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ABSTRACT

Livestock guardian dogs (LGDs) are an effective tool for limiting livestock depredation by wild and feral predators. Unfortunately, LGDs have bitten hikers, joggers, and mountain bikers. Strategies are needed to mitigate LGD-human conflicts, especially in landscapes inhabited by large, aggressive predators where the threat of livestock depredation is greatest. One recommendation is to keep groups of sheep protected by LGDs at least 400 m from high-use recreational sites, but few data exist to support or refute this strategy. We monitored sheep and LGDs with Global Positioning System collars at seven ranches during a 3-yr period to evaluate how far, and under what circumstances, LGDs roamed from their sheep. One band of sheep (i.e., flock) was studied per ranch, with a typical band composed of 600−800 mature ewes with 900−1 200 lambs. Sheep were herded in extensive grazing systems within their traditional summer or fall grazing areas in foothill and mountain landscapes of southwestern and west-central Montana. Three bands of sheep inhabited landscapes with a greater threat of depredation by gray wolves and grizzly bears, and 4 bands of sheep inhabited landscapes where the threat of depredation was mostly from coyotes. The mean and median LGD-sheep distance across all LGDs and time periods was 164 m and 86 m, respectively. LGDs roamed farther from their sheep during nighttime and crepuscular periods than during daytime; farther when the moon was more fully illuminated; farther during fall than summer; and farther in landscapes without gray wolves and grizzly bears. Female LGDs roamed farther than males. Juvenile LGDs did not roam farther than adult LGDs. Overall, our results from extensive domestic sheep grazing systems suggest that keeping range sheep 400 m away from recreation sites and rural residences will likely prevent > 90% of agonistic LGD encounters with humans.

Introduction

Range livestock agriculture and predator conservation are both fundamentally important. Properly managed livestock grazing is the most sustainable form of agriculture, requiring few inputs of nonrenewable resources while using natural biological processes to produce food, fiber, and other products that sustain human life (Vavra et al. 1994; Laycock et al. 1996; Holecheck 2009; 2013). Similarly, predation by mammalian predators is a natural biological process that helps regulate wild prey abundance, thereby sustaining ecosystem function and healthy wildlife populations (Prugh et al. 2009; Ripple et al. 2014). Unfortunately, humans and their livestock experience conflict when predators harass, injure, or kill livestock, and predators experience conflict when humans retaliate by harassing, injuring, or killing predators. Management strategies are needed to facilitate livestock-predator coexistence.

For sheep producers in the western United States, depredation by wild and feral predators is a major economic burden. For example, in Montana, Wyoming, and Idaho during 2018, predators killed 44 300 sheep valued at $7.8 million (USDA-NASS 2019a, 2019b, 2019c). The threat of depredation also inflicts indirect costs without injuring or killing sheep, through reduced sheep production (e.g., lower reproductive performance, lower weight gain, lower fleece weights) and increased costs of depredation control (Howery and DeLiberto 2004; Scasta et al. 2018).

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Effective suppression of livestock depredation often requires the integrated use of several techniques, including both lethal and non-lethal methods (Knowlton et al. 1999; Miller et al. 2016). The use of livestock guardian dogs (LGDs; *Canis familiaris*) is one tool that is currently more socially acceptable in the United States than other methods of predator control (Bruskotter et al. 2009; Slagle et al. 2017), and the use of LGDs has proven effective in the western United States. LGDs have suppressed sheep depredation by large and small predators including gray wolves *(C. lupus),* grizzly bears *(Ursus arctos horribilis),* black bears *(Ursus americanus),* mountain lions *(Felis concolor),* coyotes *(C. latrans),* bobcats *(Lynx rufus),* and red foxes *(Vulpes vulpes;* Green and Woodruff 1989, 1993; Andelt and Hopper 2000; Bangs et al. 2005; Scasta et al. 2017; Stone et al. 2017).

LGDs protect sheep by remaining near them and actively defending the sheep against predators when necessary (McGrew and Blakesley 1982; Coppinger et al. 1983; Allen et al. 2016). Barking by LGDs alerts the sheep and their human herder (i.e., shepherd) when a predator is nearby, and sheep learn to group together with LGDs when predators approach (McGrew and Blakesley 1982; Andelt 2004; Allen et al. 2016). Most coyotes, mountain lions, and black bears can be chased away relatively easily by LGDs (Jorgensen 1979; Green and Woodruff 1989). Depredation by grizzly bears and gray wolves is more difficult for LGDs to dissuade (Green and Woodruff 1989; Bangs et al. 2005).

