




Note

Elk Responses to Management Hunting and Hazing

JENNIFER D. JONES ¹, 1400 South 19th Avenue, Montana Department of Fish, Wildlife and Parks, Bozeman, MT 59718, USA
 KELLY M. PROFFITT ¹, 1400 South 19th Avenue, Montana Department of Fish, Wildlife and Parks, Bozeman, MT 59718, USA
 J. TERRILL PATERSON, Department of Ecology, Montana State University, 310 Lewis Hall, Bozeman, MT 59717, USA
 EMILY S. ALMBERG, 1400 South 19th Avenue, Montana Department of Fish, Wildlife and Parks, Bozeman, MT 59718, USA
 JULIE A. CUNNINGHAM, 1400 South 19th Avenue, Montana Department of Fish, Wildlife and Parks, Bozeman, MT 59718, USA
 KAREN M. LOVELESS,² 1400 South 19th Avenue, Montana Department of Fish, Wildlife and Parks, Bozeman, MT 59718, USA

ABSTRACT Human-wildlife conflicts are widespread around the world and result in property damage, disease spillover, financial loss, and decreased tolerance of wildlife. Increasing elk (*Cervus canadensis*) populations and land-use changes in the western United States are challenging resource managers tasked with managing conflict. Lethal and non-lethal management actions are commonly used to remove elk from conflict zones where they are not desired. We used radio-collar location data collected from female elk in 2 study areas in Montana, USA, from 2017–2020 to evaluate population- and individual-level responses to management actions (i.e., hunting, hazing) and environmental factors (i.e., weather, season, time of day). First, we used a generalized linear model with a logit link to evaluate the effects of hunting, hazing, time period, seasonality, and weather on the proportion of collared elk that used a conflict zone. Second, we used an ordinary linear model to assess the influence of hunting, hazing, seasonality, and weather on the duration of time that individual elk remained away from conflict zones. The proportion of elk using conflict zones was reduced by hunting, modestly reduced by hazing and increasing snowpack for 1 study area, increased at night, and decreased by a seasonal trend across months. The time individual elk remained away from conflict zones increased with the number of hazing events that occurred during an event and showed a modest seasonal trend increasing across months. For 1 study area, time away increased with the number of hunting days during an event and increasing snowpack, but the increase was biologically trivial. Our results indicate mixed responses of elk to hunting and hazing actions and provide evidence that management actions can influence elk use of conflict areas. Agencies trying to reduce conflicts may want to consider a combination of hunting and hazing, while accounting for site-specific characteristics to keep elk away from conflict zones. © 2021 The Wildlife Society.

KEY WORDS brucellosis, *Cervus canadensis*, damage hunt, hazing, wildlife conflict, wildlife management.

Human-wildlife conflicts occur with regularity, particularly when wildlife populations increase, change their distribution, or when changes in human land-use results in habitat loss (Messmer 2000, White and Ward 2010). Conflict often involves crop damage, property damage, and threat to the health and safety of humans or domestic livestock (Gilsdorf et al. 2002, Thirgood et al. 2005). Conflicts between growing populations of elk (*Cervus canadensis*) and landowners involved in agriculture and livestock production are frequent in many parts of the central and western United States, resulting in financial and time costs for landowners and wildlife managers (Conover 2001a, Walter et al. 2010, Smallidge et al. 2015, DeVore et al. 2016). In the Greater Yellowstone Area (GYA), the

potential for elk to transmit the disease brucellosis to livestock is an important source of wildlife conflict (Cross et al. 2007, Proffitt et al. 2011, Rayl et al. 2019). Elk are responsible for transmitting the disease to livestock in multiple recent outbreaks (Bienen and Tabor 2006, Kamath et al. 2016), and management efforts to prevent transmission from wildlife to livestock have been implemented in the GYA (Bienen and Tabor 2006, Cross et al. 2010b, Schumaker et al. 2012).

Private landowners and wildlife management agencies have several actions they can take to help prevent, decrease, or eliminate wildlife damage or disease transmission risk to livestock. These management actions to alter elk distributions can be non-lethal or lethal, year-round or seasonal. Non-lethal actions include fencing, frightening devices, and hazing, defined as the chasing of wildlife away from a specific location (Gilsdorf et al. 2002, VerCauteren et al. 2006). Lethal methods, most commonly recreational hunting, can alter elk movements (Cleveland et al. 2012)

Received: 20 December 2020; Accepted: 30 June 2021

¹E-mail: jennyjones@mt.gov

²Retired

and reduce the population, thus limiting the potential for conflict or the number of elk involved. Hunting can also have non-lethal effects and the landscape of fear concept predicts that prey will alter their behavior in response to perceived predation risk (Brown et al. 1999, Laundré et al. 2001, Preisser et al. 2005). This has been demonstrated in studies looking at elk response to natural and human predators whereby elk alter their foraging effort (i.e., location, time of day) to reduce perceived predation risk (Ciuti et al. 2012, Clinchy et al. 2016, Kohl et al. 2018). If conflict areas have high harvest risk, elk may change their behavior and select areas with lower harvest risk, potentially reducing conflict (Brown et al. 1999, Visscher et al. 2017, DeVoe et al. 2019). If lethal methods remove only a small proportion of the elk involved with conflict, it may not result in a behavioral modification because the negative consequences may not be enough to override the herd's motivation for using a resource (Cromsigt et al. 2013). The efficacy of each action can be evaluated in terms of the strength of the effect on elk behavior and distribution and the duration of the response.

A common management strategy for minimizing the transmission risk of brucellosis from elk to livestock for states in the GYA, including Montana, USA, is to maintain spatial separation of elk and livestock during the high-risk transmission period (Scurlock and Edwards 2010, Cross et al. 2015, Montana Fish, Wildlife & Parks 2020). Separation is achieved by fencing of stack yards and feedlines, actively hazing elk away from livestock pastures, and in some cases through controlled hunts aimed at altering elk movement behaviors. Despite the importance for reducing disease transmission risk and wildlife-human conflict, the effectiveness of various management tools in moving and keeping elk off specific areas is unclear, making efficient allocation of limited management effort and money difficult. Researchers have compared various management actions (e.g., hazing, hunting) and given general estimates regarding effectiveness of moving or keeping elk away from specific areas but without evaluating potentially confounding variables (e.g., weather, day of year) that likely influence the efficacy of management in different seasons and situations (Burcham et al. 1999, Kloppers et al. 2005, Cleveland et al. 2012, Found and St. Clair 2018). A better understanding of the ability of specific management actions to alter elk movement and distribution, and thus their efficacy at reducing commingling and elk to livestock transmission risk, is needed to address these conflicts more effectively.

Our objective was to evaluate the effect of management hunts and hazing on elk movement behaviors in 2 landscapes characterized by a matrix of tolerance zones (i.e., areas with no livestock where elk are allowed) and conflict zones (i.e., areas where elk are actively managed because of conflicts with private land use). Researchers have demonstrated that the immediate response to hunting and hazing is for elk to leave an area (Burcham et al. 1999, Conner et al. 2001, Kloppers et al. 2005, Cleveland et al. 2012). Given this previous work, we generally predicted that

management actions (i.e., hunting or hazing) would cause elk to leave the immediate area, but we had little information on the duration or efficacy of these actions. Therefore, our goal was to elucidate a better understanding of the strength of this effect, as measured by the number of elk in conflict zones following a management action and the length of time elk stay away. Specifically, we predicted that the number of elk in a conflict zone would be lower on days during the hunting period or immediately after hazing occurred and increase during periods of no hunting and as the number of days since hazing increased. We predicted that the duration of time elk would stay out of a conflict zone would increase if they departed during a hazing event (as compared to voluntarily departing), and with the number of hazing events that occurred while they were out of a conflict zone. We also predicted that the duration of time elk stayed away from a conflict zone would increase during the hunting period as compared to during periods of no hunting and that hunting would have a stronger influence than hazing on keeping more elk away from conflict zones for longer.

STUDY AREA

We selected 2 study areas within the Montana brucellosis Designated Surveillance Area (DSA) that employ hunting and hazing actions in efforts to maintain spatial separation between elk that may be infected with brucellosis and livestock. We defined study areas using 95% minimum convex polygons of collared elk locations during winter. The first study area was Sixmile located in the Paradise Valley (Fig. 1A). Sixmile is between the Yellowstone River and the Absaroka Mountains and is approximately 16,872 ha. Elevation ranges from 1,500 m to 2,250 m. Winter (Dec–Mar) weather in Sixmile can be extreme, with temperatures reaching -29°C and sustained winds up to 22 m/second. Sixmile is an intermontane valley predominantly covered in grasslands with fescue (*Festuca*) and wheatgrass (*Agropyron* spp.). Willow (*Salix* spp.), quaking aspen (*Populus tremuloides*), and cottonwood (*Populus* spp.) occur along Dailey Lake, Sixmile Creek, and the Yellowstone River. Coniferous forests, primarily lodgepole pine (*Pinus contorta*), Douglas-fir (*Pseudotsuga menziesii*), and Engelmann spruce (*Picea engelmannii*) begin in the foothills at higher elevations in the eastern portion of the study area.

Sixmile includes the winter range for the northern-most portion of the northern Yellowstone elk herd, a migratory herd with an estimated population of approximately 5,800 elk (Loveless 2018, Mosley and Munding 2018, Yonk et al. 2018). Elk presence in Sixmile is highly variable and weather dependent, ranging from 100 elk in mild conditions to 2,000 elk in late winter. Livestock operations with female-calf pairs that are potentially susceptible to brucellosis operate in the northern portion of the study area. Elk presence is not desired on these private properties because of the risk of brucellosis transmission and we defined these areas as conflict zones (Fig. 1A). Elk are tolerated on all property that is not a conflict zone, including a Wildlife Management Area, national forest, adjacent subdivisions,

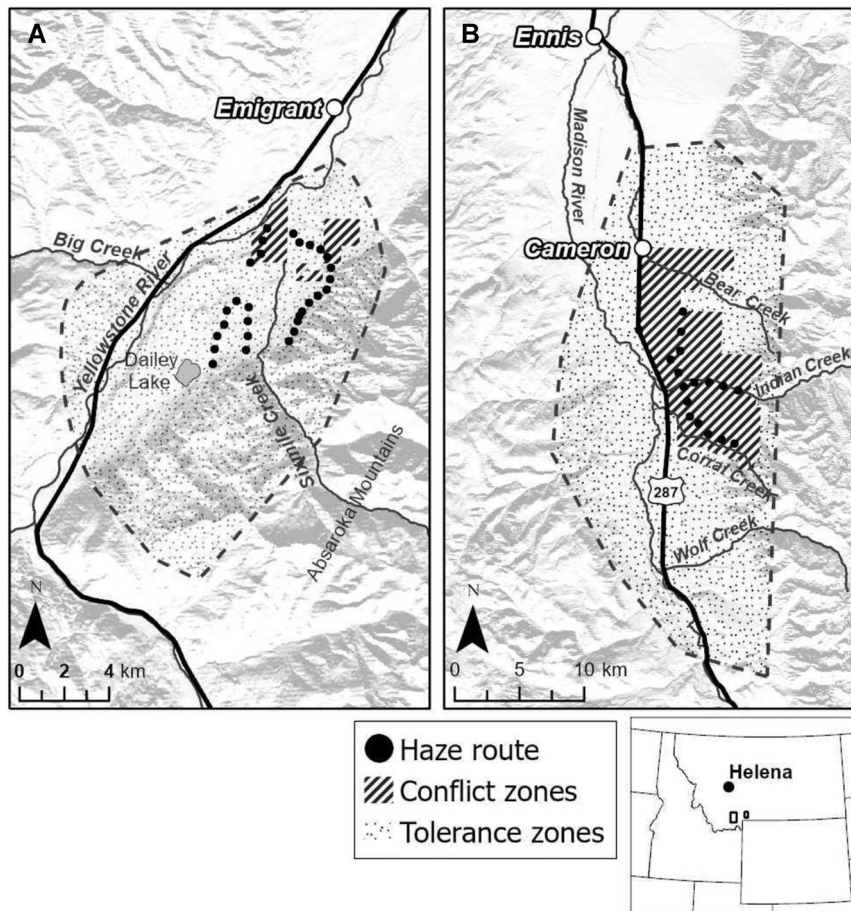


Figure 1. The Sixmile and Madison study areas in southwestern Montana, USA, 2017–2020. Typical hazing routes (black dots) and conflict zones (black hash marks) for elk are depicted.

and some nearby ranchlands without livestock. Conflict zones occupy approximately 664 ha or 4% of the study area and are entirely surrounded by tolerance zones, which occupy 16,208 ha or 96% of the study area. Elk reside either east or west of Sixmile Creek and do not generally move back and forth. Habitat conditions are similar on both sides of Sixmile Creek and within conflict and tolerance zones. There is a subdivision with 8-ha plots directly south of the conflict zone on the west side and along Sixmile Creek. The Yellowstone River and highway MT-89 may serve as a deterrent to westward movement. The Sixmile study area is also home to other ungulates, including pronghorn (*Antilocapra americana*), white-tailed deer (*Odocoileus virginianus*), and mule deer (*O. hemionus*). Carnivore species in the study area include coyote (*Canis latrans*), wolf (*C. lupus*), mountain lion (*Felis concolor*), and grizzly (*Ursus arctos*) and American black bears (*U. americanus*).

