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Original Research

Effects of Wolf Presence on Daily Travel Distance of Range Cattle☆,☆☆

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ABSTRACT

The presence of gray wolves (*Canis lupus*) can directly and indirectly affect beef cattle (*Bos taurus*) production on rangelands of the Northern Rocky Mountains. While fairly extensive knowledge exists for the direct effects of wolf predation threat (e.g., cattle death and injury losses, elevated stress), our understanding of wolf-caused changes in cattle behavior and the associated cascade of potential indirect effects on cattle resource selection, diet quality, activity budgets, and energetic relationships is still largely in its infancy. We investigated whether wolf presence affected the daily travel distance of Global Positioning System (GPS) — collared cattle under a replicated, Impact-Control study conducted in western Idaho and northeastern Oregon during 2008 — 2012. Cattle in three Control (Oregon) study areas, where wolf presence was consistently low, traveled farther per day (13.7 ± 0.396 SE km day^{-1}) than those in three Impact (Idaho) study areas (11.4 ± 0.396 SE km day^{-1}) with moderate to high wolf presence. At Control study areas, cattle traveled farthest per day in July (13.2 ± 0.355 SE km day^{-1}) and were least mobile in October (11.8 ± 0.365 SE km day^{-1}), but daily travel distances were similar across all months for cattle in Impact study areas. This observational study provides evidence suggesting cattle in mountainous grazing areas alter their spatial behavior in response to gray wolf presence. These behavioral changes have energetic consequences that could potentially impact cattle productivity and ranch economics. Additional research into the activity budget and resource selection responses of these collared cattle is required to better understand the specific mechanisms behind these daily travel distance results.

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Introduction

The presence of gray wolves (*Canis lupus*) affects beef cattle (*Bos taurus*) production on rangelands. These effects are both direct and indirect (Howery and DeLiberto, 2004; Steele et al., 2013; Ramler et al., 2014). Death and injury losses directly caused by wolf predation are well documented (NASS, 2006, 2011). Economic impacts of these losses can be quite sizable for some individual ranching operations (Oakleaf et al., 2003; Ramler et al., 2014). Wolf presence may also directly induce stress (Cooke et al., 2013) and cause changes in cattle behavior (Kluever et al., 2009; Laporte et al., 2010). While we have fairly extensive knowledge of the consequences of increased stress in cattle (e.g., dietary issues [McDowell et al., 1969; Yousef, 1985], losses in productivity [Young, 1981; West, 2003], and increased susceptibility to disease [Chirase et al., 2004; Salak-Johnson and McGlone, 2007]), our understanding of wolf-caused changes in cattle behavior and the associated cascade of potential indirect effects on resource selection, diet quality, activity budgets, and energetic relationships is still largely in its infancy. Direction and magnitudes of these indirect effects remain largely unquantified, yet they likely have strong implications for weight gain, body condition, reproductive success, and other factors affecting ranch economics.

With regard to behavioral responses, research investigating predator-prey relationships has identified several common antipredation strategies employed by cattle and other ungulates (Lima and Dill, 1990; Kluever et al., 2009; Laporte et al., 2010). Prey animals detect predators and avoid predation through increased vigilance (Underwood, 1982), but vigilance can be costly (Illius and Fitzgibbon, 1994). Bunching into larger groups increases the likelihood of successful predator detection, reduces

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the burden of vigilance for individual prey animals, and presents predators with a more formidable-appearing defense (Hamilton, 1971; Elgar, 1989; Roberts, 1996). Retreating to safer habitat or refugia sites is a strategy commonly practiced by many ungulate species (Bergerud et al., 1984; Creel et al., 2005). Flight or long-distance relocation are the most dramatic antipredation responses, but these are generally strategies of last resort. All of these antipredation strategies have something in common. All will almost certainly have some impact on the distance traveled each day by a prey animal.

Daily travel distance is an energetic response that is readily quantifiable, even on rugged and remote rangelands, using Global Positioning System (GPS)-tracking technology. Changes in daily travel distance impact the balance animals must strike between energy intake and expenditure and thus can have health and productivity consequences (Van Soest, 1982). We hypothesized that consistently elevated levels of wolf presence would lead to a reduction in daily travel distance presumably caused by increased vigilance and greater fidelity for habitats perceived to be safer from wolf predation. We tested this hypothesis in a replicated, Impact-Control study of regional scope.

Materials and methods

Approval for this study of beef cattle behavior was obtained from Oregon State University's Institutional Animal Care and Use Committee (protocol numbers 3654, 4168, and 4555). Procedures used in handling and caring for cattle adhered to the *Guide for the Care and Use of Agricultural Animals in Agricultural Research and Teaching* (FASS, 2010). Capture and handling of gray wolves for radio- and GPS-collar installation were conducted as part of routine wolf management operations by personnel from Idaho Department of Fish and Game (IDFG) and US Department of Agriculture (USDA) Animal and Plant Health Inspection Service (APHIS) Wildlife Services (WS) in accordance with IDFG-supplied training and the *IDFG Wolf Foothold Trapping Safety Protocol*.

Study Area Pairings

This research was conducted from 2008 through 2012 in six active USDA Forest Service (USFS) cattle grazing allotments ranging in extent from about 100 km^2 to > 300 km^2. Three of these study areas were located in western Idaho where well-established gray wolf populations were present before the study (Nadeau et al., 2008) and wolf presence remained consistently at moderate to high levels during each study year. The remaining three study areas occurred in northeastern Oregon at locations where wolves were either absent or at presence levels too low to be detectible before and throughout the study. The three Idaho study areas were selected first with the intent of choosing USFS allotments representative of the typical range in environmental, ecological, and managerial characteristics evident in mountainous, western Idaho cattle grazing areas. A grazing allotment in northeastern Oregon was then chosen to pair with each Idaho grazing allotment. Pairing of Idaho and Oregon study areas was based specifically on similarities in topography, parent materials, soil types, vegetation cover types, hydrology, climate, and livestock management (e.g., allotment entry/exit timing, grazing scheme, herd composition, breeding, calf age at entry). The intent of this pairing process was to control for as many of these environmental, ecological, and managerial factors as possible such that the principal difference between study areas in Idaho (Impact study areas) and those in Oregon (Control study areas) was the much higher level of wolf presence in Idaho.

