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Survival of Neonate Mule Deer Fawns in Southern Utah: Effects of Coyote Removal and Synchrony of Parturition

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ABSTRACT

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Mule deer (*Odocoileus hemionus*) are an iconic species of wildlife, and populations of mule deer across much of the western U.S. have experienced recent fluctuations in size. Factors that affect the survival and subsequent recruitment of juveniles may be the preeminent cause of population fluctuations for mule deer in many areas. Many factors, including habitat loss, extreme weather, intense predation, timing and synchrony of parturition, and competition with other species may be influencing these changes. We studied two potential factors that can influence the survival of neonate mule deer in southern Utah. To better understand how predation affects mule deer, we first implemented a study of the response of mule deer to removal of coyotes in southern Utah. We monitored survival and cause-specific mortality of neonate mule deer in areas where coyotes were removed and where they were not removed. We used multi-model inference within Program MARK and a known-fate model to estimate survival of neonate mule deer in both treatments (removal and non-removal), and to investigate factors potentially influencing survival. Our results indicated that coyote control can decrease mortality and increase survival of neonate mule deer in some situations. Removal of coyotes was most effective when removal efforts occurred for multiple consecutive years, and when control efforts occurred in or near fawning habitat.

Second, we examined how synchrony of parturition affects the survival and cause-specific mortality of neonate mule deer. Reproductive synchrony is a strategy that influences the survival of juveniles and the growth of populations. Our objective was to test three possible explanations for the synchrony of parturition in mule deer; 1) pressure of predation on newborns, 2) a hybrid of predation and environmental effects, and 3) weather and food availability. To determine the effects of the timing of parturition on the survival and predator-related mortality of neonate mule deer, we used multi-model inference within Program MARK and a known-fate model. Our results indicated that the timing of parturition influenced survival and predator-related mortality of neonate mule deer. There was a lag between the onset of parturition of mule deer and predation of mule deer by fawns; individuals born close to the onset of parturition had higher survival and lower predator-related mortality than those whose births were delayed relative to the onset of parturition. Since predators selected for neonate mule deer that were born late, predator learning may partially explain reproductive synchrony in mule deer. Environmental factors may have a greater effect than predation on the survival of early-born individuals.

Keywords: *Odocoileus hemionus*, mule deer, fawn, neonate, coyote, predator, predator control, Monroe Mountain, parturition, synchrony, birth timing, predator swamping, predator learning

ACKNOWLEDGEMENTS

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CHAPTER 1

Effects of Coyote Removal on the Survival of Neonate Mule Deer

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ABSTRACT

Mule deer (*Odocoileus hemionus*) populations across much of the western U.S. have

experienced recent fluctuations in size. Low survival of fawns and subsequent low recruitment

may be the preeminent cause of population fluctuations for mule deer in many areas. Predation

has been identified as limiting juvenile (up to 12 months of age) survival and recruitment.

Examination of survival and cause-specific mortality of neonate (0 – 6 months of age) mule deer

may further help elucidate factors contributing to population declines. To better understand how

predation affects mule deer, we implemented a study that evaluated the effects of the removal of

coyotes (*Canis latrans*) on mule deer in southern Utah. Our objective was to determine whether

removal of coyotes could improve survival of mule deer neonates. Using a four-year crossover

study design, we documented survival of neonate mule deer in areas where coyotes were

removed and where they were not. During June 2012–15, we monitored a total of 268

individuals using VHF-radio collars to determine survival. We located deceased individuals and

determined a probable cause of death based on evidence found at that location. We used multi-

model inference within Program MARK and a known-fate model to estimate survival of neonate

mule deer in both treatments (removal and non-removal), and to investigate factors potentially

influencing survival. Our results indicated that coyote control can decrease mortality and

increase survival of neonate mule deer when certain conditions are met. Removal of coyotes was

most effective when removal efforts occurred for multiple consecutive years, and when control efforts occurred in or near fawning habitat.

INTRODUCTION

Predation can play a significant role in regulating ungulate populations by influencing important population metrics, such as survival and juvenile recruitment (Connolly 1978, Linnell et al. 1995, Ballard et al. 2001). Low survival of juveniles and subsequent poor recruitment may be the preeminent cause of population fluctuations for ungulates (Connolly 1981, Unsworth et al. 1999, Andelt et al. 2004). For example, mule deer (*Odocoileus hemionus*) populations across much of the western U.S. have experienced recent fluctuations in size (Carpenter 1998, Unsworth et al. 1999, DeVos et al. 2003, Connolly et al. 2012). Many factors, including habitat loss, extreme weather, and intense predation may be influencing these changes (Ballard et al. 2001, Hurley et al. 2011). Predation has been identified as limiting juvenile (up to 12 months of age) survival and recruitment (Connolly 1978, Linnell et al. 1995). Examination of survival and cause-specific mortality of neonate (0–6 months of age) mule deer may further help elucidate factors contributing to population declines.

Many factors likely influence the relative effect of predation on populations of mule deer. Age of deer, availability of alternate prey for predators of mule deer, and density of deer populations have all been identified as important factors that can impact the relative effect of predation on populations of mule deer (Patterson et al. 1998, Patterson and Messier 2000). For example, adult female mule deer in some western states typically had high annual survival rates; however, fawns were more easily affected by biotic and abiotic stressors, and therefore, had lower and more variable annual survival rates (Gaillard et al. 1998, Unsworth et al. 1999 Lomas

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and Bender 2007). Additionally, increased availability of microtine rodents as alternate prey for predators was positively associated with survival of deer fawns (Hamlin et al. 1984). The effects predation were also lessened when deer populations were high (Ballard et al. 2001) and were greater when deer populations were low (Laundre et al. 2006).

The complexity of the carnivore community, effects of predator management, and effects of weather can also influence the impact that predators have on the survival of mule deer. The more complex a community of carnivores, the less likely removal of one species of carnivore will benefit species of prey. Additionally, the effect of one species of carnivore on the survival of neonate ungulates may change based on the number of carnivore species in a community (Griffin et al. 2011). Predator management may influence the effects of predation on mule deer by changing the ratio of predators to prey. Predator management has had mixed results, however, with some evidence for predator removals increasing survival of mule deer, whereas other studies have not provided evidence for predator removal having an effect on survival of mule deer (Harrington and Conover 2007, Hurley and Zager 2007, Hurley et al. 2011). The effects of predation can also be confounded by abiotic factors, like weather. Weather may impact the effect of predation on populations of mule deer, and these effects vary by latitude. Though they are subject to predation, mule deer are often limited by harsh winters in northern latitudes (Hurley et al. 2011), and by dry summers in southern latitudes (Bowyer 1991). Therefore, the results of previous predator management studies on survival of mule deer fawns have often been uncertain or ambiguous.

The objective of our study was to determine the effect of targeted predator control on the survival of neonate mule deer in Utah. The location of our study was ideal because of the juxtaposition that minimized the likelihood of climatic extremes (i.e., harsh winters farther north or dry summers farther south). We hypothesized that in the absence of severe weather, predation

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may reduce survival of neonate mule deer. Therefore, we predicted that targeted removal of coyotes (a common management practice) may increase survival of neonate mule deer. Further, we predicted that coyote control would have a greater effect on survival of neonate mule deer when control measures occurred in proximity to fawning and fawn rearing habitat.

STUDY AREA

Our study areas were located on Monroe Mountain in southern Utah. Monroe Mountain is approximately 70 km long (north to south) and 20 km across (east to west). Several thousand mule deer inhabit the mountain and surrounding winter range. Landownership is split between federal agencies (Forest Service and Bureau of Land Management), state lands, and private land-holdings. The mountain was divided into two study areas and a buffer zone (south study area, north study area, and a central buffer; Figure 1-1). The buffer area was an east-to-west corridor that separated the north study area from the south study area. This buffer was 5 - 10 km wide and was delineated by large canyons on the north and south where it bordered the study areas (an effort to insure independence of the treatments). Habitat types on the mountain include areas dominated by big sagebrush (*Artemesia tridentata*), mountain mahogany (*Cercocarpus ledifolius*), Gambel oak (*Quercus gambelii*), aspen (*Populus tremuloides*), pinion pine (*Pinus edulis*), Utah juniper (*Juniperus osteosperma*), ponderosa pine (*Pinus ponderosa*), and Douglas Fir (*Pseudotsuga menziesii*). Potential predators of mule deer inhabiting this area were coyotes (*Canis latrans*), cougars (*Puma concolor*), bobcats (*Lynx rufus*), and black bears (*Ursus americanus*), although black bears are uncommon.

METHODS

We determined the effects of predator removal on survival of neonate mule deer (0–6 months of age) during 2012–2015. To evaluate the effects of predator removal, we implemented an experimental crossover design. During 2012–2013 (first two years of the study), USDA Wildlife Services used standard techniques to remove coyotes from the north study area, but not from the south study area. In 2014, treatments were switched; coyote removal occurred on the south study area, but not the north study area for the final two years. Roughly equal numbers of coyotes were removed from both the north and south study areas during the first two years and last two years of the study (Mahoney 2016).

To determine survival of neonate mule deer, we captured neonates on each study area during each year. To aid in the capture of neonate mule deer, we captured adult female mule deer (via helicopter net-gunning) in March of each year from four locations on winter range of the study areas (Angle, Burrville, Thompson Basin, and Elbow Ranch; Figure 1-1). We assessed body size (hind foot length, chest and neck girth), condition (body condition score method; (Cook et al. 2007)), and age (estimated based on tooth wear and eruption pattern) of each captured individual (Severinghaus 1949, Robinette et al. 1957). Additionally, we determined body condition and pregnancy via ultrasonography (E.I. Medical Imaging portable ultrasound; (Smith and Lindzey 1982)). We fitted pregnant females with VHF collars (Telonics Inc., ATS) and vaginal implant transmitters (VIT; ATS). We used a vaginoscope to insert VITs until the antennae did not protrude from the opening of the vagina (Bishop et al. 2007).

Between the original capture of adult females and parturition, we located collared females using radio telemetry. During March and April, individuals were located sporadically from the ground and a fixed-wing aircraft. Beginning in May, we attempted to locate every female twice a week. Beginning the last week of May, we located each female at least every

other day until all VITs had been expelled. When an expelled VIT was detected (pulse rate was doubled after a reduction in temperature), we located the VIT and conducted an extensive search for the neonate(s). In addition, we opportunistically captured neonate mule deer while searching for those associated with a VIT or while observing female mule deer not previously captured.

To determine survival of neonate mule deer, we attached VHF radio collars to captured individuals. We handled neonates with latex gloves (to reduce the likelihood of transferring human scent) while we fitted collars and we recorded morphological measurements (e.g. weight and hind foot length). Additionally, we estimated the age of the individual(s) using hoof condition/length, pelage, and behavior (Haugen and Speake 1958, Robinette et al. 1973, Sams et al. 1996, Lomas and Bender 2007). Radio collars placed on individuals were designed to expand with the growing animal and drop off after approximately 8 months.

We monitored collared neonate mule deer on a schedule designed to ensure that mortalities were located promptly. Early detection of mortalities minimized the likelihood of confusion between the true cause of mortality and scavenging. Specifically, we relocated neonates at least 3 times weekly between the time of initial capture and the end of August. From September to mid-December when the Utah Division of Wildlife Resources (UDWR) captured 6-month old fawns for monitoring of state-wide survival, we relocated neonate mule deer at least once per week. We decreased monitoring frequency beginning in September because most mortality of neonate mule deer occurs in the first three months of life (Pojar and Bowden 2004, Lomas and Bender 2007).

We attempted to locate deceased animals whenever a transmitter was in mortality mode (a doubling of the pulse rate after 8 hours of no movement). After locating a collar, we searched for the deceased neonate mule deer and determined a probable cause of death based on evidence found at that location. If the probable cause of death was attributed to predation, we used a suite

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of indicators (tracks, scat, blood, drag trails, and other factors) that are predator specific (e.g. coyote, cougar, black bear) to determine what species of predator was most likely responsible for the mortality (Wade 1985, Patterson 1994, Gese and Grothe 1995). In a few cases, assignment of the predator responsible for death was ambiguous (e.g., most of the carcass was consumed and there was sign from multiple species of predators) and therefore, we classified these mortalities as unknown predation. Other cause-of-death categories included starvation, accidents, disease, and unknown.

We used multi-model inference within Program MARK and a known-fate model (White and Burnham 1999) to estimate survival of neonate mule deer in both treatments (removal and non-removal), and to investigate factors potentially influencing survival. Preliminary analysis revealed that coyotes have the greatest impact on survival of neonate mule deer during the first 16 weeks of life; therefore, we modeled survival to 16 weeks in our primary analysis. We did not use staggered entry to add neonate mule deer to our sample; rather, week-one for each mule deer neonate began at birth, regardless of calendar date (Bishop et al. 2008). We used a heirarchical approach to draw inferences regarding *a priori* hypotheses about potential influences on survival rates (Burnham 2002). We first tested for temporal effects by comparing models where survival varied linearly through time (T), quadratically through time (T²), by week (Week), and by year (Year); we also tested models that used interactions of these time components. We advanced models to the next step based on Akaike's Information Criterion adjusted for small sample sizes (AICc) if they had at least 5% weight ω_i.

In our second step, we tested for the influences of removal of coyotes by adding variables to models that advanced from our first step. Covariates related to removal of coyotes included side of the mountain (north or south; Side), treatment (Treatment), year of treatment (YrofTrtmt), number of coyotes removed within 2250 meters (the average summer range of mule deer (Webb

et al. 2013)) surrounding the capture location of each neonate (HRCKills), and lagomorph abundance (LagAbund (a measure of alternate prey for coyotes)). We obtained estimates of lagomorph abundance from a concurrent study of predators on Monroe Mountain (Mahoney 2016).