The Madison study area was located south of Ennis and east of US-287 (Fig. 1B). The Madison area is approximately 55,394 ha. Winter (Dec–Mar) weather can be extreme, with temperatures reaching -40°C and sustained winds up to 22 m/seconds. Elevation ranges from 1,700 m to 2,300 m. Madison is an intermontane valley predominantly covered in grasslands with fescue, wheatgrass, and

sagebrush (*Artemisia* spp.). Willow, aspen, and cottonwood occur along creeks. Coniferous forests, primarily lodgepole pine, Douglas-fir, and Engelmann spruce begin in the foothills at higher elevations in the eastern portion of the study area.

Madison serves as winter range for a migratory population of approximately 4,300 elk. Elk primarily winter east of US-287 up to the foothills of the Madison Mountain range, on the Bear Creek Wildlife Management Area in the north and private properties stretching south to Wolf Creek. Group sizes in the valley bottom can be very large: up to 3,700 elk (Gude et al. 2006). Like the Sixmile, elk are not desired on private property with livestock or private property with concerns regarding forage consumption (i.e., conflict zones, Fig. 1B). The Bear Creek Wildlife Management Area on the northeastern end of the study area is managed as a wintering ground for elk and other wildlife (Montana Fish, Wildlife & Parks 2018). Elk are allowed in all areas that are not conflict zones, including the Bear Creek Wildlife Management Area, adjacent subdivisions, and nearby ranchlands without livestock. Conflict zones occupy approximately 10,116 ha or 18% of the study area and are entirely surrounded by tolerance zones, which occupy 45,278 ha or 82% of the study area. Habitat conditions are

similar between conflict and tolerance zones, but there is a subdivision with 8-ha plots 4 km south of the conflict zone. Route US-287 may serve as a limited deterrent to westward movement. Madison is also home to other ungulates, including pronghorn, white-tailed deer, mule deer, and moose (*Alces alces*). Carnivore species in the study area include coyote, wolf, mountain lion, and grizzly and American black bears.

METHODS

We used helicopter net-gunning to capture 40 (>2 yr old) female elk in each study area and deployed Iridium satellite global positioning system (GPS)-collars (Vectronic Aerospace, Berlin, Germany). We captured all elk in accordance with animal welfare protocols approved by Montana Fish, Wildlife & Parks (FWP19-2013). We programmed all collars to collect a GPS location every hour from December through April, the period during that brucellosis management actions occurred. Data collection in the first season for each study area began when we collared elk: 28 February 2017 for Sixmile and 1 March 2018 for Madison.

Elk brucellosis risk management goals for the study areas included redistributing elk off private property to minimize commingling of elk and livestock through hunting and hazing. Special management hunts (rifle) occurred on and around conflict zones from approximately 1 December–15 February every year in Madison and in 2019 for Sixmile. This hunting opportunity was after the close of the general hunting season. In Madison, hunters from a roster list were called out to hunt-specific 7-day windows on conflict zones only. Hunting windows occurred back to back, meaning hunting was possible every day of the season. In 2018 all hunting was concluded prior to the capture of elk and the start of the study. Reporting of hunting effort and success for Madison was incomplete but indicated approximately 71 hunters spent 79 hunter days and harvested 71 elk in 2019 and 55 hunters spent 58 hunter-days and harvested 67 elk in 2020. There was typically only 1 hunter on the landscape at a time, with known ranges up to 5 hunters, but exact dates of hunting were unknown for multiple hunters for both years, suggesting a maximum of 10 hunters could have been on the landscape for certain dates. Hunting in Sixmile was available to any hunter with an antlerless license specific to that hunting district, and although not restricted to conflict zones, was likely restricted through landowner access because several large landowners in the area did not allow hunting. There was no reporting of hunting effort or success for Sixmile, but 1 landowner that kept personal records indicated hunting on their property was primarily restricted to a single hunter each day and that 20 hunters harvested 17 elk in 2019. Because of the lack of data in Madison and Sixmile, we assumed that all elk were potentially exposed to hunting risk every day of the hunting season. There were a few targeted special brucellosis dispersal hunts in the conflict zone on the west side of Sixmile in 2017 and 2018 that

were not included in the analysis. The dates of these hunts were unavailable, and the number of hunters was limited to fewer than 10 per year.

Elk were also redistributed off conflict zones through hazing, which is defined as the chasing of wildlife away from a specific location. The goal of hazing was to move elk off conflict zones but without a specific end destination. Hazing occurred after hunting ended on 15 February in Madison and in Sixmile after the general hunting season ended in November for 2017 and 2018. In 2019 a hunt delayed hazing until 16 February on the west side conflict zone, but hazing was ongoing all season long on the east side. The decision to haze was based on landowner requests or when management hazers observed large groups of elk on conflict zones. On days hazing did not occur, elk were able to come and go from conflict zones. Hazers in Sixmile were primarily on horseback and occasionally used all-terrain vehicles in 2017, whereas hazers in Madison exclusively used all-terrain vehicles. Hazing conducted via horseback and all-terrain vehicle was similar in speed and method with a slow approach and physical proximity to apply pressure until elk began to move off conflict zones. Hazers followed at a distance until elk moved onto tolerance zones. Elk response to hazing via horseback and all-terrain vehicle was similar. Hazing was consistently applied across years for both study areas and occurred from 0730 to 1030 in Sixmile and from 0815 to 1245 in Madison. Multiple hazing events that occurred on the same day happened twice in 2018 at Sixmile and we combined these events and treated them as a single hazing event. Topography, fencing, and access permission limited hazing to similar routes for every event (Fig. 1; route detail available online in Supporting Information). The average length of the hazing route was 6 km in Sixmile and 14 km in Madison. It was our original intent to explicitly measure hazing events with GPS tracks of each event recorded by hazers. Unfortunately, data recording was inconsistent for both study areas. We obtained the exact dates of all hazing events for Madison and Sixmile and used these dates to create a continuous predictor variable to define the number of days since the last hazing event.

We evaluated the effects of hunting and hazing on elk distributions in 2 ways. First, we counted the number of collared elk that used a conflict zone each day of the sampling period and evaluated the effects of hunting, hazing, time period (i.e., night or day), seasonality (i.e., time of year), and weather on the proportion of collared elk that used a conflict zone. We defined the sampling period as 1 December–30 April, which corresponded to the start of the management season until elk departed the winter range for spring transition ranges. We defined each day as 1800 on day $t - 1$ to 1800 on day t to correspond to approximate daily movement patterns of elk (i.e., elk typically entered a conflict zone in the evening). We further divided each day into a night (1801–0600) and day period (0601–1800) to account for the diel movement patterns of elk. For each day, during the day and night

time periods, we counted the number of collared elk with ≥ 1 location in a conflict zone (Sixmile East, Sixmile West, Madison). To account for collar loss and failure during the sampling period, we treated the proportion of collared elk that used a conflict zone daily rather than the count of elk as the response variable. We estimated this proportion as the number of collared elk that used a conflict zone on a given day as per the number of collars that transmitted ≥ 1 location on that day (Fig. 1A). In Sixmile, we treated the count of collared elk that used each conflict zone (East, West) as independent observations, and estimated the proportion of collared elk for each area each day. This was a simplification of a discrete choice process wherein each elk was realistically only able to use 1 conflict zone per sampling period (i.e., day), but we treated the probability of use for the East and West conflict zones as independent. We used a binary covariate (diel = night or day) to represent the time period within each day. To account for the within-season patterns of elk movement and use of conflict zones, we included the number of days since the beginning of the sampling period as a covariate (time). To evaluate the evidence for an effect of hunting, we created a binary predictor variable to define if the observation occurred on a day during or outside of the hunting season (hunt; 1 Dec–15 Feb). To evaluate the evidence for an effect of hazing, we created a continuous predictor variable to define the number of days since the last hazing event moved elk away from the conflict zone (haze days). To account for a weather-influencing aggregation in conflict zones, we developed a continuous covariate for the accumulated value of snow-water equivalent (SWE; Fig. S1, available in Supporting Information). Finally, for Sixmile, we included a binary covariate (conflict zone) indicating if the response was on the East or West conflict zone.

Hazing events occurred during daylight hours and we were not able to parse out the potential pre- and post-hazing effects on our counts of elk in the conflict zones because of incomplete recording of GPS hazing tracks and times (i.e., a high count in a conflict zone in the early morning prior to a hazing event was followed by a low count due to hazing on the same day). Therefore, we set the proportion of collared individuals that used a conflict zone to zero on hazing days, which narrowed our inference to assessing the effects of hunting and hazing on days following those events. Finally, exploratory analysis suggested that some collared individuals in each study area and year never visited a conflict zone. We filtered our data set to include only individuals that used a conflict zone at least once in a given year to avoid bias in our resulting parameter estimates due to inclusion of elk not associated with conflict zones.

We assessed the strength of evidence for each of these covariates using a generalized linear model with a logit link to model the proportion of collared elk that used a conflict zone on each day (PpnElk). We evaluated the Sixmile and Madison models independently to account for potential differences between study areas.

Sixmile model:

$$\begin{aligned} \text{PpnElk}_{season,t,area,night} &\sim \text{Binomial}(p_{season,t,area,night}, N_{collars_{season,t}}), \\ \text{logit}(p_{season,t,area,night}) &= \alpha^{diel} + \beta^{hunt} \times \text{hunt}_{season,t} \\ &\quad + \beta^{West} \times \text{conflict zone}_{season,t} \\ &\quad + \beta^{SWE} \times \text{SWE}_{season,t} \\ &\quad + s_{season}^{time}(\text{time}_{season,t}) \\ &\quad + s^{haze\ days}(\text{haze days}_{season,t}), \end{aligned}$$

Madison model:

$$\begin{aligned} \text{PpnElk}_{season,t,night} &\sim \text{Binomial}(p_{season,t,night}, N_{collars_{season,t}}) \\ \text{logit}(p_{season,t,night}) &= \alpha^{diel} + \beta^{hunt} \times \text{hunt}_{season,t} \\ &\quad + \beta^{SWE} \times \text{SWE}_{season,t} \\ &\quad + s_{season}^{time}(\text{time}_{season,t}) \\ &\quad + s^{haze\ days}(\text{haze days}_{season,t}), \end{aligned}$$

where *season* corresponded to the 4 seasons of observation (2017–2019 for Sixmile, 2018–2020 for Madison), *t* corresponded to the day of observation within a season, *area* corresponded to the specific conflict zone (East or West, Sixmile model only), *night* corresponded to the period of day, α^{diel} represented a daily time-specific intercept (night or day), β^{hunt} represented the effect of a hunting day, β^{West} represented an additive difference for the West conflict zone (the East conflict zone was the reference level), and β^{SWE} represented the effect of accumulated SWE. We did not have an *a priori* hypothesis for the functional form of the effect of the seasonal trend (i.e., intra-annual variation) of hazing. Therefore, we used a thin-plate spline structure with a modest number of knots (3, which we judged to be a compromise between a flexible model structure and biological interpretability) to represent a flexible functional form for the seasonal trend and effect of hazing (Wood 2017). We structured these splines to allow the seasonal trend in the proportion of collared individuals that used a conflict zone to differ among seasons (s_{season}^{time}) to account for annual spatio-temporal differences in elk distributions within the study areas. We estimated a seasonally consistent form for the influence of hazing ($s^{haze\ days}$) because we expected the effects of hazing to be consistent across years.