Study Area ID-A (Idaho) was paired with Study Area OR-A (Oregon), and this pair was intended to typify situations where cattle enter the grazing areas in early spring (April) with very young calves born in late March to mid-April. Cattle in both study areas experienced four herding events (pasture rotations) per grazing season. The most prominent topographic features of the ID-A/OR-A pair are the very steep-walled canyon slopes present between the lowest and highest elevations of the study areas. Cattle entered these study areas at their lowest elevations (520 – 753 m) and progressively worked their way upslope, scaling the steep canyon walls, reaching the highest rangelands at or shortly after the midpoint in the grazing season, and remaining at these highest elevations (1 581 – 1 932 m) until the close of the grazing season in October.

Riparian vegetation in the canyon bottoms of study areas ID-A/OR-A is dominated willow (*Salix* sp. L), sedges (*Carex* sp. L.), and rushes (*Juncus* sp. L) with Kentucky bluegrass (*Poa pratensis* L.) and cheatgrass (*Bromus tectorum* L.) occurring on stream and river terraces. The canyon walls are vegetated by bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh] A. Love) and Idaho fescue (*Festuca idahoensis* [Elmer]) associations with perennial forbs such as arrowleaf balsamroot (*Balsamorhiza sagittata* [Pursh] Nutt.), parsnipflower buckwheat (*Eriogonum heracleoides* Nutt.), Cusick's milkvetch (*Astragalus cusickii* A. Gray), and Snake River phlox (*Phlox colubrine* Wherry & Constance) occurring occasionally as co-dominants (Johnson and Simon, 1987). Pine savanna or open woodlands occur on the plateau landscape atop the canyon walls. Ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson) and bunchgrasses (e.g., Idaho fescue) form the savannas. In the open woodlands, a shrub layer of common snowberry (*Symphoricarpos albus* [L.] S.F. Blake) and/or white spirea (*Spiraea betulifolia* Pall.) and an herb layer of pinegrass (*Calamagrostis rubescens* Buckley) and Geyers sedge (*Carex geyeri* Fernald) or Idaho fescue occur under the Ponderosa pine canopy. Ridge-tops often lack forest cover and are vegetated as grasslands dominated by bluebunch wheatgrass and Idaho fescue associations. On buttes extending above the plateaus, forest vegetation is dominated by Douglas-fir (*Psedotsuga menziesii* [Mirb.] Franco) and grand fir (*Abies grandis* [Douglas ex D. Don] Lindl.) associations with forest openings vegetated by ninebark (*Physocarpus malvaceus* [Green] Kuntze) and common snowberry associations. Native graminoids like Geyers sedge and mountain brome (*Bromus marginatus* Nees ex Steud.) occur here as do seeded, introduced grasses (e.g., orchardgrass [*Dactylis glomerata* {L.}] and timothy [*Phleum pretense* {L.}]).

Soils in the canyon bottoms range from fine, smectitic, mesic pachic argixerolls to loamy-skeletal, mixed, superactive, frigid oxyaquic hapludolls (NRCS, 2017a). Loamy-skeletal, mixed, superactive, mesic lithic argixerolls and frigid lithic haploxerolls, as well as clayey-skeletal, smectitic, mesic lithic argixerolls, occur on the canyon walls. Loamy-skeletal, isotic, frigid alfic udivitrands, and vitrandic argixerolls are found on the forested highlands.

Climate at mid-elevations of the ID-A study area is likely similar to that monitored at the Snake River RAWS (SRFI1) located west of Cuprum, Idaho at 1 333-m elevation. Long-term (1998 – 2016) mean water-yr precipitation at this station was 546 mm (MesoWest, 2017a). Total precipitation values for the 2008, 2009, 2010, 2011, and 2012 water yr were 360, 441, 484, 537, and 692 mm, respectively. Long-term (1998 – 2016) mean daily air temperatures for the months of June, July, August, September, and October were 16.5°C, 23.0°C, 22.3°C, 17.0°C, and 9.6°C, respectively. The nearest climate station of comparable elevation to the OR-A study area is the Roberts Butte RAWS (BTFO3) located west of Lewis, Oregon at 1 299-m elevation. Long-term (1998 – 2016) mean water-yr precipitation at Roberts Butte is 403 mm (MesoWest, 2017b). Total precipitation values for the 2008, 2009, 2010, 2011, and 2012 water yr were 353, 297, 453, 460, and 497 mm, respectively. Long-term (1998 – 2016) mean daily air temperatures for the months of June, July, August, September, and October were 15.0°C, 20.9°C, 19.9°C, 14.8°C, and 7.9°C, respectively.

