

Behavioral Responses of Wildlife to Snowmobiles and Coaches in Yellowstone

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Abstract. Managers of Yellowstone National Park are charged with protecting some of our nation's most important natural resources, while providing for their use and enjoyment by visitors. Over 100,000 visitors entered the park by over-snow, motorized means on snowmobiles (94%) or coaches (6%) during 2003-2006. Most vehicles toured the central portion of the park where bald eagles (*Haliaeetus leucocephalus*), bison (*Bison bison*), coyotes (*Canis latrans*), elk (*Cervus elaphus*), and trumpeter swans (*Olor buccinator*) wintered in areas close to roads. We sampled 5688 interactions between groups of these species and groups of snowmobiles and coaches during 2003-2006 and used multinomial logits models, odds ratios, and predicted probabilities to identify conditions leading to behavioral responses. Bison responded less frequently (20%) to snowmobiles and coaches than swans (43%), elk (52%), coyotes (61%), or bald eagles (83%) due to fewer vigilance responses. However, the frequency of higher-intensity movement responses was similar among species (8-10%), with the exception of coyotes (24%). The likelihood of vigilance and movement responses by these species increased significantly if animals were on or near roads, animals groups were smaller, humans approached animals on foot, interaction time increased, or the numbers of snowmobiles and coaches in a group increased. There were thresholds on the odds of eliciting a response by wildlife for several of these covariates. We did not detect significant increases or decreases in the odds of movement responses for any wildlife species as cumulative over-snow vehicle traffic increased through the winter. However, the likelihood of a vigilance response by bison decreased within the winter having the largest visitation, suggesting some habituation to snowmobiles and coaches. In contrast, there was a significant increase in the odds of vigilance responses by elk as the cumulative visitation increased through the winter. Human disturbance did not appear to be a primary factor influencing the distribution and movements of the wildlife species we studied. The risk of vehicle-related mortality from snowmobiles was quite low and observed behavioral responses were apparently short-term changes that were later reversed. Bison, elk, and swans in Yellowstone used the same core winter ranges during the past three decades despite large winter-to-winter variability in cumulative exposure to OSVs. There was no evidence that snowmobile use during the past 35 years adversely affected the demography or population dynamics of bald eagles, bison, elk, or trumpeter swans (no data was available for coyotes). Thus, we suggest regulations restricting levels and travel routes of OSVs were effective at reducing disturbances to these wildlife species 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.

INTRODUCTION

Human disturbance of wildlife is widely considered a serious conservation problem when animals demonstrate strong, negative responses to human presence (Boyle and Sampson 1985, Klein et al. 1995, Knight and Gutzwiller 1995, Olliff et al. 1999). If humans significantly alter the activities or distributions of animals, then there may be increased vigilance and movement levels, reduced foraging rates, and reduced levels of parental care; each of which could reduce reproduction, survival, and population size (Stalmaster and Kaiser 1998, Duchesne et al. 2000, Steidl and Anthony 2000, Gonzales et al. 2006). However, behavioral responses and apparent avoidance may not reduce the number of animals supported in an area because animals displaced from disturbed sites in the short term may return later, resulting in the overall use of these sites being unchanged (Gill et al. 2001a). Thus, studies of disturbance need to identify major factors influencing the behavior, distribution, and forage selection of affected species and assess the role of disturbance in altering these relationships (Gill et al. 1996, Wisdom 2005). Studies also need to address whether responses to disturbance affect reproduction, survival, and abundance (Gill and Sutherland 2000, Gill et al. 2001b).

Yellowstone National Park (Yellowstone) protects some of our nation's most important natural resources that, in turn, attract millions of visitors annually for recreational activities. Thus, park managers are essentially charged with conserving resources, while providing for their use and/or enjoyment by people (National Park Service Organic Act of 1916; 16 USC 1, 2-4). Recreation may disrupt ecological processes by disturbing wildlife and resulting in altered distributions, increased energetic costs, changes in behavior and fitness, and avoidance of otherwise suitable habitat (Boyle and Sampson 1985, Knight and Gutzwiller 1995). Thus, management policies 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 an understanding of the resources, ecological processes, and human-related effects is a prerequisite for developing these policies (Parsons 2004).

