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CHARACTERISTICS OF UNGULATE BEHAVIOR AND MORTALITY
ASSOCIATED WITH WIRE FENCES

by

Justin L. Harrington

A thesis submitted in partial fulfillment
of the requirements for the degree

of

MASTER OF SCIENCE

in

Wildlife Biology

Approved:

UTAH STATE UNIVERSITY
Logan, Utah

2005

ABSTRACT

Characteristics of Ungulate Behavior and Mortality

Associated with Wire Fences

by

Justin L. Harrington, Master of Science

Utah State University, 2005

Major Professor: Dr. Michael R. Conover
Department: Forest, Range, and Wildlife Sciences

I studied the characteristics of fence mortality in pronghorn (*Antilocapra americana*), mule deer (*Odocoileus hemionus*), and elk (*Cervus elaphus*) along roads in Colorado and Utah from June 2004 to June 2005. I defined a direct-fence mortality as a carcass caught directly in a fence and an indirect-fence mortality as a carcass on the ground within 10 m of a fence. I estimated an average annual direct mortality occurrence of 0.25 mortalities/km (0.078 mule deer mortalities/km, 0.113 pronghorn mortalities/km, and 0.061 elk mortalities/km). The highest fence-mortality rates for ungulates occurred during August, which coincided with weaning of fawns on my study area. Mule deer and pronghorn both jumped fences in >81% of observed crossings and did not differ in their crossing methods ($P = 0.37$). Getting caught between the top 2 wires was the leading cause of death for fence mortalities. Mule deer suffered higher fence-mortality rates than elk or pronghorn because they crossed fences more frequently and fed in the right-of-way

of the road more often ($P < 0.001$). Juveniles were 8 times more likely to die in fences than adults. Woven-wire fence types were more lethal to ungulates (especially juveniles) than other fence types ($P < 0.001$). Woven wire with a single strand of barbed wire above it was significantly more lethal to ungulates than woven wire with 2 strands of barbed wire above it, or 4-strand barbed-wire fence ($P < 0.001$). There was a direct relationship between the frequency of fence-mortalities and ungulate abundance ($P < 0.001$). Traffic volumes had an inverse relationship with fence mortality frequencies ($P < 0.001$) and ungulate densities along the right-of-way ($P < 0.001$). Indirect mortality (i.e., carcasses within 10 m of fences) composed 66% of fence-related mortality, whereas direct-fence mortality (i.e., carcasses in fences) composed a mere 33%. Additionally, indirect-fence mortality was found to be greater along woven-wire fences, when compared to barbed-wire fence types ($P = 0.003$).

Frontispiece. Picture taken north of Craig, Colorado in July of 2004 by Emily Harrington.

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Justin Lee Harrington

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INTRODUCTION

In the western United States, fragmentation of formerly open habitat by society has been a detriment to ungulate species such as mule deer (*Odocoileus hemionus*), pronghorn (*Antilocapra americana*), and elk (*Cervus elaphus*; Rouse 1954, Mackie 1981, Scott 1992, Kie et al. 1996). Some of the most fragmentive and disruptive activities occurring in ungulate habitat include agriculture and highway construction (Mackie 1981, Clevenger et al. 2001, Forman et al. 2003). Fences associated with these practices may be 1 reason why these activities are so detrimental to wildlife.

If designed improperly, wire fences can kill ungulates by snaring their legs, restraining them in the fence until death occurs (Mackie 1981, Kie et al. 1996). This is called direct fence mortality. Wire fences may also inhibit daily and migrational movements of ungulates, causing indirect mortality (Mackie 1981, Scott 1992) and reducing carrying capacity of ungulate habitats (Rouse 1954, Kindschy et al. 1982, Kie et al. 1996, Forman et al. 2003). Indirect mortality is defined as mortality caused by the fence, even though the ungulate did not get directly caught in the fence.

At present, rotational-grazing systems are becoming popular with ranchers because these systems are more productive. Unfortunately, these rotational grazing systems require more fences (Urness 1976, Wagner 1978). Thus, increased conflict between ungulates and fences will be inevitable unless research is conducted to identify the characteristics of fences that are detrimental to ungulate passage and management techniques are developed to mitigate these conflicts.

Previous fence research has focused on pronghorn–livestock fence interactions, particularly with sheep-tight fences (Rouse 1954, Spillett et al. 1967, Mapston 1970) and

buck-and-pole fences (Scott 1992). Pronghorn are particularly susceptible to fences due to their reluctance to jump obstacles (Scott 1992). Some populations of pronghorn have declined significantly due to a combination of sheep-tight (usually woven wire) fences, harsh weather, and/or unethical hunting (Spillett et al. 1967). Pronghorn typically crawl through or under barbed wire fences (Kie et al. 1996). Due to the lack of contiguous barriers in their past habitat, pronghorn may be innately reluctant to jump vertical barriers. Spillett et al. (1967) stated that pronghorn are able to jump barriers > 2.5 m in height but seem to be unaware of their jumping ability. Rouse (1954) made similar observations. Mule deer and elk, which also live in relatively open habitats, may also exhibit the same reluctance to jump over fences. Previous research on mule deer–fence interactions has focused mainly on exclusionary methods to prevent deer damage to humans (Jones and Longhurst 1958, Reed et al. 1974, Byrne 1989, Lehnert and Bissonette 1997, Clevenger et al. 2001), rather than assessing the risks fences pose to mule deer.

Only limited research has been done on fence-crossing behavior in ungulate species (Mapston 1970, Bauman et al. 1999) and has not ascertained observations for sympatric mule deer, antelope, and elk with multiple fence types. Bauman et al. (1999) and Scott (1992) reported behavior of multiple ungulate species in relation to fences, but these studies were conducted in small areas (<5 km of fence lines), with only a single fence type. Knight et al. (1997) assessed elk preferences in crossing different types of fences and fence modifications but did not observe how ungulates cross fences or assess mule deer or pronghorn relationships with these fences. Papez (1976) conducted a study on mule deer mortality in Nevada and attributed 13% of mule deer mortalities to fence

kills but did not conduct any further research on fence-mortality characteristics. Hence, no studies have yet determined both the characteristics of fence mortality and crossing behavior of multiple ungulate species for multiple fence types over an extensive geographic area.

Many wildlife biologists believe that pronghorn are considerably more vulnerable to fence mortality than elk or mule deer, but no intensive field studies have compared fence-mortality risks of sympatric mule deer, pronghorn, and elk. Fence mortality of mule deer and elk may be underestimated because these species tend to get trapped as individuals, located in less visible areas whereas pronghorn may get caught more frequently in groups during the winter and in more open habitat (Kie et al. 1996, Forman et al. 2003). Additionally, Forman et al. (2003) reviewed literature illustrating ungulate and large carnivore avoidance of roads, which may decrease mortality frequencies in fences along roads. Coincidentally, no research has been conducted to assess the effects of landscape characteristics on fence-mortality frequencies.