Study areas ID-B and OR-B were paired to be representative of grazing areas with higher base elevations, more forested range, later cattle entry dates (late May – early June), and older calves (3 mo) at entry than the ID-A/OR-A pair. Cattle at both study areas were herded among pastures three times per season. The lowest elevations (904 – 981 m) are grasslands dominated by bluebunch wheatgrass and Idaho fescue associations or sagebrush-grasslands vegetated by mountain big sagebrush (*Artemisia tridentate* Nutt. subsp. *vaseyana*

[Rydb.] Beetle) associations (Johnson and Simon, 1987). Vegetation at mid-elevation is Ponderosa pine savanna on drier aspects and forests dominated by Douglas-fir associations on the moister aspects. At the highest elevations (1 607 − 1 633 m), the vegetation occurs as mixed conifer forests of Douglas-fir and grand fir associations. Kentucky bluegrass (*Poa pratensis* [L.]) and California oatgrass (*Danthonia californica* Bol.) occur on dry meadows. Moist meadows are dominated by tufted hairgrass (*Deschampsia cespitosa* [L.] P. Beauv.), Hood's sedge (*Carex hoodia* Boott), and thick-head sedge (*Carex pachystachya* Cham. Ex Steud.). Aspen (*Populus tremuloides* Michx.) communities may occur near springs and other moist areas. Stream riparian areas are dominated by black cottonwood (*Populus balsamifera* [L.] spp. Trichocarpa [Torr. & A. Gray ex Hook.] Brayshaw), willow (*Salix* spp. [L.]), and Kentucky bluegrass at lower elevations and willow and sedges (*Carex* spp. [L.]) at higher elevations.

Soils in the lower elevation grasslands are loamy-skeletal, mixed, superactive, frigid lithic and vitrandic haploxerolls (NRCS, 2017a). Soils underlying the Ponderosa pine savanna are loamy-skeletal, isotic, frigid vitrandic argixerolls and haploxerolls, and lithic haploxerepts. Douglas-fir stands are underlain by loamy, amorphic over isotic, frigid alfic humic vitrixerands and fine-loamy, isotic, frigid vitrandic argixerolls. Mixed conifer forests occur on loamy-skeletal, isotic, frigid andic haploxerepts and vitrandic haploxerolls.

Climatic data acquired at the Snake River RAWS (see above) is likely representative of the climate at mid-elevations within the ID-B study area. Climate at the OR-B is probably similar to that monitored at the Sparta Butte RAWS (SAFO3) located east of Keating, Oregon at 1 300-m elevation. Long-term (1998 − 2016) mean water-yr precipitation at this station was 379 mm (MesoWest, 2017c). Total annual precipitation for water yr 2008, 2009, 2010, 2011, and 2012 were 329, 451, 516, 550, and 389 mm, respectively. Long-term (1998 − 2016) mean daily air temperatures for the months of June, July, August, September, and October were 16.0°C, 20.7°C, 19.7°C, 14.7°C, and 7.8°C, respectively.

The ID-C/OR-C study area pair had the highest base elevations and the latest cattle entry dates (mid-June) of the three pairs of study areas. Calf ages at entry (3 months) were similar to that of the previous pair (ID-B/OR-B). Two herding events per season occurred in each of these study areas. Most of the study area extents are forested. The lowest elevations (1 133 − 1 249 m) are vegetated by Ponderosa pine associations while Douglas-fir and grand fir associations occur at mid-elevations. Small, wet meadows of willow and sedges also occur at these mid-elevations. Subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.) associations dominate forested areas and fescues (*Festuca* spp.[L.]), and upland sedges vegetate open areas at the highest elevations (2 504 − 2 519 m) of this study area pair.

Ponderosa pine associations are underlain by loam-skeletal, isotic, frigid vitrandic haploxerepts (NRCS, 2017a). Loamy-skeletal, amorphic over isotic, frigid alfic udivitrands and isotic, frigid vitrandic agrixerolls underly the Douglas-fir and grand fir associations. Subalpine fir forests occur on loamy-skeletal, amorphic over isotic typic vitricryands.

Climate at the higher elevations of ID-C study area is likely similar to that at the Brundage Reservoir SNOTEL site located at 1 905-m elevation south of McCall, Idaho. Long-term mean annual precipitation (1987 − 2015) is 1 271 mm for this SNOTEL site (NRCS, 2017b). Precipitation totals for the 2008, 2009, 2010, 2011, and 2012 water yr were 1 377, 1 270, 1 209, 1 516, and 1 255 mm, respectively. Long-term (1987 − 2015) mean daily air temperatures for the months of June, July, August, September, and October were 10.5°C, 16.0°C, 14.9°C, 10.3°C, and 4.1°C, respectively. Climate at the OR-C study area is probably similar to that monitored at the USDA-NRCS Taylor Green (SNOTEL) site located northeast of Medical Springs, Oregon at 1 750 m elevation. The long-term (1980 − 2015) mean annual precipitation for this SNOTEL site is 940 mm (NRCS, 2017c). Precipitation totals for the 2008, 2009, 2010, 2011, and 2012 water yr were 922, 968, 1 054, 1 250, and 871 mm, respectively. Long-term (1980 − 2015) mean daily air temperatures for the months of June, July, August, September, and October were 9.7°C, 14.7°C, 14.5°C, 10.9°C, and 4.8°C, respectively.

Cattle Data Collection

Before cattle entry into the study areas each spring (2008 − 2012), 10 mature cows (4 − 10 yr of age) of British breeds or crossbreds were randomly selected as research subjects from commercial livestock herds grazing each study area. Herd sizes ranged from 300 to 500 cow-calf pairs per study area depending on study area extent, typical forage availability and productivity, and USFS-prescribed stocking rates. Selected cows were fitted with custom GPS tracking collars (Clark et al., 2006) programmed to record the date, time, spatial position, and fix-quality parameters (e.g., Position Dilution of Precision [PDOP]) at about 5-min intervals throughout the grazing season (June − October). Handling of cattle for collar installation was conducted by safely confining each cow within a squeeze-chute facility. Care was taken to ensure proper fitting of the collars and to minimize any pain, stress, or discomfort experienced by cows during handling. Collars were removed from the cattle each fall when they exited the study areas. A new set of 10 cows from each study area was randomly selected for collaring during each study year. Each of these cows generally had multiple years of experience with the landscapes, environments, and managerial operations on their respective study areas. On the basis of our random selection process, we assumed that the activity, movement, and resource-selection patterns of these collared cows were representative of the range of variability expressed by the general cattle population within each respective herd.

