Variations of Wildlife Safety Crossings and
Their Effects for Mule Deer in Northeast Nevada

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THESIS ABSTRACT

Organisms move long distances for various reasons including foraging for food, avoidance of predators, increased breeding opportunities, to access seasonal or ephemeral resources, to access seasonal ranges, to expand ranges, or to disperse into new ranges (Bissonette and Adair 2007; Chetkiewicz et al. 2006; Fortin and Agrawal 2005). When barriers are created within a landscape, connectivity among habitat patches is disrupted, and movement between these habitat patches may be limited or eliminated (Bissonette and Adair 2007; Fortin and Agrawal 2005). Barriers to movement may lead to increased mortality, reduced reproduction, smaller populations, and lower population viability because habitat available to each individual declines and gene flow is decreased as populations become increasingly isolated (Bissonette and Adair 2007; Forman et al. 2003). Barriers can also reduce regional population numbers since suitable habitats and resources may become unavailable (Forman et al. 2003). Roads are one anthropogenic factor that can create barriers to movement by species, span over 6.4 million kilometers, and cover over 1% of the total land cover in the United States (Beckman et al. 2010). Roads also are a leading cause of habitat fragmentation and loss of connectivity among populations in North America and around the world (Beckman et al. 2010).

Because of increased habitat fragmentation, corridors have become a fundamental component of management and conservation of wildlife in North America. Traditionally, corridors have been viewed as linear strips of habitat that facilitate the movement of organisms through landscapes, but a form of corridor that has been widely accepted over the last several decades are safe crossing structures designed for wildlife in areas fragmented by roads (also known as safety crossings) (Corlatti et al. 2008; Puth &
Wilson 2001; Taylor et al. 1993). The general function of a safety crossing is to provide safe passage for animals to cross either above or below a roadway and remain out of the way of motor vehicles, which can increase safety for both wildlife and motorists (Ford et al. 2008; Kintsch and Cramer 2011).

In 2007, Nevada Department of Wildlife and Nevada Department of Transportation started the planning phases to reduce collisions between motor vehicles and migrating mule deer and restore habitat connectivity by placing several crossing structures on U.S. Highway 93 between Wells and Contact, Nevada. Two sites were selected based on known migration routes of mule deer and state reports of deer-vehicle collisions. Construction of the first set of safety crossings, located approximately 16 km north of Wells, was completed in August of 2010. This site is located at 10-Mile Summit and consists of two underpasses, one overpass, and approximately 6.4 km of exclusionary fencing. The second set of safety crossings is located approximately 32 km north of Wells at HD Summit, and was completed in August of 2011. HD Summit consists of one underpass, one overpass, and approximately 4.8 km of exclusionary fencing.

The goal of my research was to assess the efficiency of those newly constructed safety crossings and associated exclusionary fencing. Because the crossing structures were built primarily for mule deer, I used mule deer as my focal species. I placed Reconyx HyperFire Professional Cameras with infrared technology at the entrance of each crossing structure to document movement and behaviors of mule deer during migratory periods. I began collecting data during the first migration each site was ready for use without the interruption of construction, and ceased data collection in June of 2012. Since 10-Mile Summit was completed in August of 2010, data was collected
during four migrations (autumn 2010, spring 2011, autumn 2011, and spring 2012). Since HD Summit was completed in August of 2011, data was collected during two migrations (autumn 2011 and spring 2012).

In chapter 1, my objectives were to document the responses of mule deer to overpasses and underpasses, and to determine which type of structure is most effective for mule deer. I documented behavioral responses of mule deer at the entrance of each crossing structure by observing how mule deer responded to the different structures. I used the number of successful crossings as a measure of the effectiveness of each crossing structure in maintaining landscape connectivity and migration corridors. I used the number of documented traffic-related mortalities as a measure of how effective the safety crossings are in reducing wildlife-vehicle collisions. Mule deer used the crossing structures as soon as they were available. We also observed multiple species using the crossing structures, including one of the first observations of pronghorn (*Antilocapra americana*) using an overpass. Mule deer responded with more successful crossings and fewer retractions at overpasses compared with underpasses. In addition, mortalities resulting from traffic collisions with mule deer decreased with each subsequent migration.

In chapter 2, my objectives were to determine what environmental variables influenced movement and grouping behaviors of mule deer during migratory movements. I used camera data from several wildlife crossing structures to investigate how the season in which movement occurred, time of day, rate of precipitation, percent fullness of the moon, and temperature influenced the total number of crossings and group sizes of mule deer. I hypothesized that migratory movements would decrease with an increase in
percent fullness of the moon, ambient temperature, and precipitation, and movements would increase during crepuscular hours. I also hypothesized that group sizes would increase with an increase in the percent fullness of the moon, daylight hours, and rate of precipitation. Lastly, I hypothesized that group sizes would be larger during spring migrations since mule deer are more concentrated on winter ranges and likely synchronize their movements back to summer range with plant phenology. I implemented a model selection procedure to evaluate the importance of those environmental factors, developed a set of a priori models, and allowed my parameters to vary until I retained a set of models that were considered to be the best fit to the data. Movement increased during daylight hours and decreased with an increase in precipitation. Group sizes of mule deer increased with an increase in daylight, intensity of precipitation, and during spring migrations. Contrary to our predictions, we did not document any significant effect of percent fullness of the moon or temperature on movement patterns or group sizes.

Highway mitigation projects may be defined as successful when there is a reduction in wildlife-vehicle collision rates and animal movement patterns are restored between habitats fragmented by roadways (Ford et al. 2008; Fortin and Agrawal 2005; Van Wieren and Worm 2001). I demonstrated that the newly constructed safety crossings in Nevada meet those criteria for success. Mule deer used the safety crossings extensively during migratory periods, the number of successful crossings has continued to increase, and the numbers of deer-vehicle collisions have decreased with each subsequent migration. To our knowledge, there are no other studies that have evaluated overpasses and underpasses where both types of structures are within close proximity to
each other in the path of ungulates migrating between seasonal ranges. As knowledge increases about the types of structures and features that are successful for wildlife, transportation and wildlife agencies will be able to make more informed decisions on design and implementation of effective safety crossings. Additionally, this research shows changes in group sizes of mule deer with environmental factors including precipitation, seasonality, and time of day, during long-distance migrations, and support other studies that have shown similar changes in environmental factors influence the movements and behaviors of various species (deBruyn & Meeuwig 2001; Harmsen et al. 2011; Kjaer et al. 2008; Penteriana et al. 2011).

LITERATURE CITED


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precipitation were above 12 mm per/hour.
Chapter 1 – How do mule deer cross the road? Types of crossing structures and their effectiveness for migratory ungulates.

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ABSTRACT

Movement corridors have become a fundamental component of conservation and management of wildlife in North America. Indeed, a variety of regional corridor initiatives are currently underway such as safe crossing structures across highways and roads with high traffic levels for wildlife. Between 2010 and 2011 several crossing structures for wildlife in Nevada were constructed in the path of seasonal migration routes of mule deer (*Odocoileus hemionus*) to reduce deer-vehicle collisions. We monitored use of two wildlife overpasses, three wildlife underpasses, and approximately seven miles of exclusionary fencing by mule deer during migratory periods to examine the efficacy of those safety crossings. We determined which type of structure, overpass or underpass, was more effective and used more frequently by mule deer by documenting number of mule deer that used the structures and the proportion of approaches that resulted in successful crossings. Additionally, we recorded the number of mule deer mortalities located within the study site to document changes in the number of deer killed in traffic collisions with each subsequent migration. Mule deer used the crossing structures as soon as they were available. We also observed multiple species using the crossing structures, including one of the first observations of pronghorn (*Antilocapra americana*) using an overpass. Although mule deer used all of the crossing structures, we observed more successful crossings and fewer retractions at overpasses when compared with underpasses. Indeed, more than 80% of the documented crossings occurred at an overpass. Additionally, mule deer that approached an overpass successfully crossed the structure at high rates, and mule deer that approached an underpass successfully crossed the structure at much lower rates. Lastly, mortalities resulting from traffic collisions with
mule deer decreased with each subsequent migration. In summary, wildlife safety crossings are beneficial for large mammals, especially mule deer, and should be considered when attempting to mitigate the negative effects of roadways on habitat fragmentation and maintenance of movement corridors.

**KEY WORDS;** connectivity, corridor, exclusionary fencing, habitat fragmentation, mule deer, *Odocoileus hemionus*, overpass, underpass, wildlife safety crossings, wildlife-vehicle collisions.

**INTRODUCTION**

Migration between seasonal ranges is an important strategy for survival and reproduction of wildlife that live in environments with spatiotemporal variation of resources (Alerstam et al. 2003; Baguette and Van Dyck 2007; Bischof et al. 2012). Driving forces that promote migration include ecological and biogeographical factors such as seasonality in distributions of resources, competition, and predator-prey relationships (Alerstam et al. 2003; Baguette and Van Dyck 2007; Bischof et al. 2012). Long-distance movements associated with migration comes with a cost to the individual through increased possibility of mortality or increased energetic expenses, but the benefits include increased availability of resources and increased fitness that offset the overall costs of migratory movements to that individual (Alerstam et al. 2003; Baguette and Van Dyck 2007). If habitat fragmentation or physical barriers are encountered, the individual may be required to expend greater amounts of energy by increasing distance traveled or by traveling through less suitable habitat to circumvent the barrier (Alerstam et al. 2003; Baguette and Van Dyck 2007). In addition to incurring higher costs of migration, mortality rates increase with habitat fragmentation and increasing distance.
traveled, especially during long-distance migrations (Alerstam et al. 2003; Baguette and Van Dyck 2007).

Fragmentation of habitat can be caused by natural processes such as fire, but habitat fragmentation caused by humans creates unnatural edges and boundaries (Franklin et al. 2002; Forman et al. 2003). Roads are an important cause of fragmentation of habitats, and create barriers to movement for various species (Franklin et al. 2002; Forman et al. 2003). Roads span over 6.4 million kilometers, and over 1 % of the total land cover in the United States (Beckman et al. 2010). Roads also are a leading cause of habitat fragmentation and loss of connectivity among populations in North America and around the world (Beckman et al. 2010). Those negative effects of roads on wildlife and their habitats decrease species movements and connectivity, as well as increase wildlife mortality resulting from vehicle collisions (Clevenger et al. 2001; Ford et al. 2008; Huijser et al. 2007). Thus, both transportation and resource management agencies need to understand the negative effects of roads on both terrestrial and aquatic resources if they are to design effective measures to alleviate these effects (Beckman and Hilty 2010).

