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Characteristics of Ungulate Behavior and Mortality Associated with Wire Fences

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Abstract

*We studied the characteristics of pronghorn (*Antilocapra americana*), mule deer (*Odocoileus hemionus*), and elk (*Cervus elaphus*) mortalities associated with wire fences along roads in Colorado and Utah, USA, from June 2004 to June 2005. We estimated an average annual mortality occurrence of 0.25 mortalities/km for the wire fences studied (0.08 mule deer mortalities/km, 0.11 pronghorn mortalities/km, and 0.06 elk mortalities/km) or 0.5 mortalities/km of road. The highest wire fence–mortality rates in our study area occurred during August, which coincided with weaning of fawns. Mule deer and pronghorn jumped fences in >81% of observed crossings. Mortalities were largely caused by animals getting caught between the top 2 wires. Mule deer experienced higher fence-mortality rates than elk or pronghorn because they crossed fences more frequently ($P < 0.001$) and spent more time in road right-of-ways ($P < 0.001$) than the other species. Juveniles were 8 times more likely to die in fences than adults. Woven-wire fences topped with a single strand of barbed wire were more lethal to ungulates than woven wire with 2 strands of barbed wire above it or 4-strand barbed-wire fences ($P < 0.01$). There was a direct relationship between the frequency of fence mortalities and ungulate abundance ($r^2 = 0.83$). Traffic volumes were inversely related to fence-mortality frequencies ($r^2 = 0.50$) and ungulate densities along the right-of-way ($r^2 = 0.50$).* (WILDLIFE SOCIETY BULLETIN 34(5):1295–1305; 2006)

Key words

Antilocapra americana, Cervus elaphus, *elk, habitat fragmentation, highways, human–wildlife conflicts, mortality, mule deer,* Odocoileus hemionus, *pronghorn, wire fences.*

Habitat fragmentation has been identified as a major factor affecting 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). Agriculture and highway construction have been reported to be major sources of habitat fragmentation (Mackie 1981, Clevenger et al. 2001, Forman et al. 2003).

Wire fences associated with highways and pastures may exacerbate problems caused by habitat fragmentation. Ungulates attempting to cross these fences may snare their legs and be restrained until death occurs (Mackie 1981, Kie et al. 1996). Wire fences also may inhibit daily and migratory movements (Mackie 1981, Scott 1992), thus reducing carrying capacity of ungulate habitats (Rouse 1954, Kindschy et al. 1982, Kie et al. 1996, Forman et al. 2003). Better information regarding the nature of the interactions between ungulates and wire fences is needed. In particular the characteristics of wire fences that are detrimental to ungulate passage must be identified if management techniques are to be developed to mitigate these conflicts.

Previous fence research has focused on pronghorn–livestock fence interactions, particularly 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 significantly declined due to a combination of sheep-tight (usually woven-wire) fences, harsh weather, and 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. Previous research on mule deer–fence interactions has focused mainly on exclusionary methods to prevent deer damage to humans (Reed et al. 1974, Byrne 1989, Clevenger et al. 2001, Conover 2002) rather than an assessment of the risks fences pose to mule deer.

Only limited research has been done on fence-crossing behavior in ungulate species. 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 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 may be more vulnerable to fence mortality than elk or mule deer, but no intensive field studies have compared fence-mortality

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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 and 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).

Estimates of fence-mortality frequency also may be biased low because of scavenging and removal of carcasses from fences. Scavengers and mesopredators 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 (persistence time) has not been evaluated.

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. Our objectives were to determine 1) how frequently mule deer, pronghorn, and elk are killed by wire fences, 2) what characteristics increase lethality of wire fences to these ungulate species, 3) how species differ in their fence-crossing behavior, and 4) where ungulates are most likely to be killed by fences.

Study Area

Research was conducted on approximately 1,850 km^2 in northwestern Colorado and 200 km^2 in northeastern Utah, USA. Road surveys in Utah were conducted on Diamond Mountain and Blue Mountain. 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 1,770 and 2,770 m in elevation. The vegetation 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.). 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* spp.), and cottonwoods (*Populus* sp.). Areas adjacent to County Road 7 mainly were composed of sagebrush and grassland mixed with juniper woodland. Elk, mule deer, and pronghorn have been observed during our field season on all sites except for Diamond Mountain, where pronghorn were absent. The dominate land use on all study sites was grazing by domestic livestock.

