study area died while 94% of marked calves in the Del Norte study area survived. Furthermore, 59% of the Del Norte study area calves were below average birth weight and survived regardless. Because this study failed to measure maternal condition explicitly, it isn't clear how birth weight correlated to maternal conditions or how body condition compared across the two study areas, but this could be an area for further research.

A second reason for survival differing between study areas, may be due to a difference in predator density. Risk of predation is expected to be high for neonates during the first few weeks of life (Guinness et al. 1978, Clutton-Brock et al. 1982, Fairbanks 1993), and I observed this in my study, but the results were not uniform across study areas. Del Norte calves experienced no mortality due to predation in the first 14 weeks of life compared to 10% of calves in the Humboldt study area being predated upon. One explanation for this may be evident in the distribution of predators. Black bears were found to be the top predator of neonatal calves in this study and although specific values for bear abundance are unknown, areas of Humboldt County are known to contain high densities of bears (Matthews et al. 2008). Furthermore, harvest data suggests there is a higher bear density in Humboldt compared to Del Norte (Garcia and Raymond 2018). In 2016, Humboldt County accounted for 8.1% of the total bear harvest statewide, whereas Del Norte County accounted for only 1.4% (Garcia and Raymond 2018). Finally, a concurrent remote camera study in Tolowa Dunes State Park failed to document bear presence in the area where 61% of my Del Norte study area calves were marked (E. Siepker, Humboldt State University, unpublished data). The study only documented bobcats and coyotes as potential predators of neonates (E. Siepker, Humboldt State University, unpublished data). Higher predator densities are suspected to exist in other parts of Del Norte County, but without an even distribution of marks, calf survival in the Del Norte study may have been skewed as a result.

This highlights a final point: calves were disproportionally marked between the two study areas. Fewer calves were marked in the Del Norte study area due to restricted property access and difficulty accessing elk in forested areas. Less than half of marked calves occurred in Del Norte county and this study may have underestimated the amount of mortality and overestimated survival of calves as a result. Expanding this study to include data from more years and marking calves across a larger area of Del Norte County would be needed to investigate these differences more thoroughly. Regardless, calf to cow ratios have been proven to be a strong indicator of calf recruitment (Harris et al. 2008) and my estimates of lambda indicated population growth for both study areas.

Besides survival being different between the two study areas birth date was also significantly different and the results of this study indicated that birth date played an important role in survival. Contrary to what I predicted, late-born calves appeared to have an advantage over early or peak born calves. No mortality was detected in marked calves born after 8 June, regardless of study area or birth weight. The reasoning for this is unclear, but other studies have noted that late parturition occurs in a population that’s skewed towards a younger breeding population (Larkin et al. 2002) or where supplemental feeding occurs (Smith 1994). In particular, breeding that’s dominated by young males tends to extend the length of the breeding season and extends the calving season the following spring (Noyes et al. 1996, Larkin et al. 2002, Keller 2012).

The mild Mediterranean climate coupled with the fact that most elk in the Del Norte study area were near high quality forage from agriculture operations may have contributed to younger females breeding and calves being born later as a result. The mean extent of the calving season in this study was 33 days (2017 = 31 days, 2018 = 35 days), which is not abnormally long compared to other studies (Barbknecht et al. 2009, Griffin et al. 2011, Keller et al. 2014), but the objective of this study was not to document the extent calving and calf capture attempts concluded on 30 June each year. Furthermore, young calves with spots were observed in December 2018 which suggests that calving extended past June during that year. Therefore, the exact extent of birth dates is not represented in this study and calves classified as late-born in this study may not truly reflect how birth synchrony impacts calf survival. It remains unclear what factors impact birth date but studying this further may help explain the significant difference observed between study areas in this study.