To assess the goodness of fit of our model to the data and to evaluate the explanatory power of our covariates, we also fit a null model to these data and modeled the proportion of collared individuals using a conflict zone using an intercept and the conflict zone-specific adjustment for Sixmile:

$$\text{logit}(p_{season,t,area,night}) = \alpha^{diel} + \beta^{West} \times \text{West}_{season,t},$$

and only an intercept for Madison:

$$\text{logit}(p_{season,t,night}) = \alpha^{diel},$$

and compared the goodness of fit using values of R^2 for generalized linear models and the predictive power of the

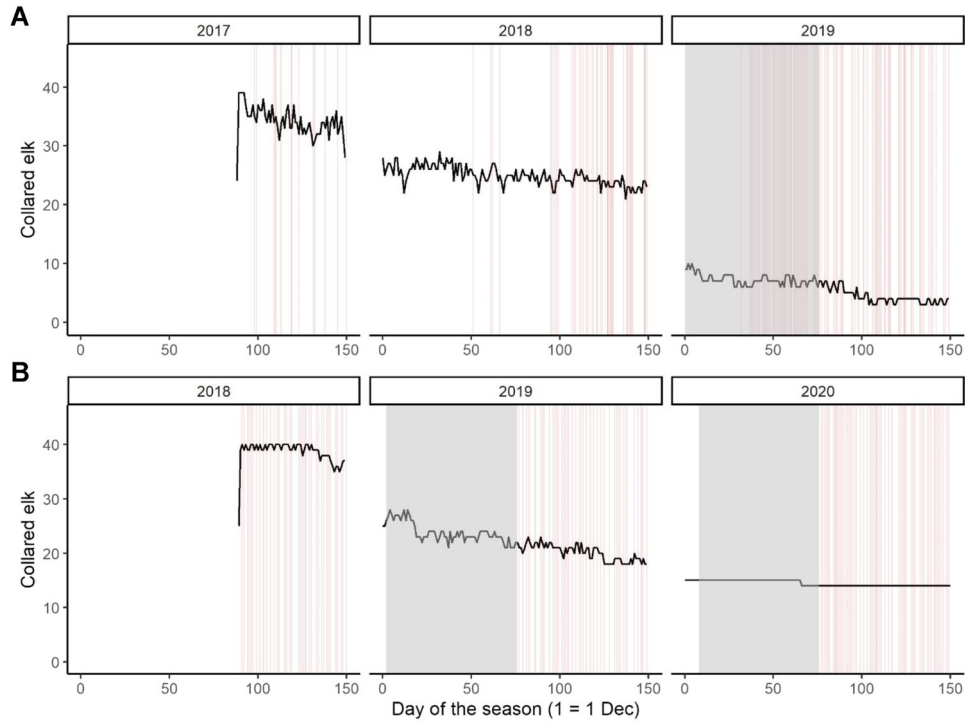


Figure 2. The number of individual elk with functioning collars (collared elk, y-axis) as a function of day of the season (x-axis) for the Sixmile (A) and Madison (B) study areas in Montana, USA, 2017–2020. The thin, vertical red lines indicate days on which ≥ 1 hazing event occurred, and the grey rectangle indicates the period during that hunting was allowed.

models using the Akaike's Information Criterion (AIC; Akaike 1973, Burnham and Anderson 2002).

Second, we assessed the influence of hunting, hazing, seasonality, and weather on the duration of time that individual elk remained away from conflict zones, following each departure from a conflict zone. We defined a sampling event as an individual leaving and then re-entering a conflict zone. For each event where an elk departed a conflict zone, we estimated the time to entry (TTE) as the number of days until the next location was within a conflict zone, and we treated TTE as our response variable. We censored any events in which a GPS-collar was off for >10 hours to avoid an over-estimation of TTE due to collar malfunction. To evaluate the effect of hunting on TTE, we created a continuous covariate for the number of hunting days based on calendar days during the hunting season that occurred during the sampling event (number of hunts). To evaluate the effect of hazing on TTE, we created a continuous covariate for the number of unique hazing events that occurred during the sampling period (number of hazes; Fig. 2). To evaluate the effect of being hazed out of a conflict zone rather than departing outside of a hazing event, we created a binary variable indicating if the departure event occurred during day period hours (i.e., 0601–1800) on a day with a hazing event (hazed out). To account for weather-effects on TTE, we included the accumulated SWE during the sampling event as a covariate (SWE; Fig. S2, available in Supporting Information). To account for the within-season patterns of elk movement and use of conflict zones, we included the time since the beginning of the sampling period (1 Dec) as a covariate (time).

We log-transformed TTE prior to analysis to account for the strong right-skew of the data (i.e., few points with very large values of TTE). We assessed the strength of evidence for each of these potential factors on TTE using an ordinary linear model and evaluated the Sixmile and Madison models independently to account for potential differences between study areas. The Sixmile and Madison models had the same structural form:

$$\log(\text{TTE}_{i,\text{season}}) \sim \text{Normal}(\mu_{i,\text{season}}, \sigma^2),$$

$$\begin{aligned} \mu_{i,\text{season}} = & \alpha + \beta^{\text{hunts}} \times \text{hunts}_{i,\text{season}} + \beta^{\text{hazed out}} \\ & \times \text{hazed out}_{i,\text{season}} + \beta^{\text{SWE}} \times \text{SWE}_{i,\text{season}} \\ & + s_{\text{season}}^{\text{time}}(\text{time}_{i,\text{season}}) \\ & + s_{\text{number of hazes}}(\text{number of hazes}_{i,\text{season}}), \end{aligned}$$

where i corresponded to $1, \dots, N_{\text{season}}$ individual sampling events in a given season (2017–2019 for Sixmile, 2018–2020 for Madison), α represented an overall intercept, β^{hunts} represented the effect of the number of hunting days during a sampling event, $\beta^{\text{hazed out}}$ represented the effect of leaving a conflict zone on a hazing day, and β^{SWE} represented the effect of accumulated SWE during the sampling event. Similar to our first analysis, we did not have an *a priori* hypothesis for the functional form for the seasonal trend or influence of hazing events, and we used thin-plate splines with a modest number of knots (3) to model the seasonal trends and effect of hazing on TTE. We structured these

Table 1. Coefficient estimates from the parametric and thin-plate spline models of the proportion of collared elk that used a conflict zone for the Sixmile and Madison elk populations of Montana, USA, 2017–2020. The coefficient estimates from the parametric model are estimated on the logit scale. Coefficients in the parametric model represent the overall intercept corresponding to the time of day (α^{day} , α^{night}), effects of hunting (hunt), and accumulated snow water equivalence (SWE). In the Sixmile model, West represents the effect of the West conflict zone as compared to the East conflict zone. Coefficients in the spline model represent a seasonal trend (time) in elk use of conflict zones each year of the study and the number of days since hazing occurred (haze days).

	Parametric model ^a				Thin-plate spline model	
	Parameter	Estimate	95% CI	P	Spline terms	P
Sixmile	α^{day}	-2.65	-2.77, -2.54	0.00	s_{2017}^{time}	0.00
	α^{night}	-2.10	-2.20, -2.01	0.00	s_{2018}^{time}	0.00
	β^{West}	-0.45	-0.56, -0.33	0.00	s_{2019}^{time}	0.01
	β^{hunt}	-0.30	-0.64, 0.04	0.09	$s^{\text{haze days}}$	0.05
	β^{SWE}	0.30	-1.98, 2.63	0.78		
Madison	α^{day}	-0.61	-0.73, -0.48	0.00	s_{2018}^{time}	0.00
	α^{night}	-0.48	-0.59, -0.37	0.00	s_{2019}^{time}	0.00
	β^{hunt}	-0.81	-1.00, -0.62	0.00	s_{2020}^{time}	0.00
	β^{SWE}	-2.41	-3.97, -0.85	0.00	$s^{\text{haze days}}$	0.00

^a The model did not test for differences between day and night, rather that there was use during both time periods.

splines to allow the seasonal trend in TTE to differ among seasons ($s_{\text{season}}^{\text{time}}$) and a seasonally consistent form for the influence of hazing ($s^{\text{number of hazes}}$).

To assess the goodness of fit of our model to the data and to evaluate the explanatory power of our covariates, we also fit a null model to these data and modeled TTE using an intercept only:

$$\text{TTE}_{i,\text{season}} \sim \text{Normal}(\mu_{i,\text{season}}, \sigma^2),$$

$$\mu_{i,\text{season}} = \alpha.$$

We compared the goodness of fit to our top model using values of R^2 and the predictive power using AIC (Akaike 1973, Burnham and Anderson 2002).

We fit the additive models using the mgcv package (Wood 2017) in the R programming environment (R Core Team 2020). It is challenging to separately interpret the terms from either generalized linear models with a non-identity link (proportion of collared animals that used a conflict zone) or a transformed response variable (TTE) that are combined with a generalized additive model. Therefore, to interpret our model results, we used graphical predictions from the models. We estimated predictions by varying 1 covariate at a time and holding other covariates at reference levels. For the proportion of collared individuals that used a conflict zone model, the reference values were conflict zone = East (Sixmile model only), diel = day, hunt = no hunt, SWE = 0, time = 120 (the middle of the management hazing season), and haze days = 0. For the TTE model, the reference values were hunts = 0 (no hunting), SWE = 0 (no accumulated SWE during a sampling event), hazed out = 0 (not hazed out), time = 120, and number of hazes = 0 (no hazing events while elk was out of conflict zone).

RESULTS

We included 81 elk-years of data from 40 elk in Sixmile and 83 elk-years from 40 elk in Madison in analyses. Collar failure, natural mortality, and hunter harvest decreased the

sample size of collared elk over time (Fig. 2). In Sixmile and Madison, 142 and 137 hazing events occurred during the sampling period, respectively (Fig. 2). During the sampling period, Sixmile had 0, 0, and 77 hunting days in 2017, 2018, and 2019, respectively. Madison had 0, 75, and 69 hunting days in 2018, 2019, and 2020, respectively. There are zero hunting days in 2018 for Madison because the study did not begin until elk were captured in late February after the hunting season had closed. The number of collared elk that used a conflict zone ≥ 1 time/season varied among years and study areas. In Sixmile in 2017, 26 out of 40 collared elk visited a conflict zone ≥ 1 time during the sampling period. In 2018, 26 out of 31 elk visited a conflict zone and in 2019, 9 out of 10 elk visited a conflict zone. In Madison in 2018, 38 out of 40 elk visited the conflict zone ≥ 1 time during the sampling period. In 2019, 25 out of 28 visited the conflict zone and in 2020, 12 out of 15 visited the conflict zone. For Sixmile, the number of TTE events was 257, 717, and 157 in 2017, 2018, and 2019, respectively. We estimated a mean TTE event duration of 2.3 days (range = 0–98.5). For Madison, the number of TTE events was 618, 578, and 347 in 2018, 2019, and 2020, respectively. We estimated a mean TTE event duration of 2.10 days (range = 0–53.1).