Wildlife-vehicle collisions are one of the major causes of mortality for many species of wildlife in human-dominated landscapes (Forman et al. 2003). For abundant species, traffic mortality is not considered to be a severe threat to population sustainability, but increased mortality from vehicle collisions has been responsible for regional declines of species that may be at low density or already in decline (Clevenger et al. 2001; Ford et al. 2008; Foster and Humphrey 1995: Jaarsma et al. 2007). All species are susceptible to traffic-related mortalities in areas that are fragmented by roads, but
species that are of greatest concern typically have low reproductive rates, long generation times, prefer open habitats, are attracted to resources located on or near roads, and often have large body sizes that create a direct safety hazard to motorists, such as large ungulates (Bissonette and Adair 2007; Forman et al. 2003). Every year thousands of large ungulates are killed and hundreds of humans are injured or killed by wildlife-vehicle collisions in areas where ungulates cross roads (Huijser et al. 2009; Nuemann et al. 2012). Official estimates may be low since some states have indicated that 50% of collisions with ungulates are reported, but likely only 30% of those collisions are reported in rural areas (Deer Crash 2011; NDOT 2006).

Most road networks were built when transportation planners focused on providing efficient transport with little regard to wildlife (Forman et al. 2003; Jaarsma et al. 2007, Beckman and Hilty 2010). With anticipated growth of the human population and ongoing investment in highways, there is now a growing interest in removing wildlife from roadways for safety reasons, in addition to maintaining landscape connectivity for populations of wildlife (Bissonette and Adair 2007; Forman et al. 2003). This concern has generated an interest in safe crossing structures for wildlife (also known as safety crossings) for use by both transportation and resource management agencies as a tool for mitigating the negative interactions between roadways and wildlife (Bissonette and Adair 2007; Forman et al. 2003; Huijser et al. 2007).

The first crossing structure designed to remove wildlife from roadways was an underpass that was built in Florida during the 1950’s (Forman et al. 2003; USDOT 2011). Since then, crossing structures of various types and sizes have been used around the world; those structures include both underpasses that pass below the road and overpasses
that pass above the road (Forman et al. 2003; USDOT 2011). Underpasses are more common because they are generally less expensive than overpasses and are known to be effective in reducing wildlife-vehicle collisions, although a time-lag of approximately three years has been documented for habituation to underpasses by ungulates (Dodd et al. 2007; Forman et al. 2003; McCollister & van Manen 2010; Sawyer et al. 2012; van der Ree et al. 2011). Regardless of the type of crossing structure, the addition of crossing structures to roadway projects may be defined as successful by a reduction in the number of wildlife-vehicle collisions and the restoration of animal movement patterns between populations fragmented by roads (Ford et al. 2008; Fortin and Agrawal 2005; Van Wieren and Worm 2001). Indeed, the installation of crossing structures can decrease the number of wildlife-vehicle collisions up to 80% (Clevenger et al. 2001; Sawyer et al. 2012). Consequently, resource management and transportation agencies have begun to incorporate crossing structures into road upgrades to reduce the risk of wildlife-vehicle collisions and restore connectivity among habitats and surrounding populations (Clevenger and Waltho. 2005; Ford et al. 2008; Huijser et al. 2007; Jaarsma et al. 2007). This cooperative approach to landscape ecology appears to be related to the awareness that changes in landscape composition and configuration often has negative effects on ecological processes, species survival, and human safety when wildlife are forced to cross roads (Alerstam et al. 2003; Clevenger 2005; Corlatti et al. 2008; Dingle & Drake 2007; Forman et al. 2003).

Exclusionary fencing is an important tool used in conjunction with crossing structures and is crucial to the effectiveness of the structure in reducing species movement onto the roadway (Sawyer et al. 2012). Without the appropriate length and
size of exclusionary fencing, crossing structures may not be as effective because fencing helps funnel wildlife to the entrance of the structure, especially with large ungulates since they exhibit strong fidelity to migration routes (Beaudry et al. 2008; Dodd & Gagnon 2010; McCollister & Van Manen 2010; Sawyer et al. 2012). Exclusionary fencing is normally placed on both sides of the roadway and is placed between structures if there is more than one (Sawyer et al. 2012; VerCauteren et al. 2006). Escape ramps for large species, also known as jump-outs, are incorporated into the exclusionary fencing to allow individuals that get stuck within the exclusionary fencing an opportunity to “jump out” and away from the roadway.

The most effective type of structure (overpass or underpass) depends on the target species. Since collisions with large ungulates are a major concern for both transportation and wildlife agencies, we investigated the differences in number of mule deer using each of the structures as well as behaviors of mule deer at the entrance of various crossing structures. Our objectives were to document the effectiveness of overpasses and underpasses, and to determine which type of structure is most effective for mule deer. We hypothesized that greater numbers of mule deer would use an overpass compared with the underpass. We also hypothesized that mule deer that approached an overpass would successfully cross the structure more often than mule deer that approached an underpass. Additionally, we hypothesized that there would be an overall reduction in traffic-related mortalities of mule deer with each subsequent migration. Finally, we predicted that the distribution of traffic-related mortalities of mule deer would be clustered near the ends of the exclusionary fencing.
METHODS

Study Area

Our study area incorporates two sites that are located along U.S. Highway 93 in northeastern Nevada between the cities of Wells (41° 07' N, 114° 58' W) and Contact (41° 46' N, 114° 45' W). The first site, 10-Mile Summit (41° 21' N, 114° 85' W), is located approximately 16 km north of Wells. This site consists of one overpass, two underpasses, and approximately 6.4 km of exclusionary fencing that extends a minimum of 0.8 km from the closest structure (Fig. 1.1). The elevation at 10-Mile Summit is 1830 meters. The second site, HD Summit (41.35° N, 114.81'), is located approximately 32 km north of Wells. This site consists of one underpass, one overpass, and approximately 4.8 km of exclusionary fencing that extends a minimum of 1.6 km from the closest structure (Fig. 1.1). The elevation at HD Summit is 1920 meters. Average temperatures range from a high of 31 °C during summer months to a low of -11 °C during winter months in this area (U.S. Climate Data). Precipitation varies throughout the year but on average receives approximately 260 mm per year with July and August being the driest months (U.S. Climate Data).

The dominant vegetation is high desert sagebrush. The most common shrub species include sagebrush (*Artemisia tridentata* Nutt. ssp. *Wyomingensis* Beetle and Young), bitterbrush (*Purshia tridentata* (Pursh) DC.), Utah juniper (*Juniperus osteosperma* (Torr.) Little), yellow rabbitbrush (*Chrysothamnus viscidiflorus* (Hook.) Nutt.), and broom snakeweed (*Gutierrezia sarothrae* (Pursh) Britton & Rusby). Grass species include crested wheatgrass (*Agropyron cristatum* (L.) Gaertn.) and Indian ricegrass (*Achnatherum hymenoides* (Roem. & Schult) Barkworth). Clover (*Trifolium L.*
sp.), yarrow (*Achillea L. sp.*), and Indian paintbrush (*Castilleja sp.*) are common forbs found throughout the study site along with the occasional prickly pear cactus (*Opuntia sp.*).

**Site Selection and Construction**

Prior to the placement of the first crossing structures within Nevada, state records were consolidated by Nevada Department of Transportation (NDOT) and Nevada Department of Wildlife (NDOW) to determine the hotspots of mule deer mortalities caused by collisions with vehicles. The majority of mortalities along U.S. Highway 93 occurred at 10-Mile Summit and HD Summit (NDOT Animal-Hit Database). Additionally, 10 mule deer were monitored with GPS store-on-board collars by NDOW to document migration routes between summer and winter ranges. Since large ungulates are known to exhibit strong fidelity to migration routes (Sawyer et al. 2012), pre-existing routes needed to be documented so that the structures and fencing were placed accordingly. Those movement data supported the mortality data and indicated that 88% of crossings over U.S. Highway 93 by mule deer with GPS collars occurred in the vicinity of 10-Mile Summit, and the remaining 12% of crossings were in the vicinity of HD Summit.

Construction of the first set of safety crossings at 10-Mile Summit was completed in August of 2010. The second set of safety crossings located at HD Summit was completed in August of 2011. Both overpasses are made of concrete arches that cross over two lanes of U.S. Highway 93. Each overpass was covered with dirt, graded to match the natural elevation at the boundaries of the public right-of-way, and seeded with natural vegetation. The overpass at 10-Mile Summit is 49 m wide and 20 m long, with a
base located 7 m above the roadway. The overpass at HD Summit is 30 m wide and 46 m long, also with a base 7 m above the roadway. The three underpasses are large spheres made from corrugated metal that pass below the roadway. Each underpass is 8 m wide, 28 m long, and 6 m tall. After instillation, dirt was placed in the base of each sphere to create a natural pathway and was graded to match the natural elevation at the boundaries of the public right-of-way on both sides. All three underpasses have a minimum 6 m x 4 m clearance opening after all grading was completed.

Exclusionary fencing was added to each side of the roadway to funnel wildlife to the entrance of each structure. This fencing spans the entire length of each study site and is located between each structure to prevent wildlife from entering the roadway. The fencing is 2.4 m tall and is made of 12.5 gauge woven wire animal fencing, also known as game fencing or field fencing. There is approximately 6.4 km of fencing at 10-Mile Summit, and 4.8 km of fencing at HD Summit. From the north fence end of 10-Mile Summit to the south fence end of HD Summit there is a break in exclusionary fencing that is approximately 8.0 km, although there is standard cattle fencing present. Additionally, access gates were added where pre-existing roads were located. Modifications of the fence ends were completed following the first autumn migration (2010) and completed in April 2011. Those modifications included additional fencing to enclose the openings at the north and south ends in order to minimize the open section along the roadway and reduce the likelihood that mule deer would become trapped between the exclusionary fencing. Moreover, a visual cattle guard was painted onto the roadway where the exclusionary fence met the highway at the south end of the study site at 10-Mile Summit.
Escape ramps were placed throughout each site. Those ramps consist of earthen berms that connect the natural grade to a break in the exclusionary fencing located approximately 0.6 m below the top of the fence. Additionally, wing-walls were added to funnel deer to the escape ramps. The wing walls were made with the same specifications as the exclusionary fencing and are at 45° angles from the roadway to the entrance of each ramp.

**Field Methods**

We collected data on responses of mule deer to the safety crossings in September 2010 through May 2012. We set up wildlife cameras to capture movement and behaviors during migratory periods and left cameras in place outside of migratory periods to capture incidental use of the crossing structures. During migratory periods, we recorded the number of mortalities caused by wildlife-vehicle collisions that occurred within the boundaries of our study area by conducting daily field observations. We collected data during the first migratory period that the structures and fencing at each study site were fully completed. We began monitoring the crossing structures at 10-Mile Summit during autumn migration in 2010 following completion of the crossing structures and exclusionary fencing. We collected data during a total of four migrations (autumn 2010, spring 2011, autumn 2011, and spring 2012). Both structures and fencing at HD Summit were completed in August of 2011; therefore we collected data during two migrations (autumn 2011 and spring 2012) at that study area. Each year we began field observations on September 15th for autumn migrations and March 1st for spring migrations, and continued field observations through December 1st and May 15th, respectively; thus, we monitored the structures for 10 weeks during each migration.
We used Reconyx HyperFire Professional Cameras (hereafter cameras) with infrared technology to document mule deer responses to the different safety crossings. Those Reconyx cameras are only triggered when motion and a change in temperature gradient are detected, which reduces the likelihood of misfires resulting from wind driven movement of vegetation. Because we were monitoring use of the structures by migratory mule deer, we placed cameras on the appropriate side of the structure to capture the approach of mule deer to the safety crossings based on seasonal migratory movement.