The history of winter recreation in Yellowstone illustrates the difficulty of balancing the trade-off between access and recreation-related effects. Snow coaches and snowmobiles were used in the park for the first time during 1955 and 1963, respectively, and park staff began grooming (i.e., packing) snow-covered roads in 1971 to facilitate their safe passage (Aune 1981, Yochim 1998). Winter recreation and snowmobile use increased dramatically in the following decades and more than 100,000 riders per year entered Yellowstone during the early 1990s (Yochim 1998, Gates et al. 2005). 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, more than 1,000 bison (*Bison 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 demography 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) resulted in conflicting legal decisions and

corresponding reactive changes in winter recreation regulations (National Park Service, U.S. Department of the Interior 2004).

The effects of road grooming on bison distribution and movements have been addressed by Bruggeman (2006), Bruggeman et al. (2006), and Fuller (2006). We sampled the behavioral responses of bald eagles (*Haliaeetus leucocephalus*), bison, coyotes (*Canis latrans*), elk (*Cervus elaphus*), and trumpeter swans (*Olor buccinator*) to snowmobiles and coaches (collectively referred to as over-snow vehicles; OSVs) during 2003-2006. We focused on these species (collectively referred to as wildlife) because of their proximity and/or perceived sensitivity to OSVs and associated human activities during winter. Our specific objectives were to determine if behavioral responses of wildlife related to the: 1) number of snowmobiles and coaches present during a human/wildlife encounter; 2) type of human activity exhibited during a human/wildlife encounter; 3) length of the human/wildlife interaction; and 4) cumulative numbers of OSVs within a winter season. We also assessed the effects of human disturbance on the distribution and demography of bison and elk by evaluating the results of companion studies conducted during 2003-2006 (Messer 2003, Garrott et al. 2006, Bruggeman 2006, Fuller 2006).

STUDY AREA

We conducted our study along road segments throughout the central portion of Yellowstone in the northern Rocky Mountains of Montana and Wyoming of the United States. However, >90% of observed interactions between groups of OSVs and groups of wildlife 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, Garrott et al. 2003, Hess 2002). This range encompassed 27,000 ha along the Firehole, Gibbon, and Madison rivers between the Norris geyser basin, Old Faithful, and West Yellowstone, Montana. Our study area also included a movement corridor for bison between Norris and Mammoth (Gates et al. 2005). Physiography was dominated by the river 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 2250-2800 m and snow depths often exceeded 91 centimeters 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.

The west-central Yellowstone system had a relatively simple faunal complex during winter, with only two abundant ungulate species and two large predators. Approximately 900-1,200 bison from the migratory central Yellowstone herd wintered in the area. The nonmigratory central Yellowstone elk population consisted of approximately 230-400 elk during our study (Garrott et al. 2006) 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. The number of wolves (*Canis lupus*) using the study area ranged between 3-4 packs totaling 30-40

animals in 2005 to 2 packs totaling 11 wolves in 2006. Black bears and coyotes also occurred in the area, but were not significant predators on adult bison or elk (Garrott et al. 2003).

Nesting, migrating, and wintering bald eagles and trumpeter swans occurred in Yellowstone during our study, including 32-34 nesting pairs of bald eagles and 18 resident swans (McEneaney 2006). Resident eagles and swans displayed strong fidelity to breeding areas and nest sites, and winter habitat was generally associated with areas of ice-free, open water (Olliff et al. 1999). Nest building by bald eagles occurred during October-April, while incubation occurred during February-March. Swans generally returned to their breeding territories between February and late May, with young hatching in late June (Olliff et al. 1999).