Methods

Frequency of Fence Mortalities

We defined a fence mortality as a mule deer, pronghorn, or elk carcass physically caught in a wire fence. To define the characteristics of fence mortalities over a broad landscape and a variety of different wire-fence types, we surveyed 621 km of roads and 1,046 km of fences. We conducted road surveys on 2 different types of survey routes to look for ungulates that were caught in wire fences. From these surveys, we could ascertain fence-mortality characteristics for each species and estimate an average occurrence of fence mortality across our study area.

Basic routes.—The first portion of our surveys included 6 basic routes that were chosen in areas where we expected higher than average fence-mortality frequencies based on our own observation of deer densities in the area and information provided by Colorado Division of Wildlife (D. Finley, Colorado Division of Wildlife, personal communication). These surveys increased our sample size of fence mortalities so we could more accurately infer what fence characteristics were affecting mortality. From the surveys done along these basic routes, we investigated the mechanisms behind fence mortality. Basic routes totaled 460 km of road with 841 km of fence. Basic route surveys were conducted biweekly from June to early October 2004 and monthly from late October to early December 2004 to minimize the chance of fence-mortality carcasses disappearing before being recorded. These routes also were surveyed once in April and once in June 2005.

Random routes.—The second portion of our surveys consisted of 10 randomly selected routes, each 16 km in length. Random routes were surveyed to obtain an annual estimate of mortalities per kilometer of fence so that they could be quantified across our study site. These random routes totaled 161 km of road and 205 km of fence. We selected random routes by road number first and then by mile marker using a random-number table. Road surveys on random routes were conducted monthly from June to December 2004, once in April 2005, and once in June 2005.

To determine the number of ungulate mortalities per kilometer of fence, we needed to determine how long a carcass remained attached to a fence (carcass persistence) after the ungulate died. Hence, whenever we found a recently killed carcass (hereafter called a new fence mortality), we checked it weekly from June to September 2004, biweekly from September to October 2004, and monthly from November to December 2004. We also checked new mortalities in April and June 2005. We determined or defined carcass persistence as a point in time 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 us with a method for estimating carcass persistence time in fences and monthly fence-mortality rates per kilometer of fence. We quantified fence mortalities within our 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.

Walking surveys.—Walking surveys were conducted on parcels of private and public land from early July until mid-August 2004 to determine if there was a difference in mortality frequency (mortalities per kilometer) between fences along roads (hereafter, referred to as road fences) and fences away from roads (hereafter, referred to as pasture fences). Walking distances ranged from 0.95 to 1.05 km in length and our surveys of pasture fences began >150 m away from roads. We compared the frequency of carcasses caught in road fences to that of pasture fences. We established 52 paired samples of walking fence-mortality surveys.

We used this information to estimate fence-mortality frequencies for pasture and road fences. We recorded the fence type, number of fence mortalities, species, age, and sex of the ungulate (if distinguishable), and estimated when (in weeks) the ungulate appeared to have died. Then we used paired t-tests to compare frequencies of fence mortality between road and pasture fences (PROC MIXED in SAS statistical software; SAS Institute 2001). With this comparison, we determined if fence-mortality frequencies were different between road fences and pasture fences.

We also counted the number of ungulate carcasses located <10 m from a fence and in a parallel transect of equal width (20 m) located 200 m away from the fence. We did not count a carcass unless >90% of its skeletal structure was present and within a 1-m radius.

Fence Characteristics at Mortality Sites

For each fence mortality, we recorded fence type, height of each wire strand in the 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 and the ground), direction ungulate was headed when it crossed the fence, species, sex, and age (i.e., juvenile or adult) of the ungulate, route name, and Global Positioning System (GPS) coordinate. All numerical measurements were measured to the nearest 0.01 m. In addition, mortality sites were photographed and flagged for future reference.

