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BLACK-TAILED DEER POPULATION ASSESSMENT IN THE MENDOCINO NATIONAL FOREST, CALIFORNIA
FINAL PROJECT REPORT – DECEMBER 2014

by

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Cover photo: Black-tailed deer doe and fawn in winter, Mendocino National Forest; Max Allen.

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BLACK-TAILED DEER POPULATION ASSESSMENT IN THE MENDOCINO NATIONAL FOREST, CALIFORNIA

PROJECT RATIONALE AND FUNDING

Columbian black-tailed deer (*Odocoileus hemionus columbianus*) (hereafter referred to as BTD) are native to California but are restricted to the northwest corner of the state between San Francisco Bay in the South, the Oregon state border in the north, the Sierra mountain range in the east, and the Pacific Ocean in the west (Pease et al. 2009). Because of its limited distribution in California, the species receives a large amount of interest from the public, particularly sport hunters, but is also sought after by photographers and other wildlife viewers. Serious concern for the welfare of California populations began several decades ago with reports of a sharp decline in hunter harvest. As the harvest continued to decline the public, including non-government organizations such as the California Deer Association and the Mendocino County Blacktail Association, and county Fish and Game Commissions approached the California Department of Fish and Wildlife (CDFW) and requested a field investigation to determine the extent and the causes of the decline and recommendations to reverse the trend and restore populations to levels seen in the 1960's (CDFW 1976 Plan for California Deer).

As a result, CDFW made the investigation of the decline of black-tailed deer in California a priority and provided financial support from accounts with dedicated big game management and conservation funds, specifically the Deer Herd Management Plan Implementation Program and Big Game Management accounts; both of which are made up of funds from the sale of big game hunting tags and therefor the majority of monetary support for the project was directly provided by hunters. The California Deer Association and the Mendocino Blacktail Association also contributed monetary support directly from donations from concerned members.

Conservation efforts have often been criticized as being only supported by sport hunters as a means of creating more game for the bag; this is not entirely untrue. But, deer are also an indicator species for the health of the ecosystem; meaning that if habitats and wild lands are maintained for deer then a host of other species benefit as well.

Realizing the need for research expertise and personnel support, the CDFW partnered with University of California Davis (UCD) researchers to conduct a field investigation to determine the extent and causes of the black-tailed deer population decline. The Mendocino National Forest and adjacent private properties were chosen as the study site because of the area's popularity for deer hunting and its ease of access for those pursuing deer from major urban areas including Sacramento, San Francisco Bay Area, and Redding. As a result, a contract between CDFW and UCD was executed on 18 June 2009 providing an initial $454,580 for 1 May 2009 through 30 June 2012. To rectify contract approval hurdles that caused a delayed start date during the initial field season, an additional $303,164 was approved for time ending 30 June 2014. As the data were being analyzed it became apparent that additional time was needed to fully develop some of the deer population analyses. Consequently, a further no-cost time extension was granted moving the final report deadline to 31 December 2014. Additional funding was graciously provided by the California Deer Association in the amount of $88,000 and the Mendocino County Blacktail Association of $5,000.

This study followed a previous study (2004 – 2007) focusing on habitat use of black-tailed deer in the Mendocino National Forest (D. Casady, CDFW) to direct habitat enhancement projects. Funding for the previous study was provided by the CDFW Deer Herd Management Plan Implementation Program ($23,113) and the California Deer Association ($29,300). Data from the previous study were made available and partially incorporated into our analyses and results.

INTRODUCTION

Widespread declines of mule deer (*Odocoileus hemionus*) and Columbian black-tailed deer across much of their distribution in western North America are a concern for both management agencies and the public. Causes of the decline are difficult to pinpoint and likely result from a combination of habitat loss, habitat degradation, and the effects of resurging predator populations (Forrester & Wittmer 2013). The population dynamics of ungulates, including BTD, are complex. In particular, the role of resource availability on population growth has long been the focus of much debate (Peek 1980, Gaillard et al. 2000, Sinclair & Krebs 2002). Likewise, the effects of predation on ungulate population dynamics is controversial (e.g., Gaillard et al. 2000, Ballard et al. 2001), especially in North America where wild ungulates are important game animals still coexisting with native predators, and resource managers face public demands to maintain high population densities (Connolly 1978).

While early studies of ungulate population dynamics were based on competing hypothesis of bottom-up effects caused by food limitation or top-down effects caused by predation (Connolly 1978, Peek 1980), it is now widely accepted that both bottom-up and top-down effects simultaneously drive ungulate populations and often interact with one another (Sinclair & Krebs 2002, Sinclair 2003). The interactions between forage and predation are likely mediated by body size (Hopcraft et al. 2010). For instance, small-bodied ungulates must rely on high-quality forage and their population dynamics are primarily driven by predation because of their high susceptibility to a relatively large number of predators (Sinclair et al. 2003, Hopcraft et al. 2010). Large-bodied ungulates on the other hand can rely on large-quantities of low-quality forage and predators have much less effect on their population dynamics. Ungulates with intermediate body size such as BTD are expected to be more strongly influenced by the interactions between forage quality and predation pressures.

The goals of this study were to determine the magnitude and causes of BTD population declines in Northern California by simultaneously evaluating the roles of bottom-up and top-down effects on vital rates (e.g., survival, pregnancy rates) and population growth. Because population dynamics in deer are driven by adult female survival and fawn survival, we focused on these aspects for our study. We also specifically investigated the role of mountain lion predation on BTD survival because lions are the primary predator of adult deer in our study area.

Specific study objectives included: 1) to estimate vital rates, causes of mortality, and abundances of adult female BTD, 2) to determine rates and causes of fawn mortality, 3) to quantify the relative contributions of habitat quality and predation on BTD mortality, and 4) to understand the predatory relationship of mountain lions on BTD.

Many of the original methods and results presented in this report have been published in peer-reviewed scientific journal articles or as part of graduate student theses and are referenced accordingly and listed in Appendix I. BTD were actively monitored in the field from June 2009 to

August 2013. Mountain lions were actively monitored in the field from June 2010 through November 2012.

STUDY AREA

The Mendocino National Forest is located in the northern Coast Range of California northwest of Sacramento midway between San Francisco Bay and the Oregon border (Figure 1). The study area encompassed approximately 1,000 km^2 (385 square miles) and included portions of Mendocino, Tehama, Glenn, and Lake Counties (39°45′N, 122°58′W); about 80% is National Forest land and the remainder is privately owned.

Two major ridges (hereafter referred to as M1 and FH7) provided the focal points of the study area (Figure 2). Elevations ranged from 396 – 2,466 m (1,300 – 8,090 ft.), with moderately rolling terrain at lower elevations and moderately steep, mountainous terrain at higher elevations. Climate in the Mendocino National Forest is considered Mediterranean and varied seasonally, with mean daily temperatures ranging from -12 to 45 °C (10 to 114 °F). Mean annual precipitation averaged 132 cm (52 in.); the majority occurring from December through March with only traces amounts from May through September. Below 1,000 m (3,280 ft.) elevation precipitation was predominantly in the form of rain, while snow was common at higher elevations and often quite deep.

Picture of the study area in the Mendocino National Forest, California

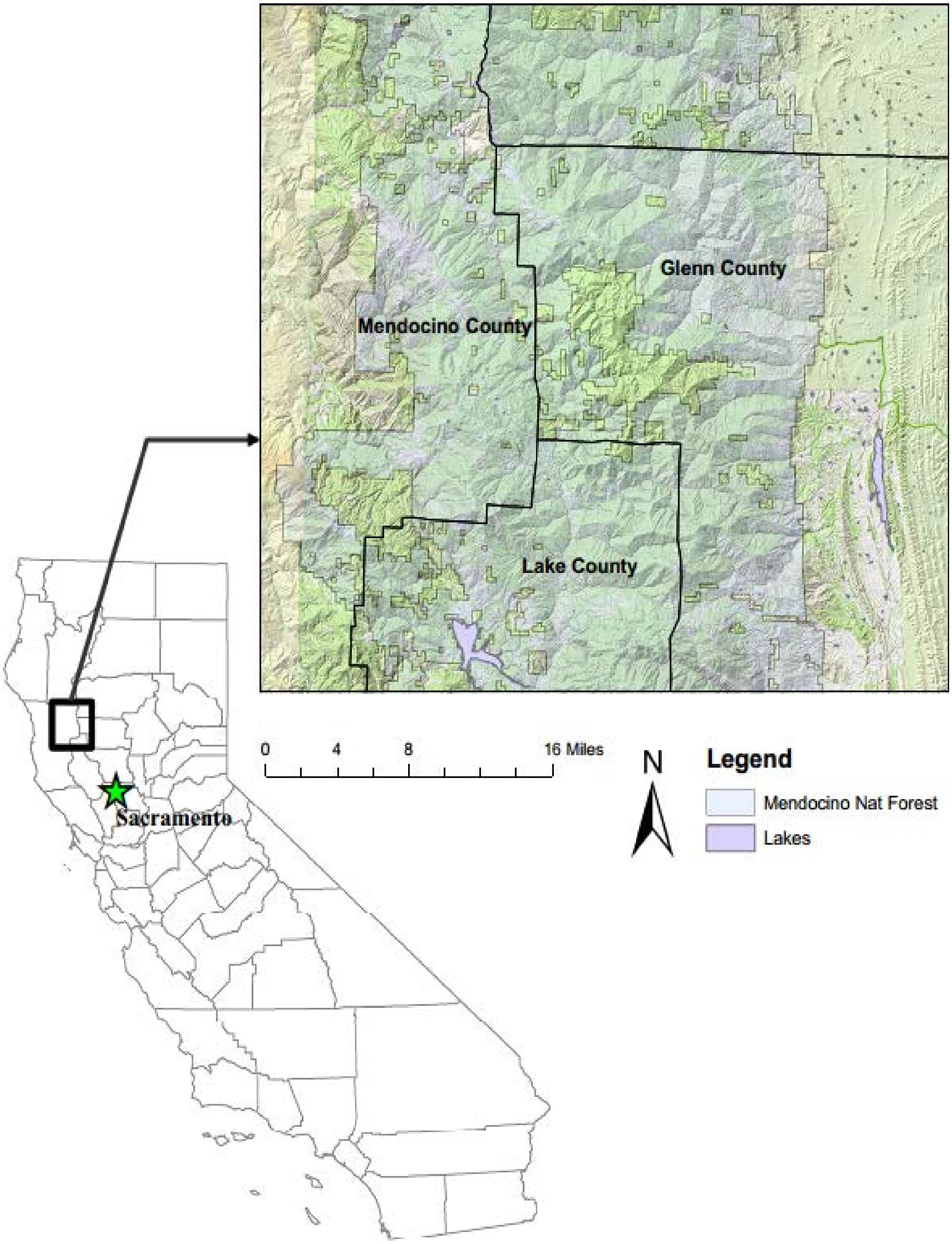

Figure 1. Location of general study area in California.

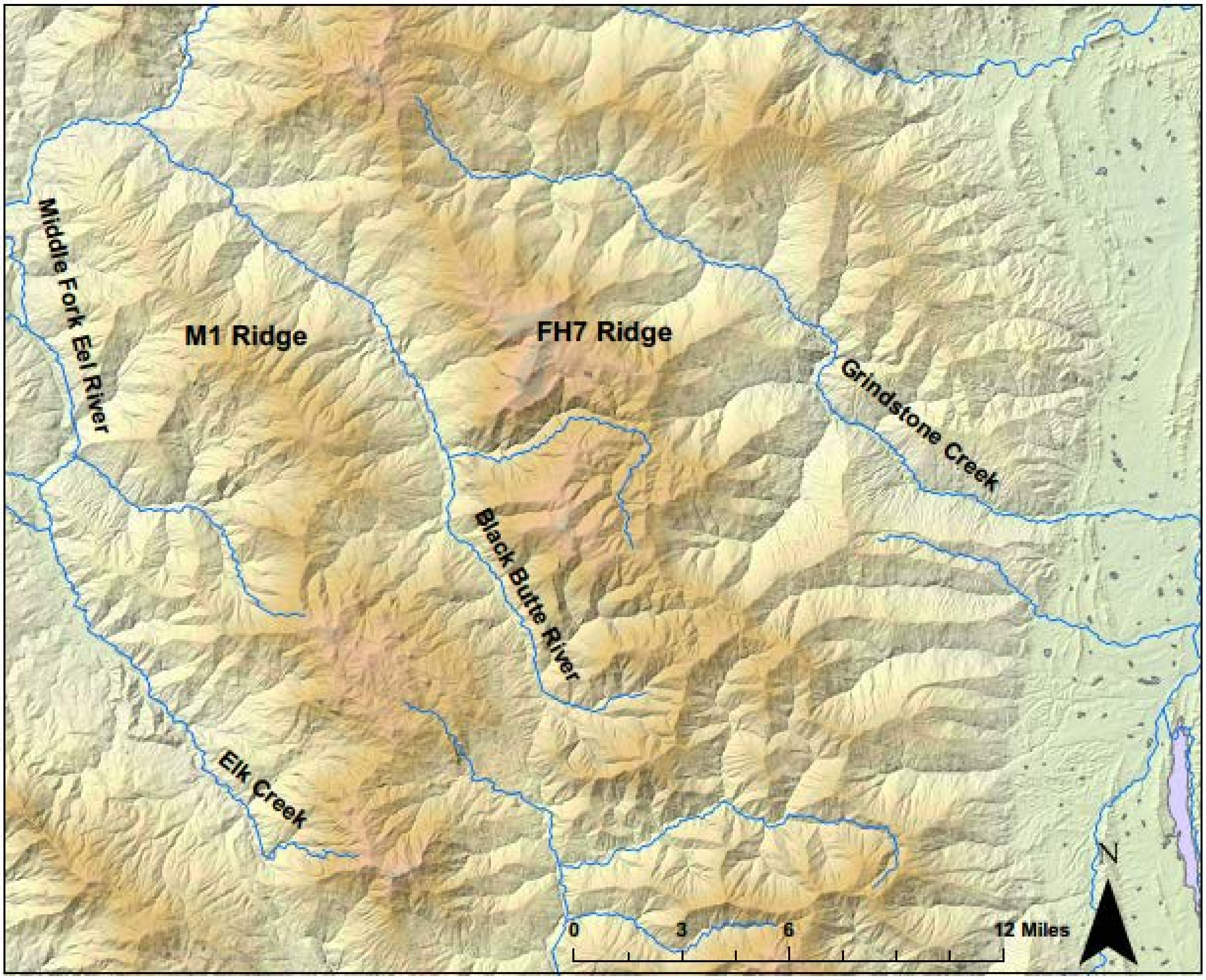

Figure 2. Location of primary study area in the Mendocino National Forest, California.

Plant communities in the study area were diverse. Major types included blue oak (*Quercus douglasii*) woodland, annual grassland, montane hardwood conifer, Douglas fir (*Pseudotsuga menziesii*), mixed chaparral, montane hardwood, ponderosa pine (*Pinus ponderosa*), Klamath mixed conifer, montane riparian and montane chaparral (Mayer & Laundenslayer 1988). Past land management activities, primarily silviculture and cattle grazing, left a mosaic dominated by even-aged conifers, with occasional mature timber stands and openings dominated by non-native grasses. Important BTD forage included many herbaceous plants, shrubs, and oaks.

BTD were the most abundant ungulate in the study area. Other ungulates observed included non-native wild pigs (*Sus scrofa*), elk (*Cervus elaphus*), and domestic cattle (*Bos taurus*). Wild pigs were observed sporadically and only at lower elevations. Elk were observed on only two occasions and were likely individuals from a reintroduced population of tule elk (*C. e. nannodes*) at Lake Pillsbury in the extreme southern end of the study area. Cattle were seasonally abundant and occupied the study area from early spring to their removal in September at the onset of deer hunting season.