MANAGEMENT IMPLICATIONS

The results of summer survival, annual survival, and recruitment indicate that calf survival in this area is high, and populations are likely increasing. These data, along with additional information, could be used to examine proposed harvest scenarios and the effect on the populations prior to enacting management decisions. This trend, however, was not uniform over both study areas. Because calf survival differed between Del Norte and Humboldt counties, management needs to be tailored to adequately address the needs of each area. In areas where elk largely occupy public lands with high densities of predators or where hunting opportunities are already established, little management is needed but should be monitored for trends diverging from the baselines established with this study. Elk in this landscape represent a population that can be managed sustainably to balance the interests of diverse stakeholders. Elk in the northern part of this study, however, largely occupy areas where they have high contact with domestic livestock, humans, and croplands. Little calf mortality was observed in this area and conflicts with humans are expected to increase if the population of elk continues to increase. Managers should focus on efforts to collaborate with stakeholders and develop plans that promote habitat for elk in low conflict areas while simultaneously using management tools such special hunts or fencing programs to reduce elk in high conflict areas.

Furthermore, this study documented a baseline for causes of mortality in the area. Managers should use this information to monitor populations and conduct future research as warranted. High adult mortality due to vehicular collisions was observed in this study.

Future research could be used to address this problem by identifying ‘hotspots’ of mortality and using tools such as wildlife crossings to improve safety and connectivity concerns. Adaptive management techniques need to be employed in the future as population dynamics can vary greatly from year to year and this study only represents a brief snapshot of a complex system.

LITERATURE CITED

Adams, B. G. 2005. Effects of maternal characteristics and climatic variation on birth masses of Alaskan caribou. Journal of Mammalogy 86:506-513.

Adams, L. G., F. J. Singer, and B. W. Dale. 1995. Caribou calf mortality in Denali National Park, Alaska. The Journal of Wildlife Management 59:584-594.

Ballard, W. B., and J. S. Whitman. 1987. Marrow fat dynamics in moose calves. The Journal of Wildlife Management 51:66.

Barber-Meyer, S. M., L. D. Mech, and P. J. White. 2008. Elk calf survival and mortality following wolf restoration to Yellowstone National Park. Wildlife Monographs 169:1–30.

Barbknecht, A. E., W. S. Fairbanks, J. D. Rogerson, E. J. Maichek, L. L. Meadows. 2009. Effectiveness of vaginal-implant transmitters for locating elk parturition sites. The Journal of Wildlife Management 73:144-148.

Barbour, M. G., T. Keeler-Wolf, and A. A. Schoenherr. 2007. Terrestrial vegetation of California. University of California Press, Berkeley.

Barnowe-Meyer, K. K., P. J. White, and J. A. Byers. 2011. Maternal investment by Yellowstone pronghorn following winter habitat deterioration. Western North American Naturalist 71:222-233.

Bender, L. C., E. Carlson, S. M. Schmitt, and J. B. Haufler. 2002. Production and survival of elk (*Cervus elaphus*) calves in Michigan. The American Midland Naturalist. 148:163-171.

Braun, C. 2005. Techniques for wildlife investigations and management. The Wildlife Society, Bethesda, Maryland, USA.

Brodie, J., H. Johnson, M. Mitchell, P. Zager, K. Proffitt, M. Hebblewhite, M. Kauffman, B. Johnson, J. Bissonette, C. Bishop, J. Gude, J. Herbert, K. Hersey, M. Hurley, P. M. Lukacs, S. Mccorquodale, E. Mcintire, J. Nowak, H. Sawyer, D. Smith, and P. White. 2013. Relative influence of human harvest, carnivores, and weather on adult female elk survival across western North America. Journal of Applied Ecology 50:295–305.

Buuveibaatar, B., J. K. Young, J. Berger, A. E. Fine, B. Lkhagvasuren, P. Zahler, and T. K. Fuller. 2013. Factors affecting survival and cause-specific mortality of Saiga calves in Mongolia. Journal of Mammalogy 94:127–136.

California Department of Fish and Wildlife. 1998. Black bear management plan. California Department of Fish and Wildlife, Sacramento, California, USA.

California Department of Fish and Wildlife. 2018. Elk conservation and management plan. California Department of Fish and Wildlife, Sacramento, California, USA.

Caughley, G. 1966. Mortality patterns in mammals. Ecology 47:906–918.

Cheatum, E. L. 1949. Bone marrow as an index of malnutrition in deer. New York State Conservation 3:19–22.

Cederlund, G. N., K. G. Hakan, and A. Pehrson. 1991. Body mass dynamics of moose calves in relation to winter severity. The Journal of Wildlife Management. 55:675-681.

Clutton-Brock, T. H., F. E. Guinness, and S. D. Albon. 1982. Red deer behavior and ecology of two sexes. The University of Chicago Press, Chicago, USA.