For the proportion of collared individuals using a conflict zone and TTE models, there was strong evidence that the more richly parameterized model outperformed the null model for both study areas. For the Sixmile models, the R^2 values of the proportion model and TTE models were higher for the model including covariates compared to the null model (0.16 vs. 0.08 for the proportion model; 0.21 vs. 0.00 for the TTE model) and the AIC values were lower for the models with covariates ($\Delta\text{AIC} = 315$ for the proportion model; $\Delta\text{AIC} = 262$ for the TTE model). Similarly, for the Madison models, R^2 values were higher for models including covariates compared to the null model (0.42 vs. 0.10 for the proportion model; 0.55 vs. 0.00 for the TTE model) and AIC values were lower for the models with covariates ($\Delta\text{AIC} = 2,489$ for the proportion model; $\Delta\text{AIC} = 1,216$ for the TTE model).

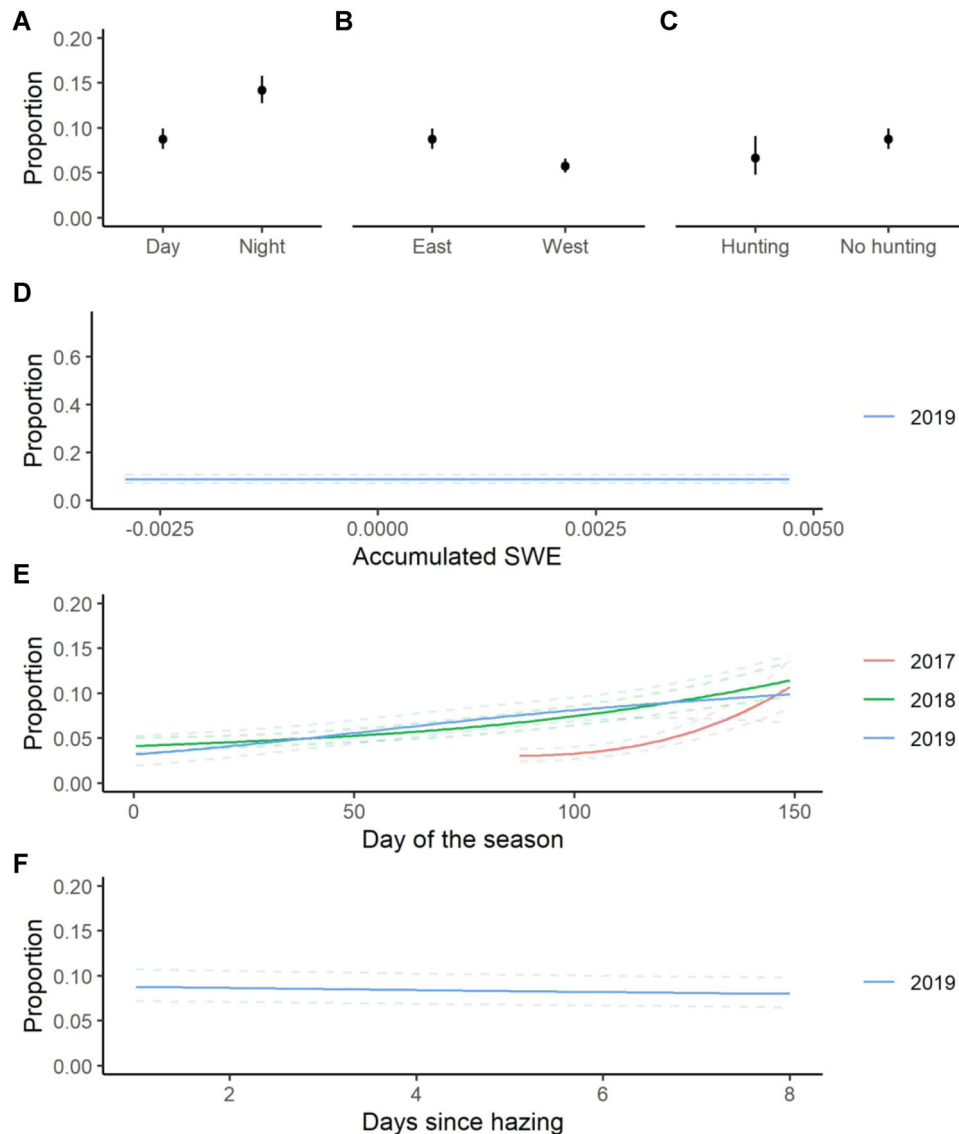


Figure 3. Predictions from the Sixmile model of relationships between the predicted proportion of collared elk using a conflict zone in Montana, USA, 2017–2019, and the categorical covariates time of day (A; day or night), location of the conflict zone (B; East or West), and hunting period (C; hunting or no hunting) and the continuous covariates of accumulated snow water equivalence (SWE) in meters (D), day of the season (E; day 0 = 1 Dec), and days since hazing in the conflict zone (F). For A–C the dot denotes the mean and the black line the 95% confidence interval. For D–F, the line denotes the mean and the dashed line the 95% confidence interval. The predictions in each panel were estimated using reference values of the other covariates.

Proportion of Collared Individuals Using a Conflict Zone

For the individuals that used a conflict zone ≥ 1 time/season, there was evidence that use of conflict zones decreased during hunting in Sixmile and Madison, although the relationship was weaker in Sixmile. In Sixmile, we predicted the proportion of individuals that used a conflict zone was 0.09 (95% CI = 0.08, 0.10) during non-hunting days and 0.07 (95% CI = 0.05, 0.09) during hunting days (Table 1; Fig. 3C). In Madison, we predicted the proportion of individuals that used a conflict zone was 0.31 (95% CI = 0.29, 0.34) during non-hunting days and 0.17 (95% CI = 0.14, 0.20) during hunting days (Table 1; Fig. 4C). There was strong evidence that the use of conflict zones was higher at night in Sixmile, and we predicted the proportion of

individuals that used a conflict zone was 0.14 (95% CI = 0.13, 0.16) at night and 0.09 (95% CI = 0.08, 0.10) during the day (Table 1; Fig. 3A). For Sixmile, elk used the West conflict zone marginally less often than the East, corresponding to a predicted proportion of 0.09 (95% CI = 0.08, 0.10) for the East conflict zone and 0.06 (95% CI = 0.05, 0.07) for the West conflict zone (Fig. 3B; Table 1). There was weak evidence for differences in day and night use of conflict zones in Madison and the predicted proportion of individuals that used a conflict zone was 0.34 (95% CI = 0.32, 0.36) at night and 0.31 (95% CI = 0.29, 0.34) during the day (Table 1; Fig. 4A). There was no evidence for an association between the proportion of individuals that used a conflict zone and SWE in Sixmile (Table 1; Fig. 3D), which contrasted the strong negative

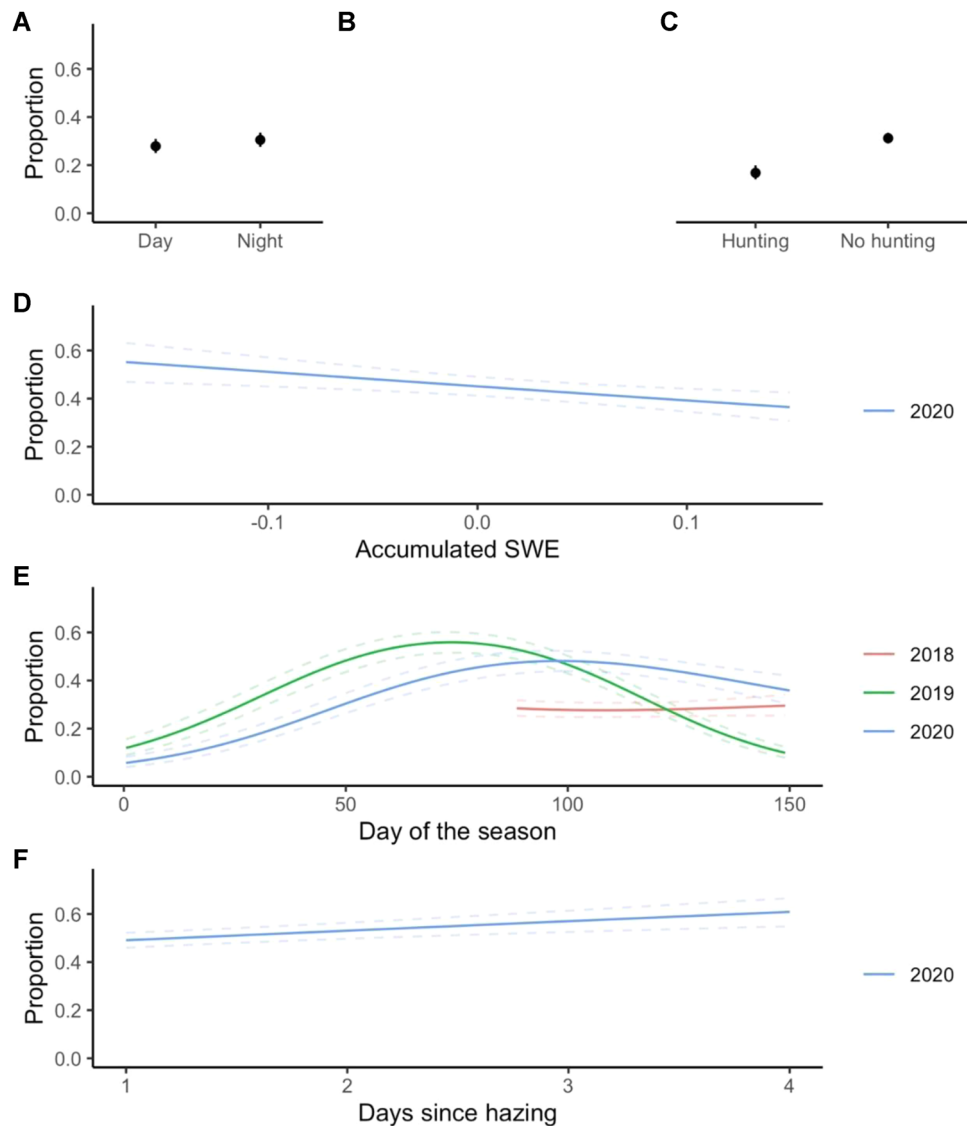


Figure 4. Predictions from the Madison model of relationships between the predicted proportion of collared elk using a conflict zone in Montana, USA, 2018–2020, and the categorical covariates time of day (A; day or night) and hunting period (C; hunting or no hunting) and the continuous covariates of accumulated snow water equivalence (SWE) in meters (D), day of the season (E, day 0 = 1 Dec), and days since hazing in the conflict zone (F). For A–C the dot denotes the mean and the black line the 95% confidence interval. For D–E, the line denotes the mean and the dashed line the 95% confidence interval. The predictions in each panel were estimated using reference values of the other covariates.

association in Madison (Table 1; Fig. 4D). In Madison, we predicted that the proportion of individuals that used a conflict zone decreased from 0.54 (95% CI = 0.50, 0.59) at the 25% percentile of the observed SWE values to 0.45 (95% CI = 0.41, 0.49) at the 75% percentile of SWE values.

From the spline component of the model, there was strong evidence for a seasonal trend in the proportion of individuals using a conflict zone in both areas (Table 1; Figs. 3E and 4E). There was no evidence for a relationship between the proportion of individuals using a conflict zone and the time since hazing in Sixmile (Fig. A1A). We predicted the proportion of individuals using a conflict zone was 0.09 (95% CI = 0.07, 0.11) the day after hazing and 0.08 (95% CI = 0.07, 0.10) 4 days after hazing (Fig. 3F). There was evidence for a modest effect of hazing in Madison and the predicted proportion of individuals using a conflict zone increased from

0.49 (95% CI = 0.46, 0.52) the day after hazing to 0.61 (95% CI = 0.55, 0.67) 4 days after hazing (Fig. 4F; Fig. A1B). For Madison, the seasonal trend component moderated the effects of hazing and was associated with a modest decline in the proportion of collared individuals using a conflict zone on the day after hazing. In late February 2020, that proportion on the day after hazing was 0.53 (95% CI = 0.48, 0.55) compared to 0.63 (95% CI = 0.57, 0.69) 4 days after hazing. Because of the seasonal trend in use patterns by elk, this predicted influence of hazing translated into different proportions in late April, where the proportion of collared individuals using a conflict zone the day after hazing was 0.40 (95% CI = 0.35, 0.45), compared to 0.52 (95% CI = 0.44, 0.59) 4 days after hazing. Although we did not specifically model differences across years, a casual qualitative review shows that inter-annual differences translated into weak

differences in seasonal trends in Sixmile and stronger differences in seasonal trends in Madison. In Sixmile, on day 120 the predicted proportion of individuals using a conflict zone was 0.05 (95% CI = 0.04, 0.06), 0.09 (95% CI = 0.08, 0.10), and 0.09 (95% CI = 0.07, 0.11), in 2017, 2018, and 2019, respectively. In Madison, on day 120 the predicted proportion of individuals using a conflict zone was 0.28 (95% CI = 0.25, 0.31), 0.30 (95% CI = 0.27, 0.33), and 0.45 (95% CI = 0.41, 0.49) in 2018, 2019, and 2020, respectively.