As gray wolf and grizzly bear populations have increased and expanded their ranges in the western United States, livestock depredations have increased (Bangs et al. 2005; Sommers et al. 2010; Wells et al. 2019; Windh et al. 2019) and more ranchers have begun using LGDs to protect their livestock. Ten percent of US sheep producers used LGDs in 2004 versus 24% of sheep producers in 2014 (USDA-APHIS 2015). In Montana, 69% of sheep producers used LGDs in 2019 (MWGA-MSU 2020). Concurrently, outdoor recreation and rural residential development have also increased, especially in the western United States (Ahmed and Jackson-Smith 2019; Thomas and Reed 2019). An unfortunate consequence has been increased confrontations between LGDs and humans. In some cases, LGDs have bitten hikers, joggers, and mountain bikers, and in at least one incident the sheep producer received criminal penalties and his civil case ended in a $1 million settlement agreement (Riccardi 2009; Lofholm 2014; Wyrick 2016). The American Sheep Industry Association (ASI) developed best management practices (BMPs) to help sheep producers optimize the use of LGDs and minimize potential conflicts with neighbors and recreationists (Reece and Brown 2011). One of these BMPs recommends that groups of sheep guarded by LGDs should be kept at least 400 m (0.25 mile) from any trailhead, campground, or picnic area during weekends, holidays, or other potentially high recreational use periods. Similarly, the US Forest Service and the Bureau of Land Management have stipulated that groups of sheep protected by LGDs must remain at least 400 m away from highly used recreational trails in some public land areas (Lofholm 2014). Few data exist to support or refute this guideline. In response, we used Global Positioning System (GPS) collars to evaluate how far, and under what circumstances, LGDs roamed from their sheep in extensively herded rangeland grazing systems.

Methods

Study area

We studied LGD behavior on seven ranches in seven different counties across southwestern and west-central Montana: Beaverhead County, Broadwater County, Lewis and Clark County, Madison County, Meagher County, Powell County, and Sweetgrass County. One band of sheep was studied per ranch, with each band composed of about 600−800 mature ewes with 900−1 200 lambs. All seven bands grazed within their traditional summer or fall grazing areas in foothill and mountain rangeland that included federal, state, and private lands. The seven grazing areas were separated from each other by $\geq$ 115 km. Vegetation and topography were typical of foothill and mountain landscapes within the Northern Rocky Mountains, with foothill grasslands, sagebrush steppe, mountain meadows, and coniferous forest vegetation types (Pfister et al. 1977; Mueggler and Stewart 1980), and recreational activity was minimal to none in the seven landscapes during our study. We acknowledge that recreational activity in the vicinity of the sheep could possibly influence LGD behavior. However, we are not aware of previous research that has addressed this question. We did not address this question because we were unable to reliably quantify the exact location, type, or intensity of human activity on extensive foothill and mountain recreational landscapes. Therefore, we purposely controlled the potential effect of this variable by confining our study within seven landscapes where recreational activity was minimal to none.

Three bands of sheep inhabited landscapes with a greater threat of depredation by gray wolves and grizzly bears, and 4 bands of sheep inhabited landscapes where the threat of depredation was mostly from coyotes. We characterized the depredation threat within the 7 landscapes (i.e., high or low threat from gray wolves and grizzly bears) based on input from state and federal wildlife agency personnel and local livestock producers.

Each band of sheep was supervised by a herder who remained with the sheep during the study period. To help control sheep movements, herders used herding dogs, primarily Border Collies and Australian Shepherds. Herding dogs accompanied the herders during the day and stayed at the herders' camps each night. In contrast, LGDs were unsupervised by the herders. LGDs were bonded to the sheep and cohabited with them 24 h/d^{-1} when the sheep were on the range, except for brief periods when herders fed dog food to LGDs near the herders' camps. It is generally recommended that LGDs not be fed at a herder's camp so as to discourage them from loitering nearby and abandoning the sheep (Green and Woodruff 1999). However, when sheep are grazing in foothill and mountain landscapes where bears and other large predators are present, dog food must be kept in heavy-duty bear-proof containers so as not to attract predators. The result is that LGDs are typically hand-fed (i.e., without a self-feeder) near the herder's camp, similar to how the herding dogs and horses are fed. Each band of sheep had 2−5 LGDs, which is common for ewe-lamb bands of this size on open range in the western United States (Green and Woodruff 1988; Andelt 2004).

Herders moved their sheep each night to a bedground located near the herder's camp because sheep are most vulnerable to depredation at night (Johnson and Griffel 1982; O'Gara et al. 1983; Stone et al. 2017). In a typical day, the herder rousted the sheep off the bedground near daylight and herded the sheep toward the day's grazing areas where the sheep remained until late afternoon or early evening. Next, sheep were moved to their bedground and bedded down around dusk each night. Bedgrounds were generally relocated to new areas on the range every 1−3 d.

Animal care

Our procedures for this study of LGD behavior adhered to the *Guide for the Care and Use of Laboratory Animals* (NAS 2011) and the *Guide for the Care and Use of Agricultural Animals in Research and Teaching* (FASS 2010). We obtained ethics approval from the Institutional Animal Care and Use Committee of Montana State University (protocol number 2011-55) and the Montana State University Agricultural Animal Care and Use Committee (protocol number 2011-AA04).

Table 1
Name, age, sex, and breed of the 13 livestock guardian dogs (LGDs) used in the data analyses, guarding sheep on 7 different ranches on foothill and mountain landscapes with higher or low presence of gray wolves and grizzly bears, during summer or fall 2012–2014 in southwestern and west-central Montana.