Estimates of fence-mortality frequency may also be biased low because of scavenging and removal of carcasses from fences. Scavengers and meso-predators use roads for foraging (Forman et al. 2003). Rapid scavenging of ungulate carcasses caught in fences may reduce the evidence of fence mortality. Unfortunately, how long a carcass remains in a fence (residence time) has not been evaluated. Additionally, occurrence of indirect-fence mortality, that which is a result of ungulates dying due to confinement with in a specific area because of the fence (Mackie 1981, Scott 1992), has not been studied and may lead to further underestimation of fence-related mortality in ungulates.

This study was designed to assess characteristics of mortality and behavior in juvenile and adult elk, mule deer, and pronghorn associated with a variety of fence types found in wildlife habitat. My objectives were to 1) determine how frequently mule deer, pronghorn, and elk are killed by fences, 2) determine what fence characteristics increase lethality of fences to these ungulate species, and 3) determine where and when ungulates are most likely to be killed by fences.

METHODS

Study Area

Research was conducted on approximately 1850 km² in northwestern Colorado and 200 km² in northeastern Utah. Road surveys in Utah were conducted on Diamond Mountain and Blue Mountain. Basic road surveys in Colorado were conducted in Moffat County on Blue Mountain (Harper's Corner Road), Highway 40 from Craig, Colorado to Maybell, Colorado; Highway 13 from Craig to County Road 4, the Great Divide area, and Highway 64–County Road 7 area near Meeker, Colorado. All sites were between 1770 m and 2770 m in elevation. The vegetative communities on Blue Mountain, Great Divide, and Diamond Mountain were predominantly sagebrush (*Artemisia* spp.), although Blue Mountain and Diamond Mountain also had areas with conifer (*Picea* spp. and *Pinus* spp.) and aspen (*Populus tremuloides*) forests. The habitat along Highway 40 was dominated by sagebrush and grassland with some intermixed juniper (*Juniperus* spp.) woodland. The landscape along Highway 40 was mainly agricultural within 5 km of Maybell. The Highway 64–County Road 7 area was adjacent to the White River and its riparian corridor. These riparian areas along Highway 64 were composed of agriculture, willows (*Salix* sp.), and cottonwoods (*Populus* sp.). Areas adjacent to County Road 7 were mainly composed of sagebrush and grassland mixed with juniper woodland. Elk, mule deer, and pronghorn have been observed during my field season on all sites except for Diamond Mountain, where pronghorn were absent.

Fence-Mortality Frequency

To look at the characteristics of fence-related mortality in ungulates over a broad landscape and a variety of different fence types, I regularly surveyed 621 km of roads and 1046 km of fences for this research project. I conducted road surveys on 2 different types of survey routes to look for mule deer, pronghorn, and elk that were caught in wire fences. From these surveys, I could ascertain fence-mortality characteristics for each species and estimate an average occurrence of fence mortality across my study area. I defined a direct-fence mortality as an ungulate carcass that was caught in a fence and an indirect-fence mortality as a carcass located within 10 m of a fence.

Basic Routes. The first portion of my surveys included 6 Basic Routes that were chosen in areas where I expected higher than average fence-mortality frequencies. These surveys increased our sample size of fence mortalities so that we could more accurately infer what fence characteristics were affecting fence mortality. From the surveys done along these Basic Routes, we investigated the mechanisms behind fence mortality. Stretches of roads for the Basic Routes were selected based on local ungulate densities and fence mortalities during the previous year. Basic Routes totaled to 460 km of road with 841 km of fence. Road surveys for fence mortality were conducted on basic sites from early June to early December of 2004, once in April of 2005, and once in June of 2005 on the specified areas. Basic Route surveys were repeated bi-weekly from June to early October of 2004 and monthly from late October to early December of 2004 to minimize the chance of fence-mortality carcasses disappearing before being recorded. These routes were also surveyed once in April and once in June of 2005.

Random Routes. The second portion of my surveys consisted of 10 randomly selected routes, each roughly 16 km in length. Random Routes were surveyed to obtain an annual estimate of fence-mortality occurrence per km of fence so that fence mortality could be quantified across our study site. These Random Routes totaled to 161 km of road and 205 km of fence. I selected Random Routes by road number first and then by starting mile marker using a random-number table. All Random Routes had to have a minimum of 16 km of road and 13 km of fence. Road surveys on Random Routes were conducted monthly from June to December of 2004, once in April, and once in June of 2005.

To assess residence time of fence mortalities, I checked newly occurring mortalities weekly from June to September of 2004, bi-weekly from September to October of 2004, and monthly from November to December of 2004. I also checked newly occurring mortalities in April and June of 2005. Residence time of fence-mortality carcasses was considered to expire when no body parts were left in the fence. An estimated disappearance date was calculated as the midpoint between the last visit to the mortality site when the carcass was present and the first visit after it was missing. This information provided me with a method for estimating carcass residence time in fences and monthly fence mortality rates per km of fence. The residence time information was used to quantify fence mortality occurrence within my study site by averaging the number of carcasses seen per trip along the random routes and multiplying it by the number of weeks in a year (52), divided by the estimated half-life (in weeks) of a carcass.

The average number of carcasses seen per trip was found by taking an average from a survey in July of 2004 and a survey in April of 2005. An annual estimation of

fence-mortality frequency along roads for Moffat County, Colorado was calculated from the 10 Random-Survey Routes on a per-km basis for each species. To estimate these frequencies, I multiplied the average carcasses seen per survey trip ($\bar{x}$) of my surveys by 52 weeks divided by the estimated half-life of a carcass (z), demonstrated by the equation $\bar{x} \times (52 \div z)$, which equals the annual mortality frequency per km of fence.

Walking Surveys. Walking surveys were conducted on parcels of private and public land from early July until mid August of 2004 to determine if there was a difference in direct-mortality frequency (mortalities per km) between fences along roads (hereafter referred to as road fences) and fences away from roads (hereafter referred to as pasture fences). Walking surveys were also used to compare frequencies of indirect-fence mortality between areas with pasture fences and areas without fences or roads. Walking distances ranged from 0.95-1.05 km in length and my surveys of pasture fences began >150 m away from roads. For direct mortality, I compared the frequency of carcasses caught in road fences to that of pasture fences. I acquired 52 paired samples of direct mortality surveys.

For indirect-mortality comparisons, I compared the frequency of carcasses within 10 m of either side of a pasture fence to the frequency of carcasses within 20-m wide walking transects conducted >200 m away from both roads and fences. An indirect mortality was not counted unless >90% of the skeletal structure was present within a 1-m radius of the mortality site. I acquired 51 paired samples of indirect mortality transects. I estimated direct- and indirect-mortality frequencies for pasture fences, road fences, and walking transects away from fences using information from my walking surveys. I recorded the fence type, number of direct- and indirect-fence mortalities, species, age,

and sex of the ungulate (if distinguishable), and how long ago (in weeks) the ungulate appeared to have died.

I used paired t-tests to compare frequencies of direct-fence mortality between road and pasture fences (PROC MIXED in SAS statistical software; SAS Institute 2001). With this comparison we would determine if direct mortality frequencies were different between road fences and pasture fences. Paired t-tests were also used to compare frequencies of indirect-fence mortality between walking transects >200 m away from fences and walking transects along pasture fences (PROC MIXED in SAS statistical software; SAS Institute 2001) to determine if the presence of a fence affected the frequency of carcasses on the ground. Fences along roads were deliberately excluded from this analysis so that the presence of road-killed ungulates did not bias our mortality estimates.