We synchronized all wildlife cameras at the beginning of each migratory period, and used the rapid fire setting with 10 continuous pictures, fast shutter speed, and no delay period. Thus, a series of photographs could be as short as 10 or >100 when individuals or large groups were in the camera range for extended periods of time.

Preliminary field tests on the cameras indicated a range of 12 m had the best performance at maximizing clarity and consistency of photos taken at night when infrared technology was required, and the range of the cameras are most limited. We staggered cameras to capture all movement at locations where the width at the entrance to the structure exceeded 12m. We placed five cameras at the entrance of the overpass at 10-Mile Summit, four cameras at the overpass at HD Summit, and one camera at each of the three underpasses. In addition, we placed one camera at each end of the fence ($n=4$) to monitor the number of individuals that traveled around the exclusionary fencing.

Cameras were operating 24 hours a day during migratory periods. We left cameras at the crossing structures outside of our study periods to document incidental use and to document other species of wildlife using the structures throughout the year. After
preliminary trials, we documented no camera failures during the duration of the study at any of the crossing structures during migratory periods.

We downloaded pictures every two weeks during migratory periods and named all pictures by camera location, date and time of the picture, and the place number of each photo in a particular series. For locations with more than one camera (i.e. the overpasses), we grouped all photographs that were taken within five minute increments. When grouping pictures in five minute increments, we carefully evaluated and compared the pictures from all cameras in that grouping to minimize the potential of double-counting individuals that were captured by more than one camera.

We classified mule deer behaviors as approaches, successful crossings, and retractions. We defined approaches as the numbers of individuals that entered the frame of the camera at the entrance of each structure. An approach resulted in a successful crossing if the individuals continued through the frame and appeared to have used the crossing structure. An approach became a retraction if the individuals turned around and returned in the direction from which they originally came (i.e. an unsuccessful crossing). If groups of deer were observed during daily field observations we documented the number of deer in each group and the behaviors that were observed. We compared any field observations with those that were captured on camera to verify accuracy of the number of mule deer that moved into the entrance of the structure, successfully crossed the structure, or retracted and returned in the direction in which they originally came.

During daily field observations we counted the number of mortalities caused by wildlife-vehicle collisions to determine if and to what extent the numbers of deer-vehicle collisions decreased with each subsequent migration. We began observations for traffic
related mortalities of deer approximately 2.4 km south of the southern fence end at 10-
Mile Summit and continued until approximately 2.4 km north of the northern fence end at
HD Summit. We observed the entire study site by driving slowly along the shoulder of
U.S. Highway 93 for the entire length of the study area. We used several cues to find
locations where wildlife-vehicle collisions may have occurred, including the physical
presence of animal carcasses, blood on the road or on the shoulder of the road, a
congregation of predators or scavengers, or broken vehicle parts such as broken blinker
casings. If one of these indicators was observed, we investigated further by walking the
vicinity until further evidence was located or we determined that no further evidence was
available. If a carcass was located, we identified the species, took pictures, and recorded
the global positioning system (GPS) coordinates of the location. If a carcass could not be
located, but obvious evidence of a wildlife-vehicle collision occurred, we documented the
evidence, took pictures, identified the species through remains when possible, and
recorded a GPS point of the location.

**Statistical Methods**

We used camera data from the entrance of all five crossing structures to analyze
responses to the structures by mule deer. Because deer that cross in the opposite
direction of the migration may have already crossed the structures, we excluded all
records of crossings that did not originate from the side of the structure that was
considered the entrance during that particular migratory period for all statistical analyses
in order to reduce the potential of double-counting the same individual. We did however,
included those deer that crossed in the opposite direction of the migration into the
descriptive summaries. We excluded all individuals that appeared to be injured from
statistical analyses and descriptive summaries since these individuals did not exhibit normal behaviors of mule deer migrating between seasonal ranges. For example; we believe an injured female temporarily used an underpass for a place of refuge and her movements in and out of the crossing structure inaccurately inflated the number of successful crossings.

For statistical analyses, we restricted our data set to the migration periods when both 10-Mile Summit and HD Summit were available for use so we had replicates and were able to incorporate two overpasses and three overpasses (i.e autumn 2011 & spring 2012). We used an analysis of variance (ANOVA; Proc GLM SAS Inst. 9.3) to compare the total number of successful crossings that occurred at each crossing structure, as well as the proportion of animals that successfully crossed each structure (i.e. the proportion of individuals that approached a crossing structure and successfully used that crossing structure). Season, study site, and structure type were main effects in both analyses. Additionally, we created several basic summaries so we could compare the total number of mule deer that successfully crossed, percentage of approaches by mule deer that successful crossed, and the percentage of the population at each study site that used each safety crossing during migratory periods.

We restricted our comparison of deer-vehicle collisions to the study area at 10-Mile Summit since we had four migrations of data collection, whereas we had only two migrations of data collection at HD Summit. We compared the records of traffic-related mortalities that were documented during daily field observations during migratory periods with data recorded in the Animal Hit Database managed by NDOT. The Animal-Hit Data Base includes reports collected by NDOT and Nevada Highway Patrol. We also
compared the numbers of reported deer-vehicle collisions in the Animal-Hit Database with a reporting rate of 50%. Although a 30% reporting rate is assumed for rural areas of Nevada, we used a 50% reporting rate since we believe the search effort by local agencies increased around the study area because of local interest about the project. Records that were not positively identified as mule deer were not included in our comparison. We plotted all deer mortalities within ArcGIS 10.0 and those data were used to determine the distribution of mortalities to determine where traffic-related mortalities of mule deer were concentrated.

RESULTS

We accrued more than 250,000 photos between four migrations and 16 cameras located at the crossing structures and ends of the exclusionary fencing. Approximately 20% of the photos contained no wildlife, 5% contained various species of wildlife and domestic species, and 75% contained mule deer. We documented a variety of species moving through, foraging, or scavenging around the entrance of the safety crossings (Table 1.1). To our knowledge, we documented the first record of an American pronghorn (*Antilocapra americana*) using an overpass on June 16\textsuperscript{th}, 2011 (Fig. 1.2). Other mammal species observed included American badger (*Taxidea taxus*), bobcat (*Lynx rufus*), coyote (*Canis latrans*), elk (*Cervus canadensis*), blacktailed jackrabbit (*Lepus californicus*), desert cottontail (*Sylvilagus audubonii*), redfox (*Vulpes vulpes*), and domestic cattle (*Bovinae* sp.), horses (*Equus* sp.), dogs (*Canis* sp.), and cats (*Felis* sp.) (Table 1.1). Avian species included Great Horned Owl (*Bubo virginianus*), Common Raven (*Corvus corax*), Black-billed Magpie (*Pica hudsonia*), Mourning Dove (*Zenaida macroura*), and various species of small passerines (Table 1.1).
When incorporating all four migratory periods, we documented 15,620 mule deer that successfully crossed over or through one of the five crossing structures during four migratory periods, and 646 mule deer that crossed a crossing structure outside of migratory periods; a total of 16,266 successful crossings by mule deer (Table 1.2). In total, we documented 13,295 (82%) mule deer that crossed over an overpass and 2971 (18%) individuals that crossed through an underpass.

When restricting our data to the autumn 2011 and spring 2012 migrations when both study sites were available, we recorded a higher mean number of total crossings at 10-Mile Summit (1781 ± 64.85) when compared to HD Summit (400 ± 74.89; \(F_{1,5} = 194.37, P < 0.0001; \text{Fig. 1.3} \)). Additionally, we documented a total of 7237 mule deer that used a crossing structure at 10-Mile Summit and 1576 mule deer that used the safety crossings at HD Summit during migratory periods. Thus, in autumn 2011 and spring 2011 we documented 82% of the population of mule deer that were migrating used a safety crossing at 10-Mile Summit and 18% of the mule deer used a crossing structure at HD Summit (Table 1.2). We observed an interaction between study site and structure (\(F_{1,5} = 246.19, P < 0.0001; \text{Fig 1.4} \)). This indicated differences in the total number of successful crossings between the structures at 10-Mile Summit but no differences between the structures at HD Summit. At 10-Mile Summit approximately 85.5% of the crossings occurred at the overpass and only 14.5% of the crossings occurred at one of the two underpasses (Table 1.3). At HD Summit approximately 47.1% of the successful crossings occurred at the overpass and 52.9% occurred at the underpass (Table 1.3). We did not detect an effect of season (\(F_{1,5} = 1.23, P = 0.3181 \)).
We also observed a higher proportion of successful crossings by mule deer (e.g. fewer retractions) at the overpasses relative to the underpasses ($F_{1,5} = 41.41$, $P < 0.0013$; Fig. 1.5). We did not detect an effect of season ($F_{1,5} = 0.48$, $P = 0.5207$), study site ($F_{1,5} = 0.46$, $P = 0.5953$), or study site by structure interaction ($F_{1,5} = 0.20$, $P = 0.6748$). We observed a high percentage of successful crossings at the overpasses the first migration they were open for use and their success rate remained high throughout the duration of the study (96% ± 2%; Table 1.4). The percentage of successful crossings at the underpasses increased with each subsequent migration or maintained the same level as the previous migration, with the exception of the underpasses at 10-Mile Summit where we detected a decrease in the percentage of successful crossings during the fourth migration (Table 1.4).

Eight hundred twenty mule deer were documented moving around the exclusionary fencing and onto U.S. Highway 93 during migratory periods. The majority successfully crossed U.S. Highway 93, but several were involved in deer-vehicle collisions. Within the 10-Mile study site, we recorded 14 mortalities within 2.5 km of the north and south ends of the fencing. We documented five mortalities outside of the exclusionary fencing and nine mortalities within the exclusionary fencing. The majority of mortalities were within 1.0 km of the fence ends ($n = 10$), two within 2.0 km, and two were located more than 2.5 km away from the fence ends but within the study site. We observed a 50% decrease in the number of mortalities of mule deer at the 10-Mile Summit study site with each subsequent migration (Fig. 1.6). Additionally, we observed 50% more mortalities than the numbers reported in NDOT’s Animal-Hit Database during the first three migrations the crossings were available for use. We did not detect any
mortalities during the fourth migration, but Nevada Highway Patrol reported one mortality near the southern fence end.

DISCUSSION

Mule Deer Use of Overpasses and Underpasses

We observed mule deer using all of the crossing structures, although a greater number of mule deer used the overpass to cross the highway relative to underpasses at 10-Mile Summit. At HD Summit, however, there was no difference in number of deer using the overpass relative to the underpass. We documented a higher percentage of successful crossings at the overpasses at both study sites, and a much lower percentage of successful crossings at all of the underpasses immediately following their availability. Mule deer had a higher rate of successful crossings the first time they encountered the overpasses relative to the underpasses and continued to do so throughout the duration of the study at both study sites. Mule deer that approached an underpass exhibited more vigilance by standing or hesitating at the entrance and fewer deer successfully used the underpasses (N. Simpson, personal observations). Conversely, mule deer that approached an overpass exhibited behaviors that indicated less vigilance; they typically did not hesitate at the entrance of the crossing structure, and moved directly over the structure (N. Simpson, personal observations).

