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Mule Deer Highway Mortality in Northeastern Utah: An Analysis of Population-Level Impacts and a New Mitigative System

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MULE DEER HIGHWAY MORTALITY IN NORTHEASTERN UTAH: AN ANALYSIS OF POPULATION-LEVEL IMPACTS AND A NEW MITIGATIVE SYSTEM

by

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ABSTRACT

Mule Deer Highway Mortality in Northeastern Utah: An

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by

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Rerouting highways to accommodate construction of the Jordanelle Reservoir in northeastern Utah caused a dramatic increase in vehicle collisions with mule deer (Odocoileus hemionus). I evaluated the effectiveness of a new system of highway crosswalk structures installed to reduce deer losses and preserve seasonal migrations. In addition, I constructed computer simulation models to investigate how highway mortality has impacted the Jordanelle deer population.

The crosswalk system restricted deer crossings to specific, well-marked areas along highways where motorists could anticipate them. Subsequent to installation, mortality declined 42.3% and 36.8% along a four-lane and two-lane highway, respectively. I was unable to statistically demonstrate that observed

mortality reductions were a direct result of the crosswalk system. The potential applicability of the structures, however, should not be dismissed. Reduced deer use of the highway right-of-way (ROW), the apparent maintenance of migratory behavior, and observations of animals crossing within crosswalk boundaries indicate the system warrants further testing. Lack of motorist response to crosswalk warning signs, the tendency for foraging deer to wander outside crosswalk boundaries, and the ineffectiveness of ROW escape gates contributed to most treatment area mortalities. I offer design modifications that address these shortcomings.

Four years of field data revealed that highway mortality at Jordanelle was inversely density-dependent, removed between 5.6% and 17.4% of the population each year, and disproportionately impacted bucks. I incorporated this information into 3 competing simulation models in which highway losses operated in a strictly additive, partially compensatory, or strictly compensatory manner. The partial compensation model most closely tracked observed population dynamics, suggesting that highway losses were not completely offset by reductions in other mortality sources. Highway mortality apparently worsened a population crash initiated by severe winter conditions, and may be slowing the recovery. The disproportionate loss of bucks along roads altered sex ratios of simulated populations. Mitigative efforts should target road-kill reductions >60% to avoid population declines predicted by the partial compensation model. Annual variation in demographic parameters offset the

impacts of highway mortality at high population levels. At low population levels, however, highway mortality was severe enough to drive declining population trends.

(92 pages)

DEDICATION

To my parents, Michael and Judith Lehnert; brother, Matthew; and sister, Sarah. Without your unconditional love, constant support, and timely encouragement, this endeavor would have meant very little to me.

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CHAPTER I

INTRODUCTION

Highway networks are continuously being upgraded and expanded to accommodate an increasing number of motorists in the United States (Federal Highway Administration 1995) and throughout the world (Groot Bruinderink and Hazebroek 1996). This expansion contributes to several problems facing wildlife populations, including habitat loss, landscape fragmentation, and direct mortality. Aside from habitat loss associated with construction of roadways and their associated clear zones, human development often accompanies paved access to new areas, leading to further habitat loss and increased human encounters with wildlife. Indirect habitat loss also occurs when animals instinctively avoid or are displaced from areas adjacent to roads. Ruediger (1996) suggested that mid-sized and large carnivores avoid using areas within 1 km and 3 km of highways in forested and open habitats, respectively. Highway avoidance behavior has also been documented in elk (Cervus canadensis) (Rost and Bailey 1979, Lyon 1983).

Highways often traverse critical habitat areas and movement corridors, causing extensive fragmentation of the landscape. Sufficiently large or busy highways may impede daily movements and form a barrier to dispersal. This may fragment populations into smaller units that experience greater demographic fluctuations and are more susceptible to local extinctions and inbreeding depression (Forman and Hersberger 1996). Efforts to maintain habitat connectivity by making roadways permeable to animal movements are important to maintain viable populations of many threatened and endangered species (Foster and Humphrey 1995, Boarman and Sazaki 1996, Noss et al. 1996).

The most noticeable impact of highways on wildlife is direct mortality resulting from collisions with automobiles. Animals displaying large home range sizes are particularly vulnerable to this disturbance as they are often forced to cross highways on a regular basis to secure necessary resources (Ruediger 1996). Migratory animal populations that travel great distances across landscapes bisected by roadways to access seasonal use areas are also at risk. In addition, some species may be attracted to the highway corridor by vegetation used to stabilize right-of-way soils and salt used in ice removal operations (Groot Bruinderink and Hazebroek 1996, Woods and Munro 1996).

The impact of roadway mortality on wildlife population dynamics is largely dependent upon the reproductive potential and rarity of the species. Collisions with vehicles have been cited as the leading cause of mortality and linked to population declines for Florida panthers (Felis concolor coryi) (Foster and Humphrey 1995, Forman and Hersberger 1996, Noss et al. 1996), Florida black bears (Ursus americanus floridana) (Forman and Hersberger 1996, Noss et al. 1996), and key deer (Odocoileus virginianus clavium) (Calvo and Silvy 1996, Forman and Hersberger 1996). Wolf (Canis lupus) and grizzly bear (U. arctos horribilis) populations south of the Canadian border may have also declined due to highway-related mortality (Forman and Hersberger 1996). More abundant species with higher reproductive potential may not be as vulnerable to population changes induced by highway mortality. The level of road-kill that these species can sustain, however, is poorly understood and largely ignored. Efforts to better understand the role highway mortality can play in shaping the dynamics of wildlife populations are needed as roadways and vehicles increasingly disrupt traditional habitats.

This study concentrated on the direct mortality of mule deer (O. hemionus) that resulted from the rerouting of highways associated with construction of the Jordanelle Reservoir in northeastern Utah. Prior to construction of the reservoir, 2 roads traversed the bottom of the Heber Valley and provided access to the surrounding communities of Kamas, Francis, and Heber City. Highway mortality along those roadways was estimated at 12 deer per year (Romin 1994). To accommodate the reservoir, portions of the 2 roads were closed and subsequently inundated. Three new highways were constructed at higher elevation to circumvent the reservoir and service the same communities. The new highways traversed areas of more active deer use and bisected seasonal migration corridors. Deer-vehicle collisions were expected to increase to 22 per year (Bureau of Reclamation 1979).

During the first year of new road operation, 174 deer were reported killed by vehicles in the study area (Romin 1994), prompting a two-phase investigation aimed ultimately at mitigating the unforeseen losses. Phase I was conducted from October 1991-October 1993 to accurately quantify the extent of roadway losses and identify areas of concentrated deer kill. Vegetative and topographic features were also analyzed with respect to deer-vehicle collision sites in order to better understand the factors influencing deer movements adjacent to and onto the highways. High kill areas were targeted as installation sites for newly designed highway crosswalks. The crosswalk system restricted deer crossings to specific, well-marked areas along the highways where motorists could anticipate them. Phase II, the focus of this thesis, evaluated the effectiveness of the experimental crossing structures at reducing vehicle collisions with deer while maintaining daily and seasonal deer movement patterns. In addition, I explored how highway losses have influenced the dynamics of the local mule deer population.

The following 2 chapters address those objectives. In chapter II, "Effectiveness of Highway Crosswalk Structures at Reducing Deer-Vehicle Collisions," I determined the efficacy of the crosswalk system and suggested design modifications that may increase its utility when further tested in other areas. In chapter III, "Modelling the impacts of highway mortality on a Utah mule deer population," I constructed and used computer simulation models to examine how highway losses may have altered the size and characteristics of the Jordanelle deer population. In addition, I explored how the population might respond to various reductions in highway mortality. The modelling exercise enabled me to identify certain levels of road-kill reduction that were required to produce desired changes in simulated population trajectories. Mitigative efforts could then target those levels of success. Together, chapters II and III discuss the success of the mitigative efforts at Jordanelle and illustrate what it means in terms of the dynamics of the local deer population.

LITERATURE CITED

Bureau of Reclamation. 1979. Central Utah Project, Bonneville Unit, Municipal and Industrial System, Final Environmental Statement, INT FES 79-55. Salt Lake City, Utah. 235 pp.

Boarman, W. I., and M. Sazaki. 1996. Highway mortality in desert tortoises and small vertebrates: success of barrier fences and culverts. Unpaginated in G. L. Evink, ed. Trends in addressing transportation related wildlife mortality: proceedings of the transportation related wildlife mortality seminar. FL-ER-58-96. Fla. Dep. Transp., Tallahassee.

Calvo, R. N., and N. J. Silvy. 1996. Key deer mortality: U. S. 1 in the Florida Keys. Unpaginated in G. L. Evink, ed. Trends in addressing transportation related wildlife mortality: proceedings of the transportation related wildlife mortality seminar. FL-ER-58-96. Fla. Dep. Transp., Tallahassee.

Federal Highway Administration. 1995. Our nation's highways: selected facts and figures. Publ. No. FHWA-PL-95-028. U. S. Dep. Transp. 48 pp.

Forman, R. T. T., and A. M. Hersberger. 1996. Road ecology and road density in different landscapes, with international planning and mitigation solutions. Unpaginated in G. L. Evink, ed. Trends in addressing transportation related wildlife mortality: proceedings of the transportation related wildlife mortality seminar. FL-ER-58-96. Fla. Dep. Transp., Tallahassee.

Foster, M. L., and S. R. Humphrey. 1995. Use of highway underpasses by Florida panthers and other wildlife. Wildl. Soc. Bull. 23:95-100.

Groot Bruinderink, G. W. T. A., and E. Hazebroek. 1996. Ungulate traffic collisions in Europe. Conserv. Biol. 10:1059-1067.

Lyon, L. J. 1983. Road density models describing habitat effectiveness for elk. J. Forestry 81:592-595.

Noss, R. F., H. B. Quigley, M. G. Hornocker, T. Merrill, and P. C. Paquet. 1996. Conservation biology and carnivore conservation in the Rocky Mountains. Conserv. Biol. 10:949-963.

Romin, L. A. 1994. Factors associated with the highway mortality of mule deer at Jordanelle Reservoir, Utah. M.S. Thesis, Utah State Univ., Logan. 83 pp.

Rost, G. R., and J. A. Bailey. 1979. Distribution of mule deer and elk in relation to roads. J. Wildl. Manage. 43:634-641.

Ruediger, B. 1996. The relationship between rare carnivores and highways. Unpaginated in G. L. Evink, ed. Trends in addressing transportation related wildlife mortality: proceedings of the transportation related wildlife mortality seminar. FL-ER-58-96. Fla. Dep. Transp., Tallahassee.

Woods, J. G., and R. H. Munro. 1996. Roads, rails, and the environment:

wildlife at the intersection in Canada's western mountains. Unpaginated in G. L. Evink, ed. Trends in addressing transportation related wildlife mortality: proceedings of the transportation related wildlife mortality seminar. FL-ER-58-96. Fla. Dep. Transp., Tallahassee.

CHAPTER II

EFFECTIVENESS OF HIGHWAY CROSSWALK STRUCTURES AT REDUCING DEER-VEHICLE COLLISIONS[1]

Abstract: I evaluated the effectiveness of a newly designed system of highway crosswalks at reducing mule deer (Odocoileus hemionus)-vehicle collisions along a two-lane and a divided four-lane highway in northeastern Utah. The crosswalk system forced deer to cross at specific, well-marked areas along the highways where motorists could anticipate them. Based on expected kill levels, mortality declined 42.3% and 36.8% along the four-lane and two-lane roads, respectively. I was unable to statistically demonstrate that observed mortality reductions were a direct result of the crosswalk system. Reduced deer use of the highway right-of-way (ROW) and observations of deer successfully crossing within crosswalk boundaries indicated that some aspects of the design served their intended purpose and may have contributed to the declines. The crosswalk system did not appear to disrupt seasonal deer movements to and from adjacent winter range. Lack of motorist response to crosswalk warning signs, the tendency for foraging deer to wander outside crosswalk boundaries, and the ineffectiveness of one-way ROW escape gates contributed to most treatment area mortalities. I offer design modifications that address these shortcomings, and may increase the utility of the approach.

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[1] Coauthored by Mark E. Lehnert and John A. Bissonette.

INTRODUCTION

Collisions between deer (Odocoileus spp.) and vehicles have become an increasing problem throughout the United States. Romin and Bissonette (1996a) estimated that at least 538,000 deer were killed along highways nationwide during 1991. This is a conservative estimate given that mortality data from several states were not available, and that many animals wander away and die undetected after being hit by a vehicle. As the nationwide network of highways continues to be upgraded and expanded (Federal Highway Administration 1995) through areas of active deer use, vehicle collisions with deer will likely increase.

The efficacy of various methods at reducing deer-highway mortality has been evaluated. Increased highway lighting was ineffective at curbing deer-vehicle accidents (Reed 1981a). Romin and Dalton (1992) found free-ranging mule deer (O. hemionus) exhibited similar behavioral responses to vehicles with and without ultrasonic warning whistles, implying they had no effect. Wood and Wolfe (1988) suggested that intercept feeding has potential to reduce deer-vehicle collisions by <50%. Tests regarding the effectiveness of Swareflex reflectors have yielded mixed results (Gladfelter 1984, Schafer and Penland 1985, Ford and Villa 1993, Reeve and Anderson 1993). The underlying assumption that deer instinctively avoid, or alter their behavior in response to the red light produced by the illuminated reflectors has been questioned (Zacks 1986, Waring et al. 1991). Properly constructed and maintained deer-proof fences can be an effective deterrent to deer trying to access roadside vegetation (Falk et al. 1978, Ludwig and Bremicker 1983, Feldhammer et al. 1986). Highway underpasses, used with deer-proof fences, have allowed animals to safely advance along habitat corridors bisected by roads (Reed et al. 1979, Ward 1982, Foster and Humphrey 1995). Deer, however, are reluctant to use relatively confining structures (Reed et al. 1975, Reed 1981b, Ward 1982), and have altered historic migration patterns to circumvent fences associated with inadequate underpasses (J. Williams, Nevada Div. Wildl., pers. commun.). High costs may preclude construction of sufficiently sized underpasses in many areas.

Further development and testing of potentially cost-effective mitigative techniques is warranted. My objective was to determine the effectiveness of a new system of highway crosswalks at reducing deer-vehicle collisions, while permitting daily and seasonal movements of the local mule deer population. The project was initiated when highways were realigned to accommodate construction of the Jordanelle Reservoir. A sixteen-fold increase in average annual deer-vehicle collisions occurred as a result. The crosswalk system was used because it could be installed easily along the existing roads at a fraction of the costs required to excavate tunnels and retrofit underpasses.

STUDY AREA

The study area was located in Summit and Wasatch counties, northeastern Utah. Elevations ranged from 1,890-2,380 m. The Jordanelle

Reservoir, located approximately 6 km southeast of Park City, was at the center of the study area. Three new highways were constructed in the area to replace preexisting roadways inundated by the reservoir. Portions of the recently built highways were used in our investigation: state route (SR) 248 from milepost (MP) 3.3 east to MP 13.5, SR 32 from MP 0.0 east to MP 9.6, and US 40 from MP 4.0 south to MP 13.1 (Fig. II-1). These roads provided direct access to the surrounding communities of Kamas, Francis, and Heber City.