In our final step, we added various individual neonate mule deer characteristics. These characteristics included sex of an individual (Sex), new hoof growth (NewGrowth), whether or not the neonate was a twin (Twin), and weight (Weight+Age)) as covariariates. We included neonate mule deer age at capture in all our models that included weight to account for the effects of age-related weight gain.

To account for potential dependence among the fate of siblings, we estimated ĉ (degree of overdispersion) by bootstrapping our data using methods described by Bishop et al. (2008). We then ranked final models based on Quasi-AICc values (QAICc) adjusted for ĉ. We checked models in our final list for uninformative parameters and then produced model-averaged estimates of β coefficients survival estimates (Arnold 2010). We judged the importance of variables in top models based on overlap in 85% confidence intervals around these β estimates (Arnold 2010).

RESULTS

During 2012–2015 we captured 287 adult female mule deer from winter-range locations surrounding Monroe Mountain. As expected, the age structure of the captured females was skewed toward younger individuals (Figure 1-2). Additionally, the range of percent ingesta free body fat (IFBF) was 2.9 – 12.1% and was normally distributed around the mean (Figure 1-3). Of the 287 females captured, 95% (N=273) were pregnant. Transmitters were inserted into 260 of these 273 pregnant females; 13 females were not used because they were recaptured and known

to summer outside the two study areas (N=5), their vaginas were too small for VIT insertion (N=5), or they experienced capture-related injury (N=3). Of the 260 animals that received VITs, 146 moved onto one of our study areas on Monroe Mountain. The remaining females transitioned onto summer range outside the study areas and could not be included in the study (Table 1-1).

Searches for neonate mule deer associated with expulsion of VITs began on 29 May, when the first VIT was expelled, and continued through early July. Based on expulsion of VITs, we obtained dates of parturition for 140 of the 146 females that remained in the study area during parturition (Figure 1-4). Five females died prior to parturition, and one female that received a VIT never gave birth. Mean dates of parturition were June 13th, 16th, 15th, and 14th for 2012–2015, respectively. Using VITs and opportunistic searching, we captured 266 neonate mule deer between the two study areas. We excluded six individuals from our sample because they were still born (N=2) or their deaths were human-caused (poaching, vehicle strike; N=4); consequently, 260 individuals were used in final analyses.

We attributed mortality of neonate mule deer to predation, starvation, disease, stillbirth, roadkill, and unknown (Table 1-2, Figure 1-5). Predation was the leading cause of mortality accounting for approximately 68% of all mortalities. Coyotes and cougars killed roughly equal numbers of neonate mule deer with all other predators accounting for only 4% of neonate mule deer mortalities (Figure 1-6). Coyotes and cougars killed a significantly higher proportion of neonate mule deer (0.16 vs 0.08 for coyotes; 0.13 vs 0.05 for cougars) on the south study area than on the north study area during all years, regardless of treatment (Figure 1-7). Approximately 90% of coyote-related mortality occurred during the first 16 weeks of neonate life (Figure 1-8). Cougar-related mortality was more evenly distributed than was coyote-related mortality throughout the six-month monitoring period.

Survival of neonate mule deer to 16 weeks averaged 65% across all years. Sex and Weight were influential variables in our models (Table 1-3). Females had a higher likelihood of survival than males. Additionally, survival of neonate mule deer increased as weight increased. None of our models contained uninformative parameters.

Number of consecutive years of treatment (YrofTrtmt) was a prominent variable in our analysis, appearing in 8 of the top 10 models (Table 1-3). Two consecutive years of coyote removal had a strong effect on survival of neonate mule deer. Survival estimates for neonate mule deer increased as the year of treatment increased (Figure 1-9).

The location of coyote removal relative to birth sites (HRCKills) appeared in 6 of the top 10 models which accounted for 40% QAICc weight. The support for HRCKills in our models indicates that proximity of coyote removal to fawning locations positively influenced the likelihood of survival of neonate mule deer (Table 1-3). The probability of a neonate mule deer surviving to 16 weeks increased considerably with increasing numbers of coyotes removed in a deer home range surrounding birth locations (Figure 1-10).

DISCUSSION

Our results support the prediction that coyote control can decrease mortality and increase survival of neonate mule deer. Survival of neonate mule deer to 16 weeks of age increased with coyote control. Predator control also resulted increased survival of neonate mule deer during summer in Idaho (Hurley et al. 2011). Predator control in the aforementioned study had the greatest effect on survival of neonate mule deer in summers where alternate prey was lacking, and deer were selected by predators. The abundance of alternate prey was not an important predictor of survival of mule deer in our study. Removal of coyotes had a positive effect on survival of neonate mule deer, regardless of the density of alternate prey. Further, subsequent

years of coyote control in the same area had a greater effect than a single year of control. This result is consistent with research on pronghorn that indicated a need for multi-year coyote removal to increase fawn survival for that species (Smith et al. 1986). Multiple years of coyote removal in Idaho had inconsistent effects on common metrics of populations of mule deer including survival of neonate mule deer, fawn-to-adult female ratios, and fawn-at-heel ratios (Hurley et al. 2011). These effects could be due to inconsistent coyote removal efforts among years. Multiple efforts to remove coyotes in the same year had no effect on fawn-to-adult female ratios or abundance of mule deer in Utah and Wyoming (Brown and Conover 2011). Even under intense coyote removal programs, coyotes have been reported to repopulate areas within months or a short number of years (Beasom 1974; Connolly 1978, 1995; Connolly and Longhurst 1975). Additionally, some coyote populations have returned to pre-treatment levels through recolonization, compensatory breeding, and increased survival rates following coyote removal (Knowlton 1972; Knowlton et al. 1999). These findings support our results that multiple years of coyote removal, with consistent removal among years, can have a greater effect on survival of neonate mule deer than a single year of control.

Juxtaposition of coyote removal on the landscape significantly influenced the likelihood of survival of neonate mule deer. In other words, the removal of coyotes relatively close to the birth site increased survival, whereas, removal of coyotes from areas distant from the birth site did not influence survival of neonates. Hurley et al. (2011) also suggested that the effects of coyote removal on the survival of neonate mule deer in summer would likely be maximized if coyotes were removed from fawning-summer range, though their suggestion applied to years when mule deer neonates were needed as alternate prey for coyotes. Coyote removal is often conducted during winter months, when snow makes coyotes more vulnerable. Since coyotes generally use the same areas in winter as they do in summer (Weaver 1979, Gantz 1990; Shivik

et al. 1996, Mahoney 2016), removing coyotes from potential fawning habitat in winter would likely benefit neonate mule deer the following summer. Our results support this prediction. This result is important because it suggests that control of coyotes should be focused in fawning habitat to successfully increase survival of neonate mule deer and subsequent recruitment into the population.

Cougars had a significant impact on the survival of neonate mule deer in our study. In fact, cougars killed roughly the same number of neonate mule deer as coyotes. Predation was the leading cause of mortality of neonate mule deer accounting for at least 68% of all mortalities. It is likely 68% underestimates the actual effects of predators. For example, it is probable that at least some of the cases we assigned to starvation were due to the mother being killed by a cougar resulting in the subsequent starvation of the neonate. In fact, we had multiple instances where we were able to determine this was the case by locating the deceased collared mother of the neonate mule deer that had starved. The result that cougars were a significant cause of mortality is supported by an examination of the selection of mule deer by coyotes and cougars that found cougars to be significant predators of young mule deer (Pierce et al. 2000). Consistent with this assertion, removal of cougars increased survival of mule deer fawns during winter and fawn-to-doe ratios increased 6–27% (Hurley et al. 2011). Removal of cougars in the aforementioned study also increased the annual survival of adult female mule deer by as much as 5.5%, while removal of coyotes in the same study did not increase the survival of adult mule deer (Hurley et al. 2011). Because of their effect on the survival of adult mule deer, cougars likely have a greater impact than coyotes on indirect mortality (e.g., starvation as described above). Because cougars can have a marked impact on mule deer populations by limiting survival of juveniles and adults (Pierce et al. 2000, Hurley et al. 2011), cougars may be even more important than coyotes for growth and regulation of deer populations. While these past studies have shown cougars to be

important predators of older fawns and adult mule deer, our results demonstrate that cougars have a significant influence on the survival of neonate mule deer as well.

Though increasing the survival rates of neonate ungulates can increase recruitment and increase the rate of population growth (Connolly 1981, Unsworth et al. 1999), it is possible that predator-related mortality is compensatory and not additive. Therefore, increased survival of neonate mule deer may not result in a population-level response. For example, survival of neonate mule deer in summer was increased with predator control in Idaho, but winter-related mortality due to winter severity was more important—swamping benefits from decreased rates of predation (Hurley et al. 2011). Predation is likely to be compensatory when populations of mule deer are at or near carrying capacity, whereas predation is more likely to be additive when populations are not at carrying capacity (Bartmann et al. 1992, Logan 1996, Ballard et al. 2001). Therefore, increasing populations of mule deer via control of coyotes has the greatest likelihood of success when and/or where winter severity is not driving recruitment and populations are below carrying capacity.

MANAGEMENT IMPLICATIONS

Mule deer are an ecologically, economically and aesthetically important species. Consequently, managing for robust deer populations is often a high priority for agencies charged with managing wildlife. Our results indicate that coyote control can increase survival of neonate mule deer. Coyote control increased survival when 1) control efforts occurred for multiple consecutive years, and 2) when control efforts occurred in or near fawning habitat. Efforts to control predators should, therefore occur, at relatively high elevation with shrubby understory consistent with the location of fawning habitat (Long et al. 2009, Freeman 2014).

The likelihood that coyote control will lead to increased survival of neonate mule deer and a positive population-level response is greatest when predator-related mortality has the greatest likelihood of being additive. In other words, control efforts are more likely to be successful when populations of deer are below carrying capacity, and winter severity or summer drought have little influence. Since we cannot predict winter severity or summer drought in advance, success of control programs may have a greater likelihood of success in regions where the likelihood of a severe winter or a summer drought is lower.