Although we did not detect an effect of migration year or season in either of our analyses, there was an increase in the percentage of successful crossings by mule deer that approached an underpass during the first 3 migrations. We interpret this increase in successful crossings at the underpasses as a habituation by those individuals that may have encountered an underpass during previous migrations. Other authors have reported
that mule deer habituation to use of crossings structures as learned behavior (Clevenger et al. 2001; Foster & Humphrey 1995). The decrease in the proportion of successful crossings during the fourth migration at 10-Mile Summit may be a result of fewer mule deer approaching those structures over time. Throughout the duration of our study we documented an increase in the total number of mule deer that approached and successfully crossed the overpass at 10-Mile Summit. Conversely, at both underpasses within the study site at 10-Mile Summit we documented a decrease in the total number of individuals that approached each underpass, leading to a decrease in the number of successful crossings. We also documented a slight increase in the percentage of the total population that successfully crossed at the overpass, and a decrease in the percentage of the total population that successfully crossed at the underpasses within the study site at 10-Mile Summit. Although additional years of data collection and marked animals are required, we surmise that mule deer may select for the overpass and avoid the underpasses within the study site at 10-Mile Summit; we predict that over time mule deer will exhibit similar behaviors at HD Summit.

There was no significant difference in the number of mule deer that crossed the overpass and underpass at HD Summit, although we observed fewer retractions at the overpasses in both study areas. Various factors likely contribute to variation in use of the structures between study sites. The number of mule deer that passed through each study site varied considerably, and significantly more mule deer crossed at 10-Mile Summit. The topography near the safety crossings also varies between study sites, especially near the overpasses. The overpass at 10-Mile Summit is located along a flat stretch of highway and is at a lower elevation than the surrounding hills on both the east and west
sides of the entrances, which allow mule deer that approach the study site to view the structure from a distance. The surrounding topography on both sides of the overpass at 10-Mile Summit also allowed for a low grade on the overpass, which allows for full view of the structure and the land on the opposite side of the highway, creating a relatively flat bridge above the roadway. Conversely, the overpass at HD Summit is located at the peak of a summit, which is higher in elevation than the surrounding hills and does not allow mule deer that approach the study site a view of the structure from a distance. Because of the location, the overpass at HD Summit has a steep grade which does not allow for full view of the structure or of the land on the opposite side of the highway until an animal reaches the middle of the crossing structure. Additionally, there is a natural spring located at the underpass at HD Summit, which may attract deer to this structure within the study site at HD Summit and somewhat confound our results. Thus, we surmise the topography and resources available within each study site, as well as the variation in the design of each overpass, may affect variation in the total number of mule deer that approach the entrance of each structure and successfully use that structure. Additional years of data collection are needed, especially at HD Summit to investigate the observed variations between study sites.

**Deer Mortalities at 10-Mile Summit**

Consistent with our hypothesis, we observed a decrease in the number of mortalities of mule deer caused by collisions with vehicles within the boundaries of our study site at 10-Mile Summit. We documented a 50% decrease with each subsequent migration the safety crossing were available for use. Although we did not have intensive monitoring of the study site prior to construction of the safety crossings and exclusionary
fencing, we detected approximately 50% more mortalities than what were reported in the Animal-Hit Database maintained by NDOT during our study periods. All mortality records reported in the Animal-Hit Database are reported by the highway mile-marker nearest to the collision site and do not note the direction from the mile marker where the collision occurred. Conversely, we recorded mortalities with GPS locations at the apparent location of the collision. Thus, we were unable to determine which records that were reported in the Animal-Hit Database matched the mortalities we recorded during daily observations. Nevertheless, we are confident that we detected the majority of the mortalities caused by collisions with vehicles in our study areas since all state reports within the study boundary occurred in the same vicinity of our marked locations, and we detected 50% more than the state reports. With this decrease in the number of deer-vehicle collisions with subsequent migrations, the cost of the construction should be recuperated by both taxpayers and management agencies with time because of the decrease in human injuries, potential fatalities, and infrastructure damage (McCollister & Van Manen 2010).

Consistent with our prediction, the majority of the mortalities were concentrated in close proximity to the end of the exclusionary fencing. Contrary to our prediction, however, we observed a higher number of mortalities inside than outside of the exclusionary fencing. Our results are similar to other areas that have documented a concentration of deer-vehicle collisions near the ends of fencing and higher rates of mortalities within exclusionary fencing on busy highways have been reported elsewhere (McCollister & Van Manen 2010). The higher number of mortalities located inside the exclusionary fencing likely indicated that some of the mule deer that went around the
ends of the fencing, moved inside the fencing, and became trapped on the highway (McCollister & Van Manen 2010). Those individuals either did not detect the ‘jump outs’ or did not identify them as an escape route. After the additional fencing and painted cattle guard was completed at 10-Mile Summit in April 2011, no further mortalities occurred within the exclusionary fencing; thus the modifications appeared to be successful in keep deer outside of the exclusionary fencing.

CONCLUSIONS

Highway mitigation projects that integrate wildlife safety crossings may be defined as successful when there is a reduction in wildlife-vehicle collision rates and restoration of animal movement patterns across roads (Ford et al. 2008; Fortin and Agrawal 2005; Van Wieren and Worm 2001). We have demonstrated by monitoring the newly constructed safety crossings in Nevada that those crossing structures are meeting those criteria for success in a short time span. Mule deer used the safety crossings extensively during migratory periods, the number of successful crossings has continued to increase, and the numbers of deer-vehicle collisions have decreased with each subsequent migration.

One of our objectives was to determine which type of structure, overpass or underpass, was most effective for allowing safe crossing of the highway by mule deer. Although mule deer used all of the crossing structures at both study sites; we observed a greater proportion of successful crossings (e.g. fewer retractions) at the overpasses. Based on our results, overpasses appear to be more effective safety crossings immediately following their construction for mule deer, and likely other species of ungulates than underpasses. Nonetheless, underpasses have been documented to be
effective following a period of habituation, usually about 3 years (Clevenger et al. 2001; McCollister & Van Manen 2010; Sawyer et al. 2012). Based on our results that period of habituation did not occur at the overpasses; nearly all of the deer that approached the overpasses during each migration, successfully crossed. To our knowledge, there are no other studies that have evaluated overpasses and underpasses where both kinds of structures were within close proximity to one another. We suspect that mule deer will exhibit strong selection for overpasses in areas where both types of crossings structures are available. Underpasses remain an effective tool in restoring connectively and reducing deer-vehicle collisions, especially when the cost or construction of an overpass is not feasible (Clevenger et al. 2001; McCollister & Van Manen 2010; Sawyer et al. 2012). Additionally, on large stretches of highway, provision of multiple crossing structures, rather than a single structure is desirable (Sawyer et al. 2012; McCollister & Van Manen 2010).

As knowledge increases about the types of structures and features that are successful for focal species, transportation and wildlife agencies will be able to make more informed decisions on design and implementation of effective safety crossings. This research provides valuable information for use in conjunction with safety crossings to effectively reduce wildlife-vehicle collisions, make roadways safer for both wildlife and motorists, restore connectivity among populations, preserve migratory corridors, and reduce fragmentation of habitats throughout human altered landscapes.

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**LITERATURE CITED**


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Nevada Department of Transportation (NDOT). 2006. Evaluation of wildlife warning systems and other countermeasures.


U.S. Climate Data; Temperature, Precipitation, Sunshine.


TABLE 1.1. Approaches and successful crossings by wildlife other than mule deer at overpasses and underpasses at 10-Mile and HD Summits in eastern Nevada, 2010 – 2012. Successful crossings are not listed for avian species, humans, domestic cattle, horses, or dogs since their movement patterns do not follow the east or west movements required to physically cross the road using a crossing structure or is restricted by fencing between grazing allotments on opposite sides of the road.

<table>
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<tr>
<th>Species</th>
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<tr>
<td>Mule Deer</td>
<td><em>Odocoileus hemionus</em></td>
<td>20,581</td>
<td>16,266</td>
</tr>
<tr>
<td>Rabbit Species</td>
<td><em>Lepus sp. &amp; Sylvilagus sp.</em></td>
<td>125</td>
<td>104</td>
</tr>
<tr>
<td>Red Fox</td>
<td><em>Vulpes vulpes</em></td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Unknown</td>
<td></td>
<td>34</td>
<td>14</td>
</tr>
</tbody>
</table>
TABLE 1.2. Total number of successful crossings by mule deer at overpasses and underpasses at 10-Mile and HD Summits on Highway 93 between Wells and Contact, Nevada, 2010-2012 during migratory periods. A total of 646 mule deer were documented using a crossing structure outside of migratory periods and were excluded from this table. Each crossing structure has a unique identifier consistent with Figure 1.1.

<table>
<thead>
<tr>
<th>Study Site</th>
<th>Crossing Structure</th>
<th>Structure Number</th>
<th>Autumn 2010</th>
<th>Spring 2011</th>
<th>Autumn 2011</th>
<th>Spring 2012</th>
</tr>
</thead>
<tbody>
<tr>
<td>10-Mile Summit</td>
<td>Underpass</td>
<td>1</td>
<td>148</td>
<td>8</td>
<td>1</td>
<td>215</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td>215</td>
<td>1</td>
<td>215</td>
</tr>
<tr>
<td></td>
<td>Overpass</td>
<td>2</td>
<td>2853</td>
<td>57</td>
<td>2</td>
<td>2716</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>2</td>
<td>2716</td>
<td>2</td>
<td>2716</td>
</tr>
<tr>
<td>10-Mile Summit</td>
<td>Underpass</td>
<td>3</td>
<td>330</td>
<td>1</td>
<td>0</td>
<td>476</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>0</td>
<td>476</td>
<td>0</td>
<td>476</td>
</tr>
<tr>
<td></td>
<td>Overpass</td>
<td>5</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>477</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>477</td>
</tr>
<tr>
<td>HD Summit</td>
<td>Underpass</td>
<td>4</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>418</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>418</td>
</tr>
<tr>
<td>HD Summit</td>
<td>Overpass</td>
<td>5</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>477</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>477</td>
</tr>
<tr>
<td><strong>Total Crossings</strong></td>
<td></td>
<td></td>
<td>3397</td>
<td>3410</td>
<td>4471</td>
<td>4342</td>
</tr>
</tbody>
</table>
TABLE 1.3. Percentage of mule deer population documented at each study site that successfully crossed at each crossing structure Highway 93 between Wells and Contact, Nevada, 2010-2012 during migratory periods. Mule deer that were documented using a crossing structure outside of migratory periods were excluded from this table. Populations are separated by study site. Each crossing structure has a unique identifier that matches Figure 1.1.

