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BEHAVIORAL RESPONSES OF BISON AND ELK IN YELLOWSTONE TO SNOWMOBILES AND SNOW COACHES

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Abstract. Managers of public lands are charged with protecting some of our most important natural resources and ecosystems, while providing for their use and enjoyment by visitors. Almost one million visitors entered Yellowstone National Park by motorized means on snowmobiles (87%) or snow coaches (13%) during 1992–2003. Most vehicles toured the central portion of the park where bison (*Bison bison*) and elk (*Cervus elaphus*) concentrate in geothermal areas. We sampled >6500 interactions between groups of these species and groups of snowmobiles and snow coaches (collectively, OSV, over-snow vehicles) during five winters (1999–2000, 2002–2004). Multinomial logits models were used to identify conditions leading to behavioral responses. Elk responded three times as often (52%) as bison (19%) during interactions with groups of snowmobiles and snow coaches due to increased vigilance responses (elk, 44%; bison, 10%). However, the frequency of higher-intensity movement responses by bison and elk were similar (6–7%, travel; 1–2%, flight; <1%, defense) and relatively low compared to other studies of ungulates and snowmobile disturbance. The likelihood of active responses by bison and elk increased significantly if animals were on or near roads, groups were smaller, or humans approached. The likelihood of an active response by bison decreased within winters having the largest visitation, suggesting some habituation to snowmobiles and snow coaches. There was no evidence snowmobile use during the past 35 years affected the population dynamics or demography of bison or elk. Thus, we suggest that regulations restricting levels and travel routes of over-snow vehicles (OSVs) were effective at reducing disturbances to bison and elk below a level that would cause measurable fitness effects. We recommend park managers consider maintaining OSV traffic levels at or below those observed during our study. Regardless, differing interpretations of the behavioral and physiological response data will continue to exist because of the diverse values and beliefs of the many constituencies of Yellowstone.

Key words: Akaike information criterion (AIC); behavior; bison; Bison bison; Cervus elaphus*; elk; multinomial logits regression; recreation; snowmobile; winter; Yellowstone National Park, USA.*

INTRODUCTION

Public lands protect some of our nation's most important natural resources and ecosystems that, in turn, attract millions of visitors annually for recreational activities. Thus, managers of these lands are essentially charged with conserving resources, while providing for their use and/or enjoyment by people (e.g., National Park Service Organic Act of 1916; 16 USC 1, 2–4). Recreation may disrupt ecological processes by disturbing wildlife and resulting in altered interspecific interactions, increased energetic costs, changes in behavior and fitness, and avoidance of otherwise suitable habitat (Boyle and Sampson 1985, Knight and Cole 1995). Thus, management policies for public lands must address the effects of recreation on wildlife and other resources to ensure that the integrity of the resources, and ecosystem processes on which they depend, are not harmed. The use of reliable science to obtain a thorough understanding of the resources, ecological processes, and human-related effects is an essential prerequisite for developing these policies (Parsons 2004).

The history of winter recreation in Yellowstone National Park (Yellowstone) illustrates the difficulty of balancing the trade-off between access and recreation-related effects. Snowmobiles were first used in Yellowstone during 1949, but regular use did not occur until the 1960s and 1970s (Yochim 1998). Private snowmobiles (1000 total) entered the park for the first time in 1963–1964, and park staff began grooming snow-covered roads in 1971 to facilitate the safe passage of snowmobiles (Aune 1981, Yochim 1998). Winter recreation and snowmobile use increased dramatically in the following decades and >140 000 riders per year entered Yellowstone during the early 1990s (Yochim 1998, Gates et al. 2005).

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Not surprisingly, a conflict arose between protecting park resources and the desires of many visitors to experience the park via snowmobile. During the severe winter of 1997, >1000 bison left the park and were killed to prevent the potential spread of brucellosis to livestock. Some of these bison left the park by traveling along roads groomed for over-snow use. This event prompted several plaintiffs to file suit, alleging that the National Park Service failed to adequately consider the effects of road grooming on bison distribution and movements and the effects of snowmobiling on the behavior, distribution, and energetics of wildlife (National Park Service, U.S. Department of the Interior 2000). A lack of rigorous empirical studies to evaluate the merits of these claims (District of Columbia 2003) has resulted in conflicting legal decisions and corresponding reactive changes in winter recreation regulations (National Park Service, U.S. Department of the Interior 2004).

Our research was designed to address one aspect of the controversy regarding winter recreation in Yellowstone, the behavioral responses of bison and elk to snowmobiles and snow coaches (collectively referred to as over-snow vehicles; OSVs). Separate analyses address the effects of road grooming on bison distribution and movements (Bruggeman et al., *in press*; J. E. Bruggeman, R. A. Garrott, P. J. White, F. G. R. Watson, R. Wallen, *unpublished manuscript*). Our specific objectives were to (1) quantify human activities associated with OSVs, (2) quantify the responses of bison and elk to OSVs, and (3) identify conditions that increase the likelihood of behavioral responses by bison and elk to OSVs.

STUDY AREA

We conducted our study along road segments throughout the central portion of Yellowstone National Park, which has been previously described by Despain (1990). However, >90% of observed interactions between groups of OSVs and groups of bison or elk occurred in the upper Madison River drainage in the west-central portion of the park. Thus, we focused the study area description on the winter range for bison and elk in this area, as defined by rigorous ground and aerial surveys during 1991–2004 (Bjornlie and Garrott 2001, Hess 2002, Garrott et al. 2003). This range encompassed 27 000 ha along the Firehole, Gibbon, and Madison rivers between the Norris geyser basin, Old Faithful, and West Yellowstone, Montana. Physiography was dominated by these drainages, with extensive meadows along the valley bottoms (Despain 1990). Large-scale fires during 1988 burned 55% of these drainages, creating a complex mosaic of burned and unburned forests at different stages of succession (Romme and Despain 1989). Major geyser basins at Midway, Norris, and Old Faithful, along with many smaller geothermal areas interspersed, 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). Elevations ranged from 2250 to 2800 m and snow depths typically exceeded 91 cm in non-geothermal areas. These deep snows drastically reduced food availability and produced severe energetic bottlenecks for herbivores during the winter (Craighead et al. 1973, Garrott et al. 2003). Snow pack typically began to accumulate in November, peaked in April, and melted off in May. Peak snow water equivalent values for the Madison Plateau SNOTEL site were 36.6 cm in 1999, 19.9 cm in 2000, 39.1 cm in 2001, 24.0 cm in 2002, 20.5 cm in 2003, and 25.0 cm in 2004. Thus, snow pack during our study was relatively high in 1999 and 2001 compared to the 37-year average of 26.6 cm, within 10% of average in 2002 and 2004, and below average during 2000 and 2003. Ambient temperatures were moderate in winters 1999–2004, with minimum daily temperatures during December through April ranging from −38° to −31°C at the Madison Plateau SNOTEL site and −42° to −36°C at the West Yellowstone SNOTEL site.

The west-central Yellowstone system had a relatively simple faunal complex, with only two abundant ungulate species (i.e., bison, elk) and two large predators (i.e., grizzly bears, wolves). Approximately 1000–1500 bison from the migratory central Yellowstone herd wintered in the area (Hess 2002). The nonmigratory central Yellowstone elk population consisted of ~300–600 elk during our study (Garrott et al. 2003) and remained within the borders of the park throughout the year (Craighead et al. 1973). Grizzly bears (*Ursus arctos*) were seasonally common during spring and autumn. Wolves (*Canis lupus*) became established during 1998 and four packs totaling ~40 wolves completely occupied the area by winter 2004. Black bears (*U. americanus*) and coyotes (*Canis latrans*) also occurred in the area, but were not significant predators on adult bison or elk (Garrott et al. 2003).