BTD shared the study area with a diverse predator community which included mountain lions (*Puma concolor*), American black bears (*Ursus americanus*), coyotes (*Canis latrans*), and bobcats (*Lynx rufus*). We also observed a range of smaller mammalian and avian scavengers including gray foxes (*Urocyon cinereoargenteus*), turkey vultures (*Cathartes aura*), and common ravens (*Corvus corvax*). Smaller prey species were ubiquitous and included lagomorphs (e.g., black-tailed jackrabbit *Lepus californicus*) and rodents (e.g., California ground squirrel *Otospermophilus beecheyi*).

METHODS

Capture, Monitoring, and Mortality Assessment

All animal capture and handling procedures were approved by the Wildlife Investigations Laboratory of the CDFW, the Institutional Animal Care and Use Committee at UCD (Protocols 15341 and 16886), and adhered to guidelines established by the American Society of Mammologists (Sikes & Gannon 2011). Mountain lion research was approved through a Memorandum of Understanding (MOU) between CDFW and UCD.

Adult Deer

Adult female BTD were captured using remote chemical immobilization via free range darting. Deer were darted opportunistically from vehicles along unpaved forest roads on the two main ridges (M1 and FH7) with Pneu-Dart® compression rifles and Pneu-Dart® disposable darts at distances ranging from 5 to 50 m (5.5 to 55 yds.), as determined by laser rangefinders. A combination of Telazol® and xylazine (DelGiudice et al. 1986) was used to chemically immobilize the animals. Ketamine HCL was administered as needed to maintain anesthesia and peripheral analgesia. After injection of the immobilizing agents, we waited a minimum of 10 minutes before retrieval to minimize stress to the animal during drug induction. Once downed deer were located their legs were bound, their eyes were covered, and they were moved to shaded location during the summer or protected area during the winter. Water was available to cool animals if needed, but overheating was rarely an issue. Blankets were routinely used during the winter to keep the animals warm and maintain safe body temperature. Deer were positioned left side down with head uphill to prevent aspiration of rumen contents, and body temperature and respiratory rate were measured at 10 minute intervals. Blood oxygen saturation was continually monitored using a Nellcor™ pulse oximeter with a lingual probe attached to the tongue. After processing, xylazine was reversed with tolazine or yohimbine. Detailed capture and handling procedures including drug dosages are described in Casady & Allen (2013).

Once immobilized, deer were weighed, measured, had their body condition assessed using modified rump fat body condition scores (rBCS) that ranged from 1 (very poor) to 5 (excellent), (Gerhart et al. 1996, Cook et al. 2010), and then aged based on tooth eruption and wear. We also extracted a canine tooth for age determination (Swift et al. 2002, Bleich et al. 2003) based on cementum annuli methods (Matson's Laboratory LLC, Missoula, MT) and collected blood and tissue samples. Based on results from either of the two aging methods and observed differences in survival probabilities (Marescot et al. 2015), we grouped deer into the following 3 age classes: yearlings (1 to 2 years old), prime-aged adults (2 to 7 years old) and senescent individuals (8 years and older).

We determined if deer were pregnant during capture using two different methods. First, we took blood from a total of 43 individuals and used progesterone levels to determine pregnancy (Wood et al. 1986). Second, we verified if does were lactating or had a fawn at heel during captures and used this information to confirm pregnancy for does captured prior to July 15th of any given year for 4 individuals. We also used ultrasound and physical examinations on 11 individuals to determine the number of fetuses in uteri. Deer were then fitted with numbered ear tags and motion-sensitive store-on-board global positioning system (GPS) collars that contained very high frequency (VHF) transmitters. Location data from a subset of the collars could be remotely uploaded via an ultra-high frequency (UHF) uplink. Collars ranged in weight and we used lighter models on smaller deer ensuring that collar weights never exceeded 3% of their bodyweight.

Collared does were monitored from the ground at least two times per week during the summer from June through September. During other times of the year, monitoring occurred every 10 to 14 days either from the ground by truck or snowmobile or by air with a fixed-wing aircraft. Collars were programmed to switch to a mortality signal after 4 hours of inactivity to facilitate mortality recovery. All collars were fitted with an automatic release mechanism programmed to uncouple and allow the collar to drop off after a maximum deployment period of 2 years.

In the event of mortality, the kill site was investigated as soon as possible to determine cause of death. Cause of death was determined using systematic criteria including disposition of the carcass, predator sign such as hair shearing, evidence of caching, bite marks, and blood (Atkinson & Janz 1994). DNA swabs from bite wounds were also taken to identify predator species following methods similar to those described in Mumma et al. (2014) and, when possible, collected a femur for marrow fat analysis as an indicator of health. If no obvious external evidence of predation was found, a necropsy was performed to determine the cause of death.

Juvenile Deer

We captured fawns from mid-June to mid-July of each year by driving along the roads and catching them opportunistically or by scanning areas with binoculars for does that may have just given birth and had fawns hidden nearby; at night we used spotlights to help locate deer.

Fawns were captured by hand or with large salmon nets. Capture personnel donned new surgical gloves for each capture to avoid contaminating fawns with human scent which might increase their chance of being detected by a predator. Upon capture, fawns were placed inside a pillowcase to reduce stress and were weighed, sexed, and then fitted with a small colored and numbered plastic tag in one ear and a VHF motion-sensitive transmitter in the other ear. Battery life of VHF ear-tag transmitters was 1 year. We estimated the age of fawns by noting the levels of dryness of the umbilical cord, standing/walking coordination, and hoof growth line measurements (Sams et al. 1996). Fawn ages were estimated as a range of days and we used the median value as the age for all analyses. Fawns were released at the capture site immediately after processing, which averaged about 10 minutes.

We determined the status of fawns as either alive or dead daily from the time of capture through mid-September and then every 7 to 14 days thereafter from either the ground or by airplane during the rest of the year. VHF ear-tag transmitters switched to mortality signal after remaining stationary for 4 hours, enabling assessment of mortality causes. Cause of mortality was determined during site investigations using criteria described above for collared does.

Mountain Lions

Mountain lions were captured between June 2010 and November 2012; the majority with trained hounds and the remainder with cage traps. During the hound captures, forest roads were driven from dawn to approximately 11:00 a.m. to locate fresh tracks in the dust during summer and in the snow during winter. If fresh tracks were discovered, the hounds were released to pursue and tree the mountain lion. Once treed, the lion was darted, restrained, and processed.

Cage traps were baited with deer carcasses and set at lion scent communication areas (scrapes) (Allen 2014) or at sites we baited with deer carcasses that had fresh lion sign. To alert us of a lion entering the trap, an old VHF radio-collar was attached to the top of the trap and fishing line was run from the collar activation magnet to the opened door. Lions going into the trap would trigger the door to close and activate the collar signal, which we could then hear with the receiving unit. Using the collar alert set-up on the door allowed us to monitor the trap without having to go out to the site and potentially spook an interested lion and also to minimize the time a captured lion spent in the trap prior to processing.

Telazol® was used as the primary immobilization agent. Ketamine was administered as needed to maintain anesthesia during processing. Once anesthetized, we determined the sex and then weighed, measured, and fitted each mountain lion with a plastic ear tag and an ARGOS satellite GPS collar. Measurements of gum-line recession was used to determine the age of captured lions (Laundré et al. 2000), and we classified them as either subadults (less than 3 years) or adults (3 years and older). Detailed capture and handling procedures are described in Allen et al. (2014a).

The ARGOS collars provided immediate accesses via computer uplink with the satellite to lion location data and allowed us to quickly investigate kill sites. Collars were programmed to acquire locations every 2 hours and we downloaded data every 3 days. Data points were mapped in ArcGIS to identify clusters of 5 or more which indicated a possible kill site. Potential point clusters had to have a minimum of 8 hours between the first and last locations, be within 150 m (492 ft.) of each other, and contain at least one crepuscular or nocturnal location (Elbroch & Wittmer 2013). In this manner, we used timely location data from the collars to locate and conduct site investigations of mountain lion kill sites.

We used the state of decay of the prey carcass and the locations of bite marks to assess whether the animal had been killed by a lion or whether the lion had been scavenging. We identified prey species by the skeletal remains and external characteristics including hair and feathers.

The age at which deer fawns were killed was estimated based on the assumption that they were born on June 16th of each year - the median birth date of fawns in our study. The age of deer from 1 to 2.5 years old at kill sites was estimated using tooth eruption patterns (Heffelfinger 2010), and the age of adults older than 2.5 years old using cementum annuli methods.

Body condition of killed adult BTD was assessed from the color of the bone marrow (Hornocker 1970) with red or red/pink being “poor”, pink being “fair”, white being “good”, and all white being “excellent”. Weights of prey species were based on published literature: for deer, we used monthly sex-specific weights for fawns, and annual sex-specific weights for adults based on data from Sitka black-tailed deer (*Odocoileus hemionus sitkensis*; Parker et al. 1993), for other mammal species we used the mean weights described in Jameson & Peeters (2004), and for bird species we used the mean weights described in Sibley (2005).

Population Estimation

Deer

Deer abundance in our study area was estimated using a mark-recapture approach applied to fecal pellet samples. Pellets were collected on summer range in four fawning areas covering a total of 150 km^2 (58 square miles). In each of the fawning areas, we defined 4 x 5 km (2.5 x 3 miles) sample plots across elevational gradients that included habitats used by both male and female deer. Within each plot, we established 4 to 6 transects 1.2 km (0.7 miles) long by 2 m (6.6 ft.) wide covering a total area of 14,400 m^2 (3.56 acres). Transects were started from a random location and then followed deer trails that were closest to a random compass bearing (Brinkman et al. 2011). We ensured that no portion of a transect was less than 1.5 km (0.9 miles) from any other transect; this minimum distance was greater than the average diameter of an adult female home range (Forrester 2014), ensuring that each transect was an independent sample unit. Discrete pellet groups were determined either by the distance between pellet groups or by the size of the pellets.

The timing of our sampling occurred after the birth of fawns each year so that our abundance and sex ratio estimates included fawns. We sampled transects twice during 2011 from late August through late September and four times during 2012 from mid-July through mid-September, with each sampling event separated by 7 to10 days in both years. Due to a forest fire that occurred during the study, two transects in 2012 had to be relocated after the first sampling period and were thus only sampled three times.

On the first survey of each transect fresh pellets were collected and the older pellets cleared from the transect area plus an additional 1 m (3.3 ft.) buffer zone on either side. On subsequent surveys, we collected pellets from groups deposited since the previous collection occasion, and then cleared the remaining pellets. For each pellet group, we recorded the date, time, location, and habitat type (Mayer & Laundenslayer 1988). Four to 6 pellets were collected from each group and stored in a plastic tube containing 95-100% ethanol. Fecal samples were genotyped (UCD Veterinary Genetics Laboratory) and then abundance and sex ratios were estimated following methods presented in Lounsberry et al. (2015).

Mountain Lions

A minimum population density of lions in our study area was calculated based on the amount overlap between home ranges (Rinehart et al. 2014). Mountain lions generally avoid one another and maintain somewhat separate home ranges, males more so than females, but there is some overlap and from the amount of overlap we can estimate a snapshot minimum population size. In order to determine the amount of overlap, home ranges were estimated using the fixed bivariate kernel method (Worton 1989) based on our 402 km^2 (155 square miles) ‘trapping area’ (Rinehart et al. 2014). After mapping the home ranges of each collared lion, we summed the proportion of overlap in the trapping area to estimate lion density. Detailed procedures are presented in Allen et al. (*in press*).

Other Predators (Black Bears, Coyotes, and Bobcats)

The relative abundance and occupancy (probability of occurrence across the landscape) of black bears, coyotes, and bobcats on summer range fawning areas were estimated using remote cameras. Locations for camera placement were chosen by placing a 12 to 14 km^2 (4.6 to 5.4 square miles) grid with 1 km^2 (0.4 square mile) cells over a map of the four fawning areas and randomly selecting grid cell centers. We set cameras within 100 m (328 ft.) of these grid centers (Rowcliffe et al. 2008) near areas of suspected animal activity including trails, closed roads, springs, and mountain lion scrapes.

An average summer home range size of 1 km^2 (0.4 square miles) (Bunnell & Harestad 1983, McCorquodale 1999) was used as the grid cell size to estimate the probability of predator use of female deer home ranges in each fawning area (MacKenzie et al. 2005). Cameras were deployed for 3 month periods beginning in mid-June of each year and ending in September. We deployed 8 to10 cameras in each of the four sampling grids for a total of 32 to 35 cameras per deployment resulting in 8,980 trap-days over three summers. One trap-day equals one camera deployed for one day.

The computer program PRESENCE (Hines 2006) was used to model both probability of use of a deer home range and detection probability for each major fawn predator. Mountain lions were not included in our analyses because there were so few of them caught on camera and we had collared lions in the area from which to get location data. Predator relative abundance was estimated for three critical periods for BTD fawns; the neonate period (mid-June to mid-July), the hiding period (mid-July to mid-August), and at heal period (mid-August to mid-September) (Wallmo 1981). Detailed methods are presented in Forrester (2014).

Survival Analysis

Multistate Capture-Mark-Recapture (CMR) Models

We conducted three separate analyses to estimate survival probabilities of BTD in the Mendocino National Forest. First, we estimated the spatial and temporal variation in cause-specific mortality rates in fawns and in yearlings, prime-aged adults, and senescent individuals using multistate capture-mark-recapture (CMR) models (Schaub & Pradel 2004). Survival analyses for fawns and adults were conducted separately because of differences in maximum deployment periods between VHF transmitters for fawns; always 1 year, and GPS collars for adults; either 2 years for 32 individuals or 1 year for 25 individuals. Finally, we used encounter histories of 23 additional adult female BTD captured during the previous study in the Mendocino National Forest conducted between 2004 and 2007 (D. Casady, unpublished data) to estimate age-specific survival probabilities of female deer greater than 1 year old over a longer time period, totaling 7 years, based on a simplified version of multistate CMR models. Detailed descriptions of all three survival analyses including model selection are given below and in Marescot et al. (2015).

Model 1: Juvenile Survival

We used multistate CMR models (Schaub & Pradel 2004) in Program E-SURGE (Choquet et al. 2009) to estimate survival probabilities (ϕ) of fawns. Based on our monitoring schedule we described monthly encounter histories resulting in 48 recapture occasions; 4 complete years from June 2009 to May/June 2013. Fawn survival models accounted for censored individuals due to collar failures that are still potentially at risk of mortality because previous research has highlighted the importance of incorporating unobservable states when modeling mortality causes (Tavecchia et al. 2012). Because of rugged terrain resulting in limited access during winter, we could not always verify the status of fawns. We thus also accounted for fawn detection probabilities to more accurately estimate their survival.

Individual fawns with known fates were assigned one of the following three states for a particular encounter occasion: alive (A+), dead due to predation (DP+), or dead due to other, unknown causes (DO+). Fawns with unknown fates were assigned one of the following three unobservable states: alive (A-), dead due to predation (DP-), or dead due to other causes (DO-). These "unobservable" states included four fawns that had transmitter malfunctions and one fawn with either a dropped or malfunctioning transmitter. Individuals dying at time *t* transitioned into an absorbing state (D) at time *t*+1 during the recapture occasion independent of cause of mortality (Gauthier & Lebreton 2008). Since other mortalities (DO) potentially included predation, the proportion of death caused by predation is likely underestimated. The transition matrix T from state *t* to another state at time *t*+1 could then be written as:

$$
T = \left[\begin{array}{cccccccc}
 & A+ & A- & DP+ & DP- & DO+ & DO- & D \\
A+ & \alpha\phi & (1-\alpha)\phi & \alpha(1-\phi)\beta & (1-\alpha)(1-\phi)\beta & \alpha(1-\phi)(1-\beta) & (1-\alpha)(1-\phi)(1-\beta) & 0 \\
A- & 0 & \phi & 0 & (1-\phi)\beta & 0 & (1-\phi)(1-\beta) & 0 \\
DP+ & 0 & 0 & 0 & 0 & 0 & 0 & 1 \\
DP- & 0 & 0 & 0 & 0 & 0 & 0 & 1 \\
DO+ & 0 & 0 & 0 & 0 & 0 & 0 & 1 \\
DO- & 0 & 0 & 0 & 0 & 0 & 0 & 1 \\
D & 0 & 0 & 0 & 0 & 0 & 0 & 1
\end{array}\right]
$$

The matrix T was decomposed into three actual transition matrices in E-SURGE. The first matrix allowed estimating α, the probability that a telemetry device functioned up to its expected lifespan of 1 year. The second matrix allowed estimating the survival process and its associated probability ϕ. The third matrix allowed estimating the probability of mortality caused by predation β (Schaub & Pradel 2004). Finally, we also estimated the detection probability of fawns, which we assumed to be constant to avoid parameter redundancy (Gimenez et al. 2003).