Characteristics of Fence Mortalities and Ungulate-Crossing Behavior

Fence-Mortality Characteristics. For each fence mortality, I recorded fence type, height of each wire strand in fence, how the ungulate was caught, catch level (i.e., the 2 wires that held the ungulate), catch height (i.e., midpoint between the 2 wires that held the ungulate), direction ungulate was headed when it crossed the fence, species, sex, and age (e.g., juvenile or adult) of the ungulate, route name, and a GPS coordinate taken at the site. All numerical measurements were measured to the 0.01 m and reported in m within the results section. In addition, mortality sites were photographed and flagged for future reference.

To identify the characteristics of fences which contributed to increased risk of ungulate mortality, I compared fence characteristics at mortality sites to those 1) directly across the road from them (adjacent sites), 2) where I observed ungulates successfully traversing a fence (crossing sites), and 3) selected at random (random sites). I selected a random site by determining a random distance within 1 km of the mortality location, using a random-number table.

Non-numeric characteristics of fence mortalities were compared among species and age classes of ungulates using chi square tests (PROC FREQ in SAS statistical software; SAS Institute 2001). Numerical fence measurements were compared among species and between age classes of fence mortalities via *F*-tests (PROC GLM in SAS statistical software; SAS Institute 2001). Numerical and non-numerical fence measurements of mortality sites were also compared to random sites, and adjacent sites, and crossing sites using chi square tests (PROC FREQ in SAS statistical software; SAS Institute 2001) and paired t-tests (PROC MIXED in SAS statistical software; SAS Institute 2001).

Fence-Crossing Characteristics. Road surveys were conducted in June of 2004, August of 2004, and April of 2005 on each of the 6 Basic Routes to assess fence-crossing behavior exhibited by free-ranging ungulates. A morning survey (dawn to 2 hours after dawn) and an evening survey (2 hours before dusk to dusk) were conducted for each month surveyed. At crossing sites I measured fence characteristics, distance of ungulate from observer, whether or not the ungulate appeared to be reacting to the presence of observer, number of attempts to cross the fence, success, method used to cross the fence, and any physical contact the ungulate made with the fence.

Chi square tests (PROC FREQ in SAS statistical software; SAS Institute 2001) were used to compare species and age differences in fence-crossing behavior, catch level (i.e., caught between which two wires), body part caught in fence, and crossing direction among species and age classes. Additionally, I compared actual crossing direction proportions to an assumed 50:50 expected distribution via a chi square test (PROC FREQ in SAS statistical software; SAS Institute 2001) to determine if there was a significant effect of road presence on the direction ungulates were traveling when they got caught.

Location of Fence Mortalities

Densities and Species Composition. I wanted to determine if fence-mortality frequencies were related to local ungulate densities. To test this, counts of live ungulates in the surrounding areas were conducted in July, September, and December of 2004 on all 6 Basic Routes to obtain a species composition and density index for these routes. Counts were only conducted on Basic Routes and not Random Routes. These counting surveys were conducted at dawn and dusk for each month being surveyed. Every time I spotted an ungulate, I recorded the species, age (juvenile or adult), time spotted, odometer reading, GPS location, distance and direction from the observer, habitat, presence of fence or fence type, presence in or outside the right-of-way, and behavior (e.g. feeding, resting, traveling) of the ungulate.

From these data, I developed indices of ungulate occurrence per km in the surrounding habitat and ungulate presence in the right-of-way per km from my morning and evening herd composition counts. I used these indices to evaluate the relationships among ungulate occurrence in the surrounding area, ungulate occurrence in the right-of-

way, and fence-mortality frequencies across sites. This information was also used to estimate relative species and age vulnerability to fence mortality by comparing proportions of species and ages among ungulate occurrence data and fence mortalities. Additionally, I used this same information to illustrate the relative risk of mortality associate with each fence type.

The ratios of fence mortalities to ungulates in the right-of-way and ungulates in the surrounding area were calculated to illustrate the relative risks of direct-fence mortality associated with each fence type. I tested for differences between samples of woven-wire and barbed-wire fences in my walking surveys to see if fence type had an effect on indirect-fence mortality. I also determined the fence types along all roads included in all survey routes so as to classify all fence types in my study area and quantify their respective lengths along each route.

I tested for differences in species and age composition of the surrounding ungulate populations along the Basic Routes to the species and age composition of fence mortalities along those routes using chi square tests (PROC FREQ in SAS statistical software; SAS Institute 2001) to sort out differences among species or age class vulnerabilities. Chi square tests were also used to compare fence type frequency among ungulate-occurrence observations, right-of-way observations, and mortality observations (PROC FREQ in SAS statistical software; SAS Institute 2001) to show any evidence for elevated risk associated with any particular fence type.

After the length of each fence type was quantified, Pearson correlation statistics were used to illustrate any relationships among fence mortalities and ungulate occurrence in the right-of-way (PROC CORR in SAS statistical software; SAS Institute 2001). The

close relationship between ungulate occurrence in the surrounding habitat and ungulate occurrence in the right-of-way was illustrated by a simple linear regression (PROC REG in SAS statistical software; SAS Institute 2001). I then proceeded to split direct-fence mortality and occurrence observations by species and age to test any differences in fence type frequency between mortality and occurrence observations via Chi Square tests so that I could see which types of fences were significantly more dangerous to particular species and age classes of ungulates (PROC FREQ in SAS statistical software; SAS Institute 2001). Additionally, paired t-tests (PROC MIXED in SAS statistical software; SAS Institute 2001) and unpaired t-tests (PROC GLM in SAS statistical software; SAS Institute 2001) were used to compare frequency of indirect-fence mortality among woven-wire fences, barbed-wire fences, and corresponding transects that did not include fences to further illustrate the effects of fence type on indirect-fence mortality.

Landscape Factors. I wanted to determine whether landscape patterns, such as watering locations and crossing corridors, influenced local mortality frequencies. To do this, I first recorded the GPS locations of fence mortalities, waterholes, and observed crossing locations on 3 of my survey routes (Diamond Mountain, Meeker, and Great Divide). Each set of points was then overlaid as a separate coverage into ARCVIEW GIS (Environmental Systems Research Institute, 1999). A 200-m buffer was then added to each set of points, and proportions of mortalities and road km inside and outside each buffer were determined prior to analyses. I determined that a 200-m buffer was the optimal size because ungulates were not observed to travel more than 150 m along a fence to find a place to cross.

I used ARCVIEW GIS (Environmental Systems Research Institute, 1999) to search for spatial relationships among GPS locations of fence mortality, observed fence crossings, and watering holes. For my GIS analysis, I used the buffering tool to place a 200-m buffer around points representing observed crossing locations and watering holes (Lambert's Conformal Conic Projection with NAD 1983 datum; Environmental Systems Research Institute, 1999). Chi square tests were then conducted to compare the proportion of direct-fence mortalities to the proportion of road-length inside and outside these buffers for each set of points (PROC FREQ in SAS statistical software; SAS Institute 2001). These tests were conducted to investigate the effects of fence-crossing corridors and watering holes on local frequencies of direct-fence mortality.