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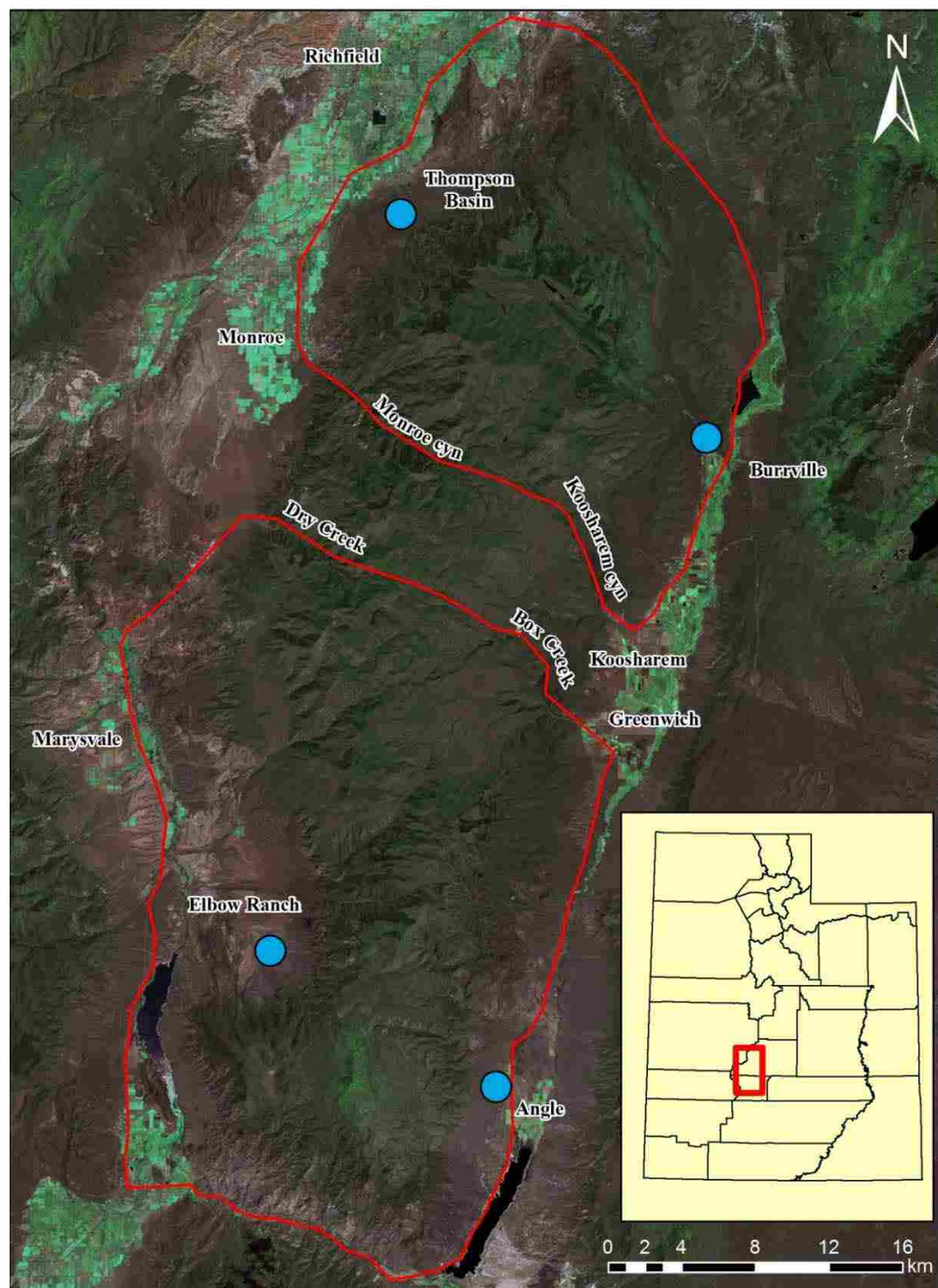
Figure 1-1. Map of Monroe Mountain, Utah with red lines delineating north (coyote removal area 2012–13) and south (coyote removal area 2014–15) study areas where we evaluated survival of neonate mule deer. Blue dots indicate general locations where adult female mule deer were captured on winter range.
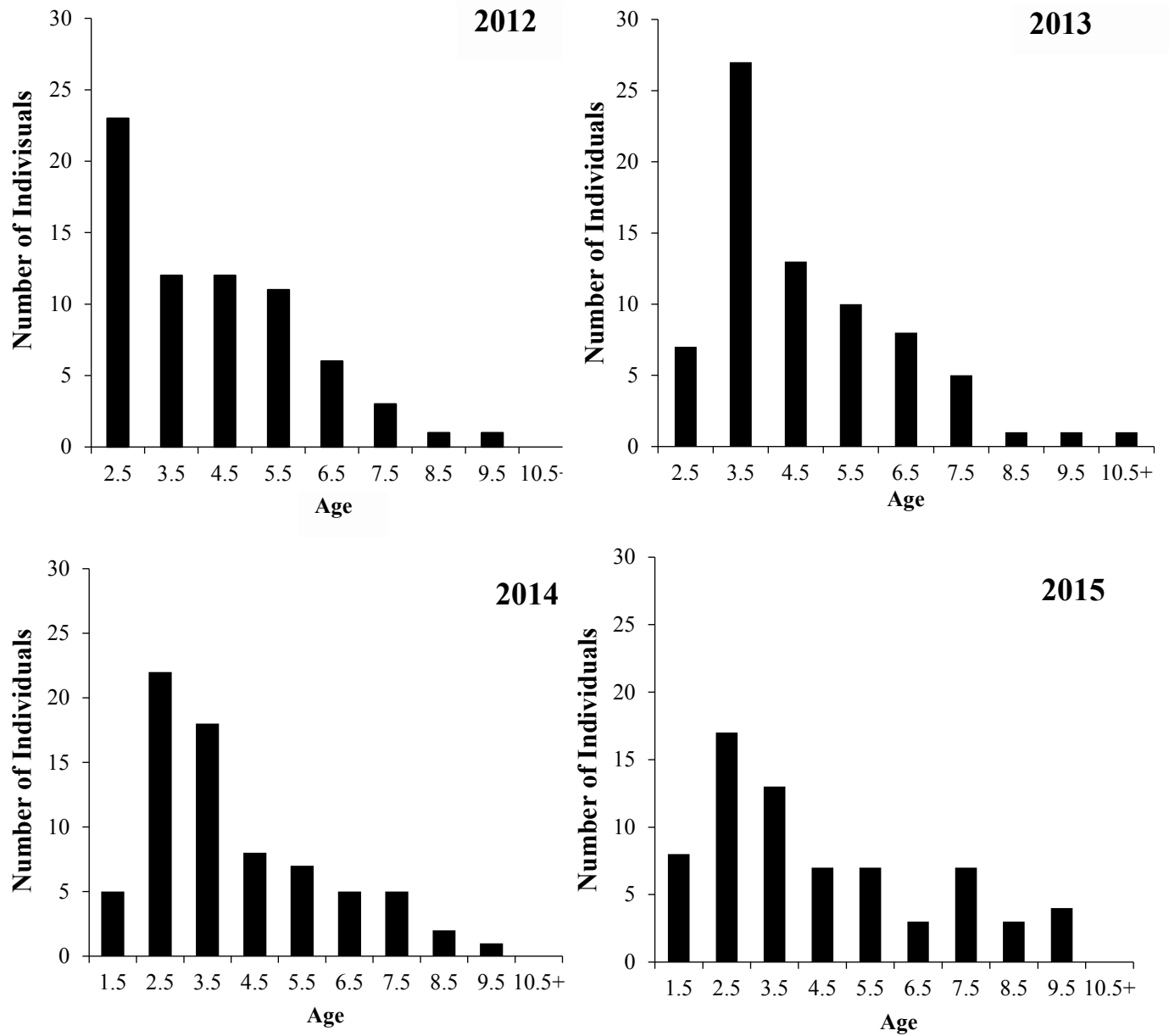
Figure 1-2. The age structure of adult female mule deer captured around Monroe Mountain during 2012–2015.
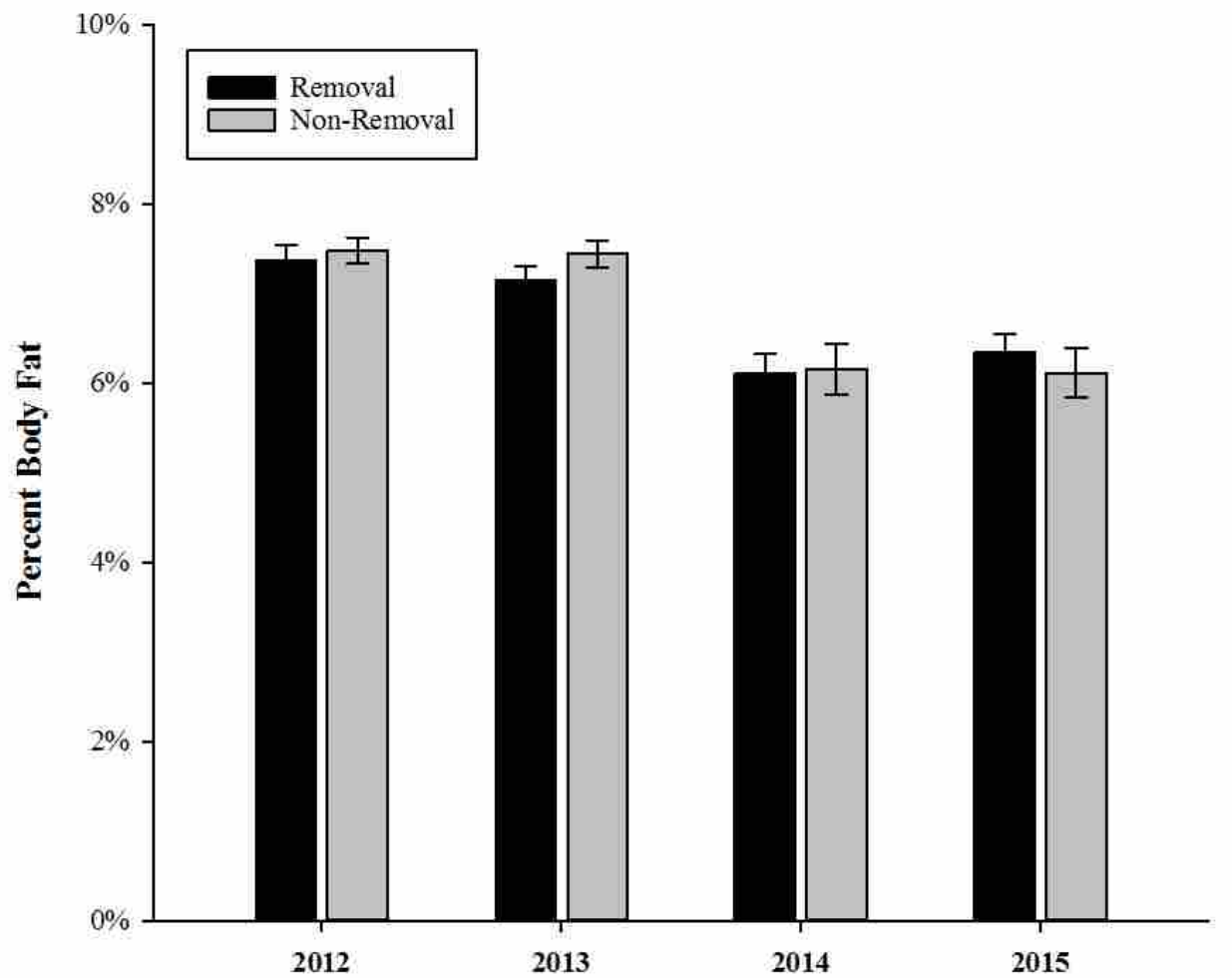
Figure 1-3. Percent ingesta free body fat of adult female mule deer captured on Monroe Mountain during March of 2012–2015. Treatments included areas where coyotes were removed (Removal) and where they were not removed (Non-removal).

