BISON AND ELK RESPONSES TO WINTER RECREATION IN

YELLOWSTONE NATIONAL PARK

by

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The National Park Service (NPS) is tasked with protecting wildlife and providing public access to parklands; winter recreation in Yellowstone National Park (YNP) has challenged NPS managers to balance this dual mandate. This study addresses bison and elk responses to winter recreation in the upper Madison River drainage of YNP. Using data on weather; winter recreation activity; elk and bison distribution, behavior, abundance, and fecal stress hormone (glucocorticoid) levels collected during the winters of 1998—1999 and 1999—2000, I developed models to analyze if variables related to winter recreation contributed to bison and elk distribution, behavior, and stress hormone levels responses. As distance between human activities and bison and elk decreased, behavioral responses increased. Both species behaviorally responded more often to people off-trail than to people on trails ($P < 0.001$ for both species), and these activities prompted more behavioral responses than activities on roads. Elk were farther from the road ($P = 0.092$) and had higher stress levels (unknown elk: $P = 0.051$; collared cow elk: $P = 0.002$) after exposure to >7,500 cumulative vehicles entering the West Yellowstone gate. Elk residing along the road segment with the greatest amount of oversnow vehicle (OSV) activity had higher stress levels (unknown elk: $P < 0.001$; collared cow elk: $P = 0.004$) and may have been displaced from habitat along the road (distance: $P = <0.001$; numbers sighted: $P = 0.082$) compared to elk residing along the less-traveled road segment. Collared cow elk stress levels increased ($P = 0.057$) while the probability of bison and elk behaviorally responding to human activities on the road decreased ($P = 0.001$ for both species) as daily vehicles entering the West Yellowstone gate increased. The predictability and frequency of OSV activities facilitated habituation to the majority of winter recreation activities. Abundance estimates indicated populations of wintering bison increased and wintering elk remained stable over 20 years. Despite varying responses to increased winter visitation since the late 1970s, bison and elk return to winter in the same area each year, coexisting with winter recreation without incurring losses at the population level.

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INTRODUCTION

Understanding and managing recreational impacts on wildlife is becoming more important as participation in outdoor activities increases and covers larger areas of land, and isolation of wildlife from humans decreases (Flather and Cordell 1995). Management policies for protected areas must balance a trade-off between public access and the impacts of human activities on animal populations. When human activities occur near wildlife, animals may show any of 4 basic responses: attraction, avoidance, habituation (Knight and Cole 1991), or no reaction. If human activity offers a reward, such as food, wildlife may be attracted to the activity. If the activity is unpredictable, rare, sporadic, or results in a negative outcome, such as harassment or injury, wildlife tend to avoid such stimuli (Aune 1981, MacArthur et al. 1982). Wildlife may habituate to stimuli, resulting in the decrease or disappearance of behavioral and/or physiological responses (Eibl-Eibesfeldt 1970), especially if the activity is predictable and frequent with no positive or negative consequences. Animals may never show any level of response to stimuli. But even when an animal lacks an observable behavioral response, a non-observable physiological stress-response may occur (MacArthur et al. 1982). A stress response may occur when an animal perceives something as a threat, triggering a cascade of hormone secretions that eventually releases adrenaline and glucocorticoids (GCs) from the adrenal gland. The short, quick release of adrenaline prepares the body for the immediate "fight or flight" response. This is followed by the slower, extended release of GCs from the adrenal cortex (MacArthur et al. 1982, Sapolsky 1992), which

reassigns the body's resources to back up the "fight or flight" response hours after the initial cognition of the threat. If this stress-response is repeated, sustained or prolonged, it can cause fatigue, hypertension, gastric ulcers, impaired disease resistance, less efficient metabolism, impaired growth, suppressed reproduction, and accelerated neural degeneration during aging (Mayes 1979, Sapolsky 1992).

Recreational activity combined with environmental factors such as deep snow, cold temperatures and reduced food availability may stress animal populations, which may result in illness or lower rates of reproduction and survival (Anderson 1995). Energy conservation during winter months is important to ungulate survival (Gates and Hudson 1979). Winter recreation activities such as snowmobiling and cross-country skiing occurring near wintering wildlife may impose disturbances of greater biological significance than other forms of recreation that occur during less energetically demanding times of the year.

In Yellowstone National Park (YNP), winter recreation is concentrated along valley bottoms where wildlife aggregate. Elk and bison winter in the valley bottoms due to reduced snow depths associated with lower elevations and the geothermal activity in these areas. In the early part of the century few people ventured into YNP during the winter, but elk and bison have been exposed to increasing levels of winter recreation since 1955, when the first snowcoach trips to Old Faithful occurred, and 1964, when the first snowmobile travelers explored the park (Meagher 1993). Since then, winter visitation has become quite popular. In the early 1970s, YNP managers began grooming the snow on roads to accommodate more snow vehicles and allowed concessioners to

operate overnight facilities for visitors and to restrict the use of oversnow vehicles (OSVs) to the road system. By the late 1970s, park-wide annual winter visitation was approximately 48,000 people, prompting the first intensive investigation of the impacts of winter recreationists on wildlife in the upper Madison River drainage of YNP by Aune (1981). He documented instances of people approaching wildlife and inhibiting wildlife movements and found that wildlife was displaced from habitat near roads and trails. These observations were relatively infrequent, however, and he observed that within the first two weeks of the winter season, animals habituated to the presence of humans, vehicles, and noise along groomed roads, and concluded that winter recreation was not a major factor influencing wildlife movement, distribution, or survival.

Since Aune's (1981) study, winter visitation has steadily increased. Between the winters of 1993—1994 and 1997—1998, the total annual number of snowmobile and snowcoach passengers and skiers coming to YNP averaged 90,748 (National Park Service 1999). Concerned with the effects of increased winter visitation, advocacy groups filed a suit against the National Park Service (NPS) in 1997. In response, the NPS agreed to prepare an environmental impact statement (EIS) addressing winter use management in YNP, Grand Teton National Park (GTNP), and the John D. Rockefeller, Jr., Parkway. Beyond the scope of the YNP/GTNP winter use management EIS, the US Department of the Interior banned snowmobiles from most National Parks in 2000, which has been met with litigation from the snowmobile industry and snowmobile enthusiast groups.

This paper addresses winter recreation activity influences on elk and bison abundance, distribution, behavior, and stress hormone levels in the upper Madison River drainage of YNP. I focused on bison and elk due to their abundance and proximity to human activity in the study area. I evaluated how OSV activity, the most common winter recreation activity, and activities afoot, such as trail and off-trail skiing and snowshoeing, affected bison and elk in the study area. As a follow up to Aune's (1981) conclusion that bison and elk habituated to winter recreation activities, I hypothesize that elk and bison avoid winter recreational activities but that these responses decrease as the animals habituate to the frequent and predictable patterns of winter recreation in the study area. I also hypothesize that while elk and bison may observably habituate behaviorally, their physiological stress levels will increase as daily and cumulative winter recreation levels increase.

I documented human activity levels, human-ungulate interactions, elk and bison distribution patterns in relation to the road corridor and areas of human activity, and measured elk and bison fecal glucocorticoid (FGC) levels as a physiological index of stress. With these data, I used regression models to test if the human activity in the study area affected elk and bison. I specifically tested if daily and cumulative numbers of vehicles entering the study area or types of winter recreation activities and human behaviors contributed significantly to elk and bison distribution, behavior, and stress hormone responses after controlling for environmental and herd characteristics that contribute to these responses. In addition to these quantitative analyses, to the extent possible, I compare current elk and bison behaviors and abundances to Aune's (1981)

baseline study to evaluate potential differences to 20 years ago, when winter visitation

was less than it is currently.

STUDY AREA

The study area was defined as the winter ranges for elk and bison within the Madison, Firehole and Gibbon drainages, referred to as the upper Madison River drainage. This area encompassed approximately 27,000 ha (Ferrari 1999) extending from Norris Geyser Basin south to Old Faithful and along the Madison River to the western boundary of the park at West Yellowstone, Montana (Figure 1). Physiography was dominated by river valleys and canyons that cut through the rhyolitic plateau (Despain 1990) with elevations that ranged from 2250–2800 meters. Extensive flat meadows lined the valley bottoms of the major drainages. The geyser basins at Norris and along the Firehole River, along with many other smaller geothermally-influenced areas, produced warm ice-free rivers, creeks and pockets where the severity of winter was reduced, allowing photosynthesizing plant communities to grow throughout the winter (Meagher 1973, Despain 1990). Lodgepole pine (*Pinus contorta*) dominated forested areas with occasional stands of Douglas fir (*Pseudotsuga mensiesii*) and spruce/fir (*Picea engelmanni/Abies lasiocarpa*) interspersed. Wet meadows were characterized by sedges (*Carex* spp.) and marsh reedgrass (*Calamagrostis* spp.) while dry meadows were characterized by sagebrush (*Artemisia* spp.) and grasses (*Festuca idahoensis, Poa* spp.) (Craighead et al. 1973, Aune 1981).

Winters were long and cold and summers were short and cool. Snow depths typically exceeded 91 cm in nonthermal areas (Eberhardt et al. 1998). The valley bottom snowpack began to melt in early March while the higher elevation plateau snowpack
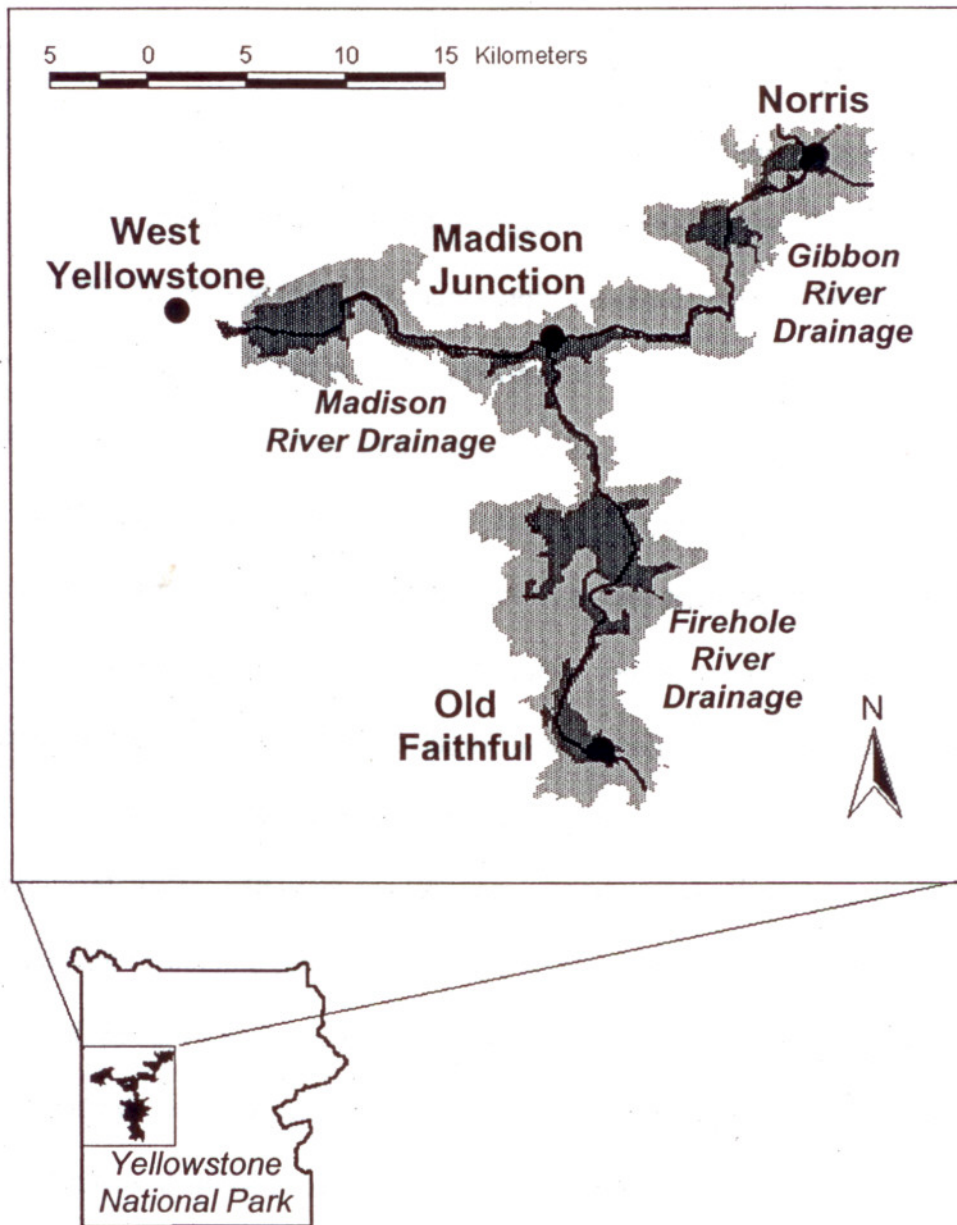
Figure 1. The upper Madison River drainage study area of Yellowstone National Park. The lighter shaded area represents the elk winter range while the darker shaded bison winter range is constricted to the valley bottoms overlapping the elk range (Ferrari 1999). Roads, indicated in black, follow the valley bottoms.