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.

Cooch, E. G., and G. C. White. 2016. Program MARK: a gentle introduction. 17th Edition. http://www.phidot.org/software/mark/docs/book/. Accessed 14 Nov 2016.

Cook, R. C., J. G. Cook, and L. D. Mech. 2004. Nutritional condition of northern Yellowstone elk. Journal of Mammalogy 85:714–722.

DeVivo, M. T., W. O. Cottrell, J. M. DeBerti, J. E. Duchamp, L. M. Heffernan, J. D. Kougher, and J. L. Larkin. 2011. Survival and cause-specific mortality of elk Cervus canadensis calves in a predator rich environment. Wildlife Biology 17:156–165.

Devineau, O., W. L. Kendall, P. F. Doherty, T. M. Shenk, G. C. White, P. M. Lukas, K. B. Burnham. 2014. Increased flexibility for modeling telemetry and nest-survival data using the multistate framework. Journal of Wildlife Management 78:224-230.

Duquette, J. F., J. L. Belant, N. Svoboda, D. E. Beyer, and P. E. Lederle. 2014. Effects of maternal nutrition, resource use and multi-predator risk on neonatal white-tailed deer survival. PLoS ONE 9(6):e100841.

Eacker, D. R., M. Hebblewhite, K. M. Proffitt, B. S. Jimenez, M. S. Mitchell, and H. S. Robinson. 2016. Annual elk calf survival in a multiple carnivore system: elk calf survival in a multiple carnivore system. The Journal of Wildlife Management 80:1345-1359.

Fairbanks, S. W. 1993. Birthdate, birthweight, and survival in pronghorn fawns. Journal of Mammalogy 74:129-135.

Flueck, W. T., J. M. Smith-Flueck, J. Mionczynski, and B. J. Mincher. 2012. The implications of selenium deficiency for wild herbivore conservation: a review. European Journal of Wildlife Research 58:761-780.

Ford, L. D., G. F. Hayes. 2007 Northern coastal scrub and coastal prairie. in M. G. Barbour, T. Keeler-Wolf, A. A. Shoenherr, editors. Terrestrial vegetation of California, third edition. University of California Press, Berkeley, USA.

Gaillard, J.-M., M. Festa-Bianchet, and N. G. Yoccoz. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. Trends in Ecology & Evolution 13:58-63.

Gaillard, J.-M., M. Festa-Bianchet, N. G. Yoccoz, A. Loison, and C. Toigo. 2000. Temporal variation in fitness components and population dynamics of large herbivores. Annual Review of Ecology and Systematics 31:367-393.

Garcia, J., and K. Raymond. 2018. Black bear take report 2016. California Department of Fish and Wildlife, Wildlife Branch, Sacramento, California, USA.

Gray, R. J. 1988. A class of K-sample tests for comparing the cumulative incidence of a competing risk. The Analysis of Statistics 16:1141-1154.

Gray, R. J. cmprsk: Subdistribuation Analysis of Competing Risks. R package version 2.2-8. https://CRAN.R-project.org/package=cmprsk. Accessed 20 July 2019.

Griffin, K. A., M. Hebblewhite, H. S. Robinson, P. Zager, S. M. Barber-Meyer, D. Christianson, S. Creel, N. C. Harris, M. A. Hurley, D. H. Jackson, B. K. Johnson, W. L. Myers, J. D. Raithel, M. Schlegel, B. L. Smith, C. White, and P. J. White. 2011. Neonatal mortality of elk driven by climate, predator phenology and predator community composition. Journal of Animal Ecology 80:1246-1257.

Guinness, F. E., T. H. Clutton-Brock, and S. D. Albon. 1978. Factors affecting calf mortality in red deer (*Cervus elaphus*). Journal of Animal Ecology 47:817-832.

Harper, J. A., J. H. Harn, W. W. Bentley, and C. F. Yocom. 1997. The status and ecology of the Roosevelt elk in California. Wildlife Monographs 16:3-49.

Harris, N. C. 2006. Monitoring survival of young in ungulates: a case study with rocky mountain elk. Thesis, University of Montana, Missoula, Montana, USA.