A set of candidate models were developed to test for temporal and spatial variability in survival probabilities of fawns. We compared models using AIC corrected for small sample sizes and selected the best model with the lowest AIC_c value (Burnham & Anderson 2002). We independently tested for effects of summer during the first 3 months of a fawn's life when the majority of mortalities occurred, season, and year and trimester (seasonal effects among years) on survival probabilities and mortality due to predation. Since female selection of fawning sites with respect to habitat may affect survival of fawns (e.g., Ballard et al. 2001), we also tested for spatial variation in both fawn survival probabilities and mortality due to predation among fawning areas, that is between fawns captured on FH7 versus M1 ridges.

Model 2: Adult deer greater than 1 year old survival

The same CMR models and transition matrices as described above were used for fawns to estimate age-specific survival of females greater than 1 year old. However, we had three additional months of data for adult BTD and thus monthly encounter histories included 51 recapture occasions rather than 48 as described for fawns. The models also differed slightly since we accounted for "unobservable" states including the probability of dropping a collar at the end of the battery lifespan (17 individuals) and the probability of collar failure (5 individuals) but contrary to fawns set the detection probability to 1 since the adults were fitted with GPS collars and we were confident of their fates.

For adult females, we compared models with the same temporal and spatial covariates as presented above for fawns. Model parameters, however, differed due to the three additional sampling occasions compared to fawns. Since previous research on ungulates including mule and black-tailed deer showed variation in survival probabilities among yearlings, prime-aged females and older individuals (Forrester & Wittmer 2013), we further tested for age-specific variation in survival probabilities. Such a focus also allowed us to test for variability in predation risk among individuals in different age classes and thus its relationship to senescence. To account for individuals transitioning across the age classes of non-breeding yearlings, prime-aged adults between 2 and 7 years old, and senescent adults of 8 years or older, we corrected age of individuals based on time elapsed since first capture (Choquet et al. 2009).

Live Encounter and Dead Recovery Models

Model 3: Adult deer greater than 1 year old survival over the entire study period

Combining the data from the 2004 to 2007 study period with those from the 2009 to 2013 period, we modeled age-specific survival probabilities of BTD greater than1 year old using live encounter and dead recovery models in E-SURGE (Choquet et al. 2009). These models are simplified versions of the multistate CMR models used for fawns and adults above because causes of mortality were not identified during the initial study period. We assigned 15 censored individuals from 2004 to 2007 and 22 from 2009 to 2013 a negative value indicating that they were removed from the analysis at last detection (Choquet and Nogue 2010). In this simplified analysis we only tested for the effects of age, season, year, trimester (season among years) and study periods.

Population Growth Rates

Lefkovich Projection Matrix

We used a post-breeding Lefkovitch projection matrix (Caswell 2001) to estimate the asymptotic growth rate of BTD in our study area. Because many ungulates including BTD are strongly age-structured, polygenous (have multiple mates), and iteroparous (have multiple reproductive cycles over the course of a lifetime) (e.g., Gaillard et al. 1998, Forrester & Wittmer 2013), we built a female only matrix, structured into 9 age classes with senescent individuals pooled into 1 class. Adult survival was limited to a maximum age of 22 years, which corresponded to the oldest deer observed in our study area (an individual killed by one of our collared mountain lions, Matson's Laboratory) (Allen 2014). Age-specific annual survival rates for fawns (ϕ_f), yearlings (ϕ_y), prime-aged (ϕ_a), and senescent individuals (ϕ_s) from the initial CMR models were used to parameterize the matrix. We assumed that females give birth for the first time on their second birthday and determined reproductive rates r from the mean proportion of females observed pregnant each year multiplied by the mean number of fawns per female and adjusted by respective age-specific survival probabilities. We estimated reproductive rates of yearlings (r_y) separately, since previous research on mule deer suggested that pregnancy rates can be lower for this age group (Monteith et al. 2014). Reproductive rates were divided by 2 to reflect per capita number of female fawns (Caswell 2001).

The resulting Lefkovitch matrix L was thus described as:

$$L = \begin{bmatrix} 0 & r_y & r_a & r_a & r_a & r_a & r_a & r_a & r_s \\ \phi_f & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & \phi_y & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & \phi_a & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & \phi_a & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & \phi_a & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & \phi_a & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & \phi_a & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & \phi_a & \phi_s \end{bmatrix}$$

where;

r_y = reproductive rate of yearlings

r_a = reproductive rate of prime-aged adults

r_s = reproductive rate of senescent adults

ϕ_f = annual survival rate of fawns

ϕ_y = annual survival rate of yearlings

ϕ_a = annual survival rate of prime-aged adults

ϕ_s = annual survival rate of senescent adults.

We used a simulation approach based on Monte Carlo iterations (Alvarez-Buylla & Slatkin 1993) to account for uncertainty in parameter estimates and population growth. We ran 10,000 Monte Carlo iterations using the rbeta function (stats v2.15.3 R package) in which survival probabilities were drawn from a beta distribution with parameters calculated in a way that expectation and standard deviations would be equal to annual survival estimates and standard errors obtained from the multistate CMR analysis. Associated variances of survival probabilities were determined based on standard errors and calculated using the delta method (Burnham & Anderson 2002). For each iteration, reproductive rates were drawn from a lognormal distribution using the mean number of pregnant females per year and related standard deviation obtained from our data. We used the R package (popbio) (Stubben & Milligan 2007) to determine the mean (±SD) asymptotic growth rate calculated from the dominant eigenvalues of the 10,000 matrices generated from the Monte Carlo iterations. We also estimated the predicted population growth rate using survival estimates for the entire study period.

Sensitivity and Elasticity Analysis

All sensitivity analyses were conducted using the function vitalsens in popbio v2.4 R package. We estimated first order sensitivities and elasticities to assess contributions of vital rates from our Lefkovitch matrix using standard methods and equations (Caswell 2001). Since sensitivities and elasticities were estimated from results of each of our 10,000 model iterations, we were able to determine variances associated with each estimate.

Lower-level elasticities (Caswell 2001) were then assessed to quantify the relative importance of proportional changes in the underlying components on population growth (Gervasi et al. 2012). We specifically looked at cause-specific mortalities associated with survival estimates of different age classes associated with survival. This allowed us to quantify the selective pressure of predators only affecting certain age groups and their subsequent contributions to the dynamics of BTD in the Mendocino National Forest. We tested whether elasticity values were robust with respect to our classification of the cause of mortality by assuming that there was no misclassification of causes of mortality, that approximately 80% of the observed other causes of adult mortality were due to predation while simultaneously assuming that approximately 50% of other causes of fawn mortality were due to predation, and that approximately 80% of the other unknown causes of fawn mortality were due to predation while assuming that approximately 50% of other causes of adult mortality were due to predation.

To do so we replaced the proportion of mortalities due to predation β with $\beta + \mu\,(1 - \beta)$, where μ is the probability of misclassifying mortalities due to predation as other mortalities. For instance, in the sensitivity and elasticity analysis based on assumption that approximately 80% of the observed other causes of adult mortality were due to predation while simultaneously assuming that approximately 50% of other causes of fawn mortality were due to predation, the random value of μ associated with adults was drawn from a uniform distribution ranging from 0.6 to 1 (mean of 0.8) while the random value of μ associated with fawns ranged from 0 to 1 (mean of 0.5).

Contributions of predation to lower level elasticities were quantified by decomposing the overall survival rate in each age class *i*, *Si* by the following expression

$$S_i = 1 - MP_i(1 - ax) - MO_i \qquad \textit{Equation 1}$$

where MP_i and MO_i represent the mortality rates due to predation and other causes in age class *i*, obtained from the product of the CMR estimates $(1 - \phi_i)\beta_i$ and $(1 - \phi_i)(1 - \beta_i)$, with the annual survival probabilities ϕ_i, and the proportion of mortalities due to predation β_i corrected by the probability μ of misclassifying mortalities. The parameter *a* referred to the amount of additive mortality. When *a* is equal to 1, mortality is fully additive and when it is equal to 0, mortality is compensatory. Finally x_i represents the proportional reduction of mortality due to predation in the case of a hypothetical management action. Multiplying mortality rate due to predation with $(1 - ax)$ then allows evaluating the elasticities of the lower level parameter and thus the demographic outcomes of a management strategy that would reduce mortality by predation (Schaub & Pradel 2004).

Bottom-Up and Top-Down Variables

Measuring Environmental Covariates

Vegetation Surveys

We surveyed all fawning areas to quantify percent cover and composition of deer forage types and to estimate biomass of shrubs, forbs, and grasses on summer ranges. Surveys were conducted along 100 m (328 ft.) transects with random starting points located on grids superimposed over maps of fawning areas. Shrub cover and species composition was estimated using the line-intercept method (Bonham 1989). Amounts of forage available to deer from shrubs was estimated using twig counts on three 1 x 3 m (3.3 x 9.8 ft.) quadrats per transect (Shafer 1963). Herbaceous biomass was estimated using the comparative yield (CY) and dry weight ranking (DWR) methods on ten 0.25 m^2 (2.7 square ft.) quadrats per transect (Haydock & Shaw 1975, Jones & Hargreaves 1979). We identified shrubs to species, classified all small flowering plants as forbs, and categorized grasses as annual or perennial. We conducted 157 line transect surveys, conducted CY and DWR surveys on 1770 quadrats, and counted all twigs equal or smaller to typical deer browse diameter on 471 quadrats. We measured 100 to 200 browsed twigs to obtain the mean species-specific browse diameter for important deer browse, including mountain whitethorn (*Ceanothus),* bitter cherry (*Prunus),* manzanita (*Arctostaphylos),* and oak (*Quercus)* species. We estimated habitat specific forage amounts for Classification and Assessment with Landsat of Visible

Ecological Groupings (CALVEG) cover types (Schwind & Gordon 2001); conifer, hardwood, mixed conifer and hardwood, shrub, and herbaceous. Habitat weighted estimates of forage were created by estimating the amount of forage for each habitat type per fawning area, summing these values from all habitat types, and then dividing by the total area. Herbaceous biomass was variable among years so herbaceous forage values were calculated for each year, while shrub biomass was less variable and average shrub browse was calculated for all years combined.

A forage availability index was created for winter range by estimating the percentage of area of CALVEG vegetation types containing high quality deer forage. High quality forage types were determined using past research (Dasmann & Taber 1956, Wallmo 1981, Livezey 1991) and included oak woodland, herbaceous meadows, and high quality shrub types. Winter ranges were delineated as minimum convex polygons from GPS locations obtained from our adult collared deer. We used these same polygons for fawn winter ranges because fawns spend their first winter with their mother (Wallmo 1981) and our transmittered fawn winter locations were within these areas.

Deer Diet Analysis

Deer fecal pellets were collected in fawning areas on transects that followed deer trails with randomly located starting points distributed across available habitat types. Diet composition was analyzed using microhistological analysis (Holechek et al. 1982, Leslie et al. 1983) and diet quality was indexed using fecal nitrogen and diaminopimelic acid (DAPA) (Hodgman et al. 1996). We used previous work (Dasmann & Taber 1956, Wallmo 1981, Kie et al. 1984) and our dietary analysis to determine the most important shrubs for deer in our study area and estimated nutritional quality for these species, including crude protein, in vitro dry matter digestibility, and tannin analysis. All diet analyses were performed by the Wildlife Habitat and Nutrition Laboratory at Washington State University.

Weather Variables

Daily precipitation and temperature data was acquired from four United States Geological Survey weather stations and snowpack depth from two California state snow monitoring areas located in the study area. We created a winter severity index that was the number of days below freezing (0 °C, 32 °F) from deer arrival on winter range to each week during the year. We accounted for difference in elevation between deer home ranges and weather stations by adjusting the temperature of the weather station nearest the winter range by the standard environmental lapse rate of 6.49 °C per 1000 meters (44 °F per 3,281 ft.) elevation. Our weather variables included winter severity index, total precipitation to date, previous total winter precipitation, and total April snowpack.

Deer Home Ranges

Home ranges of adult BTD were estimated at the 95% isopleth using the local convex hull method with the “minimum spurious hole covering” rule (Getz & Wilmers 2004, Getz et al. 2007). Summer and winter home ranges were estimated separately based on GPS locations of our collared deer. We relied on clumping patterns in the location data and excluded those that were obviously distinct elevational changes, as occurred during migration.

The weekly probability of deer leaving their home range was calculated by dividing the number of locations outside the home range by the total number of locations for each week. We chose a weekly interval because our data suggested that mountain lions in our study area on average killed

1.07 deer per week (Allen et al. 2014a). We assigned individuals to distinct summer and winter ranges using spatial gaps in the GPS data greater than twice the size of the average diameter of an adult home range and geographic features that created barriers to movement. The extent of these distinct seasonal ranges was determined using 95% minimum convex polygons from GPS locations of all collared deer within each seasonal range.

Cumulative Incidence and Cox Proportional Hazard Functions

Cumulative incidence and proportional hazards functions were used to evaluate how environmental covariates were related to fawn survival. To evaluate the possible effect of bottom-up variables on adult survival in greater detail, we modeled how mortality risk of adult female deer varied with use of familiar areas, forage availability, age class, and elevational overlap with simultaneously collared mountain lions using Cox proportional hazards models.

Model 4: Fawn Survival Based on Effects of Environmental Covariates

Cumulative incidence functions (CIFs) were used to estimate cause-specific fawn mortality and survival rates by month throughout the first year of life (Heisey & Patterson 2006). CIFs model each mortality source while accounting for the probability of dying from all other possible causes of mortality (Heisey & Patterson 2006). These functions are based on proportional hazards models (Cox 1972) and model the probability of mortality from cause *i* occurring before time *t*.

$$\mathrm{CIF}_i(t) = P(T \leq t \text{ and failure from cause } i) \qquad \textit{Equation 2}$$

We modeled fawn mortality risk with Cox proportional hazards because seasonal hazard functions could not be fit using parametric functions. We used the standard Cox proportional hazards formula

$$h(t|X_j) = h_0(t)\,exp(X_j\,\beta_x) \qquad \textit{Equation 3}$$

where t is time as specified in the model (e.g., days since birth), $h(t|X_j)$ is the hazard rate for the jth deer at time t, $h_0\,(t)$ is the baseline hazard, and the regression coefficients β_x are estimated from the risk covariates X_j for the jth deer (Cox 1972, Therneau & Grambsch 2000). The β_x are used to estimate hazard ratios that are a measure of the risk of death similar to an odds ratio. The hazard ratios are the exponential functions of the β's from equation 2 and a hazard ratio (HR) of less than or greater than 1 represents a smaller or greater risk of death respectively. We considered a HR significantly different than 1 if the 95% confidence interval did not overlap 1.

Because we captured fawns soon after birth we modeled survival as a function of age in days (Fieberg & DelGiudice 2009). We used a delayed entry design where we estimated risk beginning at birth but fawns entered the analysis at the day of capture for summer survival and the day of arrival on winter range for winter survival. We censored animals from analysis after death, after the last day on summer range (max value = 104 days of age), or after recruitment to a yearling (Hosmer et al. 2011).