Traffic volumes for county roads were assessed using a pneumatic road counter and sampling every day for ≥ 6 days (weekends always included) for each of the 11 county roads (10 unpaved and 1 paved) used in my analysis. The traffic count was then quantified into the number of cars per day for each road. I also used the Colorado Department of Transportation website to obtain traffic counts for 7 state and federal highways that were located within my study site. Fence mortality frequency (i.e., mortalities per km) and an index of ungulate densities within the right-of-way (i.e., ungulates per km) were compared to the traffic volume of the respective road via inferential statistics.

Frequencies of fence mortalities along roads of differing traffic volumes were tested by Spearman-rank correlations (PROC CORR in SAS statistical software; SAS Institute 2001). Right-of-way frequencies were also compared with traffic volumes and mortality frequencies using Spearman-rank correlations (PROC CORR in SAS statistical

software; SAS Institute 2001). These tests illustrated the relationships among fence mortality, right-of-way presence, and traffic volume along roads in my study site. I also compared these indices and fence mortality frequencies between paved and unpaved roads using F -tests (PROC GLM in SAS statistical software; SAS Institute 2001). This comparison provided an additional illustration of the effect of roads on frequency of fence mortalities and ungulate patterns in the right-of-way. Statistical significance on all tests was determined at $P \leq 0.05$.

RESULTS

I found 133 mortalities in fences along my Basic and Random Routes. I found 23 additional fence mortalities outside of these routes. There were 43 new fence mortalities found on all routes from 1 June 2004 to 17 June 2005 that were included in the 133 mortalities along our routes.

Fence-Mortality Frequency

The highest frequencies of fence mortality occurred in August and January (Figure 1). Approximately 30% of carcasses disappeared within 10 weeks and 40% within 24 weeks (Figure 2). This disappearance can be expressed mathematically by $y = -3.0(x) + 94.9$ ($r^2=0.88$; Figure 2), where y is the percent of ungulate carcasses still present in the fence and x is the number of weeks after the catch date. I used the

Figure 1. Number of new mortalities found in the 984 km of fences along all regular survey routes (Basic and Random) from June 2004 to June 2005.

Figure 2. The disappearance of fence-mortality carcasses ($n = 24$) over time.

above equation to interpolate a 25.9 week half-life for direct-fence mortalities. From this information, I calculated an average annual mortality occurrence of 0.14 ungulates/km of fence (i.e., 0.044 mule deer, 0.063 pronghorn, and 0.034 elk) along roads using the average number of carcasses seen per trip and the above residence time information.

Walking surveys were conducted on both private land (67%) and public land (33%; $n = 52$). When comparing direct-mortality frequencies in road fences ($\bar{x} = 0.25$ mortalities/km, $SE = 0.08$) to those in pasture fences ($\bar{x} = 0.40$ mortalities/km, $SE = 0.13$), I found no significant difference ($t_{51} = 1.34$, $P = 0.19$) even though fence-mortality rates were 61% higher in pasture fences. Indirect-mortality frequencies were higher ($t_{50} = 3.84$, $P < 0.001$) in transects conducted along pasture fences ($\bar{x} = 1.3$ indirect mortalities/km, $SE = 0.2$) when compared to control transects located away from fences ($\bar{x} = 0.4$ indirect mortalities/km, $SE = 0.1$).

Characteristics of Fence Mortalities and Ungulate-Crossing Behavior

Fence-Mortality Characteristics. Juveniles made up 79%, 58%, and 80% of all mule deer, pronghorn, and elk mortalities, respectively. Differences in age-specific mortality among species were significant ($\chi^2 = 6.81$, $P = 0.03$). Most mule deer (68%), pronghorn (81%), and elk (87%) got caught while attempting to jump the fence. How ungulates crossed fences when they got caught did not differ by species ($\chi^2 = 4.82$, $P = 0.09$). Additionally, 69% of juvenile and 77% of adult fence mortalities got caught while attempting to jump fences ($\chi^2 = 0.84$, $P = 0.36$). Getting caught between the top 2 wires was the leading cause of death in all species (Table 1) and all age classes (Table 2). However, elk were more likely to get caught between the second and third wires of the fence than were mule deer or pronghorn ($\chi^2 = 10.74$, $P = 0.03$; Table 1). Elk got caught by the front legs more frequently than mule deer and pronghorn ($\chi^2 = 13.78$, $P = 0.008$; Table 3). There were no differences in how juveniles and adults got caught in fences ($\chi^2 = 1.27$, $P = 0.53$; Table 4). The proportion of ungulate traveling away from the roadway when getting caught in the fence (54%) did not differ from expected rate of 50% ($n = 147$; $\chi^2 = 0.41$, $P = 0.521$).

Table 1. Percent of mule deer, pronghorn, and elk caught between different fence wires in fence-mortality samples.

Catch level	Species		
	Mule deer ($n = 78$)	Pronghorn ($n = 40$)	Elk ($n = 30$)
Between top two wires	56.4	75.0	46.7
Between second and third wires	26.9	10.0	43.3
Lower than third wire	16.7	15.0	10.0

Table 2. Percent of adults and juveniles caught between different fence wires in fence-mortality samples.

Catch level	Age Class		χ^2	P
	Juveniles (n = 112)	Adults (n = 39)		
Between top two wires	58.0	66.7	0.92	0.63
Between second and third wires	26.8	20.5		
Lower than third wire	15.2	12.8		

Table 3. Percent of mule deer, pronghorn, and elk caught by different body parts in fence mortalities.

Body part	Species		
	Mule deer (n = 82)	Pronghorn (n = 41)	Elk (n = 30)
Caught by front leg	6.1	9.8	30.0
Caught by rear leg	86.6	78.0	66.7
Caught by abdomen	7.3	12.2	3.3

Table 4. Percent of adults and juveniles caught by different body parts in fence mortalities.

Body part	Age Class	
	Juveniles (n=65)	Adults (n=15)
Caught by front leg	10.7	10.8
Caught by rear leg	81.3	86.5
Caught by abdomen	8.0	2.7

Mortality Sites versus Adjacent Sites. When all ages were combined, I found that mortality-fence height ($\bar{x}$ = 1.08, SE = 0.02) was greater than adjacent-fence height ($\bar{x}$ = 0.99, SE = 0.02) in mule deer and elk (t_{66} = 3.02, P = 0.004). For juveniles of all species,

fence height at mortality sites ($\bar{x} = 1.05$, $SE = 0.01$) was greater than that of adjacent-fence sites ($\bar{x} = 0.97$, $SE = 0.02$; $t_{61} = -3.17$, $P = 0.002$). Conversely, fence heights at mortality sites for adults ($\bar{x} = 1.34$, $SE = 0.25$) were not different from adjacent sites ($\bar{x} = 1.06$, $SE = 0.02$; $t_{23} = -0.94$, $P = 0.358$). Additionally, Figure 3 shows that 70% of fence mortalities were in fences taller than 1 m in height.