Yr	Gray wolf & grizzly bear presence	Season[1]	Ranch location (county)	LGD	Age[2]	Sex	Breed
2012	Higher	F	Beaverhead	Chuck1	Adult	Male	Komondor
	Higher	F	Beaverhead	Nick	Adult	Male	Akbash × Great Pyrenees
	Low	F	Meagher	Smokey	Juvenile	Male	Spanish Mastiff × Great Pyrenees
	Low	F	Meagher	Unknown1	Adult	Female	Miramma
	Low	F	Meagher	Unknown2	Adult	Female	Komondor
	Low	Su & F	Madison	Jasmine	Adult	Female	Akbash × Great Pyrenees
2013	Higher	Su	Powell	Tiki	Adult	Male	Akbash × Great Pyrenees
	Higher	Su	Lewis & Clark	Lewis	Adult	Male	Sharplaninatz cross
	Higher	Su	Lewis & Clark	Goliath	Juvenile	Male	Sharplaninatz
	Low	Su & F	Broadwater	Zilo	Juvenile	Male	Akbash × Great Pyrenees
2014	Higher	Su & F	Beaverhead	Rosa	Adult	Female	Akbash
	Low	F	Meagher	Sven	Adult	Male	Great Pyrenees
	Low	F	Sweetgrass	Chuck2	Juvenile	Male	Akbash

[1] F indicates Fall; Su, Summer.
[2] Adult indicates 5−9 yr old; juvenile, 1−2 yr old.

Data collection

We placed custom Global Positioning System (GPS) tracking collars (Clark et al. 2006) on 17 LGDs and 28 sheep during summer (June–August) or fall (September–November) across seven ranches and 3 yr (2012, 2013, 2014). We followed procedures similar to Akyazi et al. (2018) and Zingaro et al. (2018) and collared at least one LGD and at least one randomly selected mature ewe per band. We assumed that the collared ewe(s) in each band would exhibit spatial behavior that was representative of all the sheep in the band, especially given that the Targhee and Rambouillet sheep breeds used in our study are highly gregarious (ASI 2015). The LGDs and sheep that we monitored in the landscapes with a higher threat of depredation by gray wolves and grizzly bears had some familiarity with gray wolves and grizzly bears before our study (i.e., some LGDs and sheep may have been pursued or harassed by gray wolves or grizzly bears or been present during gray wolf or grizzly bear depredation events). Conversely, the LGDs and sheep in the landscapes with a low threat of depredation by gray wolves and grizzly bears were naïve to these predators before our study.

We programmed the GPS collars to record the date, time, spatial position, and fix-quality parameters (e.g., Position Dilution of Precision [PDOP]) at 5-min intervals, 24 h/d^{-1}. Average spatial accuracy of GPS locations was ≤ 5 m. We removed the GPS collars from the LGDs and sheep at the end of the summer or fall grazing seasons each year, at which time we downloaded the GPS data.

We augmented our field data collection by accessing the Naval Oceanography Portal (http://www.usno,navy.mil/) to obtain daily sunrise, sunset, moonrise, and moonset times for the entire field sampling period. From the same portal we obtained a daily index of lunar illumination (i.e., the fraction of the moon illuminated by the sun at midnight), which described the moon phase quantitatively. The fraction of the moon illuminated was 0.0 at new moon, 0.50 at first and last quarter, and 1.0 at full moon. We did not use daily cloud cover percentages to adjust lunar illumination values downward because previous research suggests that illumination can be increased with reflectance off high thin clouds (Hahn et al. 1995; Kyba et al. 2011).

Data analysis

We conducted our study under an Impact-Control design (Manly 2009) to contrast LGD-sheep distance in landscapes with and without much threat of depredation by gray wolves and grizzly bears. We assumed that differences in LGD-sheep distance between Impact landscapes (where the depredation threat from gray wolves and grizzly bears was greater) and Control landscapes (where the depredation threat from gray wolves and grizzly bears was low) were due primarily to differences in gray wolf and grizzly bear presence. Strict experimental control of other biotic or abiotic factors that may have been confounded with the differences in gray wolf and grizzly bear presence was not possible because gray wolf and grizzly bear presence (higher vs. low) could not be randomly assigned to the landscapes.

We screened the GPS data for gross positioning errors and removed all locations with PDOP values ≥ 10 (Clark et al. 2017). We also excluded all locations when LGDs were not out on the range with the sheep (e.g., LGD visits to veterinarian, sheep in corral). Thirteen of the GPS collars on LGDs and 26 of the GPS collars on sheep provided usable data. For ranch × grazing season combinations with usable data from more than one collared sheep, we analyzed data from only the individual ewe with the greatest number of recorded GPS locations. Altogether we analyzed > 144 000 GPS locations from 13 LGDs and > 117 000 GPS locations from 9 sheep. We used ArcMap (Version 10.3.1) to convert GPS latitude and longitude records of LGDs and sheep to Universal Transverse Mercator (UTM) coordinates. Next, we aggregated the UTM coordinates by hour and calculated hourly mean UTM coordinates for each LGD and the sheep it was guarding. We aggregated the UTM data by hour because imperfect synchrony resulted from occasions when a GPS collar failed to record its location or required extra time to acquire its location.

We calculated Euclidean LGD-sheep distance (i.e., the distance between the hourly mean UTM location of an LGD and the hourly mean UTM location of the GPS-collared ewe within the band of sheep that the LGD was guarding). These data provided 12 223 hourly mean LGD-sheep distances from 13 LGDs across 3 yr within 7 bands of sheep on 7 different ranches (Tables 1 and 2). The average and minimum numbers of LGD-sheep distances analyzed per LGD were 940 and 325, respectively (see Table 2). Six of the LGDs protected sheep in landscapes where gray wolf and grizzly bear presence was higher, and seven LGDs protected sheep in areas where gray wolf and grizzly bear presence was low and the threat of depredation was mostly from coyotes. Nine LGDs were male, four were female, and all had been spayed or neutered before our study. Four LGDs were juvenile (1−2 yr old), and nine LGDs were adult (5−9 yr old). Eight different breeds and crosses were included among the 13 LGDs (see Table 1). Previous research has documented few differences among LGD breeds in LGD behavior or predator protection effectiveness (Green and Woodruff 1988; Andelt 1992, 1999; Kinka and Young 2018, 2019).