around the perimeter of study area did not start to melt until mid-April or May (Ferrari 1999). Mean annual temperature at the western boundary of the study area is 1.7 C°, with 15.3 C° in the warmest month of July and −10.6 C° in the coldest month of January (National Oceanic and Atmosphere Administration records, as cited in Aune 1981).

Bison and elk were the most abundant large animals encountered in the study area. The elk population was primarily non-migratory, remaining within the borders of the park throughout the year (Craighead et al. 1973) and was not exposed to human hunting pressure. The study area provided primarily winter range for the central Yellowstone bison herd that numbered approximately 1,600 to 2,200 (Bjornlie and Garrott 2001, S. C. Hess unpublished data). Predators in the area included wolves (*Canis lupus*), coyotes (*Canis latrans*), and, during the non-hibernation periods, black bears (*Ursus americanus*), and grizzly bears (*Ursus arctos*). Trumpeter swans (Olor buccinator) and bald eagles (Haliaeetus leucocephalus) also occurred in the area.

Human activity in the upper Madison River drainage occurred in a predictable pattern. Vehicular travel within the study area was restricted to paved, 2-lane roads, including 22 km from the West Entrance Station to Madison Junction, 22 km from Madison Junction north to Norris Junction, and 26 km from Madison Junction south to Old Faithful. On November 1, these roads were closed to the public, and wheeled vehicle (WV) traffic was limited to YNP personnel. Once a base of snow accumulated, human travel on the roads transitioned from WVs to snowmobiles and snowcoaches, together referred to as over-snow vehicles (OSVs) and by mid-December the park opened to the public for the winter season. In mid-March the park was closed to the public, the roads

were plowed and for approximately 6 weeks WV traffic was limited to YNP personnel only. Public, non-motorized recreation was allowed for 3 weeks before the roads were opened to public WVs for the summer season in the last week of April.

Roads within the study area accommodated the most winter recreational use in the park. Of all OSVs that entered YNP, 62% arrived at the West Entrance Station (NPS 1999), 69% traveled between Madison and Old Faithful, and 36% traveled between Madison and Norris (Friemund et al. 1999). In addition to OSV road traffic, cross-country skiers, snowshoers, and other foot traffic occasionally ventured off-trail but more typically used the 80 km of available trails, mostly in the Old Faithful and Norris areas and at the geyser basin areas along the Firehole River.

METHODS

I collected data on weather; daily winter recreation activity; elk and bison distribution, behavior and abundance; and collected elk and bison fecal samples from late November to mid-May of 1998—1999 and 1999—2000.

Weather

I gathered weather data to assess winter severity effects on elk and bison behavior, distributions and FGC levels. I obtained daily snow water equivalent (SWE) measurements, an index of the mass of water contained in a column of snow, from the Natural Resources Conservation Service (NRCS) automated SNOTEL site in West Yellowstone, Montana (2,042 m) (http://www.wcc.nrcs.usda.gov/snotel/snotel.pl?sitenum=924&state=mt). I calculated average daily temperature using daily minimum and maximum air temperatures recorded at NPS weather stations located in the valleys at West Yellowstone, Madison Junction (2091 m), and Old Faithful (2264 m). I compared our SWE data to the winters Aune (1981) conducted his study and included SWE and average daily temperature as independent variables in our analyses.

Winter Recreation

I obtained the daily number of vehicles entering the NPS West Entrance Station at West Yellowstone, Montana, throughout the public OSV season and after the park opened to visitor WVs in the spring. When the park was closed to the public, I did not

quantify YNP personnel vehicles traveling through the study area and considered this activity to be the "baseline" level of human activity. When the park was opened to public visitation, the number of vehicles entering the West Yellowstone gate was additive to the baseline level of human activity. I compared our OSV visitation data to Aune's (1981). In our analyses, I included total daily vehicles entering the West Entrance gate as an independent variable. Additionally, I defined a categorical "exposure" variable, with "low" for days that the park was closed and until 7,500 cumulative vehicles entered the West Entrance gate and "high" for each day after >7,500 cumulative vehicles entered the West Entrance gate. I included this exposure variable in our analyses to test if behavior, distribution or stress hormone responses habituated to human activity after a period of initial exposure.

Elk and Bison Abundance

I estimated the elk population in the study area at the onset of each winter field season by combining replicate Lincoln-Petersen population estimates from the previous spring and replicate composition surveys conducted during the fall rut. Radio collars (36–38) were maintained on cow and calf elk on the study area during the 2 years of the study. I traveled the road system and counted all collared and uncollared elk using binoculars and a spotting scope in early morning and late evening, when elk were most visible. A continuity-corrected Lincoln-Petersen population estimate was calculated for individual surveys (Seber 1982) conducted on 10 consecutive days in April when elk were aggregated in lower elevation meadows and after most winter mortality had occurred. The mean of the spring surveys was considered the estimate of the number of

adult elk in the population entering the next winter (Rice and Harder 1977). Seven years of pre-wolf elk telemetry data showed no significant adult mortality from spring to the fall rut surveys (R.A. Garrott, unpublished data), and wolves were absent from the study system during the snowless seasons (Jaffe 2001). Fall rut replicate composition surveys were conducted on 11–12 consecutive days in late September-early October in the same manner as the spring surveys to determine the sex and age composition and estimate recruitment to the population. The proportion of cows and bulls in the adult population and the calf–cow ratio were calculated from these fall surveys. I multiplied the fall proportions of bulls, cows and calves each by the previous spring population estimate, and added these together to yield a total population estimate at the onset of winter.

I conducted censuses of the bison within the study area every 10 days during 1998—1999 and every 14 days during 1999—2000. Using intensive ground surveys techniques (Ferrari 1999, Bjornlie and Garrott 2001), the study area was divided into 72 units with 6 travel routes delineated that completely traversed all the units. Surveys lasted 2 days and consisted of 3 people separately traversing 1 route each day, locating all bison within each unit. I surveyed the Gibbon and Madison drainages 1 day and the Firehole drainage on the other day to minimize the possibility of bison moving from 1 area to another between survey days. For each group of bison observed, I recorded the date and time, location of the group recorded on USGS 7.5 minute maps in Universal Transverse Mercator (UTM) coordinates, and classified the age/sex group composition as described for the radiocollared elk locations. I compared our bison abundance estimates to Aune's (1981) bison population estimates.

Elk and Bison Behavior and Distribution

I conducted surveys from roads, trails, and in areas off–trails to collect data on elk and bison distribution in relation to roads and trails, winter recreation activities and wildlife responses. I sampled for these data on each of the 3 road segments in the study area twice a week, for a total of 6 independent surveys conducted at different times to capture daily and weekly variation in wildlife and human activities. Surveys on the road were conducted along the 3 road segments in the study area (Fig. 1) while snowmobiling or driving ≤ 50 km/hr. Trail surveys were conducted from established trails and boardwalks in the Upper Geyser Basin near Old Faithful and the Norris Geyser Basin. I conducted off–trail surveys in areas remote from roads and established trails. I surveyed approximately 10 km of trails and 10 km off–trails every 2 weeks.

For all surveys, I recorded the route surveyed and all elk and bison groups observed. For each group, I recorded distance from road, trail or observer; species; and group size. I used a laser range finder to determine perpendicular distance from road, trail, or observer. In situations beyond the capabilities of the range finder (>500 m), I estimated this distance. During road surveys, I categorized if people, including the observer, 1) stopped their vehicle; 2) stepped out on foot; or 3) ventured off the road or trail. During trail and off-trail surveys I coded if people were 1) on the trail or 2) off-trail. I used the highest human activity coded for each observation in our analysis, with the higher coded categories representing less predictable activities. I recorded elk and bison response behaviors for the majority of the group. Response behaviors were categorized as no apparent response, look/resume, ambled away, attention/alarm, and

flight (Chester 1976). I plotted proportions of the 5 behavioral responses during 6

consecutive 21-day periods when bison and elk were exposed to OSVs. Observations

from 1999—2000 were only represented in periods 2–5. Period 1 encompassed 6 days in

December 1998 when the park was not open to the public but administrative traffic had

changed to OSVs and period 6 included 7 days at the end of the normal public OSV

season in March 1999 (the 1999—2000 OSV season ended in period 5 due to lack of

snow). For logistic regression analyses, I created a binary behavioral response variable

by coding no apparent response as 0 and pooling look/resume, attention/alarm, amble

away, and flight responses together and coding these responses as 1.

Fecal Glucocorticoid Sampling

I collected feces from radiocollared cow elk, unknown elk and bison to measure

FGC levels. To obtain spatially and temporally balanced sampling of unknown elk and

bison feces, I divided the study area into 5 sampling areas: West Yellowstone to Madison

Junction; Madison Junction to approximately 11 km north of Madison Junction;

approximately 11 km north of Madison Junction to Norris; Madison Junction to

approximately 13 km south of Madison Junction; and approximately 13 km south of

Madison Junction to Old Faithful. I attempted to collect 10 fecal samples from both elk

and bison per sampling area in 2 week intervals. I attempted to collect fecal samples that

were <2 days old, using recent snowfall, tracks, and knowledge of groups recently

occupying an area to aid in our judgment of fecal sample age.