Mortality Sites versus Random Sites. When comparing mortality sites to their respective randomly chosen sites (all species pooled together), the distance between the top 2 wires was significantly less at mortality sites ($\bar{x} = 0.16$, $SE = 0.01$) than at the random sites ($\bar{x} = 0.19$, $SE = 0.01$; $t_{51} = 2.01$, $P = 0.05$). When mule deer samples were analyzed separately, I found the distance between the top 2 wires to be less ($t_{27} = -2.28$, $P = 0.03$) at the mortality sites ($\bar{x} = 0.15$, $SE = 0.02$) than at the random sites ($\bar{x} = 0.18$, $SE = 0.01$). I also found the distance between the top 2 wires to be less and the right-of-way

Figure 3. Histogram showing the proportions of mortality sites ($n = 71$) and random sites ($n = 71$) in each bin for fence height.

distance to be greater at mortality sites than random sites for juvenile mortalities (Table 5). Additionally, Figure 4 shows that 73% of fence mortalities were in fences where the distance between the top 2 wires was ≤ 20 cm.

Mortality Sites versus Crossing Sites. For all species, distance between top 2 wires (Table 6) was less at mortality sites, while fence height (Table 6) and right-of-way distance (Table 6) were greater at mortality sites than they were at crossing sites.

Ungulate-Crossing Characteristics. I observed 101 ungulates (70 mule deer, 27 pronghorn, and 4 elk) cross fences. Jumping was the most common method used in crossing fences in all species (73%, $n = 136$). Mule deer and pronghorn did not differ in their use of fence crossing methods (Table 7). However, my age-specific comparison of crossing methods yielded statistical evidence ($\chi^2 = 40.52$, $P < 0.001$) that adult mule deer and pronghorn jumped more (98%) than juveniles of those species (44%).

Figure 4. Histogram showing the proportions of mortality sites ($n = 52$) and random sites ($n = 52$) in each bin for the distance between the top 2 wires.

Table 5. Paired t-tests comparing fence characteristics at mortality sites and random sites for juveniles.

Variable	Site Type				df	t	P
	Mortality		Random				
	$\bar{x}$	SE	$\bar{x}$	SE			
Fence height (m)	1.04	0.02	1.05	0.01	38	-0.57	0.57
Distance between top 2 wires (m)	0.15	0.01	0.19	0.01	37	-3.04	0.004
Right-of-way distance (m)	16.20	2.69	10.72	0.91	38	2.04	0.05

Table 6. Means, standard errors, and t-test results comparing fence characteristics at crossing sites and mortality sites for all species.

Variable	Site Type				df	t	P
	Crossing		Mortality				
	$\bar{x}$	SE	$\bar{x}$	SE			
Fence height (m)	1.01	0.01	1.07	0.01	252	6.29	0.01
Adjacent fence height (m)	1.05	0.02	1.02	0.01	164	1.01	0.32
Distance between top 2 wires (m)	0.20	0.01	0.17	0.01	249	5.35	0.02
Right-of-way distance (m)	12.49	0.76	19.18	1.81	216	10.45	0.001

Table 7. Percent of different crossing methods in pronghorn and mule deer observations.

Crossing Method	Species-Specific Observations		χ^2	P
	Mule deer ($n = 70$)	Pronghorn ($n = 27$)		
Crossing under	2.9	7.4	1.98	0.37
Crossing through	5.7	11.1		
Jumping over	91.4	81.5		

Location of Fence Mortalities

Densities and Species Composition. Ungulate occurrence in the surrounding area and ungulate occurrence in the right-of-way were autocorrelated ($R^2 = 0.94$, $F = 545.89$,

$P < 0.001$) therefore I did not use ungulate occurrence in the right-of-way as an independent variable. I found a positive correlation between fence mortalities and ungulates occurring in the surrounding habitat ($r = 0.91$, $P < 0.001$, $n = 33$; Figure 5). Mule deer were found to use the right-of-way more often than pronghorn or elk (Table 8). This led to mule deer making up a higher proportion of fence mortalities than expected based on ungulate occurrence in the surrounding habitat (Table 9). However, when comparing fence mortalities to right-of-way observations, I found that mule deer mortality was lower than expected, whereas pronghorn and elk mortality was higher than expected (Table 10). These findings may illustrate that mule deer are at an overall higher risk because they interact with the right-of way fences more often, but in general pronghorn and elk may be at higher risk when they ultimately have to interact with fences.

Figure 5. Scatter plot of ungulate presence in the surrounding area against fence mortalities.

Table 8. Percent of each species in ungulate occurrence in the surrounding habitat compared to ungulate presence in the right-of-way.

Species	Observation Type		χ^2	P
	Habitat (n = 15597)	Right-of-way (n = 984)		
Mule deer	45.6	79.2	440.02	<0.001
Pronghorn	41.4	11.2		
Elk	13.0	9.7		

Table 9. Percent of each species in fence mortality compared to ungulate occurrence in the surrounding habitat.

Species	Observation Type		χ^2	P
	Fence mortalities (n = 114)	Habitat (n = 15597)		
Mule deer	60.5	45.6	14.76	<0.001
Pronghorn	23.7	41.4		
Elk	15.8	13.0		

Table 10. Percent of each species in fence mortality compared to ungulate occurrence in the right-of-way.

Species	Observation Type		χ^2	P
	Fence mortalities (n = 114)	Right-of-way (n = 984)		
Mule deer	60.5	79.2	21.14	<0.001
Pronghorn	23.7	11.2		
Elk	15.8	9.7		

Juveniles of all species made up a higher proportion ($\chi^2_1 = 138.87$, $P < 0.001$) of mortalities (81%) than their proportions observed in the surrounding area (30%).

Juveniles of all species also made up a higher proportion ($\chi^2_1 = 91.65$, $P < 0.001$) of fence mortalities (81%) than their proportion observed in the right-of-way (35%). These

proportions also illustrate that juveniles are 8 times more likely than adults to get caught in fences.

Fence types that included woven wire killed more ungulates (83%) than expected ($\chi^2 = 14.86, P < 0.001$), based on the proportion of ungulates in the surrounding habitat of these fences (67%). I found that woven wire with 1-strand barbed wire was considerably more deadly than woven wire topped with 2-strands of barbed wire or 4-strand barbed-wire fences (Table 11; Figure 6) when fence mortalities were compared to ungulate occurrence in the surrounding habitat. Concurring, I had similar results (Table 12; Figure 7) when comparing proportions of fence mortalities in these fence types to those of right-of-way observations. Although they only comprised 1.8% of the total distance of fences on my study area, fence types that included smooth wire and fence types that included a top rail had no mortalities.

Landscape Factors. The proportion of fence mortalities (18 %) was higher ($\chi^2 = 4.16, P = 0.04$) within 200-m of waterholes than expected based on the proportion of road length (14%). The proportion of fence crossings (28%) was significantly higher (χ^2

Table 11. Percent of fence mortality in each fence type compared to ungulate occurrence in the surrounding habitat.

