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The association between continual, year-round hunting and bellowing rate of bison bulls during the rut

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The impact of hunting (selective harvest, trophy hunting) on the demography of mammals is well documented. However, despite continual year-round hunting of bison in some populations, little is known about how the behavior of survivors may be altered. Therefore, in this initial study, we used focal-animal observations in adjacent populations of continually hunted and non-hunted Plains bison (*Bison bison bison*) in western South Dakota, to examine the potential impact of hunting on bellowing rate– an important behavior that serves to intimidate rival bulls and potentially influences mate choice by females. In addition to hunting, we investigated how the number of attendant males, number of adult females, group size, and observation day influenced bellowing rate. Bulls bellowed > tenfold more often in the protected area than in hunted areas, whereas neither hunted population significantly differed in bellowing rate. Hunting was significantly and negatively associated with bellowing rate, while all other predictors were found to have positive impacts upon bellowing rate. Furthermore, the impact of hunting on bellowing rate became more pronounced (i.e., dampened bellowing rate more strongly) as the number of attendant males increased. Our data suggest the need for studies with broader-scale geographical and temporal replication to determine the extent that continual year-round hunting has on bellowing rate of bison during the rut. If the reduced bellowing phenomenon is pervasive, then wildlife managers may need to adjust hunting rate and duration, timing (season), and the time lag between hunting events in order to insure that bison are able to express their full repertoire of natural mating behaviors.

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ABSTRACT The impact of hunting (selective harvest, trophy hunting) on the demography of mammals is well documented. However, despite continual year-round hunting of bison in some populations, little is known about how the behavior of survivors may be altered. Therefore, in this initial study, we used focal-animal observations in adjacent populations of continually hunted and non-hunted Plains bison (*Bison bison bison*) in western South Dakota, to examine the potential impact of hunting on bellowing rate– an important behavior that serves to intimidate rival bulls and potentially influences mate choice by females. In addition to hunting, we investigated how the number of attendant males, number of adult females, group size, and observation day influenced bellowing rate. Bulls bellowed > tenfold more often in the protected area than in hunted areas, whereas neither hunted population significantly differed in bellowing rate. Hunting was significantly and negatively associated with bellowing rate, while all other predictors were found to have positive impacts upon bellowing rate. Furthermore, the impact of hunting on bellowing rate became more pronounced (i.e., dampened bellowing rate more strongly) as the number of attendant males increased. Our data suggest the need for studies with broader-scale geographical and temporal replication to determine the extent that continual year-round hunting has on bellowing rate of bison during the rut. If the reduced bellowing phenomenon is pervasive, then wildlife managers may need to adjust hunting rate and duration, timing (season), and the time lag between hunting events in order to insure that bison are able to express their full repertoire of natural mating behaviors.

Key Words Hunting, demography, management, bellows, vocalizations, sensitization

Introduction

Humans have become a dominant, global evolutionary force (Palumbi 2001; Darimont et al. 2009). Our exploitation (hunting and fishing) of wild populations has induced rapid phenotypic and life-history changes (Ciuti et al. 2012; Darimont et al. 2009) on decadal time scales (Darimont et al. 2009; Coltman et al. 2003; Carlson et al. 2007). For example, in just 30 years Coltman et al. (2003) observed significant declines in ram weight and horn length of bighorn sheep (*Ovis canadensis*) due to unrestricted trophy hunting, which resulted in the production of smaller-horned, lighter rams, and ultimately fewer trophy individuals. Such rapid change can have profound impacts on the evolution and conservation of exploited populations because of their potential impact on population persistence (Yoshida et al. 2003; Fussman et al. 2007). While much attention has focused on how human exploitation induces phenotypic and life-history changes (Darimont et al. 2009; Hendry et al. 2008), there is little known about how hunting influences behaviors that are tied to reproduction of survivors in exploited populations. This takes on added importance because prescribed hunting is one of the primary mechanisms for managing ungulates (Cromsigt et al. 2013).