Time to Entry

For the individuals that used a conflict zone ≥ 2 times/season (i.e., departed and then re-entered the conflict zone), TTE was not related to hunting in Sixmile but increased TTE in Madison. In Sixmile, the TTE was not related to the number of hunting days during the sampling event (Table 2; Fig. 5B). In contrast, in Madison there was a statistically relevant relationship between the TTE and the number of hunting days; TTE increased as the number of hunting days during the sampling event increased, although the effect size was modest (Table 2; Fig. 6B). This relationship was biologically trivial and resulted in practically unreasonable predictions. For example, the predicted TTE increased from 0.39 days since leaving a conflict zone (95% CI = 0.35, 0.43) when no hunting days occurred during the sampling event to 0.88 days (95% CI = 0.77, 1.00) when 10 hunting days occurred during the sampling event. Having a predicted TTE of 0.88 days (<1 day) correspond to 10 hunting days is practically impossible given that TTE is left-truncated by the number of hunting days (i.e., TTE should be roughly greater than the number of hunting days), and we interpret this relationship as indicative of a very weak positive relationship between hunting pressure and TTE that has little biological relevance. In Sixmile, there was no evidence that TTE was related to accumulated SWE during the sampling event (Table 2; Fig. 5C). In contrast, in Madison TTE increases as accumulated SWE increased (Table 2; Fig. 6C). Time to entry increased (although at a biologically trivial amount) from 0.23 days (95% CI = 0.19, 0.27) at the 25% percentile of SWE values to 0.56 days (95% CI = 0.48, 0.66) at the 75% percentile of SWE values

in Madison. In Sixmile, TTE was not related to whether an individual was hazed out of a conflict zone (Table 2; Fig. 5A). In contrast, in Madison TTE decreased for individuals that were hazed out (Table 2), although the difference was biologically trivial. Time to entry for individuals that were hazed out was 0.28 days (95% CI = 0.26, 0.31) and 0.35 days (95% CI = 0.32, 0.39) for individuals that were not hazed out (Table 2; Fig. 6A).

From the spline component of the models, there was evidence for a seasonal trend in TTE events that was different between seasons and study areas, although the seasonal effects were modest. For Sixmile, the relationship translated into a predicted TTE on day 120 of 0.71 days (95% CI = 0.59, 0.87), 0.47 days (95% CI = 0.41, 0.54), and 0.42 days (95% CI = 0.35, 0.50) in 2017, 2018, and 2019, respectively (Table 2; Fig. 5D). In Madison, the relationship translated into a predicted TTE on day 120 of 0.35 days (95% CI = 0.32, 0.39), 0.39 days (95% CI = 0.35, 0.43), and 0.30 days (95% CI = 0.27, 0.34) in 2018, 2019, and 2020, respectively (Table 2; Fig. 6D). In contrast to the equivocal or weak evidence for effects we found for the number of hunts, SWE, and whether individuals were hazed out of conflict zones for both Sixmile and Madison, the results from the spline component of the models suggest comparatively strong relationships between the number of hazes during a sampling event and TTE (Table 2; Figs. 5E and 6E). For Sixmile, predicted TTE increased from 0.42 days (95% CI = 0.35, 0.50) with 0 hazes during a sampling event to 8.9 days (95% CI = 5.80, 13.78) with 5 hazes, to 29.47 days (95% CI = 16.04, 54.14) with 10 hazes (Fig. A2A). For Sixmile, the seasonal trend component of the model had a weak influence such that in late February in 2019, the predicted TTE with no hazes during a sampling event was 0.39 days (95% CI = 0.31, 0.49), 5 hazes was 8.27 days (95% CI = 5.38, 12.73), and 10 hazes was 27.26 days (95% CI = 14.74, 50.41), compared to those similar predictions for late April: 0 hazes = 0.53 days (95% CI = 0.36, 0.78); 5 hazes = 11.38 days (95% CI = 6.36, 12.36); 10 hazes = 37.58 days (95% CI = 18.14, 77.45). In Madison, TTE increased from

Table 2. Coefficient estimates from the parametric and thin-plate spline models of the time to entry (i.e., the duration of time spent away from a conflict zone) for the Sixmile and Madison elk populations of Montana, USA, 2017–2020. The response variable time to entry was log-transformed prior to analysis. Coefficients in the parametric model represent the overall intercept (α), the number of hunting days (hunts), accumulated snow water equivalence (SWE) during each sampling event, and the effect of being hazed out of a conflict zone as compared to leaving when there was no hazing event (hazed out). Coefficients in the spline model represent a seasonal trend (time) and the number of hazing events that occurred during each sampling event (number of hazes).

	Parametric model				Thin-plate spline model	
	Parameter	Estimate	95% CI	P	Spline terms	P
Sixmile	α	-0.45	-0.55, -0.35	0.00	s_{2017}^{time}	0.00
	β_{hunts}	0.04	-0.02, 0.09	0.20	s_{2018}^{time}	0.05
	$\beta_{hazed\ out}$	0.93	-2.45, 4.33	0.59	s_{2019}^{time}	0.01
	β^{SWE}	0.10	-0.21, 0.23	0.93	$s_{number\ of\ hazes}$	0.00
Madison	α	-0.36	-0.44, -0.28	0.00	s_{2018}^{time}	0.20
	β_{hunts}	0.21	0.19, 0.23	0.00	s_{2019}^{time}	0.05
	$\beta_{hazed\ out}$	-0.22	-0.34, -0.11	0.00	s_{2020}^{time}	0.00
	β^{SWE}	6.49	4.48, 8.49	0.00	$s_{number\ of\ hazes}$	0.00

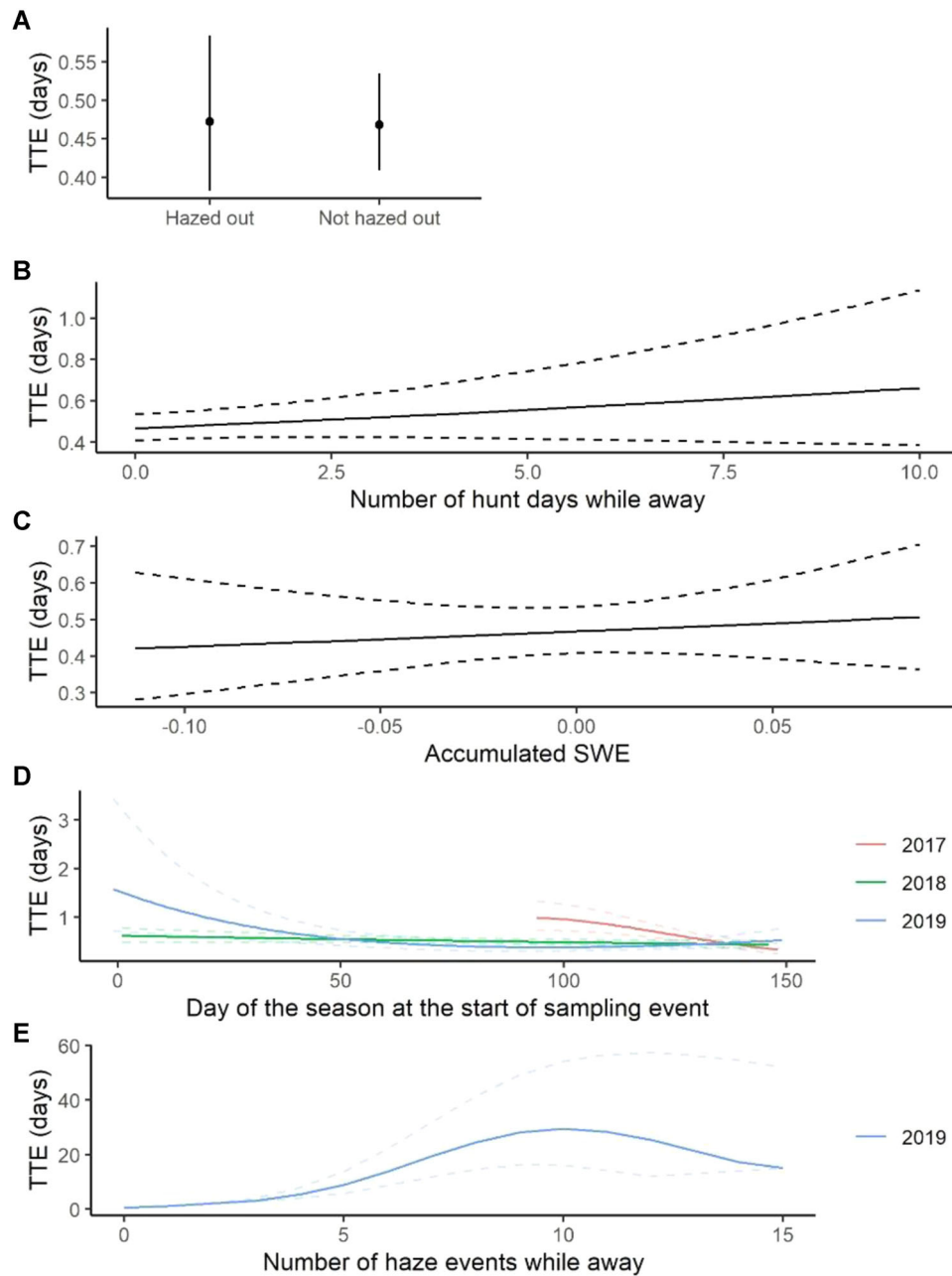


Figure 5. Predictions from the Sixmile model of relationships between the predicted time to entry (TTE) for elk in a conflict zone in Montana, USA, 2017–2019, and covariates representing the effect of being hazed out of a conflict zone as compared to leaving when there was no hazing event (A), the number of hunting days during a sampling event (B), the accumulated snow water equivalence (SWE) in meters during a sampling event (C), day of the season when the sampling event began (D; day 0 = 1 Dec), and the number of hazing events during the sampling event (E). For A the dot denotes the mean and the black line the 95% confidence interval. For B–E, the line denotes the mean and the dashed line the 95% confidence interval. For E, predictions were truncated at the maximum observed TTE (days) or number of hazing events; for example, an individual exposed to 4 hazing events while away had a minimum TTE of 4 days. The predictions in each panel were estimated using reference values of the other covariates.

0.39 days (95% CI = 0.35, 0.43) with 0 hazes during a sampling event, to 15.96 days (95% CI = 12.98, 19.64) with 5 hazes, to 107.43 days (95% CI = 78.45, 147.12) with 10 hazes (Fig. A2B). Similar to Sixmile, the seasonal trend component had a minimal influence on TTE with predictions for late February in 2020 of 0 hazes = 0.33 days (95% CI = 0.28, 0.38), 5 hazes = 13.52 (95% CI = 10.78, 16.94), and 10 hazes = 90.97 (95% CI = 65.72, 125.92) and predictions for late April of 0 hazes = 0.32 days (95%

CI = 0.26, 0.40), 5 hazes = 13.36 days (95% CI = 9.99, 17.88), and 10 hazes = 89.94 (95% CI = 61.65, 131.22).