Figure 1-4. Dates of parturition for adult female mule deer on Monroe Mountain during 2012–2015. Mean dates of parturition (red bars) were June 13th in 2012, June 16th in 2013, June 15 in 2014, and June 14th in 2015.
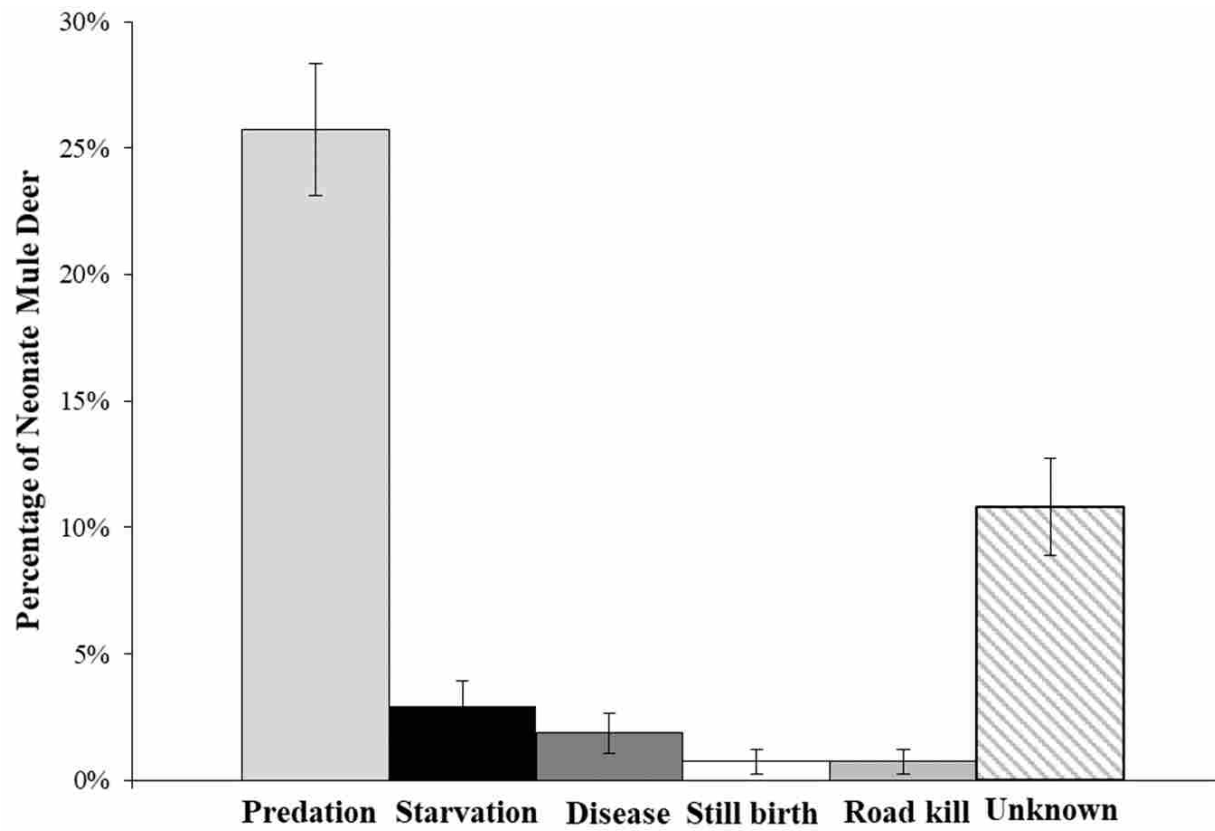
Figure 1-5. Percentage of neonate mule deer lost to each cause of mortality on Monroe Mountain during 2012–2015.
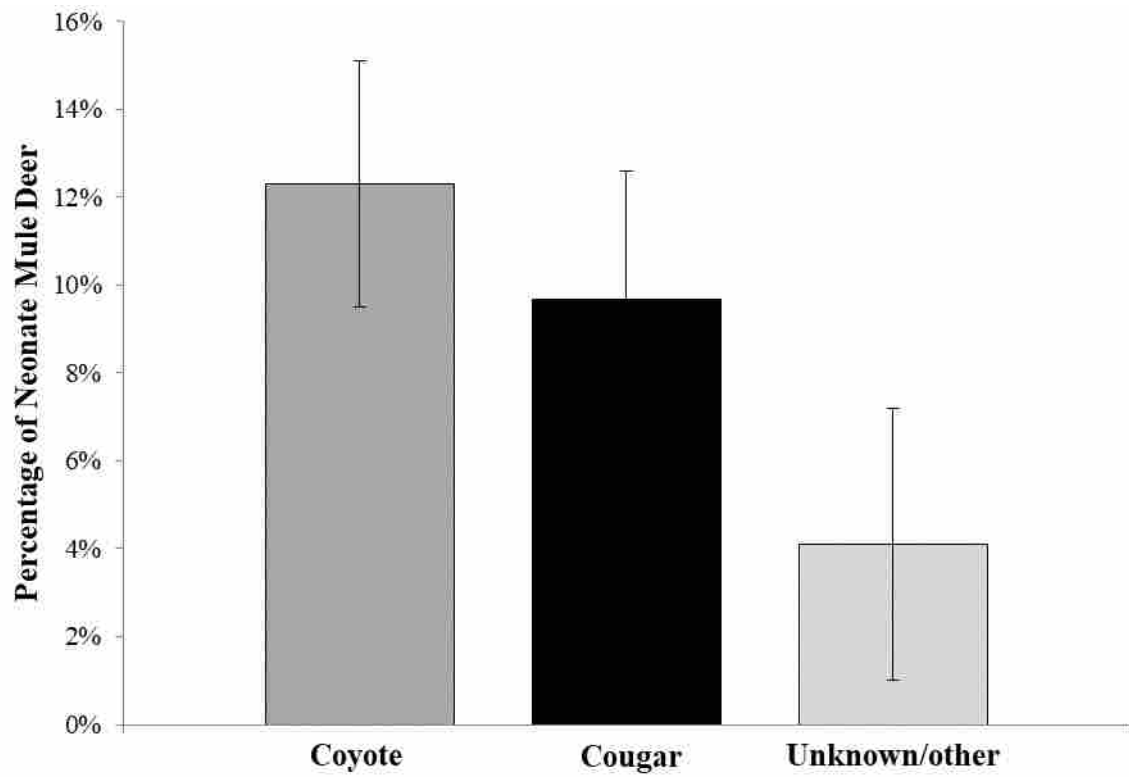
Figure 1-6. Percentage of neonate mule deer taken by each predator type on Monroe Mountain during 2012–2015.
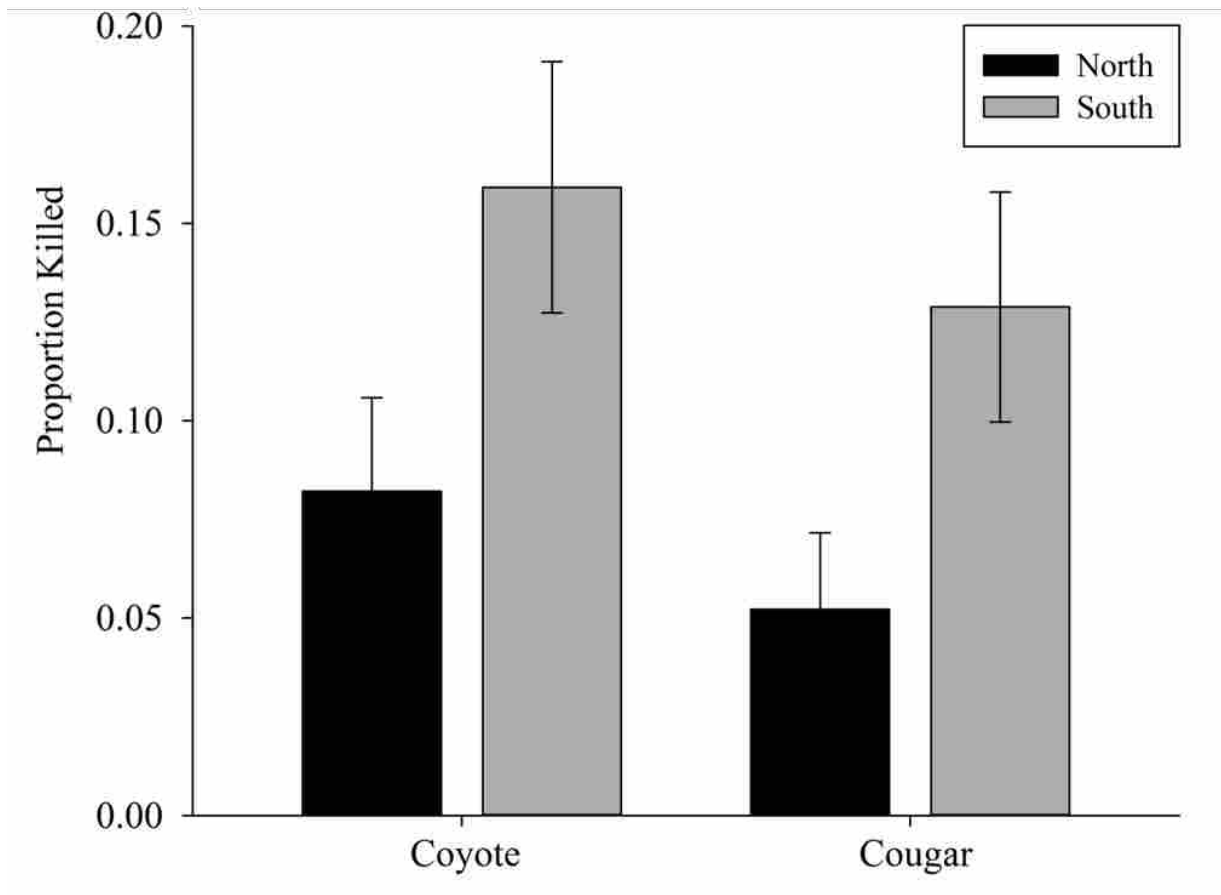
Figure 1-7. Proportion of neonate mule deer killed by coyotes and cougars (±SE) from 2012–2015 on north and south study areas on Monroe Mountain.
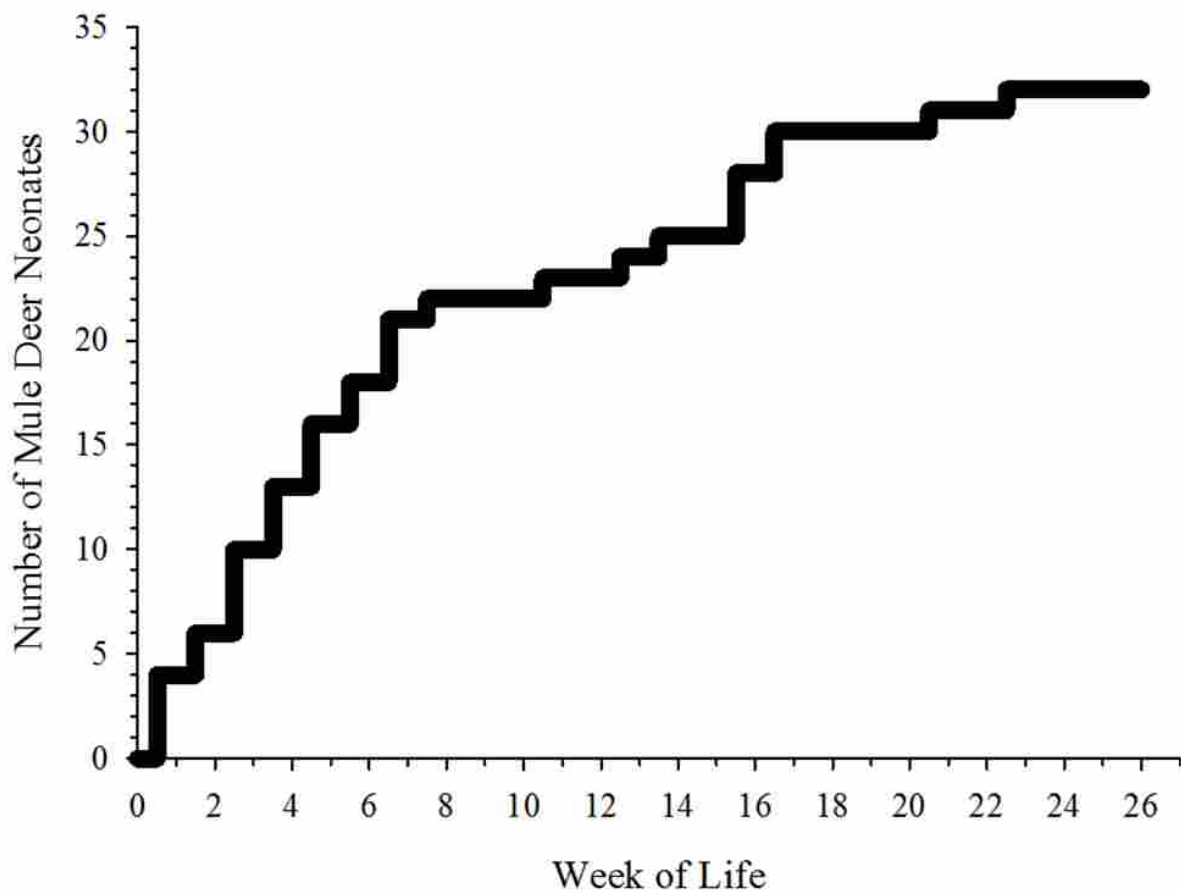
Figure 1-8. Cumulative number of neonate mule deer killed by coyotes by week of neonate mule deer life on Monroe Mountain. The numbers of neonate mule deer killed during each week after birth were pooled across all years of our study (2012–2015).
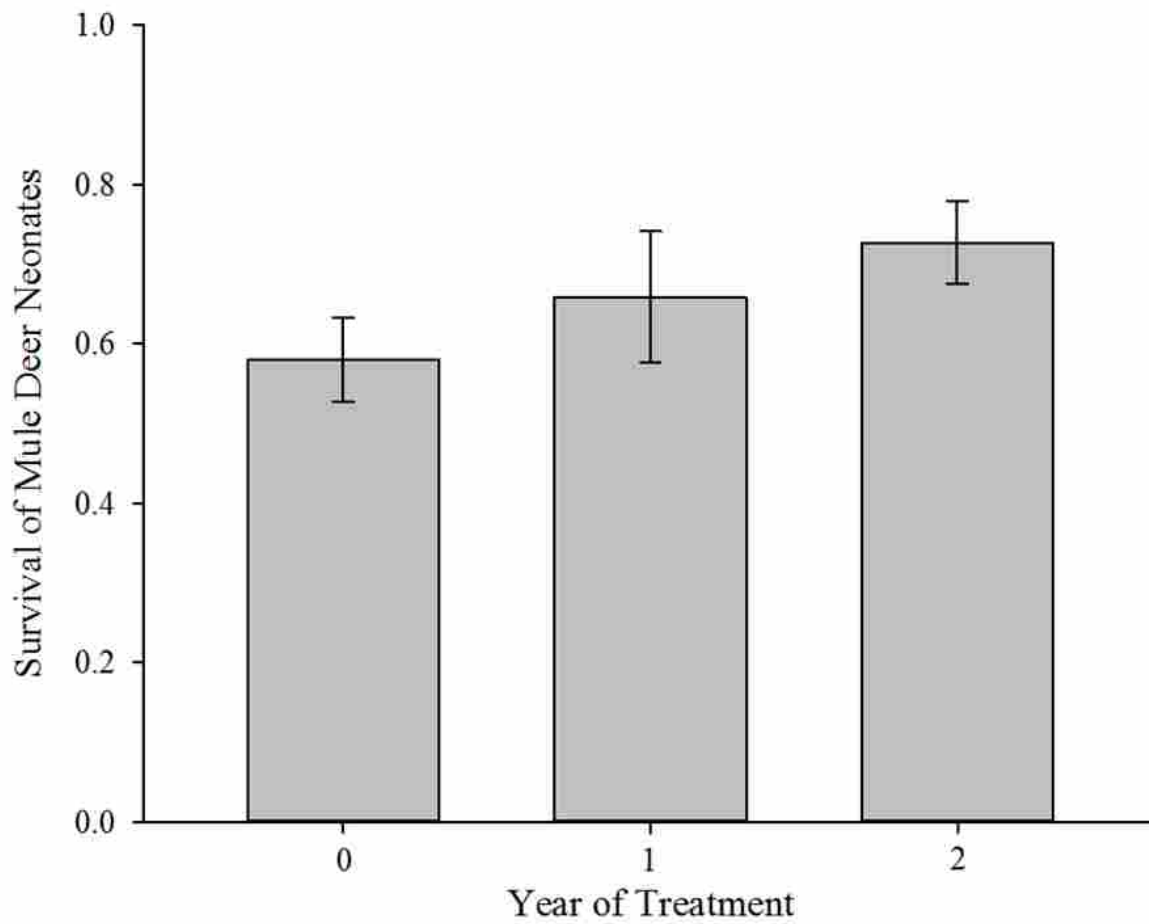
Figure 1-9. Estimated survival of neonate mule deer relative to the year of coyote removal on Monroe Mountain during 2012–2015.
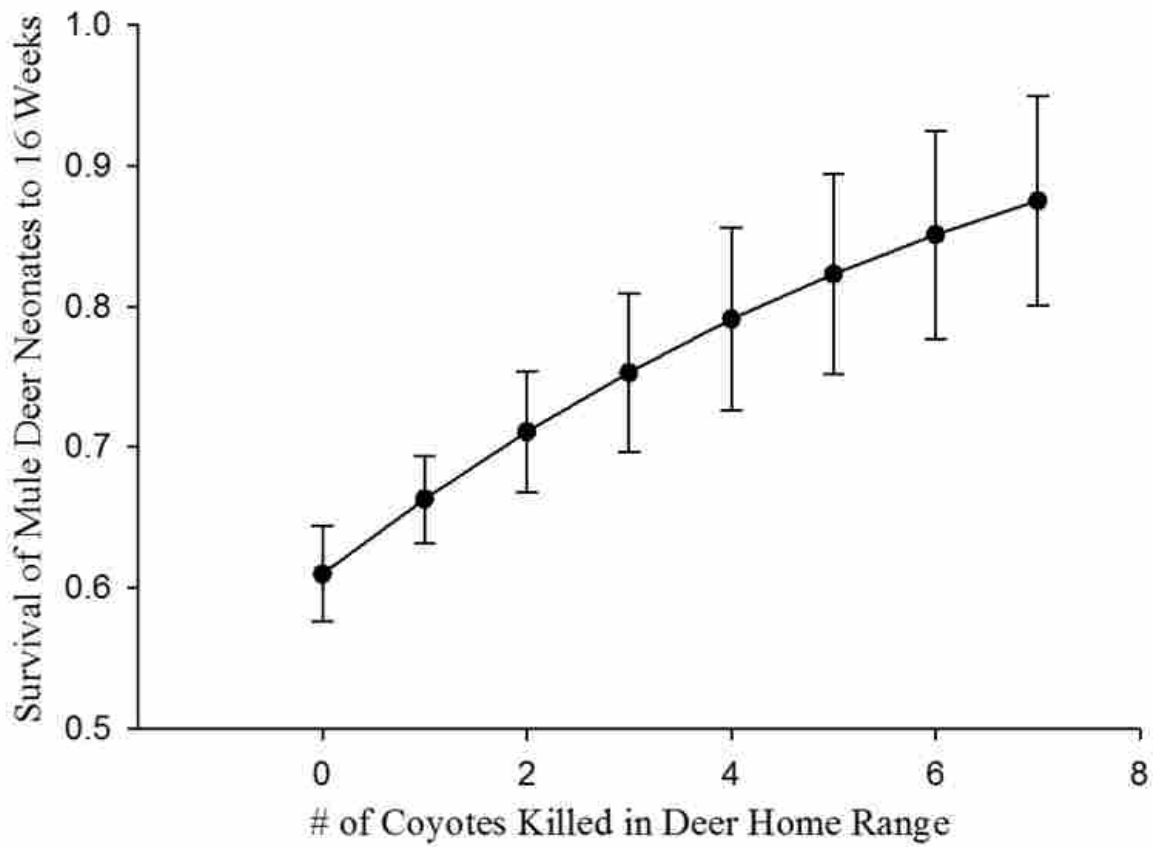
Figure 1-10. Probability of neonate mule deer surviving to 16 weeks of age on Monroe Mountain during 2012–2015 based on the number of coyotes removed within a deer home range relative to the birth sites of neonate mule deer.