Harris, N. C., D. H. Pletscher, and M. Thompson. 2007. Cause-specific mortality of rocky mountain elk calves in west central Montana. Proceedings of the symposium of the 72nd North American Wildlife and Natural Resources Conference. Wildlife Management Institute, 20-24 March 2007, Portland, Oregon, USA.

Harris, N. C., M. J. Kauffman, and L. S. Mills. 2008. Inferences about ungulate population dynamics derived from age ratios. Journal of Wildlife Management 75:1143-1151.

Hatter, I. W., and W. A. Bergerud. 1991. Moose recruitment, adult mortality and rate of change. Alces 27:65-73.

Hnilicka, P. A., J. Mionczynski, B. J. Mincher, J. States, M. Hinschberger, S. Oberlie, C. Thompson, B. Yates, D. Duane Siemer. 2004. Bighorn sheep lamb survival, trace minerals, rainfall, and air pollution: are there any connections? Symposium of North Wild Sheep and Goat Council 13:69-94.

Hosmer, D. W., S. Lemeshow, and S. May. 2011. Applied survival analysis: regression modeling of time-to-event data, second edition. John Wiley and Sons, Inc. Hoboken, New Jersey.

Howell, J. A., G. C. Brooks, M. Semenoff-Irving, and C. Greene. 2002. Population dynamics of tule elk at Point Reyes National Seashore, California. The Journal of Wildlife Management 66:478.

Husseman, J. S., D. L. Murray, G. Power, and C. M. Mack. 2003. Correlation patterns of marrow fat in rocky mountain elk bones. The Journal of Wildlife Management 67:742–746.

Janz, D. W., and D. Q. Becker. 1986. Vancouver Island elk - animal and use characteristics. Western states and provinces elk workshop. Oregon Department of Fish and Wildlife, Portland, Oregon, USA.

Jarnemo, A. 2004. Predation processes: behavioral interactions between red fox and roe deer during the fawning season. Journal of Ethology 22:167–173.

Johnson, D. E. 1951. Biology of the elk calf, *cervus canadensis nelsoni*. The Journal of Wildlife Management 15:396.

Johnstone-Yellin, T. L., L. A. Shipley, W. L. Myers, and H. S. Robinson. 2009. To twin or not to twin? Trade-offs in litter size and fawn survival in mule deer. Journal of Mammalogy. 90:453-460.

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.

Kanji, G. K. 2006. 100 Statistical tests. Sage Publications, Ltd. Thousand Oaks, California, USA.

Keech, M. A., R. T. Bowyer, J. M. Van Hoef, R. D. Boertje, B. W. Dale, and T. R. Stephenson. 2000. Life-history consequences of maternal condition on Alaskan moose. The Journal of Wildlife Management. 64:450-462.

Keller, B. J, A. D. Bleicsch, J. J. Millspaugh, C. P. Lehman, J. J. Kragel, L. P. Hansen, J. Sumners, M. A. Rumble, and G. C. Brundige. 2014. Extended duration of parturition season in North American elk (*Cervus elaphus*). The American Midland Naturalist 173:162-167.

Laake, J. L. 2013. RMark: An R Interface for Analysis of capture-recapture data with MARK. National Oceanic and Atmospheric Administration, Alaska Fisheries Science Center, National Marine Fisheries Service, Seattle, Washington, USA.

Larkin, J. L., D. S. Maehr, J. J. Cox, M. W. Wichrowski, and D. R. Crank. 2002. Factors affecting reproduction and population growth in a restored elk *Cervus elaphus nelsoni* population. Wildlife Biology 8:49-54.

Leptich, D. J., S. G. Hayes, and P. E. Zager. 1995. Coeur D'Alene elk ecology. Idaho Department of Fish and Game. Boise, Idaho, USA.

Leptich, D. J., and P. Zager. 1991. Road access management effects on elk mortality and population dynamics. Pages 126–137 in. Proceedings in elk vulnerability symposium. Montana State University, Bozeman, Montana.

Loison, A., M. Festa-Bianchet, J. Gaillard, J. T. Jorgenson, and J. Jullien. 1999. Age-specific survival in five populations of ungulates: evidence of senescence. Ecology 80:2539-2554.

Matthews, S. M., R. T. Golightly, and J. M. Higley. Mark-resight density estimation for American black bears in Hoopa, California. 2008. Ursus 19:13-21.