Management of ungulates

Many ecosystems are experiencing real [(cervids in US, Europe, and Japan;] (Côté et al. 2005), or locally perceived [(Asia, Tibetan Wild Ass (*Equus kiang*); South America, guanaco (*Lama guanicoe*) and vicuña (*Vicugna vicugna*)], increases in ungulate densities, and many of these systems require extensive management. Human hunting –either prescribed or poaching–is considered a form of predation risk that can divert time/energy from fitness-enhancing activities such as feeding, parental care, or mating (Lima and Dill 1990; Lima 1998). In fact, ungulates can show stronger behavioral responses to human hunting than to predation risk by large carnivores (Proffitt et al. 2009; Ciuti et al 2012). Other potential fitness-decreasing activities associated with hunting include increased movement and frequency of changing groups in elk (*Cervus elaphus*;

Cleveland et al. 2012; Proffitt et al. 2009), increased vigilance and movement in red deer (*Cervus elaphus*; Jayakody et al. 2008), and more frequent changes in habitat and space use in red deer, roe deer (*Cervus capreolus*), and European bison (*Bison bonasus*; Theuerkauf et al. 2008). Flight initiation distance has also been documented to significantly increase in several hunted populations of artiodactyls (Stankowich 2008).

Despite the ubiquity of harvesting ungulates for food and trophies (Proaktor et al. 2007; Ripple et al. 2015), an understanding of the population-wide effects of hunting on the behavior of survivors remains fragmentary. Events commonly associated with hunting such as firearm discharge, observing downed conspecifics, pursuit by motor vehicles, or the presence of humans in close proximity for extended periods of time may produce behavioral changes in survivors. Associations with any of these traumatic events can lead to sensitization to human presence, which in turn, may increase vigilance (e.g., increased heart rate, stress/cortisol levels), or suppress functional behaviors such as grooming, feeding, or vocalizations (MacArthur et al. 1982). To our knowledge, the potential impact of hunting on behaviors explicitly tied to male reproductive ecology (e.g., mate advertisement, threat displays to potential competitors, fighting) has not been investigated.

Ecology and management of bison

This gap in the literature is particularly important because population-level responses to human activities will be crucial to successful restoration and long-term conservation of the iconic Plains bison (*Bison bison bison*). Initial observations indicated that bulls in hunted populations were less vocal than those in a protected population (Sarno, Personal Observation). This may directly impact mating dynamics because bison form large aggregations during the breeding season (rut) when mature bulls join mixed-sex and age groups. Males exhibit a linear dominance hierarchy, with older, larger bulls dominant to smaller, younger bulls (Komers et al. 1994; Roden

et al. 2005). Dominant males temporarily consort with cows prior to or during estrus and attempt to keep all other bulls away by engaging in vocalizations, threat displays, and fights.

The most conspicuous and frequent vocalizations made by bison bulls during the rut are bellows. Bellows function to intimidate rival males (Berger and Cunningham 1994), while bellow amplitude has been linked to male body condition (Wyman et al. 2008). Importantly, amplitude and bellow quality are directly tied to mating success (Wyman et al. 2008). Vocalizations by males of different species also provide information on female reproductive status (Semple and McComb 2000), influence female mate choice (McComb 1991; Reby et al. 2010), accelerate estrus (McComb 1987), and deter rival males (Clutton-Brock and Albon 1979; Bowyer and Kitchen 1987) and predators (Tilson and Norton 1981). Therefore, any changes in bellowing behavior due to perceived predation risk (Lima and Dill 1990; Lima 1998) could have profound consequences for bison reproductive ecology (Berger and Cunningham 1994; Wyman et al. 2008).

Given the importance of bellows during the mating period, and the use of hunting as a management tool, it is essential that we understand the degree to which hunting, or associated events, influence mating behavior of survivors. Therefore, our primary objective was to use focal-animal observations to compare bellowing frequency of male bison in three populations during the rut (1 protected and 2 hunted) in western South Dakota. We hypothesized that if continual, year-round hunting of bison alters bellowing rate, then bulls in hunted populations will bellow less frequently than bulls in non-hunted populations during the rut.