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

Nonnumerical 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 nonnumerical fence measurements of mortality sites also were compared to random sites, adjacent-fence 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 Behavior of Ungulates

Road surveys were conducted in June 2004, August 2004, and April 2005 on each of the 6 basic routes to assess fence-crossing behavior exhibited by free-ranging ungulates. One morning survey (dawn to 2 hr after dawn) and an evening survey (2 hr before dusk to dusk) were conducted monthly. At crossing sites we 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 made to cross the fence, success, method used to cross the fence, and any physical contact the ungulate made with the fence.

We used chi-square tests (PROC FREQ in SAS statistical software; SAS Institute 2001) to compare species and age differences in fence-crossing behavior, catch level (i.e., caught between which 2 wires), body part caught in fence, and crossing direction among species and age classes. Additionally, we 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 were caught.

Location of Fence Mortalities

Densities and species composition.—We 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 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 on random routes. These counting surveys were conducted at dawn and dusk for each month being surveyed. Every time we spotted an ungulate, we 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, we developed indices of ungulate occurrence per kilometer in the surrounding habitat and ungulate presence within the right-of-way per kilometer from our morning and evening herd composition counts. We 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, we used this information to estimate the relative risk of mortality associated with each fence type.

The ratios of fence mortalities to ungulates in the right-of-way and the surrounding area were calculated to estimate the relative mortality risks associated with each fence type.

We also determined the fence types along all roads included in all survey routes to classify all fences in our study area and quantify their respective lengths along each route.

We tested for differences in species and age composition of the surrounding ungulate populations along the basic routes to the composition of fence mortalities along those routes using chi-square tests (PROC FREQ in SAS statistical software; SAS Institute 2001) to sort out vulnerability differences among species or age classes in their vulnerability to fences. We used chi-square tests 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 test for any differences in risk by fence type.

After the length of each fence type was quantified, we used Pearson correlation statistics to determine if fence mortalities and ungulate occurrence in the right-of-way may be related (PROC CORR in SAS statistical software; SAS Institute 2001). The relationship between ungulate occurrence in the surrounding habitat and in the right-of-way was illustrated by a simple linear regression (PROC REG in SAS statistical software; SAS Institute 2001). We then split fence-mortality and ungulate-occurrence observations by species and age and used chi-square tests to determine if fence-type frequency between mortality and occurrence observations for particular species and age classes of ungulates differed (PROC FREQ in SAS statistical software; SAS Institute 2001).

Landscape factors.—We wanted to determine whether landscape patterns, such as water sources and crossing corridors, influenced local mortality frequencies. To do this, we first recorded the GPS locations of fence mortalities, water sources, and observed crossing locations on 3 of our survey routes (Diamond Mountain, Meeker, and Great Divide). Each set of points was then overlaid as a separate coverage into ARCVIEW Global Information System (GIS) provided by Environmental Systems Research Institute (1999; Redlands, California). A 200-m buffer was then added to each set of points (Lambert's Conformal Conic Projection with NAD 1983 datum), and proportions of mortalities and road kilometer inside and outside each buffer were determined prior to analyses. We used a 200-m buffer because the ungulates we observed did not travel more than 150 m along a fence prior to crossing.

We conducted chi-square tests to compare the proportion of fence mortalities to 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 water sources on local frequencies of fence mortality.

Traffic volumes for county roads were assessed using a pneumatic road counter and sampling every day for $\geq$6 days (weekends always included) for each of the 11 county roads (10 unpaved and 1 paved) used in our analysis. The traffic count was then quantified into the number of cars per day for each road. We also used the Colorado Department of Transportation website (www.dot.state.co.us) to obtain traffic counts for 7 state and federal highways that were located within our study site during 2002–2005. Fence-mortality frequency (i.e., mortalities per kilometer) and an index of ungulate densities within the right-of-way (i.e., ungulates per kilometer) were compared to the traffic volume of the respective road via inferential statistics.

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

We found 133 mortalities in fences along our basic and random routes. These included 43 ungulates that became caught from 1 June 2004 to 17 June 2005. We also found 23 fence mortalities outside of these routes.