Following collar retrieval, the GPS data were downloaded, cropped to the fenced study area boundaries, and then objectively screened for gross positioning errors. Positions with PDOP values ≥ 10 were deemed suspect and removed from the data set. Velocities were calculated on the basis of the step length or movement distance between sequential pairs of GPS positions and the known time intervals between these positions. Positions indicating velocity ≥ 10 kph were classified as improbable and dropped from the data set. These excessive velocities were almost certainly due to GPS positioning error and were frequently associated with two-dimensional GPS fixes. Dropped positions, however, represented only about 0.3% of the original dataset.

Because collared cows occasionally entered or exited the study areas in mid-month and collars sometimes failed mid-season, the number of collars collecting data during each month varied. The mean number of

Table 1

Mean number of Global Positioning System (GPS)-collared, mature beef cows and mean number of GPS tracking positions for each month of the grazing season, as averaged across 5 study yr (2008 − 2012), within replicate pairs ($n = 3$; A, B, and C) of Impact and Control study areas (i.e., US Forest Service cattle grazing allotments) for an Impact-Control study conducted in western Idaho and northeastern Oregon.

	Treatment Levels				
	Impact		Control		
Month	Collared cows	GPS positions	Collared cows	GPS positions	Pairs
June	5.2	59 429	9.0	211 417	A
	7.8	199 453	7.0	220 405	B
	7.2	123 448	7.4	278 120	C
July	5.8	223 336	8.6	271 346	A
	9.6	351 360	6.8	278 397	B
	8.0	222 774	7.0	244 604	C
August	6.2	242 692	8.4	176 618	A
	9.2	366 543	6.6	262 409	B
	8.2	218 537	5.4	204 955	C
September	5.4	170 463	7.0	235 919	A
	8.8	325 852	6.4	230 579	B
	7.4	212 287	5.2	189 041	C
October	3.0	21 837	6.4	155 303	A
	8.4	222 168	6.2	107 664	B
	7.0	199 575	5.5	146 133	C

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viable collar data sets and mean number of GPS positions acquired for each month over 5 yr of study are provided in Table 1. For each viable collar data set, movement distance between each pair of sequential positions acquired during 24-hr periods beginning 12:00 midnight local time were summed to determine the total estimated travel distance (km) for each day of record.

These mean travel distance results suffer from two primary sources of error. Positioning error tends to inflate calculated travel distance, particularly, when collared animals are recorded as moving when they are actually stationary (e.g., bedded and standing idle). Displacement calculations tend to underestimate travel distance because actual movement paths rarely follow straight lines. Although it was not possible to determine their magnitudes, these two sources of error can be and likely were somewhat compensative.

Some explicit assumptions were made regarding the prior experience that cattle in this study had with wolves. Wolf presence in or near the Impact study areas in Idaho had been well documented in recent years preceding the study (Nadeau et al., 2008). Consequently, cattle in these study areas, including those cows selected to be GPS collared, were assumed to have some familiarity with wolf presence and some may have even experienced pursuit or harassment by wolves or were present during wolf depredation events before the study. In contrast, cattle in the Control study areas in Oregon were assumed to have been largely naïve to wolves and wolf presence before the study. Although wolves had been documented in northeastern Oregon before the study, their presence was apparently exceedingly rare and temporary (e.g., 1 − 2 wolves dispersed from Idaho to Oregon and then returned to Idaho) (Nadeau et al., 2008). Consequently, it is unlikely that cattle in the Control study areas had any prior contact or experience with wolves.

Wolf Presence Monitoring

Wolf presence levels in the Idaho and Oregon study areas were monitored throughout the study. Multiple approaches were applied because no single monitoring approach was deemed adequate for the requirements of this study. A combination of scat and sign surveys (Heinemeyer et al., 2008; Long and Zielinski, 2008), camera traps (Kays and Slauson, 2008; Swann et al., 2011; Meek and Pittet, 2014), GPS and radio tracking collars (Mech, 1982; Fuller and Snow, 1988; Ballard et al., 1995), den or rendezvous site visits (Ausband et al., 2010, 2014), incidental visual sightings, and livestock depredation reporting by study personnel and cooperating wildlife management agencies was used to assess wolf presence in time and space within our study areas. A brief description of each of these monitoring approaches is provided below. For more detail on specific approaches, the reader is directed to the cited references.

Scat and sign survey were conducted along forest roads, which traversed the major dimensions of each study area. Survey routes at each study area were selected from a population of all legally open roads with the intent of detecting wolf entry or exit from extensive areas between road courses. Wolves commonly use roadways to advertise territorial possession via scat deposition (Crete and Messier, 1987; Barja et al., 2004) and to transverse otherwise steep or complex terrain. Consequently, wolves entering or exiting areas bounded by roads will typically leave scat or track evidence of their passage and thus their presence in the area. Survey routes were monitored at regular intervals. Scat or sets of tracks detected along the route were counted, their location coordinates were recorded, and they were photographed for later confirmation of source species. Scat and tracks were then discretely marked to prevent recount during subsequent surveys.

Camera traps were used to monitor wolf presence in areas distant from roads and survey routes. These motion-triggered cameras were installed at the confluences of two or more game trails. Camera locations were selected by first generating a stratified random sample of starting locations and then selecting the nearest trail confluence to each starting location. Cameras were installed when cattle arrived on a study area and removed when cattle were removed. Photographic evidence of wolf presence was acquired day and night with the aid of infrared illumination.