Human activity in the upper Madison River drainage occurred in a predictable pattern. Vehicular travel was restricted to paved, two-lane roads between the West Entrance Station and Madison Junction (22 km), Madison Junction and Norris Junction (22 km), and Madison Junction and Old Faithful (26 km). These roads were closed to public access on 1 November each year, and wheeled vehicle traffic was limited to park staff. Once sufficient snow accumulated, traffic on the roads transitioned from wheeled vehicles to OSVs. Roads were groomed (i.e., snow packing) at least every other night, and the park was open to public OSV traffic during mid-December through mid-March. Over-snow vehicle traffic each winter consisted of commercially guided groups of OSVs, unguided groups of snowmobiles, and administrative OSVs operated by park staff and concessionaires. Most groups of snowmobiles were unguided during 1999–2003, but in winter 2004 the park instituted regulations requiring all groups of recreational snowmobiles to be guided by a trained operator. Roads were plowed during late March and early April, after which they were only open to wheeled vehicles operated by park staff or concessionaires. Roads were opened to public wheeled vehicles during the last week of April for the summer season.

METHODS

We examined the behavioral responses of bison and elk to OSVs during December–March of winters 1999, 2000, and 2002–2004 (i.e., December 1998–April 1999 = winter 1999). We focused on these species because of their proximity and/or perceived sensitivity to OSVs and associated human activities during winter. Surveys were conducted at least twice a week by a pair of observers snowmobiling or driving $\leq$50 km/h along the following nine road segments: (1) Madison to West Yellowstone; (2) Madison to Old Faithful; (3) Norris to Madison; (4) Mammoth to Norris; (5) Canyon Village to Lake Butte; (6) Fishing Bridge to West Thumb; (7) Norris to Canyon Village; (8) Fishing Bridge to South Entrance; and (9) West Thumb to Old Faithful. High OSV use segments 1–3 were surveyed during all winters except for segment 2 during 2002. Lower-use segments 4–6 were surveyed during the 2003 and 2004 winters. Segment 7 was only surveyed in 2003, while segments 8 and 9 were only surveyed in 2004. Survey times were randomly chosen during daylight hours to capture daily and weekly variation in OSV traffic and activities of bison and elk. Observers traveled a given road segment until a group (i.e., $\geq$1 animal) of bison or elk was detected. The observers stopped at a location where approaching OSVs could be observed without disturbing the animals. For each group of bison or elk, observers recorded group size and habitat and measured perpendicular distance to the road using laser rangefinders (except 2002). During 2002, perpendicular distance was visually categorized as on road (0 m), 1–20 m, 21–50 m, 51–100 m, 101–200 m, and >200 m. The midpoint was used in the modeling process. Habitats were classified as on road, meadow, geothermal, forested, or river (e.g., elk feeding on bank or in water).

Our sampling unit was an interaction between a group of OSVs and associated humans and a group of bison or elk within 500 m of the road. This definition of an "interaction zone" allowed assessment of the influence of distance of human activities on responses by bison or elk. For each interaction, observers recorded the most common human activity as: no visible reaction (N); stopped to observe animals (S); dismounted or exited the OSV (D); or approached animals (AP), which included impeding or hastening movement by chasing animals or by forcing animals ahead of vehicles. Observers recorded response behaviors of bison or elk as: no visible reaction to vehicles or humans (N); looked at OSVs or humans and then resumed their behavior (LR); attention/alarm which included rising from bed or agitation (AA); traveled away from OSVs or humans (T); flight (i.e., quick movement away; F); or defense (i.e., attacked or charged; D). Once an interaction was complete, the observers continued the survey along the road segment to locate the next group of bison or elk.

We obtained daily measurements of snow water equivalent (SWE) from the Natural Resources Conservation Service (NRCS) automated SNOTEL site on the Madison Plateau (2362 m). For each winter, we summed (1) the daily SWE measurements from 1 October through 31 April to obtain a daily cumulative value (Garrott et al. 2003), and (2) the daily number of OSVs entering the West Entrance Station at West Yellowstone, Montana for each day of the winter recreation season to obtain a daily cumulative number of OSVs.

The survey variable we modeled was the most common wildlife group response of bison or elk (n = 6508 group responses) observed during an interaction. Because the frequencies of attention/alarm (AA), travel (T), flight (F), and defense (D) responses for each species were all low, these categories were combined into a single "active" (AC) response category. Thus, we modeled three response categories: none (N; $n = 4604$), look/resume (LR; $n = 1019$), and active (AC; $n = 885$) corresponding to activities requiring an increasing amount of energy expenditure.

We formulated a candidate set of models prior to analyzing the survey data. Each model contained four or five of the following covariates recorded for each interaction between OSVs and groups of bison or elk: (1) number of animals in the group (sppnum); (2) distance of the group to the road (dist); (3) human activity (hact); (4) habitat (hab); (5) cumulative daily number of OSVs entering the West Entrance of Yellowstone (cumvis); and (6) cumulative SWE (cumswe). Only one of the cumvis or cumswe variables appeared in any model because of a strong positive within-season correlation.

Multinomial logits regression (Stokes et al. 1996, Hosmer and Lemeshow 2000, Allison 2003) was used to fit each bison and elk model because there were three response categories (N, LR, and AC). Two logits $L_a(\mathbf{x}) = \log[\pi_a(\mathbf{x})/\pi_2(\mathbf{x})]$ (a = 0, 1) were modeled where $\pi_0(\mathbf{x})$, $\pi_1(\mathbf{x})$, and $\pi_2(\mathbf{x})$ are, respectively, the probabilities of an AC response, LR response, and N response given $\mathbf{x} = (x_1, x_2, \ldots, x_p)$ is a vector of model covariates. We treated no response as the baseline response by selecting $\pi_2(\mathbf{x})$ to be in the denominator of each odds. The logit parameters were fit using the SAS LOGISTIC procedure (SAS Institute 2002). Model AIC (Akaike information criterion) statistics were also output from which $\mathrm{AIC_c}$ values were computed.

Model formulation

For each covariate, a hypothesis regarding the direction of its effect on the multinomial logit response was formulated prior to data analysis (Appendix A). Three forms of logit model effects for quantitative covariate x_i were also postulated a priori: linear, moderated, and threshold. The logit model effect is denoted $\beta_i x_i^*$ where (1) $x_i^* = x_i$ for the linear form, (2) $x_i^* = \sqrt{x_i}$ for the moderated form, and (3) $x_i^* = x_i$ for $x_i \leq T_i$ and $x_i^* = T_i$ for $x_i > T_i$ for the threshold form. The linear form assumes a fixed-rate increase or decrease per unit increase in x_i, the moderated form assumes an increasing or decreasing effect per unit increase in x_i, and the threshold form assumes a fixed-value increase or decrease per unit increase in x_i up to some threshold value T_i. The linear or moderated forms imply a continual increasing or decreasing covariate effect while the threshold form implies that the maximum effect of that covariate has been reached. For example, increasing the group size of bison or elk from one to six may reduce the odds of observing an active response, while increasing the group size from 30 to 35 may have no effect. In this case, a threshold would be more appropriate than the linear or moderated form.

We created a candidate set of 83 multinomial logit models that were judiciously formulated to cover a wide assortment of covariate combinations and contain a sufficient number of effects to represent the complexity of underlying ecological processes (Appendix B). The form for each fitted logit model from the a priori model set having main and/or interaction effects is

$$\hat{L}_a(\mathbf{x}) = b_{0a} + \sum_i b_{ia} x_j^* + \sum_i \sum_j b_{ija} x_i^* x_j^* \qquad (a = 0, 1).$$

For the categorical variables hab and hact, the x_i^* (or x_j^*) are indicator variables corresponding to categorical levels. For quantitative covariates, the x_i^* forms (linear, moderated, or threshold) may vary within a model because there is no scientific reason to believe in a one-transformation-fits-all approach to variable forms. For example, it is perfectly reasonable for one covariate to have a linear form while another covariate has a threshold form in the same model.