Frequency of Fence Mortalities

More ungulates died in fences during August (19%) and January (16%) than the other months, while the fewest fence mortalities occurred during April (2%), May (2%), and June (2%). Approximately 30% of carcasses disappeared within 10 weeks and 40% within 24 weeks. This disappearance can be expressed mathematically by $y = -3.0(x) + 94.9$ ($r^2 = 0.88$; Fig. 1), where y is the percentage of ungulate carcasses still present in the fence and x is the number of weeks after the catch date. We used the above equation to interpolate a 25.9-week half-life for fence mortalities. From this information, we 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 surveyed.

Walking surveys were conducted on both private (67%) and public land (33%). We obtained permission to access private land prior to conducting the surveys. When comparing fence-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), we found no difference ($t_{51} = 1.34$, $P = 0.19$). In addition to fence mortalities, there was a mean of 1.3 ungulate carcasses/km of fence that were located within 10 m of a fence but not caught in it. In comparison, there were 0.4 carcasses/km along transects of equal width but located away from fences.

Fence Characteristics at Mortality Sites

Juveniles made up 79%, 58%, and 80% of all mule deer (n = 82), pronghorn (n = 41), and elk (n = 30) mortalities,

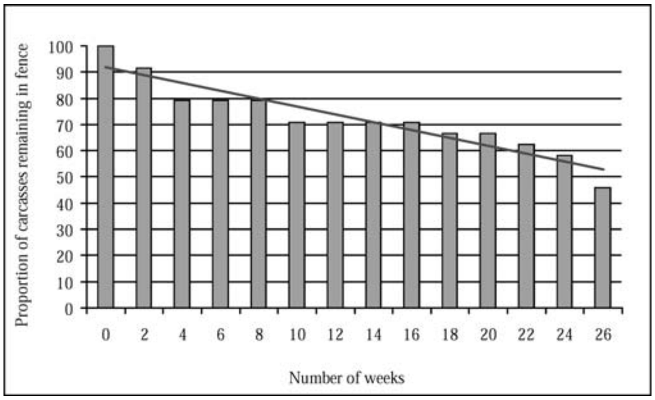

Figure 1. Disappearance of fence-mortality carcasses ($n = 24$) over time based on data collected in Utah and Colorado, USA, during 2004 and 2005.

respectively. The ratio of juveniles to adults among mortalities differed among species ($\chi^2_2 = 6.81$, $P = 0.03$). Most mule deer (68%), pronghorn (81%), and elk (87%) were caught while attempting to jump the fence. How ungulates crossed fences when they were caught did not differ by species ($\chi^2_2 = 4.82$, $P = 0.09$). Additionally, 69% of juveniles and 77% of adults were entangled in fences while attempting to jump them ($\chi^2_2 = 0.84$, $P = 0.36$).

When we examined what parts of the fences were ensnaring juvenile ungulates, we found that 58% were caught between the top 2 wires, 27% between the second and third wires, and only 15% between lower wires. Among adult ungulates, 67% were caught between the top 2 wires, 21% between the second and third wires, and 13% between lower wires. Juveniles were as likely as adults to get caught in the first and second wires ($\chi^2_1 = 0.92$, $P = 0.63$). Elk were less likely to get entangled between the first and second wires (47%) than mule deer (56%) and pronghorn (75%, $\chi^2_2 = 10.74$, $P = 0.03$). Instead, most elk died after being ensnared by lower wires.

There were no differences in what body part of juveniles and adults were caught in fences ($\chi^2_1 = 1.27$, $P = 0.53$), but elk were more likely to get caught by their front legs than mule deer and pronghorn ($\chi^2_2 = 13.78$, $P = 0.008$; Table 1). The proportion of ungulates traveling away from the roadway when getting caught in the fence (54%) did not differ from the expected rate of 50%.

Mortality sites versus adjacent-fence sites.—When all age classes and species were combined, we found that fence height at mortality sites ($\bar{x} = 1.08$ m, SE = 0.02) was greater than fence heights at adjacent-fence sites ($\bar{x} = 0.99$ m, SE = 0.02; $t_{66} = 3.02$, $P = 0.004$). For juveniles of all species, fence height at mortality sites ($\bar{x} = 1.05$ m, SE = 0.01) was greater than that of adjacent-fence sites ($\bar{x} = 0.97$ m, 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-fence sites ($\bar{x} = 1.06$, SE = 0.02; $t_{23} = -0.94$, $P = 0.35$). More than 70% of fence mortalities were in fences >1 m in height.