I collected fecal samples from a total of 45 radiocollared cow elk. Age of collared

elk, which was included as a variable in our analyses, was determined based on

cementum annuli of an upper canine tooth (Hamlin et al. 2000) extracted at the time the animal was collared. I determined the order and frequency of locating the radiocollared cow elk using a restricted randomization design (Garrott et al. 1996). With the study area divided into 6 regions, 2 field team members were randomly assigned 1 region each morning and afternoon. Radiocollared elk in those areas were then located in a randomly determined order using radio-telemetry. Animals within each region were resampled only after animals in all 6 regions were located. For each collared elk observed, I recorded date, time, and UTM location. I recorded age/sex categories of all elk associated with the marked individual (adult cows, adult bulls, and calves). When I witnessed a defecation event, after all data were recorded and the elk had moved away from the area, I collected a fecal sample from the collared cow and from other elk in the group. Upon collection, I recorded date, time of collection, species, and the identity of the animal. Fecal samples were collected in 50 mL tubes, stored at –20°C in the field and at –80°C in the laboratory until the assays were performed.

Fecal Sample Extraction and Validation of Radioimmunoassay

Fecal samples were dried using a rotary evaporator, pulverized, and 0.1-0.2 g of the resulting powder was boiled in 10 ml of 100% ethanol for 20 minutes. After centrifuging (15 minutes at 500 g), supernatant was recovered, dried and reconstituted in 1 ml methanol. This extract was vortexed for 1 minute, placed in an ultrasonic glass cleaner for 30 seconds to free adhering particles, then vortexed for 15 seconds. Extracts were stored at –80 C°.

I validated a double-antibody [125I] corticosterone radioimmunoassay (RIA; ICN Biomedicals, Costa Mesa, California, 92626 USA) for both elk and bison fecal extracts (Cekan 1975; Millspaugh 1999). This antiserum cross-reacts little with steroids other than corticosterone (deoxycorticosterone 0.34%; testosterone 0.10%; cortisol 0.05%; progesterone 0.02%; < 0.01% for all other steroids tested), the specific FGC hormone I quantified in our samples. I assayed all extracts in duplicate at dilutions of 1:50 (100 μl) for elk and 1:4 (100 μl) for bison. Serial dilutions of pooled elk fecal extracts (range =1:4 to 1:128) and pooled bison fecal extracts (range=1:4 to 1:64) yielded antibody–binding curves parallel to the standard curve (range = 25–1000 ng corticosterone/mL). Mean recovery of known amounts of corticosterone added to elk (range = 25–250 ng corticosterone/mL) and bison (range = 25-1000 ng corticosterone/mL) fecal extract was $89 \pm 1.6\%$ ($y = 4.29 + 0.89x$, $R^2 = 0.99$) and $110 \pm 2.9\%$ ($y = 17.59 + 1.10x$, $R^2 = 0.99$), respectively. Elk extract inter-assay coefficient of variation (CV) was 6.9% for a low internal control ($n = 39$, 51–68% binding) and 8.3% for a high internal control ($n = 39$, 22–34% binding) while bison extract inter-assay CV was 8.1% for a low internal control ($n = 21$, 51–67% binding) and 8.3% for a high internal control ($n = 21$, 15–29% binding). Mean intra–assay CV was 2.1% and 2.6% for elk and bison extracts, respectively. The assay sensitivity 95% confidence interval was 14.6–17.1 ng/ml (20–24% binding) for elk extracts and 10.3–16.4 ng/ml (14–23% binding) for bison extracts. Elk and bison FGC levels were expressed as ng of corticosterone hormone excreted per gram of dry feces.

Determination of Lag-time to Detectable FGC Response

In order to appropriately attribute time-dependent covariates (SWE, average daily temperature, daily and cumulative daily visitation levels) for the bison and elk FGC data analyses, we needed an estimate of the approximate lag-time from a stressful event to corresponding secretion of GCs in feces. We used the results of an adrenocorticotropin (ACTH) challenge for elk conducted by Millspaugh (1999), and conducted an ACTH challenge for bison. I isolated 2 yearling bison cows from a captive herd and collected their feces 20 hours prior and just before injecting 1 of the cows with ACTH (5–10 g Acthar gel/100 kg body mass, IM). The other bison served as a control animal. I collected samples of fecal deposits from the pen approximately every 6 hours for 49 hours post–injection. Fecal samples were collected, stored, and assayed as described above.

The captive bison injected with ACTH experienced an increase in FGC levels (Figure 2). FGC levels from fecal samples collected 20 hours prior to the injection and just prior to injection measured 343 and 207 ng/g dry feces for the treated and control bison, respectively. Peak FGC levels in samples collected 17 and 25 hours post-injection from the treated bison were observed at 742 and 740 ng/g dry feces, respectively. FGC levels dropped back down to 348 ng/g dry feces 49 hours post-injection. Using the same RIA and ACTH challenge methods, Millspaugh (1999) found the peak in cow elk FGC levels approximately 23 hours post-injection. Using this information, I attributed time-dependent variables (SWE, average daily temperature, daily and cumulative vehicle
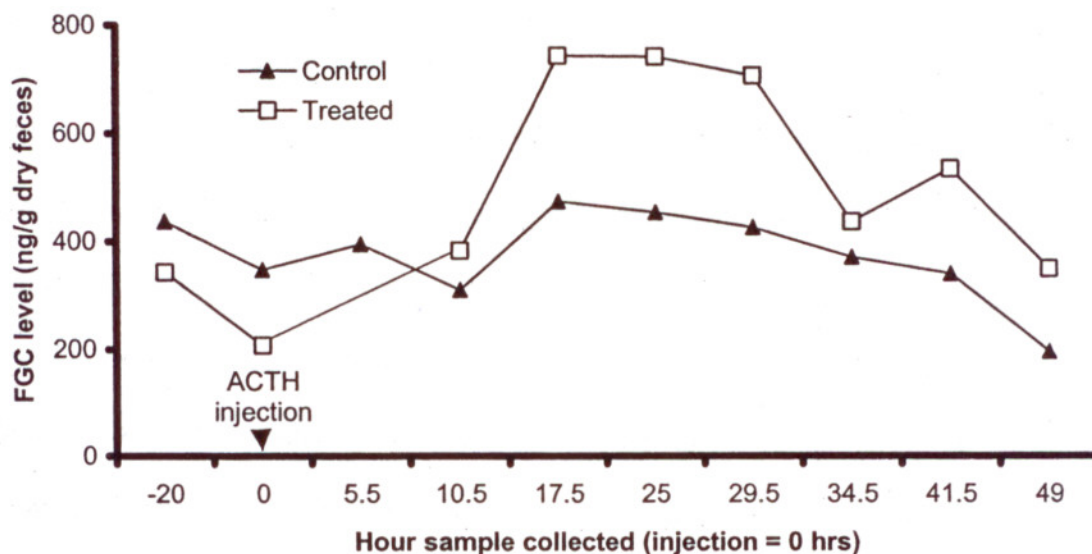
Figure 2. Fecal glucocorticoid (FGC) levels measured for an experimentally ACTH-injected cow bison and a control cow bison. The peak level of FGC secretion for the experimental bison occurred approximately 17 to 25 hours post-injection.

entering the West Yellowstone gate) from 24 hours prior to the date the fecal sample was collected when constructing the FGC models.

Analytical Methods

To test hypotheses about how winter recreation might contribute to elk and bison distribution, behavior, and stress hormone responses, I developed a priori models with variables relevant to human activities and controlled for environmental conditions and biological characteristics of elk and bison that may naturally contribute to the responses of interest. I controlled for year, cumulative season days (day 1 = Dec 1), SWE, average daily temperature, meters from road or distance from human activity, and number of animals in group. I then incorporated variables of interest representing levels and types of human activities, including road segment (West Yellowstone to Old Faithful vs.

Madison Junction to Norris), vehicle type (WV vs. OSV), number of daily vehicles entering the West Entrance gate, exposure (<7500 cumulative vehicles vs. >7500 cumulative vehicles), and human activity occurring during observations.

I developed 7 multiple linear regression models to test if human activity was related to elk and bison distribution and FGC levels. I modeled distances of elk/bison groups sighted from the road, total numbers of elk/bison sighted during road surveys, and FGC levels in unknown elk, unknown bison, and radiocollared cow elk. I log10 transformed the response variables to achieve normality. For the distance model response variable, I changed all observations of elk and bison that were on the road from 0 to 1 meter to allow for log10 transformation. For the statistically significant variables ($P \leq 0.10$) that contributed to the response in each full model, I reported partial regression results and included least means squared values for the statistically significant anthropogenic categorical variables for future comparisons.

I used logistic regression fit by maximum likelihood to test if human activity contributed to 4 models of elk and bison behavioral responses from the pooled trail/off-trail and road survey data. I started with a full model with all applicable variables. A reduced model was then run with variables achieving significant ($P \leq 0.10$) z-values from the full model. I then reassessed the importance of the variables dropped from the full model by comparing the likelihood values of the full model and reduced model, which yielded a deviance value. Small p-values ($P \leq 0.10$) from the deviance revealed that at least one of the dropped variables contributed to the response (Collett 1991). None of the deviances indicated that the dropped variables were significant contributors to the full

model and our reduced models were the final models reported. I used Minitab (Release

13) for data analyses.

RESULTS

Weather

The snowpack began to accumulate in November, peaked in April, and melted off in May though differences between the two years of our study were evident. The 1998—1999 accumulation peaked at 29 cm, 20% greater than the 33 year average peak SWE (23.1 cm) for the same location, while 1999—2000 peaked at 17.5 cm, 25% lower than the 33 year average. Peak SWE during Aune's (1981) 2 year study was 27.2 cm and 23.1 cm. Average daily temperatures ranged from –31°C to 7°C with a mean of –7 C° (SE = 0.50) in 1998—1999 and from –21°C to 7°C, averaging –5°C (SE = 0.46) in 1999—2000.

Winter Recreation

The public OSV season was 89 days from 16 December 1998 through 14 March 1999, and 82 days from 15 December 1999 through 6 March 2000 (Figure 3). Cumulative totals of 45,785 and 40,298 OSVs entered the West Entrance gate in the 1998—1999 and 1999—2000 winter seasons. Daily numbers of OSVs entering the West Entrance gate in 1998—1999 averaged 514 (SD = 208) and peaked at 1168 OSVs on 28 December while in 1999—2000, an average of 486 (SD = 222) OSVs entered the West Entrance gate daily and peaked at 1010 on 19 February. Peak visitation typically occurred on weekends and holidays while fewer vehicles entered the park on work days. For both years of this study, the threshold of 7500 vehicles changed from "low" to "high" on December 31, and was reset to "low" the day after the OSV season closed. In the

spring of both years of this study, the 7500 vehicle threshold reached the "high"

designation at the end of the first week of May, about 2 weeks after the park opened to

wheeled vehicles.