For each model there were also either nine or 27 possible combinations of quantitative covariate effect forms because sppnum, dist, and cumswe or cumvis could assume one of three forms. To address a problem of such high dimensionality, we developed a sequential model selection approach consistent with the a priori model and covariate form specifications. We began by fitting all 83 bison or elk models with linear forms for the quantitative covariates and selecting the 10 best models for each species having the smallest $\mathrm{AIC_c}$ values. Next, we replaced the linear form of one covariate with its moderated form yielding a new set of models that preserved each model's structure. $\mathrm{AIC_c}$ values were calculated for these models. Similarly, the same linear effect was replaced with a threshold form and the $\mathrm{AIC_c}$ values of the resulting models were calculated. We estimated the threshold value by checking a set of potential threshold values and retaining the one that yielded the lowest $\mathrm{AIC_c}$ value. Increments of 5 m for dist, one animal for sppnum, 500 OSVs for cumvis, and 100 cm for cumswe were used to select a threshold. It was unnecessary to conduct the sequential assessment for all 83 original models because replacing a linear form with a moderated or threshold form either improved or worsened the $\mathrm{AIC_c}$ values for all models containing that covariate.

Once we had 30 $\mathrm{AIC_c}$ values corresponding to the 10 best models for linear, moderated, and threshold forms of the first covariate, we selected the 10 models with the best $\mathrm{AIC_c}$ values from this set and repeated the sequential assessment process for the second quantitative covariate, yielding another 30 $\mathrm{AIC_c}$ values. The models with the 10 best $\mathrm{AIC_c}$ values were retained, and this process was repeated until all quantitative covariates were examined with linear, moderated, and threshold forms. The final 10 models with the best $\mathrm{AIC_c}$ values were assessed to determine relationships between covariates, interactions, and responses by bison or elk.

We conducted post hoc analyses to see if a model existed whose effects were consistent with the a priori hypotheses but yielded a significantly improved $\mathrm{AIC_c}$ value. The quantitative covariate daily number of OSVs entering the West Entrance (visits) and the categorical covariate with an indicator for each winter in the study (year) were incorporated into these exploratory analyses. Parsimonious post-hoc bison and elk models consistent with the assessment results for the a priori models were used to generate predicted probability plots and odds ratios.

Odds ratios and predicted probabilities

For each multinomial logit model, predicted logit values and odds ratios can be calculated. The estimated odds ratios $\mathrm{OR}_1(\mathbf{x}_1, \mathbf{x}_2) = [\hat{\pi}_0(\mathbf{x}_1)/\hat{\pi}_2(\mathbf{x}_1)]/\hat{\pi}_0(\mathbf{x}_2)/\hat{\pi}_2(\mathbf{x}_2)$ and $\mathrm{OR}_2(\mathbf{x}_1, \mathbf{x}_2) = [\hat{\pi}_1(\mathbf{x}_1)/\hat{\pi}_2(\mathbf{x}_1)]/\hat{\pi}_1(\mathbf{x}_2)/\hat{\pi}_2(\mathbf{x}_2)$ for covariate vectors $\mathbf{x}_1$ and $\mathbf{x}_2$ were used for interpretation of results. For each quantitative variable, $\mathbf{x}_1$ and $\mathbf{x}_2$ were selected so the odds ratio was calculated for a one unit of measurement increase. For each categorical variable, $\mathbf{x}_1$ and $\mathbf{x}_2$ were selected so the odds ratio was calculated for a categorical change from its baseline (i.e., no response (N) for hact and meadow (M) for hab).

Odds ratios, however, only provide partial information. It is also useful to examine patterns in the predicted probabilities $\hat{\pi}_0(\mathbf{x})$, $\hat{\pi}_1(\mathbf{x})$, and $\hat{\pi}_2(\mathbf{x})$, for a given covariate $\mathbf{x}$. Predicted response probabilities can be directly compared, while odds ratios comparisons are relative to a baseline response. Because there were an infinite number of possible covariates conditions, predicted response probabilities were calculated for two scenarios defined by judiciously created sets of covariate levels. The scenarios represent varying levels of distance to road, group size, and within-season date, while allowing examination of all human activity and habitat effects on the bison or elk group response. In Bison Scenario I, we explored the response of bison during an interaction with OSVs and humans at different distances (i.e., 5 and 100 m), in different habitats (i.e., forested, meadow, or thermal), and at three times during the winter (start of

TABLE 1. Model selection results for the top 10 bison a priori models.

Model(i) = covariates + sppnum × dist + dist × hab + the terms below	K	$\Delta\text{AIC}_\text{c}$	w_k
1 dist × hact + sppnum × hab	40	0.000	0.650
2 dist × hact	34	1.436	0.317
3 dist × hact + sppnum × hab + sppnum × hact	46	7.657	0.014
4 dist × hact + sppnum × hact	40	8.310	0.010
5 dist × hact + sppnum × hab + hact × hab	58	10.051	0.004
6 dist × hact + hact × hab	52	10.408	0.004
7 + sppnum × hab + hact × hab	52	13.768	0.001
8 dist × hact + sppnum × hact + hact × hab	58	15.421	0.000
9 + sppnum × hact + hact × hab	53	19.046	0.000
10 + sppnum × hab + sppnum × hact + hact × hab	58	21.031	0.000

Notes: Abbreviations are: dist, distance of group from road; sppnum, number of animals in group; hab, habitat; hact, human activity; cumvis, cumulative daily number of OSVs (over-snow vehicles). Each model contains covariates = sppnum ($T = 7$ bison) + dist ($T = 125$ m) + hact + hab + cumvis where T is a variable threshold, K is the number of model parameters, w_k is the AIC model weight, and $\text{AIC}_\text{c} = 3974.4$ for model 1. w_p is the AIC predictor weight for the column covariate ($w_\text{p} = 1$ for all effects appearing in covariates). The w_p values for the dist × hact, sppnum × hab, sppnum × hact, and hact × hab potential model effects are 0.999, 0.669, 0.025, and 0.009, respectively.

season, 31 January, and 28 February). In Bison Scenario II, the impact of different bison group sizes (1, 4, or 7 bison) was explored at a fixed point during each winter (28 February) with bison groups at 50 m from the road. The structure of Elk Scenario I was similar to the bison scenarios, except that there was an additional habitat (aquatic), group sizes were 2, 8, or 14 elk, and distances of 5 and 50 m were used. For Elk Scenario II, group sizes of 2, 8, and 14 elk were used. The cumulative OSVs for 31 January and 28 February were, respectively, 22 905 and 40 156 for 1999, 22 159 and 37 616 for 2000, 23 026 and 42 218 for 2002, 10 963 and 20 272 for 2003, and 6948 and 12 465 for 2004. Probability estimates were averaged over the five winter seasons.

RESULTS

The public OSV season lasted 89 days in 1999, 82 days in 2000, 82 days in 2002, 72 days in 2003, and 88 days in 2004. The mean and standard deviation (SD) of daily OSVs entering the West Entrance Station were 514 ± 208 OSVs in 1999, 486 ± 222 OSVs in 2000, 593 ± 269 OSVs in 2002, 320 ± 114 OSVs in 2003, and 178 ± 59 OSVs in 2004. Maximum daily numbers were 1168 OSVs on 28 December 1998, 1010 on 19 February 2000, 1874 on 30 December 2001, 573 on 20 February 2003, and 330 on 15 February 2004. Peak visitation typically occurred on weekends and holidays, while fewer vehicles entered the park on weekdays. Cumulative OSVs entering the West Entrance Station totaled 45 785 in 1999, 40 298 in 2000, 46 855 in 2002, 23 073 in 2003, and 15 846 in 2004. The substantial decrease in visitation during 2003 and 2004 likely resulted from poor snow pack, regulations imposing daily limits on snowmobiles entering the park (720 in 2004), and public uncertainty about the status of OSV recreation within the park (National Park Service, U.S. Department of the Interior 2004).

We observed 6508 encounters between groups of bison or elk and OSVs in unguided groups (pre-2004), commercially guided groups of OSVs (2004 only), or administrative groups of park and concessionaire staff. Twenty-five percent of humans on OSVs that observed groups of bison or elk showed no visible reaction and did not stop, 64% stopped to observe but remained on or inside their OSV, 7% stopped and dismounted their OSVs, and 4% approached, impeded, or hastened the movement of bison or elk with the OSVs. For bison, 81% of responses to OSVs and associated human activities were categorized as no apparent response, 8% look/resume, 2% attention/alarm, 7% travel, 1% flight, and <1% defensive. For elk, 48% of responses were categorized as no apparent response, 32% as look/resume, 12% as attention/alarm, 6% as travel, 2% as flight, and <1% as defensive.