<table>
<thead>
<tr>
<th>Study Site</th>
<th>Crossing Structure</th>
<th>Structure Number</th>
<th>Autumn 2010</th>
<th>Spring 2011</th>
<th>Autumn 2011</th>
<th>Spring 2012</th>
<th>Total Crossings</th>
</tr>
</thead>
<tbody>
<tr>
<td>10-Mile Summit</td>
<td>Underpass</td>
<td>1</td>
<td>4.6</td>
<td>6.3</td>
<td>3.5</td>
<td>2.2</td>
<td>4.1</td>
</tr>
<tr>
<td>10-Mile Summit</td>
<td>Overpass</td>
<td>2</td>
<td>85.7</td>
<td>79.7</td>
<td>89.2</td>
<td>87.1</td>
<td>85.5</td>
</tr>
<tr>
<td>10-Mile Summit</td>
<td>Underpass</td>
<td>3</td>
<td>9.7</td>
<td>14.0</td>
<td>7.3</td>
<td>10.7</td>
<td>10.4</td>
</tr>
<tr>
<td>HD Summit</td>
<td>Underpass</td>
<td>4</td>
<td>-</td>
<td>-</td>
<td>49.2</td>
<td>59.2</td>
<td>52.9</td>
</tr>
<tr>
<td>HD Summit</td>
<td>Overpass</td>
<td>5</td>
<td>-</td>
<td>-</td>
<td>50.8</td>
<td>40.8</td>
<td>47.1</td>
</tr>
</tbody>
</table>
TABLE 1.4. Percentage of mule deer that approached each structure and successfully crossed each structure at 10-Mile and HD Summits on Highway 93 between Wells and Contact, Nevada, 2010-2012. This table excludes all records of crossings that did not originate from the side of the structure that was considered the entrance during that particular migratory period. Each crossing structure has a unique identifier that matches Figure 1.1.

<table>
<thead>
<tr>
<th>Study Site</th>
<th>Crossing Structure</th>
<th>Structure Number</th>
<th>Autumn 2010</th>
<th>Spring 2011</th>
<th>Autumn 2011</th>
<th>Spring 2012</th>
</tr>
</thead>
<tbody>
<tr>
<td>10-Mile Summit</td>
<td>Underpass</td>
<td>1</td>
<td>34.3</td>
<td>55.6</td>
<td>64.1</td>
<td>34.1</td>
</tr>
<tr>
<td>10-Mile Summit</td>
<td>Overpass</td>
<td>2</td>
<td>96.2</td>
<td>98.4</td>
<td>94.3</td>
<td>94.1</td>
</tr>
<tr>
<td>10-Mile Summit</td>
<td>Underpass</td>
<td>3</td>
<td>26.9</td>
<td>49.8</td>
<td>49.3</td>
<td>39.5</td>
</tr>
<tr>
<td>HD Summit</td>
<td>Underpass</td>
<td>4</td>
<td>-</td>
<td>-</td>
<td>45.4</td>
<td>61.0</td>
</tr>
<tr>
<td>HD Summit</td>
<td>Overpass</td>
<td>5</td>
<td>-</td>
<td>-</td>
<td>94.5</td>
<td>96.3</td>
</tr>
</tbody>
</table>
FIGURE 1.1. Crossing structures are indicated by deer crossing signs; for overpasses (green) and underpasses (yellow) at 10-Mile and HD Summits on Highway 93 between Wells and Contact, Nevada, 2010-2012. Each crossing is numbered with unique identifiers which match the crossing structures in each summary table.
FIGURE 1.2. American pronghorn used the overpass at 10-Mile Summit for the first time on June 16th, 2011.
FIGURE 1.3. Mean ± SD for the number of mule deer that crossed within each study site. Observed mean number of total crossings at 10-Mile Summit and HD Summit ($F_{1,5} = 194.37, P < 0.0001$), on Highway 93 between Wells and Contact, Nevada, 2010-2012.
FIGURE 1.4. Mean ± SD for the mean number of mule deer that crossed each structure within each study site. Observed mean number of total crossings at the overpasses and underpasses ($F_{1,5} = 249.53, P < 0.0001$), and interaction between study site and structure ($F_{1,5} = 246.19, P < 0.0001$) at 10-Mile and HD Summits on Highway 93 between Wells and Contact, Nevada, 2010-2012.
FIGURE 1.5. Mean + SD for the proportion of approaches that successfully crossed. Observed higher proportion of successful crossings at the overpasses when compared to the underpasses ($F_{1,5} = 41.41, P < 0.0013$) at 10-Mile and HD Summits on Highway 93 between Wells and Contact, Nevada, 2010-2012.
FIGURE 1.6. Documented and estimated mortalities of mule deer caused by vehicle collisions within the boundaries of the 10-Mile study site on U.S. Highway 93 between Wells and Contact, Nevada, 2010-2012. We observed a 50% decrease in the number of documented mortalities of mule deer at the 10-Mile Summit study site with each subsequent migration. Additionally, we documented 50% more mortalities than the numbers reported in the Animal-Hit Database maintained by NDOT during the first three migrations the crossings were available for use by mule deer and other wildlife.
Chapter 2 – Variation in group sizes of migratory mule deer: observations from safety crossings.

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ABSTRACT

Various environmental factors such as lunar cycle, temperature, time of day, and precipitation have been shown to affect movement behaviors of various species. Although movement activity and herd size of ungulates have varied with changes in environmental factors, literature is scarce with regard to how environmental variables influence movements and behaviors of ungulates during migration. We used camera data from several wildlife crossing structures to investigate which environmental variables influenced movement and behaviors of mule deer that migrate between seasonal ranges. We hypothesized that percent fullness of the moon, rate of precipitation, time of day, ambient temperature, and season in which movement occurred would affect movements and behavior of mule deer during migration. We implemented a model selection procedure to evaluate those effects, developed a set of a priori models, and allowed our parameters to vary until we retained a set of models that were considered to be the best fit to the data. Group sizes of mule deer that moved over or through a crossing structure increased with an increase in daylight and intensity of precipitation, and increased during spring migrations. Neither percent fullness of the moon nor ambient temperature had any effect on movement patterns or group sizes of migrating mule deer. Our research shows that environmental factors can affect movements and grouping behaviors of mule deer during long-distance migrations.

KEY WORDS: corridor, environmental influences, fragmentation, group size, migratory movements, mule deer, *Odocoileus hemionus*, ungulate, wildlife crossing structures.
INTRODUCTION

Migration has been described at a variety of scales including small movements of microorganisms within a water column to large scale movements by vertebrates between breeding and wintering ranges (Dingle and Drake 2007). Regardless of the scale of the movement, migration is generally considered to be an adaptation to exploit resources and different habitats ultimately to increase fitness (Alerstam et al. 2003; Baguette and Van Dyck 2007; Berger 2004; Dingle and Drake 2007). For the purpose of this paper, we define migration consistently with Berger (2004) as seasonal to-and-fro movements of individuals between regions where resources and conditions are seasonally unsuitable to regions that are more suitable. Driving forces for long-distance migration include ecological and biogeographical factors including changes in seasonality, reduced competition, predator-prey relationships, and changes in spatiotemporal distributions of resources (Alerstam et al. 2003; Baguette and Van Dyck 2007; Bischof et al. 2012).

Movement costs associated with long-distance migrations can be separated into mortality and deferred costs (Baguette and Van Dyck 2007; Simpson 2012). Mortality of dispersing individuals might occur due to predation or the exhaustion of energetic reserves, whereas deferred costs reduce the fitness of immigrants after they have completed their migration (Baguette and Van Dyck 2007; Simpson 2012). Nonetheless, the benefit of increased resource availability reduces the overall costs associated with migratory movements and migrants often have higher fitness than residents (Bischof et al. 2012).

Organisms are motivated to move for various reasons including foraging for food, avoidance of predators, increased breeding opportunities, access seasonal or ephemeral
resources, access seasonal ranges, expand ranges, or disperse into new ranges (Bissonette and Adair 2007; Chetkiewicz et al. 2006; Fortin and Agrawal 2005). Various environmental components have been shown to affect movement behaviors by animals including changes within seasons, time of day, precipitation, lunar cycle, and temperature (Bischof et al. 2012; Hetem et al. 2012; Kjaer et al. 2008; Lea et al. 2010; Nathan et al. 2008; Speicher et al. 2011). For example, an increase in lighting and visibility caused by a full moon has resulted in increased movements of both predator and prey species since the activity patterns of predators coincide with periods when prey species are most vulnerable (Harmsen et al. 2011; Kjaer et al. 2008; Speicher 2011).

In addition, risk of predation has been hypothesized as a reason for prey species to form groups or move as a herd, especially among ungulates (Lung & Childress 2006; Marino 2010; Pays 2012). Prey species benefit from group formation through early detection of predators, which allows each individual the opportunity to increase foraging with increased overall vigilance of the group (Pays et al. 2012). Indeed, an inverse relationship between group size and vigilance has been documented with various species of ungulates (Lung 2006; Morano 2010; Pays et al. 2012; Pulliam & Caraco 1984).

The ability of an individual to complete a long-distance migration is largely determined by the energetic requirements needed to successfully make long-distance movements (Bischof et al. 2012; Sawyer & Kauffman 2011). A variety of species, including migratory birds and ungulates, are known to rest and replenish energetic requirements at habitat patches along or near migratory routes where resources are more abundant and nutritious, also known as “stopovers” (Sawyer & Kauffman 2011). Individuals making long-distance migrations may accumulate at these stopover areas and
create larger groups due to the concentration of individuals within these habitat patches. Movements of large ungulates have been correlated with forage quality, especially during the spring growing season (Bischof et al. 2012; Sawyer & Kauffman 2011). Forage is most nutritious during the initial phases of growth, just prior to green-up; therefore ungulates migrate in synchrony with vegetation phenology to maximize energy intake (Bischof et al. 2012; Sawyer & Kauffman 2011). Thus, group size could be a factor of more individuals moving towards summer ranges and timing of their movements with the phenological peaks of food abundance (Bischof et al. 2012; Sawyer & Kauffman 2011).

Regardless of the reason, the probability of movement between habitat patches or seasonal ranges determines the functional connectivity of the landscape (Bissonette and Adair 2007; Forman et al. 2003; Fortin and Agrawal 2005; Simpson 2012). When barriers are created, movements may stop or lead to detours where the crossings of barriers are avoided or reduced resulting in increased expenditure of energy (Alerstam et al. 2003; Simpson 2012). Roads are a leading cause of habitat fragmentation and loss of connectivity among populations in North America and around the world (Beckman et al. 2010; Simpson 2012). Because of increased fragmentation caused by human expansion, corridors, including wildlife crossing structures, have become a fundamental component of management and conservation of wildlife in North America (Simpson 2012). Wildlife cameras used to document species use of crossing structures allows extensive data collection at points of concentration of animal activity, especially during migratory periods (Dodd & Gagon 2010; McCollister & Van Manen 2010; Sawyer et al. 2011). Camera data can provide detailed information about species behaviors and timing of movements. Therefore, data collected by wildlife cameras at crossing structures where
animals are concentrated during migratory movements can be used to identify environmental factors that affect movement and behaviors of various species.