Table 1-1. The distribution of female mule deer captured from four regions of wintering range around Monroe Mountain during 2012–2015. Numbers in parentheses are deer that migrated from Angle to Burrville (between sides) during winter.

	Capture Location			
	Thompson	Burrville	Angle	Elbow
Females inserted w/ VITs	62	53	101	44
Females migrating	29	16	53	10
Females in Buffer	0	2	0	2
VIT females remaining*	32	30(+5)*	47(-5)	32
Fawns Captured from VITs	29	25(+2)	52(-2)	26

* this number includes only those females that moved onto one of the Monroe Mountain study areas. One doe captured at Burrville never gave birth.

Table 1-2. The distribution and probable causes of mortality of neonate mule deer that were captured on Monroe Mountain during 2012–2015.

	2012 Fawns Per Study Area		2013 Fawns Per Study Area		2014 Fawns Per Study Area		2015 Fawns Per Study Area	
	REMOVAL	NON-REMOVAL	REMOVAL	NON-REMOVAL	REMOVAL	NON-REMOVAL	REMOVAL	NON-REMOVAL
Total Captured	34	27	35	32	39	33	36	32
Still Births	0	2	0	0	0	0	0	0
Predation Mortalities	5	9	4	13	16	7	11	4
Coyote	5	6	0	4	7	4	5	2
Cougar	0	2	2	3	8	3	6	2
Unknown	0	1	2	6	1	0	0	0
Road Kill Mortalities	1	0	0	0	0	1	0	0
Disease/Deformity	2	0	0	1	1	0	1	0
Starvation	3	2	0	2	0	0	1	0
Unknown Mortality	3	2	2	3	5	6	4	4

Table 1-3. Model selection results for neonate mule deer through 16 weeks of age on Monroe Mountain during 2012–2015. Variables in our top models include linear time trend (T), side of the mountain (Side), year of coyote removal treatment (YrofTrtmt), number of coyotes removed within a deer home range relative to fawn birth sites (HRCKills), sex (Sex), weight at capture (Weight), and age at capture (Age).

Model	QAICc	Δ QAICc	AICc ω_i	K	QDeviance
{S(T+Side+YrofTrtmt+Sex+Weight+Age)}	679.6116	0	0.1512	7	665.5771
{S(T+Side+HRCKills+Side*HRCKills+YrofTrtmt+Sex+Weight+Age)}	679.9357	0.3241	0.12858	9	661.8803
{S(T+Side+YrofTrtmt+Weight+Age)}	680.9298	1.3182	0.07822	6	668.904
{S(T+Side+HRCKills+Side*HRCKills+YrofTrtmt+Weight+Age)}	681.2247	1.6131	0.0675	8	665.1804
{S(T+Side+HRCKills+Side*HRCKills+Sex+Weight+Age)}	681.2311	1.6195	0.06728	8	665.1869
{S(T+Side+YrofTrtmt+Sex)}	681.6154	2.0038	0.05552	5	671.597
{S(T+Side+YrofTrtmt)}	681.8101	2.1985	0.05037	4	673.7978
{S(T+Side+HRCKills+Side*HRCKills+Weight+Age)}	681.8181	2.2065	0.05017	7	667.7837
{S(T+Side+HRCKills+Side*HRCKills+YrofTrtmt+Sex)}	682.0013	2.3897	0.04578	7	667.9669
{S(T+Side+HRCKills+Side*HRCKills+YrofTrtmt)}	682.0491	2.4375	0.0447	6	670.0233

CHAPTER 2

Effects of Timing and Synchrony of Parturition on the Survival of Neonate Mule Deer

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ABSTRACT

Mule deer (*Odocoileus hemionus*) are an iconic species in the western U.S. with intriguing life history strategies, including reproductive synchrony. Multiple hypotheses exist to explain why reproductive synchrony may have evolved. One hypothesis suggests reproductive synchrony is a strategy to minimize the likelihood of predation. A surge of prey may swamp predator populations, thereby increasing the likelihood that an individual survives. Stabilizing selection in parturition occurs as animals born before or after this surge have a greater likelihood of mortality via predation. Prey switching, due to predator learning, is another factor that may influence parturition of mule deer by causing directional selection in parturition by decreasing likelihood of survival of late-born individuals. Alternatively, weather or the availability of adequate resources may drive synchrony of parturition. Timing of resource availability may restrict early parturition (lack of available forage for lactation and growth) and late parturition (necessity to reach a critical body mass prior to winter). Our objective was to test these hypotheses to explain the synchrony of parturition in mule deer. During June of 2012–15, we recorded birth dates of 260 mule deer fawns on Monroe Mountain in south-central Utah. We fitted fawns with VHF-radio collars and monitored their survival for the first several months of life. To determine the effects of the timing of parturition on the survival and predator-related mortality of neonate mule deer, we used multi-model inference within Program MARK and a

known-fate model. Our results indicated that the timing of parturition influenced survival and predator-related mortality of neonate mule deer. There was a lag between the onset of parturition of mule deer and predation of mule deer by predators; individuals born close to the onset of parturition had higher survival and lower predator-related mortality than those whose births were delayed relative to the onset of parturition. We found support for the hypothesis that predator learning influences parturition in mule deer by causing directional selection. Environmental factors may be more important than predation in regulating early parturition.

INTRODUCTION

Reproductive synchrony is an intriguing life history strategy employed by many species of plants and animals (Janzen 1971, Ims 1990a, Simmonds 2017). Reproductive synchrony is characterized by neighboring individuals of the same species producing many young in a relatively short amount of time, and is often driven by important environmental and social cues (Ims 1990b). Reproductive synchrony is a strategy that influences the survival of juveniles and the growth of populations (Keller et al. 2015). Because reproductive synchrony is widespread among plants and animals, it must increase the fitness of species that employ this strategy.

In general, there are two potential mechanisms or hypotheses to explain the evolution of reproductive synchrony in animals; 1) timing and/or synchrony of parturition may result from predation on newborns, and 2) synchrony is driven by weather and food availability (seasonality in climate) (Rutberg 1987, Mysterud et al. 2002). Synchrony may be driven by one of these factors alone, or a combination of these mechanisms (Guinness et al. 1978). For example, predators alone may impact synchrony by targeting early and late-born individuals (Estes 1976, Adams et al. 1995). Conversely, extreme weather may influence early-born individuals (Bunnell

1980) while predation may influence late-born individuals due to the time necessary for predators to recognize the influx of available prey (Ballard et al. 1991, Testa et al. 2000).

Species with synchronous parturition often have reduced predator-related mortality and increased survival of neonates due to predator swamping (Sinclair et al. 2000). In other words, a surge of prey may swamp a predator population, reducing the overall proportion of juveniles taken by predators. In this case, individuals born before or after this surge are subjected to greater risk of predation. For example, neonate wildebeest (*Connochaetes taurinu*) born at the peak of the parturition period were more likely to survive than those born earlier or later (Estes 1976). Since neonates are only vulnerable for a short time following birth, condensed parturition reduces the overall time predators can access neonates (Whittaker and Lindzey 1999, Testa 2002). However, if parturition is drawn-out, susceptible neonates are available for a longer time period. Consequently, we see reduced survival of offspring born to individuals that give birth during periods of high vulnerability. Under this scenario, we would expect stabilizing selection to occur, with a greater likelihood of mortality due to predation as parturition departs from the peak date.

Prey switching, due to predator learning, is a factor that may cause directional selection in parturition of ungulates by selecting against late-born individuals. Predation of caribou calves by wolves was delayed relative to the onset of parturition (Adams et al. 1995). This delay may have been the result of the time required for wolves to detect the availability of newborn calves or late-born calves being of greater profit to wolves due to increased aggregations of caribou calves (Adams et al. 1995). Additionally, moose calves that were born late were more likely to be killed by predators than calves that were born early suggesting that prey switching and predator learning were likely responsible for the increased risk of predation on late-born individuals (Keech 2000, Testa 2000, 2002). It is evident from these examples that predators can

affect the likelihood of survival of late-born individuals. However, this timing of predation alone would not drive synchrony—rather, this would lead to directional selection in favor of early births.

Weather or the availability of adequate resources may drive synchrony of parturition. For example, the peak parturition period for ungulates in temperate regions usually takes place late enough for adequate forage to be available and early enough for sufficient growth of juveniles before the onset harsh winter conditions (Bunnell 1980, Clutton-Brock et al. 1982). Therefore, individuals born early may have reduced survival because resources are not sufficient for their mothers to successfully nurse, or they may be subjected to temperatures below those required for proper thermoregulation (Bunnell 1980). Individuals born later in the season may have a competitive disadvantage (Clutton-Brock et al. 1987) or delayed development of body mass (Holand et al. 2003, Saether et al. 2003) causing reduced survival during the subsequent winter (Gaillard et al. 1996, Loison et al. 1999). Under this scenario, we would expect selection against early and/or late-born individuals.

Mule deer (Odocoileus hemionus) are an iconic species in the western U.S. that exhibit reproductive synchrony (Freeman et al. 2014). The typical parturition season for mule deer lasts approximately one month, with the mean birth date ranging from late May to late July (Butler et al. 2009, Long et al. 2009), but often occurring in June (Bowyer 1991, Pojar and Bowden 2004, Freeman et al. 2014). The onset of parturition may begin from mid-May to late June, and conclude from mid-June to mid-August. Though parturition season is typically one month in length, up to 95% of births can take place in a two-week period (Pojar and Bowden 2004). The synchrony of parturition in many populations make mule deer an ideal species for an examination of factors that regulate this reproductive strategy.

Our objective was to test the alternate hypotheses to explain the synchrony of parturition in mule deer. If predator swamping was driving synchrony, we predicted that neonate mule deer born near the peak of the parturition period would have lower likelihood of being killed by predators than those born before or after the peak. If predator learning and prey switching were responsible for directional selection, we predicted that late-born individuals would have higher predator-related mortality than those born early. If synchrony was influenced by weather and food availability, we predicted that neonate mule deer born during the peak of the parturition period were more likely to survive than those born before or after the peak—regardless of predation. Understanding the factors that influence the synchrony of birth in mule deer can give us greater insight into the ecology of an economically and aesthetically important ungulate species.

STUDY AREA

Our study took place on Monroe Mountain in south-central Utah (39°10' - 39°46' N and 111°50' – 112°15' W). Monroe Mountain is approximately 70 km long (north to south) and 20 km across (east to west). Several thousand mule deer inhabited the mountain and surrounding winter range. Land ownership is split between federal agencies (Forest Service and Bureau of Land Management), state lands, and private land-holdings. Elk *(Cervus elaphus)* and pronghorn (*Antilocapra americana*) were the only additional wild ungulates that occupied this range, though domestic livestock, cattle and sheep, also seasonally occupied this range. Potential predators of mule deer inhabiting this area were mountain lions (*Puma concolor*), bobcats (*Lynx rufus*), black bears (*Ursus americanus*) and coyotes (*Canis latrans*). Elevations across this unit ranged from 1603 m near the town of Richfield, Utah to 3421 m at Monroe peak. Mule deer use of winter range to summer range generally followed this elevation gradient. Habitat types varied

across the mountain and included areas dominated by big sagebrush (*Artemesia tridentata*), mountain mahogany (*Cercocarpus ledifolius*), Gambel oak (*Quercus gambelii*), aspen (*Populus tremuloides*), pinion pine (*Pinus edulis*), Utah juniper (*Juniperus osteosperma*), ponderosa pine (*Pinus ponderosa*), and Douglas Fir (*Pseudotsuga menziesii*).

METHODS

As part of a larger study, we determined parturition date and survival of neonate mule deer during 2012–2015. To aid in the capture of neonate mule deer, we captured adult female mule deer (via helicopter net-gunning (Barrett et al. 1982, Krausman et al. 1985, White and Bartmann 1994)) in March of each year from four locations on winter range of the study areas (Angle, Burrville, Thompson Basin, and Elbow Ranch; Figure 2-1). We determined pregnancy via ultrasonography (E.I. Medical Imaging portable ultrasound; (Smith and Lindzey 1982)). We fitted pregnant females with VHF collars (Telonics Inc., ATS systems) and vaginal implant transmitters (VIT; ATS systems). We used a vaginoscope to insert VITs until the antennae did not protrude from the opening of the vagina (Bishop et al. 2007, Freeman et al. 2014).

Between the original capture of adult females and parturition, we located collared females using radio telemetry. During March and April, individuals were located sporadically using radio telemetry from the ground and a fixed-wing aircraft. Beginning in May, we attempted to locate every female twice a week. Beginning the last week of May, we located each female at least every other day until all VITs had been expelled. When an expelled VIT was detected (pulse rate was doubled), we located the VIT and conducted an extensive search for the neonate(s). In addition, we opportunistically captured neonate mule deer while searching for those associated with a VIT or while observing female mule deer not previously captured.