Model selection and exploratory analysis

For bison, the two best models resulting from the sequential model selection process had AIC_c values of 3974 and 3976, with Akaike model weights of $w_k = 0.65$ and 0.32. All other models had $\text{AIC}_\text{c} > 7.6$ (Table 1). The 10 best AIC_c–based models included group size (sppnum), distance from road (dist), human activity (hact), habitat (hab), and cumulative visitation (cumvis), with threshold values of 125 m for distance and seven bison for group size (Table 1). The six best models ?1 included the sppnum × dist, dist × hab, and dist × hact interactions with Akaike predictor weights of $w_\text{p} = 1$, 1, and 0.999, respectively (Table 1), though the sppnum × dist interaction was not statistically significant ($P = 0.36$). The best a priori model also included the sppnum × hab interaction with its $w_\text{p} = 0.67$ (Table 1). The negative parameter estimates and significant P values (Appendix D) support the a priori hypotheses that the odds of an AC response decrease with increasing bison group size and with increasing distance to road.

For elk, the two best models resulting from the sequential model selection process had AIC_c values of 3855 and 3856, with Akaike model weights of $w_k = 0.51$ and 0.28. All other models had $\text{AIC}_\text{c} > 2.7$ (Table 2). The 10 best AIC_c–based models included sppnum

Table 2. Model selection results for the top 10 elk a priori models.

Model(i) = covariates + dist × hab + sppnum × hab + the terms below	K	$\Delta\text{AIC}_\text{c}$	w_k
1 $\sqrt{\text{cumvis}}$ + sppnum × dist + dist × hact	46	0.000	0.509
2 cumswe + sppnum × dist + dist × hact	46	1.200	0.279
3 $\sqrt{\text{cumvis}}$ + sppnum × dist	40	2.763	0.128
4 cumswe + sppnum × dist	40	4.683	0.049
5 sppnum × dist + dist × hact + sppnumhact	50	6.967	0.016
6 $\sqrt{\text{cumvis}}$ + sppnum × dist + dist × hact + sppnum × hact	52	7.780	0.010
7 cumswe + sppnum × dist + dist × hact + sppnum × hact	52	8.730	0.006
8 $\sqrt{\text{cumvis}}$ + sppnum × dist + sppnum × hact	46	10.840	0.002
9 $\sqrt{\text{cumvis}}$ + dist × hact + sppnum × hact	50	13.977	0.000
10 cumswe + dist × hact + sppnum × hact	50	14.837	0.000

Notes: Abbreviation is: cumswe, cumulative snow water equivalents. See Table 1 for other abbreviations. Each model contains covariates = sppnum ($T = 14$ elk) + dist + hact + hab where T is a variable threshold, K is the number of model parameters, w_k is the AIC model weight, and $\text{AIC}_\text{c} = 3855.2$ for model 1. w_p is the AIC predictor weight for the column covariate ($w_\text{p} = 1$ for all effects appearing in covariates). For cumswe, $T = 2500$ cm. The w_p values for the $\sqrt{\text{cumvis}}$, cumswe, sppnum × dist, dist × hact, and sppnum × hact potential model effects are 0.649, 0.335, 0.999, 0.821, and 0.036, respectively.

(threshold = 14 elk), dist, hact, hab, and either a moderated form for cumvis or a threshold of 2500 cm for cumulative snow water equivalent (cumswe; Table 2). The eight best models included the sppnum × dist, dist × hab, and sppnum × hab interactions, with Akaike predictor weights of $w_\text{p} = 0.999$, 1, and 1, respectively (Table 2). The best a priori model also included the dist × hact interaction with $w_\text{p} = 0.82$ (Table 2). Appendix C provides additional details regarding the sequential model selection process.

The a priori and exploratory analyses initially indicated a significant positive cumulative visitation (cumvis) AC logit model effect for bison (Appendices D and E) and a nonsignificant effect for elk (Appendices F and G), which were counter to our predictions. Because the cumulative visitation varied considerably over the five study winters, we incorporated a seasonal interaction (cumvis × year) into exploratory models for bison and elk. The results were dramatic with the best AIC_c values decreasing from 3974 to 3845 for bison and 3855 to 3694 for elk. The cumvis × year interaction effects were negative for 1999 and 2000 and positive for 2002 and 2003 (Appendices E and G). Also, the cumvis estimate was now significantly negative for bison (Appendix E), which is a reversal of the positive cumvis estimate when we ignored year-to-year visitation (Appendix D). Thus, AIC criteria must be used and interpreted cautiously because the a priori model set may not include one or more highly influential variables that reveal potentially important effects and, possibly, reverse conclusions regarding the sign of parameter effects. This is especially true for high-dimensional problems for which the potential number of model variables is large.

For both the a priori (Appendices D and F) and exploratory analysis (Appendices E and G) models, the AC-logit estimates for hact and hab are consistent with the a priori hypotheses. That is, for hact, the parameter estimates for the active response logits for both bison and elk were positive if humans approached the animals and negative if humans did nothing. For hab, the estimates were positive when bison or elk were in direct contact with humans or OSVs that were on the road and negative (given the zero-sum constraint), but not necessarily equal, for other habitats. These hypotheses were not supported for the LR-logit estimates.

When present in the best a priori models and exploratory analysis models, the interaction effects were consistent with our predictions (Appendix A). The effect of distance for both bison and elk on the odds of an active response was not as great for meadow and thermal habitats in contrast to the more-protected forested habitat. This is reflected in the smaller dist × hab estimates for meadow and thermal areas than for a forested habitat (Appendices E and G). For bison, the odds of eliciting a response when approaching animals was smaller the further bison were from humans and OSVs (i.e., a negative dist × hact estimate when hact = AP; Appendix E). This result was not seen in the elk model with the estimate being nonsignificant (Appendix G). For both bison and elk, when animals were on the road, increasing group size lowered the odds of eliciting an active response (i.e., negative sppnum × hab estimates when hab = RD; Appendices E and G). For elk, the effect of group size on the odds of an active response was not as large at greater distances (i.e., negative sppnum × dist estimate; Appendix G).

The hypotheses that the effect of distance would not be as large with larger groups of bison or elk (dist × sppnum), and that the effect of approaching animals would not be as great in forested habitats with more cover than in open meadows or geothermal areas (hact × hab), were not supported by the data for the AC logit models.

The cumvis × year interaction appearing in both exploratory analysis models (Appendices E and G) indicates the impact of visitation on bison and elk group responses varied across winters. Interpretation is difficult because cumulative visitation was highly variable across the five winters. This means that any specific cumvis OSV count (e.g., 10 000 OSVs) will occur at different days in different winters. Thus, there is no simple generalized interpretation of the effects.

In summary, for the exploratory analyses, a cumvis × year effect was added while the sppnum × dist interaction was removed from the best a priori bison model in the exploratory analyses, leaving a model with the covariates sppnum, dist, hact, hab, and cumvis (with threshold values of 125 m for distance and seven bison for group size) and interactions sppnum × hab, dist × hact, dist × hab, and cumvis × year (Appendix E). For elk, effects for year and cumvis × year were added to the best a priori elk model leaving a model with the covariates sppnum, dist, hact, hab, and cumvis and interactions sppnum × dist, sppnum × hab, dist × hact, dist × hab, and cumvis × year (Appendix G).

Odds ratios and predicted probabilities

There were significant decreases in the odds of active responses by bison and elk as group size and distance to the road increased. The odds of observing no response relative to an active response by bison or elk were 4.6 and 2.2 times greater, respectively, for each additional animal in the group. Also, the odds of observing no response relative to an active response by bison or elk were 87 and six times greater, respectively, for each 100-m increase in distance of the nearest animal in the group to the road (Appendices D and F). There was a strong association between responses by bison or elk and both habitat type and human activity. If a bison or elk group was on the road, then the odds of an active response was 136 and 74 times greater, respectively, than if they were off-road in meadow habitat. The odds of an active response by bison and elk were 15 and seven times greater, respectively, when humans approached animals than if they did not respond (Appendices D and F).