The risk of summer and winter fawn mortality was modeled separately because seasonal ranges were spatially separated and as a result of their increase in body size fawns were at risk from a smaller number of predator species during winter. Covariates of mortality risk during summer were estimated either within seasonal home ranges of individuals or distinct fawning areas and included biomass of oak and herbaceous forage, relative predator abundance, previous winter precipitation, spring precipitation, as well as sex, age and weight at capture, and twin status of fawns. Covariates of mortality risk during winter were again estimated either within seasonal home ranges of individuals or distinct population ranges and included amount of oak and shrub habitat types on winter range, cumulative winter precipitation, cumulative days below freezing, average weekly elevation, and a predation risk index that was the difference between average weekly elevation of deer and mountain lions (Allen et al. 2014a). We used pairwise correlation coefficients to assess if covariates were correlated (correlation >0.5). We evaluated all possible model subsets from remaining covariates (Whittingham et al. 2006, Arnold 2010) and used Akaike Information Criterion adjusted for small sample sizes (AIC_c) to rank models (Burnham & Anderson 2002). We considered a model to be strongly supported if the AIC_c score was < 4 AIC_c from the next model (Burnham & Anderson 2002). We used Akaike weights (*wi*) to calculate the relative importance of all covariates and model averaging methods to calculate average hazard ratios, standard errors, and confidence intervals from all models if no model was strongly supported (Burnham & Anderson 2002, Johnson & Omland 2004).

We tested possible linear and non-linear interactions using fractional polynomials (Royston & Sauerbrei 2004). We tested the assumption of proportional hazards for covariates in the model using graphical methods and Shoenfeld residual plots (Grambsch & Therneau 1994). If the proportional hazard assumption was violated, we assessed covariate fit and form using Martingale residuals and transformed variables or stratified the model by the appropriate variable (Hosmer et al. 2011). If variables that changed over time violated the proportional hazard assumption we split our dataset at the failure times and interacted the variables with a time function (Hosmer et al. 2011). We chose the appropriate time function by fitting a locally weighted scatterplot smoothed (lowess) graph of the Martingale residuals against the covariates interacted with various time functions, and used the function that created the most linear plot (Therneau & Grambsch 2000, Cleves et al. 2010). We assessed model fit by plotting the cumulative hazard function against the Cox-Snell residuals and testing for a 1:1 fit (Therneau & Grambsch 2000). We assessed if outliers unduly affected the model by graphing DFBETA residuals (Cleves et al. 2010) and likelihood displacement values (Collett 2003) against analysis time.

The cause-specific risk of bear and coyote predation was modeled using CIFs with the semi-parametric method formulated by Fine & Gray (1999). This method models the CIF for cause *i* as the cumulative sub-hazard function for that cause alone, and covariate effects for cause *i* can be interpreted similarly to a Cox proportional hazards model. We tested assumptions of the CIF models with the same methods as the Cox proportional hazards models, selected models using AIC_c, and used model averaging if we did not find one best model (Burnham & Anderson 2002). All statistical tests were performed in STATA ver. 12.1 (StataCorp, College Station, TX).

Model 5: Adult Survival Based on Effects of Environmental Covariates

We again used cumulative incidence functions (CIFs) and Cox proportional hazards to evaluate the effects of environmental covariates on the summer, winter, and annual cause-specific mortality rates of adult BTD. Both methods have been described in detail above. Note that we calculated associated standard errors using the delta method (Coviello & Boggess 2004). First, we used CIFs to calculate the summer, winter, and annual cause-specific mortality rates of deer. In particular, we examined how forage availability, proximity to predators, weather, individual characteristics and the probability of spending time outside the home range affected the risk of mortality using an *a* *priori* set of models. We used the amount of summer herbaceous and oak forage and the area of herbaceous and oak CALVEG cover types within a seasonal home range in the “forage” model. We used the distance between the mean monthly elevation of mountain lions and deer (Allen et al. 2014a) in the “proximity to predators” model. We created a “weather” model with precipitation and the number of freezing days as time varying covariates for each weekly encounter date. The “individual deer” model consisted of age class and the probability a deer was inside or outside the 95% isopleth of its seasonal home range. We also tested for combinations of each of the variables (e.g., forage + proximity to predators + weather). Prior to our analysis, we ensured covariates were not highly correlated (i.e., correlation coefficients $<|0.7|$).

The risk of mortality was then modeled using Cox proportional hazards. We considered a hazard ratio significantly different than 1 if 1 was not included within the 95% confidence interval. We used a delayed entry design with left and right censored data with survival time based on biological years (Fieberg & DelGiudice 2009) beginning on June 1st where deer entered the analysis at capture and exited upon death or dropping their GPS collar (Hosmer et al. 2011).

The probability a deer stepping outside the 95% isopleth of its seasonal home range was estimated using a multiple failure Cox proportional hazards model (Therneau & Grambsch 2000). Deer were counted as outside of their range if any locations fell outside the home range on the day selected for the encounter history. In this application of the model the hazard ratio was an odds ratio that measured the probability of leaving the home range, and the β_x were used to estimate the odds ratios for each covariate. We used the same model set described in the survival analysis above.

We tested the assumption of proportional hazards for covariates in Cox hazards and CIF models using graphical methods and Shoenfeld residual plots (Grambsch & Therneau 1994). If time varying variables violated the proportional hazard assumption we interacted the variables with an appropriate time function (Therneau & Grambsch 2000, Cleves et al. 2010, Hosmer et al. 2011). We assessed model fit by plotting the cumulative hazard function against the Cox-Snell residuals and testing for a 1:1 fit (Therneau & Grambsch 2000).

Models were selected using Akaike Information Criterion adjusted for small sample sizes (AIC_c) and present models within 4 AIC_c units of the best model (Burnham & Anderson 2002). We considered nested models as competitors for best model only if parameters in the model were significant at the 0.1 level or if parameters were not merely a subset of the competing model (Burnham & Anderson 2002, Arnold 2010). If multiple non-nested models were within $\Delta 4$ AIC_c of the best model we report model-averaged parameters (Burnham & Anderson 2002).

Post-hoc analyses were conducted to test if lower survival probabilities of senescent deer could be attributed to differences in home range composition and habitat selection between age classes. We tested for differences in the amount of forage inside home ranges of prime-aged and senescent individuals using repeated measures analysis of variance, or Friedman’s test for repeated measures if variables could not be transformed to meet normality assumptions, with age class as the independent variable and amount of specific habitats as dependent variables. We tested if the amount of forage within a home range was normally distributed with the Shapiro-Wilk test and used Bartlett’s test to determine if variance was homoscedastic.

RESULTS

Capture, Monitoring, and Mortality

Adult Deer

We captured a total of 61 adult female deer from 2008 - 2013. Including the 23 additional deer captured during the previous study by D. Casady (CDFW) from 2004 - 2007, a total of 85 successful captures (one deer was captured twice) occurred in the study area between 2004 and 2013. Three deer died during capture and are not included in subsequent analyses. Two deaths were due to respiratory failure of previously compromised individuals with congested lungs confirmed by necropsy, and one death resulted from a dart penetrating the abdominal cavity. The average weight of deer captured was 45.63 kg (100.6 lbs.) and ranged from 29.5 – 68.0 kg (65 – 150 lbs.). See Appendix II for detailed drug dosages, handling times, and vital statistics. High body temperature readings averaged 38.3 °C (100.9 °F) and overheating was usually not a concern; 38.3 °C (101 °F) is considered normal (CDFW Wildlife Investigations Lab 2010) and 40 °C (104 °F) and above considered elevated and cause for concern (Kreeger et al. 2002). Our greatest challenge during capture and processing was maintaining blood oxygen levels above 70% which is considered within safe margins (Kreeger et al. 2002); 100% is considered normal for non-drugged animals (CDFW Wildlife Investigation Lab 2010). It was especially difficult when captures occurring in early summer when animals were in late-stage pregnancy. The combination of xylazine - a respiratory depressant, coupled with fetal crowding which reduces the thoracic area available for lung expansion, made maintaining safe blood oxygen levels challenging. As a result, we refined handling methods, monitoring, and drug doses to maintain safe levels and prevent capture related mortalities. These refinements are presented in Casady and Allen (2013).

The total sample for the 2009-13 period consisted of 57 deer, 26 of which used high elevation summer habitat on the M1 ridge and 31 of which used summer habitat along the FH7 ridge. Yearlings constituted 5%, prime-aged individuals aged 2 to 7 years constituted 77%, and senescent individuals constituted 18% of the 2009-2013 sample. We observed a similar age structure when we added the 23 individuals captured between 2004 and 2007 to our analysis: 8% yearlings, 77% prime-aged individuals, and 15% senescent individuals.

Pregnancy rates averaged 0.87 ±0.05 (87%) across years and pregnant females carried an average of 1.9 fawns. For population growth estimates, we assumed reduced pregnancy rates of 0.60 (60%) for yearlings based on proportional differences between yearlings and older individuals presented in Monteith et al. (2014).

Adult deer were monitored an average of 397 days prior to collars dropping off at the end of their battery life, animal death, or collar malfunction (Appendix III). GPS location data was retrieved for 50 individuals. The number of locational fixes retrieved from collars totaled 149,324 and ranged from 144 to 7,873. Fix success rates averaged 83% and ranged from 55% to 99%.

The average seasonal home range size for all deer more than 2 years old was 0.71 km^2 (175.4 acres). Summer home ranges averaged 0.61 km^2 (150.7 acres) and were slightly smaller than winter home ranges which averaged 0.86 km^2 (212.5 acres). There was no difference in home range sizes of prime-aged and senescent deer during summer or winter. Yearlings, however, utilized slightly larger summer and winter ranges than the other age classes. Seasonal home ranges of individual deer have been summarized in Appendix IV.

Field investigations were conducted to determine the cause of all collared deer deaths. Investigations of mortality sites on summer range were performed in an average of 8 days. Due to inclement weather, deep snow, and rough terrain, winter investigations took an average of 147.5 days.

Predation accounted for 57% of the 21 adult collared deer mortalities we investigated with mountain lions taking 11 and black bears taking one. The deer killed by a black bear was likely a nutritionally stressed individual. Of the remaining mortalities, two (10%) were due to poaching and seven (33%) were due to unknown causes. Eight individuals died during 2004-2007 thus increasing the total mortalities to 29.

Juvenile Deer

We captured a total of 137 fawns, 71 of which were captured on the M1 ridge and 66 on the FH7 ridge (Appendix V). The mean capture date over all years was June 27 with a range from 6 June to 19 July. Seventy-two fawns were female, 64 male, and 1 fawn of unknown sex after having originally been identified as male. The average weight at capture was 3.66 kg (8.01 lbs.) and ranged from 2 to 7.03 kg (4.4-15.5 lbs.). The estimated average age at capture was 4.81 days and ranged from 1 to 10 days. Mean capture age and capture weight were not significantly different among years or between the M1 and FH7 ridges. One fawn died of capture related injuries and was excluded from all subsequent analyses. Of the remaining 136 fawns, 42 were twins and 94 were singles. We did not capture both fawns of all sets of twins.

Fawn mortalities during summer were investigated within an average of 1.1 days while mortalities that occurred during the winter were investigated within an average of 24.2 days following the detection of a mortality signal from the ear-tag radio transmitter. Again, inclement weather and limited accessibility due to snow delayed investigations in winter. Predation was the primary cause of fawn mortality with black bears contributing the largest single source. The majority (61%) of total mortality and of predation mortality (69%) occurred within 30 days of birth. During summer, there were low numbers of mortalities assessed as unknown predators (5% of summer mortality) or unknown cause (8% of summer mortality). Only 22% of annual mortality occurred on winter range, and most known causes were attributed to predation. Although we could not assess the cause of mortality in most instances, no winter mortalities were attributed to malnutrition.

Mountain Lions

We captured a total of 5 female and 2 male mountain lions (Table 1). Ages ranged from 1.5 to 6 years for females and 3 to 8 years for males. Females were an average of 37.72 kg (83.6 lbs.) and ranged from 29.9 kg (66 lbs.) to 49.4 kg (109 lbs.). The average weight for males was 50.07 kg (110.4 lbs.) and ranged from 36.3 kg (80 lbs.) to 63.5 kg (140 lbs.). During the course of the study, three of the five females died. The 6 year old female (F1) died from a reproductive tract infection which was verified by a CDFW Wildlife Investigations Lab veterinarian. F17 died from a non-capture related fall onto sharp rocks, probably during the pursuit of prey, and F43 died during recapture when she jumped from the tree after being darted and drowning in a nearby stream. Rescue breathing was attempted without success. Additionally, one male mountain lion died during the study. The 3 year old was found severely injured and starving as a result of a fight with another lion - shortly thereafter a mortality signal was detected.

Table 1. Capture information of 7 adult mountain lions captured in the Mendocino National Forest, 2009 – 2013.

Lion ID	Sex	Capture Event	Age (yrs)	Weight	Status and reason for mortality
F1	Female	1	6	37.2 kg (82 lbs.)	Dead due to reproductive tract infection
		2	6	32.7 kg (72 lbs.)	
F17	Female	1	1.5	29.9 kg (66 lbs.)	Dead due to non-capture related fall
		2	1.7	33.1 kg (73 lbs.)	
F19	Female	1	3.5	35.8 kg (74 lbs.)	Alive at end of study
F23	Female	1	4.5	49.4 kg (109 lbs.)	Alive at end of study
		2	4.7	47.2 kg (104 lbs.)	
F43	Female	1	3.1	38.1 kg (84 lbs.)	Drowned during recapture
M33	Male	1	7	57.6 kg (127 lbs.)	Killed by another male lion
		2	7.8	56.2 kg (124 lbs.)	
		3	8	63.5 kg (140 lbs.)	
M36	Male	1	3	36.3 kg (80 lbs.)	Alive at end of the study
		2	3	45.8 kg (101 lbs.)	

Deer Sex Ratios and Abundance

Of the 761 deer fecal pellet samples that yielded full genotypes, we identified 342 unique individuals with an overall sex ratio of 2.72 females per male or 37 males per 100 females. Sex ratios differed between years with 3.68 females per male in 2011 and 2.72 females per male in 2012. Analysis of Huggins model estimates of abundance indicated a significant interaction between sex and year ($P = 0.05$), suggesting that sex ratios differed between years.

We used the effective area estimate to convert abundance estimates to per-transect density indices, which we could then average across fawning areas. In 2011, density estimates ranged from 7.80 (SE ± 2.60) to 18.20 (±6.88) males/km^2 (3.0 to 7.0 per square mile) and from 24.58 (±3.48) to 52.45 (±10.75) females/km^2 (9.5 to 20.2 per square mile). In 2012, density estimates ranged from 11.40 (±3.26) to 26.38 (±12.22) males/km^2 (4.4 to 10.2 per square mile) and from 14.36 (±3.40) to 41.58 (±9.83) females/km^2 (5.5 to 16.0 per square mile) across fawning areas.

The average abundance and density estimates in the 4 fawning areas were highly correlated with the numbers of individuals sampled, both for females ($r = 0.98$) and males ($r > 0.99$). Similarly, the numbers of females were highly correlated with numbers of males across fawning areas, both in terms of numbers of individuals sampled ($r = 0.91$) and abundance estimates ($r = 0.88$). Thus, changes in sex ratios detected between the two years appear to have affected all fawning areas similarly. A more detailed description of the results can be found in Lounsberry et al. (2015).

Mountain Lion Abundance

In our study area, we estimated a minimum population density of 1.74 lions/402 km^2 (0.43/100 km^2) (0.011 per square mile or 1.12 per 100 square miles) based on 95% kernel home ranges of 266 ±116 km^2 (102.7 square miles) for four adult females, 102 km^2 (39.38 square miles) for one sub-adult female, 348 km^2 (134.4 square miles) for one adult male, and 142 km^2 (54.83 square miles) for one sub-adult male. From these density estimates we can extrapolate that there were roughly 4.3 adult mountain lions in the study area (1000 km^2, 385 square miles) at any given time during our investigation.