Table 1. Percentage of adults and juveniles as well as mule deer, pronghorn, and elk caught by different body parts at mortality sites. These observations were made in Utah and Colorado, USA, during 2004 and 2005.

Body part caught	Age class		Species		
	Juveniles ($n = 65$)	Adults ($n = 15$)	Mule deer ($n = 82$)	Pronghorn ($n = 41$)	Elk ($n = 30$)
Front leg	10.7	10.8	6.1	9.8	30.0
Rear leg	81.3	86.5	86.6	78.0	66.7
Abdomen	8.0	2.7	7.3	12.2	3.3

Mortality sites versus random sites.—When comparing mortality sites to their respective random sites, the distance between the top 2 wires was less at mortality sites ($\bar{x} = 0.16$ m, SE = 0.01) than random sites ($\bar{x} = 0.19$ m, SE = 0.01; $t_{51} = 2.01$, $P = 0.05$) when all species were pooled together. Additionally, 73% of fence mortalities were in fences where the distance between the top 2 wires was ≤20 cm.

Mortality sites versus crossing sites.—When data from all species were combined, fence height and the width of the right-of-way were greater at mortality sites than crossing sites (Table 2). The distance between the top 2 wires was less at mortality sites than at crossing sites.

Fence-Crossing Behavior of Ungulates

We observed 101 ungulates (70 mule deer, 27 pronghorn, and 4 elk) cross fences. Mule deer crossed fences more than the other 2 species ($P < 0.001$). Jumping was the most common method used in crossing fences in all species (88%). The precentage of mule deer that crossed under (3%), crossed through (6%), or jumped over (91%) fences did not differ ($\chi^2_2 = 1.98$, $P = 0.37$) from the percentage of pronghorn that crossed under (7%), crossed through (11%), or jumped over (82%) fences. When all species were combined, more adults (98%) jumped fences than juveniles (44%; $\chi^2_2 = 40.52$, $P < 0.001$).

Location of Fence Mortalities

Densities and species composition.—Ungulate occurrence in the surrounding area and ungulate occurrence within the right-of-way were autocorrelated ($r^2 = 0.94$, $F = 545.89$, $P < 0.001$), and therefore we did not use ungulate occurrence in the right-of-way as an independent variable. Fence mortalities and ungulate density were correlated ($r^2 = 0.83$, $P < 0.001$, $n = 33$). Mule deer had a greater propensity than pronghorn or elk to be within the right-of-way based on their numbers in the adjacent habitat ($\chi^2_2 = 440.02$, $P < 0.001$; Table 3). Concomitantly mule deer constituted a higher proportion of fence mortalities than expected based on ungulate occurrence in the adjacent habitat ($\chi^2_2 = 14.67$, $P < 0.001$; Table 4). However, when comparing fence mortalities to right-of-way observations, we found that mule deer mortality was lower than expected, whereas pronghorn and elk mortality were higher than expected (Table 4). These findings suggest that mule deer may have an overall higher risk because they cross right-of-way fences more

Table 2. Means, standard errors, and *t*-test results comparing fence characteristics at fence-mortality sites to sites where ungulates successfully crossed fences when data for all species were combined. These observations were made in Utah and Colorado, USA, during 2004 and 2005.

Variable	Crossing sites $\bar{x}$	Crossing sites SE	Mortality sites $\bar{x}$	Mortality sites SE	df	*t*	*P*
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

often but, in general, pronghorn and elk may be at higher risk per fence-crossing attempt.