On 25 days of this study, OSV counts exceeded the 1979 winter peak of 738 daily

OSVs entering the West Entrance gate (Aune 1981). Cumulative daily OSV visitation

during this study was approximately double that reported by Aune (1981) when 19,563

and 20,539 OSVs entered the West Entrance gate during 1978—1979 and 1979—1980,

respectively.
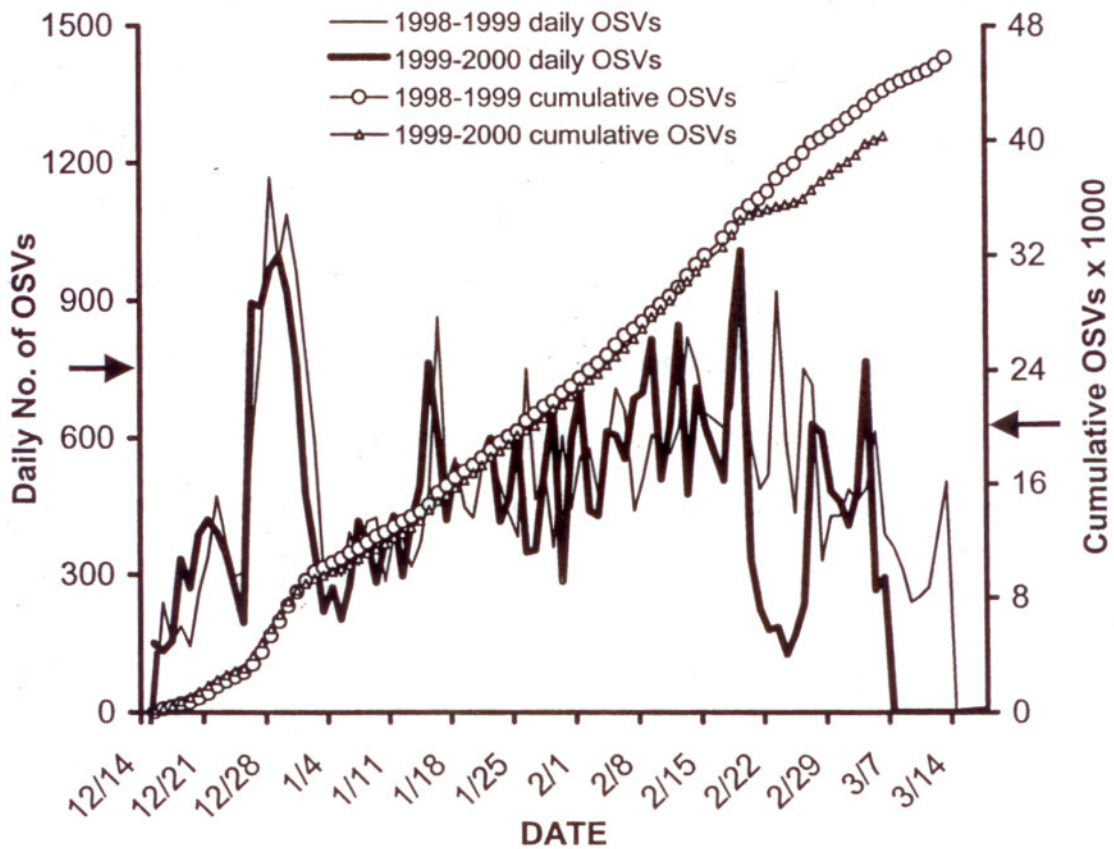
Figure 3. Total daily over-snow vehicles (OSVs) and cumulative daily OSVs entering the study area from the West Yellowstone entrance gate during the 1998—1999 and 1999—2000 winter seasons. Peaks of daily OSVs recorded at Old Faithful and the total cumulative OSVs that entered the park at West Yellowstone, Montana, during Aune's (1981) study are indicated with arrows on the appropriate axes for comparison.

Elk and Bison Abundance

I estimated the elk population at 428 ± 103 in April 1998 and 420 ± 49 in April 2000. Combining the mean spring estimates with the fall sex-age composition surveys, I estimated the fall elk population, prior to winter mortality, at 600 and 552 for 1998 and 1999. In January 1980, Aune (1981) counted 612 elk in the study area using aerial and ground survey methods. In addition to his study, other population estimates of the elk in the study area include 6 aerial censuses conducted between 1965—1974 by the NPS, ranging from 440 to 590 elk (Aune 1981), and Eberhardt et al. (1998) arrived at 4 estimates ranging from 537 to 821 elk in the study area from a combination of aerial and ground surveys conducted between 1993—1997.

Between December and May I completed 16 and 11 bison surveys in 1998—1999 and 1999—2000, respectively. As snowpack increased, bison moved from the deeper snows in the other areas of their range outside the study area to the moderated conditions in the study area's valley bottoms where forage was more easily obtained. The bison counts reflected this seasonal influx, ranging from 464 to 921 in 1998—1999 and 241 to 1167 in 1999—2000, peaking at the end of March in both years. Aune (1981) counted a range of 78 to 352 bison in 6 surveys conducted between December and April of 1978—1979 and 1979—1980.

Elk and Bison Distribution

I conducted a total of 194 road surveys, covering 4494 km, and recorded numbers of animals and distances from road for 1811 and 884 groups of bison and elk,

respectively. Bison were sighted on the road 81 times while elk were observed on the road only 14 times. Mean distances (± SD) of bison and elk groups along each of the study area road segments, when plotted against categories of daily OSV traffic entering the West Yellowstone gate, do not indicate avoidance of the road as OSV traffic increased (Figures 4 and 5).

The model for log 10 numbers of bison seen on a given day (adjusted $R^2 = 0.095$; Table 1) revealed that more bison were observed on the road from West Yellowstone to Old Faithful (least squares mean = 2.03) than from Madison Junction to Norris (least squares mean = 1.80; partial regression, $t_{154} = 2.60$, $P = 0.002$) and later in the season than earlier ($t_{154} = 1.76$, $P = 0.081$). The model of log 10 distances of bison groups from road, while not explaining much variability in the response (adjusted $R^2 = 0.03$; Table 1), showed bison were closer to the road in 1998—1999 (least squares mean = 1.85) than in 1999—2000 (least squares mean = 1.94; partial regression, $t_{1803} = 2.60$, $P = 0.009$), and later in the season than earlier ($t_{1803} = -1.95$, $P = 0.051$), and as SWE increased ($t_{1803} = -2.54$, $P = 0.011$). The model for log 10 numbers of elk sighted on a given day also performed poorly, with an adjusted $R^2 = 0.008$ (Table 2), but indicated fewer elk were sighted on the road segment from West Yellowstone to Old Faithful (least squares mean =1.24) than from Madison Junction to Norris (least squares mean = 1.36; partial regression, $t_{150} = 1.75$, $P = 0.082$).
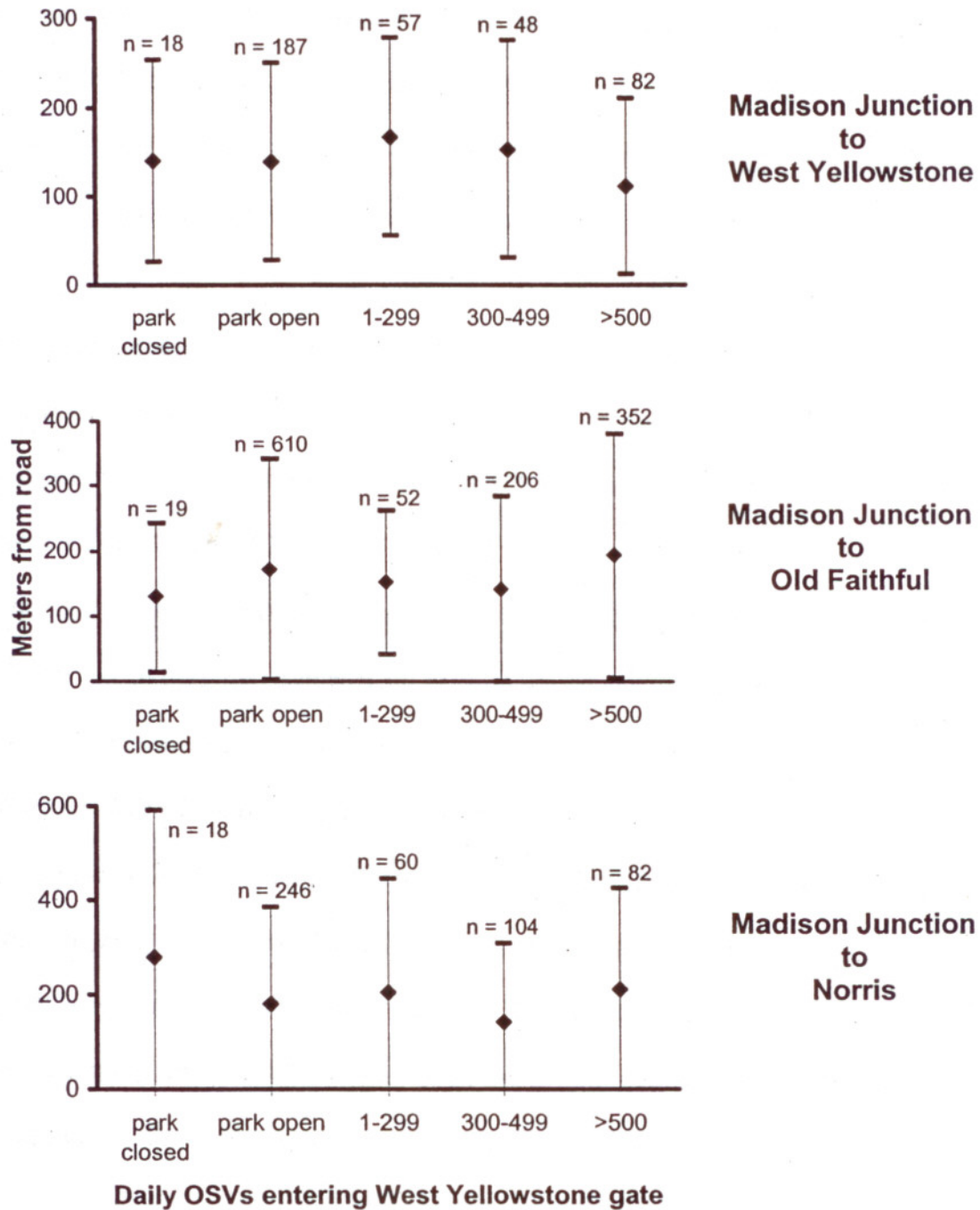
Figure 4. Bison distances (mean ± SD) from the three road segments in the upper Madison River drainage of Yellowstone National Park plotted against categorical levels of oversnow vehicle (OSV) traffic that entered the West Yellowstone gate during the winters of 1998—1999 and 1999—2000. Categories included periods when the park was closed to public OSV travel compared to when the park was open to public OSV travel, and when 1-299, 300-499, and >500 OSVs entered the study area via the West Yellowstone gate.
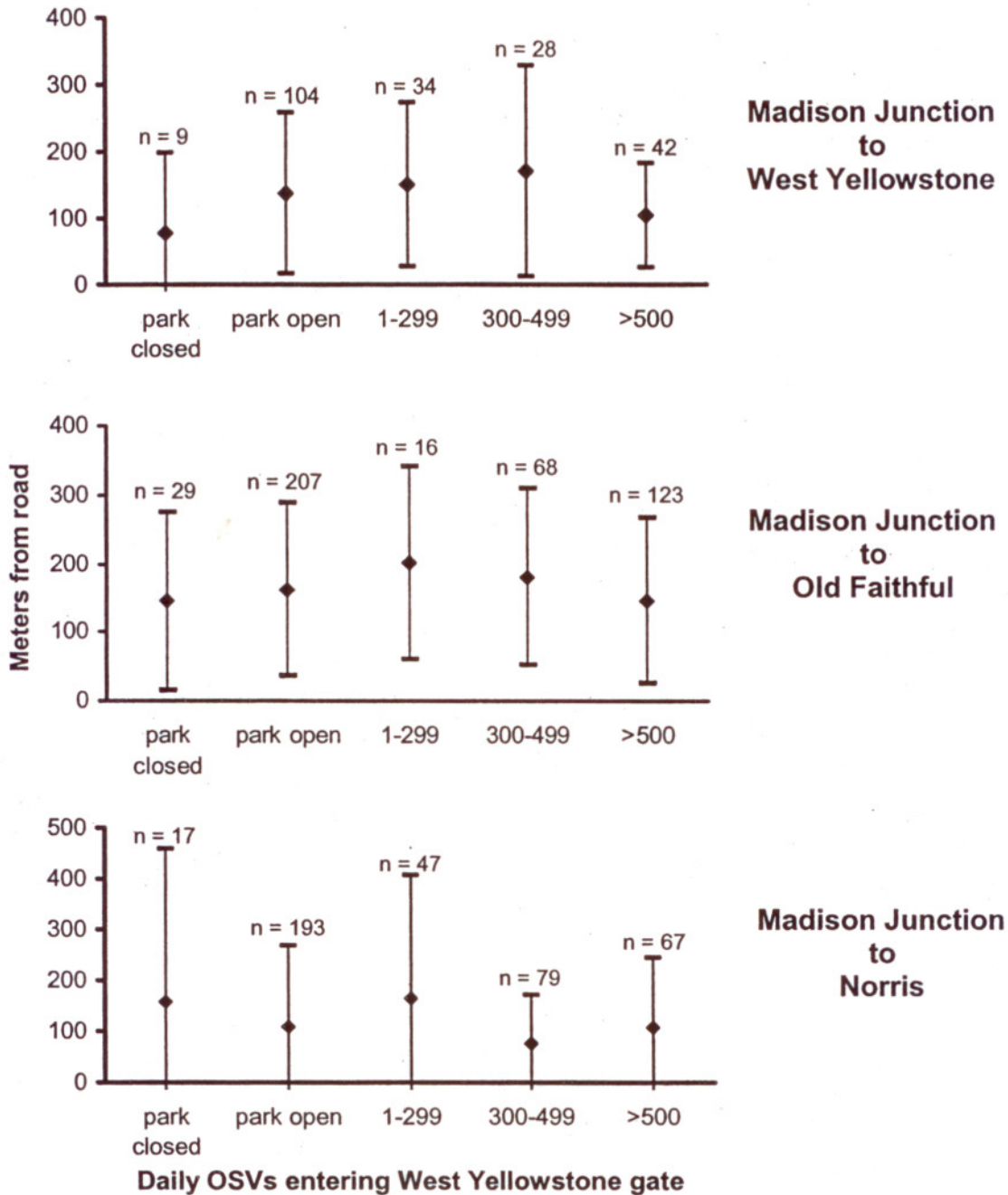
Figure 5. Elk distances (mean ± SD) from the three road segments in the upper Madison River drainage of Yellowstone National Park plotted against categorical levels of oversnow vehicle (OSV) traffic that entered the West Yellowstone gate during the winters of 1998—1999 and 1999—2000. Categories included periods when the park was closed to public OSV travel compared to when the park was open to public OSV travel, and when 1-299, 300-499, and >500 OSVs entered the study area via the West Yellowstone gate.