DISCUSSION

Management actions to reduce wildlife conflict are commonly employed world-wide (Messmer 2000, Walter et al. 2010), and their effectiveness improves with a greater understanding of the effects of various actions in different situations and how best to apply those actions. There was

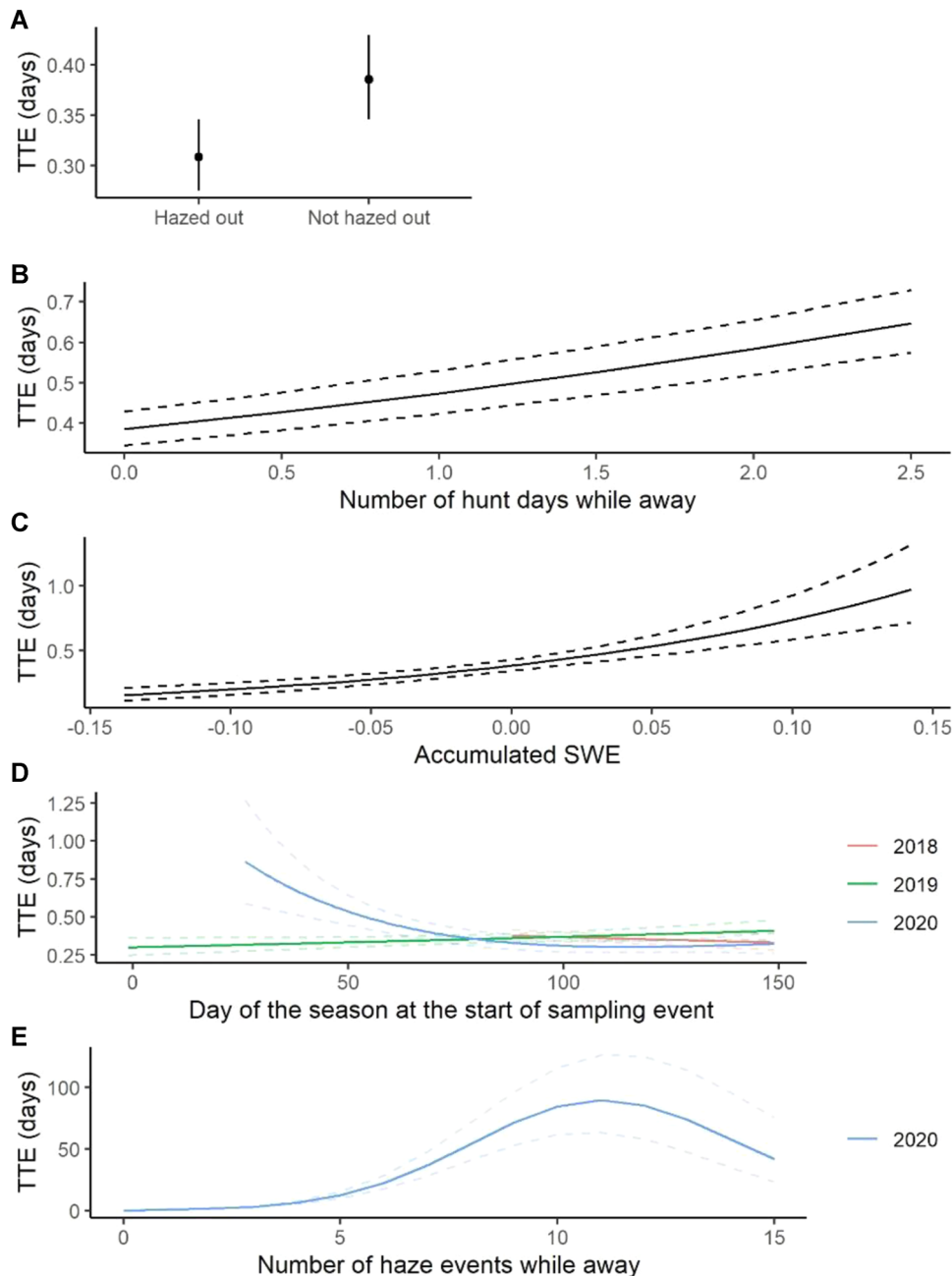


Figure 6. Predictions from the Madison model of relationships between the predicted time to entry (TTE) for elk in a conflict zone in Montana, USA, 2017–2019, and covariates representing the effect of being hazed out of a conflict zone as compared to leaving when there was no hazing event (A), the number of hunting days during a sampling event (B), the accumulated snow water equivalence (SWE) in meters during a sampling event (C), day of the season when the sampling event began (D; day 0 = 1 Dec), and the number of hazing events during the sampling event (E). For A the dot denotes the mean and the black line the 95% confidence interval. For B–E, the line denotes the mean and the dashed line the 95% confidence interval. For E, predictions were truncated at the maximum observed time to entry (days) or number of hazing events; for example, an individual exposed to 4 hazing events while away had a minimum time to entry of 4 days. The predictions in each panel were estimated using reference values of the other covariates.

some evidence that hunting and hazing effectively reduced elk use of conflict zones; however, results varied by study area, suggesting that different management techniques to reduce conflict are needed in different areas and for different situations. Our results presented evidence that hazing may keep individuals out of conflict zones for a period but offered little evidence that hazing affected the overall number of animals using a conflict zone. There was evidence for a positive association between the incidence of hazing and

time elk are away from a conflict zone, suggesting that for hazing to be effective it must be applied frequently. Whether an elk was hazed out of a conflict zone or left on their own did not affect the duration of their time away, indicating that hazing is only temporarily effective against individuals by removing them from a conflict zone. Hunting decreased the number of elk using conflict zones, making it more effective than hazing at the population level, but at the individual level hunting was associated with a biologically

trivial increase in the time individuals stayed off conflict zones for 1 study area and was not associated with TTE for the other study area.

Hazing is commonly applied to redistribute wildlife away from conflict zones (Holevinski et al. 2007, Walter et al. 2010), and although our results suggest hazing keeps individual elk away from conflict zones longer, it does little to decrease the number of elk using conflict zones. The strongest support for hazing as a management tool was that more hazing events while an elk was away kept the elk out of a conflict zone longer. Consistent hazing applied at high rates reduces conflict with African lions (*Panthera leo*) and Japanese macaques (*Macaca fuscata*; Honda et al. 2019, Petracca et al. 2019), implying that how a tool is applied may be as important as the tool chosen. Unexpectedly, individuals that were hazed out of the Madison conflict zone returned sooner than those that left on their own. Several elk that were not hazed off the conflict zone stayed away for a long time (e.g., 53 days), potentially influencing this relationship and making it appear that hazing led to faster return times. Individual variation in affinity for conflict zones may also explain why some elk return to a conflict zone quickly (e.g., same day) and others stay away for extended periods. Some elk may prefer the habitat in the conflict zone and be habituated to hazing so that they return immediately after a haze is concluded, whereas other elk have little interest in the conflict zone and may only occasionally wander through. The application of behavioral ecology and the consideration of individual traits, such as a bold personality that may lead to habituation, has gained increased attention in wildlife management and suggests tailoring actions such as targeted hazing and culling of specific problematic individuals to reduce population-level conflict (Merrick and Koprowski 2017, Swan et al. 2017, Found, St. Clair, 2018, Honda et al. 2018, Garvey et al. 2020).

Our results offer limited evidence that the number of elk using a conflict zone decreases after a hazing event, with a weak effect in Madison and no effect in Sixmile. Our small sample size may not have been able to detect a change in the proportion of use immediately after a hazing event, other than to note that it is lower overall than during the pre-hazing events. For Sixmile, such a small proportion of collared elk were using conflict zones that variation in the data itself may make it difficult to detect any effects. Hazing was also frequent, such that large numbers of collared elk were rarely allowed to accumulate on conflict zones. The effect of hazing may be like a switch that depresses use with no clear trend in how that use then rebounds after hazing. For wildlife conflicts with serious consequences (i.e., disease, financial loss), frequent applications of hazing, may be successful at keeping elk away from conflict zones for longer durations. Our analysis considered hazing as a binary event (on or off) rather than a continuous response related to the frequency of hazing. Our simplification was forced because of the challenges of obtaining field data and may be a poor representation of the actual effect of hazing. Future studies should carefully record the start and end times of all hazing events.

Disturbances by humans (i.e., hazing, hunting) can influence social structure, group size, and behavior (Manor and Saltz 2003, Setsaas et al. 2018), which in turn may influence the efficacy of management actions (Petracca et al. 2019). The arrangement of wildlife on the landscape (i.e., number of groups, group size) and the layout of tolerance and conflict zones may influence the efficacy of hazing. Sixmile tends to have numerous smaller groups of elk (e.g., 100–300 elk) and 2 relatively small conflict zones spaced apart. Madison tends to have just a few very large groups (e.g., 800–1,500 elk; Proffitt et al. 2011) and the conflict zone is a large contiguous block in the valley bottom. If groups in Sixmile are moving independently, 1 group may be hazed off a conflict zone today, and a different group may use the conflict zone tomorrow, keeping the proportion of users low but stable. In Madison, the large conflict zone and group sizes make it easier for a large proportion of collars to use the conflict zone on a given day and a greater likelihood that all those collars are hazed out. Irrigated fields, although present in conflict and tolerance zones, likely drew elk into conflict zones in both Madison and Sixmile. Managers hoping to use hazing to redistribute elk off conflict zones may need to consider the number and size of elk groups and the size of the conflict zone relative to tolerance zones to estimate the efficacy of hazing and how often hazing needs to be applied.

The effectiveness of hunting to reduce wildlife conflicts has been documented in a variety of species including wild boar (*Sus scrofa*; Geisser and Reyer 2004), white-tailed deer (Conover 2001b), American black bears (Garshelis et al. 2020), and elk (Cleveland et al. 2012). Our results support hunting as an effective tool to alter elk distribution and decrease use of conflict zones, although the results were stronger in Madison than at Sixmile. During periods of hunting, the number of elk using a conflict zone decreased in both study areas, albeit only slightly in Sixmile, and there was no biologically relevant relationship with the time animals remained away. These disparities may be explained by differences in hunting pressure; the hunting areas are larger in Madison and access to private land is prearranged through Montana Fish, Wildlife & Parks, which may result in more hunters on the landscape. The Madison landscape also contains large open fields, compared to rolling hills in the Sixmile landscape. Although we generally assumed that hunting pressure on Sixmile was lower and more inconsistent compared to Madison, we did not have a more explicit measure of hunting pressure. Explicit quantification of hunting pressure (i.e., density of hunters, hunter-days, number of elk harvested) would greatly benefit future research and aid managers and landowners in understanding the pressure needed for effective redistribution of elk. Collar failure and mortalities also greatly reduced our sample size for Sixmile when hunting occurred, possibly contributing to our finding only a weak relationship between the proportion of elk using conflict zones and hunting. Future research should evaluate how site-specific characteristics such as topography, the matrix of tolerance and conflict zones, and attractants such as irrigated fields or feedlines may influence the efficacy of management actions to redistribute elk.

Our results indicate increased use of conflict zones at night for elk at Sixmile, rendering them unavailable to hunters, which may dampen any hunting effect. Conflicts typically increase at night, especially in the absence of management actions or deterrents (Woodroffe et al. 2005, Gusset et al. 2009, Herr et al. 2009). Visscher et al. (2017) reported that elk subjected to hunting pressure increased use of refuges during the day and foraged on agricultural fields of high predation risk during night. The concept of hunting for fear has suggested that extended or non-traditional hunting methods be used to move elk away from conflict areas (Cromsigt et al. 2013). Issuing kill permits that allow landowners to harvest elk at night may offer a way to address increased use of conflict zones at night. The number of elk removed by hunting in both study areas was small and did not result in population reduction.