Fence type	Observation Type		χ^2	P
	Fence mortalities (n = 96)	Occurrence (n = 11805)		
WW ^a with 1-strand BW ^b	53.1	32.2	21.93	<0.001
WW with 2-strand BW	34.4	39.4		
4-strand BW	12.5	28.4		

^a WW = woven wire

^b BW = barbed wire

Figure 6. Mean ratios of fence mortalities to ungulate occurrence (number observed per km) in the surrounding habitat.

^a WW = woven wire, BW = barbed wire, TMW = Triangle mesh wire

= 4.16, $P = 0.04$) within 200-m of waterholes based on the proportion of road length

(11%). The proportion of fence mortalities (26%) was also higher ($\chi^2 = 5.77$, $P = 0.02$)

within 200 m of observed crossing locations based on road length proportions (9%).

When compared to unpaved roads, paved roads had more cars per day (CPD;

Table 12. Percent of fence mortality in each fence type compared to ungulate presence in the right-of-way.

Fence type	Observation Type		χ^2	P
	Fence mortalities (n=96)	Right-of-way (n=719)		
WW ^a with 1-strand BW ^b	53.1	33.8	17.01	<0.001
WW with 2-strand BW	34.4	38.0		
4-strand BW	12.5	28.2		

^a WW = woven wire

^b BW = barbed wire

Figure 7. Mean ratios of fence mortalities to ungulate occurrence (number observed per km) in right-of-way.

^a WW = woven wire , BW = barbed wire, TMW = Triangle mesh wire

Table 13), fewer ungulates present within the right-of-way per km (U/km; Table 13), and fewer fence mortalities per km (M/km; Table 13). Spearman-rank correlation tests were used because the relationship between CPD and M/km was curvilinear in nature (Figure 8); as was the relationship between CPD and U/km (Figure 9). For all roads combined,

Table 13. Effect of road type on traffic volume, fence mortalities, and number of ungulates in the right-of-way.

Variable	Road Type				df	F	P
	Paved		Unpaved				
	$\bar{x}$	SE	$\bar{x}$	SE			
Cars per day	732.3	233.7	46.7	11.8	1, 16	10.88	0.005
Mortalities per fence km	0.1	0.0	0.2	0.0	1, 16	10.40	0.005
Right-of-way presence per fence km	0.4	0.1	1.2	0.3	1, 15	7.18	0.017

Figure 8. Scatter plot of fence mortalities per km of fence (M/km) against cars per day (CPD), with the resulting relationship included.

Figure 9. Scatter plot of fence ungulates in the right of way per km of fence (A/km) against cars per day (CPD), with the resulting relationship included.

my analyses resulted in a negative correlation between CPD and M/km ($r = -0.70$, $P < 0.001$), a negative correlation between CPD and U/km ($r = -0.74$, $P < 0.001$), and a strong positive correlation between M/km and U/km ($r = 0.84$, $P < 0.001$).

When comparing woven-wire pasture fences with barbed-wire pasture fences from my walking surveys, I found higher rates of indirect-fence mortality along woven-wire fences, whereas there were no differences between their respective control transects (Table 14). When woven-wire and barbed-wire pasture fences were compared to their paired control transects, woven-wire fences had significantly higher rates of indirect-fence mortality as opposed to barbed-wire fences (Table 15). There was a similar indirect-mortality rate between barbed-wire fences and their paired controls (Table 15).

Table 14. Number of carcasses per km within 10 m of barbed-wire and woven-wire fences and 20-m wide transects conducted away from barbed-wire and woven-wire fences.

Sample type	Fence Type				<i>df</i>	<i>t</i>	<i>P</i>
	Barbed wire		Woven wire				
	$\bar{x}$	SE	$\bar{x}$	SE			
Along fence (<i>n</i> = 38,14)	0.3	0.1	1.6	0.2	51	9.90	0.003
Away from fence (<i>n</i> = 38,13)	0.5	0.2	0.4	0.1	50	0.85	0.36

Table 15. Number of carcasses per km within 10 m of fences and 20-m wide transects conducted away from fences for both barbed-wire and woven-wire fences.

Fence type	Sample Type				df	t	P
	Along fences		Away from fences				
	$\bar{x}$	SE	$\bar{x}$	SE			
Woven-wire fences	1.6	0.2	0.4	0.1	37	4.74	<0.001
Barbed-wire fences	0.2	0.1	0.5	0.2	12	-1.24	0.24

DISCUSSION

How Often Are Ungulates Killed by Fences?

Based on a carcass half life of 25.9 weeks, I calculated an annual fence mortality rate of 0.14 mortalities/km of fence (0.044 mule deer/km, 0.063 pronghorn/km, and 0.034 elk/km) for direct mortalities caught in right-of-way fences across my study area. This estimate of fence mortality is corrected for carcass disappearance. Fence mortalities disappeared primarily because of scavenging. I observed turkey vultures (*Cathartes aura*), golden eagles (*Aquila chrysaetos*), common ravens (*Corvus corax*), black-billed magpies (*Pica pica*), and ground squirrels (*Spermophilus sp.*) scavenging on carcasses. Canid scat and tracks were observed at numerous fence-mortality sites. In addition, some fence mortalities may have disappeared because of humans. Most ungulates that get caught in fences will damage the fence in their attempts to escape. Ranchers and road workers notice the damaged fence and remove the carcass (even if just bones are present) to repair the fence.

To estimate the additional error associated with missing fence mortalities while driving, I compared the rate of mortalities found/km observed from driving my Basic Routes to the rate of mortalities/km observed during my walking surveys. Given that my walking surveys were randomly distributed throughout my Basic Routes, I consider the difference in proportion between the 2 estimates the amount of error associated with missing carcasses while driving. From this, I estimated that I saw 55% of all fence mortalities along the road while driving, which means the corrected annual mortality rate

estimation is 0.25 mortalities/km of fence (0.078 mule deer mortalities/km, 0.113 pronghorn mortalities/km, and 0.061 elk mortalities/km).

To estimate an average rate of indirect mortality due to fences, I first subtracted the mean annual indirect-mortality rate found away from fences (0.82 indirect mortalities/km) from the mean indirect-mortality rate found along fences (2.51 indirect mortalities/km). This adjusted annual rate (1.69 indirect mortalities/km) from our walking surveys was 208% of direct mortalities (0.8 direct mortalities/km) found in our walking surveys. From this information, I estimated an annual rate of 0.52 indirect mortalities/km based on the assumption that the half-life of an indirect mortality is similar to a direct mortality. When added, direct and indirect mortality equaled 0.77 mortalities/km.

Some of these indirect mortalities may have been initially direct mortalities that scavengers or people removed from the fences. However, most of the indirect mortalities were found to be in body positions indicative of an ungulate curling up and dying on the ground, whereas fence mortalities taken out of the fence would have had straightened legs and marks where wire strands had cut into their flesh. Additionally, different portions of direct fence mortality carcasses were removed at different times by scavenging. Usually the legs not caught in the fence would disappear first, followed by the head, and then the abdomen would be taken. This scavenging process would eliminate the possibility of finding >90% of a carcass within a 1-m radius on the ground.