Relative Abundances of Other Predators

Predators were abundant on female BTD summer ranges with the exception of mountain lions. All predators showed a trend of higher abundance during June and early July when fawns were most vulnerable, but there was considerable variation among ridges and thus fawning areas and among years in the same fawning area. Bears had the highest relative abundance, measured as monthly detection rate, across all years and fawning areas (1.59, SE = 0.12), followed by coyotes (0.62, SE = 0.08), and bobcats (0.27, SE = 0.06).

See Table 2 for detailed relative predator abundances by year, time period, and fawning area. Mountain lions were only detected at remote camera stations deployed across the four identified fawning areas four times and thus were not included in analyses.

Table 2. Relative abundance of bears, coyotes, and bobcats by time period and fawning area.

	Area	Bear			Coyote			Bobcat		
		June/July	July/Aug	Aug/Sept	June/July	July/Aug	Aug/Sept	June/July	July/Aug	Aug/Sept
2010	Cherry Hill	1.39	0.00	1.27	1.50	0.20	0.60	1.10	0.20	0.15
	Coyote Rock	1.42	1.54	1.55	1.71	0.96	0.37	1.42	0.05	0.00
	Cold Spring	0.71	1.21	0.75	0.19	1.43	0.08	0.10	0.00	0.42
	Plaskett Meadows	2.24	0.96	1.64	1.41	0.48	1.03	0.12	0.16	0.14
2011	Cherry Hill	3.92	1.88	1.92	0.00	0.47	0.24	0.00	0.09	0.00
	Coyote Rock	3.28	1.59	1.72	0.00	0.34	1.48	0.16	0.00	0.49
	Cold Spring	0.91	1.55	0.78	0.45	0.22	0.26	0.00	0.52	0.13
	Plaskett Meadows	1.12	1.85	1.34	0.84	0.58	0.97	1.12	0.12	0.22
2012	Cherry Hill	1.49	1.50	2.36	0.46	0.25	0.37	0.11	0.00	1.12
	Coyote Rock	2.22	1.88	1.60	0.49	0.50	0.37	0.12	0.13	0.37
	Cold Spring	2.18	1.57	0.82	0.26	0.60	1.29	0.13	0.36	0.47
	Plaskett Meadows	2.10	1.61	1.32	0.99	0.62	0.22	0.25	0.00	0.11

Note: Mountain lions were not detected frequently enough to be included. Relative abundance was calculated as the monthly detection rate (# predator detections/camera days * 30). The time periods used corresponded to life history periods of black-tailed deer fawns and were the neonate period (mid-June to mid-July), the hiding period (mid-July to mid-August), and following their mother (mid-August to mid-September).

Mountain Lion Predation

We conducted field investigations of 598 of 609 (98%) identified GPS clusters within an average time period of 6.78 days that ranged from 0 to 60 days after the mountain lion left its kill. We identified 352 kills, of which 82% were BTD. The remaining 18% consisted of two black bears and 62 small-to-medium sized animals including rabbits, jackrabbits, various rodents and birds (Figure 3).

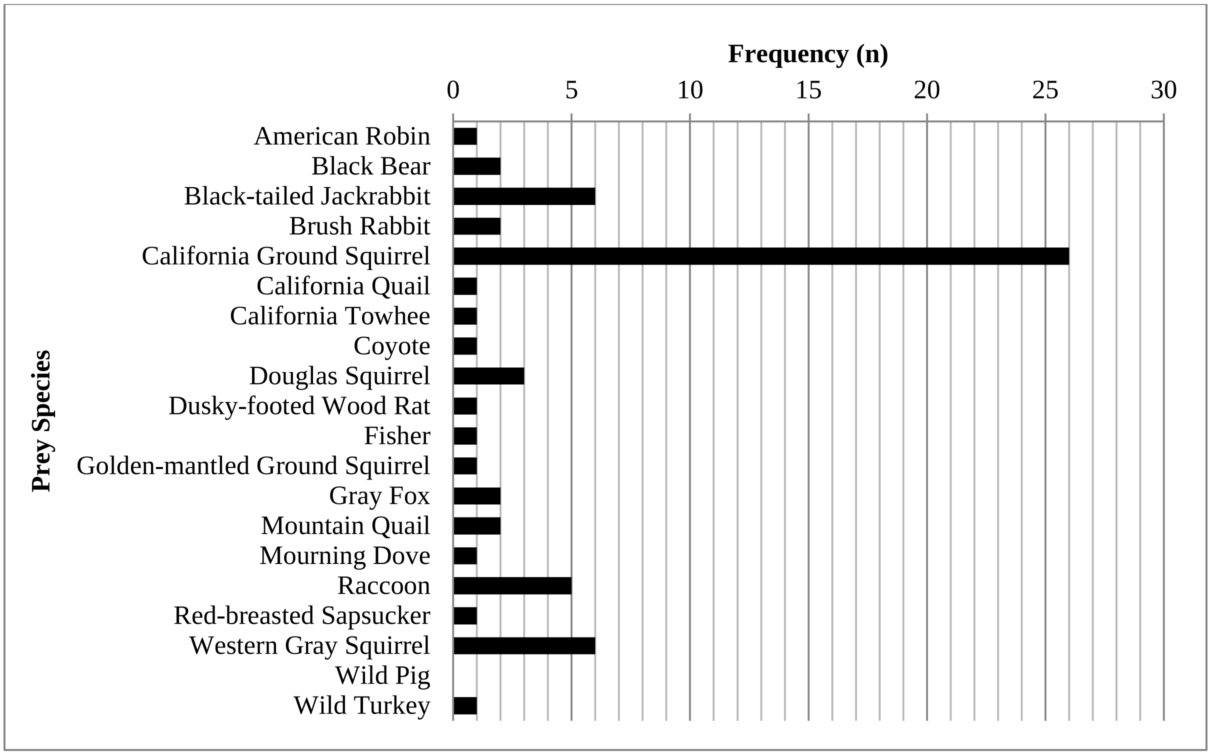

Figure 3. The frequency of non-deer prey species eaten by mountain lions.

California ground squirrels were the most abundant non-BTD prey item consumed by our collared lions. Distant seconds were black-tailed jackrabbits, gray squirrels, and raccoons. It is interesting to note that no wild pig kills were found during our investigations. We also recorded on remote cameras four acts of mountain lions scavenging.

Overall, BTD contributed 98.6% of prey by weight. Adults contributed approximately 74.4% of BTD kills, while fawns contributed 39.8% in summer and 27.5% in fall. The overall kill rate for BTD was 1.07 (95% CI = 0.77-1.38) individuals per week and 5.78 kg (12.74 lbs.) (95% CI = 4.16-7.40 kg) per day. However, kill rates for BTD varied by season with summer and fall kill rates significantly higher than winter or spring.

The time a mountain lion stayed at an adult BTD kill significantly differed among seasons ($P <$ 0.0001) with winter times longer than spring, summer, or fall times. Also, detection of a BTD kill by black bears varied significantly by season ($P < 0.0001$) with 87.2% in summer, 80.3% in fall, 31.6% in winter, and 70.3% in spring. We also found a strong inverse relationship between adult BTD carcass handling times by lions and detection rates of the kills by black bears ($P = 0.0114$, $R^2 = 0.98$) (Table 3). In essence, the more likely a lion kill was to be detected by a black bear, the lower amount of time the lion spent at the kill.

Table 3. Numbers of deer killed per week, weight killed per day, daily movement, elevation of deer kills, and handling times for mountain lions.

	Number of Deer Kill Rate (deer/week)	Mass Kill Rate (kg/day)	Mean Daily Movements (km/day)	Elevation of deer kills (meters)	Handling time (hours)
Season	Mean (95% CI)	Mean (95% CI)	Mean (95% CI)	Mean (95% CI)	Mean (95% CI)
Winter	0.85 (0.51-1.20)	6.00 (3.95-8.05)	6.88 (4.71-9.04)	1006 (840-1172)	102.2 (85.0-119.4)
Spring	0.88 (0.56-1.20)	5.63 (3.73-7.52)	6.54 (4.55-8.53)	1012 (857-1166)	74.0 (58.6-89.5)
Summer	1.32 (1.03-1.62)	6.40 (4.67-8.14)	7.13 (5.23-9.03)	1307 (1167-1446)	52.1 (37.6-66.5)
Autumn	1.27 (0.98-1.55)	6.74 (5.05-8.43)	7.78 (6.03-9.53)	1168 (1031-1305)	58.0 (44.3-71.7)

Note: Average monthly values for variables used in our analyses of variation across seasons. Values were averaged for each individual mountain lion for each month they were monitored, and then pooled by season to test if lion behaviours varied across seasons.

The elevations at which deer were killed by mountain lions also varied by season (*P* < 0.0001). Kills during summer occurred at higher elevations than in winter, spring, or fall and there was a strong relationship between the monthly elevations at which lions killed BTD and the monthly elevations of our collared BTD (*P* = 0.0012, R^2 = 0.67) (Figure 4).

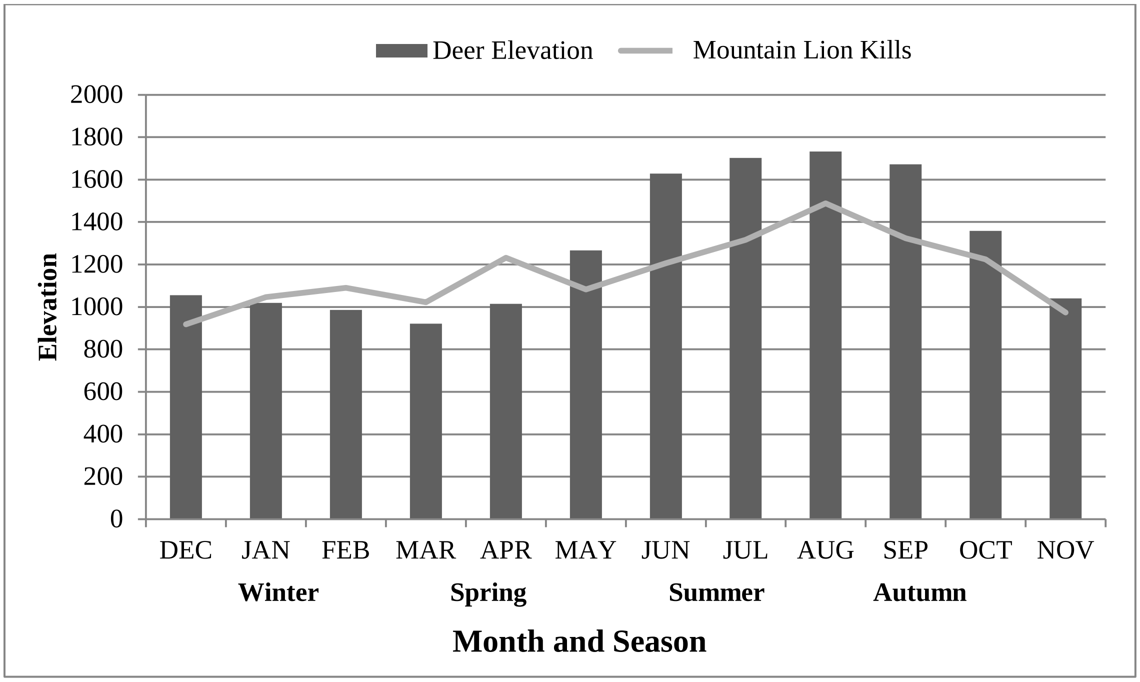

Figure 4. Average elevations by month of deer locations and mountain lion deer kills.

Adult Female Deer Survival

The two best CMR models included multiplicative effects of age and trimester, and additive effects of age and summer survival across years on both survival and cause-specific mortality probabilities. Because not all parameters were identifiable in these models, we estimated age-specific survival probabilities from a plausible model ($\Delta AIC_c = 2$) that accounted for additive effects of season and age. In general, survival probabilities were higher during winter (yearlings = 0.91 ±0.18, prime-aged adults = 0.96 ±0.03, senescent individuals = 0.91 ±0.07) than during summer (yearlings = 0.87 ±0.04, prime-aged adults = 0.94 ±0.02, senescent individuals = 0.87 ±0.02). Effects of predation were strongly age dependent; the ΔAIC_c of the model ignoring such effects was implausible (i.e., $\Delta AIC_c > 50$). The seasonal proportion of mortalities caused by predation ranged from 0.99 ±0 to 1 for yearlings, from 0.33 ±0.28 to 0.84 ±0.17 for prime-aged adults and from 0.31 ±0.30 to 0.82 ±0.22 for senescent individuals. Predation was the primary cause of mortality (i.e., $\beta > 0.5$) for all individuals at least 1 year old in spring and summer.

Age-specific annual survival probabilities for females greater than 1 year of age averaged 0.56 ±0.18 for yearlings, 0.77 ±0.13 for prime-aged adults, and 0.55 ±0.08 for senescent individuals. Annual mortality rates due to predation for females greater than 1 year were 0.43 ±0.17 for yearlings, 0.12 ±0.07 for prime-aged adults, and 0.23 ±0.07 for senescent individuals.

Even though both survival and predation parameters were identifiable for all age classes, estimated probabilities of predation of yearlings were high and approaching 1 with associated standard errors of zero. These results suggest that the effect of predation on yearlings could have been overestimated likely as a result of small sample sizes.

Finally, age-specific survival probabilities for the entire data (2004-07; 2009-13) were 0.80 ±0.04 for yearlings, 0.78 ±0.03 for prime-aged females and 0.63 ±0.03 for senescent individuals.

Juvenile Survival

The best CMR model indicated that survival probabilities varied between the two main ridges and across seasons and years. Seasonal fawn survival on FH7 ranged from 0.10 (±0.09) to 0.99 (±0.01). Seasonal fawn survival on M1 ranged between 0.26 (±0.16) and 0.99 (±0.01). The probability of fawns being killed by predators was higher during summer (0.81± 0.07 on FH7 and 0.78 ±0.07 on M1) than during other seasons (0.28 ±0.10 on FH7 and 0.26 ±0.10 on M1). Predation alone was insufficient to explain observed spatiotemporal variability in survival, given that in the second best model ($\Delta AIC_c = 1$) the proportion of death due to predation only varied between summer and the remaining seasons independently of the year and of the fawning area. Annual fawn survival averaged 0.24 ±0.16 across years and fawning area. The annual probability of fawns dying due to predation was 0.47 ±0.26.

Population Decline

The estimated asymptotic growth rate for the BTD population in the Mendocino National Forest for the period from 2009 to 2013 was 0.82 (SD = 0.13) and from 2004 to 2013 was 0.89 (SD = 0.11). In other words, the population was declining at the high annual rate of 11% to 18% between 2004 and 2013.

Sensitivities and Elasticities

First-Order Sensitivities and Elasticities

Population growth during our study was approximately twice as sensitive to changes in survival of prime-aged adults ($E_a = 0.53 \pm 0.01$) than to combined changes in fawn survival, and fecundity of yearlings and adults ($E_f + E_{fy} + E_{fa} = 0.15 + 0.01 + 0.13 = 0.29 \pm 0.01$). Among all vital rates, survival of senescent individuals contributed least to population growth.

Lower Level Sensitivities and Elasticities

When decomposing overall survival estimates (see *Equation 1*) and investigating resulting lower level elasticities, population change was most sensitive to predation of fawns independent of assumed amounts of misclassified mortalities due to predation. Fawn mortality due to predation continued to have the greatest demographic effect even when pooling elasticities for all 3 adult age classes ($E_{\mathrm{MP}f} = 0.38$ versus $E_{\mathrm{MP}y} + E_{\mathrm{MP}a} + E_{\mathrm{MP}s} = 0.25$).