METHODS

Study Area

Badlands National Park (non-hunted population)

Badlands National Park (13 N 715522, 4859069; 194.25 km^2) includes a population of bison not subject to annual hunting mortality, and is located approximately 113 km east of Rapid City, and 13 km south of Wall, South Dakota. We conducted behavioral observations in the Sage Creek Wilderness Area, located in the Northern Unit of the park. The study area varied from 800–1100 m in altitude and the landscape is characterized as relatively flat, open grassland with intermittent rolling hills, draws, mesas, and buttes (National Park Service 2003). The dominant grassland species was Western wheatgrass (*Agropyron smithin*). Wheatgrass/green needlegrass (*Nasella viridula*) associations occurred on small hills, slopes, and buttes. Rocky mountain juniper forests (*Juniperus scopulorum*) were the most common forest type and dominated the drier slopes, butte edges, and upper draws of the study area (National Park Service 2003).

Badlands National Park is characterized by hot, dry summers, and cold, dry winters. Weather is variable and temperature extremes range between −40°– 47° C. Average yearly precipitation is nearly 40 cm and most occurs between April and September. Average daily maximum temperature during the warmest month (July) was 33°C (BNP National Weather Service record of river and climatological observations).

Pine Ridge Reservation (two hunted populations)

Pine Ridge Reservation (413N, 699106, 4766549) bison pastures (hunted populations) are located in the central and southwestern portion of the reservation in Bennett County, South Dakota. Pastures varied in elevation from 762–1219 m. Annual precipitation varied from 33–48 cm and summer/winter temperatures mirrored those of Badlands National Park (Graham and Gingerich 2013). Bison on Pine Ridge Reservation are harvested throughout the year.

Yellow Bear Pasture (14 N, 262726, 4796154; 39 km^2) is the site of one of the hunted bison populations and is located approximately 30 km southeast of Kyle, South Dakota and 85 km southeast of Badlands National Park. The landscape is open and undulating and was dominated by cheat grass (*Bromus tectorum*), western wheatgrass, buffalograss (*Bouteloua*

134 *dactyloides*), and little bluestem (*Schizachyrium scoparium*). Canyons also were present and
135 canyon ridge-tops were dominated by ponderosa pine (*Pinus ponderosa*). Other common tree
136 species included Rocky Mountain juniper, green ash (*Fraxinus pennsylvanica*), and Eastern
137 cottonwood (*Populus deltoides*; Graham and Gingerich 2013).

138 Slim Buttes Pasture (13 N, 682624, 4793169; 49.7 km^2) contains the second hunted bison
139 population on Pine Ridge and is located approximately 20 km northwest of Pine Ridge, South
140 Dakota, and 155 km southwest of Badlands National Park. The same grasses that were found in
141 Yellow Bear Pasture also were present in Slim Buttes. Eastern cottonwood and Rocky Mountain
142 juniper were the dominant tree species (Graham and Gingerich 2013).

143 **Hunting events**

144 Hunts were conducted year-round in Slim Buttes Pasture and Yellow Bear Pasture with .
145 270 or .25-06 caliber centrefire rifles. In each bison pasture there was a minimum of 2-3 hunting
146 events per month (T. Ecoffey, United States Department of Agriculture, personal
147 communication). The number of animals taken and the duration of hunts varied. During
148 ceremonial hunts, shooters usually approached bison in motor vehicles (2–3 vehicles with 4–5
149 people total) to within 50–100 m. Non-lactating cows and 2-3 year-old bulls were usually
150 selected during hunts, though older bulls (> 5 years old) were also removed. During these short
151 ceremonial hunts only one or two bison were taken, and most hunts lasted approximately two
152 hours (Graham and Gingerich 2013).