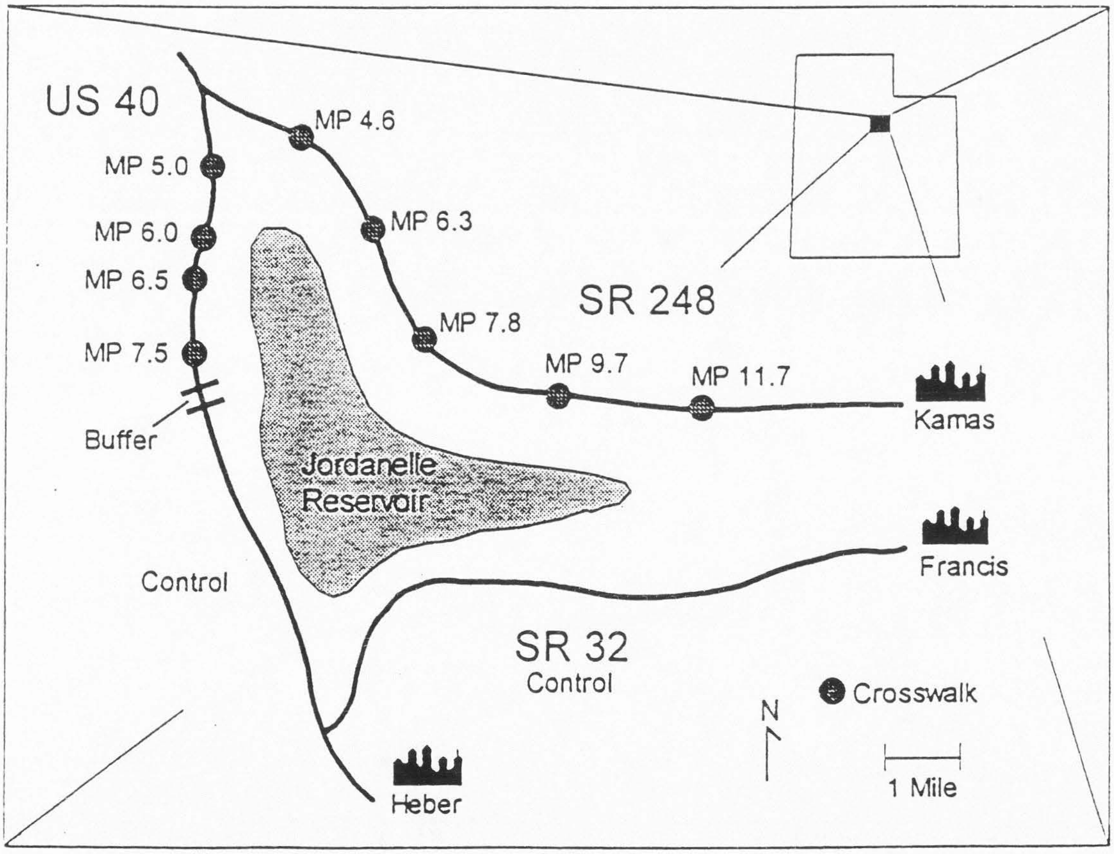


Fig. II-1. Milepost (MP) locations of crosswalk structures along experimental sections of study area roads surrounding the Jordanelle Reservoir, Utah, 1991-1995. Control sections are also illustrated.

Oakbrush (Quercus gambelii) clones and sagebrush (Artemisia spp.)-grass communities dominated the flora along the drainage slopes and foothill regions. Riparian communities, consisting predominantly of cottonwood (Populus angustifolia) trees and willow (Salix spp.) thickets, occupied the lower valley areas along the margins of the Provo River. Pastureland also was common throughout the lower valley regions.

Mule deer used resources in the study area throughout the spring, summer, and fall seasons, and remained there for the duration of the year contingent upon winter conditions. During milder winters, deer remained in the area and concentrated their activities on south-facing slopes. More severe winters forced deer into the lower valley areas where foraging resources were more accessible.

METHODS

Description of Crosswalk System

As with underpasses, animals using the crosswalk system were funneled with deer-proof fencing to designated areas where they were allowed to cross. However, instead of passing underneath the highway, deer travelled across the highway surface. The intention was to restrict the location of deer-crossings to specific, well-marked areas along the highways where motorists could anticipate them.

Right-of-ways (ROW) were fenced off with 2.3-m high fencing to direct

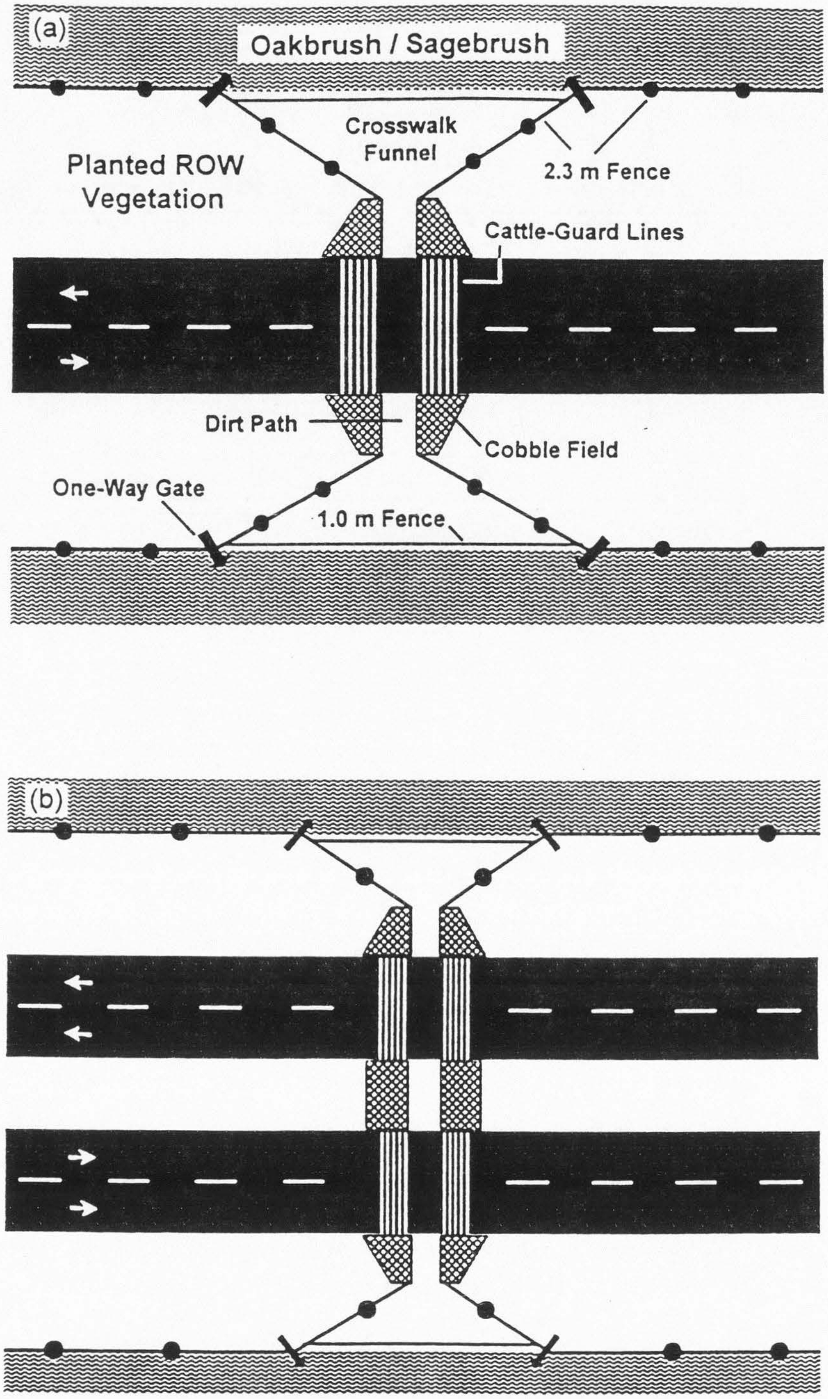


Fig. II-2. (a) Major features associated with the crosswalk system on a two-lane highway. Crosswalk features were the same on a (b) four-lane, divided highway, except the animal was required to negotiate 4 lanes of traffic and a median during its crossing attempt. The median path was demarcated by additional river cobbles. White arrows on the road surface indicate the direction vehicles were travelling.

the animals to the designated crosswalk zones (Fig. II-2). Upon arriving at these locations, deer were able to jump a 1.0-m high fence and enter the crosswalk funnel constructed of additional 2.3-m fencing. Once in the funnel, the animal could choose to forage on ROW vegetation, or continue to approach the road. The funnel fencing extended towards the highway and converged into a narrow opening 9.1 m from the highway surface. Federal highway regulations specified that a 9.1-m fence-free zone be maintained adjacent to the highway. Once through the narrow funnel opening, deer encountered 2 features associated with the crosswalks: a dirt path bordered on both sides by a field of rounded river cobbles (20 cm-30 cm dia.) and painted cattle-guard lines on the road surface. The path bordered by cobbles was used by deer as they continued to approach the road. Previous field observations have shown that cobbles were effective at deterring deer movements (L. Dalton, Utah Div. Wildl. Resour., pers. commun.). The painted lines were incorporated into the design to delineate crosswalk boundaries for oncoming motorists, and may have served as a visual cue to guide deer directly across the highway. Once across the road, the deer encountered another 9.1-m long dirt path demarcated by river cobbles, and a narrow fence opening allowing entry to the crosswalk funnel and distant habitat.

Vegetation in and along cobble paths was eliminated to discourage deer from remaining or congregating near the road surface. A series of 3 warning signs, spaced 152 m apart, was installed at each crosswalk to advise motorists travelling in either direction that they were entering a crossing zone. Four one-way gates at each crosswalk were intended to enable deer that became trapped along the highway corridor to escape the ROW.

Costs for materials and installation of each crosswalk, excluding ROW fencing and one-way gates, were estimated at $28,000 per structure on a four-lane, divided highway and $15,000 per structure on a two-lane highway. Excavating underpasses along already existing four-lane (5.49 m x 5.49 m x 42.67 m) and two-lane (4.57 m x 4.57 m x 27.43 m) roadways would cost approximately $173,000 and $92,000, respectively (B. Parker, Utah Dep. Transp., pers. commun.). Dimensions for the above structures meet the openness guidelines proposed by Reed et al. (1979).

To evaluate the system, I (1) monitored highway mortality levels in experimental and control areas before and after crosswalk installation, (2) used spotlight censuses to document deer use of the highway ROW and indirectly determine if the crosswalk system impeded seasonal deer migrations, (3) assessed deer behavior and movement patterns in crosswalk zones, (4) conducted speed assessments to evaluate motorist response to crosswalk warning signs, and (5) evaluated the efficacy of the one-way gates at enabling trapped deer to escape the ROW.

Road Mortality in Experimental and Control Areas

Highway mortality levels were monitored along study area roads for 3 years (Oct 1991-Sep 1994) prior to crosswalk installation. Construction of 5 crosswalks, with deer-proof fencing and one-way gates, was completed along SR 248 during September 1994. Fencing and 4 crosswalks were installed along the northern half of US 40 at the same time (Fig. II-1). Crosswalks were constructed in areas where deer kill tended to be most concentrated during the preinstallation phase of the study (Romin and Bissonette 1996b). State route 32 was designated as the corresponding control road (i.e., no fencing or crosswalks installed) for SR 248. Both roads are two-lane highways with occasional passing lanes on steep climbs. Highway US 40 was a four-lane, divided highway. The southern half was left unfenced to serve as the control for the test section to the north. A 0.64-km buffer separated the experimental and control sections of US 40. I documented highway mortality patterns along the 3 roads for an additional 15 months following crosswalk installation.

The experimental design enabled me to examine the usefulness of the crosswalks on SR 248 and US 40. Due to funding and logistical constraints, I had no replication of the 2 road types. Further, the control on US 40 was not strictly independent of the test section. As a result, I was limited in the statistical procedures I could use, and in the inferences I was able to draw.

I drove study routes $\geq$1 time/week to record the date and location to the nearest 161 m of deer killed by vehicles. Personnel from the state wildlife agency and a private contracting company assisted with road-kill data collection.

I conducted twice monthly spotlight censuses to monitor deer densities along study area roads. An assistant used a 400,000 candlepower, handheld spotlight to illuminate deer from a vehicle travelling 30-40 kph. Once deer were detected, I stopped the vehicle and used a 20x spotting scope to tally the animals. I also recorded whether deer were located on the highway ROW. I used rangefinder readings to estimate the observable area sampled during counts so densities could be computed.

I modified Reeve and Anderson's (1993) formula to calculate the expected number of deer killed in the experimental areas after installation of the crosswalks (K_{Eexp}). I explicitly accounted for differential changes in deer density between the treatment and control areas subsequent to crosswalk installation. I computed K_{Eexp} under the assumption that the crosswalk system had no influence on deer-vehicle collisions:

$$K_{Eexp} = [K_C(K'_E / K'_C)]\,[(N'_C / N_C)(N_E / N'_E)] \qquad (1)$$

where K_C = the number of deer killed in the control area after crosswalk installation, K'_E = the number of deer killed in the experimental area before crosswalk installation, K'_C = the number of deer killed in the control area before crosswalk installation, N'_C = the sum of seasonal deer densities recorded in the control area before crosswalk installation, N_C = the sum of seasonal deer densities recorded in the control area after crosswalk installation, N_E = the sum of seasonal deer densities recorded in the experimental area after crosswalk installation, and N'_E = the sum of seasonal densities recorded in the experimental area before crosswalk installation. I then quantified the percent change in highway mortality (Δ) that occurred after the system was in place:

$$\Delta = ((K_{Eobs} / K_{Eexp}) - 1)100\% \qquad (2)$$

where K_{Eobs} = the observed number of deer killed in the experimental area after crosswalk installation. Negative values of Δ indicate reductions in highway mortality. Each road type (two-lane versus four-lane) was analyzed separately.

Equations (1) and (2) were also used to quantify changes in the percentage of deer seen on the ROW during spotlight censuses before and after system installation.

I used paired comparison tests between mortality observed during the before and after crosswalk installation time periods to evaluate whether the crosswalk system reduced mortality. I used a randomization procedure (Manly 1991) to quantify the likelihood that observed reductions in mortality occurred by chance alone. Again, each road type was analyzed separately. I first computed the difference (Y_i) between the number of deer killed in the experimental and control area for each season of the study:

$$Y_i = X_{Ei} - X_{Ci} \qquad (3)$$

where X_{Ei} = the number of deer killed in the experimental area during season i, and X_{Ci} = the number of deer killed in the control area during season i. I then calculated the average Y_i for the time periods before (Y_{Bi}, $\underline{n}$ = 12) and after (Y_{Ai}, $\underline{n}$ = 5) crosswalk installation. Subtracting the after average from the before average yielded the test statistic (D_{Obs}).

I then randomly assigned 12 seasonal Y_i's to the before time period and the remaining 5 to the after time period. I computed average Y_i's for the before and after time frames using the randomly allocated data. Subtracting the before and after averages yielded a random difference (D_{Ran}). I repeated the process of shuffling the data and calculating a D_{Ran} value 5,000 times to generate a distribution of random differences. The percentage of randomizations that produced a D_{Ran} greater than or equal to D_{Obs} was the probability that observed reductions in highway mortality occurred by chance alone (i.e., the p-value for the test). I used the RT software program to conduct the analysis (Western EcoSystems Technology, Inc. 1991).