Idaho Department of Fish and Game (IDFG) and Oregon Department of Fish and Wildlife routinely captured and instrumented wolves with radio or GPS telemetry collars to facilitate monitoring for wolf management (e.g., pack relocation for pup counts, home-range delineation, and winter population census). Radiotelemetry data were collected biweekly via fixed-wing aircraft flights. Position data from GPS collars were acquired at 12-hr intervals via satellite communications. During most of the study period, each documented wolf pack operating near or within the study areas had at least one radio- or GPS-instrumented pack member.

Wolf den and/or rendezvous sites were documented within or near each of the Impact study areas. Site occupancy data were acquired during annual site visits by IDFG or Nez Perce Tribe field staff. Incidental sightings or direct observations of wolves were routinely recorded by study personnel and/or cooperating cattle producers and range riders who traversed each study area during almost all days of the grazing season. Livestock depredation reports from IDFG and USDA APHIS were acquired for all Impact study areas. Data from documented incidents were compiled and classified according to confirmation level (i.e., confirmed, probable, or suspected wolf depredation), wolf pack involved, livestock species involved, number of individuals killed or injured, and date and location of incident. Incidental direct observations of wolves harassing and/or pursuing cattle in the study areas were also recorded.

Wolf presence on a study area, based on all of these data sources, was classified into three presence levels: low, moderate, and high within a relevant sampling period (e.g., grazing season or month within a grazing season). A conclusive determination of wolf absence on these rugged, remote study areas was generally impossible. Consequently, the low-presence class was assigned to sample periods when no wolf presence was recorded in the study area despite rigorous monitoring. Sample periods were classified as having a moderate level of wolf presence when scat, camera-trap photos, telemetry-tracking data, visual sightings, and/or den or rendezvous site occupancy indicated wolves were present in the study area, but no cattle pursuit events or depredations had been recorded. The high-presence class was assigned to periods when documented cattle pursuit events and/or depredations occurred in the study area. Simply put, if any cattle in the study area were documented as obviously and acutely aware of wolf presence through physical interaction, then the affected period was assigned to the high-presence class. Typically, the pursuit events or depredations required to prompt a high-presence classification were also accompanied by evidence of persistent wolf presence (e.g., numerous scat, frequent sighting). In some cases, confirmed livestock depredations ended up triggering lethal control actions by wolf management agencies. Consequently, time periods classified to the high-presence level could immediately be followed by periods of low wolf presence because the local wolf population had been temporarily reduced by lethal control.

All of the Oregon study areas were consistently classified to the low wolf presence level because no wolf presence was documented there during the course of the study. All the Idaho study areas, however, were classified to either the moderate or high wolf presence classes during at least one month (June − October) of each of the 5 study years (Table 2). For more detail regarding wolf presence observations, the reader is directed to Table S1 (available online http://dx.doi.org/10.1016/j.rama.2017.06.010) which provides a monthly summary of wolf presence events detected at each Impact study area during June − October for study years 2008 − 2012.

Statistical Analyses

This study was conducted under an Impact-Control design (Manly, 2009). The principal aim of this design was to contrast the daily travel

Table 2
Gray wolf presence levels (low, moderate, or high) in Idaho study areas by month within year as assessed using a combination of scat and sign surveys, camera traps, Global Positioning System and radiotelemetry tracking collars, den or rendezvous site visits, direct observation, and livestock depredation data. See Table S1 (online supplemental materials, available at http://dx.doi.org/10.1016/j.rama.2017.06.010) for details on wolf presence contributing to these monthly classifications.

		Months				
Study area	Yr	June	July	August	September	October
ID-A	2008	Moderate	High	High	Low	Low
	2009	High	High	High	Moderate	High
	2010	High	High	High	Low	Moderate
	2011	High	High	High	High	Low
	2012	High	Low	High	High	High
ID-B	2008	Low	Low	Moderate	Low	Low
	2009	Moderate	Moderate	Low	Moderate	Moderate
	2010	Low	Moderate	Low	Low	Low
	2011	Low	Moderate	Moderate	Low	Low
	2012	Low	Moderate	Low	Low	Low
ID-C	2008	Low	Moderate	Low	Low	Low
	2009	Low	Low	Moderate	Low	Low
	2010	Low	Moderate	Low	Low	Low
	2011	Low	Moderate	Moderate	Low	Low
	2012	Low	Low	Moderate	Moderate	Low

distance responses of GPS-collared cattle in Impact (Idaho) study areas, where wolf presence levels were generally higher, with responses in Control (Oregon) study areas where wolf presence was consistently low. As noted earlier, considerable effort was applied in pairing each individual Impact study area to a corresponding Control study area based on environmental, ecological, and managerial attributes. Nevertheless, the reader is reminded that while a weight of evidence case can be argued that any differences in cattle daily travel distance between Impact and Control study areas were due primarily to differences in wolf presence, study-area pairing did not provide strict experimental control of other biotic or abiotic factors, which may have been confounded with the wolf presence differences. This kind of strict control of nuisance variables could only be obtained by randomized assignment of the wolf-presence treatment, which obviously would be difficult, if not impossible, to do within the context of a regional-scale experiment.