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 ($\chi^2_1 = 14.86$, $P < 0.001$) based on the proportion of ungulates in the surrounding habitat of these fences (67%). We found more mortalities in woven-wire fences topped with 1-strand barbed wire than other fence types (Table 5). Although they only comprised 1.8% of the total distance of fences on our 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 ($\chi^2_1 = 4.16$, $P = 0.04$) within 200 m of waterholes than expected based on the proportion of road length within 200 m of a waterhole (14%). The proportion of fence crossings (28%) was significantly higher ($\chi^2_1 = 4.16$, $P = 0.04$) $<$200 m from water sources than expected based on the proportion of road length $<$200 m from water sources (11%). The proportion of fence mortalities (26%) also was higher ($\chi^2_1 = 5.77$, $P = 0.02$) within 200 m of observed crossing locations than expected based on road-length proportions within 200 m of them (9%).

When compared to unpaved roads, paved roads had more cars per day, fewer ungulates present within the right-of-way per kilometer (ungulates per kilometer), and fewer fence mortalities per kilometer (Table 6). For all roads combined, our analyses resulted in a negative correlation between cars per day and mortalities per kilometer ($r^2 = 0.49$, $P < 0.001$), a negative correlation between cars per day and ungulates per kilometer ($r^2 = 0.54$, $P < 0.001$), and a positive correlation between fence mortalities per kilometer and ungulates per kilometer ($r^2 = 0.76$, $P < 0.001$).

Table 3. Percentage of each species occurrence in the adjacent habitat compared to ungulate presence within the right-of-way. These observations were made in Utah and Colorado, USA, during 2004 and 2005.

Species	Observation type: Habitat (n = 15,597)	Observation type: Right-of-way (n = 984)	χ^2	*P*
Mule deer	45.6	79.2	440.02	<0.001
Pronghorn	41.4	11.2		
Elk	13.0	9.7		

Discussion

Frequency of Fence Mortalities

For our study area, we 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 right-of-way fence mortalities. This estimate is based on a carcass half-life of 25.9 weeks. Fence mortalities disappeared primarily because of scavenging. We observed turkey vultures (*Cathartes aura*), golden eagles (*Aquila chrysaetos*), common ravens (*Corvus corax*), black-billed magpies (*Pica pica*), and ground squirrels (*Spermophilus* spp.) scavenging on carcasses. Canid scat and tracks were observed at numerous fence-mortality sites. In addition, humans may have removed some fence mortalities. Most ungulates caught in fences will damage the fence in their attempts to escape. Ranchers and road workers informed us that when they noticed the damaged fence, they would remove the carcass (even if just bones are present) when repairing the fence.

To estimate the error associated with missing fence mortalities while driving, we compared the rate of mortalities found per kilometer observed from driving our basic routes to the rate of mortalities per kilometer observed on our walking surveys of right-of-way fences. Given that our walking surveys were randomly distributed throughout our basic routes, we consider the difference in proportion between the 2 estimates the amount of error associated with missing carcasses while driving. From this, we estimated that we saw 55% of all fence mortalities along the road while

Table 4. Percentage of each species found as fence mortalities compared to their occurrence in adjacent habitat and within right-of-ways. These observations were made in Utah and Colorado, USA, during 2004 and 2005.

Species	Observation type: Fence mortalities (n = 114)	Observation type: Adjacent habitat (n = 15,597)	Observation type: Right-of-way (n = 984)
Mule deer	60.5	45.6	79.2
Pronghorn	23.7	41.4	11.2
Elk	15.8	13.0	9.7

Table 5. Percentage of ungulate mortalities found in each fence type compared to their occurrence in habitat adjacent to each fence type. These observations were made in Utah and Colorado, USA, during 2004 and 2005.

	Observation type			
Fence type[a]	Fence mortalities ($n = 96$)	Habitat ($n = 11{,}805$)	χ^2	P
WW with 1-strand BW	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; BW = barbed wire.

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).

We also found 1.3 ungulate carcasses/km located <10 m from a fence but not attached to it. This rate was higher than the 0.4 carcasses/km found in transects of equal width located away from fences. Some of these carcasses near fences may have initially been fence mortalities that scavengers or people removed from the fences. However, most of the carcasses were intact and found in a curled position. This suggested to us that the ungulate probably died while on the ground. In contrast, when an ungulate was killed in a fence and taken out of it, the carcass had straightened legs and marks where wire strands had cut into their flesh. Some indirect fence 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 also may have been kills that predators made by cornering ungulates into fences. The majority (>90%) of indirect mortalities were fawns, and most of these 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, the high density of carcasses near fences indicate that fences can kill ungulates by methods other than ensnaring them. Although we 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 confining them in a particular area for prolonged periods of time (Mackie 1981, Scott 1992). By doing so, impassable fences may 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 (Urness 1976).