Deer Behavior in the Crosswalks

I used night-vision goggles to observe deer behavior and movements in crosswalk areas during evening time periods. I used a wooden blind in areas that offered a clear view of the crosswalk and provided adequate cover for camouflage. When such conditions were absent, I conducted observations from a vehicle parked along the highway shoulder. I blocked out vehicle windows so the observer could not be seen from the outside. Observation times were dependent upon weather conditions and lunar phases, because relatively clear skies with sufficient moonlight were required for effective operation of night-vision equipment.

I compared deer behavior in the crosswalk areas to behavior observed along control roads to evaluate if the system altered roadside behavior. I used observations in control areas as an index of how deer behaved in experimental areas prior to installation of the crosswalk system. I limited observations along the control roads to high kill zones, because crosswalks were installed in similar areas along the experimental roads. Eight crosswalks were selected for this analysis; 4 along both two-lane SR 248 and four-lane, divided US 40. Four control sites were selected along each of the corresponding control roads to make the comparisons.

Variables quantified included major activity observed on the ROW, length of time spent on the ROW, and tendency for foraging deer to step onto the road. Activity was categorized as either foraging or traveling. Travelling animals did not forage while on the ROW. I also evaluated whether river cobbles and cattle-guard striping were effective at restricting deer movements to the designated crossing areas. I made comparisons of dominant activity in the crosswalk and control regions using a two-tailed Fisher exact test. I used a one-tailed Fisher exact test to test for differences in the proportion of deer that stepped onto the roadway while foraging. I estimated power for Fisher's exact test when sample sizes were small (Zar 1984). I used a one-way analysis of variance (ANOVA) with subsamples to test for differences in the length of time that foraging deer spent on the ROW in the crosswalk and control areas. Because of unequal subsamples, I computed the $\underline{F}$-test for the treatment effect using Sattherwaite's approximation (Ostle and Malone 1988). I analyzed each road type separately.

Deer Use of One-Way Escape Gates

I constructed earthen track beds at 12 randomly selected one-way gates to determine gate effectiveness. I analyzed tracks and cleared the beds ≥1 time/week over the study period. Track bed analysis was discontinued from January through March 1995 because most deer had migrated to winter ranges.

When analyzing track beds, I recorded the number of approaches and passages, as well as approaches and passages in the wrong direction. I defined gate effectiveness in terms of the percentage of approaching animals that passed through the gates, and the gate's ability to prevent passages in the wrong direction, also expressed as a percentage.

Motorist Response to Warning Signs

I assessed motorist response to crosswalk warning signs by measuring vehicle speed. Personnel from the state transportation department conducted speed assessments in accordance with the design I specified. I focused the analysis between the hours of 2100-0500. During this period visibility was reduced and speed reductions were more essential to avoid a deer-vehicle collision.

I evaluated 4 crosswalks along both SR 248 and US 40. Each crosswalk was paired with a location in the corresponding control area similar in road topography (e.g., hills and curves). In the crosswalks, I measured average vehicle speed at warning signs located 304.8 m before the crosswalk and at the crossing site itself. In the corresponding control areas, I measured speed at 2 points located 304.8 m apart. I conducted speed assessments simultaneously on each of the 8 paired sites, thereby blocking the design to reduce variability due to differing weather conditions on different nights. Using an ANOVA for a randomized block design, I tested the null hypothesis that speed changes observed in the crosswalk areas were equal to speed changes seen in the control areas.

RESULTS

Road Mortality in Experimental and Control Areas

During the 3 years prior to installation of fencing and crosswalks, 148 and 123 deer were killed in what were to become the experimental and control sections of US 40, respectively. During the 15 months that the crosswalk system was in place, 63 deer were killed in the control area. Expected kill level in the experimental area (K_{Eexp}) was 79.7 animals. An observed kill of 46 deer suggested a 42.3% reduction in highway mortality (Δ) since implementing of the crosswalk system. The majority (59.1%) of these deer were killed outside crosswalk boundaries.

Randomization results revealed that the observed reduction in mortality along US 40 could not be attributed to effectiveness of the crosswalk system ($D_{Obs} = 5.4$, $\underline{P} = 0.112$). There was an 11.2% chance the reduction occurred by chance alone.

Mortality totalled 111 and 75 deer along experimental SR 248 and control

SR 32, respectively, during the 3 years prior to mitigative efforts. Thirty-four deer were killed along SR 32 during the 15 months that the crosswalks and fencing were in place along SR 248. Expected kill level along SR 248 (K_{Eexp}) was 57.0 deer. An observed kill of 36 deer suggested a 36.8% reduction in highway mortality (Δ) since installing the crosswalk system. The majority (75.0%) of these deer were killed outside crosswalk boundaries.

Randomization results indicated that the observed reduction in mortality along SR 248 could not be attributed to effectiveness of the crosswalk system (D_{Obs} = 2.6, P = 0.198). There was a 19.8% chance the reduction occurred by chance alone.

Deer Behavior in the Crosswalks

Dominant Activity in Crosswalk and Control Areas.—The fencing and crosswalks did not appear to reduce the tendency for deer to use the ROW for foraging. The proportion of deer observed foraging was not significantly different between the crosswalk and control sites along the two-lane roads (P = 0.104) nor for comparisons along the four-lane, divided highway (P = 0.387). Small sample sizes along US 40, however, may have prevented me from detecting a significant difference (power = 0.246). In this case, 50% (n = 10) of the deer entered the crosswalks to forage, compared to 72.7% (n = 11) that foraged in the control sites.

Tendency for Foraging Deer to Walk on Highway.—While foraging on the ROW, deer in the crosswalk areas were more likely to walk onto the road surface than deer in the control sites. This relationship was highly significant for the two-lane road comparisons ($\underline{P}$ = 0.004). Small sample sizes, however, may have prevented me from detecting similar statistical differences along US 40 ($\underline{P}$ = 0.086, power = 0.637). In this case, 80% ($\underline{n}$ = 5) of deer foraging in crosswalk zones walked onto the road, whereas only 25% ($\underline{n}$ = 8) did so while foraging in the control areas. Deer foraging in the crosswalk areas would typically walk onto the road to circumvent the river cobbles and gain access to resources within the ROW.

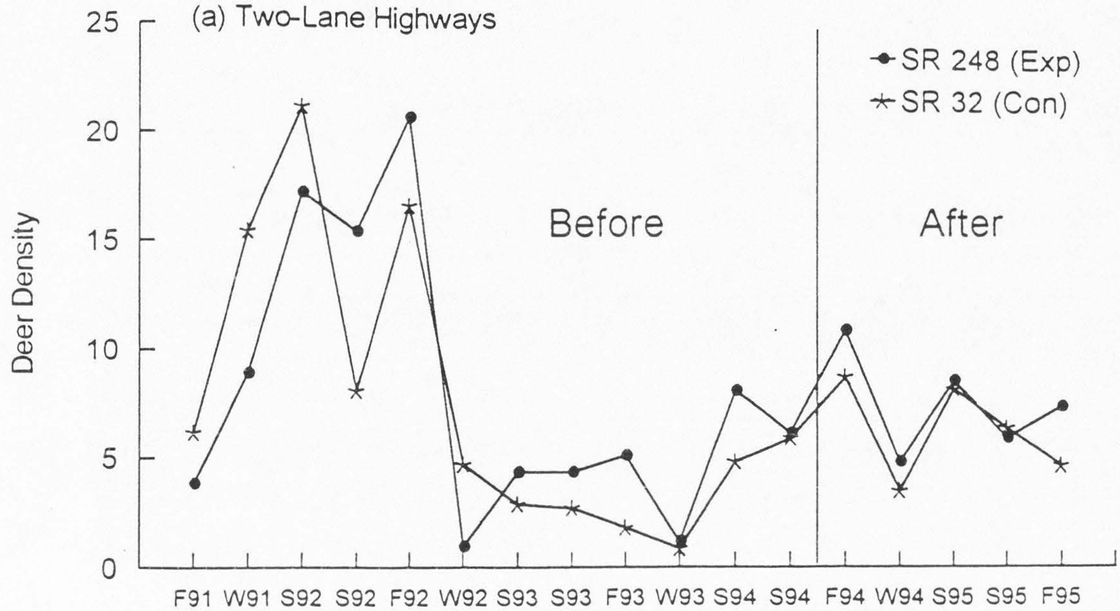
Time Spent Foraging on the Highway ROW.—Deer in crosswalk zones along SR 248 spent significantly more time foraging on the ROW than deer foraging in control sites along SR 32 ($\underline{F}$ = 6.23; 1,6.98 df; $\underline{P}$ = 0.041). Average time spent foraging on the SR 248 ROW was 66.2 minutes (SE = 8.9, $\underline{n}$ = 13). The majority (76.5%) of this time was spent outside the funnel along the highway corridor. Foraging bouts averaged 22.1 minutes (SE = 5.2, $\underline{n}$ = 9) on the ROW in the SR 32 control sites. Along US 40 I failed to reject the null hypothesis that crosswalk area deer foraged for the same amount of time as deer in the control sites ($\underline{F}$ = 0.0002; 1,4.21 df; $\underline{P}$ = 0.989). Mean foraging times of 26.5 minutes (SE = 7.9, $\underline{n}$ = 4) and 32.0 minutes (SE = 6.3, $\underline{n}$ = 5) were documented for deer on the ROW in crosswalk and control zones, respectively. The majority (74.5%) of the time spent foraging in the experimental section of US 40 took place outside the crosswalk funnels. Vegetation available in the crosswalk funnels did not appear adequate.

Crossing Attempts in SR 40 and SR 248 Crosswalks.—I documented 9 instances where deer entered the crosswalks to attempt a road crossing; 6 along US 40 and 3 along SR 248. The first 3 attempts occurred within 2 months after crosswalks were completed. All 3 deer wandered outside the confines of the crosswalk and became trapped in between the 2.3-m high fencing. Over time, however, deer apparently became familiar with the crosswalk design. The subsequent 6 attempts involved animals that travelled within the boundaries of the river cobbles and cattle-guard stripes. Two of these animals, however, were hit by vehicles along US 40 during their crossing attempt. Overall, deer travelled faster on the highway while crossing in US 40 crosswalks (2.28 m/sec) compared to crossings made in SR 248 crosswalks (0.99 m/sec).

Spotlight Census Data

Eighty-two spotlight censuses were conducted during the study—53 prior to crosswalk installation and 29 during the 15 months that the crosswalks were in place. Seasonal deer densities observed along the experimental and control regions of each road type tracked each other closely over the course of the study (Fig. II-3). The close association between experimental and control area densities suggests that deer movements to and from adjacent winter range were not impeded by fencing associated with the crossing system.

I used spotlight data to determine the percentage of deer observed on the ROW in the experimental and control areas before and after installation of



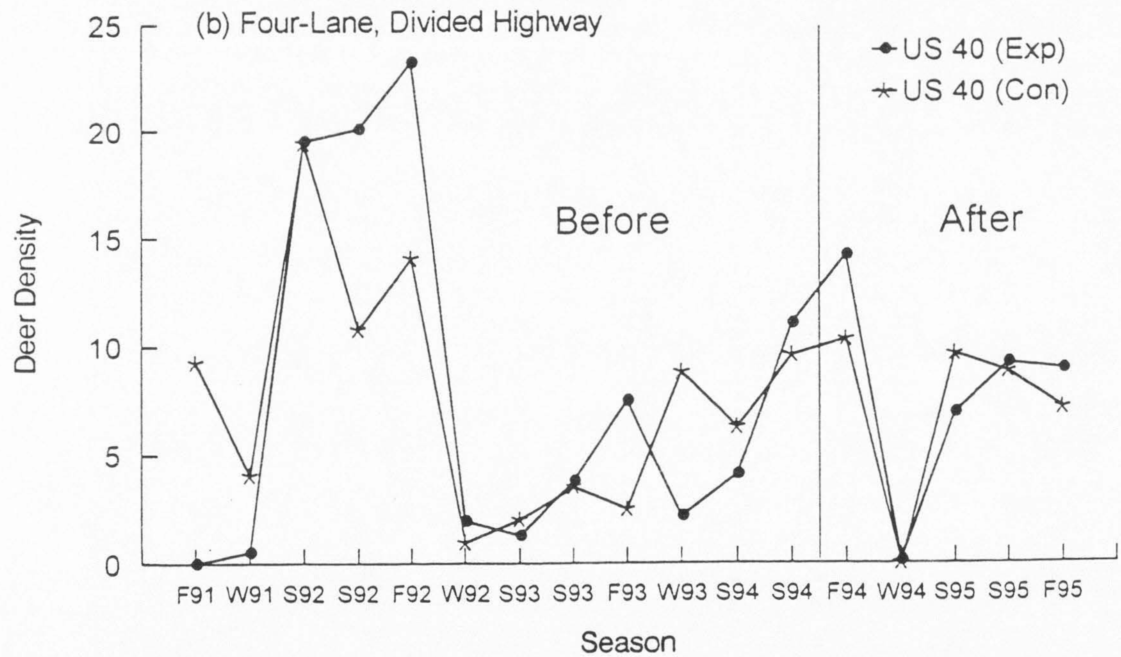


Fig. II-3. Seasonal deer densities (deer/km^2) calculated from spotlight censuses in the experimental and control areas of the (a) two-lane and (b) four-lane, divided highways at Jordanelle Reservoir, Utah, 1991-1995.

the crosswalks and fencing. Based on expected experimental area percentages, I documented a 54.6% and 34.1% reduction (Δ) in deer use of the ROW along US 40 and SR 248, respectively. A considerable number of deer were still accessing the ROW by wandering outside crosswalk boundaries and exploiting fence defects along both road types.

Deer Use of One-Way Escape Gates

I analyzed each of the 12 track beds 82 times over the study period. I recorded 243 instances where deer approached the gates while trapped on the ROW. Forty (16.5%) of these animals proceeded to jump through the gate to escape the ROW. The remaining 203 deer were forced to find alternative means of escape. None of the 128 deer that approached the gates from the wrong direction passed through the tines to access the ROW.

Motorist Response to Warning Signs

Motorists did not exhibit speed reductions while travelling through the crosswalk zones. Observed changes in vehicle speed were not different from changes observed in paired sites along the control roads (F = 0.151; 1,7 df; P = 0.738). Direct visual observations indicated that motorists (n = 1,683) were more likely to turn on their high-beam lights (1.84%) while approaching the crosswalks rather than apply the brakes (0.59%). However, the majority (95.42%) of observed motorists exhibited no response of any observable type to crosswalk warning signs.

DISCUSSION

Mortality Reductions

Although I was unable to statistically demonstrate that observed mortality reductions were a direct result of mitigative efforts, I believe that some aspects of the crosswalk system worked as intended and contributed to this decline. Building upon these successes and redesigning those aspects of the system that failed may improve the utility of this technique.

The river cobbles and cattle-guard stripes appeared to be effective at guiding deer movements when they entered the crosswalks to attempt a crossing. Deer that entered the crosswalks to forage, however, frequently walked onto the road and wandered outside crosswalk boundaries in search of abundant roadside vegetation. This behavior was conducive to increased vehicle encounters with deer when compared to control area foraging patterns. The 2.3-m high fencing reduced overall deer use of the highway ROW by 42%, possibly compensating for the undesired foraging behavior that predisposed individual deer to vehicle traffic. Further reductions in deer use of ROW resources may further reduce highway losses.