We handled neonate mule deer with latex gloves (to reduce the likelihood of transferring human scent) while we recorded morphological measurements (e.g. weight and hind foot length) and determined and verified the age of the individual(s). The VITs allowed us to determine dates of parturition for neonate mule deer. To determine dates of parturition for individuals caught opportunistically, we estimated the age of the individual(s) using hoof condition/length, pelage, and behavior (Haugen and Speake 1958, Robinette et al. 1973, Sams et al. 1996, Lomas and Bender 2007). To determine survival of neonate mule deer, we fitted VHF radio collars to captured individuals. Radio collars placed on individuals were designed to expand with the growing animal and drop off after approximately 8 months.

In order to determine the effects of predators on the survival of neonate mule deer, we monitored collared individuals on a schedule designed to ensure that mortalities were located promptly. Early detection of mortalities minimized the likelihood of confusion between the true cause of mortality and scavenging. Specifically, we relocated neonates at least 3 times weekly between the time of initial capture and the end of August. Beginning in September, we relocated neonate mule deer at least once per week. We decreased monitoring frequency beginning in September because most mortality of neonate mule deer usually occurs in the first three months of life (Pojar and Bowden 2004, Lomas and Bender 2007, Freeman 2014).

In order to determine an accurate cause of death for neonate mule deer, we attempted to locate animals whenever a transmitter was in mortality mode (a doubling of the pulse rate). Radio collars switched to mortality mode after remaining stationary for 8 hours. After locating a collar in mortality mode, we searched for the deceased neonate mule deer and determined a probable cause of death based on evidence found at that location. If the probable cause of death was attributed to predation, we used a suite of indicators (tracks, scat, blood, drag trails, and other factors) that are predator specific (e.g. coyote, cougar, black bear) to determine

what species of predator was most likely responsible for the mortality (Wade 1985, Patterson 1994, Gese and Grothe 1995). In some cases, assignment of the predator responsible for death was ambiguous (e.g., most of the carcass was consumed and there was sign from multiple species of predators) and therefore, we classified these mortalities as unknown predation. Other cause-of-death categories included starvation, disease, and unknown.

To determine the effects of the timing of parturition on the survival and predator-related mortality of neonate mule deer, we used multi-model inference within Program MARK and a known-fate model (White and Burnham 1999). Preliminary analysis revealed that coyotes have the greatest impact on survival of neonate mule deer during the first 16 weeks of life; therefore, we modeled survival to 16 weeks in our primary analysis. We did not use staggered entry to add neonate mule deer to our sample; rather, day-one for each neonate mule deer began at birth, regardless of calendar date (Bishop et al. 2008). We used a heirarchical approach to draw inferences regarding *a priori* hypotheses about potential influences on survival rates (Burnham 2002). In our first step, we tested the characteristics of sex of an individual (Sex), whether the neonate was a twin (Twin), and weight (Weight+Age). We included age of neonate mule deer at capture in all our models that included weight to account for the effects of age-related weight gain. We also tested models that used interactions of these components. We advanced models to the next step based on Akaike's Information Criterion adjusted for small sample sizes (AICc) if they had at least 5% weight ω_i.

We then tested the temporal effects of parturition by adding timing variables examining 1) whether the parturition date of a neonate mule deer was before, during, after the peak parturition period (Peak); 2) the deviation of each individual date of parturition (in days) from the overall mean date of parturition (DevMnDt); and 3) each individual date of parturition relative to the annual onset of parturition (DySncOnst). We also included squared terms for

DevMnDt2 and DySncOnst2 to investigate support for potential asymptotic relationships. Dates of parturition classified as early, peak, and late approximated 25, 50, and 25% of births (Adams et al. 1995) each year. To further identify any potential differences in timing of parturition, we compared the mean date of parturition of individuals that survived to 16 weeks of age to the mean date of parturition of individuals that were depredated by that time.

RESULTS

Searches for neonate mule deer associated with expulsion of VITs began on 29 May, when the first VIT was expelled, and continued through early July. Based on expulsion of VITs, we obtained dates of parturition for 140 of the 146 females that remained in the study area during parturition (Figure 2-2). Five females died prior to parturition, and one female that received a VIT never gave birth. The range of the parturition period for neonate mule deer that were captured during 2012–2015 was from May 29 to June 30 (Figure 2-3). Mean dates of parturition were June 13th, 16th, 15th, and 14th for 2012–2015, respectively. The average annual mean date of parturition was 13 days after the onset of parturition. We captured $\geq$ 60 neonate mule deer each year, yielding 266 neonate mule deer across all years of our study; 133 neonate mule deer were captured using VITs, and 133 were captured from opportunistic searching. We excluded six neonate mule deer from our sample because they were stillborn (N=2), or their deaths were human-caused (poaching, vehicle strike; N=4). Consequently, 260 neonate mule deer were used in our final analyses.

We attributed mortality of neonate mule deer to predation, starvation, disease, and unknown (Table 2-1). Predation was the leading cause of mortality accounting for approximately 68% of all mortalities. Coyotes and cougars killed roughly equal numbers of neonate mule deer with all other predators accounting for only 4% of neonate mortality (Figure 2-4). The timing of

coyote and cougar kills was somewhat different. Approximately 90% of coyote-related mortality during our monitoring period occurred during the first 16 weeks of neonate mule deer life (Figure 2-5). Although approximately 75% of cougar-related mortality during our monitoring period also occurred during the first 16 weeks of neonate mule deer life (Figure 2-5), cougar-related mortality was more evenly distributed throughout the monitoring period than was coyote-related mortality (Figure 2-6). There was a considerable lag between the onset of parturition and the onset of predation on neonate mule deer. In fact, the earliest predation event did not occur until the peak of parturition or twelve days after the onset of parturition (Figure 2-6). Consistent with this timing of predation, the mean date of parturition for neonate mule deer that were depredated by 16 weeks of age averaged 1.5 days later than individuals that survived to 16 weeks of age.

In order to determine which factors were influencing parturition, we analyzed survival and predator-related mortality of neonate mule deer. Survival of neonate mule deer to 16 weeks averaged 65% across all years. Sex and Weight were influential variables in our models (Table 2-2). Females had a higher likelihood of survival than males. Additionally, survival of neonate mule deer increased as weight increased. Number of days since the onset of parturition (DySncOnst, DySncOnst2) was a prominent variable in our analyses, with DySncOnst or DySncOnst2 appearing in 8 of the top 10 models (Table 2-2). Models that included these variables accounted for 67% QAICc weight. The support for DySncOnst in our models indicates that the probability of a neonate mule deer surviving to 16 weeks decreased as the time between the onset of parturition and the date of parturition of an individual increased (Figure 2-7). When we included only predator-related mortality in our analysis, we observed that the likelihood of predation of neonate mule deer increased with increasing number of days between the onset of

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parturition and the birth of an individual (Figure 2-8). None of our models contained uninformative parameters.

DISCUSSION

Timing of parturition influenced survival and predator-related mortality of neonate mule deer. Individuals born close to the onset of parturition had higher survival and lower predator-related mortality than those whose births were delayed relative to the onset of parturition. As births got later, the likelihood of survival decreased and the likelihood of being killed by a predator increased. Our results are consistent with an examination of predation of moose calves wherein the likelihood of moose calves being killed by a predator increased as the number of days since the onset of parturition increased (Testa 2002). Consistent with our model results, mean dates of parturition of neonate mule deer that survived to 16 weeks were earlier than those that were killed by predators. The difference of 1–2 days in timing of parturition between these groups may not seem like a large advantage against predation. However, neonate mule deer gain mobility quickly after birth, and individuals that were 3–4 days of age were often difficult to capture by hand on the ground. The marked increase in mobility in a short time after birth is characteristic of other ungulates as well (Adams et al. 1995, Patterson et al. 2016). Since predators selected for late-born individuals, it is likely that predators influenced parturition by means of directional selection. However, if predation selects against late-born individuals, opposing ecological forces must be at work against early-born individuals to keep the parturition season consistent and synchronous (Bowyer et al. 1998, Testa 2002).

The observed lag between the onset of parturition and the onset of predation on neonates significantly influenced the likelihood of survival of neonate mule deer. There are multiple possible explanations for why such a lag exists. There may be a learning period before predators

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key in on the flush of available prey or become proficient at successfully capturing neonates (Ims 1990a, Adams et al. 1995, Keech et al. 2000). Alternatively, predators may be concentrating on the availability of alternate prey during the onset of parturition for mule deer. Consistent with this assertion, increased survival of fawns was correlated with increased availability of microtine rodents as alternate prey for coyotes in Montana (Hamlin et al. 1984). Alternate prey can also compose a large portion of the diet of cougars (Cunningham et al. 1999). In any case, it appears that the timing of parturition has a pronounced effect on the likelihood of survival relative to predation. The greater likelihood of predation on late-born individuals is likely a selective force for earlier births (Testa 2002).

Our results are consistent with the predator learning hypothesis. Predators selected for neonate mule deer that were born late on Monroe Mountain. If predation is not affecting early-born ungulates, ecological pressures other than predation must be countering the observed effect of predation on late-born individuals to maintain synchrony (Testa 2002, Patterson et al. 2016). Therefore, environmental factors may have a greater effect than predation on the survival of early-born individuals. For example, climatic variables linked to factors like plant phenology can be critical in determining the timing and synchrony of parturition of ungulates (Bunnell 1980, Rutberg 1987, Linnell et al. 1995, Adams and Dale 1998, Bowyer et al. 1998, Keech et al. 2000). We did not observe any effect of climatic variables on early-born individuals in our study, however. Relatively mild winters during our study may have prevented any effects of climatic variables on the survival of early-born mule deer. Alternatively, the timing of parturition in our study population may be experiencing directional selection. The ideal date of parturition may be shifting to one earlier than historically observed, though we likely would not observe this effect during a four-year study. The potential effects of the onset of winter were not examined in our study, but could be another factor selecting against late-born individuals (Bowyer et al. 1998,

Keech et al. 2000, Solberg et al. 2007). By selecting for late-born individuals, predators had a marked impact on the timing of parturition of mule deer on Monroe Mountain. The support we found for the predator learning hypothesis is evidence that predation can have a significant impact on the survival of late-born individuals, and may contribute to the reproductive synchrony observed in populations of mule deer.

Age and body condition of adult female ungulates can also influence timing of parturition and survival of their offspring, and deserve consideration. Young female caribou and moose gave birth later than older females (Adams et al. 1995, Adams and Dale 1998, Patterson et al. 2016). Additionally, female moose with greater rump fat were more likely to give birth earlier than females with less rump fat (Testa and Adams 1998, Keech et al. 2000). Condition of adult female ungulates is also linked to the birth mass of their offspring (Robinette et al. 1973). As we observed, higher birth mass was associated with increased survival of neonate mule deer (Lomas and Bender 2007, Bishop et al. 2009). Individuals that are heavier at birth may be better equipped to evade predators soon after birth than lighter individuals. These individuals may also have higher survival through their first winter because body mass of fawns before winter is a predictor of survival to recruitment (Bartmann et al. 1992, Unsworth et al. 1999, Lukacs et al. 2009). Further research is needed to address the effects of maternal age and condition on the timing of parturition and survival of neonate mule deer.