Fence Characteristics at Mortality Sites

We wanted to identify fence characteristics that contributed to their lethality to ungulates. To do so, we compared the fence characteristics at mortality sites to fence characteristics at 1) sites where we saw ungulates successfully cross a fence, 2) sites directly across the road from mortality sites, and 3) randomly selected sites. More ungulate mortalities, particularly in juveniles, were associated with woven-wire fences than those made of only barbed wire. Sundstrom (1967), Mackie (1981), and Kie et al. (1996) reported that juveniles are particularly impacted by woven-wire fences because these fences posed more of a barrier. In our study site, we recorded no mortalities in smooth-wire fences and fences including a top rail in their construction. However, these fence types were too uncommon to allow statistical comparisons.

We found higher mortalities in woven-wire fences that were topped by a single strand of barbed wire than woven-wire fences topped by zero strands of barbed wire or woven wire topped by 2 strands of barbed wire. We believe that woven-wire fences with a single strand of barbed wire pose a greater mortality risk because of the coupling of the rigidity of woven wire and the snagging ability of barbed wire. In many of the observed fence mortalities, the barbed wire, when twisted into the woven wire, would snag into the flesh of the ungulate and cinch the ungulate's leg so tightly into the top rung of the woven-wire fencing that the ungulate could not pull its leg free. However, when woven-wire fences were topped by 2 strands of barbed wire, the ungulate would usually get its legs caught between these 2 strands. When 2 strands of barbed wire were twisted together, they often had enough give that an ungulate could jerk itself out of the fence with minor injuries. Additionally, a woven-wire fence by itself may be too stiff to twist around the 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, and most of these fence regulations specify distances >0.30 m between the top 2 wires (Denney 1964). This coincides with recommendations given by Anderson (1980), the United States Bureau of Land Management (1985), and Kie et al. (1996). Our

Table 6. Effect of road type on traffic volume, fence mortalities, and number of ungulates in the right-of-way. These observations were made in Utah and Colorado, USA, during 2004 and 2005.

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

Figure 2. Photo of typical jumping technique exhibited by mule deer on our study area. (Photo courtesy of Emily Harrington).

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 our study area are greater than the respective recommended fence heights for all 3 species. Hence, we have no evidence that these fence-height recommendations are inappropriate. Additionally, our histograms on fence height and distance between the top 2 wires show that if these fence recommendations were put into practice, the ungulate mortality risk may be mitigated.

Figure 3. Photo of typical jumping technique exhibited by pronghorn on our study area. (Photo courtesy of Emily Harrington).

Figure 4. Photo of typical jumping technique exhibited by elk on our study area. (Photo courtesy of iLoveOregon.com).

Fence-Crossing Behavior of Ungulates

We found no evidence that mule deer and pronghorn differ in their fence-crossing methods. When comparing crossing observations between the 2 species, we found jumping was used most frequently by both. This contradicts previous reports (Rouse 1954, Spillett et al. 1967, Scott 1992, Kie et al. 1996) 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 our study area, 81% of pronghorn jumped fences and 19% went through or under fences. Additionally, Spillett et al. (1967) estimated that 0.82 m was the maximum fence height that adult pronghorn could readily jump. We observed >20 pronghorn jump fences >1.0 m in height without making contact with the fence.

Perhaps the pronghorn in our study site were better at fence jumping than pronghorn occupying open plains or flat deserts because the geography of our study site was different. Our study area was mostly rugged, broken by gullies, ravines, and covered in sagebrush. Our study site also had a higher density of fences than most pronghorn habitat in Colorado and Utah. In our study area, pronghorn may have gained more experience jumping over obstacles at an earlier age than pronghorn in open, flat terrain with fewer fences.

The different ungulate species differed in their jumping styles. In contrast to mule deer and pronghorn, elk had a more stiff-legged style of jumping fences (Figs. 2–4). Due to their more lumbering type 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. We 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.