Despite heavier traffic volumes, higher vehicle speeds, and nearly twice the distance to negotiate while crossing, the mortality reduction along US 40 was greater than the SR 248 reduction. Foraging activity within the ROW appeared to decline along the US 40 treatment area subsequent to crosswalk installation. This pattern was not apparent along SR 248 relative to behavioral observations along the corresponding control road. Reduced foraging along US 40 was also reflected in the greater reduction in deer observed on the ROW during spotlight censuses. Along SR 248, the observed reduction in ROW deer may have been partially offset by the increased foraging times displayed by the animals that managed to access it. Fewer and shorter foraging bouts outside crosswalk boundaries and quicker highway crossing times within the boundaries characterized deer behavior in US 40 crosswalks, and may explain the greater mortality reduction. Efforts to improve the design of the crosswalk system should target these components of deer behavior.

In terms of absolute numbers, 54 deer-vehicle collisions were avoided over the 15-month posttreatment period. Ignoring the human injuries and fatalities that may have occurred, this amounted to a $135,700 savings in lost wildlife resources and vehicle damage (Romin and Bissonette 1996a). At the current mortality reduction rates, the $812,565 spent for materials and installation of the 9 crosswalks, as well as 42 km of 2.3-m high fencing and 36 one-way gates, will be amortized within 6 years.

Recommendations for Improvement

Most deer-vehicle collisions in the treatment areas were attributed to lack of motorist response to crosswalk warning signs, the tendency for foraging deer to wander outside crosswalk boundaries in search of roadside vegetation, and the ineffectiveness of one-way gates at enabling deer to escape the ROW. These shortcomings must be addressed to increase the utility of the system.

Even though warning signs explicitly warned of the crosswalk, and indicated the distance to it, many drivers may have mistaken them for typical game-crossing signs to which motorists pay little attention (Reed 1993, Williams 1964). Flashing lights, triggered by deer entering the crossing zones, could be attached to crosswalk signs, and may help distinguish them from traditional warning signs. The use of pavement "rumble strips" and cautionary speed limit signs may also help draw attention to the crosswalk location. Because the increased success of this mitigative approach is heavily dependent upon motorists reducing vehicle speed in designated crossing zones, future testing of the crosswalk system should be reserved for relatively low-speed, low-volume highways that service local residents who would encounter deer in crosswalks frequently enough to recognize the need to slow down. Although mortality reductions along US 40 were more pronounced, I feel that further gains in effectiveness are limited by the heavy traffic volume and high speeds associated with this divided four-lane highway.

The crosswalks were designed so that desired ROW forage would be available to animals in the crosswalk funnel. Most foraging animals, however, quickly left the funnel and circumvented the cobbles by means of the road surface to access more abundant resources along the ROW. Comparison of this behavior to patterns displayed by animals foraging in the control areas indicated that the crosswalk design may have increased the percentage of foraging deer that walk onto the road. Once on the ROW, the animals were trapped in between the 2.3-m high fencing and could wander along the highway corridor and attempt to cross in areas where motorists were not expecting them. Because most deer were killed outside the designated crossing zones, this behavior likely led to most treatment area mortalities.

Strategic fence placement may reduce the inclination for animals to use crosswalks as a means of accessing vegetation along the ROW (Fig. II-4). Currently, the 2.3-m high fence lies as far as 100 m from the highway surface, and forms a barrier at the interface between the ROW resources deer are attracted to and the oakbrush and sagebrush communities characteristic of the area (Fig. II-2a). If 2.3-m high fencing was positioned closer to the highway,

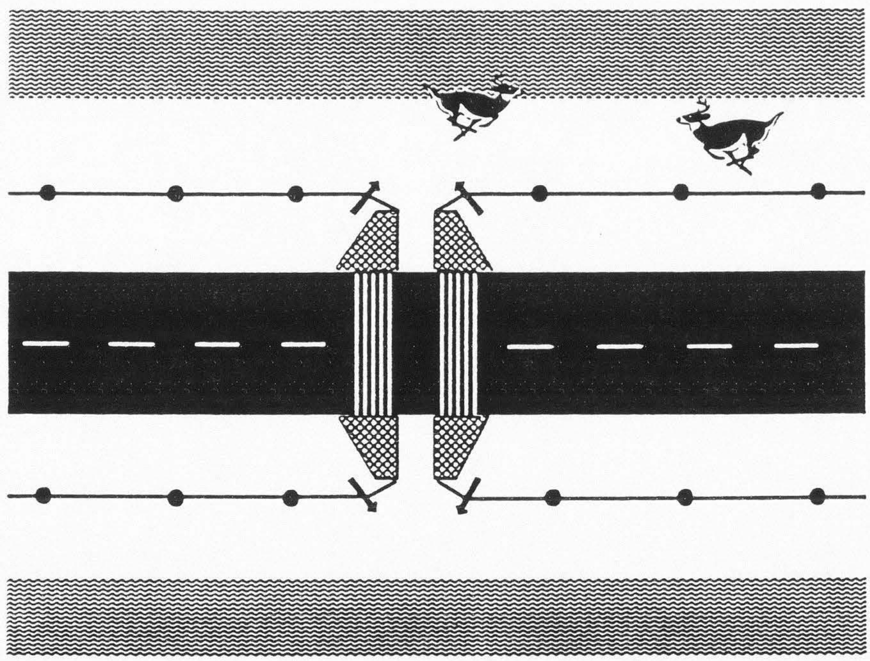


Fig. II-4. Proposed modification in placement of the 2.3-m high fenceline intended to make desired right-of-way vegetation available to animals on the non-highway side of the fence. Original fence position is illustrated in Fig. II-2.

then desired ROW vegetation would be available to deer on the non-highway side of the fence. Repositioning the ROW fenceline for a few hundred meters on each side of the crosswalk may be sufficient, but should be tested. Replacing vegetation that remains on the highway side of the fence with a less palatable species may further reduce the tendency for deer to wander outside the crosswalk boundaries in search of forage.

Unlike results from a previous study (Reed et al. 1974), track bed analysis indicated that deer were reluctant to use the one-way gates they encountered. Many animals remained on the ROW for extended periods of time until they found an alternative means of escape. An alternative would be to incorporate the use of earthen or other type ramps that lead to the top of the fence and allow deer to jump to the safety of the other side. Earthen ramps are used successfully in Wyoming (H. Harju, Wyoming Game and Fish, pers. commun.).

CONCLUSION

This study represents the initial implementation and testing of the crosswalk system. High costs associated with the project precluded the spatial replication that most statistical tests require. As a result, I had limited ability to determine whether observed mortality reductions were driven by mitigative efforts. The potential applicability of the crosswalk system, however, should not be dismissed. Reduced deer use of the highway ROW, the apparent maintenance of migratory behavior, and observations of travelling animals remaining within crosswalk boundaries indicate that the system warrants further testing. This study served as a baseline analysis to identify shortcomings in the design so improvements can be made. The crosswalk system should be tested in multiple settings before the upper limits of success and its applicability for widespread use, or lack thereof, can be defined. Given that high construction costs often preclude the use of underpasses in many areas, further investigations into crosswalks as a less costly alternative are warranted. However, because complete reductions in mortality are unlikely with this technique, crosswalks should only be used when the cost of underpasses or overpasses is too high.

Other researchers are likely to face the same statistical challenges when testing modified versions of the crosswalk system. Carefully designed studies within the context of the larger project, however, can reveal if design modifications produce desired changes in deer behavior and motorist response patterns. These smaller scale behavioral analyses enabled me to identify deficiencies in the original system. This information is essential to ensure that time and money are not wasted in future efforts.

LITERATURE CITED

Falk, N. W., H. B. Graves, and E. D. Bellis. 1978. Highway right-of-way fences as deer deterrents. J. Wildl. Manage. 42:646-650.

Federal Highway Administration. 1995. Our nation's highways: selected facts and figures. Publ. No. FHWA-PL-95-028. U. S. Dep. Transp. 48 pp.

Feldhammer, G. A., J. E. Gates, D. M. Harman, A. J. Loranger, and K. R. Dixon. 1986. Effects of interstate highway fencing on white-tailed deer activity. J. Wildl. Manage. 50:497-503.

Ford, S. G., and S. L. Villa. 1993. Reflector use and the effect they have on the number of mule deer killed on California highways. Rep. No. FHWA/CA/PD-94/01. Calif. Dep. Transp., Sacramento. 12 pp.

Foster, M. L., and S. R. Humphrey. 1995. Use of highway underpasses by Florida panthers and other wildlife. Wildl. Soc. Bull. 23:95-100.

Gladfelter, L. 1984. Effect of wildlife highway warning reflectors on deer-vehicle accidents. Iowa Highway Res. Board Proj. HR-210. Iowa Dep. Transp. 11 pp.

Ludwig, J., and T. Bremicker. 1983. Evaluation of 2.4-m fences and one-way gates for reducing deer-vehicle collisions in Minnesota. Transp. Res. Rec. 913:19-22.

Manly, B. F. J. 1991. Randomization and Monte Carlo methods in biology. Chapman and Hall, London. 281 pp.

Ostle, B., and L. C. Malone. 1988. Statistics in research: basic concepts and techniques for research workers. Iowa State Univ. Press, Ames. 664 pp.

Reed, D. F. 1981a. Effectiveness of highway lighting in reducing deer-vehicle collisions. J. Wildl. Manage. 45:721-726.

_____. 1981b. Mule deer behavior at a highway underpass exit. J. Wildl. Manage. 45:542-543.

_____. 1993. Efficacy of methods advocated to reduce cervid-vehicle accidents: research and rationale in North America. Colo. Div. Wildl. Resour., Fort Collins. 13 pp.

_____, T. M. Pojar, and T. N. Woodard. 1974. Use of one-way gates by mule deer. J. Wildl. Manage. 38:9-15.

_____, T. N. Woodard, and T. M. Pojar. 1975. Behavioral response of mule deer to a highway underpass. J. Wildl. Manage. 39:361-367.

_____, _____, and T. D. I. Beck. 1979. Regional deer-vehicle accident research. Rep. No. FHWA/CO/RD-79/11. Colo. Div. Wildl. Resour., Denver. 61 pp.

Reeve, A. F., and S. H. Anderson. 1993. Ineffectiveness of Swareflex reflectors at reducing deer-vehicle collisions. Wildl. Soc. Bull. 21:127-132.

Romin, L. A., and J. A. Bissonette. 1996a. Deer-vehicle collisions: status of state monitoring activities and mitigation efforts. Wildl. Soc. Bull. 24:276-283.

_____, _____. 1996b. Temporal and spatial distribution of highway mortality of mule deer on newly constructed roads at Jordanelle Reservoir, Utah. Great Basin Nat. 56:1-11.

_____, and L. B. Dalton. 1992. Lack of response by mule deer to wildlife warning whistles. Wildl. Soc. Bull. 20:382-384.

Schafer, J. A., and S. T. Penland. 1985. Effectiveness of Swareflex reflectors in reducing deer-vehicle accidents. J. Wildl. Manage. 49:774-776.

Ward, A. L. 1982. Mule deer behavior in relation to fencing and underpasses on Interstate 80 in Wyoming. Transp. Res. Rec. 859:8-13.

Waring, G. H., J. L. Griffis, and M. E. Vaughn. 1991. White-tailed deer roadside behavior, wildlife warning reflectors, and highway mortality. Applied Animal Behaviour Science. 29:215-223.

Western EcoSystems Technology, Inc. 1991. RT: a program for randomization testing. Version 1.02. Cheyenne, Wyo. 17 pp.

Williams, J. E. 1964. Deer, death and destruction. Colo. Outdoors 13:1-3.

Wood, P., and M. L. Wolfe. 1988. Intercept feeding as a means of reducing deer-vehicle collisions. Wildl. Soc. Bull. 16:376-380.

Zacks, J. L. 1986. Do white-tailed deer avoid red? An evaluation of the premise underlying the design of Swareflex wildlife reflectors. Transp. Res. Rec. 1075:35-43.

Zar, J. H. 1984. Biostatistical analysis. Prentice-Hall, Englewood Cliffs, N.J. 718 pp.

CHAPTER III

MODELLING THE IMPACTS OF HIGHWAY MORTALITY ON A UTAH MULE DEER POPULATION[2]

Abstract: A four-year field study was conducted to define the characteristics of mule deer (Odocoileus hemionus) mortality along highways surrounding the Jordanelle Reservoir in northeastern Utah. Highway mortality rates were inversely density-dependent, removed between 5.6% and 17.4% of the population each year, and had a disproportionate impact on male animals. I incorporated this information into 3 competing simulation models and used them to investigate how highway mortality has impacted the local mule deer population. The models differed mechanistically in terms of whether highway losses were incorporated in a strictly additive, partially compensatory, or strictly compensatory manner. The partial compensation model most closely tracked the observed dynamics of the population, suggesting that not all highway losses were offset by reductions in other sources of mortality. Highway mortality appeared to have accentuated the population crash initiated by severe 1992-1993 winter conditions, and may be slowing the subsequent recovery. The disproportionate kill of bucks along the highways altered sex ratios of simulated populations. A 60% reduction in highway mortality was necessary to halt the population decline predicted by the partial compensation model. Monte Carlo

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[2] Coauthored by Mark E. Lehnert, John A. Bissonette, and James W. Haefner.

error analysis, however, revealed that mitigative efforts should target higher levels of reduction to ensure that desired population responses occur. Annual variation in demographic parameters caused by environmental stochasticity was able to offset the impacts of highway mortality when simulated populations were relatively high. At low population levels, however, highway mortality rates were severe enough to drive declining trends in the population. This study demonstrated that highway mortality can significantly alter long-term population trends and characteristics. Highway losses should be incorporated into management plans for populations prone to vehicle traffic.

INTRODUCTION

Deer (Odocoileus spp.)-vehicle collisions are commonly expressed in terms of animals killed annually (Carbaugh et al. 1975, Allen and McCullough 1976, Romin and Bissonette 1996a), human injuries and fatalities (Mansfield and Miller 1975, Allen and McCullough 1976, Sicuranza 1979, Hansen 1983), and costs associated with automobile damage (Pils and Martin 1979, Hansen 1983, Decker et al. 1990, Witmer and deCalesta 1992, Romin and Bissonette 1996a). The long-term consequence of these encounters on the dynamics of local deer populations, however, is largely unknown. Although highway losses are the second most common source of deer mortality observed by wildlife personnel (Reed 1981), many state natural resource agencies have not kept consistent records of these encounters (Romin and Bissonette 1996b). Knowledge of how this often overlooked mortality source can influence population trends and characteristics may aid in long-term forecasting and provide insight for deer management decisions.

Highway mortality levels increased dramatically in northeastern Utah when roadways were realigned to accommodate construction of the Jordanelle Reservoir. Deer-vehicle collisions rose from an estimated 12 per year to as high as 278 recorded in a single year. Accurately assessing the impacts of this increased level of mortality depends largely on knowing whether it is additive or compensatory. In other words, will increases in highway mortality be offset by decreases in another source of mortality? The idea of compensatory mortality was first introduced by Errington (1945, 1946) while studying northern bobwhite quail (Colinus virginianus) and muskrats (Ondatra zibethicus). Specifically, Errington (1946, p. 235) stated:

> [W]e may see that a great deal of predation is without truly depressive influence. In the sense that victims of one agency simply miss becoming victims of another, many types of loss--including loss from predation--are at least partly intercompensatory in net population effect.

This concept ultimately served as the underlying premise for most recreational deer hunting. The extent to which harvest removals can trigger reductions in other mortality sources, however, has been questioned (Connolly 1981a, Caughley 1985).