153 During non-ceremonial, commercial hunts, up to 8 animals were removed in 6 hours.
154 Here, a mobile abattoir was utilized, whereby animals were first driven into a holding pasture
155 where two people approached bison to within 25–50 m before discharging their rifles. Carcasses

were removed from the pasture and processed at which time shooters re-entered the pasture and repeated the procedure until eight bison were removed. Remaining animals were then re-released into the pasture (T. Ecoffey, United States Department of Agriculture, personal communication).

Data Collection

We defined bellowing rate as the total number of distinct bellows recorded by the observer during 15-minute observations. Bellows were quantified using a stopwatch and a manual hand counter. We conducted 245, 15-min focal observations (Altmann 1974) of mature bulls between dawn and dusk from 1 July to 13 August 2013 using Vortex binoculars and Leica spotting scopes. Group size was defined by the number of animals within 50 m of the focal bull. All mature bulls, whether bellowing or not, that were accompanying a cow were considered to be participating in the rut, and therefore could be included as focal animals. We minimized pseudo-replication by identifying animals based on tag numbers and natural markings. Where animals were not marked, we visited different groups for each observation. We observed bison as close as we could safely approach them throughout the day (50 m), while attempting to avoid oversampling during any particular time of day. Bison did not appear to be bothered by the presence of stationary vehicles as cows and calves routinely passed by parked vehicles of tourists within 3-5 m. Bulls also passed by parked vehicles within 3-5 m while bellowing and fighting other bulls as well as accompanying cows. Therefore, we do not believe that the data were influenced by the presence of observers in motor vehicles. In order to standardize the time period that we observed the rut among pastures, we limited our observations to three weeks after the date of initially observing bellows by bulls. Consequently, observation day (described below in the analysis) indicated the progress of the rut (i.e., the number of days that had elapsed after the day that the first bellow was observed).

We also collected data on group composition and number of attendant males (mature bulls within 50 m of the focal bull). We characterized adult sex ratios and numbers of bison in each population utilizing data collected by Badlands National Park and Oglala Sioux Parks and Recreation Authority (OSPRA) personnel during fall roundups. Each of the three study sites are independent as all pastures were surrounded by fences.

Ethics Statement

Sensitization can be considered an important indirect effect of hunting; therefore, we observed animals only in areas where bison were subjected to regular human visitation. Data collection did not involve restricted habitat or interference with other species, and was in compliance with institutional (Hofstra University IACUC # 13/14-5) and national guidelines for ethical conduct in the care and use of nonhuman animals in research. We obtained permission to conduct fieldwork in Badlands National Park (Permit #: BADL-2013-SCI-0009).

Data analysis

Initially, a series of descriptive statistics of the data were generated. Due to high skew (3.7) and kurtosis (22.2) of bellowing rate, a series of attempted transformations, including square root, log, and numerous others along with the application of the Johnson family of transformations were run, but failed to substantially improve the non-normality of the data. Therefore, we utilized non-parametric bivariate statistics along with Poisson regression, to appropriately model the distribution of bellowing rate. Additionally, scatterplots of bellowing rate and each predictor variable (number of attendant males, number of adult females, group size, observation day (i.e., number of days elapsed since beginning behavioral observations and

hunting) were investigated in order to ensure linearity as well as the absence of outliers. Linearity was indicated in all cases, with a single extreme outlier found with respect to bellowing rate. However, the removal of this outlier failed to substantially change the results of all analyses conducted; therefore, no cases were removed from the analyses.

Spearman's correlations were initially performed in order to determine the strength, significance, and direction of the relationship between bellowing rate and the predictor variables. An $|r| > 0.75$ was used as the threshold for indicating serious multicollinearity (Mun 2008). We used a Mann-Whitney *U* test to compare bellowing rate between the two hunted and one protected population, while a Kruskal-Wallis ANOVA with multiple comparisons was used to assess any differences in bellowing rate between the three populations. Finally, two Poisson regressions were conducted in order to determine the extent to which the number of attendant males, number of adult females, group size, observation day, and hunting (yes/no) impacted bellowing rate. These multivariate regressions served to determine the impact of each predictor on the outcome of bellowing rate, while holding all other predictors in the model constant. The initial model only included main effects. The second model included an interaction between the number of attendant males and hunting. All analyses were performed using Stata 13.1.