We assigned one of three time periods (daytime, nighttime, or crepuscular) to each of the 12 223 LGD-sheep distances. We defined daytime as 1 h postsunrise to 1 h presunset; we defined nighttime as 1 h postsunset to 1 h presunrise; and we defined cre-

Table 2
Mean (standard deviation) distance, median distance, and number of hourly mean locations analyzed for 13 individual livestock guardian dogs (LGDs) and the sheep they were guarding. LGD-sheep distances were recorded during summer and fall 2012–2014 on foothill and mountain rangeland in southwestern and west-central Montana.

LGD	Mean LGD-sheep distance (m)	Median LGD-sheep distance (m)	Minimum LGD-sheep distance (m)	Maximum LGD-sheep distance (m)	Hourly mean locations (n)
Chuck1	175 (370)	68	1	1 970	329
Nick	118 (127)	70	3	1 300	576
Smokey	198 (345)	78	1	1 936	806
Unknown1	293 (312)	197	6	1 985	1 438
Unknown2	287 (362)	173	7	1 965	772
Jasmine	136 (179)	72	4	1 713	1 230
Tiki	93 (98)	63	2	985	1 119
Lewis	79 (68)	60	2	556	325
Goliath	213 (322)	106	2	1 994	876
Zilo	96 (123)	66	1	1 887	1 994
Rosa	162 (252)	104	1	1 981	849
Sven	108 (138)	73	4	1 927	859
Chuck2	174 (230)	89	2	1 576	1 050
Total					12 223
Mean	164 (70)	94 (43)	3 (2)	1 675 (458)	940 (450)

puscular as the two 2-h periods surrounding sunrise and sunset (Rockhill et al. 2013). We also assigned a lunar illumination value to each of the 12 223 LGD-sheep distances. Lunar illumination values ranged from 0 to 1 based on the fraction of the moon illuminated by the sun at midnight of the day when the LGD-sheep distance was recorded.

To evaluate the effects of season (summer, fall); LGD sex (male, female); LGD age (juvenile, adult); time of day (daytime, nighttime, crepuscular); and the threat of depredation by gray wolves and grizzly bears (low, higher), we used chi-square likelihood ratio tests to compare the null model with the respective single-variable candidate models (Program R, version 3.5.1, R Foundation for Statistical Computing, Vienna, Austria). We included individual LGDs as a random effect in all models to limit type I error from repeated observations of the same experimental units (Burnham and Anderson 2002). We used log-transformed data for these comparisons because LGD-sheep distance was not normally distributed, and we back-transformed the results for presentation.

We used generalized linear mixed models (GLMMs) to identify the principal factors influencing LGD-sheep distance (Program R, version 3.5.1, R Foundation for Statistical Computing, Vienna, Austria). Again, we used log-transformed responses to meet distributional assumptions of GLMMs, and we present results on the real scales for data interpretation. We included seven explanatory variables: predator presence (i.e., gray wolf and grizzly bear presence), season, LGD sex, LGD age, time of day, lunar illumination, and the interaction between lunar illumination and time of day. We included this interactive variable because we hypothesized that lunar illumination would not affect LGD behavior during daytime. We were unable to include additional interactive variables of interest, such as interaction between LGD sex and predator presence or interaction between LGD age and predator presence, because in landscapes with a higher threat of depredation by gray wolves and grizzly bears, we had usable data from only one juvenile LGD and one female LGD.

All of our explanatory variables had a priori biological relevance. Accordingly, we began with a fully parameterized model and then used backward stepwise elimination based on Akaike Information Criterion corrected for small sample size (AIC_c) to iteratively build and evaluate candidate models (Burnham and Anderson 2002). As we did with the single-variable models described earlier, we included individual LGDs in all of our candidate models as a random effect to account for repeated observations from the same LGDs and limit type I error (Burnham and Anderson 2002). We considered the model with the lowest AIC_c value to be the model that best explained LGD behavior. Additional mod-

els with $\Delta\ AIC_c \leq 2$ were also examined (Burnham and Anderson 2002).

Results

Across all 13 LGDs in our 3-yr study, LGD-sheep distance averaged 164 m (SE = 2.24 m). The overall median LGD-sheep distance was 86 m. Among individual LGDs, mean LGD-sheep distance varied from 79 m to 293 m and the median LGD-sheep distance among the 13 LGDs varied from 60 m to 197 m (see Table 2). The minimum LGD-sheep distance per LGD averaged 3 m, and the maximum LGD-sheep distance per LGD averaged 1 675 m (see Table 2). Seventy-eight percent of all LGD-sheep distances in our study were $\leq$ 200 m, 82% were $\leq$ 300 m, and 92% were $\leq$ 400 m (see Table 3).