Determination of how mortality factors interact within a population demands a controlled experiment where mortality rates from various sources can be manipulated individually and measured accurately. The type of interaction observed over 1 range of densities, however, is likely to change as population size fluctuates. Because density-dependence is the primary mechanism driving compensatory responses (Bartmann et al. 1992), detection of density-dependent mortality sources indicates that compensation can occur. Fluctuating environmental conditions, however, can overpower the influence of these regulating mechanisms and prevent their detection in free-ranging populations. Without knowledge of how mortality sources interact, it is difficult to predict the impacts of an increasing mortality agent. Modelling offers a unique opportunity to incorporate highway losses under various scenarios and explore the consequences on population dynamics. The scenario that most closely tracks observed population dynamics may provide insight into real-world mechanisms, although empirical studies are needed to confirm them.

I used computer simulation models to explore how highway mortality rates characteristic of the Jordanelle area could influence mule deer (O. hemionus) population dynamics. My goal was not to make absolute quantitative predictions, but rather to explore how highway mortality can alter trends in projected population trajectories. The models provided insight regarding the potential consequences of highway losses under additive and compensatory frameworks, and enabled me to address 3 specific questions: (1) How has highway mortality altered the size and characteristics of the Jordanelle deer population?; (2) how might the Jordanelle population respond to reductions in highway mortality?; and (3) can the stochastic nature of the environment and the variability it creates in reproduction and mortality dampen the impacts of highway mortality, or is highway mortality sufficiently high to drive patterns in the Jordanelle population? Many changes that result from increases in a mortality source may take several years to manifest themselves. The modelling approach enabled me to examine some of those long-term changes.

STUDY AREA

The study area was located approximately 6 km southeast of Park City in northeastern Utah. The Jordanelle Reservoir, located at the center of the study area, captured water flowing out of the Uinta mountains via the Provo River for subsequent municipal use. I collected data along portions of 3 roads surrounding the Jordanelle Reservoir: state route (SR) 248 from milepost (MP) 3.3 east to MP 13.5, SR 32 from MP 0.0 east to MP 9.6, and US 40 from MP 4.0 south to MP 13.1. Construction of these highways was completed in 1989 to service the surrounding communities of Kamas, Francis, and Heber City. Preexisting roadways were subsequently inundated by the reservoir.

Mule deer inhabited the area and were killed along the highways throughout the year. Heavy snows, however, pushed most animals onto adjacent winter ranges. State route 32 ran adjacent to an active wintering area.

METHODS

Overall Approach

A field study was conducted from October 1991-November 1995 to define the characteristics of highway mortality in the Jordanelle area. In particular, I determined whether highway mortality rates varied in relation to deer density and analyzed for differential impacts on bucks, does, and fawns. I incorporated this information into 3 competing simulation models constructed using the C programming language. The models differed mechanistically in terms of whether highway losses were incorporated in a strictly additive, partially compensatory, or strictly compensatory manner. The models provided insight into the impacts of highway losses under the 3 mortality scenarios. I selected the model that most closely tracked the observed dynamics of the Jordanelle population to address my questions of interest.

Defining and Monitoring the Jordanelle Deer Population

I defined the Jordanelle deer population to include deer that might encounter or cross the roads while travelling through their home range. Only deer occupying home ranges adjacent to or bisected by the roadways were considered in my estimate of the population. I did not radio collar deer, but as an approximation I used a circular home range with a 1.6-km diameter to determine the amount of land under consideration adjacent to the 3 study area roads. This was representative of female winter and spring home range sizes observed in other areas (Dickinson and Garner 1980, Kufeld et al. 1988). I used densities observed during spotlight censuses to estimate the total number of deer in that area at a particular time. I conducted the counts twice monthly over the course of the field study to document trends in the size and sex ratios of the population.

I determined the proportion of bucks, does, and fawns in the initial population used in model simulations from posthunt (Nov-Dec) spotlight classifications. I based the percentage of yearling males and females in the initial population on data from other studies. I did not use the age structure of road-killed animals to estimate these percentages because yearling animals may be disproportionately represented in roadway losses as a result of dispersal-related behavior and movement patterns (Putman 1988).

Model Structure and Assumptions

The models were deterministic in nature, and consisted of finite difference equations that operated on a one-year time step to calculate the values of the state variables. The state variables included the number of fawns, yearling males and females, and adult males and females present in the June population prior to the fawning season. Fawns at this time were about to become yearlings and yearlings were about to become adults. Inputs to the state variables were in the form of newly born fawns or survival of animals into the next age class. Losses were caused by highway mortality and non-highway mortality agents. Equations used to monitor changes in the state variables are presented in the appendix at the end of the chapter.

Each simulation time step began with parturition and ended immediately before parturition the following year. After yearling and adult females dropped their fawns, all animals advanced to the next age class. I then removed a percentage of each sex and age category from the population according to rates specified for annual highway and non-highway-related mortality. Non-highway mortality rates included the contributions of all mortality agents impacting the population (predation, hunting, disease, winter kill, old age, etc.), except highway losses. Once the removals occurred, the number of animals remaining in each sex and age class was stored for subsequent analysis. The cycle was repeated for the desired number of time steps.

I assumed that emigration and immigration events balanced over time and did not incorporate them into the models. This assumption may hold for yearling males, but is likely to fail when yearling females are considered (Hamlin and Mackie 1989). Current knowledge of dispersal mechanisms is based largely on theoretical models that lack empirical validation (Johnson and Gaines 1990), making prediction and accurate incorporation into modelling exercises difficult.

I implicitly incorporated density-dependent mechanisms into non-highway mortality rates of the strictly compensatory and partially compensatory models. In the strictly compensatory model, increased highway mortality was completely offset by decreased non-highway mortality, such that annual survival rates remained constant. Under this scenario, highway mortality had no additional impact on the population. In the partially compensatory model, only 50% of highway losses were offset by reductions in other mortality sources. The strictly additive model contained no density-dependent mortality factors. In this case, I simply added highway mortality rates to rates from non-highway-related sources. I excluded density-dependent reproduction from all models based on available evidence (Keith 1974, Hamlin and Mackie 1989, Mackie et al. 1990) and the known sensitivity of models to assumed levels of density-dependence (Conroy 1993).

I constructed a stochastic version of the most predictive of my models to explore how impacts of highway losses may be offset by variation in mortality and reproductive rates caused by fluctuating environmental conditions. Results obtained from the stochastic model were based on the mean and 95% confidence intervals from 10,000 simulations. I linked an environmental submodel to the existing population model to simulate the temperature and precipitation conditions to which the population was exposed. Hamlin and Mackie (1989) found annual fawn survival was closely tied to forage production variables prior to birth that included July-April precipitation and mean May temperature. Incorporating winter severity indices into their regression added very little predictive power. These variables influenced the timing of forage development, as well as the actual yield. Cool temperatures delayed plant development so that high quality forage was available to fawns preparing to enter the winter season. These variables also affected the physical condition of adults and may lead to variation in winter mortality rates (Hobbs 1989) and subsequent fawn production (Robinette et al. 1977, Zwank 1979, Trainer et al. 1981).

I obtained historic temperature and precipitation data from a weather station located approximately 6 km northwest of the study area. I used the data to define 5 temperature and precipitation categories that would affect forage growth and subsequently influence winter survival and spring reproduction. I specified "normal" May temperatures to be within 1 standard deviation (SD) of the mean. "Good" and "poor" temperature conditions were between ±1 and 2 SDs from the mean, and "very good" and "very poor" temperatures were greater than ±2 SDs from the mean. Based on the large standard deviation associated with the precipitation data, I delineated the 5 categories using the mean ±0.5 or 1 SD. I determined the percentage of data that fell within each of the 5 categories for May temperature and July-April precipitation data separately. I generated a single combined frequency distribution by averaging the proportions of temperature and precipitation data observed within each category. Available data precluded a more rigorous approach to incorporating random effects.

I associated a corresponding set of reproductive and non-highway mortality rates for the different age and sex classes with each of the 5 spring growing conditions. The range of parameters used was based on the range of values observed in the literature. I therefore assumed that variation in annual reproduction and non-highway mortality rates was driven by summer and fall forage conditions that prepare the animals for the approaching winter. Poor forage conditions led to low fat reserves and heavy winter mortality. I did not assume that mortality rates were determined by winter die-offs alone because contributions from other sources of mortality were incorporated into the absolute parameter values. Highway mortality was not influenced by changing environmental conditions.

Parameterizing Model Equations

I performed field examinations of road-killed does from February 1995 through August 1995 to estimate reproductive parameters for yearling (bred at 1.5 years of age) and adult (bred at ≥2.5 years of age) age classes. I assumed that reproductive contributions from fawns were negligible (Robinette et al. 1977, Zwank 1979, Trainer 1981, Smith 1983). I quantified pregnancy rates as the proportion of females that were carrying fetuses or showed visible signs of lactation. When possible, I determined the number and sex of fetuses that each pregnant doe was carrying. I used a chi-square test to test for departures from a 1:1 fetal sex ratio. I multiplied fetal rates of pregnant does by the age specific pregnancy rate to determine the reproductive contribution from each doe in the population. Under a polygynous mating system, I assumed that all does were bred over the range of densities simulated in the models. I examined premolar replacement to estimate age of each doe in the field (Robinette et al. 1957a). I extracted front incisors and used cementum annuli techniques (Low and Cowan 1963) to verify field estimates and accurately categorize females into the 2 age brackets.

I estimated non-highway mortality rates for fawns, yearling and adult females, as well as yearling and adult males using a weighted average of values taken from the literature. I quantified the proportion of surviving fawns that were female based on my observed fetal sex ratio and information gathered from the literature regarding sex differential mortality of fawns.

I estimated annual highway mortality rates using data gathered on highways surrounding the Jordanelle Reservoir. I divided the observed number of deer killed during each year (May-Apr) by the highest spring population estimate obtained through spotlight censuses. Spring densities were typically the highest observed, thus giving a conservative estimate of highway mortality rates. I obtained an equation relating highway mortality rate to population size by linear regression on log-transformed data. I incorporated this equation into the models. I evaluated disproportionate levels of highway mortality on bucks, does, and fawns by comparing the sex ratio of annual highway kill to the sex ratio of the population immediately prior to the October firearm season. Late summer and early fall spotlight censuses provided this information. I drove study area roads at least once per week to document the date, location, sex, and age of each deer killed by vehicles. Personnel from UDWR and a private contracting company assisted with road-kill data collection.

Selecting the Most Predictive Model

I identified the most predictive model by qualitatively comparing simulated output over 4 time steps to actual June population levels recorded through spotlight censuses from 1992-1995. I based selection criteria on the model's ability to track observed increases or decreases in the population.

Uncertainty Analysis

I conducted a sensitivity analysis on the deterministic version of the most predictive model to determine the relative influence of each parameter on model output. I individually increased and decreased each parameter by 10%. I expressed the corresponding impact on model output (total population size after 20 years) as the standardized change in model response to standardized change in the parameter value (S):

$$S = ((O_N - O_A) / O_N) / ((P_N - P_A) / P_N)$$

where O_N = model output using the nominal parameter value, O_A = model output using the altered parameter value, P_N = nominal parameter value, and P_A = altered parameter value.

To investigate higher-order effects that arise from uncertainty in all parameters operating simultaneously, I conducted a Monte Carlo error analysis (Gardner et al. 1981). Specifically, I used the procedure to assess predictions of the deterministic model regarding population responses to various levels of highway mortality reduction. I ran 10,000 simulations using parameter values that were randomly drawn from triangular distributions at the start of each simulation. I defined the triangular distribution for each parameter based on information obtained from the literature. I pooled available data for each parameter to define the range of possible values (i.e., the base of the triangle).

The median value observed in the literature defined the peak of the triangular distribution. I excluded demographic rates that were indicative of extreme environmental conditions. I recorded the total population size at the end of each random simulation and analyzed the results based on the cumulative distribution functions.

RESULTS

The Jordanelle Deer Population and Associated Parameter Values

The initial population used in modelling exercises consisted of 2,329 animals occupying a 151.6-km^2 area adjacent to the 3 study area roads. Based on posthunt spotlight classifications, the proportion of bucks, does, and fawns in the initial population was set at 2.8%, 60.2%, and 37.0%, respectively (Table III-1). The buck and doe components of the population were further divided into yearling and adult age classes. The proportion of deer in the yearling age bracket was estimated at 0.41 for males and 0.20 for females (Hamlin and Mackie 1989).

Pregnancy rates for the yearling and adult females at Jordanelle were 76.5% ($\underline{n}$ = 17) and 93.3% ($\underline{n}$ = 30), respectively. Twenty-one does were carrying fetuses at the time they were killed. Fetal rates for pregnant yearlings and adults were 1.33 ($\underline{n}$ = 6) and 1.67 ($\underline{n}$ = 15), respectively. Multiplying the number of fetuses per pregnant doe by the corresponding pregnancy rate estimated the mean number of fetuses produced by each doe in the population.

Table III-1. Percentage of mule deer bucks, does, and fawns observed during posthunt spotlight censuses at Jordanelle Reservoir, Utah, 1991-1995.

	Bucks	Does	Fawns
1991	3.8	57.7	38.5
1992	0.8	71.9	27.3
1994[a]	4.5	53.4	42.1
1995	2.2	57.8	40.0
Average	2.8	60.2	37.0

[a] Posthunt data from 1993 consisted of one spotlight census where 11 animals were observed. This sample was judged to be insufficient for determination of population sex ratios.

As commonly reported, I found that the reproductive rate for yearlings (1.02 fetuses/doe) was considerably lower than the adult rate (1.56 fetuses/doe). I compared my results to values from other studies (Table III-2). Reproductive rates used in the stochastic version of the best model were based on findings from these studies (Table III-3).

I observed a 1:1 sex ratio among 32 fetuses (χ^2 = 0.00, 1 df, P = 1.00). Other studies typically reported a slight preponderance of males in fetal classifications (Robinette and Gashwiler 1950, Robinette et al. 1977, Medin and Anderson 1979), although Trainer et al. (1981) observed a ratio of 86 males:100 females. None of these differences were statistically significant. Fetal sex ratios are thought to reflect nutrition, with the proportion of female fetuses increasing with the nutritional plane of the does (Robinette et al. 1957b, Connolly 1981b). Assuming a 1:1 sex ratio of fawns at birth and slightly higher

Table III-2. Reproductive rates from selected mule deer herds by state and locale.

		Fetuses/Doe[a]		
Location	Source	Yearlings	Adults	Combined
Utah				
Jordanelle Reservoir	This study	1.02 (17)	1.56 (30)	1.36 (47)
LaSal Mountains	Smith 1983	1.15 (20)	1.84 (94)	1.72 (114)
Oak Creek	Robinette et al. 1977	0.68 (90)	1.58 (257)	1.32 (359)
Antimony	Julander et al. 1961	0.63 (8)	1.42 (19)	1.19 (27)
Statewide	Robinette et al. 1977	1.06 (370)	1.67 (863)	1.50 (1,349)
Statewide	Zwank 1979	1.23 (30)	1.91 (154)	1.80 (184)
California				
Interstate	Salwasser 1978	1.07 (17)	1.80 (79)	1.67 (96)
Colorado				
Middle Park	Gili 1972	1.27 (26)	1.85 (146)	1.76 (172)
Middle Park	Robinette et al. 1977	0.82 (38)	1.64 (103)	1.42 (141)
Cache la Poudre	Medin and Anderson 1979	1.01 (42)	1.58 (163)	1.46 (205)
Idaho				
Sublett	Julander et al. 1961	1.56 (9)	1.96 (24)	1.85 (33)
Cassia	Davis 1966	1.25 (8)	1.82 (28)	1.69 (36)
Montana				
Missouri River Breaks	Hamlin and Mackie 1989	1.16 (28)	1.73 (166)	1.65 (194)
National Bison Range	Nellis 1968			1.50 (151)
Oregon				
Steens Mountain	Trainer et al. 1981	0.69 (26)	1.75 (190)	1.62 (216)
Washington				
Okanogan County	Zeigler 1978	1.57 (14)	1.70 (47)	1.67 (61)

[a] Sample size given in parentheses

Table III-3. Summary of parameters used in the deterministic and stochastic versions of the models.