We used data from remote cameras at crossing structures established on a migratory corridor of a population of mule deer (Odocoileus hemionus) in northeastern Nevada to investigate how environmental cues influence the behaviors of mule deer during migration. Our objectives were to determine what environmental variables influenced movement and behaviors of mule deer during migratory movements. We hypothesized that season in which movement occurred; time of day, rate of precipitation, percent fullness of the moon, and ambient temperature would affect movement and behavior of mule deer migrating between seasonal ranges. We predicted that migratory movements would decrease with an increase in percent fullness of the moon, ambient temperature, and precipitation. We predicted that migratory movement would increase during crepuscular hours, and would fluctuate between seasons. We also predicted that group sizes would increase with an increase in the percent fullness of the moon, daylight hours, and rate of precipitation. Lastly, we predicted group sizes would be larger during spring migrations since mule deer are more concentrated on winter ranges and likely synchronize their movements back to summer range with plant phenology, and surf the green wave (Bischof 2012).

METHODS

Study Area

Our study area incorporates two sites located along U.S. Highway 93 in northeastern Nevada between the cities of Wells (41° 07' N, 114° 58' W) and Contact (41° 46' N, 114° 45' W; Simpson 2012). Ten-Mile Summit (41° 21' N, 114° 85' W), is
located approximately 16 km north of Wells, and consists of one overpass, two underpasses, and approximately 6.4 km of exclusionary fencing (Fig. 2.1). The elevation at 10-Mile Summit is 1830 meters. The second site, HD Summit (41.35° N, 114.81°), is located approximately 32 km north of Wells, and consists of one underpass, one overpass, and approximately 4.8 km of exclusionary fencing (Fig. 1). The elevation at HD Summit is 1920 meters. Average temperatures range from a high of 31 °C during summer months to a low of -11 °C during winter months in this area (U.S. Climate Data). Precipitation varies throughout the year but on average receives approximately 260 mm per year with July and August being the driest months (U.S. Climate Data).

Dominant habitat type is high desert sagebrush (Artemisia tridentate Nutt. ssp. Wyomingensis Beetle and Young). The most common shrub species include sagebrush, bitterbrush (Purshia tridentate (Pursh) DC.), Utah juniper (Juniperus osteosperma (Torr.) Little), yellow rabbitbrush (Chrysothamnus viscidiflorus (Hook.) Nutt.), and broom snakeweeds (Gutierrezia sarothrae (Pursh) Britton & Rusby). Grass species include crested wheatgrass (Agropyron cristatum (L.) Gaertn.) and Indian ricegrass (Achnatherum hymenoides (Roem. & Schult) Barkworth). Clover (Trifolium L. sp.), yarrow (Achillea L. sp.), and Indian paintbrush (Castilleja sp.) are common forbs found throughout the study site along with the occasional prickly pear cactus (Opuntia sp.).

Field Methods

We collected data on the movement of mule deer at the crossing structures in September 2010 through May 2012. We collected data during the first migratory period that the structures and fencing at each study site were fully completed. We began monitoring the crossing structures at 10-Mile Summit during the autumn migration in
2010 following completion of the crossing structures and exclusionary fencing for a total of four migrations (autumn 2010, spring 2011, autumn 2011, and spring 2012). Both structures and fencing at HD Summit were completed in August of 2011; therefore we collected data during two migrations (autumn 2011 and spring 2012) at that study area.

We used Reconyx HyperFire Professional Cameras (hereafter cameras) with infrared technology to document migratory movement of mule deer at each of the crossing structures. Those Reconyx cameras are only triggered when motion and a change in temperature gradient are detected, which reduces the likelihood of misfires resulting from wind driven movement of vegetation. We placed cameras on the appropriate side of the structure to capture the approach of mule deer to the safety crossings based on seasonal migratory movements. We staggered cameras to capture all movement at locations where the width at the entrance to the structure exceeded the range of the cameras during night hours (approximately 12 m). Thus, we placed five cameras at the entrance of the overpass at 10-Mile Summit, four cameras at the overpass at HD Summit, and one camera at each of the three underpasses. We synchronized all wildlife cameras at the beginning of each migratory period, and used the rapid fire setting with 10 continuous pictures, fast shutter speed, and no delay period. Thus, a series of photographs could be as short as 10 or >100 when individuals or large groups were in the camera range for extended periods of time. Cameras were operating 24 hours a day during migratory periods and we documented no camera failures during the duration of the study at any of the crossing structures. We left cameras at the crossing structures outside of our study periods to document incidental use and to document other species of wildlife using the structures throughout the year, but we restricted data in these analyses.
to observations between September 15\textsuperscript{th} and December 1\textsuperscript{st} for autumn migrations and March 1\textsuperscript{st} and May 15\textsuperscript{th} for spring migrations; for a total of 10 weeks during each migration.

We downloaded pictures every two weeks during migratory periods and named all pictures by camera location, date and time of the picture, and the place number of each photo in a particular series. Photographs were filed based on structure location, date, and time. For locations with more than one camera (i.e. the overpasses), we grouped photographs in five minute increments. When files had more than one series of photos taken by multiple cameras we carefully evaluated each series to avoid double-counting individuals that were captured by more than one camera. When grouping pictures in five minute increments, we carefully evaluated and compared the pictures from all cameras in that grouping to minimize the potential of double-counting individuals that were captured by more than one camera. We documented the average temperature that was recorded within each series of photographs, the time of day, and season of each record. We documented mule deer behaviors as approaches, successful crossings, and retractions. We defined approaches as the numbers of individuals that enter the frame of the camera. We described an approach that resulted in a successful crossing if the individuals continued through the frame and appeared to have used the safety crossing. We defined retractions as the number of individuals that turned around and returned in the direction from which they originally came (i.e. an unsuccessful crossing).

Species engaged in long-distance migrations tend to move all hours of the day, so we evaluated how migratory movements and herding behaviors varied within 24 hour time periods. We used a data base controlled by the U.S. Naval Observatory
(http://aa.usno.navy.mil/data/docs/RS_OneYear.php) to collect data on sunrise and sunset times for the city of Wells. We assigned all movement records of mule deer into three categories to determine the time of day when the crossings occurred (crepuscular, day, or night; hereafter time interval). We defined crepuscular hours as ±2 hours from sunrise and sunset (Stewart et al. 2002; 2006). Thus, time intervals varied with changes in the timing of sunrise and sunset of each calendar date.

We collected weather data from a database that is controlled and operated by Nevada Department of Transportation; Vaisala IceCast IceNet – road/rail/runway (http://birice.vaisala.com/IceNet/displayCustomerLoginForm.do). We used data collected by a weather station located at the peak of HD Summit. Although accumulation of precipitation is normally seen in the literature, this particular weather station records the rate of precipitation in mm per hour. Additionally, we were interested in how the rate of precipitation influenced movement and grouping behaviors during precipitation events rather than an accumulation of precipitation. We retrieved the highest rate of precipitation during a three hour interval (0:00-2:59, 3:00-5:59, 6:00-8:59, etc.) for each day of our study period. We added the rate of precipitation into each record of animal activity that fell within those three hour intervals. Thus, if a record of animal activity was documented on September 29th 2011 at 6:21am, we used precipitation data from Vaisala IceCast IceNet associated with the interval of 6:00-8:59 on September 29th 2011.

The amount of light at night should be an important variable to species that may migrate during night hours, so we evaluated the influence of the lunar cycle on migratory movement of mule deer. The effect of cloud cover on illumination could not be measured; therefore our analysis assumes that fluctuations in the amount of light caused
by cloud cover would not have a strong influence on the interaction of migratory movements with moon phase. We used Quick Phase Pro (QuickPhase Pro Inc. 3.3.5) to collect data on the percentage of fullness of the moon for each night of our study period as a measure of illumination. All moon data that was calculated in Quick Phase Pro was based on the coordinates of Wells, Nevada (41° 07' N, 114° 58' W).

**Statistical Methods**

We investigated environmental parameters that affect migratory movement of mule deer, and implemented a model selection procedure to evaluate those effects (Morano et al. 2012). We developed a set of a priori models and allowed our parameters to vary until we retained a set of models that were considered the best fit to the data (Morano et al. 2012). We used a generalized linear model with restricted estimated maximum likelihood (SAS Inst. 9.3). Our models included both fixed effects and covariates (Table 2.1). We assigned all models the fixed effects of study site and the type of structure where the crossings were documented since previous analysis concluded these two parameters have strong effects on the number of crossings (Simpson 2012). Since we were interested with habituation to the crossing structures, and season was shown to have no effect in previous analyses (Simpson 2012), we added the fixed effects of subsequent migration from which the structure was first available for use (1st, 2nd, 3rd, or 4th). We also included time interval as a fixed effect. Lastly, we included average temperature, the percentage of fullness of the moon, and the intensity of precipitation as covariates in our models.

We used Akaike’s Information Criterion (AICc) adjusted for small sample sizes to evaluate model support (Burnham & Anderson 2010). We used AICc scores because
they utilizes the maximum likelihood for each model via the term $-2\ln(L)$ and a penalty term for the number of parameters in the model (Burnham & Anderson 2010; Williams et al. 2002). Thus, the model with the lowest AIC$_C$ score is determined to follow the principle of parsimony utilizing the smallest possible number of parameters to adequately represent variation in the data (Box & Jenkins 1970; Burnham & Anderson 2010; Williams et al. 2002). We calculated AICc weights ($w_i$) of all models to determine the best supported model (Burnham & Anderson 2010). Parameter estimates ($\beta_i$) from the top model were used to determine which environmental variables were important in migratory movement of mule deer, and confidence intervals that did not overlap 0 were considered to be significant.

After we determined which factors were important to movement of migratory mule deer based on $\Delta$AIC$_C$ scores and model weights, we conducted a post hoc analysis, and used an analysis of variance (ANOVA; Proc GLM SAS Inst. 9.3) to determine the mean group size of mule deer that used a crossing structure during each time interval and during precipitation events. Study site, structure type, subsequent migration, and time interval were main effects in the ANOVA. Finally, we summarized the mean number of mule deer that successfully crossed during each time of day and the mean group size documented during those periods.

RESULTS

Based on the change in AIC$_C$ scores and model weights, the top model contained effects of study site, structure type, time interval, subsequent migration, rate of precipitation, and temperature (Table 2.2). Our second ranked model, and the only other model within 2 AIC$_C$ units of the top model, included all of the same parameters of the
top model except temperature (Table 2.2). The removal of temperature from the top model decreased the model weight, but the beta values were almost identical for both models (Table 2.2). Additionally, the confidence intervals of temperature in the top model overlapped 0 ($\beta_i=0.0151$, 95% CI = -0.0581 to 0.0280) indicating temperature does not have a significant effect on group size during migratory movement of mule deer. All other models had model weights $\leq 0.01$ and were not within 2 $\text{AIC}_C$ units from the top model (Table 2.2). Thus, our best model contained the effects of study site, structure type, time interval, subsequent migration, and rate of precipitation and excluded temperature (Table 2.3).