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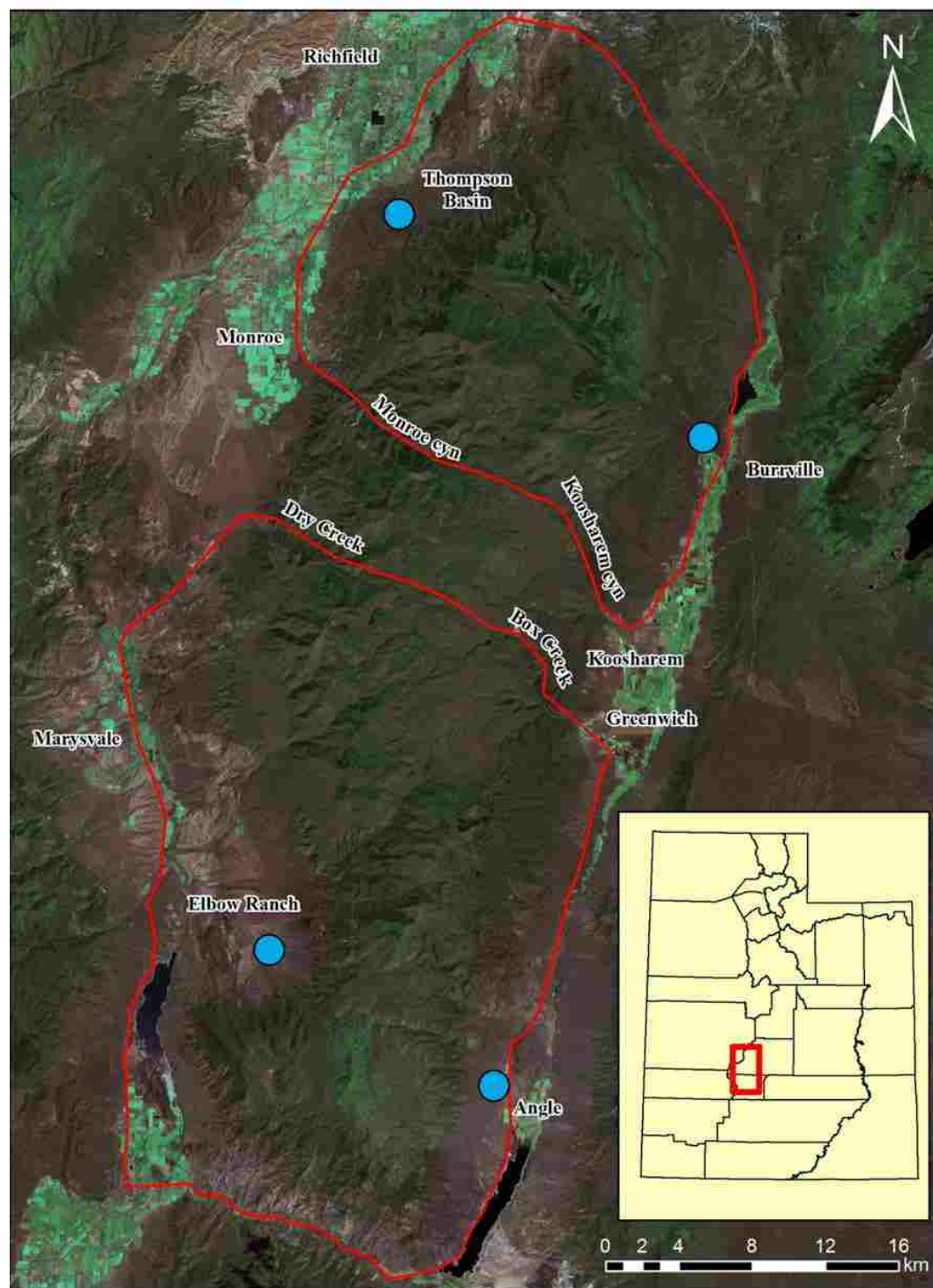
Figure 2-1. Map of Monroe Mountain, Utah with red lines delineating north (coyote removal area 2012–13) and south (coyote removal area 2014–15) study areas where we evaluated survival of neonate mule deer. Blue dots indicate general locations where adult female mule deer were captured on winter range.
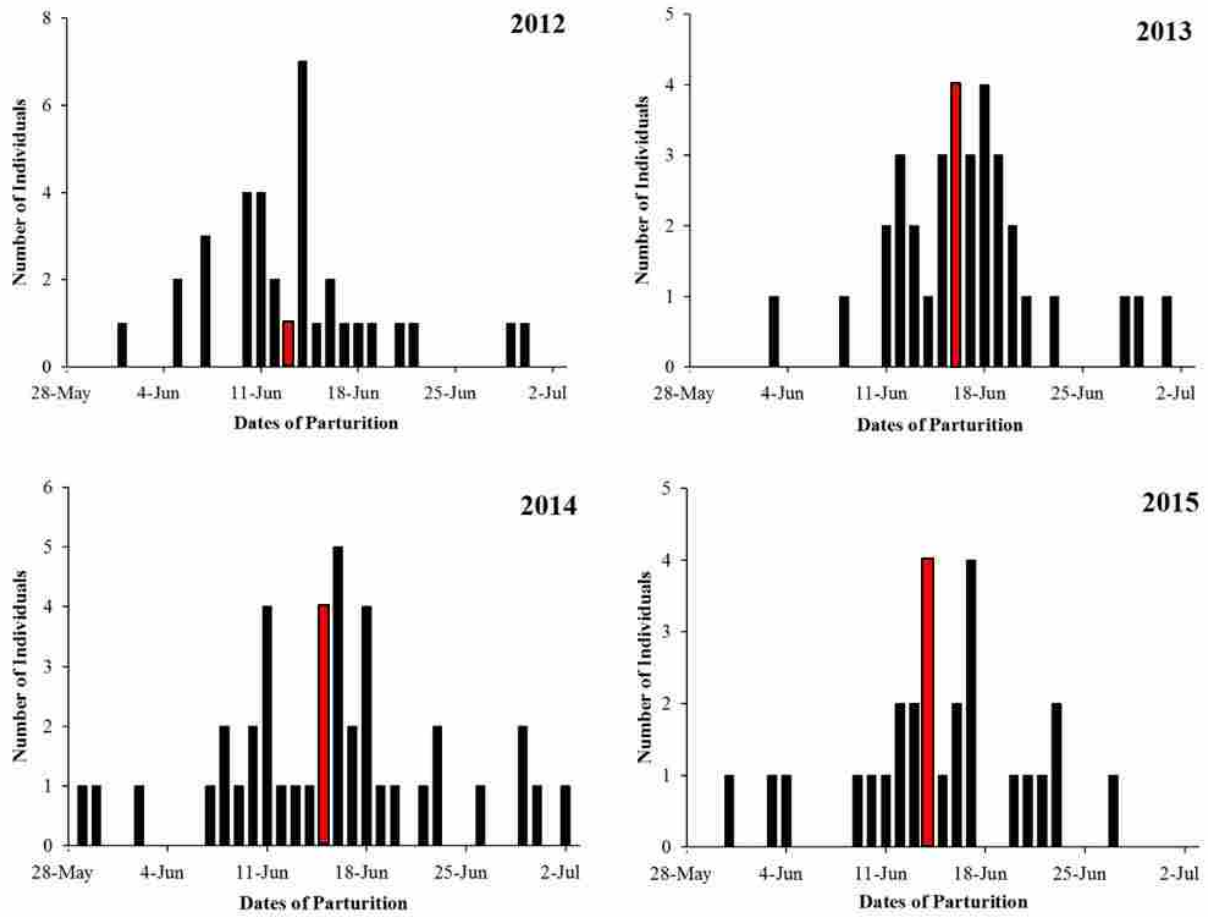
Figure 2-2. Dates of parturition for adult female mule deer on Monroe Mountain during 2012–2015. Mean dates of parturition (red bars) were June 13th in 2012, June 16th in 2013, June 15th in 2014, and June 14th in 2015.
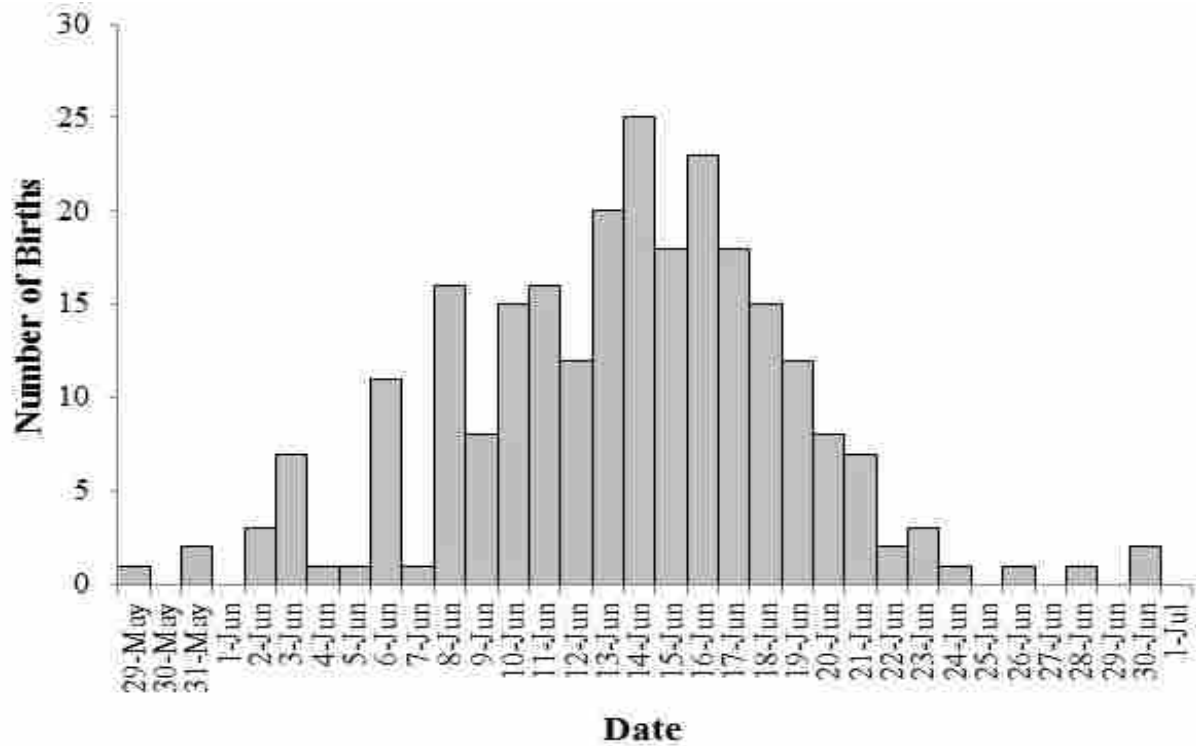
Figure 2-3. Distribution of dates of parturition, and number of births for each date, of neonate mule deer captured on Monroe Mountain during 2012–2015.
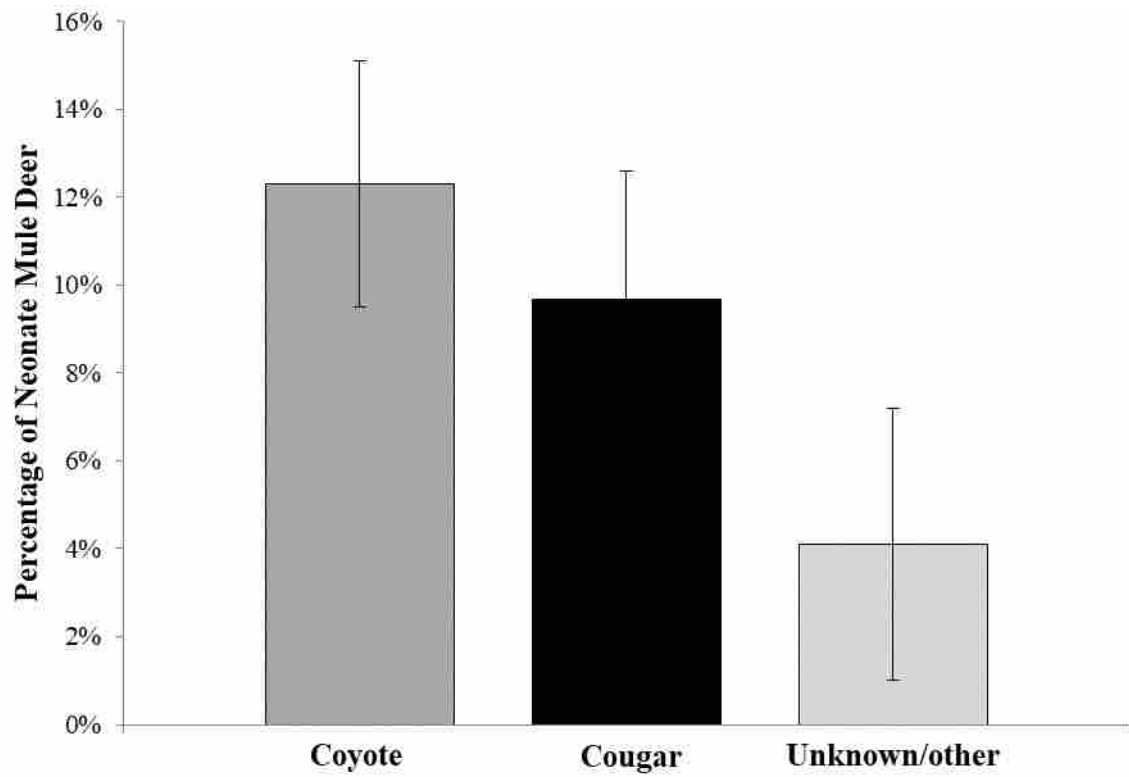
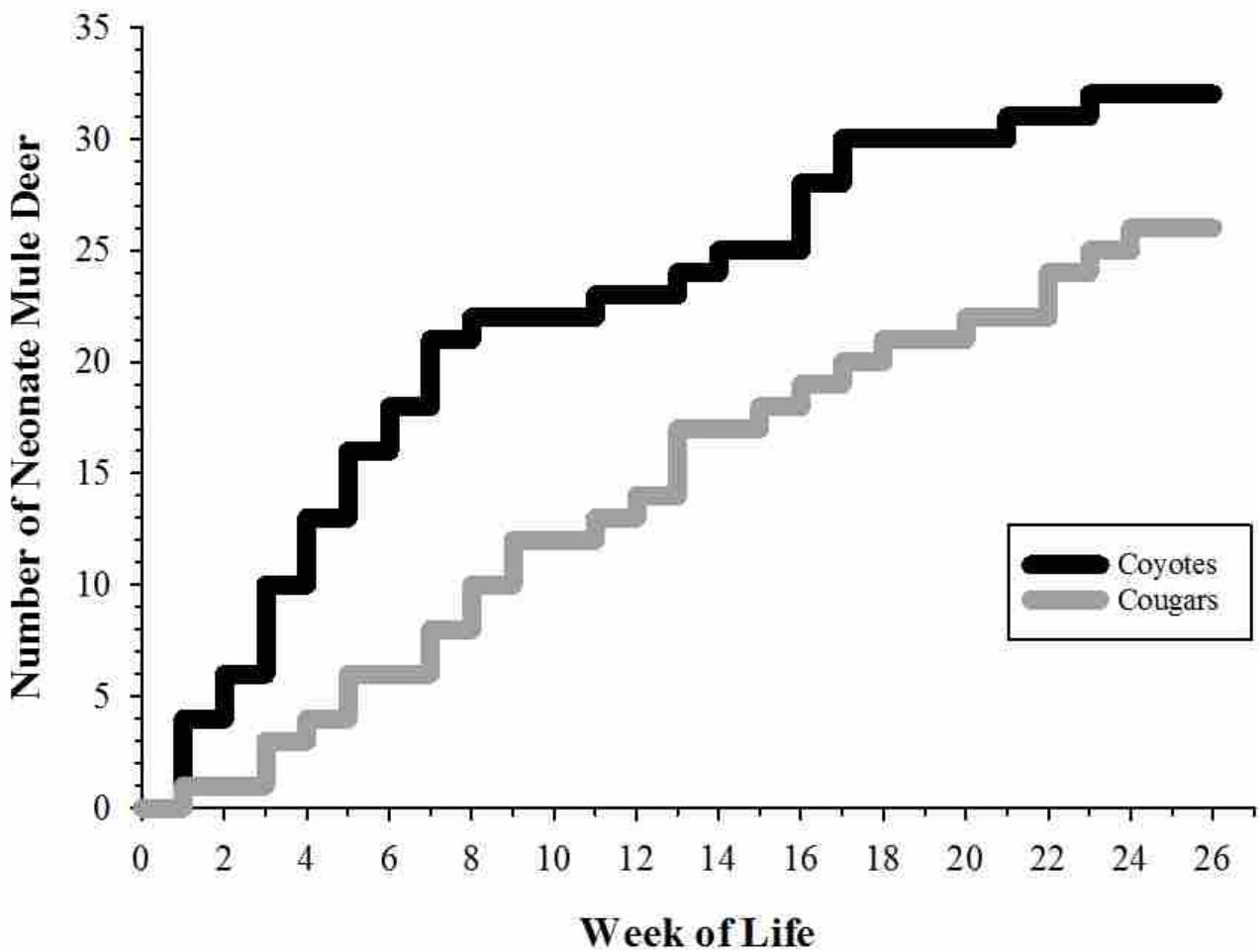Figure 2-4. Percentage of neonate mule deer taken by each predator type on Monroe Mountain during 2012–2015.