Human activity in the upper Madison River drainage occurred in a predictable pattern. Vehicular travel was restricted to paved, 2-lane roads that were closed in early November each year, and wheeled 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 2003, but in winter 2004 (beginning in December 2003 in response to a court ruling) the park initiated regulations requiring all groups of recreational snowmobiles to be guided by a trained operator, limited daily snowmobile numbers, and moved towards requiring most sleds to be the cleanest and quietest commercially available. To prepare the park for the summer, roads were plowed from early March through 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 wildlife to OSVs during December-March of winters 2003-2006 (i.e., December 2004-March 2005 = winter 2005). Surveys were conducted at least twice a week by a pair of observers snowmobiling ≤ 50 km/h along the following 9 road segments: 1) Madison to West Yellowstone (22 km); 2) Madison to Old Faithful (26 km); 3) Madison to Norris (23 km); 4) Norris to Mammoth (26 km); 5) Canyon Village to Lake Butte (26 km); 6) Fishing Bridge to West Thumb (34 km); 7) Canyon Village to Norris (19 km); 8) Old Faithful to West Thumb (27 km); and 9) South Entrance to West Thumb (43 km). High OSV use segments 1-4 were surveyed during all winters. Lower-use segments 5-6 were surveyed during 2003-2005 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 wildlife. Observers traveled a given road segment until a group (i.e., ≥ 1 animal) of wildlife was detected. The observers stopped at a location where approaching OSVs could be observed without disturbing the animals. For each group of wildlife, observers recorded group size and habitat and measured perpendicular distance to the road using laser rangefinders. Habitats were aquatic, burned forest, unburned forest, meadow, or geothermal. We also generated an indicator variable recording whether or not a bison, coyote, or elk group was on the road.

Our sampling unit was an interaction between a group of OSVs and associated humans and a group of wildlife within 500 meters of the road. For each interaction, observers recorded the most extreme human group activity as: 1) no visible reaction; 2) stopped to observe animals; 3) dismounted or exited the OSV; 4) approached animals on foot; or 5) impeded or hastened movement by chasing animals or by forcing animals ahead of vehicles. The approach and impede/hasten categories were combined for all animals except bison because of low frequencies of impede/hasten activities.

Observers recorded the response behaviors of wildlife as: 1) no visible reaction to vehicles or humans; 2) looked at OSVs or humans and then resumed their behavior; 3) alarm/attention posture, including rising from bed or agitation; 4) traveled away from OSVs or humans; 5) flight (i.e., quick movement away); or 6) defense (i.e., attacked or charged). They also recorded the number of snowmobiles and coaches and if the OSV group was administrative or guided. Once an interaction was complete, the observers continued the survey along the road segment to locate the next group of wildlife. Wildlife group responses resulting from a reaction to the observer were excluded from the analyses.

We obtained daily measurements of snow water equivalent from the Natural Resources Conservation Service's automated SNOTEL site at West Yellowstone (2,042 meters). We summed the daily snow water equivalent measurements from 1 October through 31 April for each winter to obtain a daily cumulative value (Garrott et al. 2003). We also summed the daily number of OSVs entering the west, south, or east gates for each day of the winter recreation season to obtain a daily cumulative number of OSVs. Data was not available from the north entrance gate.

The survey variable we modeled was *wresp*, the most common wildlife group response ($n = 5,688$) observed during a human/wildlife interaction. We combined the travel, flight, and defense responses into a single "movement" category because their frequencies were low, but represent activities requiring the greatest amount of energy expenditure. We combined the attention/alarm and look-and-resume responses into a single "vigilance" category because they involved increased alertness, but required less energy than a movement response. If the wildlife group did not respond to the human activity, then it was categorized as "none." Thus, we modeled three response categories for each species – none ($n = 3,646$), vigilance ($n = 1,556$), and movement ($n = 486$) – corresponding to activities requiring an increasing amount of energy expenditure.

Model formulation

Candidate sets of models were formulated prior to analyzing the survey data (Appendix A). We developed a base model with terms that were included in every *a priori* model based on their importance in previous analyses (Borkowski et al. 2006). Base model terms included: 1) year (*year*); 2) animal group size (*sppnum*); 3) distance from road (*dist*); 4) human group activity (*hact*); 5) human/wildlife interaction time (*intxn*); 6) number of snowmobiles (*sb*); 7) number of coaches (*coach*); 8) *sppnum*dist* interaction (bison, elk, and swans only due to sample size constraints); and 9) an on-road indicator for the wildlife group (*onroad*; non-avian species only). We then added combinations of the following covariate effects to this base model: 1) habitat (*hab*); 2) cumulative OSV visitation (*cumvis*); and 3) interactions *sppnum*hab*, *year*cumvis*, *dist*hact*, *sppnum*hact*, *intxn*dist*, and/or

*intxn*sppnum*. There was only 1 habitat for swans (aquatic). Also, only 2 interactions (*year*cumvis* and *intxn*dist*) could be estimated for bald eagles and coyotes because of the limited number of observations.