Using the fitted logit models, we calculated the predicted probabilities for two scenarios for both bison and elk. In Bison Scenario I, we studied bison habituation by comparing response probabilities at the start of the winter season (cumvis = 0) to those on 31 January and 28 February. We varied the distance of bison from near (5 m) or on road (Fig. 1) to 100 m from the road (Fig. 2). The group size was fixed at one animal. Predicted AC response probabilities decreased across the winter with a 2–6% decrease from the start of the season to 28 February across all human responses and habitats. This is matched by a similar increase in the probabilities for no (N) response. As long as the bison group was away from the road, the predicted probability of an active bison response was very low across all habitat and human response conditions.

The impact of different bison group sizes (1, 4, or the threshold value of seven bison) was explored in Bison Scenario II. The effect of group size was negligible on AC response probabilities for forested and thermal habitats (Fig. 3). However, for meadows (the predominant habitat), the AC probabilities decreased slightly with increasing group size. There was also a noticeable reduction in the probabilities of an LR response with increasing group size for all habitats and human responses. These plots highlight the presence of the group size by habitat interaction in the bison logit models.

In Elk Scenario I, we studied elk habituation by comparing response probabilities at the start of the winter season (cumvis = 0) to those on 31 January and 28 February. We varied the distance of elk from near (5 m) or on road (Fig. 4) to 50 m from the road (Fig. 5). The group size was fixed at two animals. There were negligible changes in predicted AC response probabilities from the start of the season to 28 February across all human responses and habitats. The effect that distance had on the probability of an AC or LR elk response was minimal. This was a result of the dist × hab interaction. The dist estimate was -1.755 while the dist × hab estimates for hab = A, F, TH, and M are 1.52, 1.57, 1.61, and 1.80, respectively (Appendix G). Thus, for each of these four habitats the individual within habitat dist effects (dist + dist × hab) were very close to 0. The only noticeable effect of distance occurred if the elk were on the road (hab = RD).

In Elk Scenario II, the impact of different elk group sizes (2, 8, or the threshold value of 14 elk) was explored. The effect of group size on AC response probabilities was highly dependent on habitat (Fig. 6). For aquatic and forested habitats, the probability of an AC response increased with increasing group size. However, for meadows and thermal areas, the AC probabilities decreased with increasing group size. A larger reduction in the probabilities of an LR response occurred with increasing group size for all habitats and human responses.

DISCUSSION

Bison and elk in Yellowstone behaviorally responded to OSVs and associated human activities with increased vigilance (i.e., look/respond, alert/attention), travel (i.e., walking away) and, occasionally, flight or defense. The likelihood and intensity of these responses differed by species, with elk responding three times as often (52%) as bison (19%). This difference was due to increased vigilance responses by elk (44%) compared to bison (10%). The frequency of higher-intensity movement responses by bison and elk were similar at 6–7% travel, 1–2% flight, and <1% defensive. The likelihood and intensity of responses by bison and elk increased significantly if animals were on or near roads, groups were smaller, or animals were approached by humans or their movements were impeded or hastened by vehicles. Bjornlie and Garrott (2001) reported 60% of encounters between bison and OSVs when bison were traveling on groomed roads resulted in negative responses, with animals being moved by vehicles along extended distances of road or diverted into snow off the road. Also, Aune (1981) and Hardy (2001) indicated elk were temporarily displaced ~60 m from busy road segments (e.g., Madison to Old Faithful) as cumulative traffic increased.

Few studies have documented the effects of OSVs on bison or elk. However, the frequency and intensity of

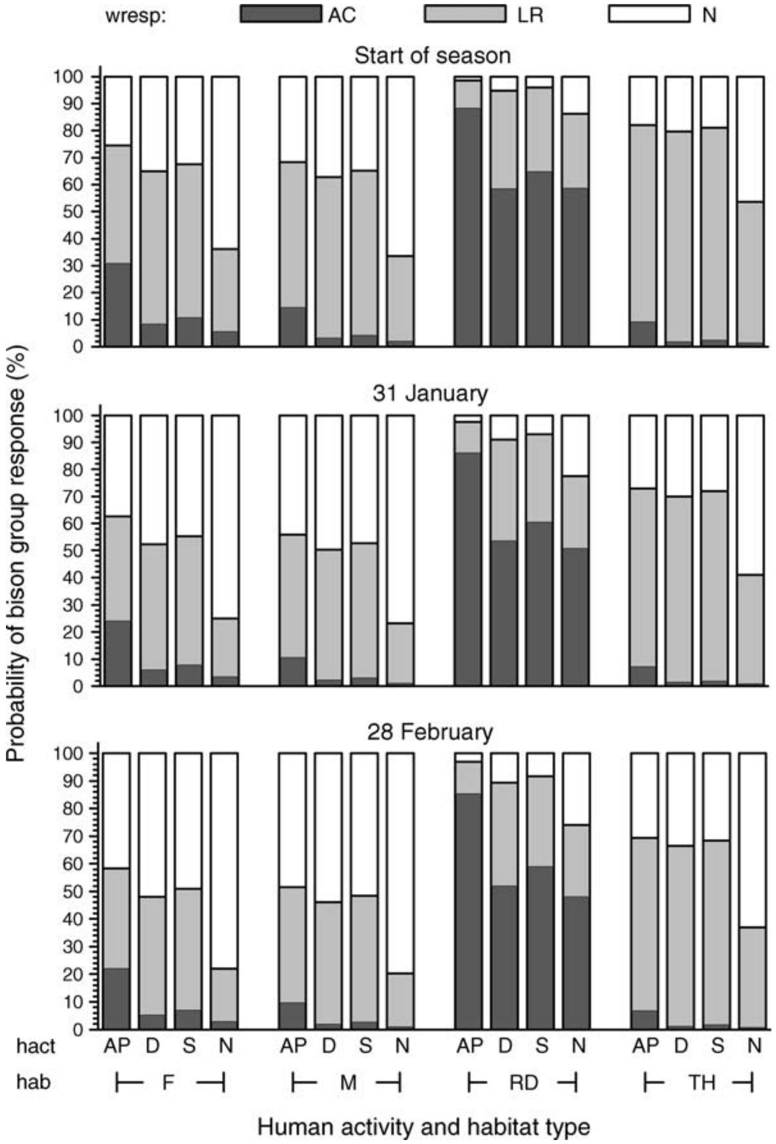

FIG. 1. Predicted probability plots of bison group responses for each human response and habitat combination at start of season, 31 January, and 28 February. Distance to road is fixed to be at 5 m (or actually on the road for hab = RD), and the group size is fixed at one animal. The probabilities are averages calculated across the five winters. Habitat (hab) abbreviations are: F, forested; M, meadow; RD, road; TH, thermal. Human activity (hact) abbreviations are: AP, approached animals; D, dismounted or exited over-snow vehicles (OSVs); S, stopped to observe animals; N, no visible reaction to animals. Wildlife group responses (wresp) are: AC, active response; LR, looked at OSVs or humans and resumed their behavior; N, no visible reaction to vehicles or humans.

movement responses by bison and elk in our study were small compared to other studies reporting substantially higher degrees of avoidance and responses to snowmobiles by bison (Fortin and Andruskiw 2003), moose (*Alces alces*; Colescott and Gillingham 1998), mule deer (*O. hemionus*; Freddy et al. 1986), reindeer (*Rangifer tarandus*; Tyler 1991, Reimers et al. 2003), and white-tailed deer (*Odocoileus virginianus*; Dorrance et al. 1975, Richens and Lavigne 1978, Eckstein et al. 1979). For example, Fortin and Andruskiw (2003) reported that in Prince Albert National Park, Saskatchewan, Canada, 3% of bison reacted to human presence by approaching, 46% by looking while remaining in place, and 51% by fleeing the area. Bison were as likely to flee from a person on foot as a snowmobile, and the probability of flight by groups that included bison less than a year old increased as the snowmobile approached, reaching 50% at 257 m.