Several factors, however, are commonly known to strongly influence the distance cattle and other large herbivores travel each day, and these could be readily examined as covariates in our analysis of treatment effects. Steepness of the terrain, proximity of drinking water sources, and vegetation characteristics (e.g., quality and availability of forage and cover) can all affect cattle mobility and distribution patterns (Mueggler, 1965; Cook, 1966; Roath and Krueger, 1982; Gillen et al., 1984; Ganskopp and Vavra, 1987; Bailey et al., 1996; Ganskopp et al., 2000; Ganskopp, 2001; Porath et al., 2002). As such, it was useful to determine whether the wolf-presence treatment affected cattle daily travel distance above and beyond the varying effects of slope, water distribution, and vegetation factors. For this work, we derived percentage slope rasters for each study area from 30-m digital elevation models sourced from the USGS National Elevation Dataset (NED; USGS, 2017a). Surface water feature locations on each of the study areas were extracted from the USGS National Hydrography Dataset (NHD; USGS, 2017b). Cloud-free satellite imagery (Landsat 5 TM) acquired in 2008, 2010, and 2011 during the peak forage production period (late June — early July; USGS, 2017c) was used to derive Normalized Difference Vegetation Index (NDVI) values at 30-m ground sample distance for each study area. Suitable imagery were not available for all study areas during study years 2009 and 2012. The NDVI values are indicative of vegetation greenness and provide a useful proxy to direct measurements of forage availability and vegetation cover. A GIS was then used to create covariate data sets by assigning slope, nearest distance to water features, and NDVI values to all cattle GPS locations.

A candidate set of 20 mixed models for the cattle daily travel distance response was evaluated using the GLIMMIX procedure in SAS v.9.4 (SAS, 2013). Akaike information criterion (AIC; Akaike, 1973) scores were used to select the best performing model for further analysis. This final model included treatment (Impact vs. Control study areas), study-area pair, month of grazing season, and their interactions as fixed effects. Treatment had three replicates (study areas) for each of the two levels. Study-area pair had three levels (A, B, and C), and month had five levels (June — October). Although GPS tracking data were collected on some study areas for longer than 5 months (e.g., study areas ID-A and OR-A), to maintain consistency, only data from the June — October period were used in these analyses. Slope, distance to water, and NDVI2008 covariates were also included in the model as fixed effects. Candidate models that included the NDVI2008 covariate consistently outperformed models that included either the NDVI2010 or NDVI2011 covariates. Study year with five levels (2008 — 2012) and its interaction with treatment and month, as well as the interaction among animal (total of 237 collared individuals), treatment, and study-area pair, were included in the mixed model as random effects. A variance component covariance structure was used to model random effects. Model denominator degrees of freedom were computed using the Kenward-Roger method (Kenward and Roger, 1997). Examination of residual plots indicated no substantial departures from normality, and no data transformation was necessary. The Tukey-Kramer adjustment was used for pair-wise comparisons of least-squares means (Kramer, 1956).

Results and Discussion

Collared cattle in the Control (Oregon) study areas (13.7 ± 0.396 SE km day^{-1}) traveled farther per day than those in Impact (Idaho) study areas (11.4 ± 0.396 SE km day^{-1}; Table 3). Cattle daily travel distance was similar among study-area pairs A (12.3 ± 0.376 SE km day^{-1}), B (12.4 ± 0.370 SE km day^{-1}), and C (12.8 ± 0.392 SE km day^{-1}), which represented three different but regionally typical ecological and managerial situations. Daily travel distance differed among some month combinations (Table 3). Cattle traveled farthest per day during July and were least mobile in October (Table 4). Treatment interacted with month (see Tables 3 and 5). Differences in daily travel distances were detected among months at Control study areas, but travel distances were similar across months at Impact study areas.

While distance to surface water and vegetation greenness (NDVI2008) strongly influenced the daily travel distance of cattle, effect of terrain slope was not significant at the 0.05 alpha level (see Table 3). Cattle traveled farther per day as distance to surface water increased (coefficient estimate: 0.00173 ± 0.000292 SE). As vegetation greenness increased, so did daily travel distance (coefficient estimate: 12.0 ± 0.290 SE). The NDVI2008 variable had, by far, the largest effect size among the three covariates.

Table 3
Type 3 *F*-test results for a mixed model evaluating the fixed effects of wolf presence (treatment), study-area pair, month and covariates (terrain slope [%], nearest distance to surface water feature [m], and Normalized Difference Vegetation Index ([NDVI, index values]) on cattle daily travel distance (km) responses under an Impact-Control design involving 3 study areas in western Idaho (Impact) and 3 study areas in northeastern Oregon (Control) during the mo June, July, August, September, and October of a 5-yr study (2008 — 2012).

Effect	Num. DF	Den. DF	*F* value	Pr > F
Treatment	1	3.899	20.17	0.0116
Pair	2	217.2	0.83	0.4389
Treatment · pair	3	216.8	4.79	0.0092
Month	4	16.09	6.65	0.0023
Treatment · month	4	16.57	7.94	0.0009
Pair · month	8	23971	83.88	<0.0001
Treatment · pair · month	8	24161	27.50	<0.0001
Slope	1	24852	3.16	0.0756
Distance to water	1	24780	35.04	<0.0001
NDVI	1	24889	1525.21	<0.0001

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Table 4

Least-squares means and 95% confidence limits from a mixed model of cattle daily travel distance (km) responses for each month of a 5-month grazing season, averaged across 5 study years (2008-2012), at study areas (i.e., USFS cattle grazing allotments) included in an Impact-Control study conducted in western Idaho and northeastern Oregon.

Months	LS[†] Means	Lower CL	Upper CL
	-----------km per day-----------		
June	12.2^{bc}	11.4	13.0
July	13.2^{a}	12.4	14.0
August	13.0^{ab}	12.2	13.8
September	12.5^{abc}	11.6	13.3
October	11.8^{c}	11.0	12.6

[†] Least-squares means with different letter codes were significantly different at the 0.05 alpha level.