Interaction of Bottom-Up and Top-Down Effects on Survival

Deer Diet Composition

The four fawning sites we investigated were identified throughout our study as “Cherry Hill”, “Coyote Rock”, “Cold Springs”, and “Plaskett Meadows” based on names taken from a topographic map of the National Forest.

Diet was averaged between years for the four fawning areas under study and was mostly composed of shrubs (Cherry Hill=88%, Coyote Rock=83.1%, Cold Spring=85.8%, Plaskett Meadows=53.6%), while forbs contributed only a small proportion (Cherry Hill=2.1%, Coyote Rock=3.9%, Cold Spring=4.8%, Plaskett Meadows=11.5%). Oak leaves composed most of the diet in summer in all areas except for Plaskett Meadows (Cherry Hill=76.1%, Coyote Rock=65.4%, Cold Spring=73.6%, Plaskett Meadows=21.8%) (Table 4).

Table 4. Diet composition (%) of BTD by fawning area in the Mendocino National Forest, California during the years of 2010-2013.

Forage Type	Cherry Hill (M1)	SE	Coyote Rock (M1)	SE	Cold Spring (FH7)	SE	Plaskett Meadows (FH7)	SE
Quercus spp.	76.1	0.03	65.4	8.03	73.6	7.53	21.8	7.16
Ceanothus spp.	6.5	0.80	1.6	0.15	3.8	0.98	8.5	0.70
Other Shrubs	5.4	0.93	16.1	4.68	8.4	6.54	23.2	3.36
Conifers	1.0	0.67	2.9	0.78	1.4	0.52	5.0	1.80
Forbs	2.1	0.35	3.9	1.28	4.8	2.36	11.5	3.54
Grasses	0.9	0.38	1.0	0.67	2.7	1.19	4.4	1.44
Lichen	6.2	0.44	6.5	2.71	2.8	1.89	14.2	2.79
Other Forage	1.8	0.39	2.6	0.38	2.4	0.61	11.3	1.40

We determined deer diet based on microhistological analysis of deer fecal pellets (Holechek & Gross 1982, Leslie et al. 1983) collected in the study area as described by Forrester (2014). A list of local plants and tissue samples of requested species were sent to the Wildlife Habitat and Nutrition Lab at Washington State University to aid with identification. Diet composition was similar across fawning areas with the exception of Plaskett Meadows which had a lower proportion of oak leaves ($P = 0.043$) and a higher proportion of other shrub species ($P = 0.047$) than other fawning areas.

Forage quality of Brewer’s oak (*Quercus garryana breweri*) and mountain whitethorn (*Ceanothus cordulatus*), the species most frequently eaten by BTD in our study area, were estimated from plant samples collected from each fawning area. Samples of each species were collected from four to six separate locations per fawning area, and from several different plants at each location. Multiple leaves were harvested from each plant from twigs smaller than the average deer browse diameter for the species (Forrester 2014). The combined samples from each fawning area were analyzed for crude protein, gross energy (calories/gram), in-vitro dry matter digestibility (% IVDM), detergent fiber levels, and tannins (Martin & Martin 1982). Samples from distinct fawning areas were blended for analysis to obtain fawning area averages. Since averages did not vary among fawning areas, we calculated averages for each species across all fawning areas

(Table 5). Mountain whitethorn had significantly higher gross energy than Brewer's oak (*P* <0.001), but lower % IVDM 86 (*P* = 0.028), protein (*P* = 0.047), and higher tannin concentrations (*P* = 0.048).

Table 5. Digestibility and protein content of Brewer's oak (*Quercus garryana*) and mountain whitethorn (*Ceanothus cordulatus*) in fawning study areas of the Mendocino National Forest.

Shrub spp.	% Crude Protein	Gross Energy (cal/gm)	% IVDM	% Neutral Detergent Fiber	% Acid Detergent Fiber	% Acid Detergent Lignin	Tannin
Brewer's oak	17.2	4746	68.4	36.6	21.8	7.5	0.11
Mountain whitethorn	11.2	5062	56.9	26.3	18.3	7.0	0.16

We surveyed all study fawning areas in 2010 and 2011 to quantify percent cover of BTD shrub and herbaceous forage types (Table 6). Mountain whitethorn and Brewer's oak had the highest percent cover followed by white fir and snow berry (*Symphiocarpus* spp.). Willows (*Salix* spp.) had the lowest percent cover.

Table 6. Percentage of cover of the most common species on summer fawning areas 2010-2011.

Cover Type or Species Name	Scientific Name	Overall Percent Cover
Barren	NA	47.1
Herbaceous	NA	13.1
Whitethorn Ceanothus	*Ceanothus cordulatus*	8.1
Brewer's Oak	*Quercus garryana breweri*	7.1
White Fir	*Abies concolor*	5.4
Snow Berry spp.	*Symphiocarpus* spp.	3.3
Red Fir	*Abies magnifica*	1.9
Live Oak spp.	*Quercus agrifolia/Q. wislizeni/Q. chrysolepis*	2.1
Gooseberry/Currant spp.	*Ribes* spp.	1.4
Whiteleaf Manzanita	*Arctostaphylos viscida*	1.4
Wild Rose	*Rosa* spp.	1.1
Fern spp.	*Polystichum* and *Pteridium* spp.	0.8
Bitter Cherry/Choke Cherry	*Prunus* spp.	0.8
Ponderosa Pine	*Pinus ponderosa*	0.8
Willow spp.	*Salix* spp.	0.7

Additional Survival Models

Adult Deer

We pooled data across years to evaluate mortality risks as there were no significant differences in survival among years. All environmental covariates met proportional hazard assumptions. Three competing models were within Δ4 AIC_c of the top model so we averaged model parameters. The probability of leaving an individual home range was the best predictor of mortality risk. Individuals with a 40% probability of stepping outside their respective home ranges within a given week were four times more likely to die (Table 7). Of the 21 observed mortalities, 13 occurred outside respective 95% home range isopleths. Distances of mortalities to nearest home range boundaries averaged 1,171 m (SE = 325 m) (0.72 miles), with 8 mortalities greater than 700 m

(0.43 miles) outside identified home ranges. Mortality risk was reduced by 3% for each additional 0.01 km^2 (2.5 acres) of herbaceous habitat within a home range and by 10% for every 100 m (328 ft.) difference in average monthly elevations of our simultaneously collared mountain lions. Senescent individuals were two times more likely to die than prime aged deer, although the 95% confidence interval for the hazard ratio slightly overlapped 1.

Table 7. Results of Cox proportional hazards models.

Covariate	Hazard Ratio	Standard Error	95% Confidence Interval
Probability of leaving home range	1.42	0.09	1.19 – 1.69
Herbaceous area in home range (ha)	0.97	0.02	0.94 – 1.00
Young Age Class	3.22	0.63	0.94 – 11.06
Senescent Age Class	2.38	0.48	0.93 – 6.10
Mountain Lion Overlap	0.90	0.04	0.82 – 0.98

Mortality risk for deer remained constant for most of the year but declined in spring (Figure 5). Weather, biomass of summer forage, and amount of oak habitat within individual home ranges did not predict variation in mortality risk.

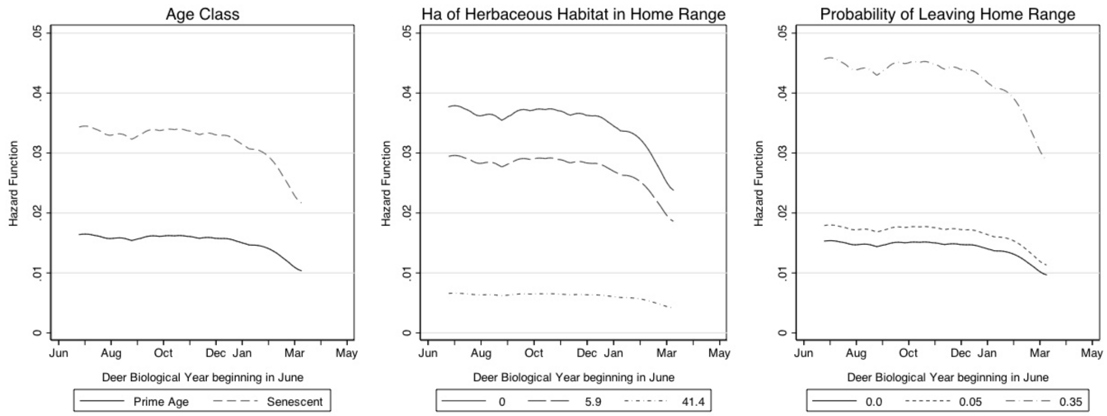

Figure 5. Hazard rates for age class, forage area within home range, and the probability of leaving the home range for adult female BTD. Values for hectares of herbaceous habitat and probability of leaving the home range are the 10%, 50%, and 90% quantiles.

A single model explaining the probability of an individual leaving its home range was strongly supported ($w_i = 0.93$). After controlling for the amount of precipitation and freezing days, both of which reduced the probability that BTD would leave their home ranges, the amount of herbaceous forage habitat within home ranges and the biomass of herbaceous and oak forage on summer range reduced the probability of stepping outside identified ranges (Table 8). Deer were also 65% more likely to leave their home range during winter despite the significantly larger range size ($P <$ 0.001). Age class had no impact on the likelihood of leaving home ranges in either summer or winter.

Table 8. Cox proportional hazards model results for the top model of the probability of leaving the home range for adult female BTD.

Covariate	Odds Ratio	*P* value	95% Confidence Interval
Seasonal Range	1.65	0.005	1.162 – 2.349
Herbaceous area in home range	0.99	0.019	0.987 – 0.998
Summer home range herbaceous biomass	0.95	0.049	0.906 – 0.999
Summer home range oak browse biomass	0.97	0.024	0.948 – 0.996
Cumulative Precipitation	0.98	0.049	0.957 – 0.999
Cumulative days below freezing	0.99	<0.001	0.996 – 0.998

Note: Odds ratios greater or less than 1 indicate an increase or decrease in probability of leaving the home range, respectively, and *P* -values indicate if the hazard ratio is significantly different than 1.

There was no difference in the amount of forage habitat within home ranges of prime-age and senescent individuals in either summer ($P = 0.99$) or winter ($P = 0.78$). Senescent deer weighed more than prime-aged deer in our study area ($P = 0.02$).

Juvenile Deer

We limited the Cox proportional hazards analysis evaluating mortality risks in summer to the three cohorts captured from 2010 to 2012 since we did not collect environmental covariates for the 2009 cohort. We pooled data across years after confirming that summer survival differences among years were not significant. Capture weight and age were correlated ($r > 0.5$) and capture weight was retained for the model because it was more accurately measured in the field. Correlation coefficients were less than -0.5 between herbaceous forage and both overall shrub cover and *Ceanothus* species. We retained herbaceous forage for modeling because herbaceous forage is critical summer forage for mule deer (Wickstrom et al. 1984, White 1992), and dropped *Ceanothus* since these species did not contribute much to summer diets. We also dropped percent cover because it was measured as vegetation composition and not specifically as deer cover. All remaining environmental covariates met proportional hazards assumptions, and capture weight was modeled as a linearly increasing and time varying covariate since it increased with age.

There was no clear best model for summer mortality risk so we summed Aikake weights (w_i) and estimated model averaged parameters to determine the importance of covariates. Capture weight and the amount of oak forage within fawning areas explained the most variation in mortality and were negatively related to mortality risk. Herbaceous forage and twin status also explained variation in mortality; twins were 54% more likely to die than single fawns and increasing herbaceous forage showed a trend toward decreased mortality risk. Predator abundance, fawn sex, and spring and winter precipitation were not well supported in mortality risk models (Table 9).

Table 9. Cox proportional hazards ratios for summer hazards models for fawn BTD.

Summer Mortality Risk Covariates	Summed Model Weights (w_i)	Model Avg. Hazard Ratios	Model Avg. SE	Model Avg. 95% CI
Capture Weight	0.98	0.98	0.01	0.97 – 0.99
Oak Forage Biomass	0.97	0.86	0.05	0.77 – 0.95
Twin Status	0.76	1.54	0.22	1.00 – 2.39
Herbaceous Forage Biomass	0.62	0.92	0.06	0.82 – 1.03
All Predators Relative Abundance	0.37	0.94	0.08	0.81 – 1.09
Sex	0.33	1.07	0.10	0.89 – 1.30
April Precipitation	0.29	0.96	0.08	0.81 – 1.13
Winter Precipitation	0.27	1.00	0.01	0.99 – 1.01

Predation risk from bears during summer was not strongly explained by any covariates, but relative bear abundance had the strongest support ($w_i = 0.64$). No predator abundance or forage covariates showed a significant effect on predation risk (Table 10). Predation risk from coyotes during summer was lower in areas with more oak forage. No other covariate significantly affected coyote predation risk. The coyote predation risk CIF was higher on the FH7 ridge compared to the M1 ridge ($P = 0.006$) while the bear predation risk CIF was not different ($P = 0.307$).

Table 10. Summer predation risk of BTD fawns from black bears and coyotes.

	Black Bear Models				Coyote Models			
Covariates	w_i	SHR	SE	95% CI	w_i	SHR	SE	95% CI
Coyote Relative Abundance	0.54	0.86	0.25	0.53 – 1.41	0.29	0.96	0.23	0.63 – 1.47
Bear Relative Abundance	0.64	0.89	0.15	0.66 – 1.20	0.36	0.88	0.17	0.66 – 1.16
Herbaceous Forage Biomass	0.27	0.99	0.03	0.93 – 1.05	0.40	0.94	0.02	0.84 – 1.07
Oak Forage Biomass	0.32	0.98	0.03	0.93 – 1.03	0.89	0.77	0.13	0.60 – 0.98
Capture Weight	0.33	0.94	0.07	0.82 – 1.06	0.48	0.80	0.19	0.56 – 1.13
Twin Status	0.35	1.15	0.14	0.88 – 1.51	0.33	1.17	0.22	0.80 – 1.73
Sex	0.35	0.87	0.14	0.67 – 1.13	0.29	1.12	0.19	0.80 – 1.56

For our analysis evaluating the influence of environmental covariates on winter mortality risk we pooled data due to a lack of differences among years. All covariates in winter hazards models met proportional hazards assumptions. There was no single best model for winter mortality risk, so we report model averaged parameters and summed AIC_c weights for covariates from all subsets of models (Arnold 2010). Sex of fawns was the strongest predictor of mortality, and the amount of shrub habitat and predation risk index were also related to mortality risk, although not significantly (Table 11). Winter severity, precipitation, and the amount of oak habitat in winter home ranges were not related to mortality. We did not model predation-specific mortality risk in winter due to the high number of unknown mortalities.

Table 11. Winter mortality results from all possible subsets of Cox proportional hazards models for BTD fawns.

Winter mortality risk covariate	w_i	Hazard Ratios	SE	95% CI
Sex	0.91	0.27	0.56	0.09 – 0.80
Total Browse	0.78	1.14	0.07	0.99 – 1.31
Mountain Lion Risk	0.66	1.44	0.24	0.90 – 2.30
Winter Severity	0.38	1.00	0.0001	1.00 – 1.01
Precipitation	0.35	0.98	0.02	0.94 – 1.02
Total Oak	0.29	1.01	0.01	0.98 – 1.03
Twin Status	0.28	0.90	0.18	0.63 – 1.29

DISCUSSION

Our overall findings yielded four important results. First, we found age-specific variation in survival and survival probabilities of all age classes of deer were significantly lower than typically reported for the species (Forrester & Wittmer 2013). Despite high reproductive rates, the BTD population in the Mendocino National Forest is thus currently expected to be in decline. Second, we found strong top-down effects influencing survival of all age groups. Fawns were particularly affected by predation from black bears and coyotes, much of which occurred over the first 30 days of their life. Adults were primarily killed by mountain lions and observed kill rates were among the highest reported in the literature (Knopff et al. 2010, Allen et al. 2014a). We speculate that high kill rates of adult BTD are a consequence of kleptoparasitism from black bears (Allen et al. 2014b, Elbroch et al. 2015). Third, we found evidence of interactions between bottom-up and top-down effects. For example, the amount of oak forage on summer ranges explained variability in mortality risks of fawns, particularly with respect to coyotes. In addition, adult BTD with reduced forage available within their home ranges were more likely to step outside identified home range boundaries where they were at greater risk of mortality (Forrester et al. *in press*). Both observations are in agreement with the predation-risk sensitive foraging theory combining bottom-up and top-down effects (Sinclair & Arcese 1995). Fourth, despite the low observed survival over both short and longer time frames, there currently remain relatively high deer densities on the Mendocino National Forest.