Figure 2-5. Cumulative number of neonate mule deer killed by coyotes and cougars by week of neonate mule deer life on Monroe Mountain. The numbers of neonate mule deer killed during each week after birth were pooled across all years of our study (2012–2015).
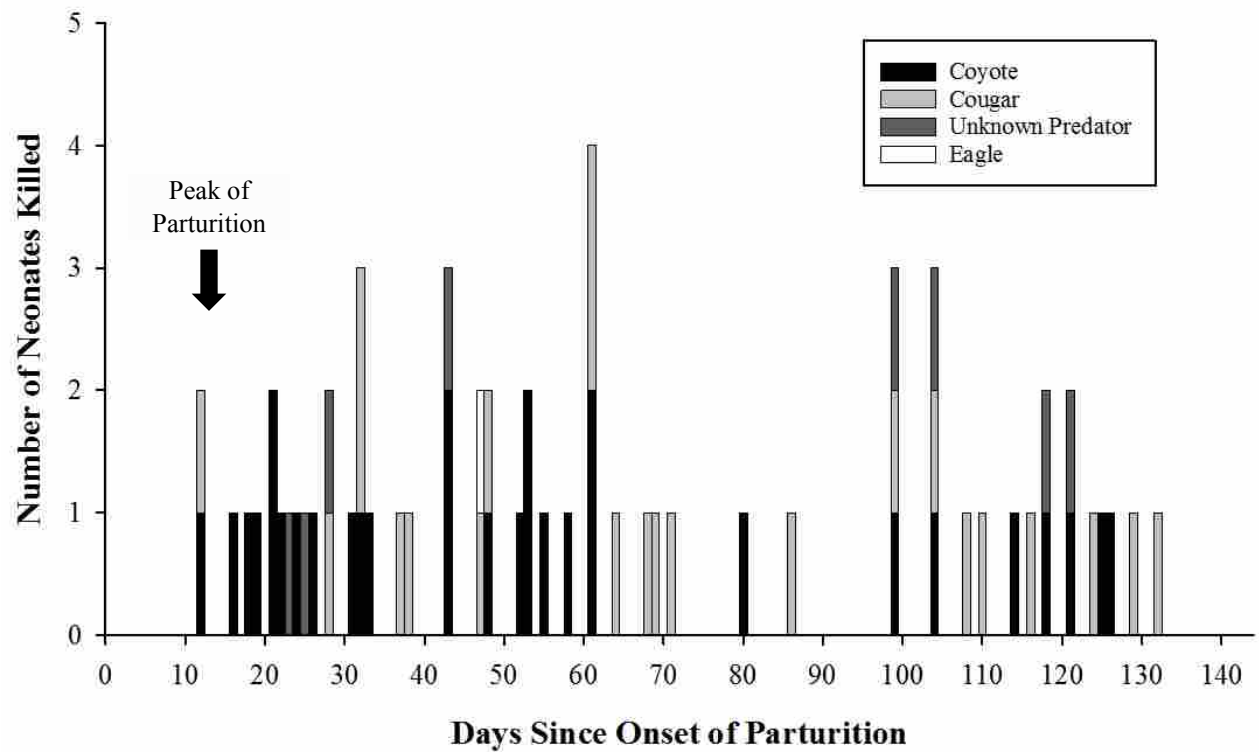
Figure 2-6. Timing of predator kills of neonate mule deer on Monroe Mountain during 2012–2015. Results from each year were aligned on the earliest date of parturition of neonate mule deer.
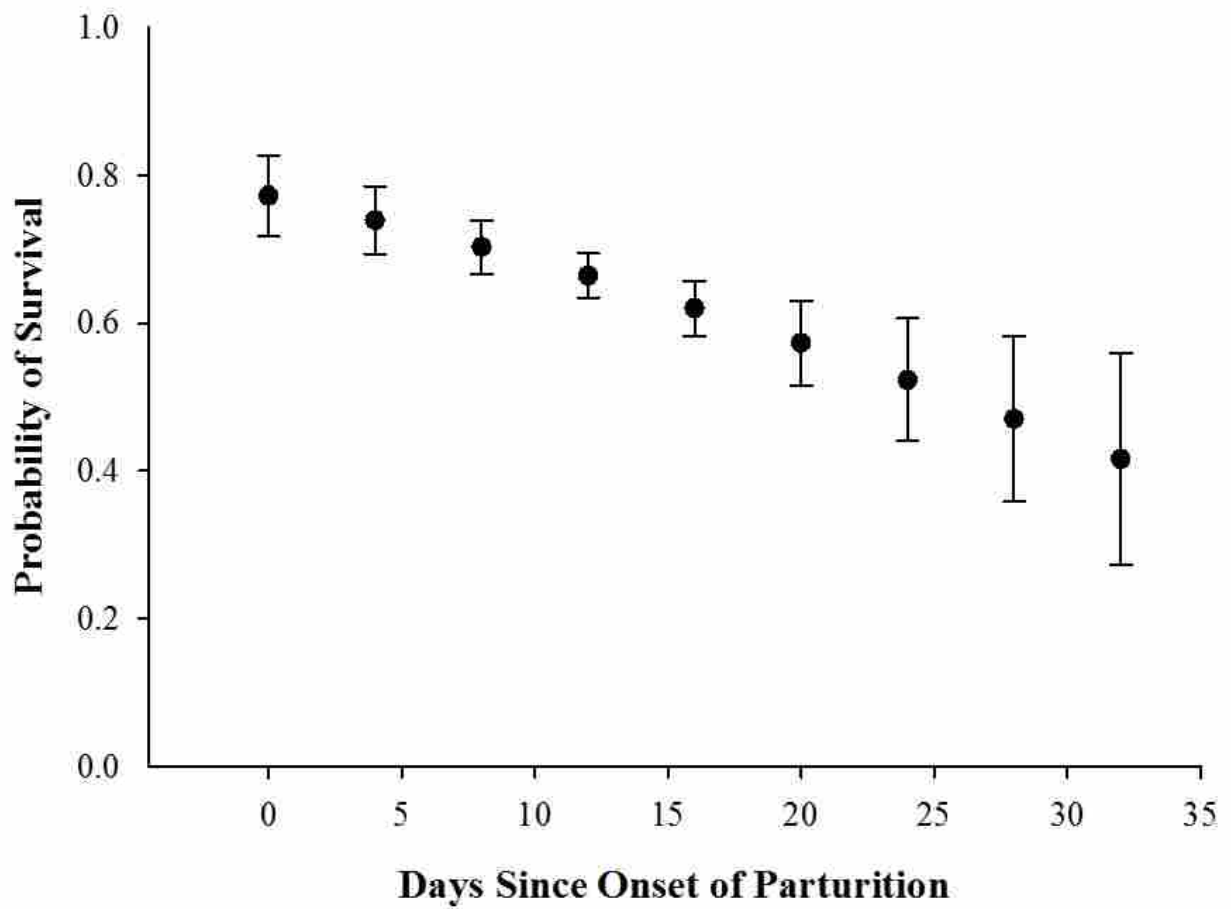
Figure 2-7. Probability of survival of neonate mule deer to 16 weeks of age based on individual birth date relative to the onset of parturition on Monroe Mountain during 2012–2015.
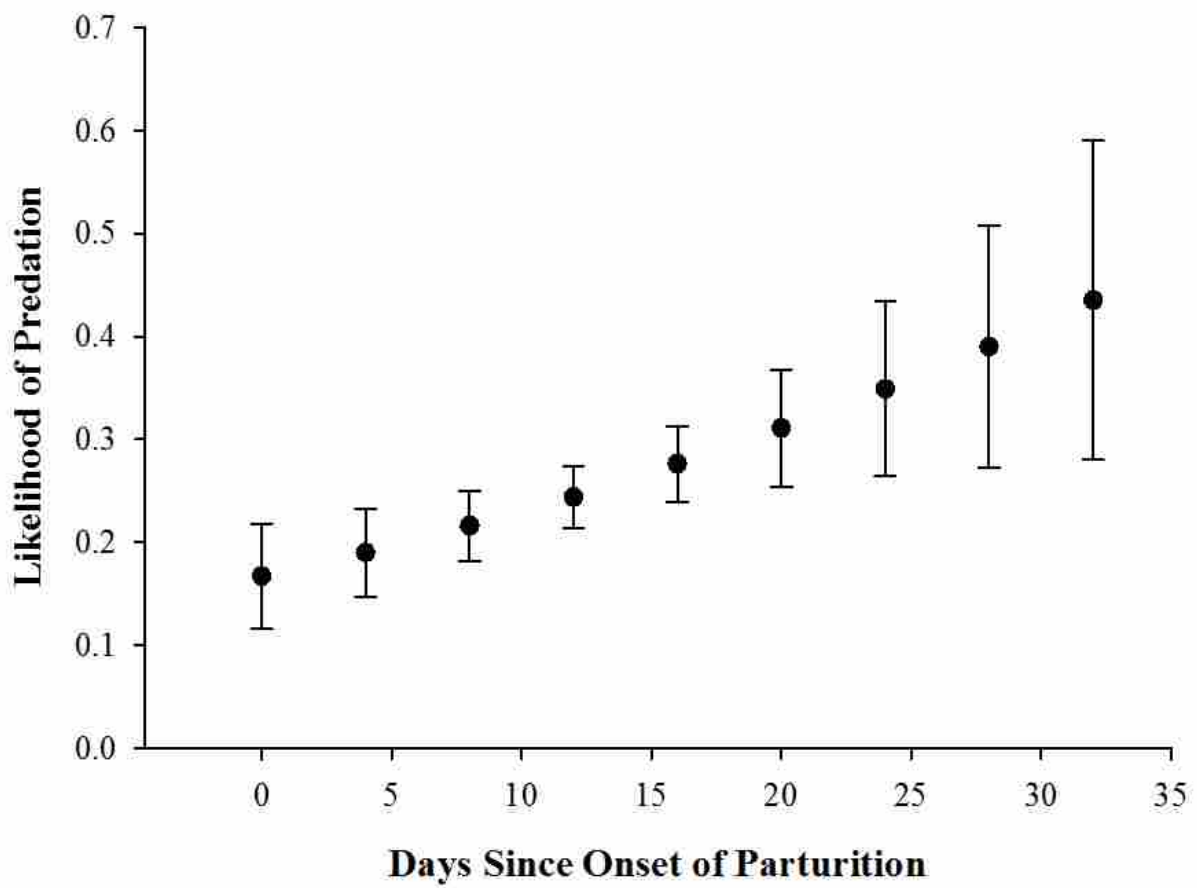
Figure 2-8. Probability of predation during the first 16 weeks of life of neonate mule deer. Estimates are based on individual birth date relative to the onset of parturition on Monroe Mountain during 2012–2015.

Table 2-1. The probable causes of mortality of neonate mule deer that were captured on Monroe Mountain during 2012–2015.

Year	2012	2013	2014	2015
Total Captured	56	67	71	66
Predation Mortalities	16	17	23	15
Coyote	11	4	11	7
Cougar	2	5	11	8
Unknown	1	8	1	0
Starvation	3	0	0	1
Disease	2	0	1	1
Unknown Mortality	3	2	5	4

Table 2-2. Model selection results for neonate mule deer through 16 weeks of age on Monroe Mountain during 2012–2015. Variables in our top models include date of parturition relative to the onset of parturition (DySncOnst, DySncOnst2), whether the individual was a twin (Twin), sex (Sex), weight at capture (Weight), and age at capture (Age).

Model	QAICc	Δ AICc	AICc ω$_i$	K	QDeviance
{S(Weight+Age+Sex+DySncOnst)}	1233.5255	0	0.14948	116	1000.3045
{S(Weight+Age+DySncOnst)}	1233.8703	0.3448	0.12581	115	1002.6702
{S(Weight+Age+Sex+DySncOnst+DySncOnst2)}	1234.5258	1.0003	0.09065	117	999.2836
{S(Weight+Age+Sex+DySncOnst2)}	1234.899	1.3735	0.07522	116	1001.678
{S(Weight+Age+DySncOnst2)}	1235.1149	1.5894	0.06752	115	1003.9148
{S(Weight+Age+Sex)}	1235.1918	1.6663	0.06498	115	1003.9917
{S(Weight+Age+DySncOnst+DySncOnst2)}	1235.3372	1.8117	0.06042	116	1002.1162
{S(Weight+Age+Twin+Sex+DySncOnst)}	1235.5388	2.0133	0.05463	117	1000.2966
{S(Weight+Age+Twin+DySncOnst)}	1235.8822	2.3567	0.04601	116	1002.6612
{S(Weight+Age)}	1236.1229	2.5974	0.04079	114	1006.9436