Table 1. Regression coefficients of variables that contributed significantly ($P \leq 0.10$) to models of bison behavior, distribution, and stress hormone levels in the upper Madison River drainage in Yellowstone National Park during the winters of 1998-1999 and 1999-2000. Statistically insignificant variables included in the full model are blank while "n/a" indicates variables not included in the model. Categorical variable coefficients are interpreted relative to a lower numerically coded reference level, indicated parenthetically. The behavioral response logistic regression model coefficients are from the best-fit reduced model with only the statistically significant variables from the full model.

| Response Variables — Independent Variables	Behavioral response vs. no response		Distribution		Physiological Stress: Corticosterone level
	Road Surveys	Trail and Off-trail surveys	Distance from Road	Numbers of bison observed	
Daily vehicles entering West Yellowstone gate	-0.001				
Wheeled vehicles (vs. over-snow vehicles)		n/a			0.171
Exposure to >7500 cumulative vehicles (vs. <7500)					
Cumulative season days			-0.002	0.001	-0.001
1999-2000 (vs. 1998-1999)		-0.528	0.105		-0.069
West Yellowstone to Old Faithful (vs. Madison Junction to Norris)		n/a		0.237	
Number in group	-0.034	-0.044		n/a	n/a
Meters from road	-0.020	n/a	n/a	n/a	n/a
Human activity near group of bison		n/a	n/a	n/a	n/a
Meters from humans	n/a	-0.851	n/a	n/a	n/a
Human off-trail (vs. on trail)	n/a	1.873	n/a	n/a	n/a
Snow water equivalent	n/a	n/a	-0.007		-0.004
Average daily temperature	n/a	n/a	n/a	n/a	

Table 2. Regression coefficients of variables that contributed significantly ($P \leq 0.10$) to elk behavior, distribution, and stress hormone responses in the upper Madison River drainage in Yellowstone National Park during the winters of 1998-1999 and 1999-2000. Statistically insignificant variables included in the full model are blank while "n/a" indicates variables not included in the model. Categorical variable coefficients are interpreted relative to a lower numerically coded reference level, indicated parenthetically. The behavioral response logistic regression model coefficients are from the best-fit reduced model with only the statistically significant variables from the full model.

Response Variables	Behavioral response vs. no response		Distribution		Physiological Stress: Corticosterone level	
Independent Variables	Road Surveys	Trail and Off-trail surveys	Distance from Road	Numbers of Elk observed	Random elk	Collared elk
Daily vehicles entering West Yellowstone gate	-0.001					<0.000
Wheeled vehicles (vs. over-snow vehicles)		n/a				0.073
Exposure to >7500 cumulative vehicles (vs. <7500)			0.115		0.045	0.088
Cumulative season days	-0.007				-0.001	
1999-2000 (vs. 1998-1999)	0.399				-0.042	-0.206
West Yellowstone to Old Faithful (vs. Madison Junction to Norris)	0.372	n/a	0.225	-0.125	0.058	0.05
Number in group	-0.060		0.015	n/a	n/a	n/a
Meters from road	-0.007	n/a	n/a	n/a	n/a	n/a
Human activity near group of elk		n/a	n/a	n/a	n/a	n/a
Meters from humans	n/a	-0.749	n/a	n/a	n/a	n/a
Human off-trail (vs. on trail)	n/a	4.395	n/a	n/a	n/a	n/a
Snow water equivalent	n/a	n/a				-0.005
Average daily temperature	n/a	n/a	n/a	n/a		-0.008
Age	n/a	n/a	n/a	n/a	n/a	0.009

The model for elk log 10 distances from road (adjusted $R^2 = 0.074$; Table 2) indicated elk were sighted further from West Yellowstone to Old Faithful road segments (least squares mean = 2.01) than along the road from Madison Junction to Norris (least squares mean = 1.78; partial regression, $t_{876} = 6.25$, $P < 0.001$) and with larger group sizes ($t_{876} = 5.66$, $P < 0.001$). This model also showed that elk were further from the road after >7500 cumulative vehicles passed through the West Entrance gate (least squares mean = 1.94), given all the other variables in the model (<7500 cumulative vehicles least squares mean = 1.86; $t_{876} = 1.69$, $P = 0.092$). Coefficients, standard errors, and P-values can be found in Appendix 1.

To summarize these results focusing on anthropogenic variables of interest, bison numbers and distribution in relation to the road were not influenced by levels or types of winter recreation in the study area. Fewer elk were observed at greater distances along the busier road segment from West Yellowstone to Old Faithful compared to the road segment from Madison Junction to Norris, and elk were distributed further from the road after >7,500 cumulative vehicles had entered the West Yellowstone gate.

Elk and Bison Behavior

I recorded behavioral observations of 1812 bison and 877 elk groups during road surveys and 377 bison and 220 elk groups during 309 km of trail and 228 km of off-trail surveys throughout the entire study. The total proportions of no apparent response, look/resume, attention/alarm, amble away, and flight observations were plotted against categorical levels of OSVs that entered the West Yellowstone gate as an index of trends

related to increasing winter public visitation (Figures 6 and 7). Bison rarely responded to