RESULTS

Mean bellowing rate was an order of magnitude higher in the non-hunted Badlands National Park population ($\acute{x}$ = 53.3, *SD* = 61.5) than in the hunted Pine Ridge populations ($\acute{x}$ = 5.0, *SD* = 15.8). The median difference between the protected and hunted populations was significant ($z = 9.0$, $p < .0001$). Mean bellowing rate also differed between sites. Badlands National Park was highest ($\acute{x}$ = 53.3, *SD* = 61.5) and was followed by Yellow Bear ($\acute{x}$ =

7.2, *SD* = 19.8), and Slim Buttes pastures, respectively ($\acute{x}$ = 2.2, *SD* = 7.4) on Pine Ridge. The Kruskal-Wallis ANOVA comparing the three associated medians was statistically significant ($\chi^2(2) = 81.4$, $p < .001$). While significant differences existed in bellow rate between Badlands National Park, Yellow Bear Pasture, and Slim Buttes Pasture ($p < .0001$), bellow rate in Yellow Bear and Slim Buttes pastures was similar ($p > .05$).

All Spearman's correlations between bellowing rate and the predictor variables were significant except those between bellowing rate and the number of attendant males and adult females (Table 1). Correlations between the number of attendant males and the remaining predictor variables were also significant. Negative, yet statistically significant correlations existed between group size, observation day and hunting. There was also a strong, positive correlation between hunting and observation day.

The results of the first Poisson regression (Table 2) indicate that all predictor variables significantly influenced bellowing rate. Number of attendant males, number of adult females, group size, and observation day (i.e., progress of the rut) positively impacted bellowing rate, while hunting suppressed bellowing rate. For example, the incidence rate ratios (IRR) indicate that average bellowing rate in the hunted populations was about 5% that of the protected population. In contrast, average bellowing rate was predicted to increase by 5% with the addition of each attendant male. The variance inflation factors, taken from an identically specified linear regression model, indicated no substantial multicollinearity using the commonly-used cutoff of 5 (Oyana and Margai 2015).

The second Poisson regression analysis (Table 3) incorporated the interaction between hunting and number of attendant males. All main effects were again significant as was the interaction between hunting and the number of attendant males. Because the direction of the hunting* # attendant males interaction was positive, the impact of hunting on bellowing rate

246 becomes more pronounced (i.e., dampens bellowing rate more strongly) as the number of
247 attendant males increases. As a result of this significant interaction effect, the number of attendant
248 males was dichotomized on the basis of the mean # of attendant males/group. This
249 dichotomization revealed a substantial difference in mean bellowing rate when the number of
250 attendant males was > the mean number of attendant males ($\acute{x}$ = 4.3) (Hunting: $\acute{x}$ = 8.6,
251 *SD* = 19.9; No hunting: $\acute{x}$ = 121.5, *SD* = 117.1); however, when the number of attendant
252 males was < the mean number of attendant males, the difference in mean bellow rate was > twice
253 as large (Hunting: $\acute{x}$ = 1.6, *SD* = 9.3; No hunting: $\acute{x}$ = 46.0, *SD* = 48.9). No substantial
254 multicollinearity was indicated, though this was reduced substantially by first standardizing the
255 main effects associated with the interaction effect and using these standardized measures in the
256 calculation of the interaction. Both Poisson regression models were statistically significant ($p <$
257 0.0001). The *R*-squared of both models was above 0.50.