Parameter definition	Symbol	Units	Deterministic value	Stochastic values based on May temp. and July-April precipitation					Source[a]
				Very poor	Poor	Normal	Good	Very good	
Birth rate, yearlings	yr	fawns/female/year	1.02	0.75	0.90	1.02	1.14	1.29	This study, Table III-2
Birth rate, adults	ar	fawns/female/year	1.56	1.40	1.48	1.56	1.64	1.72	This study, Table III-2
Non-highway mortality rate, fawns	fm	fraction/year	0.64	0.88	0.78	0.64	0.50	0.40	Trainer et al. 1981, Hamlin and Mackie 1989, Beale 1991 unpubl. data
Non-highway mortality rate, yearling males	ymm	fraction/year	0.36	0.55	0.45	0.36	0.32	0.27	Hamlin and Mackie 1989
Non-highway mortality rate, yearling does	ymd	fraction/year	0.20	0.32	0.26	0.20	0.15	0.10	White et al. 1987, Hamlin and Mackie 1989
Non-highway mortality rate, adult males	amm	fraction/year	0.53	0.65	0.59	0.53	0.47	0.41	Hamlin and Mackie 1989
Non-highway mortality rate, adult does	amd	fraction/year	0.17	0.29	0.23	0.17	0.12	0.07	White et al. 1987, Hamlin and Mackie 1989
Proportion of surviving fawns that are female	p	unitless	0.52	0.52	0.52	0.52	0.52	0.52	See text

[a] Values used in the stochastic model were selected from the range of results observed in the literature. These values were not reported as being specific to the environmental conditions to which they were assigned.

mortality of male fawns (Connolly 1981b), I estimated that 52% of fawns surviving their first year were female.

Non-highway mortality rates used in the deterministic and stochastic versions of the models are presented in Table III-3. The higher mortality rate of adult males versus yearling males was attributed to selective hunting pressure and higher winter losses associated with the post-rut condition of dominant individuals. I assigned yearling females a higher mortality rate than adult females. Yearling females typically occupy more open habitat during the summer and fall while adults raise fawns in more secure areas. Yearlings may be more vulnerable to harvest during this time (Hamlin and Mackie 1989).

The parameter values I used were characteristic of rates observed in western mule deer populations. By incorporating data from other areas, I have deliberately sacrificed the precision by which the model will mimic any particular system and increased generality, or the number of systems subsumed by the model (Levins 1966).

Characteristics of Highway Mortality

Observed seasonal highway mortality rates were inversely related to population size (F = 12.93; 1,15 df; P = 0.003; R^2 = 0.46) (Fig. III-1a). As population size decreased at Jordanelle, a higher proportion of animals were removed from the population along the highways. Annual highway mortality rates appeared to follow this same pattern, although the relationship was not significant given only 3 years of complete data were available (F = 33.74;

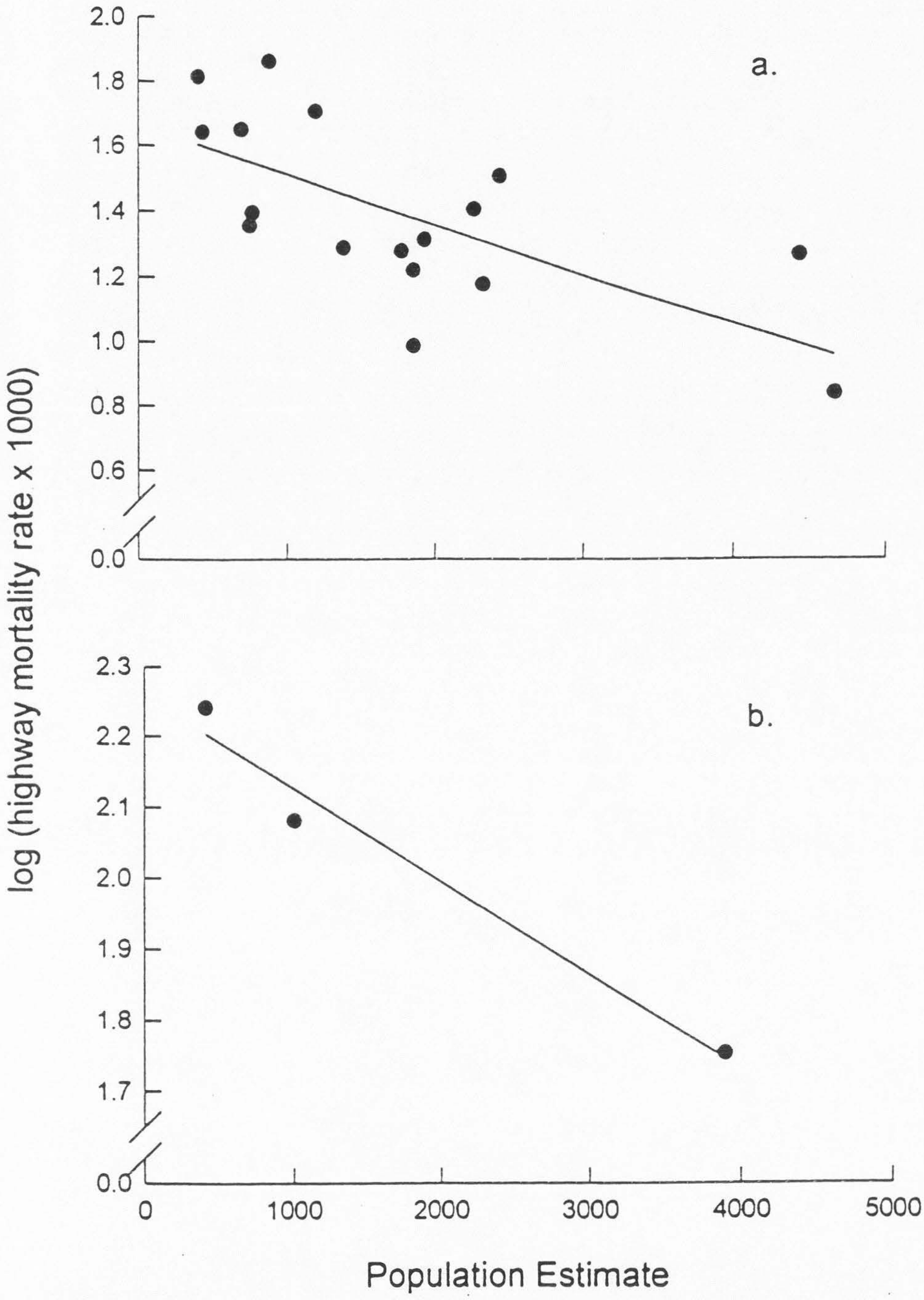

Fig. III-1. Inverse relationship between highway mortality rates and population size at the Jordanelle Reservoir, Utah, 1991-1995. Seasonal rates (a) were based on data collected from fall 1991 through fall 1995. Annual mortality rates (b) were calculated using May-April road-kill data (1992-1995) and the highest spring population estimate.

1,1 df; $\underline{P}$ = 0.109; $\underline{R}^2$ = 0.97) (Fig. III-1b). Based on the pattern apparent in the seasonal rates, I assumed that annual highway mortality rates displayed the same inversely density-dependent response. Observed annual highway mortality rates at Jordanelle ranged from 5.6% at high population levels (25.7 deer/km^2) to 17.4% at lower population levels (2.6 deer/km^2). A regression line fitted to the log-transformed values of the 3 data points was used in the models to determine the annual rate of highway mortality based on population size at the beginning of the time step. The initial population of 2,329 animals (15.4 deer/km^2) was exposed to a 9.0% highway mortality rate.

Certain sex and age classes were disproportionately represented in the road-kill data relative to their occurrence in the prehunt population (Table III-4). On average, bucks tended to be killed at nearly twice the rate that they occurred in the population. Fawns were underrepresented in the kill, partly due to the hiding behavior displayed during their first 6 to 8 weeks of life (Geist 1981). Does tended to be killed in roughly the same proportion as they occurred in the population. These relationships were incorporated into the mechanisms of the 3 models.

Selecting the Most Predictive Model

To determine which of the 3 models most closely tracked the observed population dynamics, I needed to incorporate heavy mortality recorded during the 1992-1993 winter field season. A 69% reduction in population size between June 1992 and June 1993 was recorded using spotlight censuses. The UDWR

Table III-4. Percentage of mule deer bucks, does, and fawns observed in both prehunt spotlight censuses and May-April highway mortalities at Jordanelle Reservoir, Utah, 1992-1995.

	Bucks		Does		Fawns	
	Census	Kill	Census	Kill	Census	Kill
1992	11.9	22.5	52.9	60.8	35.2	16.7
1993	5.6	15.6	63.8	57.8	30.6	26.6
1994	9.7	19.8	49.9	52.8	40.7	27.4
1995[a]	16.0	26.9	46.1	57.1	37.9	16.0
Average	10.8	21.2	53.1	57.1	36.1	21.7

[a] Kill percentages based on data from May 1, 1995 through March 15, 1996.

estimated a similar 70% reduction in population levels due to the severe winter conditions (Romin and Bissonette 1996a). To account for this occurrence and approximate actual mortality, I increased non-highway mortality rates for fawns by 30%, yearling and adult males by 45%, and yearling and adult females by 35% for the first year of the simulation. The resulting mortality rates were representative of extreme values in the literature and likely reflected rates at Jordanelle.

The 3 models behaved considerably different from one another (Fig. III-2). This suggests that knowing the additive or compensatory interactions between mortality factors is important to accurately forecast long-term population trends. The partial compensation model most closely tracked the observed population dynamics (Fig. III-2). In this model, 50% of the animals killed along the highways would have died from other non-highway-related causes. The remaining 50%, however, would have survived to the next age class and reproduced. Although this suggests highway mortality is only partially offset by reductions in other mortality sources over the range of densities I observed, it does not confirm it. Another model operating under completely different mechanisms may have predicted the observed dynamics just as well. The strictly additive model tracked the severity of the 1993 population crash better than the partial compensation model. Highway losses may have been completely additive at that time. The continued downward projection of the additive model, however, did not agree with the observed population increase.

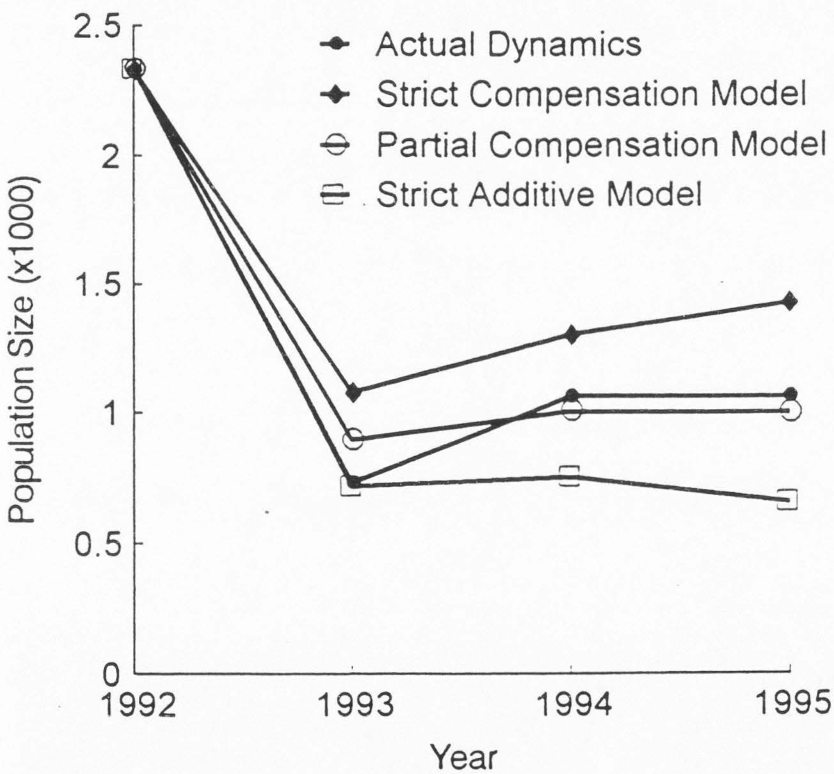

Fig. III-2. Predictions of the 3 competing simulation models versus observed mule deer population dynamics at Jordanelle Reservoir, Utah.

Sensitivity Analysis

Changes in yearling and adult male mortality rates had little influence on the behavior of the partial compensation model (Table III-5). This reflected my assumption that surplus males were available to breed all females over the range of densities I observed. The loss of 1 male simply meant that another would take his place. The model was also relatively insensitive to alterations in yearling female reproduction and mortality. Reproductive contributions from yearling females were minor compared to inputs from adult females. As expected, the model was sensitive to rates associated with adult females. A 10% change in adult female mortality or birth rate resulted in a 57% change in total population size after 20 time steps. The model was highly responsive to changes in fawn mortality rate and the proportion of fawns surviving their first year that were female. The values chosen for these rates were representative of real-world mule deer populations (Table III-3).

Impact of Highway Mortality on the Jordanelle Population

I investigated what the Jordanelle population may have looked like had the high levels of highway mortality not occurred. Figure III-3 displays the observed dynamics of the Jordanelle population and output from the strict compensation model. The strict compensation model depicts what the population was capable of in the absence of highway losses. The sex ratios corresponding to actual population levels were generated by the partial

Table III-5. Relative change in model output (total population size after 20 years) to alterations in individual parameter values.

Parameter	Symbol	Nominal value	Output using nominal value	Altered value (+/- 10%)	Output using altered value	Ratio of output change: parameter change (S)
Birth rate, yearlings	yr	1.02	1,225	1.122	1,327	0.83
				0.918	1,137	0.72
Birth rate, adults	ar	1.56	1,225	1.716	1,924	5.71
				1.404	778	3.65
Non-highway mortality rate, fawns	fm	0.64	1,225	0.704	437	6.43
				0.576	3,351	17.36
Non-highway mortality rate, yearling males	ymm	0.36	1,225	0.396	1,203	0.18
				0.324	1,248	0.19
Non-highway mortality rate, yearling does	ymd	0.20	1,225	0.220	1,079	1.19
				0.180	1,389	1.34
Non-highway mortality rate, adult males	amm	0.53	1,225	0.583	1,206	0.16
				0.477	1,257	0.26
Non-highway mortality rate, adult does	amd	0.17	1,225	0.187	784	3.60
				0.153	1,923	5.70
Proportion of surviving fawns that are female	p	0.52	1,225	0.572	1,921	5.68
				0.468	783	3.61
Highway mortality rate	hwy	equation	1,225	1.1(equation)	961	2.16
				0.9(equation)	1,537	2.55

compensation model, which most closely predicted observed dynamics. Comparing the output reveals that highway mortality may have accentuated the crash caused by severe 1992-93 winter conditions, and may be slowing the subsequent recovery. Changes in the population's sex ratios may have been caused by highway mortality. Bucks tend to comprise 10.8% of the prehunt spotlight censuses, yet account for more than 21% of the annual highway losses (Table III-4). The disproportionate kill of male animals along the highways explains the differences in sex ratios between the 2 simulations.