human activity along roads. Elk responded more often than bison to human activity
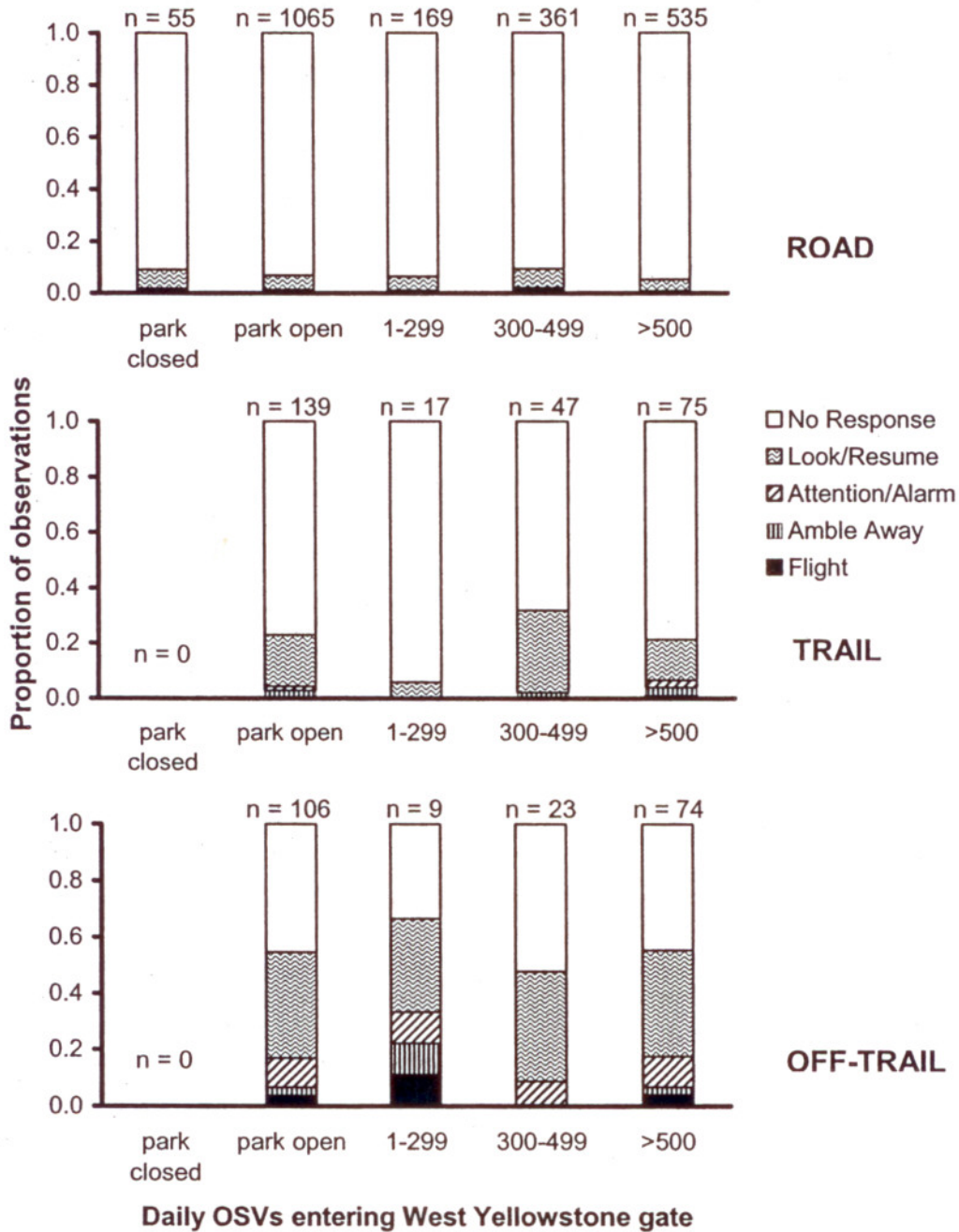
Figure 6. Bison behavioral responses to human presence and activity recorded during road, trail, and off-trail surveys conducted throughout the 1998—1999 and 1999—2000 over snow vehicle (OSV) seasons in the upper Madison drainage of Yellowstone National Park. Human presence (x-axis) was categorized into periods when the park was closed to the public compared to when the park was open to public OSV travel, and when 1-299, 300-499, and >500 daily OSVs entered the study area via the West Yellowstone gate.
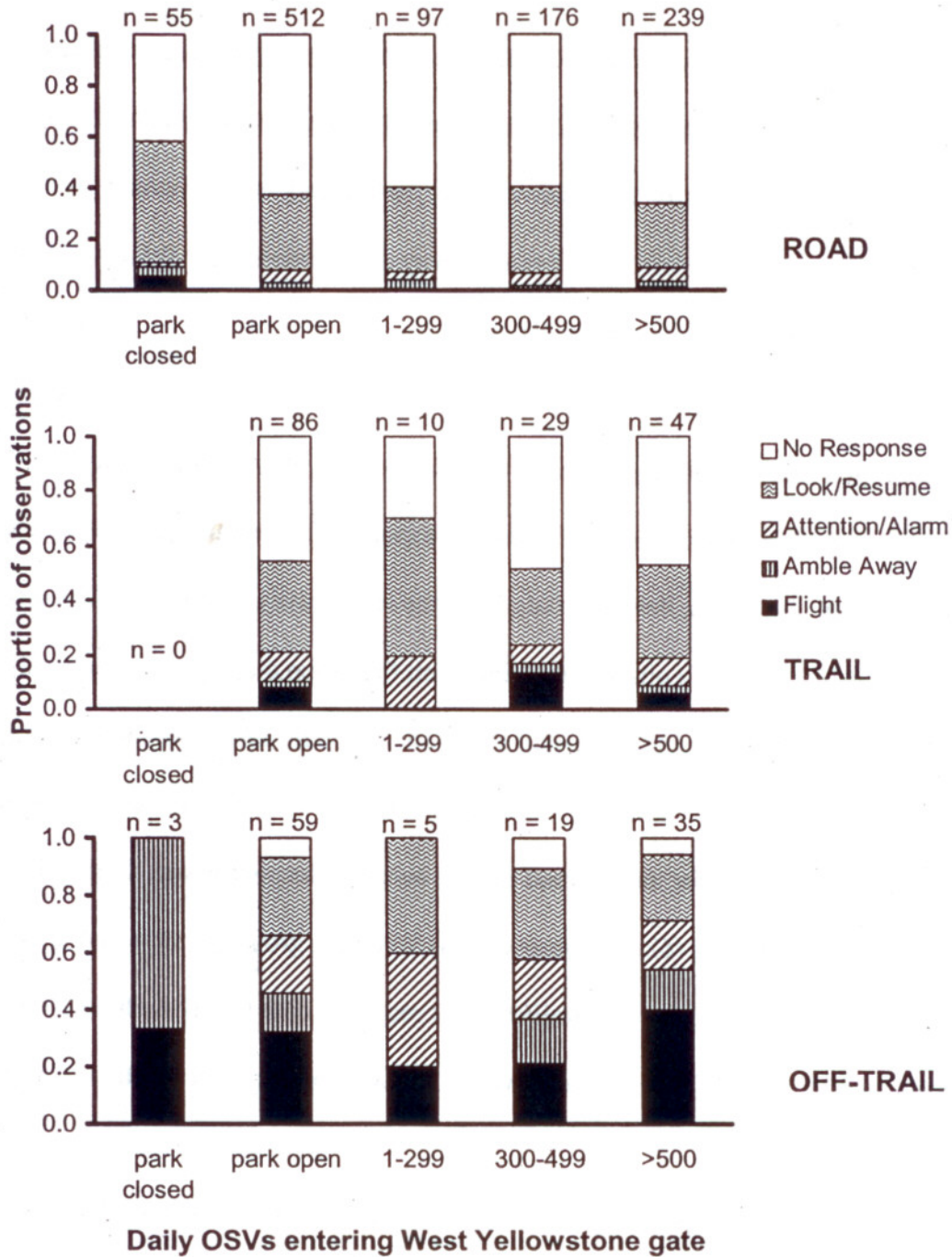
Figure 7. Elk behavioral responses to human presence and activity recorded during road, trail, and off-trail surveys conducted throughout the 1998—1999 and 1999—2000 over snow vehicle (OSV) seasons in the upper Madison drainage of Yellowstone National Park. Human presence (x-axis) was categorized into periods when the park was closed to the public compared to when the park was open to public OSV travel, and when 1-299, 300-499, and >500 daily OSVs entered the study area via the West Yellowstone gate.

along the roads, but most of the road observations for elk were no apparent response. The proportion of elk no apparent response observations along the road was lowest during periods of park closure. Elk and bison exhibited a higher proportion of look/resume, attention/alarm, amble away, and flight behavioral responses during trail and off-trail surveys compared to the road survey observations. Elk almost always responded to some degree to people off-trail.

I divided the behavioral response data to create a binary response variable for logistic regression by pooling the look/resume, attention/alarm, amble away, and flight responses together and coding all of these as responses (1), versus the no apparent responses (0). For bison, behavior data from the road surveys included 157 responses (8.7%) and 1655 (91.3%) observations in which the group displayed no apparent response. For the pooled trail/off-trail survey data, the response variable included 135 (37.4%) events and 226 observations (62.6%) coded as no apparent reaction for bison. The response variable for the elk road survey behavior responses was divided in to 331 (37.7%) events and 546 (62.3%) observations when the group displayed no apparent reaction to humans. The pooled trail/off-trail response data for elk included 109 (49.5%) events and 111 (50.5%) observations when there was no apparent reaction to human presence and activity.

The reduced logistic regression models, composed only of statistically significant variables ($P \leq 0.10$) from the full model, provided the best model of strength (P-value) and association (coefficient sign) of non-anthropogenic and anthropogenic variables to behavioral responses of bison (Table 1) and elk (Table 2) in the study area. The road data

model achieved 85.6% concordance and indicated bison responded more often when groups were closer to roads ($P < 0.001$) and when there were fewer animals in the group ($P < 0.001$). Bison responded less often when the numbers of daily vehicles entering the West Yellowstone gate increased ($P = 0.001$). The trail and off-trail behavior model had a 79.7% concordance and showed that bison responded more often in 1999—2000 than in 1998—1999 ($P = 0.043$), with fewer animals in the group ($P = 0.004$), when bison were closer to human activity ($P < 0.001$), and when people were off-trail vs. on trail ($P < 0.001$).

The elk road behavior response model, with 73.9% concordance, revealed elk responded to human presence and activities more often when the group was closer to the road ($P < 0.001$), when there were fewer animals in the group ($P = 0.001$), later in the winter ($P < 0.001$), and in 1999—2000 than in 1998—2000 ($P = 0.013$). Elk exhibited responses along the road from West Yellowstone to Old Faithful more often than from Madison Junction to Norris ($P = 0.023$), and responded less often as the numbers of daily vehicles entering the West Yellowstone entrance gate increased ($P = 0.001$). The trail and off-trail behavioral response model achieved 87.8% concordance and indicated elk responded more often when closer to human activity ($P < 0.001$) and when human activity was off-trail vs. on trail ($P < 0.001$). Coefficients with standard errors and P-values for variables in the full and reduced elk and bison behavior models can be found in Appendix 2 & 3.

Using calculated probabilities of behavioral responses for bison and elk from the logistic regression models for road survey data, I plotted the probability of behavioral

responses against categorical levels of daily OSVs entering the West Entrance gate

(Figure 8). These plots show the highest probabilities of behavioral responses occurred

when the park was closed and the lowest probabilities of behavioral responses occurred

after more than 500 OSVs entered the West Entrance on a given day, given all the

variables used the model.

To summarize elk and bison behavioral responses to anthropogenic variables

included in these analyses, elk responded behaviorally more often along the busier road

segment between West Yellowstone and Old Faithful than between Madison Junction

and Norris, which had less than half the traffic. At the same time, the models indicated

both bison and elk were less likely to respond behaviorally as the daily number of

vehicles entering the West Entrance gate increased. Bison and elk responded less often

to people on trail than to people off-trail.
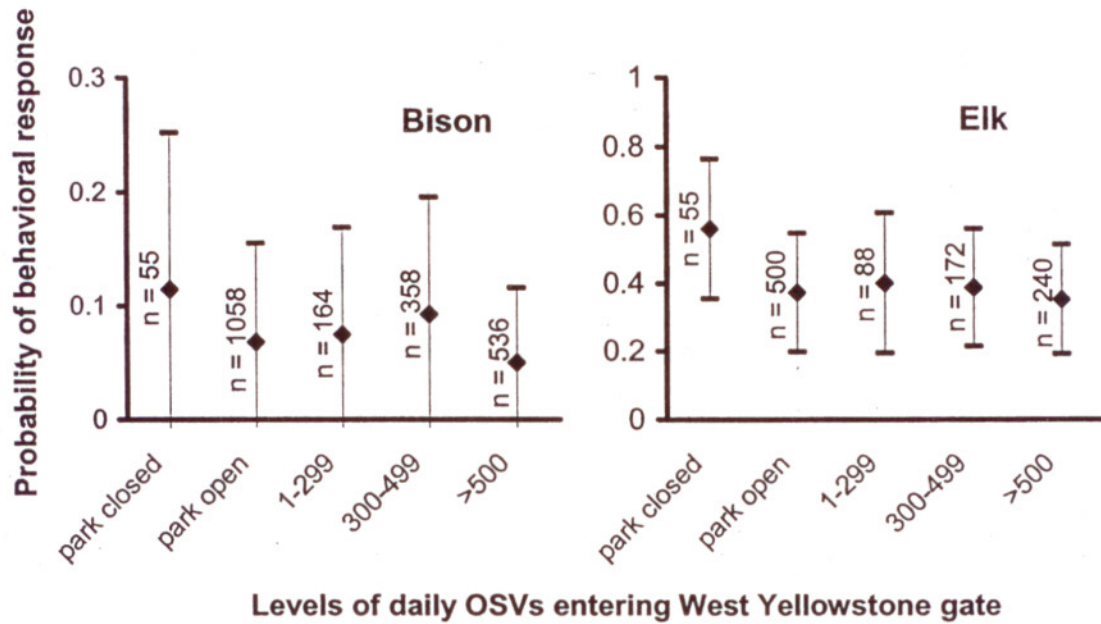
Figure 8. Probabilities (mean ± SD) of bison and elk behaviorally responding to human presence and activity during the oversnow vehicle (OSV) winter seasons of 1998—1999 and 1999—2000 in the upper Madison River drainage of Yellowstone National Park. The probabilities, derived from the logistic regression analyses of road survey observational data, are plotted against levels of OSVs entering the West Yellowstone, Montana, entrance gate, and included comparison of when the park was closed to the public compared to when the park was open to public OSV travel, and when 1-299, 300-499, and >500 daily OSVs entered the study area via the West Yellowstone gate.