Mean LGD-sheep distance was greater during nighttime and crepuscular periods (182 and 180 m, respectively) than during daytime (142 m; $P < 0.001$; Table 4), and LGD-sheep distance was greater when the moon was more fully illuminated (Fig. 1). Mean LGD-sheep distance was greater for female LGDs than males (220 vs. 134 m, respectively; $P = 0.004$; see Table 4). Distinctive differences in LGD-sheep distances were less apparent between summer and fall ($P = 0.100$; see Table 4) and between LGDs inhabiting areas where gray wolf and grizzly bear presence was low or higher ($P = 0.187$). LGD-sheep distance did not differ between juvenile and adult LGDs ($P = 0.874$; see Table 4).

We evaluated 10 candidate models to describe LGD roaming behavior (Table 5). The model containing LGD sex, time of day, and degree of lunar illumination received the most support ($\Delta\ AIC_c = 0$, $w_i = 0.61$; see Table 5 and Fig. 1), and a chi-square likelihood ratio test indicated strong support for the top model over the null model ($P < 0.001$). A second model had $\Delta\ AIC_c \leq 2$ ($\Delta\ AIC_c = 1.84$, $w_i = 0.24$), but the second model only differed by one term; therefore we considered that term (season) noninformative (Arnold 2010). Our interpretation was reinforced by a chi-square likelihood ratio test that indicated strong support for the top model over the second-ranked model ($P = 0.030$).

Discussion

LGD-sheep distance in our study averaged 164 m. Our result is corroborated by other studies of extensively grazed sheep from around the world (United States, Italy, Norway) in which LGD-sheep distance averaged < 265 m (Linhart et al. 1979; Coppinger et al. 1983; Hansen and Smith 1999). It is worth noting that
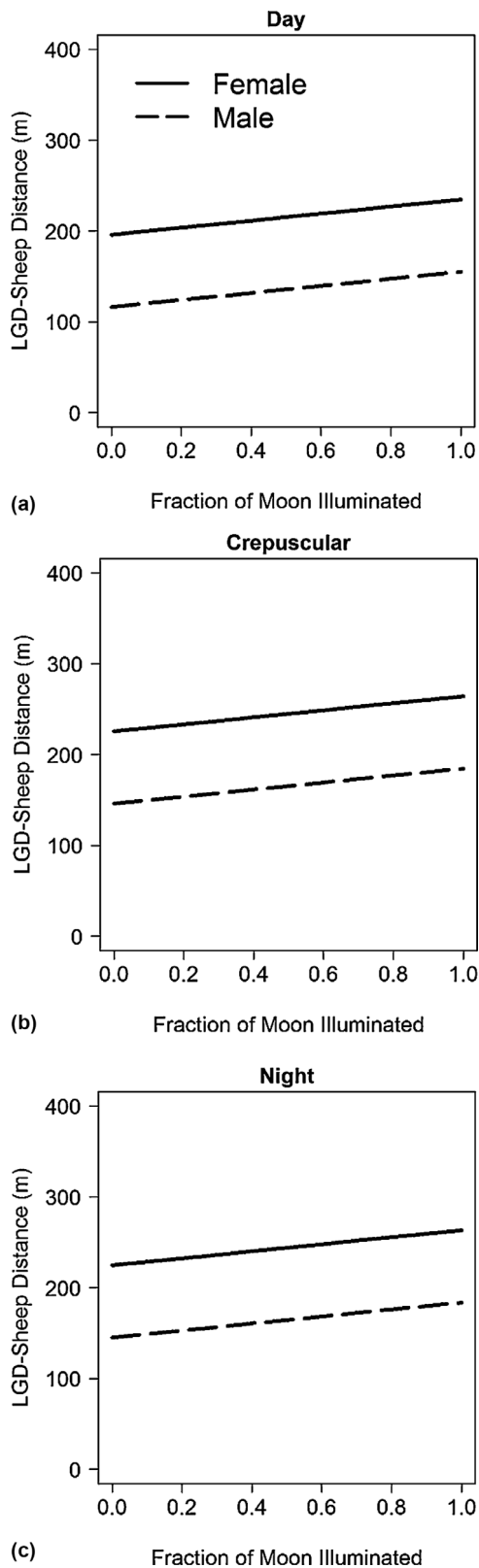
Table 3
Percentage distribution of the distances between livestock guardian dogs (LGDs) and the sheep they were guarding during summer or fall 2012–2014 on foothill and mountain rangeland in southwestern and west-central Montana ($n = 12\ 223$ hourly mean locations).

LGD-sheep distance (m)	Time of day						Total		
	Crepuscular		Daytime		Nighttime				
	Female $n = 625$	Male $n = 1$ 076	Female $n = 1$ 825	Male $n = 3$ 694	Female $n = 1$ 839	Male $n = 3$ 164	Female $n = 4$ 289	Male $n = 7$ 934	All $n = 12$ 223
					%				
≤ 100	33	66	48	70	38	58	42	64	56
101-200	27	19	24	19	25	24	25	21	22
201-300	16	8	13	5	15	9	14	7	10
301-400	9	3	6	2	7	3	7	3	4
401-500	3	1	3	1	5	2	4	1	2
501-600	3	1	2	1	3	1	2	1	3
601-700	2	< 1	1	< 1	2	1	2	1	1
701-800	1	< 1	< 1	< 1	1	< 1	1	< 1	< 1
801-900	1	< 1	< 1	< 1	< 1	< 1	< 1	< 1	< 1
901-1 000	1	< 1	< 1	< 1	1	< 1	< 1	< 1	< 1
> 1 000	4	2	3	2	3	2	3	2	2
Total	100	100	100	100	100	100	100	100	100

Table 4
Mean (standard deviation) distances between livestock guardian dogs (LGDs) and the sheep they were guarding during summer or fall 2012–2014 on foothill and mountain rangeland in southwestern and west-central Montana, USA ($n = 12\ 223$ hourly means). Comparisons among ages of LGDs, sexes of LGDs, seasons of the year, times of day, and relative presence of gray wolves and grizzly bears on the landscape.