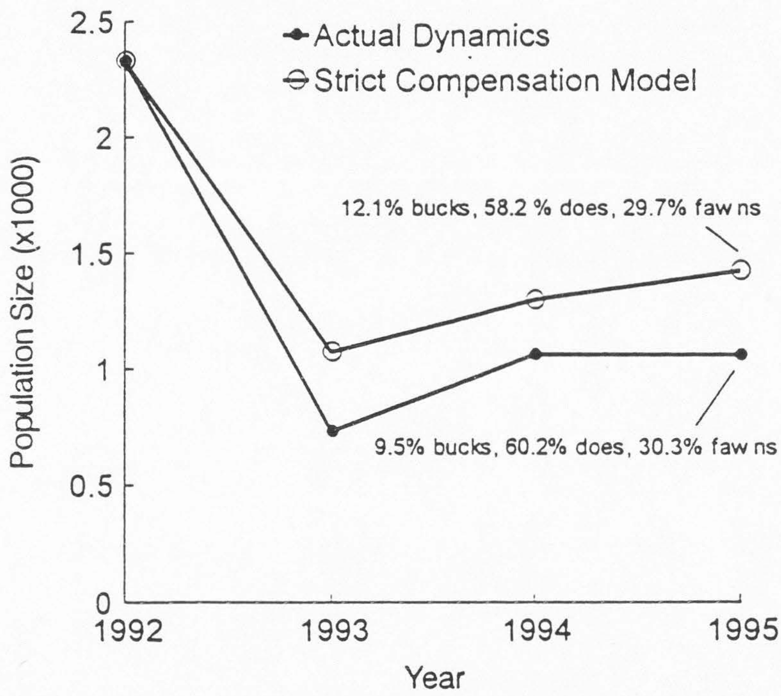

Fig. III-3. Observed population dynamics versus predictions of the strict compensation model. The strict compensation model illustrates what the population may have looked like in the absence of highway losses. Highway mortality apparently worsened the crash initiated by severe 1992-1993 winter conditions, and may be slowing the recovery. The disproportionate kill of bucks along highways altered simulated population sex ratios.

Response to Road-Kill Reductions

Highway mortality levels at Jordanelle declined by 40% since installing a newly designed system of highway crosswalks (Lehnert and Bissonette, Utah St. Univ., unpubl. data). I investigated population-level changes that might occur as a result of reducing losses by this percentage, and explored the level of reduction necessary to reverse the long-term population decline predicted by the partial compensation model at the pretreatment highway mortality rates (Fig. III-4).

The simulated population responded quickly to reductions in highway mortality (Fig III-4). A 60% reduction in the rate of highway mortality was required to halt the decline displayed by the simulated population at the pre-

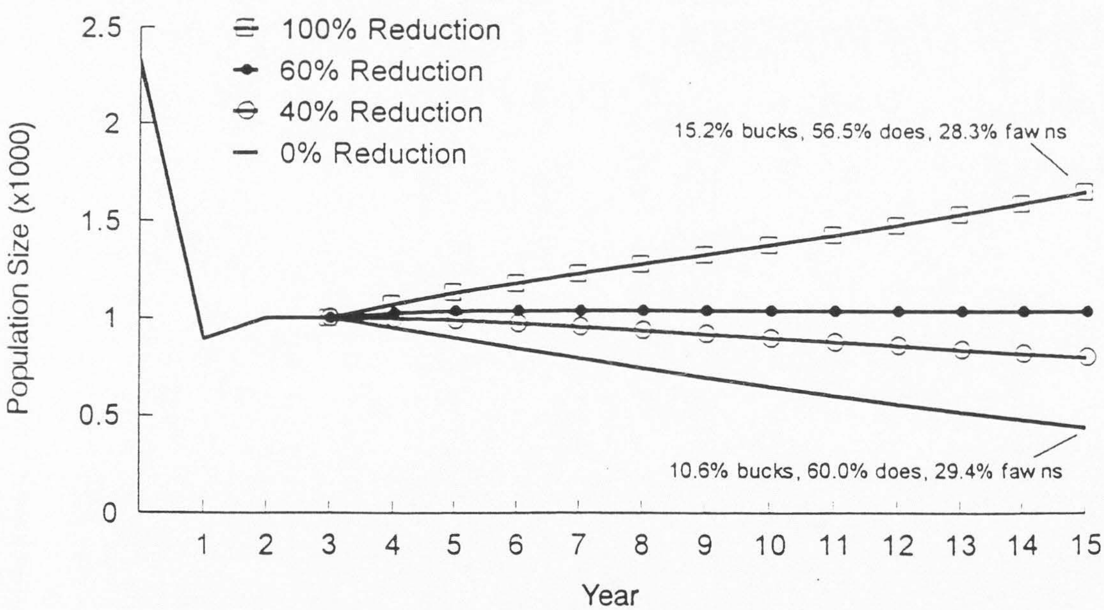

Fig. III-4. Simulated population response to various reductions in the highway mortality rate. Mortality reductions were initiated in year 3. The percentage of bucks is expected to increase as highway mortality is reduced.

treatment mortality rates. Further reductions allowed for population growth. A complete reduction in highway losses enabled the simulated population to recover to precrash conditions in 21 years. As highway mortality is progressively reduced, the relative proportion of bucks in the population is predicted to increase. The model predicted that the observed 40% reduction in vehicle collisions with deer would not be sufficient to reverse the predicted population decline. Assuming the model is a realistic representation of the Jordanelle population, improvements in the design of the crosswalk system appear to be justified from the standpoint of population viability.

Given the range of uncertainty inherent in each parameter value, error analysis was used to assess predictions of the deterministic model. With no reduction in highway mortality, 90.7% of the Monte Carlo simulations using parameter values randomly drawn from specified frequency distributions yielded a declining population (Fig. III-5a). This was consistent with deterministic predictions and illustrates the need for successful mitigation. At the 40% reduction level, the likelihood of a declining population given the uncertainty in the parameter values was 62.4% (Fig. III-5b). Efforts to improve the original design of the crosswalk system and further reduce highway losses are warranted. The level of reduction needed to reverse the predicted population decline, however, is not certain. At the 60% reduction level specified by the deterministic model, one can still expect to observe a declining population 41.8% of the time given the uncertainty surrounding each parameter value (Fig.

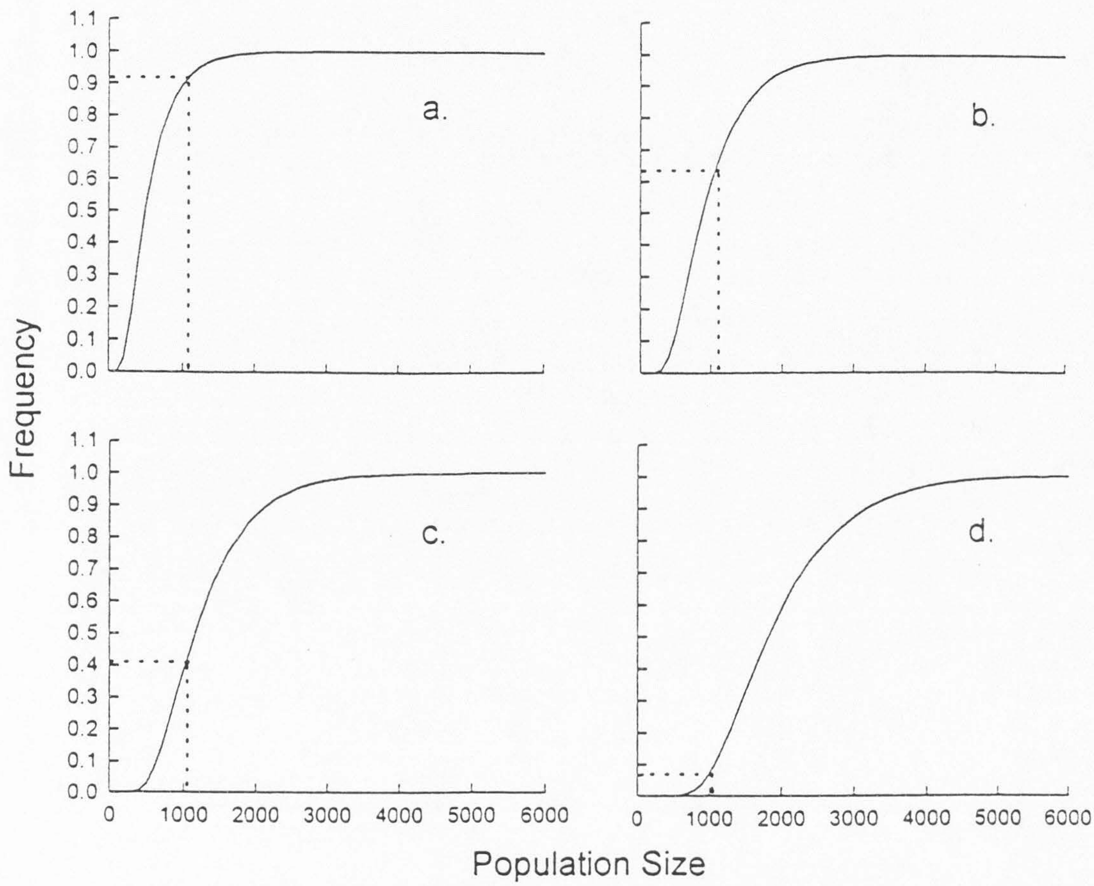

Fig. III-5. Cumulative frequency distributions derived from 10,000 simulations using parameter values randomly drawn from specified distributions during Monte Carlo error analysis. Dotted lines address the probability (y-axis) of observing a population that declined over 12 years even after reducing highway mortality rates by (a) 0%, (b) 40%, (c) 60%, and (d) 100%. The stable population size is 1,037 animals.

III-5c). Mitigative efforts should therefore target higher rates of highway mortality reduction to better ensure that the desired population response is achieved. With an 80% reduction in highway mortality, there is a 22.8% chance that the population will still decline. Even reducing highway losses 100% does not guarantee population expansion (Fig. III-5d). There is an 8.5% chance the population will decline even after completely eliminating highway losses.

Influence of a Variable Environment

Based on historic temperature and precipitation data, I determined the probability of occurrence of very poor (6.2%), poor (9.7%), normal (65%), good (9.9%), and very good (9.2%) climatic conditions that influenced forage growth and ultimately determined the level of winter mortality and spring reproduction.

Annual variation in reproduction and non-highway mortality rates caused by environmental variability enabled simulated populations to reach higher levels when compared to predictions made by the deterministic version of the model. This likely reflected the higher probability of very good forage conditions arising in a given year compared to very poor conditions. The tendency for environmental variation to offset or dampen the impact of highway losses, however, was contingent upon initial population size (Table III-6). This determined the rate of highway mortality to which the population was exposed. At high population levels, highway mortality rates were relatively low. Variability in reproduction and mortality enabled these populations to increase well above the predictions of the deterministic model. At an initial population size of 3,000

Table III-6. Projected population size after 25 time steps using the deterministic and stochastic versions of the partial compensation model.

	Projected Population Size	
Initial Population Size	Deterministic	Stochastic[a]
5,000	9,478	11,039 (10,875-11,202)
3,000	2,016	3,367 (3,290-3,444)
1,000	143	195 (191-200)

[a] The mean of 10,000 simulations is presented. Confidence intervals (95%) are shown in parentheses.

animals, environmental variability appeared to dampen the impact of highway losses and enabled the population to expand. This population declined under the deterministic mechanisms. As population size decreased further, however, the impacts of highway mortality became more severe and tended to drive the system, largely because they were operating independent of environmental changes. At these higher levels of roadway mortality, environmental variation simply slowed the decline predicted by the deterministic model, but could not reverse them.

DISCUSSION

My results indicated that highway mortality levels characteristic of the Jordanelle area were capable of altering trends in mule deer dynamics, especially at relatively low population densities. The contrasting predictions of the 3 competing simulation models indicated that knowing the additive and compensatory interactions between mortality agents is important to accurately predict long-term population trajectories.

Selection of the partial compensation model as the most predictive suggests, but does not confirm, that not all highway losses are offset by reductions in other sources of mortality over the range of deer densities I observed. In other words, highway mortality at Jordanelle was partially additive. This, in conjunction with its inversely density-dependent nature, may have accentuated the population crash initiated by severe 1992-1993 winter conditions, and appears to be slowing the subsequent recovery. The disproportionate kill of male animals along the highways altered sex ratios in simulated populations. Greater susceptibility of males to deer-vehicle encounters during the breeding and hunting seasons has been reported (Jahn 1959, Allen and McCullough 1976, Goodwin and Ward 1976, Romin and Bissonette 1996a), and largely explains the disproportionate kill. The partial compensation model indicated a 60% reduction in highway mortality was required to reverse the predicted long-term population decline. Error analysis, however, revealed a 41.8% chance of still observing a population decline after reducing highway losses by 60% due to uncertainty in parameter values used in the deterministic model. Mitigative efforts should therefore target greater mortality reductions to better ensure that desired population responses occur. Variation in reproduction and mortality caused by changing environmental conditions were able to offset the impacts of highway losses when initial population levels were relatively high (i.e., low highway mortality rates). At low population levels, however, highway mortality was severe enough to drive declining trends in the population.

The models I constructed represented a series of hypotheses regarding relationships and parameters that were important in driving mule deer population dynamics over the range of densities I studied. My purpose was not to mimic the complexity of real-world systems, but rather to construct a useful simplification in order to address the questions of interest. Correspondence of model output to actual observations does not confirm the relationships and assumptions incorporated into the models (Conroy 1993). By running the simulations, I generated predictions regarding the ability of highway mortality to alter population trends and characteristics. I also used the models to predict how the Jordanelle population might respond to reductions in highway losses. These predictions need to be empirically tested. My intent was to examine the potential impacts of highway mortality in a controlled setting, and subsequently determine if empirical investigations were warranted in the real world. My results suggests that they are.

MANAGEMENT IMPLICATIONS

Many decisions involving wildlife resources are made using models designed to evaluate the potential consequences of implementing various management strategies. Parameter values are typically manipulated to give some idea of the changes required in the real system to produce a desired state. Failure to include or accurately measure 1 or more factors that are important in driving the dynamics of the system can result in management decisions that fail to produce the desired state or, even worse, are detrimental to sustained use of the resource. My results suggest that in areas where deer-vehicle accident rates are high, failure to incorporate the rates and characteristics of highway losses into mortality parameters may lead to discrepancy between the desired state of the system and that realized when management plans are implemented. Efforts to accurately quantify the extent of highway losses are warranted to more effectively manage populations prone to vehicle traffic.

Population reduction has been suggested as a means of lowering the occurrence of deer-vehicle collisions (Allen and McCullough 1976, Sicuranza 1979, Leedy and Adams 1982). Careful planning should precede implementation of this practice in areas where highway mortality rates display the inversely density-dependent pattern I observed at Jordanelle. Harvesting the population below a certain point may increase highway mortality rates sufficiently enough to drive further declines in the population. This assumes highway losses are not completely compensated by reductions in other mortality sources.

LITERATURE CITED

Allen, R. E., and D. R. McCullough. 1976. Deer-car accidents in southern Michigan. J. Wildl. Manage. 40:317-325.

Bartmann, R. M., G. C. White, and L. H. Carpenter. 1992. Compensatory mortality in a Colorado mule deer population. Wildl. Monogr. 121. 39 pp.