The comparatively less frequent and lower intensity responses by bison and elk in Yellowstone suggest there is a certain level of habituation to OSVs and associated human activities. Habituation occurs when an animal learns to refrain from responding to repeated stimuli that are not biologically meaningful (Eibl-Eibesfeldt 1970). Wildlife may become conditioned to human

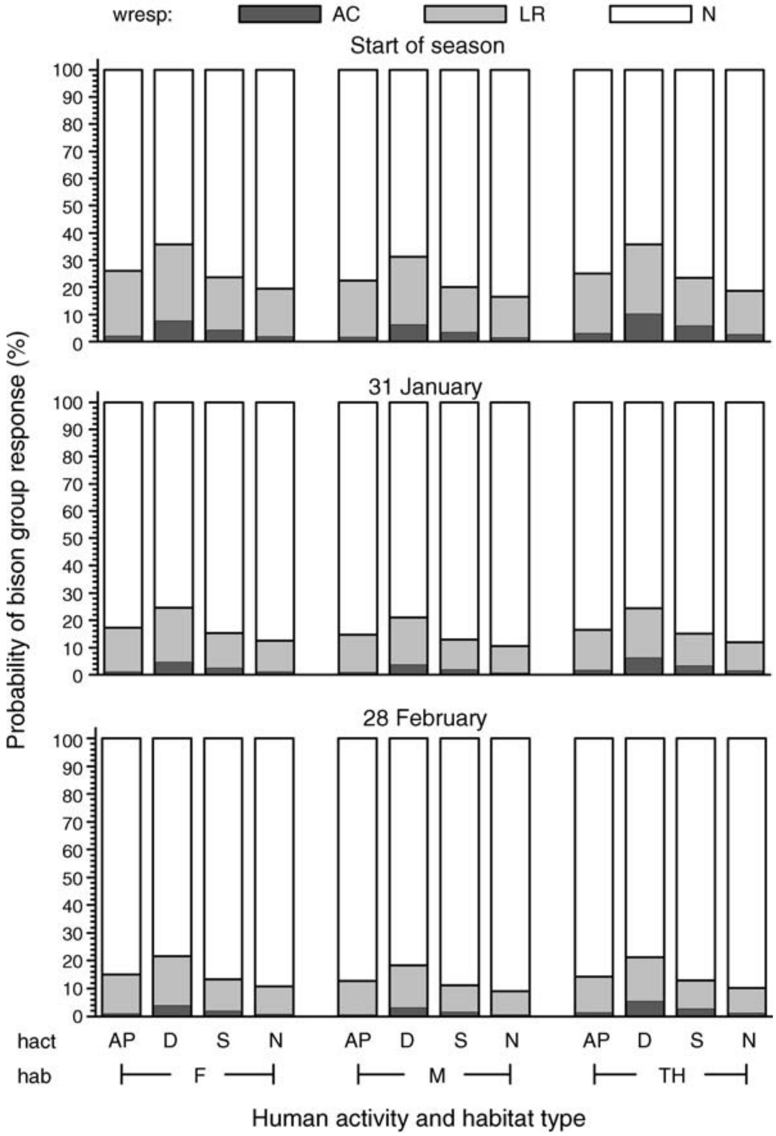

FIG. 2. Predicted probability plots of bison group responses for each human response and habitat combination at start of season, 31 January, and 28 February. Distance to road is fixed to be at 100 m, and the group size is fixed at one animal. The probabilities are averages calculated across the five winters. See Fig. 1 for abbreviations.

activity when the activity is controlled, predictable, and not harmful to the animals (Schultz and Bailey 1978, Thompson and Henderson 1998). The likelihood of an active response by bison decreased within winters having the highest visitation, suggesting some further habituation to OSV recreation with increasing exposure to vehicles during the season. Aune (1981) and Hardy (2001) also concluded bison and elk habituated to the presence and patterns of human activity in Yellowstone. Though large winter-to-winter variability in cumulative exposure to OSVs exists, bison and elk in Yellowstone have continued to utilize the same core winter range during the past three decades, and bison distribution has apparently not been influenced by OSV recreation activities or levels (Hardy 2001). All OSVs traveled through our study area in predictable ways, remaining confined to roads and typically without humans threatening or harassing elk and bison. Few people ventured far from roads, established trails, or areas of concentrated human activities (e.g., warming huts, geyser basin trails). These characteristics of winter recreation are likely to facilitate behavioral habituation by wintering bison and elk to OSV traffic (Hardy 2001). Hence, winter recreational activities in national parks should be conducted in a predictable manner.

While OSVs often elicited no observable behavioral response by bison and elk, recreational activities can also cause physiological responses such as elevated heart

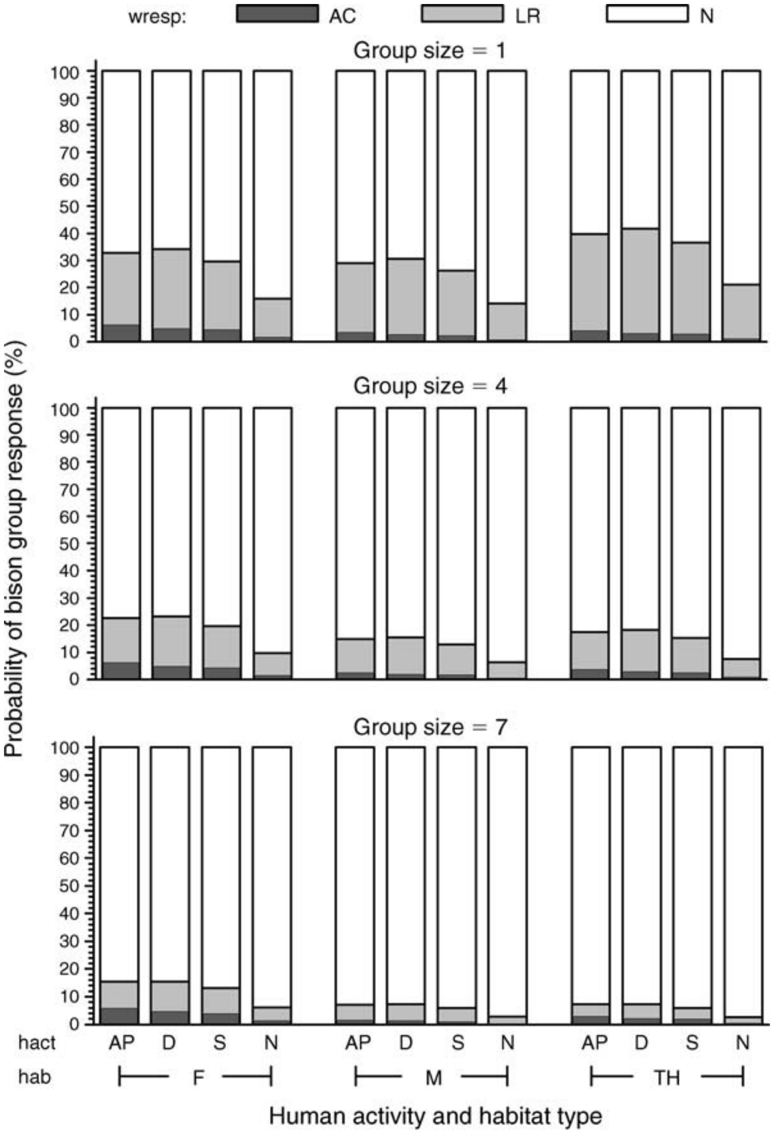

FIG. 3. Predicted probability plots of bison group responses for each human response and habitat combination at bison group sizes of 1, 4, and 7 animals. Distance to road is fixed at 50 m and the date is set at 28 February. The probabilities are averages calculated across the five winters. See Fig. 1 for abbreviations.

rate, blood pressure, breathing rate, and release of adrenaline. The adrenal cortex secretes glucocorticoids (GC) that alter metabolic pathways for the production of ATP and divert energy from physiological processes not required for immediate survival. The secretion of GC is beneficial to an animal in the short term, but chronic GC elevation can inhibit digestion and growth, result in decreased resistance to disease, and produce an array of pathologies, including reproductive suppression, ulcers, and muscle wasting (Munck et al. 1984, Sapolsky 1992). Thus, more severe or prolonged responses to human activity could have fitness costs such as decreased survival and reproduction. In a companion investigation to this study, we measured fecal GC levels of bison and elk in the Madison-Firehole-Gibbon area of Yellowstone during winters of 1999 and 2000. Glucocorticoid levels in elk varied significantly with age, mean daily temperature, and snow pack (Hardy 2001). After controlling for these effects, Creel et al. (2002) reported preliminary results from the first year (1999) of the study, concluding that GC levels of marked elk increased significantly as the daily number of snowmobiles in the area increased. Also, GC concentrations were higher in response to snowmobiles than wheeled vehicle traffic during spring after roads were plowed.