Time interval and subsequent migration were fixed effects that appeared in both of our top models. Thus, we conducted a post hoc analysis to determine how the time of day and subsequent migration influenced movement of migratory mule deer. We documented 15,620 mule deer that successfully crossed over or through one of the five crossing structures during four migratory periods, and 646 mule deer outside of migratory periods; a total of 16,266 successful crossings by mule deer (Simpson 2012; Table 2.4). We observed the greatest number of mule deer that moved during daylight hours, with the lowest number of mule deer moving during night hours (Fig. 2.3). In addition, we observed larger group sizes during daylight hours and the smallest group sizes during night hours (Fig. 2.2; $F_{2,2975} = 65.71$, $P < 0.0001$). Finally, we observed larger group sizes of mule deer during spring migrations when compared to autumn migrations (Fig. 2.4; $F_{3,2975} = 32.11$, $P < 0.0001$).

The rate of precipitation was the only covariate that was supported in both of our top two models. Thus, we conducted a post hoc analysis to determine how precipitation
was influencing migratory movement. The majority of movement occurred when there was no measurable precipitation (n=14,363). As the rate of precipitation increased, the number of mule deer that crossed a structure decreased and movement stopped completely when rates of precipitation reached more than 12 mm per hour (Fig. 2.5). Conversely, average group size increased with an increase in the rate of precipitation (Fig. 2.6).

**DISCUSSION**

Although we did not detect a difference in the number of crossings between seasons, we observed larger group sizes of mule deer during spring migrations compared with autumn migrations. There may be several factors that attribute to the larger group sizes documented during spring migrations. During winter months nutritious forage is limited, animals may be limited by energetic costs of moving through snow, and distributions of mule deer and other ungulates are restricted (Stewart et al. 2010). Thus, mule deer become more concentrated on winter ranges and are more widely distributed on summer ranges when resources are more abundant (Stewart et al. 2010). When migrating from summer ranges to winter ranges individuals are more spread-out over the landscape and therefore may arrive at the crossings at different times, creating smaller groups. Conversely, during the spring, female ungulates that are pregnant often have strong birth site-fidelity and may be responding to the urgency to return to their fawning grounds prior to parturition (Wiseman et al. 2006). Moreover, animals that are more clumped in distribution on winter range may be more likely to move together in synchrony with vegetation phenology to maximize energetic intake, and surf the green wave back to summer range (Sawyer & Kauffman 2011, Bischof et al. 2012). Thus,
group size could be a factor of more individuals timing their movements with the phenological peaks of food abundance (Bischof et al. 2012; Sawyer & Kauffman 2011).

We documented peaks of movement during the day, just outside of crepuscular hours in the morning and late afternoon. Movement behaviors during long-distance migrations appear to fluctuate somewhat from normally observed behaviors because ungulates are often the most active during crepuscular hours while animals are foraging (Kjaer et al. 2008). We surmise that during migration ungulates are active for a longer time within a 24 hour period when compared to activity levels when they are within their home range. Nevertheless, while migrating, individuals still must meet nutrition requirements throughout their migration (Bischof et al. 2012). Thus, foraging activity during migration occurs at stopovers locations between long-distance movements (Sawyer and Kauffman 2011). Consistent with our prediction, we documented larger group sizes during daylight hours. Although we did not examine vigilance behavior, we surmise the increase in group size during daylight hours may partially be attributed to a predator-avoidance strategy since vigilant behaviors have been attributed to risk of predation, and decrease with an increase in the size of the group (Lung & Childress 2006). Further investigation on vigilance and group size of mule deer at the crossing structures may lead to greater understanding about differences in group sizes associated with the timing of movements.

Consistent with our hypothesis, we documented a decrease in successful crossings by mule deer and an increase in group size with an increase in the rate of precipitation. There are studies that have investigated changes in movements within home-ranges that may have been driven by accumulation of precipitation (Bello et al. 2004), but to our
knowledge there are no studies that have investigated how the rate of precipitation influences movement rates and grouping behaviors of migratory species. We surmise that with an increase in precipitation prey species become more vulnerable because of reduced visibility and hearing, and movement becomes more risky. Thus, mule deer may form larger group sizes and eventually stopping movement altogether when the risk of movement becomes too high.

Contrary to our hypothesis, we did not detect an effect of the percent fullness of the moon, presumed to affect nighttime illumination and visibility (Harmsen et al. 2011; Penteriani 2011; Kjaer et al. 2008). Although some studies have detected changes in movement patterns or behaviors of species correlated with changes in illumination by the moon, these studies were focused on small scale movements usually within individual home ranges (Harmsen et al. 2011; Penteriani 2011; Kjaer et al. 2008). We suspect that during large scale movements, such as long-distance migrations, the illumination by the moon is not as influential as it may be during activities within home ranges. The effects of moon phase on activity patterns by deer and movement are divided, since some studies did not find any influence of moon phase and illumination on deer activity while others reported that movements by deer both increased and decreases during brighter moons depending on surrounding habitat (Beier and McCullough 1990; Kjaer et al. 2008).

We did not detect a significant effect of temperature on movement, although movement by ungulates has been known to decrease with an increase in temperatures (Rivrud et al. 2010). Nevertheless, the effects of temperature are weaker within shorter time scales (weekly – daily) when compared to longer time scales (monthly-biweekly) (Rivrud et al. 2010). Since our study periods consist of 10 week intervals, and most of
the movement occurs within 3-4 weeks of each study period, our time scale may not be appropriate to address if temperatures have an effect on ungulates during migration.

Vigilance behaviors in ungulates have been attributed to variation in the risk of predation, and have been known to decrease with an increase in group size (Lung & Childress 2006; Marino 2010; Pulliam and Caraco 1984). The decrease in vigilance with an increase in group size is thought to reflect a decrease in perceived predation risk (Lung & Childress 2006; Marino 2010). With an increase in group size, each individual can decrease its own scanning rate in response to the vigilance of others, and can spend more time foraging (Marino 2010; Pays et al. 2012). Nevertheless, there are constraints on group size, including energetic costs associated with an increase in resource competition when moving with other individuals (Marino 2010; Pays et al. 2012). Thus, group sizes have been documented to vary throughout the course of the day with subgroups merging and dispersing frequently to gain access to more resources (Pays et al. 2012). Another drawback to increased group size is a decrease in the rate of movement since group cohesion can only exist if all individuals within the group synchronize their movements (Pays et al. 2012). As a group becomes larger, the group as a whole slows down; a theory thought to correlate with an increase in potential paths with a larger number of individuals (Pays et al. 2012). When ungulates make long-distance movements, moving quickly throughout the landscape may be critically important, and forage quality is limited along the migratory route (Pays et al. 2012). Thus, there must be a balance of the costs and benefits of increased group sizes. Group stability for ungulates has been documented between 5-10 individuals within home ranges (Pays et al. 2012). Our results appear to be consistent with Pays et al. (2012) for migratory movement. Although we
documented the occasional group that contained more than 100 individuals during spring migrations, the mean number of individuals within a group between all seasons was 5-10 individuals.

Despite the large number of studies on general movements and grouping behaviors of ungulates, the literature is scarce on those factors during long-distance migration. Our study shows that there are various environmental factors, especially intensity of precipitation that affects movements and behaviors of mule deer during long-distance migrations. Our results support other studies that have shown changes in environmental factors influence the movements and behaviors of various species (deBruyn & Meeuwig 2001; Harmsen et al. 2011; Kjaer et al. 2008; Penteriana et al. 2011). Components of movements and behaviors include external environmental factors, the internal state of the individual, locomotion, timing, and navigation (Lea et al. 2010; Nathan et al. 2008). Consequently, movements and behaviors result from interplay of those basic components, especially during long-distance migration (Lea et al. 2010; Nathan et al. 2008). Further studies should investigate the movement paths during migrations, stop-over points, and grouping behaviors of mule deer migrating between seasonal ranges which may bring further understanding to the mechanisms that control movement and grouping behaviors during migratory movement.

ACKNOWLEDGMENTS

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LITERATURE CITED


U.S. Climate Data; Temperature, Precipitation, Sunshine.


TABLE 2.1. Description, abbreviation (Abbr), and categories of parameters that were investigated in models addressing environmental factors that influenced group size of mule deer during migratory movement at crossing structures located at 10-Mile and HD Summits in eastern Nevada, 2010 – 2012.

<table>
<thead>
<tr>
<th>Abbr</th>
<th>Model Parameter</th>
<th>Description</th>
<th>Effect Type</th>
</tr>
</thead>
<tbody>
<tr>
<td>SITE</td>
<td>Study Site</td>
<td>Study site where crossings were documented 10-Mile Summit or HD Summit</td>
<td>Fixed Effect</td>
</tr>
<tr>
<td>STRUCTYP</td>
<td>Structure Type</td>
<td>Kind of structure where crossings were documented Overpass or Underpass</td>
<td>Fixed Effect</td>
</tr>
<tr>
<td>TIME</td>
<td>Time Interval</td>
<td>Time of day when crossing was documented Crepuscular, Day, or Night</td>
<td>Fixed Effect</td>
</tr>
<tr>
<td>SUBMIG</td>
<td>Subsequent Migration</td>
<td>Order of migration from when the structure was first available for use 1st, 2nd, 3rd, or 4th</td>
<td>Fixed Effect</td>
</tr>
<tr>
<td>PRECIP</td>
<td>Rate of Precipitation</td>
<td>Max rate of precipitation that occurred during a 3 hour interval 0.0 through 1.0 inches per hour</td>
<td>Covariate</td>
</tr>
<tr>
<td>TEMPC</td>
<td>Average Temp °C</td>
<td>Average temperature when occurrence was documented -18 through 36 degrees Celsius</td>
<td>Covariate</td>
</tr>
<tr>
<td>MOON</td>
<td>Moon Illumination</td>
<td>The percentage of the moon that was full 0 through 100 percent full</td>
<td>Covariate</td>
</tr>
</tbody>
</table>
TABLE 2.2. Results of model selection (top 10 models) addressing environmental factors that influenced the group size of mule deer during migratory movement at crossing structures located at 10-Mile and HD Summits in eastern Nevada, 2010 – 2012. Fixed effects of site and structure were included in all models evaluated, while all other variables were manipulated. See Table 2.1 for parameter descriptions.