Fecal Glucocorticoid Sampling

I collected a total of 355 fecal samples from radiocollared cow elk, 632 fecal samples from unknown elk, and 473 fecal samples from unknown bison. Elk FGC levels ranged from 35 to 627 ng/g dry feces. Mean FGC for unknown elk was 200 ng/g dry feces (SD = 85) while the average for the collared elk samples was 214 ng/g dry feces (SD = 89; overall range: 35–627 ng/g dry feces). Mean bison FGC (range: 256–5463 ng/g dry feces) was 860 ng/g dry feces (SD = 421). I plotted bison and elk FGC levels

(mean ± SD) against daily levels of OSVs entering the West Entrance gate (Figure 9); these plots did not reveal any obvious trends indicating OSV levels affect elk and bison stress hormone levels.

The bison FGC analysis suggested 4 variables contributed significantly to FGC responses ($P \leq 0.10$; Table 1). Bison log 10 FGC levels were higher in 1998—1999 than in 1999—2000 (partial regression, $t_{464} = -2.89$, $P = 0.004$), earlier than later in the winter ($t_{464} = -2.09$, $P = 0.037$), and when SWE levels were lower ($t_{464} = -1.82$, $P = 0.069$). After controlling for these effects, bison log 10 FGC levels were higher when WVs were present (least squares mean = 3.01) than when OSV were present (least squares mean = 2.84; $t_{464} = -3.39$, $P = 0.001$). The bison model yielded a low adjusted $R^2 = 0.077$, and the random elk model also had a low adjusted $R^2 = 0.087$ (Table 2). The FGC levels for random elk were higher in 1998—1999 (least squares mean = 2.27) than in 1999—2000 (least squares mean = 2.21; partial regression, $t_{612} = -2.10$, $P = 0.037$) and as the season progressed ($t_{612} = -2.30$, $P = 0.022$). Beyond these non-anthropogenic effects, log 10 FGC levels for random elk were higher after >7,500 cumulative vehicles (least squares mean = 2.25) entered the West Yellowstone gate (least squares mean for <7,500 cumulative vehicles = 2.22; $t_{612} = 1.95$, $P = 0.051$) and on the road segment from West Yellowstone to Old Faithful (least squares mean = 2.27) than from Madison Junction to Norris (least squares mean = 2.21; $t_{612} = 3.75$, $P < 0.001$).
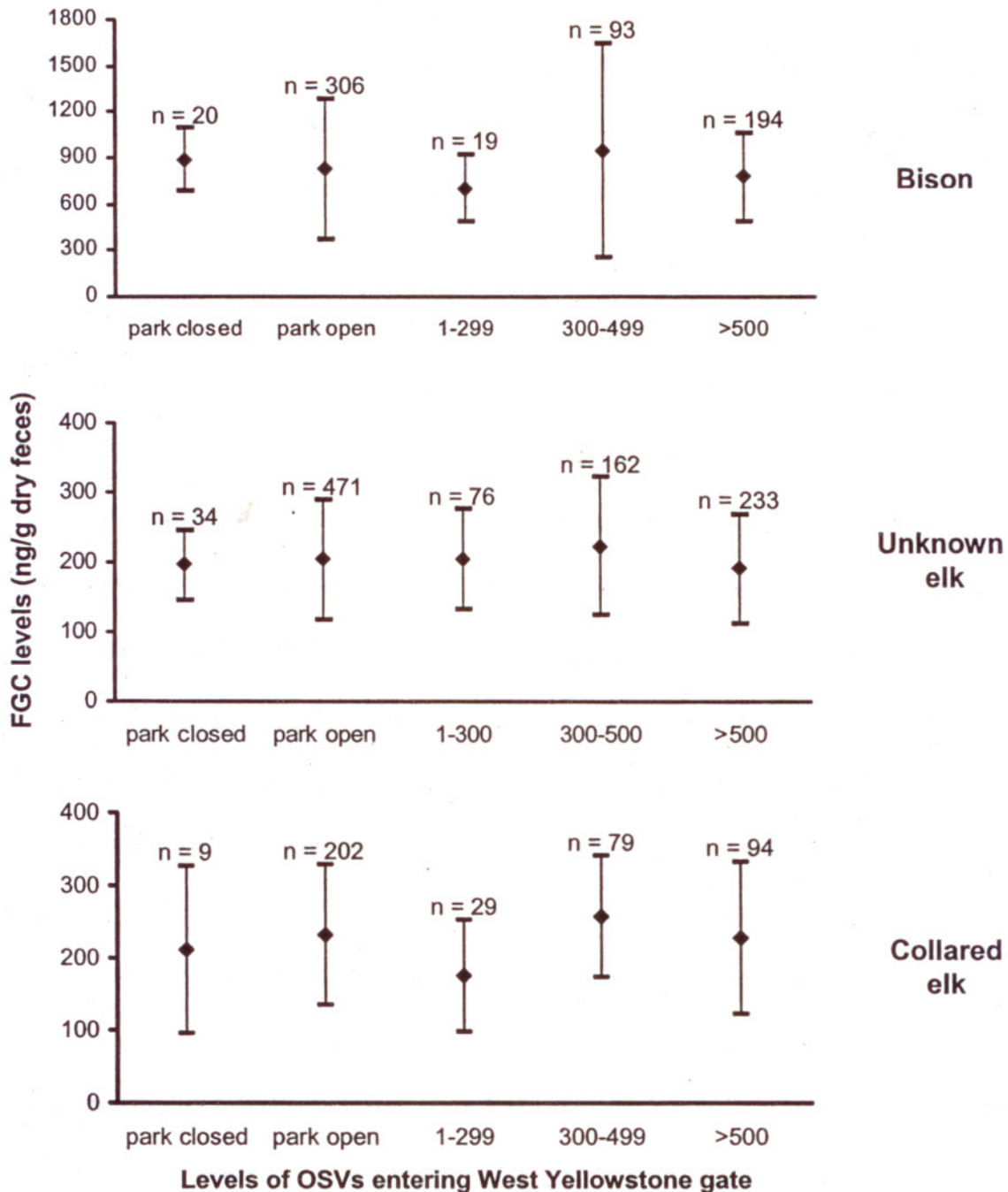
Figure 8. Unknown bison and elk and collared elk fecal glucocorticoid (FGC) levels (mean ± SD) plotted against levels of oversnow vehicles (OSVs) entering the upper Madison drainage through the West Yellowstone entrance gate during the 1998—1999 and 1999—2000 winter seasons in Yellowstone National Park. Levels of OSVs were categorized into periods when the park was closed compared to when the park was open to public OSV travel, and when 1-299, 300-499, and >500 daily OSVs entered the study area via the West Yellowstone gate.

With the ability to control for age and sex, the collared elk FGC model achieved an adjusted $R^2 = 0.372$ with 8 variables significantly ($P \leq 0.10$) contributing to the log 10 FGC response variable (Table 2). Collared cow elk FGC levels increased with age (partial regression, $t_{333} = 3.53$, $P < 0.001$) and colder temperatures ($t_{333} = -4.88$, $P < 0.001$) and decreased as SWE increased ($t_{333} = -2.22$, $P = 0.027$). Log 10 FGC levels in collared elk were lower in 1999—2000 (least squares mean $= 2.18$) than in 1998—1999 (least squares mean $= 2.39$; $t_{333} = -4.88$, $P < 0.001$). After controlling for these variables, FGC levels were higher with greater numbers of daily vehicles ($t_{333} = 1.91$, $P = 0.057$), after >7,500 cumulative vehicles (least squares mean $= 2.33$) entered the West Yellowstone gate than "low" exposure periods (<7,500 cumulative vehicles least squares mean $= 2.24$; $t_{333} = 3.14$, $P = 0.002$), and along the road segments from West Yellowstone to Old Faithful (least squares mean $= 2.31$) compared to the road from Madison Junction to Norris (least squares mean $= 2.26$; $t_{333} = 2.91$, $P = 0.004$). Our model indicated that log 10 FGC levels were higher when WVs were present (least squares mean $= 2.32$) vs. when OSVs were present (least squares mean $= 2.24$; $t_{333} = 2.91$, $P = 0.004$), given all the other variables in the model. Coefficients with standard errors and P-values for variables in the elk and bison FGC models can be found in Appendix 4.

To summarize, the FGC analysis did not detect significant impacts of winter recreation activity on bison FGC levels. Unknown elk FGC levels were higher after exposure to >7500 vehicles and residing along the busier road segment from West Yellowstone and Old Faithful although the unknown elk FGC data did not distinguish a difference between OSVs and WVs. Collared cow elk FGC levels increased after >7500

cumulative vehicles and with increasing daily numbers of vehicles passing through the

West Yellowstone gate. Collared cow elk between West Yellowstone and Old Faithful

had higher FGC levels than collared cow elk between Madison Junction and Norris.

Given all the other variables in this model, the two year dataset of collared elk FGC

levels indicated FGC levels were higher when WVs were present than when OSVs were

present.

DISCUSSION

Craighead, et al. (1973) and Meager (1973) emphasized the influence of geothermal areas and warm streams in providing winter range to wildlife in the Upper Madison River drainage of YNP. Aune (1981) documented concentrated wildlife distribution in the 5,608 hectares of core winter range due to increased food availability and reduced energetic demands. This core winter range was concurrently shared with winter recreation activities and resulted in inhibited wildlife movements and temporary displacement of wildlife near trails during periods of heavy traffic (Aune 1981). Overall, though, Aune (1981) concluded that wildlife habituated to the presence and patterns of human activity in the upper Madison River drainage of YNP (Aune 1981). This study documented twice as much winter visitation as Aune's (1981) study. Despite the increased exposure to OSVs, bison and elk have continued, over the years and throughout this study, to utilize this same core winter range, overlapping with winter recreation similar to 20 year ago.

Bison distribution in the study area did not appear to be influenced by winter recreation activities or levels. Fewer elk were observed at greater distances along the West Yellowstone to Old Faithful road segment with heavier traffic. These results indicated by the elk distribution models may be due to sampling bias as detectability typically decreases as distance increases (Buckland et al. 1993). Differences in topography and forest cover between the West Yellowstone to Old Faithful area versus the Madison Junction to Norris area may have contributed to fewer elk sighted at greater

distances from the West Yellowstone to Old Faithful road. Displacement of elk due to the presence of large groups of bison and the Nez Perce wolf pack along the route to Old Faithful (Jaffe 2001) may also have played a role in displacing elk away from the West Yellowstone to Old Faithful road. Beyond these considerations, the results of the elk distribution models may indicate increased traffic displaced elk. Elk were further from all study area roads after >7,500 cumulative vehicles had entered the West Yellowstone gate, another indicator that elk were displaced in response to greater cumulative amounts of traffic, although the analysis did not detect a difference in elk distributional responses during the OSV season compared to the WV season. Aune (1981) found temporary displacement of wildlife was within 60 m from roads and trails and amounted to approximately 972 hectares (17%) of the total core winter range. Dorrance et al. (1975) documented white-tailed deer exposed to heavy snowmobile traffic on the weekends and lighter snowmobile traffic during week days were sighted near trails less often on days with higher snowmobile traffic volumes (Dorrance et al. 1975). Despite this response, these deer returned to the areas they had fled after several hours and home range size, movement, and activity were not measurably affected. Habituation may facilitate temporary displacement as opposed to complete abandonment of suitable habitat, but during severe winters, even the smallest displacement and loss of habitat could be detrimental to wildlife survival (Dorrance, et al. 1975, Aune 1981).