These patterns were not evident when data from both years of the study were analyzed (Hardy 2001). Levels of GC in marked elk were significantly lower during 2000 than 1999, though OSV traffic was not significantly

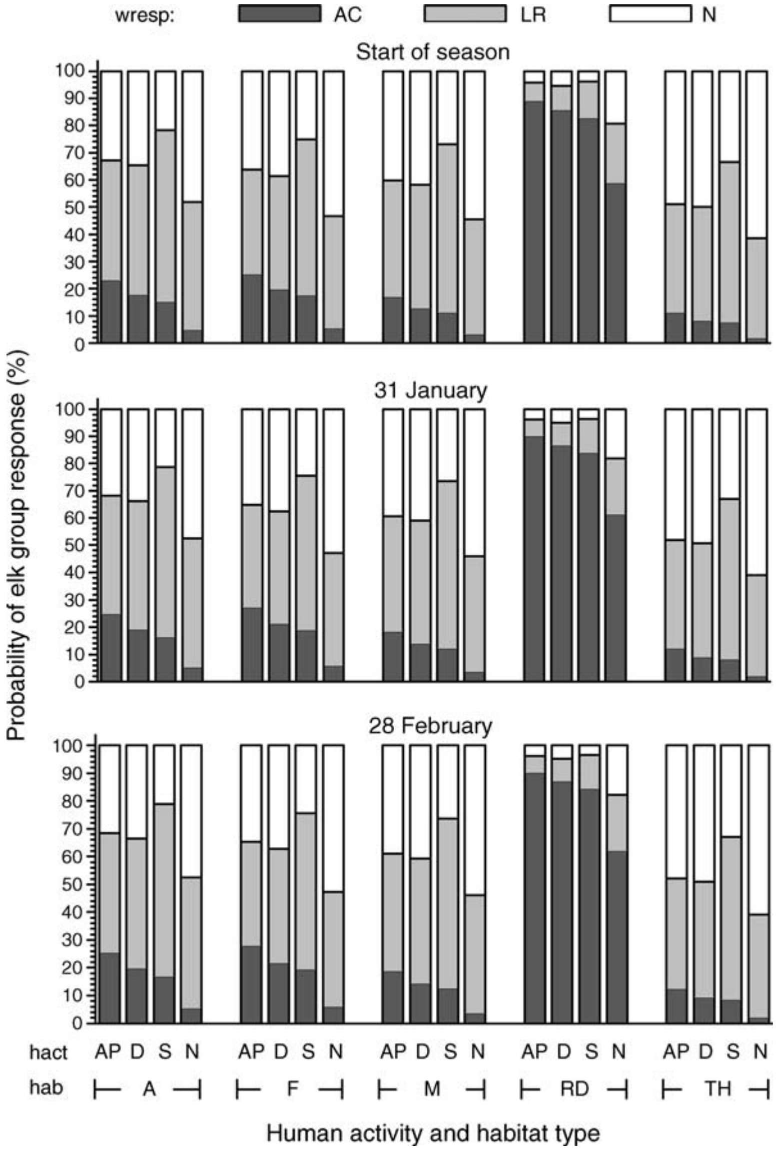

FIG. 4. Predicted probability plots of elk group responses for each human response and habitat combination at start of season, 31 January, and 28 February. Distance to road is fixed to be at 5 m (or actually on the road for hab = RD), and the group size is fixed at two animals. The probabilities are averages calculated across the five winters. Abbreviations are as in Fig. 1, with the addition of A (aquatic) as a habitat type.

different between winters (1999, 45 785 cumulative and 514 daily [SD 208]; 2000, 40 298 cumulative and 486 daily [SD 222]). There were no obvious trends between daily traffic of OSVs and GC levels, and GC levels were higher in response to wheeled vehicles than snowmobiles. In addition, Hardy (2001) sampled bison during both years and did not detect any significant effects of OSV recreation on fecal GC levels. These disparities are not surprising given recent findings that many factors influence cortisol excretion independent of direct effects on adrenal responses, including age, sex, seasonal patterns in GC secretion, body condition, diet, social ranking, and reproductive status (Millspaugh and Washburn 2004). Thus, an increase in GC secretion does not automatically equate to a state of distress or deleterious responses (Romero 2004). Biologists must carefully consider confounding factors and the relationship between fecal GC concentrations and population performance or biological costs when interpreting effects of environmental or human-induced disturbances on wildlife (Millspaugh and Washburn 2004).

We did not conduct detailed energetics measurements or modeling to evaluate the relative energy costs of bison or elk interactions with OSVs in relation to their total daily energy expenditures because numerous assumptions are required and poorly defined parameter

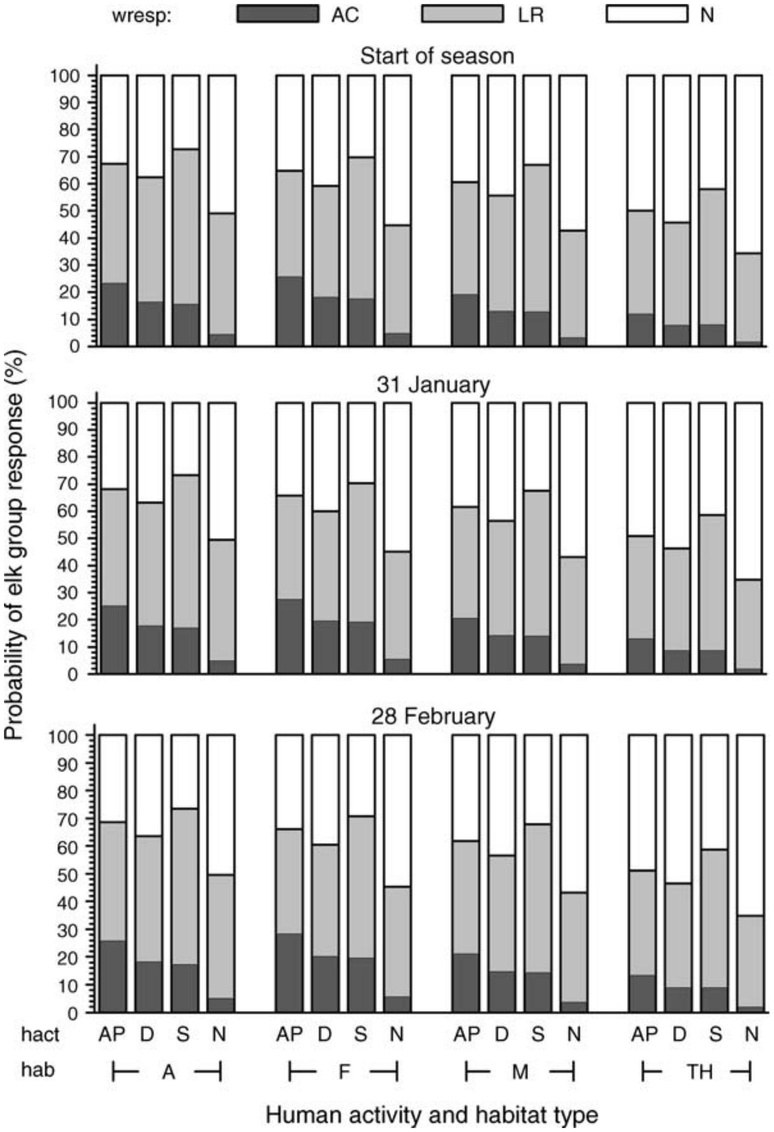

FIG. 5. Predicted probability plots of elk group responses for each human response and habitat combination at start of season, 31 January, and 28 February. Distance to road is fixed to be at 50 m, and the group size is fixed at two animals. The probabilities are averages calculated across the five winters. See Figs. 1 and 4 for abbreviations.