Impact versus Control

A number of explanations could be proposed for why daily travel distance was greater for cattle in Control than Impact study areas. Generally, this response indicates a difference in how cattle partitioned their time budgets. Cattle in Control study areas must have spent a larger proportion of their time engaged in mobile behaviors such as foraging or traveling to water, as opposed to stationary behaviors (e.g., bedding, ruminating, grooming, scanning for predators), compared with cattle in Impact study areas. For example, if drinking water sources were fewer and/or more dispersed in Control than Impact study areas, cattle in Control study areas would likely have spent more time traveling among water and other focal sites (e.g., upland foraging areas, mineral licks), thereby tending to travel farther per day than cattle in Impact study areas (Valentine, 1947; Williams, 1954; Roath and Krueger, 1982; Senft et al., 1987). However, when the distance to water covariate data from this study were examined, there was no clear contrast between Impact and Control treatment levels in terms of mean distances between collared cattle locations and water features (Table 6). While distance to water did exert a highly significant effect on cattle mobility in general (see Table 3), it seems unlikely, based on results in Table 6, that this covariate contributed substantially to the observed difference in daily travel distance between Impact and Control study areas.

Vegetation conditions can influence cattle mobility (Senft et al., 1987; Clark et al., 2017a, 2017b). In this study, daily distance traveled by cattle increased with increasing vegetation greenness (see Table 3). Yet when the NDVI covariate data were examined, there was no evidence of contrast between Impact and Control study areas (see Table 6). It is rather doubtful, consequently, that variability in vegetation greenness motivated the observed difference in cattle mobility between Impact and Control study areas.

Table 5

Least-squares means and 95% confidence limits from a mixed model of cattle daily travel distance (km) responses for each treatment by month combination, averaged across 5 study years (2008-2012).

Treatment Level	Months	LS[†] Means	Lower CL	Upper CL
		-----------km per day-----------		
Control	June	14.2^{ab}	13.2	15.2
	July	14.7^{a}	13.7	15.7
	August	14.0^{abc}	13.0	15.0
	September	13.5^{abcd}	12.4	14.5
	October	12.2^{bcde}	11.2	13.2
Impact	June	10.2^{e}	9.20	11.2
	July	11.8^{cde}	10.8	12.8
	August	11.9^{bcde}	10.9	12.9
	September	11.5^{de}	10.5	12.5
	October	11.4^{de}	10.3	12.4

[†] Least-squares means with different letter codes were significantly different at the 0.05 alpha level.

Table 6

Mean and standard deviation values for terrain slope, distance to surface water features, and Landsat-derived Normalized Difference Vegetation Index (NDVI) or greenness at cattle Global Positioning System locations within pairs of Impact and Control study areas.

Study areas	Treatment levels	Slope	Distance to water	NDVI
		----%----	----m----	----value----
ID-A	Impact	17.7 ± 8.73	176 ± 95.9	0.423 ± 0.104
OR-A	Control	17.7 ± 10.4	199 ± 84.7	0.428 ± 0.0879
ID-B	Impact	11.4 ± 5.27	168 ± 105	0.441 ± 0.124
OR-B	Control	17.4 ± 7.58	122 ± 70.1	0.453 ± 0.0772
ID-C	Impact	18.2 ± 6.24	175 ± 100	0.458 ± 0.102
OR-C	Control	19.4 ± 7.98	104 ± 48.7	0.454 ± 0.0742

Topography, particularly terrain slope, can strongly influence cattle distribution patterns (Mueggler, 1965; Cook, 1966; Gillen et al., 1984; Ganskopp and Vavra, 1987). Consequently, one would intuitively expect slope to play a principal role in governing cattle mobility. Yet in our mixed model, the terrain slope covariate did not have a significant effect on the daily travel distance response. This finding is more understandable if one considers that cattle are proficient at finding and using least-effort pathways within complex and sloping terrain (Ganskopp et al., 2000). This ability allows cattle to at least partially avoid the energetic limitations on daily travel distance that would otherwise be imposed by steep slopes. It is not too surprising then that terrain slope was not a strong predictor of daily travel distance in this study. Furthermore, no clear differences in slope at cattle GPS location were evident between Impact and Control study areas (see Table 6). Consequently, terrain slope does not appear to have promoted the observed treatment difference in daily travel distance.

Climate, soils, floristic composition, grazing management, and animal husbandry practices are all known to affect cattle mobility (Clary et al., 1978; Stuth, 1991; Bailey et al., 2008; Rubio et al., 2008) and thus potentially could have contributed to the treatment difference. However, as noted in the Methods section, considerable care and effort was applied when pairing Impact and Control study areas with the intent of controlling these potentially confounding factors. On the basis of the data available, it seems unlikely that any of these environmental, ecological, or managerial factors played a substantial role in the observed treatment effect.

If, based on the discussion above, one assumed our efforts to pair Impact and Control study areas were adequately successful in controlling most of the influence from nuisance variables, then the differing response by cattle to the Impact-Control treatment should primarily be due to the difference in wolf presence levels. Increased vigilance by cattle in Impact study areas could, at least partially, explain the lower daily travel distances observed there relative to Control study areas. Vigilance generally takes the form of remaining stationary, head up, watching, and listening for the approach of danger (Welp et al., 2004; Kluever et al., 2009). Vigilance tends to interrupt nonstationary behaviors such as foraging and walking and thus would decrease daily travel distance unless foraging and/or traveling budgets were enlarged to compensate for these interruptions (Underwood, 1982; Howery and DeLiberto, 2004; Kluever et al., 2009). As a ruminant, cattle must spend considerable time each day ruminating (e.g., 6.5 hr; Braun et al., 2013), which places limits on how much their foraging and traveling budgets can be adjusted to compensate for vigilance (Illius and Fitzgibbon, 1994). If these trade-offs between vigilance and mobile activities cannot be balanced, energy costs will exceed intake and productivity will be impacted (Lima and Dill, 1990; Howery and DeLiberto, 2004). In contrast, cattle in Control study areas, under much lower predation threat, would likely be less vigilant. Foraging and traveling activities, consequently, would suffer less interruption and daily travel distances would tend to be longer.