Elk exposed to more traffic along the West Yellowstone to Old Faithful road were more behaviorally sensitive than elk between Madison and Norris, similar to the distribution model results. Again, the presence of wolves, interspecific competition with

bison, and differences in vegetative cover and topographic characteristics between these two road segments may play roles in this outcome. Flight responses of ungulates have been observed to be dependent on whether or not the animal was in dense vegetative cover or not (Richens and Lavigne 1978). Perhaps displacement of elk along the West Yellowstone to Old Faithful road decreased exposure to the predictable route and regular timing of traffic that is key to the habituation learning process (Eibl-Eibesfeldt 1970). But even as both elk and bison throughout the study area behaviorally responded less often as exposure to daily traffic increased, elk along the busier road segment appeared to be more behaviorally sensitive than elk along the road segment with less traffic.

Opportunities for visitors to walk on boardwalks and trails in the geyser basins near the road are more abundant along the route from West Yellowstone to Old Faithful compared to the Madison to Norris route. Bison and elk in the upper Madison River drainage of YNP were most behaviorally sensitive to human activities off-trail, then to human activities on trails. Human activities occurring on the road incurred the smallest proportion behavioral responses. Off-trail travel was relatively uncommon compared to people following established routes, and even though off-trail travelers do not typically intend to threaten wildlife, this unpredictable and infrequent activity usually startles animals (Lyon and Ward 1982, MacArthur et al. 1982, Singer and Beattie 1986, Cassirer et al. 1992, Papouchis et al. 2001). Human activities occurring repeatedly and restrictedly to predictable routes such as trails and boardwalks can moderate animal responses to these activities (Papouchis et al. 2001), but with this said, ungulates tend to display more disturbance reactions toward people on foot compared to people on

snowmobiles (Richens and Lavigne 1978, Aune 1981) or in automobiles (Cassier et al. 1992, Papouchis et al. 2001). Although the difference in elk behavioral responses between the West Yellowstone to Old Faithful and the Madison Junction to Norris routes was detected in the road survey data analysis, it is possible that the greater exposure to human activities afoot along the West Yellowstone to Old Faithful route may have contributed to the increased level of elk behavioral responses compared to the Madison Junction to Norris route.

Not surprisingly, the closer bison and elk were to any type of human activity, including vehicular travel on roads, the more likely they were to behaviorally respond. Bjornlie and Garrott (2001) studied bison use of the groomed road system in the upper Madison River drainage and documented 60% of the encounters between bison and OSVs when bison were traveling on the groomed snow roads resulted in negative reactions. The depth of the analyses conducted for my study did not incorporate the quantification of wildlife-human interactions on the roadway specifically, but I occasionally observed animals being moved by vehicles along extended distances of road or into deep snow off the road in order to avoid the activity. Aune (1981) documented similar instances, but recognized wildlife habituated to OSV activity outside of direct interactions that typically occurred on roads or with off-trail human activities. Studies have shown deer habituate to snowmobiles but will respond to the activity when in the immediate vicinity of snowmobile trails (Bollinger et al. 1973, Dorrance et al. 1975, Eckstein et al. 1979). Richens and Lavigne (1978) found that in early winter, white-tailed deer ran from snowmobiles encountered while traveling on trails more often

compared to later in the winter either as a function of depleted physical condition that arises as the winter proceeds or deer habituation to snowmobiles. I detected no seasonal trend in elk responses to OSV traffic, but did find that bison and elk behavioral responses diminished as daily levels of vehicular traffic increased. Similar to the distribution analysis, I did not detect differences in either bison and elk behavioral responses comparing periods of OSV travel to periods of WV travel.

The only statistical difference between periods of OSV and WV travel was revealed in the bison and collared cow elk FGC data. These data indicated bison and collared cow elk stress levels were higher during periods of WV travel than during periods of OSV travel. With no other variables related to winter recreation contributing significantly to bison stress levels, bison stress levels did not appear to respond to winter recreation activity. Higher stress levels detected during periods of WV travel occurred during the transition from late winter to early spring, when animal energetic reserves are at their lowest. As snowpack recedes, forage availability increases along the bottom of the valleys and bison and elk congregate in these open meadows along the roads (Bjornlie and Garrott 2001). Inter- and intra-specific competition in these meadow areas, physiological depletion (Wingfield and Ramenofsky 1999), and closer proximity to WV traffic may contribute to higher FGC levels in bison and elk compared to the OSV season. The latter two explanations are less viable considering the FGC analyses included a variable to detect cumulative seasonal effects and the distribution analyses failed to detect statistical evidence of a difference between the OSV and WV seasons. Another possible explanation may be that people are more prone to leave the road as the

snow recedes and bison and elk may perceive this as novel and unpredictable human activity to which they have not habituated.

Using both seasons' collared cow elk FGC data, I detected higher stress levels during periods of exposure to WVs, but using only the 1998—1999 collared cow elk FGC data from this study, Creel et al. (2001), found the opposite: higher stress levels correlated with exposure to OSVs rather than WVs. Creel et al. (2001) cautiously interpreted this result due to the small number of samples from the WV period (n = 14) compared to the sample size from the OSV period (n = 111), but statistical significance was achieved. For this study, I pooled the data from both years of the study to obtain generalized results and employed additional variables that the Creel et al. (2001) analysis did not include. For those reasons, the Creel et al. (2001) analysis is not directly comparable to results from this study. But I contend the difference in SWE between the two years, with an above average SWE year in 1998—1999 and below average SWE year in 1999—2000, offers a compelling explanation for the different outcomes in collared elk FGC responses to the different vehicle types. That difference leads me to consider that in winters with heavier snowpack, elk FGC levels may be more sensitive to OSV stimuli. The Creel et al. (2001) analysis found that FGC levels increased as SWE increased during the 1998—1999 season while this study found the opposite effect, which does not make biological sense. Again, the pooling of the 2 years of different data may account for this discrepancy.

Controlling for age and sex in the collared cow elk FGC data analysis resulted in our best predictive model and revealed that cow elk FGC levels increased when daily

traffic entering the West Yellowstone gate increased, a parallel finding to the Creel et al. (2001) analysis. Following trends seen in the distribution and behavior analyses, unknown elk and collared cow elk stress levels were higher from West Yellowstone to Old Faithful compared to the Madison Junction to Norris route. The non-anthropogenic considerations listed previously might contribute to the higher stress levels in elk along the West Yellowstone to Old Faithful road, or it may also be due to the higher levels of traffic on that route. Throughout the entire study area, unknown and collared elk FGC levels were higher after >7,500 cumulative vehicles entered the study area through the West Yellowstone gate.

To summarize, bison and elk behaviorally habituated to increased traffic, tempered by the fact that close proximity to any human activity provoked behavioral responses. Elk in the upper Madison River drainage study area are non-migratory due to the availability of year-round habitat. The incentive of available food, in conjunction with frequent and predictable patterns of vehicular traffic without direct negative impacts such as human hunting pressure, may induce elk habituation to the human activity on the roads. But elk responses along roads with higher traffic volumes may indicate limits to elk habituation. Elk along the busiest winter road in the park appeared to be displaced to some degree, behaviorally responded more often, and had higher FGC levels than elk residing along the road segment that comparatively has half the amount of traffic. Elk physiological responses increased with increased exposure to vehicle stimuli.

It is important to put these statistical results into a biological context. First, I point out that the distribution models and the models for unknown bison and elk FGC

levels yielded low R^2 values, suggesting these model's statistically significant variables may have little biological consequence overall. But statistical significance in complex ecological studies with little or no control over variables is difficult to achieve, therefore I do not abandon the interpretation of statistically significant anthropogenic effects. The fundamental biological question is, how do these anthropogenic influences on bison and elk populations influence their fitness and survival? Recreational activities can cause immediate changes in wildlife behavior, which can result in long-term effects such as altered vigor, productivity, demographics, abundance, distribution, survivorship, and changes in community species composition and interactions (Knight and Cole 1995), and chronic stress responses can subsequently affect resistance to disease, survival, and reproductive output (Sapolsky 1992). Bison abundance estimates from this study indicated bison wintering in the study area have increased since Aune's (1981) study. Even with the presence of wolves in the study area since 1996 (Jaffe 2001), elk abundance estimates in the study area appear to be relatively stable over the past 30 years. These abundance estimates indicate that despite increases in winter recreation since its inception, and despite detectable elk responses to OSVs, any biological effects due to anthropogenic influences are currently being compensated for at the population level.

Characteristics of human activity such as the timing, predictability, frequency, magnitude, and location, as well as abiotic factors such as topography, vegetation and weather, can have varying effects on wildlife (Richens and Lavigne 1978, Aune 1981, Knight and Cole 1995). Wildlife may become conditioned to human activity when the

activity is controlled and predictable and does not harm the animals (Schultz and Bailey 1978, Mace and Waller 1996, Thompson and Henderson 1998). Habituation occurs when an animal learns passively to refrain from responding to repeated stimuli that are biologically unmeaningful to the animal (Eibl-Eibesfeldt 1970). For the most part, OSVs traveled through the study area in predictable and regular fashion, confined to roads, typically without humans threatening or harassing elk and bison. Compared to the amount of activity on the roads, few people ventured far from trails and areas of human activity. These characteristics of winter recreation in YNP facilitated habituation in wintering bison and elk to OSV traffic. In contrast, human activity on trails, and off-trail activities induced behavioral responses in both bison and elk. While bison and elk exhibited responses to winter recreation, winter recreation in YNP is coexisting with wintering bison and elk without causing declines in population levels.

MANAGEMENT IMPLICATIONS

The road that accommodates the greatest amount of OSV traffic traverses important wildlife winter habitat. Because of this, winter recreation activities should be conducted in a contained and predictable manner to allow animals to habituate to the human presence and activities. Because bison and elk behaviorally respond to people deviating from known, predictable routes, management measures that encourage visitors to stay on roads and established trails will reduce wildlife disturbance rates.

The collection of fecal samples to conduct radioimmunoassays analysis of FGC steroid hormone levels has been shown to be an effective, non-invasive method to measure physiological stress (Ostovar 1998, Millspaugh 1999). The indication that elk FGC levels increased with increasing levels of traffic provides a reminder that non-observable physiological responses to human activity do occur and have the potential to undermine the overall health of species that are sensitive to increased stimuli. While the levels of winter recreation witnessed during this study did not appear to induce a chronic stress response in elk, it is feasible that elk FGC levels could increase if winter visitation were to continue to increase. Long-term monitoring of bison and elk FGC levels may help to detect variables and thresholds that induce a chronic stress response. This study did not measure bison and elk calf stress hormone levels. However this may be a more sensitive indicator of stress in the population, and increased stress levels in this segment of the population could possibly lead to reduced recruitment. I recommend that

management consider employing an FGC monitoring program that specifically monitors for cows and calves to watch for changes in stress hormone responses that may be a result of winter use management changes. This effort could concurrently contribute to the field of stress physiology and guide the NPS in decision-making processes that might affect bison and elk exposure to anthropogenic stimuli.

The results of this study may not be applicable to other species or other locations. This study focused only on two of the most abundant and visible species in YNP. Their relative ubiquity in the study area may indicate a higher tolerance of human activity compared to other populations beyond this study area, or other species in the study area or elsewhere. Wolves, coyotes, ravens, eagles, trumpeter swans, various duck species, and even grizzly and black bears are all examples of animals that may be affected by winter use management in YNP. The NPS should consider further studies on other species that share habitat with winter recreationists.

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