258 **Discussion**

259 Bulls in the hunted populations on Pine Ridge Reservation bellowed an order of
260 magnitude less frequently than bulls in the non-hunted Badlands National Park population; yet
261 bellowing rates between the hunted populations on Pine Ridge were not statistically different.
262 Hunting had a large negative effect on bellowing rate and was the only variable to do so. Bellows
263 function to intimidate rival males (Berger and Cunningham 1994), while bellow amplitude and
264 quality are directly tied to mating success (Wyman et al. 2008). Dominant bulls accompany cows
265 in estrus (Lott 2002, Mooring et al. 2004, 2006a) during the rut, and dominance status increases
266 the probability of producing offspring (Mooring and Penedo 2014). Since bellows are used to
267 intimidate potential rivals, dominant bulls accompanying females in estrus are generally those

that bellow most frequently during the rut, and have the greatest probability of producing offspring.

We suspect that the consistent number (2-3) of hunting events/month on Pine Ridge, combined with pursuit by - and/or forced close proximity to - motor vehicles and humans for 6 to 18 hours/month, may be impacting bellowing behavior. Because bison are generally found in the open, perhaps the best strategy in a risky environment is to remain quiet even during a season when it is advantageous to vocally advertise for mates. Pregnancy rates of ≥ 3.5 year-old females in Yellow Bear pasture is approximately 40% (OLC Bison Management Plan 2013), while that in Badlands National Park is 90% (E.Childers, Badlands National Park, pers. comm). While we do not know the reason for this disparity, it is a possible and disconcerting demographic impact of continual, year-round hunting.

Perceived predation risk (Frid and Dill 2002) and disturbance (Gutzwiller et al. 1994) diverts time and energy from fitness-enhancing activities, including mating displays in a number of species. Male Tungara frogs (*Engystomops pustulosus*) stifle mating calls and sometimes abandon mate advertisement in response to perceived predation (Ryan 1985). Male Great snipes (*Gallinago media*) abandon leks when disturbed or perceive risk to predation (Fiske and Kålås 1995). Among ungulates, overall reproductive success of mule deer (*Odocoileus hemionus*) and caribou (*Rangifer tarandus*) decreased when they were disturbed by ATV's and low-flying aircraft (Yarmoloy et al. 1988; Harrington and Veitch 1992).

All remaining explanatory variables predicted increased bellowing rate. The addition of each attendant male predicted an increase in bellowing rate by approximately 5%. Berger and Cunningham (1994) also reported a positive relationship between the number of attendant males and bellowing rate. Although bellowing rate increased as the number of attendant males increased, it did not occur with equal magnitude in the hunted (Pine Ridge) populations vs the non-hunted (Badlands National Park) population. When there were > 4.3 attendant males (mean

number of attendant males/group), bellowing rate by bulls in the hunted populations was 14 times less than that of bulls in the non-hunted population. When there were < 4.3 attendant males, bellowing rate by bulls in the hunted populations dropped to nearly 29 times less than that of bulls in the non-hunted population. Bulls in the two hunted populations clearly exhibit dampened bellowing rate, and the effect is more pronounced when there are few attendant males.

The passage of each observation day (indicative of the progress of the rut) was predicted to increase bellowing rate by 5.5%. We observed all populations for three weeks following the date that we recorded the first bellow in each population. Since the estrus state of cows influences bellowing rates of bulls (Berger and Cunningham 1994), we infer that as the number of observation days accrued, more females entered into estrus. Group size and the number of adult females in groups also positively influenced bellowing rates, but to a much lesser extent and their impact can be considered negligible.

Implications for Conservation

Ungulates can show behavioral responses to human hunting, that are, at times, even stronger than responses to large carnivores (Proffitt et al. 2009; Ciuti et al 2012). Bison in Yellow Bear and Slim Buttes pastures on Pine Ridge may be sensitized to continual, year-round hunting. These findings should be of particular conservation relevance to bison because bellow amplitude and quality have been directly associated with mating success (Wyman, 2006), while also functioning to deter rival males during the mating season (Berger and Cunningham 1994). Because vocalizations impact mating success, any changes in behavior could alter critical population-genetic parameters like effective population size (Wright 1931) and the capacity for populations to exhibit adaptive evolution. The IUCN Bison Specialist Group emphasizes the importance that bison express the full complement of natural mating behaviors (Gates et al. 2010) and stresses consideration of possible genetic consequences of all management actions, especially those for smaller herds; bellowing behavior is one such component that should be considered.