In addition to vigilance, cattle in Impact study areas, like other ungulates experiencing wolf predation threat, may retreat to safer habitats or

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refugia to avoid predation (Bergerud et al., 1984; Creel et al., 2005; Hebblewhite et al., 2005). Fidelity for safer habitat types could reduce daily travel distance, particularly, if cattle were reluctant to traverse discontinuities separating patches of safer habitat. Reluctance to leave safer habitat, however, may also impact cattle diet quality and thus productivity if these habitats offer less or lower-quality forage than riskier habitats (Lima and Dill, 1990).

Ungulates like cattle may also aggregate into larger group sizes to dilute predation risk (Hebblewhite and Pletscher, 2002). Bunching into larger groups could also influence daily travel distance. According to the group vigilance hypothesis (Roberts, 1996), collective detection by the group may allow individuals to relax their vigilance (Elgar, 1989; but see Lima, 1995) and thus forage more efficiently with fewer interruptions. The cohesiveness of the group, however, would tend to emphasize stationary or slow-speed behaviors over traveling because individual cattle would be reluctant to move beyond the bounds of the group (Hamilton, 1971; Pulliam and Caraco, 1984). Individuals moving as a group could tend to move shorter distances overall than if these individuals were pursuing their own explorations. Combined, antipredator behaviors like increased vigilance, fidelity for safe habitats, and bunching into larger groups would all lead to relative decreases in daily travel distance such as we observed between our Impact and Control study areas.

Temporal Variability

Cattle in this study traveled farther per day during the middle of the grazing season (July) and were least mobile at the close of the season (October). Cattle did, however, travel less during June than July, which is probably a response to greater, more homogenous availability of high-quality graminoid forages across the landscape during June than July (McIlvanie, 1942; Skovlin, 1967). With nutritious food readily at hand in June, cattle would not have had a dietary motivation to travel. However, as these graminoid species set seed in July and their forages began to senesce and dry, associated declines in palatability would likely have induced more extensive foraging. While soil moisture limitations on open slopes and ridges would cause forages there to senesce early and rapidly, forages on deeper soils and more mesic exposures, swales, and riparian systems would retain greater nutritional quality and palatability later into the season (Wilson, 1982; Seagle and McNaughton, 1992). This increased landscape-scale heterogeneity of forage quality in July would likely have motivated greater exploratory foraging, interpatch traveling bouts, and daily travel distances (de Knegt et al., 2007; Utsumi et al., 2009). Daily travel distance of cattle was statistically similar among the months July, August, and September. This suggests that extensive foraging and enhanced mobility continued to be energetically profitable during these months (Charnov, 1976; Bailey et al., 1996; WallisDeVries et al., 1999). By October, however, forage quality and palatability would have become more universally depressed across the landscape. Under these conditions, cattle probably adapted a strategy of energy conservation (Clark et al., 2017a) with a larger proportion of their time budgets dedicated to stationary behaviors (e.g., ruminating coarse, bulky forages) and, thus, a consummate decrease in daily travel distance.

It is interesting that these monthly differences in daily travel distance were evident at the Control but not the Impact study areas. This finding may suggest cattle in Impact study areas did not respond to increases in heterogeneity of forage quality by increasing their mobility. A potential explanation for this lack of expected mobility during July, August, and September would be a strong fidelity by cattle for habitats perceived to be safer from predation threat and the resulting localization of cattle movement to within these habitats. For example, open slopes and pine savannas with extensive viewsheds allow cattle to detect the approach of large predators and thus provide greater security from ambush than more mesic areas characterized by heavier forest and/or tall shrub cover. Unfortunately, these “safer,” open habitats would also tend to experience earlier and more pronounced declines in forage quality than more mesic but risker habitats (Skovlin, 1967). While cattle can compensate for subpar forage quality by selective grazing (Holechek et al., 1981), this capacity has limits, particularly, when mobility is otherwise constrained. If wolf presence in the Impact study areas was indeed constraining cattle movement to safer habitats at the expense of nutritional needs, this would almost certainly have impacts on cattle productivity. Prolonged and concentrated cattle use of these same habitat areas could also promote resource damage. A resource-selection analysis is required to evaluate this site-fidelity hypothesis and its implications. Although beyond the scope of the present paper, this analysis has been undertaken by the authors and will be the subject of a forthcoming paper.

Conclusions and implications

This study provides evidence that cattle in mountainous grazing areas and consistently exposed each year to moderate to high gray wolf presence exhibited shorter daily travel distances than cattle in areas of consistently low wolf presence. Pairing of Impact and Control study areas appeared to adequately control for effects of other environmental, ecological, and managerial factors, which potentially could have become confounded with treatment effects on cattle mobility. Lower daily travel distances observed for cattle in the Impact study areas likely resulted from a combination of antipredator behaviors including increased vigilance, fidelity for safer habitats, and aggregation into larger but less mobile groups. Seasonal variability in daily travel distance was observed but only at Control study areas, which suggests wolf presence in Impact study areas may have constrained cattle mobility responses to seasonal increases in landscape-scale heterogeneity of forage quality and palatability. Additional research into the activity budget and resource selection responses of these cattle is required to better understand the actual mechanisms operating behind these daily travel distance results. Further evaluation of this finding is important because while antipredator behaviors may lessen risks of wolf predation, they can also have adverse impacts on cattle productivity and environmental health.

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