In our study juveniles were 8 times more likely than adults to die in fences. Many of the juvenile fence mortalities occurred during August when we often observed juveniles following females back and forth between foraging and resting areas. These daily movements often require the young to cross fences. Unfortunately, juveniles may be inexperienced at negotiating fences, and their mothers may not realize how much of a barrier a fence may pose for their offspring. Juveniles trying to crawl or squeeze through may get stuck by their hips and cannot escape. Another dangerous time for juveniles may be when they have grown too large to crawl through woven-wire fences and are forced to jump fences before they have developed the strength and size to do so successfully. 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. Most of these ungulates were caught trying to jump fences. During winter, snow depths often exceeded 0.5 m at our study sites, and such conditions probably cause nutritional stress in local ungulates both because most of their food is covered by snow and more energy is required to travel (Wickstrom et al. 1984, Parker et al. 1984, 1996, Hobbs 1989).

Under such conditions, deer 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 could cause ungulates to make contact with the fence, and sometimes become entangled. As deer and pronghorn jump, they commonly tuck their front legs underneath their abdomen. However, their rear legs remain perpendicular with the ground, which causes the lower tarsal bones in the rear legs to protrude, thus increasing their vulnerability (Figs. 3, 4). 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 felt the wire touching their abdomens, we observed them trying to kick their back legs while still in the act of jumping in an attempt to push off from the top wire of the fence to gain more height. Sometimes this effort was successful in giving the ungulate the extra boost it needed to clear the fence. However, if the ungulate missed the top wire with its feet, its feet can get caught between the top 2 wires. Once the ungulate is caught, it hits the ground and kicks with its back legs, thrashing about and 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. We do not know what proportion of ungulates are able to free themselves and what proportion cannot.

Location of Fence Mortalities

We found that fence mortalities along roads were inversely related to traffic volumes. We believe this relationship existed because the number of ungulates present within the right-of-way per kilometer also was inversely related to traffic volumes. Mule deer and pronghorn are wary animals and flee from a road's right-of-way whenever a vehicle approaches. Hence, these animals can peacefully feed along roads only where traffic is sparse. We believe it is for this reason that ungulate densities within right-of-ways were negatively correlated with traffic volumes rather than due to any differences in vegetation between high-traffic-volume and low-traffic-volume roads. These findings also point to the greater need of fence mitigation in areas with low traffic volumes or in areas with high ungulate densities. For instance, it may be more worthwhile to modify fences so they are less lethal to ungulates along dirt roads than paved roads.

We found higher rates of fence mortalities within 200 m of water sources and sites where we observed ungulates crossing fences. These findings suggest that it would be worthwhile to focus fence alterations around water sources 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

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, Conover et al. 1995, 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 (Conover et al. 1995). Andrews and Rowley (1998) estimated that deer and elk caused US$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 (Conover et al. 1995, Conover 1997, 2002), which we 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, we estimated an annual cost of $61/km of right-of-way fence in our study area due to fence mortalities ($16 for mule deer, $24 for pronghorn, and $21 for elk) or $122/km of road because roads have fences on both sides. These values cannot be extrapolated to roads throughout the West because of high ungulate densities in our study areas.

In our study woven-wire fences pose a greater mortality risk to juveniles than other fence types. Woven wire is common on fawning grounds in our study area and is a factor in reducing fawn survival during the weaning period. 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.

Our results indicate the most effective way to alter fences so they are less hazardous to ungulates is to replace woven wire with barbed or smooth wire. This should be done especially 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 them 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 United States Bureau of Land Management [1985] for recommendations on the distance between the top 2 wires in areas with 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 reduce the probability of both livestock leaning over them and free-ranging ungulates getting caught between these strands. Fence height also should be minimized whenever possible. To reduce the lethality of woven-wire fences to juveniles, they could be raised 13–18 cm off the ground to allow passage of fawns under the fence. This would also reduce the need to top a woven-wire fence with a strand of barbed 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 densities of ungulates, 3) near watering sources, 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 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, departments of transportation, and wildlife agencies) to collaborate in mitigation efforts so that damage to all entities can be reduced with as little effort and conflict as possible.

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