Parameter	LGD-sheep distance (m)	Chi-square[1]	P[1]
LGD age			
Juvenile	151 (245)	0.03	0.874
Adult	172 (249)		
LGD sex			
Female	220 (288)	8.37	0.004
Male	134 (217)		
Season			
Summer	130 (196)	2.79	0.100
Fall	186 (273)		
Time of day			
Daytime	142 (230)	117.16	< 0.001
Crepuscular	180 (273)		
Nighttime	182 (256)		
Gray wolf & grizzly bear presence			
Low	175 (254)	1.74	0.187
Higher	141 (232)		

[1] Chi-square values and P values from likelihood ratio tests comparing the null model to the univariate model of effects. All models included random intercepts for individual LGDs.

our result and the results of the studies cited earlier differ dramatically from a recent study in which LGD-sheep distance averaged 626 m (Young et al. 2019). The large discrepancy is probably due to methodology. We recorded LGD and sheep locations at 5-min intervals and averaged them hourly to minimize temporal mismatches between the sheep and LGD locations. Alternatively, Young et al. (2019) recorded sheep locations once per h and recorded LGD locations once every 2.5 h or once every 5 h. Next, Young et al. (2019) defined LGD and sheep locations as simultaneous when LGD and sheep locations were recorded within 1 h of each other. Thus, in Young et al. (2019) LGD and sheep locations mismatched temporally by 1 h could have resulted in an LGD-sheep distance of up to 2.7 km even if the sheep and LGD never separated spatially and traveled side-by-side for 1 h at the average walking speed of domestic sheep (2.7 km/h; Squires et al. 1972).

LGDs need to be attentive and remain near their sheep in order to react when predators approach (Coppinger et al. 1983). LGDs also need to move away from their sheep occasionally to detect when predators are in close proximity (i.e., patrolling behavior) (Linhart et al. 1979; Hansen and Smith 1999; Green and Woodruff 1983). When more than one LGD is present, LGDs often work together, with one or more LGDs remaining close to the sheep while others move to detect or challenge predators (McGrew and Blakesley 1982; van Bommel and Johnson 2015; Allen et al. 2016). Consequently, LGD-sheep distances are expected to vary within and among LGDs. Hansen and Smith (1999), for example, documented that average LGD-sheep distance of individual, uncontrolled LGDs varied from 5 to 500 m during summer nights on forested mountain range in central Norway. In our study the average LGD-sheep distance of individual LGDs varied from 79 to 293 m, which suggests that sheep producers may wish to purposely select LGDs that tend to remain closer to their sheep if the producer's sheep regularly graze near popular recreational sites or near rural residences. Previous research suggests that LGD-sheep

Table 5
Fit statistics for models of livestock guardian dog (LGD) roaming behavior while guarding sheep during summer or fall 2012–2014 on foothill and mountain rangeland in southwestern and west-central Montana ($n = 12\ 223$ hourly mean locations). Models are ranked by Akaike Information Criterion (AIC_c), K is the number of fixed effects, ΔAIC_c is the difference of each model's AIC_c value from that of the highest ranked model, and w_i is the Akaike weight (sum of all Akaike weights = 1.00).

Model	K[1]	AIC_c	ΔAIC_c	w_i	Cumulative w_i
Lunar illumination + Time of day + Sex	7	34 380.18	0	0.61	0.61
Lunar illumination + Time of day + Sex + Season	8	34 382.02	1.84	0.24	0.85
Lunar illumination + Time of day	6	34 384.02	3.83	0.09	0.94
Lunar illumination + Time of day + Sex + Season + Predator presence	9	34 385.48	5.30	0.04	0.99
Lunar illumination + Time of day + Sex + Season + Predator presence + Age	10	34 387.70	7.52	0.01	1.00
Lunar illumination × Time of day	8	34 389.54	9.36	0.00	1.00
Time of day	5	34 465.05	84.87	0.00	1.00
Season + Time of day	6	34 467.54	87.36	0.00	1.00
Lunar illumination	4	34 487.62	107.43	0.00	1.00
Lunar illumination + Season	5	34 491.12	110.94	0.00	1.00
Null	3	34 566.66	186.47	0.00	1.00

[1] All models included random intercepts for individual LGDs.

Day

(a)

Crepuscular

(b)

Night

(c)

Fig. 1. Predicted responses for distances between livestock guardian dogs (LGDs) and the sheep they were guarding during summer or fall 2012–2014 on foothill and mountain rangeland in southwestern and west-central Montana. Responses by male and female LGDs are shown relative to lunar illumination during daytime (**A**), crepuscular periods (**B**), and nighttime (**C**).

distances tend to be less when, as pups, LGDs develop close social bonds with sheep (Espuno et al. 2004; Zingaro et al. 2018).