McCorquodale, S. M. 2013. A brief review of the scientific literature on elk, roads, & traffic. Washington Department of Fish and Wildlife, Olympia, USA. http://wdfw.wa.gov/publications/01491/wdfw01491.pdf. Accessed 12 Dec 2016.

Mitchell B., and G. A. Lincoln. 1973. Conception dates in relation to age and condition in two populations of red deer in Scotland. Journal of Zoology 171:141-152.

Monteith, K. L., V. C. Bleich, T. R. Stephenson, B. M. Pierce, M. M. Conner, J. G. Kie, and R. T. Bowyer. 2014. Life-history characteristics of mule deer: effects of nutrition in a variable environment. Wildlife Monographs 186:1-56.

Munz, P. A., and D. D. Keck. 1950. California plant communities - supplement. Journal of Systematic and Evolutionary Biology 2:199-202.

Muhly, T. B., M. Hebblewhite, D. Paton, J. A. Pitt, M. S. Boyce, M. Musiani. 2013. Humans strengthen bottom-up effects and weaken trophic cascades in a terrestrial food web. PLoS ONE 8(5):e64311.

National Oceanic and Atmospheric Administration [NOAA]. 2018. National Centers for Environmental Information. Monthly summaries for Humboldt County, California. <https://www.ncdc.noaa.gov/cdo-web/datasets>. Accessed 14 July 2018.

Noyes, J. H., B. K. Johnson, L. D. Bryant, S. L. Findholt, and J. W. Thomas. 1996. Effects of bull age on conception dates and pregnancy rates of cow elk. The Journal of Wildlife Management 60:508-517.

O'Gara, B. W., K. C. Brawley, J. R. Munoz, and D. R. Henne. 1983. Predation on domestic sheep on a western Montana ranch. Wildlife Society Bulletin 11:253–264.

Parker, K. L., P. S. Barboza, and M. P. Gillingham. 2009. Nutrition integrates environmental responses of ungulates. Functional Ecology. 23: 57-69.

Phillips, G. E., and A. W. Alldredge. 2000. Reproductive success of elk following disturbance by humans during calving season. The Journal of Wildlife Management 64:521-530.

Pradel, R. 1996. Utilization of capture-mark-recapture for the study of recruitment and population growth rate. Biometrics 52:703-709.

Quintana, N. T. 2016. Predator-prey relationships between Rocky Mountain elk and black bears in northern New Mexico. Dissertation, Texas Tech University, Lubbock, Texas, USA.

Rabe, M. J., S. S. Rosenstock, and J. C. DeVos. 2002. Review of big-game survey methods used by wildlife agencies of the western United States. Wildlife Society Bulletin 30:46-52.

Raganella-Pelliccioni E., L. Boitani, and S. Toso. 2006. Ecological correlates of roe deer fawn survival in a sub-Mediterranean population. Canadian Journal of Zoology 84:1505-1512.

Raithel, J. D., M. J. Kauffman, and D. H. Pletscher. 2007. Impact of spatial and temporal variation in calf survival on the growth of elk populations. The Journal of Wildlife Management 71:795–803.

Rearden, S. N., R. G. Anthony, and B. K. Johnson. 2011. Birth-site selection and predation risk of Rocky Mountain elk. Journal of Mammalogy 92:1118–1126.

Redwood National and State Parks. 2000. General management plan/general plan Redwood National and State Parks. Humboldt and Del Norte Counties, California, USA.

Redwood National and State Parks. 2015. 2014 Herd unit classification and management of Roosevelt elk. Redwood National and State Parks. Orick, California, USA.

Redwood National and State Parks. 2016. 2015 Herd unit classification and management of Roosevelt elk. Redwood National and State Parks. Orick, California, USA.

Rutberg, A. T. 1987. Adaptive hypotheses of birth synchrony in ruminants: an interspecific test. The American Naturalist 130:692–710.

Sarns, M. G., R. L. Lochmiller, E. C. Hellgren, W. D. Warde, and L. W. Varner. 1996. Morphometric predictors of neonatal age for white-tailed deer. Wildlife Society Bulletin 24:53–57.