Carbaugh, B., J. P. Vaughan, E. D. Bellis, and H. B. Graves. 1975. Distribution and activity of white-tailed deer along an interstate highway. J. Wildl. Manage. 39:570-581.

Caughley, G. 1985. Harvesting of wildlife: past, present, and future. Pages 3-14 in S. L. Beasom and S. F. Roberson, eds. Game harvest management. Caesar Kleberg Wildlife Research Inst., Kingsville, Tex.

Connolly, G. E. 1981a. Limiting factors and population regulation. Pages 245-285 in O. C. Wallmo, ed. Mule and black-tailed deer of North America. Univ. Nebraska Press, Lincoln.

_____. 1981b. Assessing populations. Pages 287-345 in O. C. Wallmo, ed. Mule and black-tailed deer of North America. Univ. Nebraska Press, Lincoln.

Conroy, M. J. 1993. The use of models in natural resource management: prediction, not prescription. Trans. N. A. Wildl. and Nat. Resour. Conf. 58:509-519.

Davis, J. A. 1966. Reproduction of the Cassia deer herd in Idaho. M.S. Thesis. Univ. of Idaho, Moscow. 60 pp.

Decker, D. J., K. M. Loconti-Lee, and N. A. Connolly. 1990. Deer-related vehicular accidents in Tompkins County, New York: incidence, costs and implications for deer management. Trans. Northeast Sect., The Wildl. Soc. 47:21-26.

Dickinson, T. G., and G. W. Garner. 1980. Home range use and movements of desert mule deer in southwestern Texas. Proc. Annu. Conf. Southeast. Fish and Wildl. Agencies 33:267-278.

Errington, P. L. 1945. Some contributions of a fifteen-year study of the northern bobwhite to a knowledge of population phenomena. Ecol. Monogr. 15:1-34.

_____. 1946. Predation and vertebrate populations. Quart. Rev. Biol. 21:144-177, 221-245.

Gardner, R. H., R. V. O'Neill, J. B. Mankin, and J. H. Carney. 1981. A comparison of sensitivity analysis and error analysis based on a stream ecosystem model. Ecol. Modelling 12:173-190.

Geist, V. 1981. Behavior: adaptive strategies in mule deer. Pages 157-243 in O. C. Wallmo, ed. Mule and black-tailed deer of North America. Univ. Nebraska Press, Lincoln.

Gill, R. B. 1972. Middle Park deer study: productivity and mortality. Pages 179-198 in Game research report, July 1972, part 2. Colorado Div. Wildl., Denver.

Goodwin, G. A., and A. L. Ward. 1976. Mule deer mortality on Interstate 80 in Wyoming: causes, patterns, and recommendations. Pages 1-4 in USDA Forest Service Res. Note RM-332. Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo.

Hamlin, K. L., and R. J. Mackie. 1989. Mule deer in the Missouri River Breaks, Montana: A study of population dynamics in a fluctuating environment. Job Compl. Rep. Proj. W-120-R. Montana Dep. Fish, Wildl. and Parks, Helena. 401 pp.

Hansen, C. S. 1983. Costs of deer-vehicle accidents in Michigan. Wildl. Soc. Bull. 11:161-164.

Hobbs, N. T. 1989. Linking energy balance to survival in mule deer: development and test of a simulation model. Wildl. Monogr. 101. 39 pp.

Jahn, L. R. 1959. Highway mortality as an index of deer-population change. J. Wildl. Manage. 23:187-197.

Johnson, M. L., and M. S. Gaines. 1990. Evolution of dispersal: theoretical models and empirical tests using birds and mammals. Annu. Rev. Ecol. Syst. 21:449-480.

Julander, O., W. L. Robinette, and D. A. Jones. 1961. Relation of summer range condition to mule deer herd productivity. J. Wildl. Manage. 25:54-60.

Keith, L. B. 1974. Some features of population dynamics of mammals. Proc. Internat. Cong. Game Biol. 11:17-58.

Kufeld, R. C., D. C. Bowden, and D. L. Schrupp. 1988. Habitat selection and activity patterns of female mule deer in the Front Range, Colorado. J. Range. Manage. 41:515-522.

Leedy, D. L., and L. W. Adams. 1982. Wildlife considerations in planning and managing highway corridors. Rep. No. FHWA-TS-82-212. Federal

Highway Admin., Offices of Research and Development. 93 pp.

Levins, R. 1966. The strategy of model building in population biology. American Scientist 54:421-431.

Low, W. A., and I. M. Cowan. 1963. Age determination of deer by annular structure of dental cementum. J. Wildl. Manage. 27:466-471.

Mackie, R. J., K. L. Hamlin, D. F. Pac, G. L. Dusek, and A. K. Wood. 1990. Compensation in free-ranging deer populations. Trans. N. A. Wildl. and Nat. Res. Conf. 55:518-526.

Mansfield, T. M., and B. D. Miller. 1975. Highway deer-kill district 02 regional study. Internal Report. Caltrans, Sacramento, Calif. 49 pp.

Medin, D. E., and A. E. Anderson. 1979. Modeling the dynamics of a Colorado mule deer population. Wildl. Monogr. 68. 77 pp.

Nellis, C. H. 1968. Productivity of mule deer on the National Bison Range, Montana. J. Wildl. Manage. 32: 344-349.

Pils, C. M., and M. A. Martin. 1979. The cost and chronology of Wisconsin deer-vehicle collisions. Rep. 103. Wis. Dep. Nat. Resour. Res. 5 pp.

Putman, R. 1988. The natural history of deer. Cornell Univ. Press, Ithaca, N.Y. 191 pp.

Reed, D. F. 1981. Conflicts with civilization. Pages 509-535 in O. C. Wallmo, ed. Mule and black-tailed deer of North America. Univ. Nebraska Press, Lincoln.

Robinette, W. L., and J. S. Gashwiler. 1950. Breeding season, productivity, and fawning period of the mule deer in Utah. J. Wildl. Manage. 14:457-469.

_____, J. S. Gashwiler, J. B. Low, and D. A. Jones. 1957b. Differential mortality by sex and age among mule deer. J. Wildl. Manage. 21:1-16.

_____, N. V. Hancock, and D. A. Jones. 1977. The Oak Creek mule deer herd in Utah. Utah Div. Wildl. Resour. Publ. No. 77-15. 148 pp.

_____, D. A. Jones, G. Rogers, and J. S. Gashwiler. 1957a. Notes on tooth development and wear for Rocky Mountain mule deer. J. Wildl. Manage. 21:134-153.

Romin, L. A., and J. A. Bissonette. 1996a. Temporal and spatial distribution of highway mortality of mule deer on newly constructed roads at Jordanelle Reservoir, Utah. Great Basin Nat. 56:1-11.

_____, and _____. 1996b. Deer-vehicle collisions: status of state monitoring activities and mitigation efforts. Wildl. Soc. Bull. 24:276-283.

Salwasser, H. 1978. Interstate wildlife study. Interim Rep. No. 4. Univ. of Calif., Berkeley. 114 pp.

Sicuranza, L. P. 1979. An ecological study of motor vehicle-deer accidents in southern Michigan. M.S. Thesis, Michigan State Univ., Lansing. 63 pp.

Smith, R. B. 1983. Mule deer reproduction and survival in the LaSal Mountains, Utah. M.S. Thesis. Utah State Univ., Logan. 102 pp.

Trainer, C. E., J. C. Lemos, T. P. Kistner, W. C. Lightfoot, D. E. Toweill. 1981. Mortality of mule deer fawns in southeastern Oregon, 1968-1979. Wildl.

Res. Rep. No. 10. Oreg. Dep. Fish and Wildl., Portland. 113 pp.

White, G. C., R. A. Garrott, R. M. Bartmann, L. H. Carpenter, and A. W. Alldredge. 1987. Survival of mule deer in northwest Colorado. J. Wildl. Manage. 51:852-859.

Witmer, G. W., and D. S. deCalesta. 1992. The need and difficulty of bringing the Pennsylvania deer herd under control. Proc. East. Wildl. Damage Control Conf. 5:130-137.

Zeigler, D. L. 1978. The Okanogan mule deer herd. Biol. Bull. No. 15. Washington State Game Dep. 106 pp.

Zwank, P. J. 1979. Reduced recruitment in Utah mule deer relative to winter condition. Publ. 79-11. Utah Div. Wildl. Resour. 80 pp.

APPENDIX

The models were based on a set of simple equations that tracked the inputs to and outputs from each of the 5 state variables. These variables included the number of fawns (FAWN), male yearlings (MYEAR), female yearlings (FYEAR), male adults (MADULT), and female adults (FADULT). Refer to Table III-3 for a description of each parameter used to control the rate of input and output in the equations.

Inputs to the fawn age class were from reproductive contributions of yearling (yinput) and adult (ainput) females present in the population at the end of the previous time step (t-1):

$$\text{yinput} = \text{yr}\ (\text{FYEAR}_{t-1})$$

$$\text{ainput} = \text{ar}\ (\text{FADULT}_{t-1})$$

Combining the number of fawns produced by the 2 age classes yielded total annual fawn production (totinput):

$$\text{totinput} = \text{yinput} + \text{ainput}$$

The number of fawns present in the population at time t (FAWNS_t) was computed by subtracting non-highway and highway related losses from the total number of fawns produced at the start of the time step:

$$\text{FAWN}_t = \text{totinput} - (\text{fm}\ (\text{totinput})) - (\text{hwyf}\ (\text{totinput}))$$

where hwyf = highway mortality rate adjusted for the underrepresentation of fawns in highway kill relative to their occurrence in the population

The number of animals present in the other state variables was calculated by a similar procedure. Inputs to these age and sex classes was in the form of survival of animals into the next age class. In other words, fawns that survived to the end of 1 time step became yearlings in the next. Similarly, yearlings survived to become adults. Surviving adults remained in that age bracket.

$$FYEAR_t = FAWN_{t-1}(p) - (ymd\ (FAWN_{t-1}\ (p))) - (hwyd\ (FAWN_{t-1}\ (p)))$$

where hwyd = highway mortality rate for does.

$$MYEAR_t = FAWN_{t-1}(1-p) - (ymm(FAWN_{t-1}\ (1-p))) - (hwym\ (FAWN_{t-1}\ (1-p)))$$

where hwym = highway mortality rate adjusted to account for the disproportionate kill of males relative to their occurrence in the population.

$$FADULT_t = FADULT_{t-1} + FYEAR_{t-1} - (amd\ (FADULT_{t-1} + FYEAR_{t-1}) - (hwyd\ (FADULT_{t-1} + FYEAR_{t-1})$$

$$MADULT_t = MADULT_{t-1} + MYEAR_{t-1} - (amm\ (MADULT_{t-1} + MYEAR_{t-1}) - (hwym\ (MADULT_{t-1} + MYEAR_{t-1})$$

CHAPTER IV

CONCLUSION

Deer (Odocoileus spp.)-vehicle collisions have become an increasing problem throughout the United States (Romin and Bissonette 1996). In northeastern Utah, highway mortality of mule deer (O. hemionus) increased dramatically when roadways were realigned to accommodate construction of the Jordanelle Reservoir (Romin 1994). A newly designed system of highway crosswalks was installed in an attempt to reduce deer losses along highways and preserve the daily and seasonal movement patterns of the local deer population. I evaluated the effectiveness of the experimental mitigative system. In addition, I used computer simulation models to investigate how increased highway mortality has influenced the size and characteristics of the Jordanelle population, and explored how the population might respond to reductions in highway losses.

The crosswalk system restricted deer-crossings to specific, well-marked areas along the highways where motorists could anticipate them. Subsequent to installation, highway mortality declined 42.3% and 36.8% along a four-lane, divided and two-lane road, respectively. High costs associated with the project precluded the spatial replication required by most statistical tests. As a result, I was unable to statistically demonstrate that the observed mortality reductions were a direct result of the crosswalk system. The potential applicability of the system, however, should not be dismissed. Reduced deer use of the highway right-of-way (ROW), the apparent maintenance of migratory behavior, and observations of animals crossing within crosswalk boundaries indicate that some aspects of the system served their intended purpose and likely contributed to the declines. Lack of motorist response to crosswalk warning signs, the tendency for foraging deer to wander outside crosswalk boundaries in search of roadside vegetation, and the ineffectiveness of one-way ROW escape gates contributed to most treatment area mortalities. I offered design modifications that address these shortcomings, and may increase the utility of the approach.

The long-term consequences of highway losses on the dynamics of local deer populations are poorly understood and largely ignored. A four-year field study was conducted to define the characteristics of deer mortality along roads in the Jordanelle area. Highway mortality was found to be inversely density-dependent, removed between 5.6% and 17.4% of the population each year, and had a disproportionate impact on male animals. I incorporated this information into 3 competing computer simulation models and used them to simulate the dynamics of the population under the influence of highway mortality. The models differed mechanistically in terms of whether highway losses were incorporated in a strictly compensatory, partially compensatory, or strictly additive manner.

The models behaved considerably different from one another, indicating that accurate forecasting of population trajectories using models is heavily dependent upon an understanding of how mortality factors interact in a system. The partial compensation model most closely tracked the observed dynamics of the Jordanelle population. In this model only 50% of highway losses were offset by reductions in other sources of mortality. In other words, highway mortality at Jordanelle appeared to be partially additive over the range of densities that I studied. Highway losses apparently accentuated a population crash caused by severe 1992-1993 winter conditions, and may be slowing the subsequent recovery. The disproportionate kill of bucks along the roads was able to alter sex ratios of simulated populations. The Jordanelle population was predicted to have a higher percentage of bucks in the absence of highway losses. Environmental stochasticity, and the variability it creates in reproduction and mortality, was able to offset the impacts of highway mortality when initial population sizes were relatively high. As population size decreased, highway mortality rates became severe enough to drive the dynamics of the system.

The 40% reduction in highway mortality observed subsequent to installing the crosswalk system is not expected to reverse the long-term population decline predicted by the partial compensation model at pretreatment mortality rates. Assuming the model is an accurate representation of the Jordanelle population, efforts to improve the effectiveness of the crosswalk system are justified from the standpoint of population viability. Simulation results indicate that a 60% reduction in the highway mortality rate is needed to stop the predicted decline. Monte Carlo error analysis, however, suggested that mitigative efforts should target higher levels of mortality reduction to ensure that desired population responses occur. Understanding how uncertainty inherent in each parameter value propagates during simulations is an important component of modelling exercises.

The results of this research are intended to promote continued investigations into the crosswalk system as a less costly alternative to traditional overpasses and underpasses. This study served as a baseline analysis to identify shortcomings in the original design so that modifications can be made. Only through further modification and testing can we define the upper limits of success that the crosswalk system can achieve, and determine its applicability for widespread use, or lack thereof. In addition, I hope that my modelling results will prompt wildlife personnel to consider highway losses when developing management strategies for deer populations prone to vehicle traffic. Effective long-term management and sustained use of wildlife resources is dependent upon an understanding of all factors that influence them. As highway networks continue to expand, roadway mortality can be expected to play a more defining role in shaping the dynamics of wildlife populations. Empirical studies aimed at better understanding the influence of highway losses in real-world systems are warranted.

LITERATURE CITED

Romin, L. A. 1994. Factors associated with the highway mortality of mule deer at Jordanelle Reservoir, Utah. M.S. Thesis, Utah State Univ., Logan.

83 pp.

_____, and J. A. Bissonette. 1996. Deer-vehicle collisions: status of state monitoring activities and mitigation efforts. Wildl. Soc. Bull. 24:276-283.