Population dynamics of BTD in the Mendocino National Forest

Survival of adult female BTD older than 1 year of age in our study, a population with no antlerless harvest, experienced the lowest annual survival rates reported to date in the literature. Based on models that ignored age structure in the population (for comparison with previous studies) but included observed seasonal effects, we found a combined mean annual adult survival rate of 0.71 (±0.07) over the duration of our study (Marescot et al. 2015). This estimate was 15% lower than the mean annual adult female survival of 0.84 (CV = 0.06) for the species averaged across 21 published studies (reviewed in Forrester & Wittmer 2013). Survival estimates remained very low (mean = 0.77 ± 0.13) even when we only considered survival of prime-aged females between 2 and 7 years of age. To our knowledge, only 3 previous studies have reported annual adult survival rates of less than 0.80 for mule and BTD (McNay & Voller 1995, Bleich & Taylor 1998, Robinson et al. 2002). Adult survival did not vary significantly over the four years of monitoring. The very low observed survival of yearlings during our four year study (0.56 ±0.18) was likely an artifact of small sample sizes. Once we combined our data with those collected during the previous study, yearling survival (0.80 ±0.04) was no longer significantly lower than that of prime-aged adults (0.78 ±0.03). The noticeable reduction in survival of senescent individuals, those 8 years and older; however persisted across all survival analyses we conducted. Survival estimates over the longer time frame of both study periods confirm an overall population decline of BTD in the Mendocino National Forest albeit with a lower degree of confidence (mean lambda = 0.89 ±0.11).

Predation accounted for at least 57% of observed adult mortalities, the majority of which (92%) were attributed to mountain lions. Overall, mountain lion predation was the dominant contributor and thus proximate cause of the observed low adult survival including those of prime-aged females. The relative impact of predation was similar to other studies reporting low adult survival for mule and BTD. However, previous studies identified predation as the primary cause of mortality during winter when adult deer are expected to be in poorer body condition and thus more susceptible to predators (e.g., McNay & Voller 1995, Robinson et al. 2002). Our study suggested greater vulnerability to predation during summer when GPS location data showed that mountain lions followed migrations of adult deer to high elevation summer ranges. Structurally diverse habitats on summer ranges may have also increased vulnerability of deer to ambush predators such as mountain lions (Sih et al. 1998, Pierce et al. 2004). However, differences in monitoring intensity resulted in a greater number of unidentified causes outside the summer season and thus the potential to underestimate the effect of lion predation during winter.

Concurrent to low adult survival, BTD in our study also experienced approximately 17% lower annual survival of fawns than typically reported (0.24 versus 0.29; Forrester & Wittmer 2013). The low fawn survival was primarily a consequence of high predation from a diverse number of predators during summer. Fawn survival was more consistent than generally reported but still exhibited significant spatiotemporal variability over the duration of our study. For instance, fawn survival varied between ridges and thus fawning areas. However this variation was apparently independent of differences in predation. Finally it is noteworthy that results from our lower-level sensitivity and elasticity analysis pointed towards growth rates being mostly influenced by low fawn survival. This is contrary to our current understanding of ungulate population dynamics and likely a consequence of fawn survival being consistently low rather than varying substantially over time (Gaillard & Yoccoz 2003). Furthermore, our results showed that adult survival was low and variable rather than high and constant. Thus life history traits for BTD in the Mendocino National Forest have probably not been canalized by environmental variability because of the high selective pressure exerted by multiple predators.

Given the low survival rates for individuals from all age classes including fawns it is not surprising that the deer population in the Mendocino National Forest is currently predicted to decline dramatically. The decline is occurring despite relatively high fecundity rates that saw greater than 85% of adult females older than 2 years pregnant every year. While Forrester & Wittmer (2013) suggested that high fecundity rates enable mule and BTD to compensate for low fawn survival, the reproductive potential was insufficient to account for the combination of low fawn and adult survival. Such a pattern has been described for many small ungulate populations exhibiting similar rates of decline as those observed in our study and that identified predation as the primary cause of mortality (e.g., Wittmer et al. 2005, 2013; Johnson et al. 2010). The predicted significant negative asymptotic growth associated with high predation rates strongly suggests that top-down effects are responsible for declines. Unsustainable predation may have affected the population over longer time frames. While no information on causes of mortality were collected during the early project, the consistency in survival patterns observed suggest that predation may have negatively affected this population for longer periods of time.

The potential contribution of black bears to low vital rates and resulting population decline of BTD warrants special attention. First, black bears were distributed across the entire study area and likely occur at high densities. These results suggest that deer are unable to avoid interactions with black bears at the landscape level (Elbroch et al. 2015). Second, the large numbers of fawns killed by bears highlight their direct impact on BTD population declines. Third, the high elasticity of fawn mortality from predation increases the importance of bear predation, which almost exclusively preyed on fawns. Overall, bears were the most significant fawn predator despite fawns only being vulnerable for the first 30 days of their lives. Finally, we hypothesize that carcass stealing from black bears was at least partially responsible for high observed kill rates of mountain lions.

Our hypothesis is based on the following observations:

1) Kill rates of mountain lions were highest during seasons where bears are most active while handling times showed the opposite pattern (Allen et al. 2014a);
2) Based on video cameras deployed at 58 mountain lion kills, we determined that mountain lions did not return to 72.4% of their kills once they were discovered by bears (Allen 2014);

3) Mountain lions essentially stopped feeding on kills once they were discovered by black bears (Allen 2014, Allen et al. 2014b);
4) Mountain lion kill rates were higher than predicted based on energetic requirements (Elbroch et al. 2014);
5) Mountain lions did not use competition refuges and were unable to conceal their kills from black bears via caching (Elbroch et al. 2015).

Interaction of bottom-up and top-down effects

Several results supported our prediction of bottom-up and top-down effects jointly influencing BTD in the Mendocino National Forest. Most importantly, we found adult deer with access to greater amounts of forage within their small seasonal home ranges as well as access to higher quality summer range less likely to leave their home range during weekly monitoring intervals and thus use "risky areas" with greater probability of death (Forrester et al. *in press*). Food availability contributed to risk of mortality in that those individuals able to restrict their movements to and from high quality forage areas were less likely to be detected and killed by mountain lions. This outcome is an expected benefit associated with site familiarity (Piper 2011).

Forage and habitat availability during summer also explained observed spatial variation in mortality and risk of predation from coyotes of older fawns. In particular, risk of predation from coyotes was lower in areas with more oak forage. Older fawns in better condition may have been able to escape coyotes more easily or mothers in better physical condition may have been able to defend against coyotes more effectively (Lingle et al. 2005, Lingle et al. 2008). Oak forage was likely linked to better summer condition because it made up the majority of the summer diet and was used in much higher proportion than its availability. Furthermore, oak leaves had lower tannins and higher protein content than *Ceanothus* spp., the next most common shrub observed in the diets of deer in our study area. Protein is critical for early growth of fawns and is just as important for summer nutrition as digestible energy (Parker et al. 2009). There seemed to be no carryover effects of nutrition from the preceding winter since there was no detectable difference in body condition of adult females across the study area at the beginning of the summer. Other mechanisms for the observed link between oak forage and lower coyote predation could be an increased escapability in open habitats (Geist 1981), or coyotes switching to alternate prey in habitats dominated by oaks (Hamlin et al. 1984; Hurley et al. 2011).

Other results also support our conclusion that both bottom-up and top-down effects influenced BTD. For example, while fawn weights in our study were lower than those of captive fawns from does with ad libitum access to food, thus potentially pointing towards food limitation, pregnancy and fetal rates were still higher than averages reported for the species across their distribution (Forrester & Wittmer 2013). In addition, body condition of adult females in the study area in early summer was approaching a level of "good" (mean rBCS = 2.8 on a 1-5 scale). Fat reserves in early summer, however, should be near the low point for the year (White 1992, Parker et al. 2009), and a good body condition does not provide evidence for nutritional limitation (Pierce et al. 2012). Combined, these results were consistent with the interplay of top-down and bottom-up effects expected in a mid-sized ungulate such as BTD (Hopcraft et al. 2010).

Population size

Given that survival rates observed in this study point towards a strongly declining population, results from our fecal pellet DNA analyses are encouraging in that they suggest that deer in the

Mendocino National Forest still occur at substantial densities (Lounsberry et al. 2015). While DNA results based on fecal samples collected on high quality summer ranges cannot be used to estimate absolute abundances in the study area, they can be compared to density estimates from other areas using similar methodologies. Based on these comparisons (e.g., Brinkman et al. 2011) it appears that densities remain high despite the observed prolonged period of population decline.

We interpret these findings as evidence that our study coincided with population declines expected based on previous hypotheses of multi-decadal fluctuations typical for deer in the Western United States (Leopold et al. 1947, Forrester & Wittmer 2013). We added to this hypothesis by showing that interactions of bottom-up and top-down effects can contribute to these observed fluctuations. Our observation of size-partitioned predation as well as indirect interactions among bears and mountain lions point towards complex community interaction consistent with current ecological theory (De Roos et al. 2008).

CONCLUSIONS AND RECOMMENDATIONS

Like other deer populations in the western United States, the Mendocino deer population has undergone cyclic fluctuations in population size. Aldo Leopold explicitly identified the area occupied by the Mendocino population as an overpopulated deer range in the 1940's (Leopold et al. 1947). Deer populations peaked again in the 1960's and 1970's and record harvests were taken by hunters in the counties that comprise our study area (Booth et al. 1982).

Our results show that BTD in the Mendocino National Forest are currently declining in abundance. We found evidence that the decline is caused by high mortalities due to predation in all age classes. We also found bottom-up effects contributing to the decline. In particular, results supported predictions of the predation-sensitive foraging hypothesis in adults where individuals with suboptimal access to food take greater risks that lead to greater probabilities of being killed by a predator. Based on the past history of BTD in the area and persistence of deer over evolutionary times, we suggest that the current decline is part of longer-term fluctuations described by earlier researchers.

We offer the following recommendations with regard the future management actions and research endeavors:

1. Continue the limited antlered adult male only harvest regime until the population has made substantial positive changes in population trends. Antlerless harvest is not recommended at this time.

2. Track population change annually until population recovers. Conduct yearly helicopter based mark-resight sampling with GPS collars to estimate adult abundance, adult female survival, and fawn recruitment.

3. Map and enhance/or maintain summer and winter range areas; especially known fawning areas. Create habitat use models to identify additional areas to enhance and maintain.

4. Determine the underlying mechanisms that regulate the observed long-term abundance cycles in black-tailed deer populations.

5. Determine if a similar downward trend in population growth is apparent in black-tailed deer populations adjacent to the Mendocino National Forest study site including private properties enrolled in the California Department of Fish and Wildlife Private Lands Habitat Enhancement and Management Program which provides antlerless hunting.

6. Determine the direct effects of black bear abundance and seasonal habitat use on black-tailed deer population dynamics; especially in regard the recent prohibition of the use of trained hounds during hunting and the subsequent reduction in bear harvest.

7. Investigate the apparent differences in fawn survival probabilities between Brewer’s oak and conifer/chaparral dominated habitat areas in terms of predation by coyotes.

8. Monitor changes in mountain lion abundance and its effect on deer population dynamics.

9. Investigate the effects of kleptoparasitism by bears on mountain lions over a large scale.

10. Quantify the relationship between fawn survival and summer habitat use in black-tailed deer.

SUMMARY

1) Between 2009 and 2013, we captured 137 black-tailed deer (*Odocoileus hemionus columbianus*) fawns and 57 adult females 1 year of age and older in the Mendocino National Forest and fitted them with VHF and GPS collars, respectively. During captures we determined pregnancy rates and, when possible, the number of fetuses carried by pregnant does. We also sampled deer fecal pellets on identified high-quality summer ranges in both 2011 and 2012 and estimated deer population densities based on fecal DNA.

2) We used encounter histories and information about the cause of deer mortality to quantify age- and cause-specific survival probabilities based on multistate capture-mark-recapture (CMR) models. We measured a range of environmental covariates including seasonal quality and quantity of forage to explain observed spatial and temporal variation in survival patterns. Based on available vital rates we estimated predicted population growth rates using matrix models.

3) We captured a total of 7 mountain lions (*Puma concolor*) over the duration of our study and fitted them with ARGOS satellite enabled GPS collars. Real-time information from the collars allowed us to immediately determine and investigate possible kill sites. Based on intensive field investigations, we determined the diet composition and kill rate of each lion in the Mendocino National Forest. We used a home-range approach to estimate snapshot population densities.

4) We found strong age-specific survival probabilities (fawns = 0.24 ±0.16, yearlings = 0.56 ±0.18, prime-aged adults = 0.77 ±0.13, senescent individuals = 0.55 ±0.08). Predation was the primary cause of fawn mortality, and black bear predation was the largest single source of mortality. Mountain lion predation was the primary cause of mortality of adult females equal to or greater than1 year old. Does had an average pregnancy rate of 0.87 ±0.05 during our study and carried 1.9 fawns. The estimated asymptotic growth rate for the period from 2009-13 was 0.82 (SD = 0.13).

5) Deer contributed 98.6% of prey biomass to the diet of mountain lions with estimated kill rates of 1.07 (95% CI = 0.77-1.38) per week. High observed kill rates were somewhat mediated by

lower than expected densities of mountain lions, including the known kittens, of 0.68/100 km^2 (1.76/100 mi^2) in the study area. Higher kill rates together with reduced handling times during seasons when black bears were active point towards the possibility of kill rates being elevated due to carcass stealing by bears.

6) Despite the strong top-down effects we observed, bottom-up effects modified risk of deer mortality. Adult female deer with greater access to oak habitats experienced lower fawn mortality from coyotes. Deer with larger amounts of forage within their identified home ranges were less likely to die of any cause, including predation.

7) Results from our fecal pellet DNA analyses confirm current negative population trends based on available estimates of vital rates, but also suggest that black-tailed deer still occur at substantial densities in the Mendocino National Forest. In particular, we found relative densities of 7.80 (±2.60) to 18.20 (±6.88) males/km^2 (3.01 to 7.02 / mi^2) and 24.58 (±3.48) to 52.45 (±10.75) females/km^2 (9.49 to 20.25 / mi^2) in high quality summer range.

8) Our results show that deer in the Mendocino National Forest are currently declining in abundance. We found evidence that the decline is caused by high mortalities due to predation in all age classes. We also found bottom-up effects contributing to the decline. Based on the past history of black-tailed deer in the area and their persistence over evolutionary time, we suggest that the current decline is part of longer-term fluctuations described by earlier researchers.

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APPENDIX I: List of peer-reviewed publications resulting from the Mendocino black-tailed deer population assessment project.

1) **Student theses**:

Allen, L.M. 2014. The ecology and behaviour of pumas (*Puma concolor*) in northern California, U.S.A. PhD Dissertation, Victoria University of Wellington, Wellington, New Zealand.

Forrester, T.D. 2014. Effects of predation and forage availability on the survival of black-tailed deer (*Odocoileus hemionus columbianus*) in the Mendocino National Forest, California. PhD Dissertation, University of California, Davis, USA.

2) **Peer reviewed journal publications** (including *in press*):

Allen, M.L., Elbroch, L.M. & Wittmer, H.U. 2013. Encounter competition between a mountain lion, *Puma concolor*, and a western spotted skunk, *Spilogale gracilis*. Canadian Field-Naturalist 127:64-66.