Time of day

LGDs in our study remained, on average, about 40 m farther from their sheep during nighttime and crepuscular periods than during daytime. We attribute this difference to greater patrolling behavior, given that most sheep depredations by gray wolves, grizzly bears, and coyotes occur at night and during crepuscular periods (Johnson and Griffel 1982; O'Gara et al. 1983; Stone et al. 2017). Our results are consistent with Zingaro et al. (2018), who documented that LGDs in Italy were farther from their sheep when the risk of depredation was greater. The increased LGD-sheep distance that we documented during crepuscular periods versus during daytime is also consistent with previous research in the French Alps, where LGDs were regularly observed moving away from their sheep during early morning to defecate and urinate and then returning to their sheep (Landry et al. 2014). LGDs on Australian rangelands also moved away from their sheep during early morning (4 A.M. to 8 A.M.) (van Bommel and Johnson 2014). Our results differ from Gipson et al. (2012), who reported that LGD-sheep distance in western Oklahoma was less at night during the second yr of their 2-yr study (27 m at night vs. 58 m during daytime). However, these data were collected from only one LGD within one 1.3-ha pasture during a 2-wk period (Gipson et al. 2012).

Nighttime LGD-sheep distance in our study averaged 182 m. Our result is comparable with Linhart et al. (1979), who documented that LGDs at night in western Montana and south-central North Dakota generally stayed within 200 m of the sheep bedground. Hansen and Smith (1999) documented that LGD-sheep distance averaged 261 m during summer nights on forested mountain range in central Norway.

Daytime LGD-sheep distance in our study averaged 142 m, which was notably more than daytime LGD-sheep distances during summer in the central Appenine Mountains of Italy, an environment similar to our study area (Coppinger et al. 1983). Only one of 33 LGDs in the Italian study had an average daytime LGD-sheep distance > 100 m (Coppinger et al. 1983). The shorter LGD-sheep distances recorded by Coppinger et al. (1983) likely reflect a difference in methodology. We used one GPS-collared ewe per band of sheep to calculate LGD-sheep distance, whereas Coppinger et al. (1983) visually estimated the distance between an LGD and the nearest sheep in the flock. We expect that the nearest sheep would, on average, be closer to an LGD than the representative GPS-collared sheep that we used in our study.

Lunar illumination

LGD-sheep distance of both male and female LGDs was greater when the moon was brighter, with average LGD-sheep distance of both male and female LGDs increasing about 50 m from zero to full lunar illumination. Yet even when the moon was brightest, LGD-sheep distance averaged < 200 m for males and < 300 m for females, less than the 400-m distance that ASI recommends sheep be kept from high-use recreational areas (Reece and Brown 2011).

We interpreted the positive correlation between LGD-sheep distance and lunar illumination as a response by LGDs to depredation risk. LGDs respond to predators, in part, by chasing predators away from their sheep (Jorgensen 1979; Green and Woodruff 1989), and depredation risk from top predators is greatest when the moon is bright, likely because increased moonlight increases the ability of predators to see their prey (Theuerkauf et al. 2003; Griffin et al. 2005; Pratas-Santiago et al. 2016).

We documented that LGD-sheep distance and lunar illumination were positively correlated during daytime, as well as during

nighttime and crepuscular periods. In addition, LGD-sheep distance was lower during daytime when compared with similar fractions of lunar illumination during either nighttime or crepuscular periods. Together, this suggests that LGDs displayed a delayed response to the decreased depredation risk present during daylight, and it suggests that LGDs were responding more to depredation risk than to the direct effect of lunar illumination. If LGDs roamed farther from their sheep to protect them during nights and crepuscular periods when the moon was bright and depredation risk was greater, we speculate that LGDs may have required several hours to subsequently decrease LGD-sheep distance as depredation risk subsided during daylight. This delayed response could account for the positive correlation during daytime that we observed between LGD-sheep distance and lunar brightness. A similar time lag in animal behavioral response to moon phases was observed in southwestern Spain, where European rabbits *(Oryctolagus cuniculus)* apparently required several days to adjust their behavior in response to increased nighttime predation during full moons by their top predator, Iberian lynx *(Lynx pardinus;* Penteriani et al. 2013).

LGD sex

Female LGDs in our study roamed, on average, about 86 m farther from their sheep than male LGDs. Our result differs from previous studies in Italy and Turkey that documented no difference in LGD-sheep distance between female and male LGDs (Akyazi et al. 2018; Zingaro et al. 2018). All LGDs in our study were either spayed or neutered. Neutered male LGDs tend to remain closer to their sheep than sexually intact male LGDs, and neutered male LGDs are less distracted by wild or feral female canids in estrus (Timm and Schmidz 1989; Green and Woodruff 1990). Also, spayed female LGDs are less likely to attract wild or feral male canids, and spayed LGDs do not need to be removed from guard duty to whelp and rear pups (Timm and Schmidz 1989). In a survey of livestock producers in 47 US states and 7 Canadian provinces, spayed or neutered LGDs were judged equally effective as sexually intact LGDs (Green and Woodruff 1988).

Season

LGDs in our study roamed, on average, 56 m farther from their sheep during summer than during fall. We are unaware of any previous investigations of seasonal effects on LGD-sheep distance, although a comparison of home range sizes of LGDs in Australia observed no difference between summer versus fall-winter (van Bommel and Johnson 2014).