Scrucca, L., A. Santucci, and F. Aversa. 2007. Competing risk analysis using R: an easy guide for clinicians. Bone Marrow Transplant. 40:381-387.

Shallow, J. R., M. A. Hurley, K. L. Monteith, and R. T. Bowyer. 2015. Cascading effects of habitat on maternal condition and life-history characteristics of neonatal mule deer. Journal of Mammalogy 96:194-205.

Shilling, F. 2016. Impact of wildlife-vehicle conflict on drivers and animals. University of California Davis, Road Ecology Center. <https://roadecology.ucdavis.edu/files/content/news/CA_WVC_Hotspots_2016.pdf>. Accessed 12 Dec 2016.

Shilling, F., C. Denney, D. Waetjen, K. Harrold, P. Farman, and P. Perez. 2018. Impact of wildlife-vehicle conflict on California drivers and animals. University of California Davis, Road Ecology Center. <http://lpfw.org/wp-content/uploads/2018/09/CA_WVC_Hotspots_2018_0.pdf>. Accessed 19 January 2020.

Singer, F. J., A. Harting, K. K. Symonds, and M. B. Coughenour. 1997. Density dependence, compensation, and environmental effects on elk calf mortality in Yellowstone National Park. The Journal of Wildlife Management 61:12–25.

Smith, B. L., and S. H. Anderson. 1998. Juvenile survival and population regulation of the Jackson elk herd. The Journal of Wildlife Management 62:1036-1045.

Smith, B. L., R. L. Robbins, and S. H. Anderson. 1997. Early development of supplementally fed, free-ranging elk. The Journal of Wildlife Management 61:27-40.

Starns, D. H., 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.

Therneau, T. 2015. A package for survival analysis in R. version 2.38, URL: https://CRAN.R-project.org/package=survival. Accessed 20 July 2019.

Thorne, T. E., R. E. Dean, W. G. Hepworth. 1976. Nutrition during gestation in relation to successful reproduction in elk. The Journal of Wildlife Management. 40:330-335.

Toweill, D. E., and J. W. Thomas. 2002. North American elk: ecology and management. Second edition. Wildlife Management Institute, Washington, DC, USA.

Unsworth, J. W., L. Kuck, M. D. Scott, and E. O. Garton. 1993. Elk mortality in the clearwater drainage of northcentral Idaho. The Journal of Wildlife Management 57:495-502.

Waring, R. H., J. F. Franklin. 1979. Evergreen coniferous forests of the Pacific Northwest. Science. 204:1380-1386.

Weckerly, F. W. 1999. Social bonding and aggression in female Roosevelt elk. Canadian Journal of Zoology 77:1379–1384.

Weckerly, F. W., A. E. Julian, and K. Schmidt. 2013. Group size dynamics of female Roosevelt elk in Redwood National and State Parks, California. https://digital.library.txstate.edu/handle/10877/5981. Accessed 10 Sep 2016.

Weckerly, F. W., and M. A. Ricca. 2000. Using the presence of sign to measure habitats used by Roosevelt elk. Wildlife Society Bulletin 28:146–153.

Wengert, G. 2000. Demography, range, habitat, condition and parasites of the Roosevelt elk (*Cervus elaphus roosevelti*) of Sinkyone Wilderness State Park, Mendocino County, California. California State Parks. California Department of Parks and Recreation, North Coast District, Eureka, California, USA.

White, C. G., and R. A. Garrott. 1990. Analysis of wildlife radio-tracking data. Academic Press, Inc., San Diego, California, USA.

White, C. G., P. Zager, and M. W. Gratson. 2010. Influence of predator harvest, biological factors, and landscape on elk calf survival in Idaho. Journal of Wildlife Management 74:355–369.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46:120–139.

Zager, P., C. White, and M. W. Gratson. 2002. Elk ecology study IV: factors influencing elk calf recruitment; job #s 1–3; pregnancy rates and condition of cow elk; calf mortality causes and rates; predation effects on elk calf recruitment. Federal Aid in Wildlife Restoration - job progress report, Idaho Department of Fish and Game. Boise, Idaho. USA.

Zager, P., C. White, and G. Pauley. 2007. Elk ecology study IV: factors influencing elk calf recruitment, project W-160-R-33, subproject 31, completion report. Idaho Department of Fish and Game. Boise, Idaho. USA.