Allen, M.L., Elbroch, L.M., Casady, D.S. & Wittmer, H.U. 2014a. Seasonal variation in the feeding ecology of pumas (*Puma concolor*) in northern California. Canadian Journal of Zoology 92:397-403.

Allen, M.L., Elbroch, L.M., Wilmers, C.C. & Wittmer, H.U. 2014b. Trophic facilitation or limitation? Comparative effects of pumas and black bears on the scavenger community. PLoS ONE 9(7):e102257.

Allen, M.L., Elbroch, L.M., Casady, D.S. & Wittmer, H.U. *in press*. The feeding ecology of mountain lions in Mendocino National Forest, California. California Fish and Game.

Allen, M.L., Elbroch, L.M., Wilmers, C.C. & Wittmer, H.U. *in press*. The comparative influences of large carnivores on the acquisition of carrion by scavengers. American Naturalist.

Casady, D.S. & Allen, M.L. 2013. Handling adjustments to reduce chemical capture–related mortality in black-tailed deer. California Fish and Game 99:104-109.

Elbroch, L.M., Allen, M.L., Lowrey, B.H. & Wittmer, H.U. 2014. The difference between killing and eating: ecological shortcomings of puma energetic models. Ecosphere 5:53.

Elbroch, L.M., Lendrum, P., Allen, M.L. & Wittmer, H.U. 2015. Nowhere to hide: pumas, black bears, and competition refuges. Behavioral Ecology. DOI: 10.1093/beheco/aru189.

Forrester, T.D. & Wittmer, H.U. 2013. A review of the population dynamics of mule deer and black-tailed deer *Odocoileus hemionus* in North America. Mammal Review 43:292-308.

Forrester, T.D., Casady, D.S., & Wittmer, H.U. 2014. Home sweet home: fitness consequences of site familiarity of female black-tailed deer. Behavioral Ecology and Sociobiology. DOI: 10.1007/s00265-014-1871-z.

Lounsberry, Z.T., Forrester, T.D., Olegario, M.T., Brazeal J.L., Wittmer, H.U. & Sacks, B.N. 2015. Estimating sex-specific abundance in fawning areas of a high-density Columbian black-tailed deer population using fecal DNA. Journal of Wildlife Management 79(1):39-49.

Marescot, L., Forrester, T.D., Casady, D.S. & Wittmer, H.U. 2015. Using multistate capture-mark-recapture models to quantify effects of predation on age-specific survival and population growth in black-tailed deer. Population Ecology. DOI: 10.1007/s10144-014-0456-z.

APPENDIX II. Dosages, weights, induction and reversal times, and physiological parameters of female black-tailed deer chemically immobilized via remote darting with a mixture of telazol and xylazine and xylazine reversals tolazine hydrochloride or yohimbine.

Animal Number	Telazol (mg)	Telazol (mg/kg)	Xylazine (mg)	Xylazine (mg/kg)	T:X ratio	Weight (kg)	Ketamine Supplement (mg)	Reversal (mg)[1]	Reversal (mg/kg)	Induction (min)[2]	Handling (min)	Reversal PDI[3] (min)	Up[4] (min)	High Temp (F)	Heart Rate (b/min)	Respiratory Rate (b/min)	SpO2[5] (%)
1485	120	2.30	91	1.74	1:0.8	52.2	-	250	4.79	3	87	87	3	101.0	45-46	32-36	79-85
5728	100	1.97	100	1.97	1:1	50.8	-	200	3.94	-	174	176	0	-	-	-	-
5728-1	93	2.56	100	2.75	1:1.1	36.3	-	150	4.13	3	130	58	32	-	-	-	-
5730	200	4.12	200	4.12	1:1	48.5	-	10 (y)*	0.21	20	118	105	0	101.2	-	30	-
5731	200	3.53	200	3.53	1:1	56.7	-	15(y)	0.26	10	113	98	15	104.3	-	28	-
5732	200	5.18	100	2.59	1:2	38.6	-	10(y)	0.26	3	135	135	4	101.8	-	32	-
5733	100	1.92	100	1.92	1:1	52.2	-	14(y)	0.27	10	105	102	3	102.5	-	34	-
5734	100	2.10	100	2.10	1:1	47.6	-	200	4.20	4	115	101	14	101.1	32-38	30-36	-
5735	100	2.45	100	2.45	1:1	40.8	-	180	4.41	3	89	88	1	101.3	74	68	-
5736	50	0.88	100	1.76	1:2	56.7	-	200	3.53	5	113	110	3	-	-	-	-
5737	55	1.10	100	2.00	1:1.8	49.9	-	220	4.41	5	78	75	3	99.9	-	24	-
5738	55	1.03	100	1.88	1:1.8	53.1	-	200	3.77	-	-	135	0	105.7	82	84	-
5739	100	1.84	150	2.76	1:1.5	54.4	-	150	2.76	-	135	135	-	101.9	60-80	70-80	-
5740	130	2.92	130	2.92	1:1	44.5	-	250	5.62	10	80	72	8	100.9	48-56	28-30	85
5740	100	2.14	100	2.14	1:1	46.7	-	200	4.28	5	124	114	10	-	-	-	-
5741	93	1.52	100	1.63	1:1.1	61.2	-	400	6.54	-	101	100	1	95.7	60	-	-
5742	143	4.10	100	2.86	1:0.7	34.9	-	300	8.60	-	187	75	-	99	60	-	-
5743	100	2.12	100	2.12	1:1	47.2	-	330	6.99	6	105	103	0	101	48-50	26-26	-
5744	100	2.27	100	2.27	1:1	44.0	-	200	4.54	25	88	88	4	100.6	40	38	-
5745	200	4.16	100	2.08	1:0.5	48.1	-	200	4.16	-	89	86	3	101.3	52	22-44	-
5747	100	2.40	100	2.40	1:1	41.7	-	200	4.80	3	95	77	17	99.7	28-52	42-54	-
7037	130	3.82	130	3.82	1:1	34.0	-	100	2.94	4	158	115	43	102.8	55-60	44-60	72-80
7079	270*	5.67	270	5.67	1:1	47.6	-	150	3.15	10	94	75	41	100.5	48-63	30-45	65-85
7216	120	2.03	120	2.03	1:1	59.0	200	200	3.39	36	95	90	5	100.8	67	-	89-89
7227	110	2.47	84	1.89	1:0.8	44.5	-	200	4.49	3	86	78	10	101.7	61-67	-	85-91
7274	130	4.35	99	3.31	1:0.8	29.9	-	200	6.69	1	138	109	30	100.0	44-46	-	80-86

7276	130	3.02	130	3.02	1:1	43.1	-	250	5.8	3	137	111	26	100.4	63-68	52-60	80-85
7285	130	2.73	99	2.08	1:0.8	47.6	100	100	2.10	5	95	54	66	100.5	44-51	-	42-89
7298	120	2.82	91	2.14	1:0.8	42.6	-	200	4.69	3	69	97	4	100.9	36-46	36-48	76-87
7303	130	2.78	130	2.78	1:1	46.7	-	200	4.28	4	93	86	5	100.2	42-108	40	75-91
7308	130	3.05	130	3.05	1:1	39.9	-	100	2.51	3	113	83	30	101.7	48-60	72-91	62-72
7314	120	3.39	91	2.57	1:0.8	35.4	-	200	5.65	5	107	95	19	99.9	52	60	77
7318	120	2.59	91	1.96	1:0.8	46.3	-	200	4.32	3	121	75	6	99.9	44-60	56-60	86-94
7331	130	3.29	130	3.29	1:1	39.5	-	200	5.06	5	135	125	11	101.8	62-73	48	74-84
7447	130	3.05	99	2.32	1:0.8	42.6	-	200	4.69	3	80	67	16	99.0	46-78	28	73-87
7449	110	2.20	84	1.68	1:0.8	49.9	-	200	4.00	12	72	60	12	101.4	43-48	17	82-96
7581	166	3.52	200*	4.24	1:1.2	47.2	-	200	4.24	70	166	132	34	103.3	58	50-50	-
7582	100	1.99	150*	2.98	1:1.5	50.3	-	200	3.98	27	131	120	11	102.8	40	36-44	-
7583	130	2.99	210*	4.83	1:1.6	43.5	-	200	4.60	3	166	148	17	97.9	38-41	-	76-95
7584	140	3.43	140	3.43	1:1	40.8	-	200	4.90	3	103	92	11	99.7	59-66	80-88	-
7585	130	2.56	130	2.56	1:1	50.8	-	150	2.95	3	123	73	51	101.0	54-64	-	58-70
7586	130	3.58	130	3.58	1:1	36.3	-	160	4.41	3	168	166	2	102.6	50-80	30-36	64-74
7588	130	2.73	130	2.73	1:1	47.6	-	200	4.20	8	122	117	5	102.7	62-69	28-30	68-88
7593	140	3.51	140	3.51	1:1	39.9	-	180	4.51	15	75	68	17	-	-	-	-
7597	130	3.02	130	3.02	1:1	43.1	-	200	4.64	-	77	68	35	100.2	52	44	-
7616	130	4.41	99	3.36	1:0.8	29.5	-	150	5.08	3	157	88	72	100.2	43-45	48	70-82
7879	220*	4.21	220	4.21	1:1	52.2	-	230	4.41	50	130	95	35	104.3	-	90	-
7882	130	3.67	130	3.67	1:1	35.4	-	100	2.82	3	65	63	2	101.4	49-100	42	81-90
7884	130	3.05	130	3.05	1:1	42.6	-	100	2.35	19	137	130	7	103.3	36-44	40	88-94
7885	130	3.26	130	3.26	1:1	39.9	-	200	5.01	8	162	147	15	99.2	41-42	-	58-72
7924	150	3.52	150	3.52	1:1	42.6	-	200	4.69	3	115	99	19	101.5	42-46	32	88-90
8796	130	2.49	130	2.49	1:1	52.2	-	300	5.75	8	75	76	9	100.5	64-68	60-72	-
8797	130	2.86	130	2.86	1:1	45.4	-	200	4.40	10	62	62	0	100.8	40-44	-	52-68
8798	150	2.87	150	2.87	1:1	52.2	-	250	4.79	8	159	70	89	101.5	68-79	60	-
8800	170	2.84	270*	4.51	1:1.6	59.9	-	260	4.34	42	119	109	10	100.6	60-72	48-64	-
8801	130	2.75	130	2.75	1:1	47.2	-	300	6.35	4	79	75	64	101.5	64-92	52-52	-
8802	120	2.49	220*	4.57	1:1.	48.1	-	100	2.08	3	214	139	75	97.3	48	44	-

					8												
8803	130	3.49	130	3.49	1:1	37.2	-	250	6.72	5	140	90	50	100.3	52-60	64-80	-
8804	220	4.62	220	4.62	1:1	47.6	-	100	2.10	12	92	90	2	99.4	40-41	66-88	-
8805	230	5.34	230	5.34	1:1	43.1	-	200	4.64	55	-	120	-	98.8	44-68	-	76-92
8806	120	2.12	220*	3.88	1:1.8	56.7	-	130	2.29	3	146	133	13	100.5	44-68	40-44	-
8808	130	3.97	130	3.97	1:1	32.7	-	200	6-12	10	119	75	44	100.4	65-70	50-50	-
8809	130	2.33	200*	3.58	1:1.5	55.8	-	250	4.48	47	144	132	14	99.8	46-66	32-60	-
8810	130	2.49	130	2.49	1:1	52.2	-	300	5.75	15	95	65	30	-	-	-	-
8812	120	2.82	91	2.14	1:0.8	42.6	-	200	4.69	3	138	86	12	100.3	53-55	28-32	79
8813	130	3.41	130	3.41	1:1	38.1	-	180	4.72	3	118	65	53	100.9	44	44	-
8815	130	2.65	130	2.65	1:1	49.0	-	220	4.49	7	77	78	1	100.7	-	19	-
8816	270*	6.01	270	6.01	1:1	44.9	-	100	2.23	33	137	126	11	102.1	36-90	18-24	45-92
8817	120	2.88	120	2.88	1:1	41.7	-	100	2.40	7	118	90	28	103.1	54-60	24-28	-
8818	110	2.29	84	1.75	1:0.8	48.1	100	200	4.16	5	75	63	10	100.9	52-60	40-56	84-90
8819	130	2.70	130	2.70	1:1	48.1	-	210	4.36	2	131	118	9	105.2	34-50	-	65-86
8820	150	2.87	150	2.87	1:1	52.2	-	150	2.87	3	150	144	6	97.8	44-58	40	83-95
8821	130	3.82	130	3.82	1:1	34.0	-	150	4.41	-	-	51	18	100.1	56	-	82-83
8822	260*	4.78	260	4.78	1:1	54.4	-	240	4.41	10	123	157	26	102.0	52-64	48-60	-
8823	130	3.37	130	3.37	1:1	38.6	-	200	5.18	-	140	118	22	-	-	-	-
8826	130	2.51	130	2.51	1:1	51.7	-	230	4.45	10	89	96	3	101.6	59-76	-	71-81
8828	130	2.60	130	2.60	1:1	49.9	-	270	5.41	3	126	104	35	99.9	48-52	44-60	-
8829	130	2.68	130	2.68	1:1	48.5	-	300	6.18	2	182	116	68	99.2	50-55	28-32	70-81
8833	130	4.69	130	4.69	1:1	27.7	-	100	3.61	6	95	95	6	101.2	63-65	92	62-81
8834	130	1.91	130	1.91	1:1	68.0	-	150	2.20	10	137	122	15	99.1	42	-	-
8835	120	2.62	120	2.62	1:1	45.8	-	100	2.18	4	96	84	2	100	44-48	36-50	-
8836	150	4.53	150	4.53	1:1	33.1	-	140	4.23	5	123	101	22	101.6	49-60	33	85-91
8837	150	5.24	150	5.24	1:1	28.6	-	130	4.54	10	150	121	39	101.2	53-60	36-40	86-92
A255	200	5.06	100	5.06	1:1	39.5	-	200	5.06	5	75	80	1	101.9	36-40	50-54	-
A278	100	1.69	100	1.69	1:1	59.0	-	400	6.78	5	111	112	4	100.4	49-58	38-44	-
A279	100	1.84	100	1.84	1:1	54.4	-	200	3.68	5	110	104	11	102.3	45	42-52	-
85 events	Telazol (mg)	Telazol (mg/kg)	Xylazine (mg)	Xylazine (mg/kg)	T:X ratio	Weight (kg)	Ketamine Supplement (mg)	Reversal (mg)[1]	Reversal (mg/kg)	Induction (min)[2]	Handling (min)	Reversal PDI[3] (min)	Up[4] (min)	High Temp (F)	Heart Rate (b/min)	Respiratory Rate (b/min)	SpO2[5] (%)
n	82	82	79	79	75	86	3	82††	82††	77	83	86	83	79	57	38	39
Mean†	129.1	2.95	128.90	2.96	1:1	45.63	133.33	197.68	4.39	10.30	116.82	98.60	19.0	100.9	54.94	47.08	79.56
SE	3.50	0.10	4.59	0.11	0.03	7.95	33.33	6.95	0.14	1.52	3.47	2.93	2.22	0.18	1.40	2.60	1.33
CV	0.25	0.32	0.32	0.34	0.24	0.17	0.43	0.29	0.29	1.29	0.27	0.28	1.06	0.02	0.19	0.34	0.10

[1] (y) denotes the use of yohimbine rather than tolazine hydrochloride

[2] Induction time is the time between injection and unconsciousness

[3] PDI = Time post dart injection

[4] Up = Time until animal was coherent with head up

[5] SpO_2 = dissolved blood oxygen

*** Additional dose required to achieve unconsciousness**

† Does not include animals that required an additional dose post dart injection

†† Includes only animals that were administered tolazine hydrochloride