Changes in mating behavior (e.g., propensity to advertise for mates, intimidate, and/or fight rival males) can alter breeding opportunities – or possibly even effectively remove certain individuals from the breeding pool. Population-wide responses to hunting, like fear, are probably transmitted more quickly in social species (Cromsigt et al. 2013) like bison, where many individuals (on occasion) can witness conspecifics being downed by humans at close range. Therefore, we suggest that researchers and managers consider the potential that continual, year-round human hunting has to induce behavioral changes in survivors of exploited populations, especially those behaviors that are linked to mating success via mate advertisement and acquisition. Future research could include a fully replicated examination of bellows in hunted and non-hunted areas, while examining potential differences in the rate and physical parameters (e.g., amplitude, rate, pitch, timbre) of bellows. If reduced bellowing is pervasive, then wildlife managers may need to adjust hunting rate and duration, timing (season), and the time lag between hunting events in order to insure that bison are able to express their full repertoire of natural mating behaviors.

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Table 1(on next page)

Spearman's Rank Correlation

Table 1 Spearman’s correlations between bellowing rate and possible predictor variables of Plains bison in South Dakota, 1 July – 13 August, 2013.

1

Variables	1	2	3	4	5
Bellows[1]					
# Attendant Males[2]	-.078				
Group Size[3]	.257***	.177**			
Day[4]	-.235***	.573***	-.240***		
Hunting[5]	-.576***	.475***	-.218***	.671***	
# Adult Females	-.043	.442***	.676***	.099	.210**

2 *Note*. *p<.05, **p<.01, ***p<.001; *df* = 242 in all cases.

Table 2(on next page)

Poisson Regression

Table 2 Poisson regression analysis for bellowing rate of bison bulls from two hunted populations and one non-hunted population in South Dakota, from 1 July – 13 August 2013.

Variables	IRR	*SE*	*z*	*p*	VIF
Constant	11.559	.667	42.44	<.001	
#Attendant Males	1.053	.003	17.20	<.001	1.35
Group Size	1.002	.000	11.88	<.001	2.34
Day	1.055	.003	19.36	<.001	2.41
Hunting	.053	.003	-58.43	<.001	2.28
# Adult Females	1.004	.000	9.39	<.001	1.95

Note. $N = 243$, LR $\chi^2(5) = 7085.60$, $p < .0001$; Pseudo $R^2 = .5259$. Data shown are incident rate ratios, standard errors, *z*-statistics, *p*-values, and Variance Inflation Factors (VIF) (derived from an identically specified linear regression analysis).

Table 3(on next page)

Poisson Regression with Interaction

Table 3 Poisson regression analysis of the interaction between hunting and number of attendant males on bellowing rate of bison bulls from two hunted populations and one non-hunted population in South Dakota, from 1 July – 13 August 2013.

Table 3 Poisson regression analysis of the interaction between hunting and number of attendant males on bellowing rate of bison bulls from two hunted populations and one non-hunted population in South Dakota, from 1 July – 13 August 2013.

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Variables	IRR	*SE*	*z*	*p*	VIF
Constant	1.153	.095	1.73	.083	
# Attendant Males (Std.)	1.614	.029	27.07	<.001	1.49
Group Size	1.002	.000	11.79	<.001	2.39
Day	1.060	.003	21.50	<.001	2.41
Hunting (Std.)	.236	.006	-57.91	<.001	2.30
# Adult Females	1.004	.000	9.68	<.001	1.95
Hunting *#Attendant males	1.227	.014	18.24	<.001	1.23

Note. $N = 243$, LR $\chi^2(6) = 7348.93$, $p < .0001$; Pseudo $R^2 = .5455$. Data shown are incident rate ratios, standard errors, *z*-statistics, *p*-values, and Variance Inflation Factors (VIF) (derived from an identically specified linear regression analysis).