Some indirect mortalities were probably ungulates weakened by injuries, disease, or malnutrition that no longer had the strength to cross the fence, and because of this, died next to it. Some may also have been kills that predators made by cornering

ungulates into fences (Knowlton 1968, Byers 2003). The vast majority (>90%) of indirect mortalities were fawns that probably got separated from their mothers when the mothers crossed the fence and the fawns could not. This mainly happened with woven-wire fences.

Regardless of their cause, indirect mortalities indicate that fences can kill ungulates by methods other than ensnaring them. My previous calculations indicate that direct mortality was a minority of total fence mortality. Although I did not measure it, another threat that fences pose to ungulates is lessening the ability of ungulates to move across the landscape and in some cases may confine them in a particular area for prolonged periods of time (Mackie 1981, Scott 1992). By doing so, impassable fences reduce the ability of ungulates to exploit the resources contained within their home range in an optimal fashion, thereby reducing their ability to survive and reproduce.

What Is the Economic Cost of Fence Mortalities?

When ungulates get caught in fences, they often destroy or damage the fences in their efforts to escape. Fence damage causes economic harm to landowners (Lacey et al. 1993, Andrews and Rowley 1998) due to both livestock losses and the time or materials required to fix the damaged fences. Unfortunately, few studies have quantified economic losses from these conflicts. Andrews and Rowley (1998) estimated that deer and elk caused \$3,341 worth of fence damage per Oregon rancher in 1997. Lacey et al. (1993) found an average annual loss of \$282 per rancher in southwestern Montana due to fence damage by wildlife.

Of course, the main loss from ungulate–fence conflicts is not damage to the fence, but the death of the ungulate, which I estimated at \$209 for mule deer, \$209 for pronghorn, and \$349 for elk. This information was derived by using a \$209 estimated value of mule deer (Loomis et al. 1989) and adjusting the values for pronghorn and elk based on the ratio of hunting tag prices for each species in Colorado. Based on these estimates of ungulate values, I estimated an annual cost of \$61/km of fence for direct mortalities (\$16 for mule deer, \$24 for pronghorn, and \$21 for elk) and \$188/km for both direct and indirect mortalities. This information may be useful for constructing cost-share programs in mitigating ungulate-fence conflicts.

Why Do Ungulates Get Caught in Fences?

Many fence mortalities occurred during August when juveniles start to follow their mothers back and forth between foraging areas and resting areas. These daily movements often require the young to cross fences. Unfortunately, juveniles are inexperienced at negotiating fences, and their mothers may not realize how much of a barrier a fence may pose for their offspring. In their desperation to keep up with their mothers, young juveniles try to crawl through fences and may use such force to squeeze through that they get stuck by their hips, and cannot escape. Another dangerous time for juveniles is when they have grown too large to crawl through woven-wire fences, and they are forced to jump fences before they have developed the strength and size to do so successfully. Hence, it is not surprising that in my study site, juveniles were 8 times more likely than adults to die in fences. Sundstrom (1967), Mackie (1981), and Kie et al.

(1996) also stated that fences pose a higher risk to juveniles than to adults, although they did not quantify this risk.

Another peak in fence mortalities occurred during January when many fawns and adults were caught. Most of these ungulates were caught trying to jump fences. During mid-winter at my study site, ungulates are nutritionally stressed and weak. Under such conditions, they need to minimize their expenditure of energy and therefore may use as little energy as possible to jump a fence. Due to this, some individuals err on the side of being too conservative in their jumping efforts. This causes the ungulate to make contact with the fence and sometimes they become entangled. As deer and pronghorn jump, they commonly tuck their legs underneath their abdomen, which causes the lower tarsal bones in the rear legs to be protruding and vulnerable (Figures 10 and 11). If an animal does not jump high enough, the top wire will scrape along its abdomen so that the top wire passes beneath the body but above its rear legs. When some ungulates feel the wire touching their abdomens, I observed them to extend their back legs while still in the act of jumping in an attempt to kick off from the top wire of the fence to gain more height. Sometimes this effort is successful in giving the ungulate the extra boost it needs to clear the fence. However, if the ungulate misses the top wire with its feet, it gets caught between the top 2 wires. Once the ungulate is caught, it hits the ground and kicks with its back legs, thrashing about trying to free itself. Sometimes these efforts are successful and the animal frees itself. Other times, the wires twist tight enough around the legs that the animal is held fast. I do not know what proportion of the ungulates are able to free themselves and what proportion cannot. However, once upside-down with its rear end above its head, the ungulate will not live long due to circulator failure.

Figure 10. Picture (by Emily Harrington) of typical jumping technique exhibited by mule deer on my study area.

Figure 11. Photo (by Emily Harrington) of typical jumping technique exhibited by pronghorn on my study area.

Are There Interspecific Differences in Fence-Crossing Behavior?

I found no evidence that mule deer and pronghorn were any different in their fence-crossing methods. When comparing crossing observations between the 2 species, I found jumping was the method used most frequently. This contradicts previous reports (Scott 1992, Kie et al. 1996, Spillet 1967, and Rouse 1954), suggesting pronghorn rarely jump fences. Mapston (1970) stated that only 21% of pronghorn jumped fences in his observations whereas the rest went through or under fences. In my study area, 81% pronghorn jumped fences and 19% went through or under fences. Additionally, Spillet et al. (1967) estimated that 0.82 m was the maximum fence height that adult pronghorn could readily jump. In my study, pronghorn easily jumped fences >1.0 m in height without making contact with the fence.

Perhaps the pronghorn in my study site were better at fence jumping than pronghorn occupying open plains or flat deserts because the geography of my study site was different. My study area was mostly rugged, broken by gullies, ravines, and covered in sagebrush (*Artemisia spp.*). My study site also had a high density of fences. In my study site, pronghorn may have gained more experience jumping over obstacles at an earlier age than pronghorn in open, flat terrain with fewer fences. The inability of pronghorn located elsewhere to jump over fences may be a result of conditions that are not conducive to learning. These conditions may include infrequent fences in their habitat and seasonal migrations between heavily fenced landscapes and landscapes with few or no fences. It is also possible that pronghorn at my study site are better jumpers than those located elsewhere because they were in better health due to excellent forage

conditions on my study site or to genetic differences. Pronghorn within my study site that cannot jump fences would have a considerably lower probability of survival than those that can because there are high fence densities across my study site and these pronghorn are not known to migrate into areas with few or no fences. Due to my pronghorn living in fenced landscapes constantly throughout the year, the effects of fences upon these pronghorn were stronger. Hence, natural selection may have been taking place and as a result, better jumping ability is manifested in the pronghorn on my study site.

There were different jumping styles exhibited by different species on my study area. In contrast to mule deer and pronghorn, elk had a more stiff-legged style of jumping fences (Figure 12). Due to their more lumbering style of jumping, elk were more likely than mule deer and pronghorn to use their larger body mass to plow through fences, which caused more damage to fences. They also were more likely to get caught by their front legs than mule deer or pronghorn. Based on their occurrence in the study site, individual mule deer had a higher probability of getting caught in fences than either elk or pronghorn. I also found that mule deer were more often found within road right-of-ways than the other 2 species. Due to this, it appears that mule deer have a higher probability of being caught in a fence simply because they crossed fences and fed in the right-of-way more often than pronghorn and elk. Kie et al. (1996) also stated that fences have caused far greater mortality to mule deer than to pronghorn, though he cited no specific data to support this.