Understanding how adverse weather conditions may affect elk movements can help anticipate changes in elk use of conflict zones and the level of management actions needed. Snowpack may influence wildlife distribution through locomotion restrictions, energetic demands, and decreased access to forage resources (Reed et al. 2009, Brodie et al. 2014, Beumer et al. 2017, Honda and Kozakai 2020). Our results indicate that increasing snowpack, as measured by SWE, reduced the number of elk using the conflict zone in Madison despite its lower elevation than surrounding tolerance zones. This may be attributed to decreased animal movements as snowpack increased, hunting pressure, and the availability of other acceptable options in tolerance zones on the landscape. Longer hazing distances (e.g., 14 km) as compared to the Sixmile area (e.g., 6 km) could also place elk far from the conflict zone, and when coupled with limited movement could lead to a reduction in use of the conflict zone. The lack of an association between snowpack and elk use of conflict zones in Sixmile may be due to the smaller overall area that always leaves elk near a conflict zone. Local conditions, including the proximity of irrigated farmlands or livestock feedlines, may override any influence of weather and may need to be considered on a case-by-case basis when investigating the potential effect of adverse weather conditions on wildlife conflict.

Disease transmission risk from wildlife to livestock is a common concern associated with wildlife conflict and may be the impetus for management actions (White and Ward 2010, Nyhus 2016). Understanding how management actions alter disease transmission risk has value in improving the efficacy of those actions. Although we did not quantify the reduction in brucellosis transmission risk achieved from management-related changes in elk use of conflict zones, abortion risk is greatest in March–May (Cross et al. 2015), and the seasonal trend data suggests that elk use of conflict zones is highest in March but begins to taper in April as elk begin migrating to transitional ranges. Transmission risk is affected by many factors including elk population size, seroprevalence, elk migration patterns, forage quality and availability (i.e., irrigated fields), and size and distribution of the livestock operations (Cross et al. 2010a, Proffitt et al. 2015, Kauffman et al. 2016, Rayl et al. 2019). Higher elk population size and

seroprevalence increase risk, whereas early migration patterns reduce it. We speculate the modest reductions in elk use of conflict zones that resulted from hunting and hazing may have reduced the risk of transmission but did not eliminate it. Quantifying the reduction of risk, particularly during the high-risk months of March and April, would increase the efficacy of management actions and is work that would be a good next step.

MANAGEMENT IMPLICATIONS

Wildlife managers and private landowners attempting to redistribute elk away from conflict zones should consider a combination of strategies and may need to adjust strategies based on site-specific characteristics. Lethal management actions such as hunting appear to have more of an effect at the population level, whereas harassment such as hazing, when frequently applied, affects individual responses. The differences in elk responses to hazing and hunting between Sixmile and Madison suggest that each site and its characteristics, such as irrigated fields, size of available tolerance zones, and topography, may influence elk responses to management actions. Managers should employ a combined approach, applying hunting when seasonally appropriate and frequent hazing whenever elk are using a conflict zone. The influence of snowpack in decreasing elk use of conflict zones suggests increasing hazing frequency during snow-free months is needed to keep elk away from conflict zones. Elk use of conflict zones often increased at night when management actions are typically suspended. Automated frightening devices or increased use of kill permits that allow landowners to remove elk at night could help deter use of conflict zones. Overall, any effect of redistributing elk away from conflict zones may be ephemeral. Even modest redistribution effects, however, may be important to private property owners experiencing conflict.

ACKNOWLEDGMENTS

We thank the landowners that allowed access to their property for elk capture, monitoring, and collar retrieval; B. J. Manners, N. P. Ostler, W. G. Burns, M. Thompson, and G. Thompson for hazing; N. S. Cadwell for flying; the Quicksilver capture crew; and Montana Fish, Wildlife & Parks game wardens that assisted with landowner contacts and capture operations. J. A. Gude provided valuable insight through review of this manuscript. Financial support for this project was provided by revenues from the sale of Montana hunting and fishing license, Montana Department of Livestock, and the Rocky Mountain Elk Foundation.

LITERATURE CITED

- Akaike, H. 1973. Information theory as an extension of the maximum likelihood principle. Pages 267–281 in B. N. Petrov and F. Csaki, editors. Second international symposium on information theory. Akademiai Kiado, Budapest, Hungary.
- Beumer, L., Ø. Varpe, and B. B. Hansen. 2017. Cratering behaviour and faecal C:N ratio in relation to seasonal snowpack characteristics in a High-Arctic ungulate. *Polar Research* 36:1286121.
- Bienen, L., and G. Tabor. 2006. Applying an ecosystem approach to brucellosis control: can an old conflict between wildlife and agriculture be successfully managed? *Frontiers in Ecology and the Environment* 4:319–327.

- Brodie, J. F., E. Post, J. Berger, and F. Watson. 2014. Trophic interactions and dynamic herbivore responses to snowpack. *Climate Change Responses* 1:4.
- Brown, J. S., J. W. Laundré, and M. Gurung. 1999. The ecology of fear: optimal foraging, game theory, and trophic interactions. *Journal of Mammalogy* 80:385–399.
- Burcham, M., W. D. Edge, and C. L. Marcum. 1999. Elk use of private land refuges. *Wildlife Society Bulletin* 833–839.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multi-model inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.
- Ciuti, S., J. M. Northrup, T. B. Muhly, S. Simi, M. Musiani, J. A. Pitt, and M. S. Boyce. 2012. Effects of humans on behaviour of wildlife exceed those of natural predators in a landscape of fear. *PLOS ONE* 7:e50611.
- Cleveland, S. M., M. Hebblewhite, M. Thompson, and R. Henderson. 2012. Linking elk movement and resource selection to hunting pressure in a heterogeneous landscape. *Wildlife Society Bulletin* 36:658–668.
- Clinchy, M., L. Y. Zanette, D. Roberts, J. P. Suraci, C. D. Buesching, C. Newman, and D. W. Macdonald. 2016. Fear of the human “super predator” far exceeds the fear of large carnivores in a model meso-carnivore. *Behavioral Ecology* 27:1826–1832.
- Conner, M. M., G. C. White, and D. J. Freddy. 2001. Elk movement in response to early-season hunting in Northwest Colorado. *Journal of Wildlife Management* 65:926–940.
- Conover, M. R. 2001a. Resolving human-wildlife conflicts: the science of wildlife damage management. CRC Press, Boca Raton, Florida, USA.
- Conover, M. R. 2001b. Effect of hunting and trapping on wildlife damage. *Wildlife Society Bulletin* 29:521–532.
- Cromsigt, J. P. G. M., D. P. J. Kuijper, M. Adam, R. L. Beschta, M. Churski, A. Eycott, G. I. H. Kerley, A. Myrsterud, K. Schmidt, and K. West. 2013. Hunting for fear: innovating management of human-wildlife conflicts. *Journal of Applied Ecology* 50:544–549.
- Cross, P. C., E. K. Cole, A. P. Dobson, W. H. Edwards, K. L. Hamlin, G. Luikart, A. D. Middleton, B. M. Scurlock, and P. J. White. 2010a. Probable causes of increasing brucellosis in free-ranging elk of the Greater Yellowstone Ecosystem. *Ecological Applications* 20:278–288.
- Cross, P. C., M. R. Ebinger, V. Patrek, and R. Wallen. 2010b. Brucellosis in cattle, bison, and elk: management conflicts in a society with diverse values. Pages 81–94 *in* J. Johnson, editor. *Knowing Yellowstone: science in America's first national park*. Taylor Trade Publishing, Lanham, Maryland, USA.
- Cross, P. C., W. H. Edwards, B. M. Scurlock, E. J. Maichak, and J. D. Rogerson. 2007. Effects of management and climate on elk brucellosis in the Greater Yellowstone Ecosystem. *Ecological Applications* 17:957–964.
- Cross, P. C., E. J. Maichak, J. D. Rogerson, K. M. Irvine, J. D. Jones, D. M. Heisey, W. H. Edwards, and B. M. Scurlock. 2015. Estimating the phenology of elk brucellosis transmission with hierarchical models of cause-specific and baseline hazards. *Journal of Wildlife Management* 79:739–748.
- DeVoe, J. D., K. M. Proffitt, M. S. Mitchell, C. S. Jourdonnais, and K. J. Barker. 2019. Elk forage and risk tradeoffs during the fall archery season. *Journal of Wildlife Management* 83:801–816.
- DeVore, R. M., M. J. Butler, M. C. Wallace, S. L. Liley, A. A. Mertz, S. E. Sennie, and P. S. Gipson. 2016. Elk resource selection patterns in a semiarid riparian corridor. *Journal of Wildlife Management* 80:479–489.
- Found, R., and C. C. St. Clair. 2018. Personality influences wildlife responses to aversive conditioning. *Journal of Wildlife Management* 82:747–755.
- Garshelis, D. L., K. V. Noyce, and V. St-Louis. 2020. Population reduction by hunting helps control human-wildlife conflicts for a species that is a conservation success story. *PLOS ONE* 15:e0237274.
- Garvey, P. M., P. B. Banks, J. P. Suraci, T. W. Bodey, A. S. Glen, C. J. Jones, C. McArthur, G. L. Norbury, C. J. Price, J. C. Russell, and A. Sih. 2020. Leveraging motivations, personality, and sensory cues for vertebrate pest management. *Trends in Ecology & Evolution* 35:990–1000.
- Geisser, H., and H.-U. Reyer. 2004. Efficacy of hunting, feeding, and fencing to reduce crop damage by wild boars. *Journal of Wildlife Management* 68:939–946.
- Gilsdorf, J. M., S. E. Hygnstrom, and K. C. VerCauteren. 2002. Use of frightening devices in wildlife damage management. *Integrated Pest Management Reviews* 7:29–45.
- Gude, J. A., R. A. Garrott, J. J. Borkowski, and F. King. 2006. Prey risk allocation in a grazing ecosystem. *Ecological Applications* 16:285–298.
- Gusset, M., M. J. Swarner, L. Mponwane, K. Keletile, and J. W. McNutt. 2009. Human-wildlife conflict in northern Botswana: livestock predation by endangered African wild dog *Lycaon pictus* and other carnivores. *Oryx* 43:67–72.
- Herr, J., L. Schley, and T. J. Roper. 2009. Stone martens (*Martes foina*) and cars: investigation of a common human-wildlife conflict. *European Journal of Wildlife Research* 55:471–477.
- Holevinski, R. A., P. D. Curtis, and R. A. Malecki. 2007. Hazing of Canada geese is unlikely to reduce nuisance populations in urban and suburban communities. *Human-Wildlife Conflicts* 1:257–264.
- Honda, T., H. Iijima, J. Tsuboi, and K. Uchida. 2018. A review of urban wildlife management from the animal personality perspective: the case of urban deer. *Science of the Total Environment* 644:576–582.
- Honda, T., and C. Kozakai. 2020. Mechanisms of human-black bear conflicts in Japan: in preparation for climate change. *Science of the Total Environment* 739:140028.
- Honda, T., N. Yamabata, H. Iijima, and K. Uchida. 2019. Sensitization to human decreases human-wildlife conflict: empirical and simulation study. *European Journal of Wildlife Research* 65:71.
- Kamath, P. L., J. T. Foster, K. P. Drees, G. Luikart, C. Quance, N. J. Anderson, P. R. Clarke, E. K. Cole, M. L. Drew, and W. H. Edwards. 2016. Genomics reveals historic and contemporary transmission dynamics of a bacterial disease among wildlife and livestock. *Nature Communications* 7:1–10.
- Kauffman, M., D. Peck, B. Scurlock, J. Logan, T. Robinson, W. Cook, K. Boroff, and B. Schumaker. 2016. Risk assessment and management of brucellosis in the southern greater Yellowstone area (I): a citizen-science based risk model for bovine brucellosis transmission from elk to cattle. *Preventive Veterinary Medicine* 132:88–97.
- Kloppers, E. L., C. C. St. Clair, and T. E. Hurd. 2005. Predator-resembling aversive conditioning for managing habituated wildlife. *Ecology and Society* 10(1):31.
- Kohl, M. T., D. R. Stahler, M. C. Metz, J. D. Forester, M. J. Kauffman, N. Varley, P. J. White, D. W. Smith, and D. R. MacNulty. 2018. Diel predator activity drives a dynamic landscape of fear. *Ecological Monographs* 88:638–652.
- Laundré, J. W., L. Hernández, and K. B. Altendorf. 2001. Wolves, elk, and bison: reestablishing the “landscape of fear” in Yellowstone National Park, U.S.A. *Canadian Journal of Zoology* 79:1401–1409.
- Loveless, K. 2018. Hunting district 313 elk survey (Gardiner to 6-Mile creek). Montana Fish, Wildlife & Parks, Helena, USA.
- Manor, R., and D. Saltz. 2003. Impact of human nuisance disturbance on vigilance and group size of a social ungulate. *Ecological Applications* 13:1830–1834.
- Merrick, M. J., and J. L. Koprowski. 2017. Should we consider individual behavior differences in applied wildlife conservation studies? *Biological Conservation* 209:34–44.
- Messmer, T. A. 2000. The emergence of human-wildlife conflict management: turning challenges into opportunities. *International Biodeterioration & Biodegradation* 45:97–102.
- Montana Fish, Wildlife & Parks. 2018. Bear Creek Wildlife Management Area management plan. Montana Fish, Wildlife & Parks, Helena, USA.
- Montana Fish, Wildlife & Parks. 2020. Elk management in areas with brucellosis: 2020 Work Plan. Montana Fish, Wildlife & Parks, Helena, USA.
- Mosley, J. C., and J. G. Munding. 2018. History and status of wild ungulate populations on the Northern Yellowstone Range. *Rangelands* 40:189–201.
- Nyhus, P. J. 2016. Human-wildlife conflict and coexistence. *Annual Review of Environment and Resources* 41:143–171.
- Petracca, L. S., J. L. Frair, G. Bastille-Rousseau, J. E. Hunt, D. W. Macdonald, L. Sibanda, and A. J. Loveridge. 2019. The effectiveness of hazing African lions as a conflict mitigation tool: implications for carnivore management. *Ecosphere* 10:e02967.
- Preisser, E. L., D. I. Bolnick, and M. F. Benard. 2005. Scared to death? The effects of intimidation and consumption in predator-prey interactions. *Ecology* 86:501–509.
- Proffitt, K. M., N. Anderson, P. Lukacs, M. M. Riordan, J. A. Gude, and J. Shamhart. 2015. Effects of elk density on elk aggregation patterns and exposure to brucellosis. *Journal of Wildlife Management* 79:373–383.