Gray wolves and grizzly bears

LGDs often successfully chase coyotes, mountain lions, black bears, and to a lesser extent grizzly bears, away from the sheep they are guarding (Jorgensen 1979; Green and Woodruff 1989). In Montana, coyotes, mountain lions, and bears may be naturally wary of large canines such as LGDs because these predators coevolved in landscapes with gray wolves (Bangs et al. 2005). In contrast, gray wolves exhibit much less fear of LGDs and gray wolves in packs often attack and kill LGDs (Bangs et al. 2005). Accordingly, we have observed few old and bold LGDs in areas of Montana inhabited by gray wolf packs. LGDs in our study remained, on average, 34 m closer to their sheep in landscapes where gray wolf presence was higher, although this difference was not distinctive statistically. We speculate that the LGDs in our study may have learned that it is safer and more effective to remain slightly closer to the sheep and the herder when the landscape is inhabited by wolf packs.

Some European researchers and shepherds believe that brown bears *(Ursus arctos)* and wolves are not dissuaded by LGDs unless LGDs chase bears and wolves long distances (Urbigkit and Urbigkit 2010). For example, in Norway LGDs chased a brown bear *(Ursus arctos)* for 25 min until the bear was 1 km away from the flock (Hansen and Bakken 1999), and in Bulgaria LGDs were observed chasing wolves until they were 2 km from their sheep (Dohner 2007:140). These observations might imply that LGDs on average would roam farther from their sheep in landscapes inhabited by gray wolves and grizzly bears. Our results did not indicate this to be true, but we did observe that LGDs occasionally roamed far from their sheep with or without the presence of gray wolves and grizzly bears. Every LGD in our study had at least 1 hourly mean LGD-sheep distance that exceeded 550 m, and seven LGDs had at least 1 hourly mean LGD-sheep distance that exceeded 1.9 km. Included among these seven LGDs were four males and three females from six different breeds (Akbash, Great Pyrenees, Komondor $(n = 2)$, Miramma, Sharplaninatz, and Spanish Mastiff × Great Pyrenees).

LGD age

LGD-sheep distance in our study was similar for adult (5- to 9-yr-old) versus juvenile (1- to 2-yr-old) LGDs. Our result differed from Zingaro et al. (2018), who documented that older LGDs remained closer to their sheep than did younger LGDs, but most of the LGDs monitored by Zingaro et al. (2018) were juveniles (i.e., 22 of 29 LGDs were ≤ 2 yr old and 14 of the 22 juveniles were ≤ 1 yr old).) Zingaro et al. (2018) speculated that the younger LGDs roamed farther from their sheep because they were not yet strongly bonded socially to the sheep they were guarding. Indeed, LGDs commonly require 12−24 mo of bonding with sheep, beginning at 1−2 mo of age, before they become effective guardians (Redden et al. 2015).

Management implications

LGDs are an effective tool for facilitating livestock-predator coexistence, simultaneously minimizing, but not eliminating, negative consequences to both livestock and predators (van Eeden et al. 2017; Spencer et al. 2020; Whitehouse-Ted et al. 2020). As such, LGDs are fundamentally important to predator conservation and to sustaining range sheep production in extensive grazing systems. Conflicts can occur, however, between LGDs and humans. We examined the behavior of LGDs while protecting range sheep as one step toward refining strategies for mitigating conflicts among LGDs, recreationists, and rural residents in the western United States. An existing BMP suggests that groups of sheep guarded by LGDs should be kept at least 400 m from high-use recreational sites (Reece and Brown 2011). Our results indicated that this buffer does not need to be expanded in foothill and mountain landscapes inhabited by gray wolves and grizzly bears. And although LGD-sheep distances in our study differed distinctly between male and female LGDs, daytime versus nighttime or crepuscular periods, and new versus full moons, our results suggest that keeping range sheep 400 m away from recreation sites and rural residences will likely prevent > 90% of potentially agonistic encounters between LGDs and humans. Even during full moons when LGD-sheep distance was greatest, LGD-sheep distance averaged < 200 m for males and < 300 m for females. Overall, LGD-sheep distance in our study averaged 164 m and the median LGD-sheep distance was 86 m.

LGD-sheep distance did vary among individual LGDs, suggesting that sheep producers may want to select LGDs that remain closer to their sheep if their sheep regularly graze near high-use recreational sites or near residential areas. We noted that the sheepherders who collaborated with us in this study, without the ben-

efit of GPS measurements and by observation alone, could readily identify those individual LGDs that tended to travel farther from their sheep versus those LGDs that tended to remain closer to their sheep. Average LGD-sheep distance varied from 79 m to 293 m among the 13 LGDs in our study, while the median LGD-sheep distance among the 13 LGDs in our study varied from 60 m to 197 m.

Finally, we recommend that sheep producers, government agencies, and private landowners post signs and distribute brochures to inform recreationists and others when LGDs are present and to advise people about actions they can take to avoid human-LGD conflicts (USDA-APHIS 2010a, 2010b). We also suggest that future research should explore 1) the effects of wolves and grizzly bears on LGD aggressiveness toward humans, 2) the effects of varied LGD training and bonding techniques on LGD roaming behavior and aggressiveness toward humans, and 3) strategies to confine LGDs near their sheep (e.g., virtual fencing technology) and the associated impacts of these strategies on depredation deterrence by LGDs.

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