Figure 12. Picture (courtesy of iLoveOregon.com) of typical jumping technique exhibited by elk on my study area.

Which Fence Characteristics Contribute to Ungulate Mortality?

I wanted to identify fence characteristics that contributed to their lethality to ungulates. To do so, I compared the fence characteristics at mortality sites to fence characteristics at 1) sites where I saw ungulates successfully cross a fence, 2) sites directly across the road from mortality sites, and 3) randomly selected sites. When I compared fence types, I discovered that fences containing woven wire were significantly more dangerous than those made of only barbed wire. This was true for both indirect- and direct-fence mortality. In the literature, woven-wire fences are considered

detrimental to both mule deer and pronghorn (Connolly 1981, Spillett et al. 1967).

Riddle and Oakley (1972) found that dead pronghorn were located along woven-wire fences more frequently than expected based on the proportion of fence types within their samples. My analyses showed that woven-wire fences were especially lethal to juveniles. Sundstrom (1967), Mackie (1981), and Kie et al. (1996) all agreed that juveniles are particularly impacted by woven-wire fences because they are smaller and weaker than adults, and fences pose a more significant barrier to them. In my study site, the safest of all fence types appeared to be smooth-wire fences and fences including a top rail in their construction, but these fence types were too uncommon to allow statistical comparisons.

I found that woven-wire fences that were topped by a single strand of barbed wire were more dangerous than woven-wire fences topped by 0 strands of barbed wire, and woven wire topped by 2 strands of barbed wire. The reason that woven-wire fences with a single strand of barbed wire are so lethal may be due to the coupling of the rigidity of woven wire and the snagging ability of barbed wire. In many fence mortalities, the barbed wire, when twisted into the woven wire, would snag into the flesh of the ungulate and lock the ungulate's leg into the top rung of the woven-wire fencing. However, when woven-wire fences were topped by 2 strands of barbed wire, the ungulate would usually get its legs caught between these two strands. When 2 strands of barbed wire were twisted together, they were often flimsy enough so that the ungulate could jerk itself out of the fence with minor injuries. Furthermore, a woven-wire fence by itself is too stiff to twist around a leg of an ungulate, and without the extra strand(s) of barbed wire, these fences were usually short enough for most ungulates to cross with ease.

Many state highway departments have regulations on right-of-way fence characteristics (Denney 1964), and most of these fence regulations specify distances >0.30 m between the top 2 wires. This coincides with recommendations given by Anderson (1980), the U.S. Bureau of Land Management (1985), and Kie et al. (1996). My results on spacing of the top 2 wires support these specifications. Fence height recommendations in the literature vary from 0.91 m (Rouse 1954) for areas with pronghorn to 1.07 m (Anderson 1980) for areas with mule deer or elk. The mean fence heights at fence-mortality sites in my study area are greater than the respective recommended fence heights for all 3 species. Hence, I have no evidence that these fence-height recommendations are inappropriate. Additionally, my histograms on fence height and distance between the top 2 wires show that if these fence recommendations were put into practice, considerable ungulate mortality would be averted.

Where Do Fence Mortalities Occur?

I wanted to identify where most fence mortalities were occurring because it would be these sites where modifying fences to make them safer to ungulates would create the greatest benefit. I found that fence mortality sites were highly correlated with ungulate numbers in the surrounding areas. Also, the frequency of fence mortalities along right-of-way fences decreased as traffic volumes increased. This relationship probably existed because the number of ungulates present within the right-of-way per km also decreased as traffic volumes increased. These findings point to the greater need of fence mitigation in areas with high ungulate densities and along roads with low traffic volumes. For

instance, it would be more worthwhile to modify fences so that they were less lethal to ungulates along dirt roads than paved roads.

I found higher rates of fence mortalities within 200 m of watering sites and within 200 m of sites where I observed ungulates crossing fences. These findings suggest that it would be worthwhile to focus fence alterations around watering sites or within areas where ungulates are known to cross fences, such as within corridors where ungulates are known to migrate between their summer and winter ranges.

MANAGEMENT IMPLICATIONS

The risk that woven-wire fences pose to juveniles is clearly illustrated by my results. Woven wire is common on fawning grounds across the Intermountain West and may be an additive factor in reducing recruitment during the fawn-weaning period. However, many ranges previously grazed by sheep are now only grazed by cattle and woven wire is not needed to retain cattle. The presence of woven-wire fences both increases the risk of ensnaring juveniles as they try to cross fences and separates mother ungulates from juveniles, which increases the risk of predation and starvation to juveniles.

My results indicate that the most effective way to alter fences so that they are less hazardous to ungulates is to replace woven-wire with barbed-wire or smooth-wire. This especially should be done on ranges that are fenced with woven wire but only grazed by cattle. If this cannot be done, then the lethality of woven-wire fences can be reduced by topping it with 0 or 2 strands of smooth or barbed wire. When a top wire is used above a woven-wire fence, increasing the distance between the top 2 wires decreases ungulate mortality (see Denney [1964] or U.S. Bureau of Land Management [1985] for recommendations on the distance between the top 2 wires in areas with wild ungulates). Ideally these top wires should be smooth rather than barbed, but this suggestion is likely to be met with resistance by landowners because fences topped with smooth wire rather than barbed wire are more likely to be pushed down by livestock leaning over them. If this is a concern, adding a strand of barbed wire within 1-3 cm of the top of the woven wire would also reduce the probability of both livestock leaning over them and wild

ungulates getting caught between these strands. Fence height should also be minimized whenever possible, especially in woven-wire fences where juvenile ungulates that are too large to go through are forced to jump over before they are ready. To combat this problem, woven-wire fences could be raised 13-18 cm off the ground to allow passage of fawns under the fence. This would allow passage of fawns and reduce the need to add strands of barbed wire above woven wire to increase its height.

Modification of fences should begin in areas where fence mortalities are the highest. These are 1) in summer ranges where juveniles are concentrated (limit woven wire especially), 2) in areas with high ungulate densities, 3) near watering sites, 4) where ungulates frequently cross fences, and 5) along roads with low traffic volumes, such as dirt roads. By concentrating in these high-risk areas, the cost of modifying fences may be less than the economic costs associated with direct- and indirect-fence mortalities and fence repair, especially given that the cost to modify fences can be amortized across many years. It would behoove stakeholders (e.g. fence owners and wildlife agencies) to collaborate in mitigation efforts so that damage to both entities can be reduced with as little effort and conflict as possible.

Pronghorn in my study area seemed more willing and better able to jump fences than pronghorn located elsewhere. If it can be substantiated that some pronghorn populations have exceptional jumping ability, then wildlife biologists should consider using animals from these populations when restocking areas with high fence densities or where high levels of fence mortality have been observed in the past. Future research should focus on identifying populations that manifest better jumping ability so that they

can be used to supplement struggling ungulate populations (especially pronghorn) that have observable problems with negotiating fences.

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