- Proffitt, K. M., J. A. Gude, K. L. Hamlin, R. A. Garrott, J. A. Cunningham, and J. L. Grigg. 2011. Elk distribution and spatial overlap with livestock during the brucellosis transmission risk period. *Journal of Applied Ecology* 48:471–478.
- R Core Team. 2020. R: a language and environment for statistical computing. R Foundation for Statistical Computing.
- Rayl, N. D., K. M. Proffitt, E. S. Almborg, J. D. Jones, J. A. Merkle, J. A. Gude, and P. C. Cross. 2019. Modeling elk-to-livestock transmission risk to predict hotspots of brucellosis spillover. *Journal of Wildlife Management* 83:817–829.
- Reed, B., M. Budde, P. Spencer, and A. E. Miller. 2009. Integration of MODIS-derived metrics to assess interannual variability in snowpack, lake ice, and NDVI in southwest Alaska. *Monitoring Protected Areas* 113:1443–1452.
- Schumaker, B. A., D. E. Peck, and M. E. Kauffman. 2012. Brucellosis in the Greater Yellowstone area. *Human-Wildlife Interactions* 6:48–63.
- Scurlock, B. M., and W. H. Edwards. 2010. Status of brucellosis in free-ranging elk and bison in Wyoming. *Journal of Wildlife Diseases* 46:442–449.
- Setsaas, T., L. Hunninck, C. R. Jackson, R. May, and E. Røskoft. 2018. The impacts of human disturbances on the behaviour and population structure of impala (*Aepyceros melampus*) in the Serengeti ecosystem, Tanzania. *Global Ecology and Conservation* 16:e00467.
- Smallidge, S. T., H. J. Halbritter, T. T. Baker, N. K. Ashcroft, D. S. Cram, and J. M. Fowler. 2015. Elk and livestock in New Mexico: issues and conflicts on private and public lands. Range Improvement Task Force, New Mexico State University Cooperative Extension Service.
- Swan, G. J. F., S. M. Redpath, S. Bearhop, and R. A. McDonald. 2017. Ecology of problem individuals and the efficacy of selective wildlife management. *Trends in Ecology & Evolution* 32:518–530.
- Thirgood, S., R. Woodroffe, and A. Rabinowitz. 2005. The impact of human-wildlife conflict on human lives and livelihoods. *Conservation Biology Series* 9:13.
- VerCauteren, K. C., M. J. Lavelle, and S. Hygnstrom. 2006. Fences and deer-damage management: a review of designs and efficacy. *Wildlife Society Bulletin* 34:191–200.
- Visscher, D. R., I. Macleod, K. Vujnovic, D. Vujnovic, and P. D. Dewitt. 2017. Human risk induced behavioral shifts in refuge use by elk in an agricultural matrix. *Wildlife Society Bulletin* 41:162–169.
- Walter, W. D., M. J. Lavelle, J. W. Fischer, T. L. Johnson, S. E. Hygnstrom, and K. C. VerCauteren. 2010. Management of damage by elk (*Cervus elaphus*) in North America: a review. *Wildlife Research* 37:630–646.
- White, P. C. L., and A. I. Ward. 2010. Interdisciplinary approaches for the management of existing and emerging human-wildlife conflicts. *Wildlife Research* 37:623–629.
- Wood, S. N. 2017. Generalized additive models: an introduction with R. CRC Press, Boca Raton, Florida, USA.
- Woodroffe, R., S. Thirgood, and A. Rabinowitz, editors. 2005. People and wildlife, conflict or co-existence? Cambridge University Press, Cambridge, United Kingdom.
- Yonk, R. M., J. C. Mosley, and P. O. Husby. 2018. Human influences on the Northern Yellowstone Range. *Rangelands* 40:177–188.

Associate Editor: Michael Wisdom.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's website.

APPENDIX A: SUMMARY OF COLLARED ELK IN CONFLICT ZONES

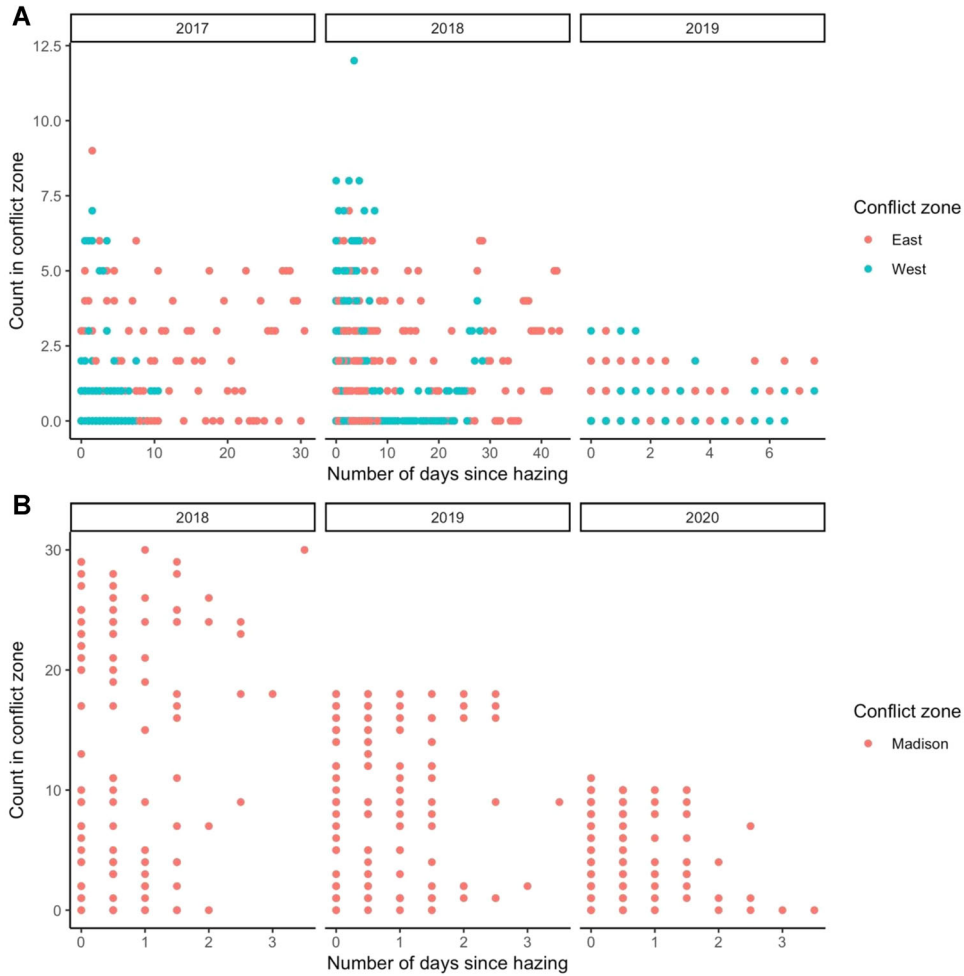


Figure A1. Summary of collared elk counts in a conflict zone as a function of the number of days since hazing for the Sixmile (A) and Madison study areas (B) in southwest Montana, USA, 2017–2020. Counts for Sixmile are summarized independently for the East (pink) and West (blue) conflict zones.

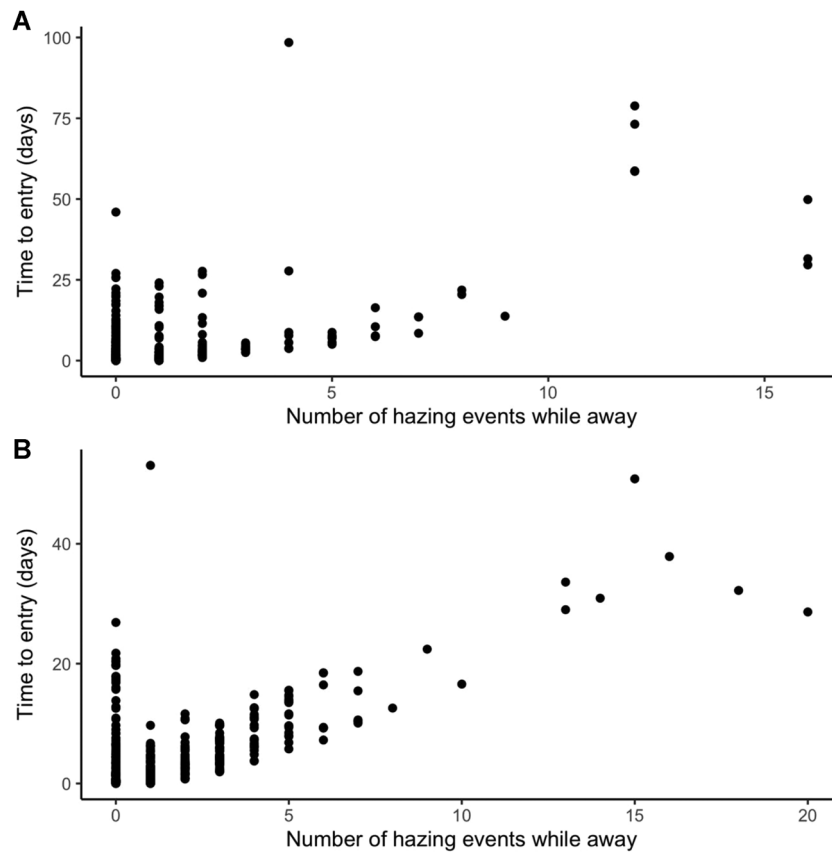


Figure A2. Summary of time to entry (days) for elk in conflict zones as a function of the number of hazing events during the sampling event for Sixmile (A) and Madison (B) study areas in southwest Montana, USA, 2017–2020.