<table>
<thead>
<tr>
<th>Rank</th>
<th>Model</th>
<th>No. of Parameters</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>wAIC</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>SITE + STRUCTYP + DAYPER + SUBMIG + RAIN + TEMPC</td>
<td>6</td>
<td>20859.8</td>
<td>0.0</td>
<td>0.5850</td>
</tr>
<tr>
<td>2</td>
<td>SITE + STRUCTYP + DAYPER + SUBMIG + RAIN</td>
<td>5</td>
<td>20860.6</td>
<td>0.8</td>
<td>0.3921</td>
</tr>
<tr>
<td>3</td>
<td>SITE + STRUCTYP + DAYPER + SUBMIG + RAIN + TEMPC + MOON</td>
<td>7</td>
<td>20867.8</td>
<td>8.0</td>
<td>0.0107</td>
</tr>
<tr>
<td>4</td>
<td>SITE + STRUCTYP + DAYPER + SUBMIG + RAIN + MOON</td>
<td>6</td>
<td>20868.4</td>
<td>8.6</td>
<td>0.0079</td>
</tr>
<tr>
<td>5</td>
<td>SITE + STRUCTYP + DAYPER + SUBMIG + TEMPC</td>
<td>5</td>
<td>20870.7</td>
<td>10.9</td>
<td>0.0025</td>
</tr>
<tr>
<td>6</td>
<td>SITE + STRUCTYP + DAYPER + SUBMIG</td>
<td>4</td>
<td>20871.6</td>
<td>11.8</td>
<td>0.0016</td>
</tr>
<tr>
<td>7</td>
<td>SITE + STRUCTYP + DAYPER + SUBMIG + TEMPC + MOON</td>
<td>6</td>
<td>20878.7</td>
<td>18.9</td>
<td>0.0001</td>
</tr>
<tr>
<td>8</td>
<td>SITE + STRUCTYP + DAYPER + SUBMIG + MOON</td>
<td>5</td>
<td>20879.5</td>
<td>19.7</td>
<td>0.0001</td>
</tr>
<tr>
<td>9</td>
<td>SITE + STRUCTYP + DAYPER + RAIN + TEMPC</td>
<td>5</td>
<td>20926.0</td>
<td>66.2</td>
<td>0.0001</td>
</tr>
<tr>
<td>10</td>
<td>SITE + STRUCTYP + DAYPER + RAIN</td>
<td>4</td>
<td>20927.5</td>
<td>67.7</td>
<td>0.0001</td>
</tr>
</tbody>
</table>
TABLE 2.3. Parameter estimates ($\beta_i$), standard errors, and 95% confidence intervals from our top model from a model selection addressing environmental factors that influenced group size of mule deer during migratory movement at crossing structures located at 10-Mile and HD Summits in eastern Nevada, 2010 – 2012.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Category</th>
<th>$\beta_i$</th>
<th>SE</th>
<th>95% Confidence Interval</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td></td>
<td>2.0741</td>
<td>0.6309</td>
<td>0.8370 - 3.3111</td>
</tr>
<tr>
<td>Study Site</td>
<td>10-Mile Summit</td>
<td>0.7160</td>
<td>0.4503</td>
<td>-0.1669 - 1.5990</td>
</tr>
<tr>
<td>Study Site</td>
<td>HD Summit</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Structure Type</td>
<td>Overpass</td>
<td>3.2747</td>
<td>0.3328</td>
<td>2.6221 - 3.9272</td>
</tr>
<tr>
<td>Structure Type</td>
<td>Underpass</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Time Interval</td>
<td>Day</td>
<td>4.0000</td>
<td>0.4026</td>
<td>3.2106 - 4.7894</td>
</tr>
<tr>
<td>Time Interval</td>
<td>Crepuscular</td>
<td>1.4911</td>
<td>0.3434</td>
<td>0.8177 - 2.1644</td>
</tr>
<tr>
<td>Time Interval</td>
<td>Night</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Migration</td>
<td>1&lt;sup&gt;st&lt;/sup&gt;</td>
<td>-1.6439</td>
<td>0.4637</td>
<td>-2.5531 - 0.7348</td>
</tr>
<tr>
<td>Migration</td>
<td>2&lt;sup&gt;nd&lt;/sup&gt;</td>
<td>0.7153</td>
<td>0.5179</td>
<td>-0.3003 - 1.7308</td>
</tr>
<tr>
<td>Migration</td>
<td>3&lt;sup&gt;rd&lt;/sup&gt;</td>
<td>-2.7296</td>
<td>0.4640</td>
<td>-3.6395 - 1.8197</td>
</tr>
<tr>
<td>Migration</td>
<td>4&lt;sup&gt;th&lt;/sup&gt;</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Rate of Precipitation</td>
<td></td>
<td>10.1188</td>
<td>3.9889</td>
<td>2.2975 - 17.9402</td>
</tr>
</tbody>
</table>
TABLE 2.4. Total number of successful crossings by mule deer at overpasses and underpasses at 10-Mile and HD Summits on Highway 93 between Wells and Contact, Nevada, 2010-2012 during migratory periods. A total of 646 mule deer were documented using a crossing structure outside of migratory periods and were excluded from this table. Each crossing structure has a unique identifier consistent with Figure 2.1.

<table>
<thead>
<tr>
<th>Study Site</th>
<th>Crossing Structure</th>
<th>Structure Number</th>
<th>East Crossings</th>
<th>West Crossings</th>
<th>East Crossings</th>
<th>West Crossings</th>
<th>East Crossings</th>
<th>West Crossings</th>
<th>East Crossings</th>
<th>West Crossings</th>
</tr>
</thead>
<tbody>
<tr>
<td>10-Mile Summit</td>
<td>Underpass</td>
<td>1</td>
<td>148</td>
<td>8</td>
<td>1</td>
<td>215</td>
<td>116</td>
<td>6</td>
<td>3</td>
<td>78</td>
</tr>
<tr>
<td></td>
<td>Overpass</td>
<td>2</td>
<td>2853</td>
<td>57</td>
<td>2</td>
<td>2716</td>
<td>3043</td>
<td>52</td>
<td>39</td>
<td>3242</td>
</tr>
<tr>
<td>10-Mile Summit</td>
<td>Underpass</td>
<td>3</td>
<td>330</td>
<td>1</td>
<td>0</td>
<td>476</td>
<td>253</td>
<td>1</td>
<td>1</td>
<td>403</td>
</tr>
<tr>
<td>HD Summit</td>
<td>Underpass</td>
<td>4</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>418</td>
<td>74</td>
<td>21</td>
<td>320</td>
</tr>
<tr>
<td>HD Summit</td>
<td>Overpass</td>
<td>5</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>477</td>
<td>31</td>
<td>1</td>
<td>234</td>
</tr>
<tr>
<td><strong>Total Crossings</strong></td>
<td></td>
<td></td>
<td><strong>3397</strong></td>
<td><strong>3410</strong></td>
<td><strong>4471</strong></td>
<td><strong>4342</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
FIGURE 2.1. Crossing structures are indicated by deer crossing signs; for overpasses (green) and underpasses (yellow) at 10-Mile and HD Summits on Highway 93 between Wells and Contact, Nevada, 2010-2012. Each crossing is numbered unique identifiers which match the crossing structures in each summary table.
FIGURE 2.2. Mean + SD for the mean group size of mule deer during each day period. We observed larger group sizes during day hours and the smallest group size during night hours ($F_{2,2975} = 63.57, P < 0.0001$) at 10-Mile and HD Summits on Highway 93 between Wells and Contact, Nevada, 2010-2012. Different letters of bars indicate significant differences.
FIGURE 2.3. Total crossings by mule deer throughout all migratory periods during a 24 hour cycle at 10-Mile and HD Summits on Highway 93 between Wells and Contact, Nevada, 2010-2012.
FIGURE 2.4. Mean ± SD for the mean group size of mule deer during each migratory period. We observed the largest group sizes during the spring migrations and smallest group sizes during autumn migrations ($F_{3,2975} = 32.11, P < 0.0001$) at 10-Mile and HD Summits on Highway 93 between Wells and Contact, Nevada, 2010-2012. Different letters of bars indicate significant differences.
FIGURE 2.5. Total crossings by mule deer throughout all migratory periods during precipitation events at 10-Mile and HD Summits on Highway 93 between Wells and Contact, Nevada, 2010-2012.
FIGURE 2.6. Mean group size of mule deer during precipitation events at 10-Mile and HD Summits on Highway 93 between Wells and Contact, Nevada, 2010-2012. We observed larger group sizes when precipitation was stronger and smaller group sizes when there was no precipitation ($F_{4,29750} = 32.11, P < 0.0001$). No movement was documented when rates of precipitation were above 12 mm per/hour.
Highway mitigation projects may be defined as successful when there is a reduction in rates of wildlife-vehicle collisions and restoration of animal movement patterns across roads (Ford et al. 2008; Fortin and Agrawal 2005; Van Wieren and Worm 2001). We demonstrated that several newly constructed safety crossings in Nevada met those criteria for "success". We monitored five crossing structures, 2 overpasses and 2 underpasses with wildlife cameras. Mule deer used the safety crossings extensively, especially during migratory periods. The number of successful crossings has continued to increase, and the number of deer-vehicle collisions has decreased with each subsequent migration. Additionally, our results showed that overpasses are more effective safety crossings for mule deer and likely other species of ungulates than underpasses. Mule deer used the overpasses more frequently, and exhibited less hesitation and resistance when compared with the underpasses. Although the overpasses in Nevada had a higher proportion of successful crossings by mule deer upon first encounter, underpasses were still an effective tool in restoring connectively and reducing deer-vehicle collisions, especially when the cost or construction of an overpass is not feasible (Clevenger et al. 2001; McCollister & Van Manen 2010; Sawyer et al. 2012).

To our knowledge, there are no other studies that have evaluated overpasses and underpasses where both kinds of structures were within close proximity to each other in the path of ungulates migrating between seasonal ranges. We suspect that if mule deer exhibit strong selection for overpasses, the underpasses may become more of an incidental crossing than the overpasses. If those underpasses are used less frequently with time, transportation and resource management agencies may not need to install.
underpasses in areas where overpasses are available. Nevertheless, in large stretches of highway, provision of multiple crossing structures, rather than a single structure is desirable (Sawyer et al. 2012; McCollister & Van Manen 2010). As knowledge increases about the types of structures and features that are successful for wildlife, transportation and wildlife agencies will be able to make more informed decisions on design and implementation of effective safety crossings.

Using wildlife cameras to capture movement of species at the crossing structures provided us the opportunity to look at various behaviors, such as group size, that the use of GPS collars does not allow. GPS collars can provide detailed movement information, but those collars only provide information about a single individual, whereas wildlife cameras provided us with information on timing of movements and behaviors on thousands of individuals. Our results documented changes in movements and grouping behaviors of mule deer associated with environmental variables. Migratory movement varied with the rate of precipitation and time of day. Moreover, group sizes of migrating mule deer were greatest during spring, during daylight hours and with increasing intensity of precipitation. We believed the increase in group sizes during spring migration, is partially a result of mule deer being concentrated on winter ranges, and timing their movements with the phenological peaks of food abundance (Bischof et al. 2012; Sawyer & Kauffman 2011). Forage is most nutritious during the initial phases of growth; therefore ungulates migrate in synchrony with vegetation phenology to maximize energy intake (Bischof et al. 2012; Sawyer & Kauffman 2011).

Despite the large number of studies on general movements and grouping behavior of ungulates, the literature is scarce on the occurrence of those factors during long-
distance migration. Thus, our study may be one of the first that investigated how environmental factors influenced movements and grouping behavior of ungulates. Further studies should investigate movement paths during migrations, stop-over points, and grouping behavior of mule deer migrating between seasonal ranges, which may bring further understanding to the mechanisms that control long-distance movement. This research provides valuable information for use in conjunction with safety crossings to effectively reduce wildlife-vehicle collisions, make roadways safer for both wildlife and motorists, restore connectivity among populations, preserve migratory corridors, and reduce fragmentation of habitats throughout human altered landscapes.

LITERATURE CITED