estimates could strongly affect model output (Beissinger and Westphal 1998). As Creel et al. (2002) suggested, however, it is still logical to ask if the behavioral responses we observed to OSV recreation in Yellowstone are adversely affecting the population dynamics or demography of bison and elk. Over-snow vehicle recreation increased exponentially from 5000 to >120 000 riders during 1968–2004 (Gates et al. 2005). Over this same period, counts of central Yellowstone bison increased exponentially from ~400 to 3400 bison, including an increase from 1700 to 3400 bison during our study (1999–2004). Also, population estimates for central Yellowstone elk fluctuated around a dynamic equilibrium of ~500–550 elk during 1968–2004 (λ = 0.99–1.01) and remained between 300 and 660 elk during our study (Garrott et al. 2006). The annual survival of adult female elk in this population exceeded 90% and calf : cow ratios indicated healthy recruitment prior to the restoration of wolves in 1998 (Garrott et al. 2003). Thus, any adverse behavioral and energetic effects of OSV recreation to these ungulate populations have apparently been compensated for at the population level. Fortin and Andruskiw (2003) reached a similar conclusion for bison in Prince Albert National Park, Saskatchewan, Canada. They found no evidence that the frequency of disturbance imposed on bison by snowmobiles, trucks, or foot traffic had an important effect on resource use or bison density among meadows.

Resolution of the debate regarding winter recreation in Yellowstone depends, in part, on quantitative evaluations

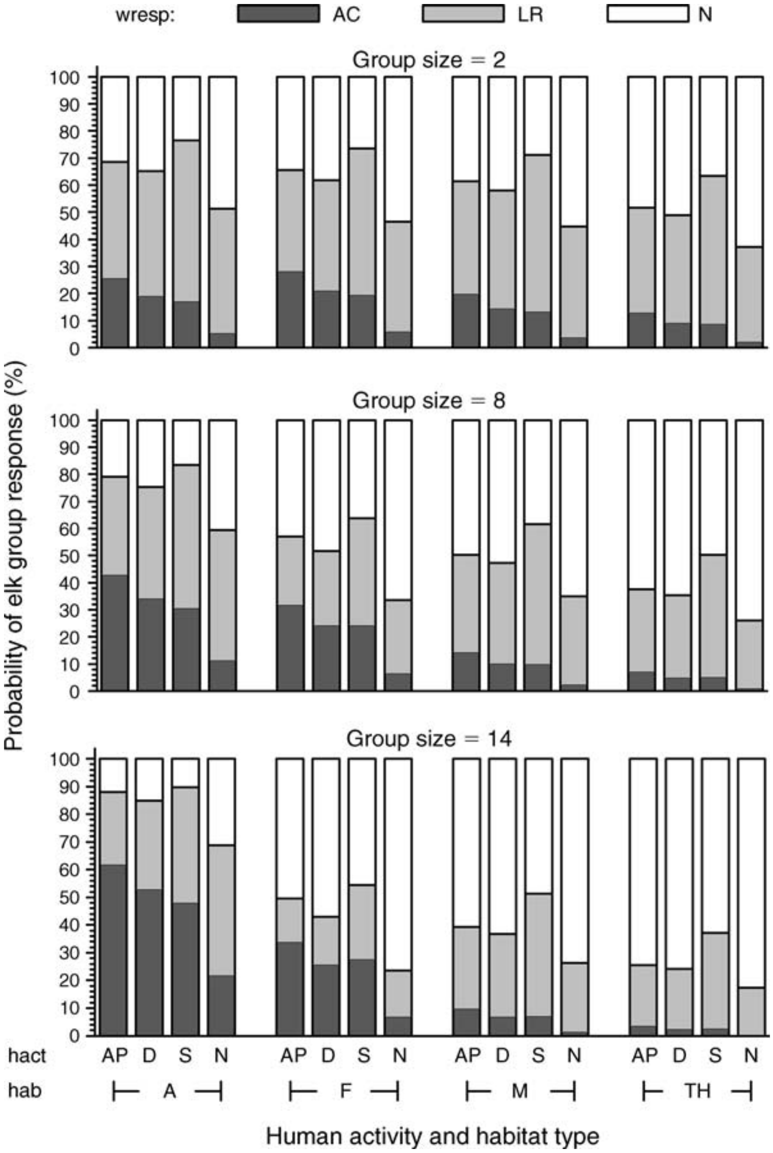

FIG. 6. Predicted probability plots of elk group responses for each human response and habitat combination at bison group sizes of 2, 8, and 14 animals. Distance to road is fixed at 25 m and the date is set at 28 February. The probabilities are averages calculated across the five winters. See Figs. 1 and 4 for abbreviations.

of the effects of OSVs on wildlife. However, science cannot resolve issues where policy is advocated due to values judgments and perceptions about what is appropriate in national parks (Sarewitz 2004). As Creel et al. (2002) discussed, various constituencies have strong values and beliefs about the primary purpose of the park (i.e., recreation vs. conservation) and acceptable levels of impact (i.e., behavioral vs. physiological vs. population). At one extreme, it is argued that ungulate responses to activities associated with OSVs are minor and of little consequence given the absence of a measurable decrease in abundance. At the other extreme, it is argued that human activities that induce behavioral and stress responses should be curtailed. Bison and elk are acutely aware of their surroundings and any human activities in close proximity likely elicit some response, even if it is not detectable by an observer. Thus, it is unrealistic to expect winter recreation or administrative travel by park staff to be totally benign, regardless of whether the activity is skiing, snowshoeing, snowmobiling, or driving an automobile (e.g., Aune 1981, Cassirer et al. 1992, Hardy 2001). As a result, park managers must seek ways to minimize, to the greatest degree practicable, adverse impacts on park resources and values (National Park Service 2000).

This study documented that winter visitors traveling on OSVs were essentially confined to the groomed roads, typically behaved appropriately when viewing wildlife, and rarely approached wildlife except when animals were on or immediately adjacent to the road. These attributes have allowed elk and bison in Yellowstone to habituate somewhat to OSV recreation, commonly demonstrating no observable response, and rarely displaying "fight or flight" responses when animals were off road. Further, available data provide no evidence that levels and patterns of OSV traffic during the past 35 years adversely affected the population dynamics or demography of elk and bison. Thus, we suggest regulations restricting the levels and travel routes of OSVs during our study were effective at reducing disturbances to bison and elk below a level that would cause measurable fitness effects. We acknowledge the potential for fitness effects to develop if OSVs or other stressors become more severe or prolonged. Thus, we recommend park managers consider maintaining OSV traffic levels at or below those observed during our study. Regardless, numerous studies have shown that scientific findings rarely persuade people to alter their values or beliefs (e.g., Meadow et al. 2005). Thus, we suspect that varying interpretations of the behavioral and physiological response data will continue to exist because of the diverse values and beliefs of the many constituencies of Yellowstone National Park.

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APPENDIX A

The a priori predictions for covariates included in the candidate set of multinomial logit models (*Ecological Archives* XXX-XXX).

APPENDIX B

The a priori candidate set of 83 multinomial logit models (*Ecological Archives* XXX-XXX).

APPENDIX C

Results of the sequential approach for evaluating various forms of the quantitative covariates (*Ecological Archives* XXX-XXX) .

APPENDIX D

SAS statistical software output from the a priori model for bison best supported by the data (*Ecological Archives* XXX-XXX).

APPENDIX E

Output from exploratory analyses of the bison model best supported by the data, including odds ratios and their reciprocals (*Ecological Archives* XXX-XXX).

APPENDIX F

SAS statistical software output from the a priori model for elk best supported by the data (*Ecological Archives* XXX-XXX).

APPENDIX G

Output from exploratory analyses of the elk model best supported by the data, including odds ratios and their reciprocals (*Ecological Archives* XXX-XXX).