The covariate estimates for the quantitative variables group size, distance from road, and cumulative visitation were hypothesized to be negative for the movement logit $L_0(x)$ and vigilance logit $L_I(x)$, while the estimates for interaction time and number of snowmobiles and coaches were hypothesized to be positive. In other words, these logits (or, equivalently, the odds) were expected to decrease as group size, distance to the road, or cumulative number of OSVs increased. The logits were also expected to decrease as the human/wildlife interaction time, number of snowmobiles or coaches decreased.

Estimated effects for the categorical on-road indicator covariate were hypothesized to be positive for the two logits when bison, coyote, or elk groups were on the road. Formulating *a priori* hypotheses for the categorical covariates human activity and habitat were more complicated because the multiple parameter estimates were constrained to sum to zero. We expected animals to respond more frequently and intensively as human activity became more directed and pronounced towards the wildlife group. Thus, we hypothesized the parameter estimate for the movement and vigilance logits would be positive if humans approached wildlife on foot and negative if humans did nothing. For habitat, we expected estimates to be negative when wildlife groups were in cover (e.g., forest) and positive when wildlife groups were in open habitats (i.e., meadow, thermal, aquatic). Habitat was not considered for coyotes and only forest, burned forest, and meadow habitats were considered for bald eagles because of the limited numbers of observations across the habitat categories.

Given the complexity of the Yellowstone ecological system and potential recreational effects, it would be surprising for an additive effects model to adequately represent the relationship between the covariates and the wildlife group response. In other words, there is no reason to assume that the effect of one covariate on the response is independent of the levels of another covariate. Hence, we also formulated predictions for 7 interactions between covariates. We hypothesized: 1) the effects of cumulative OSV visitation on the wildlife response would vary across winters (*cumvis*year*) because of differences in visitation numbers across years; 2) the negative effect of distance would be smaller for larger wildlife groups (*sppnum*dist*) because group size would no longer be a large mitigating factor when groups were far enough away from the road (i.e., the magnitude of the reduction in the odds due to increasing the group size becomes smaller the farther the group is from the road); 3) the negative effect of distance would be larger for longer interaction times (*dist*intxn*) because interaction time would no longer be a large mitigating factor when groups were far enough away from the road; 4) the negative effect of group size would be larger for longer interaction times (*sppnum*intxn*) because interaction time would no longer be a large mitigating factor when groups were larger; 5) the effects of distance to mitigate a wildlife response would vary based on the human activity (*dist*hact*) because the odds of eliciting a response when approaching wildlife should be smaller the further animals were from humans and OSVs; 6) the effects of group size to mitigate a wildlife response would vary based on the human activity (*sppnum*hact*) because the odds of eliciting a response when humans approach animals should be smaller as group size increases.; and 7) the effects of group size to mitigate a wildlife response would vary based on the habitat (*sppnum*hab*) because the odds of eliciting a response when humans approach animals should be smaller for less open habitats (e.g., forest).

Multinomial logits regression (Stokes et al. 1996, Hosmer and Lemeshow 2000, Allison 2003) was used to fit each model for each species because there were three response categories (N, V, and M). 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 M response, V response, and N response given $\mathbf{x} = (x_1, x_2, \dots, x_p)$ is a vector of model covariates. The ratio $\pi_a(\mathbf{x})/\pi_2(\mathbf{x})$ is called an odds. We treated no response as the baseline response by selecting $\pi_2(\mathbf{x})$ to be in the denominator of each odds. For example, if $\pi_0(\mathbf{x})/\pi_2(\mathbf{x}) = 2$, then the probability of an M response is twice the probability of an N response given covariate conditions \mathbf{x} . We modeled the logarithm of the odds (i.e., the logit) rather than the odds themselves because the parameter estimates under this transformation are approximately normally distributed for large samples. The logit parameters were fit using the SAS LOGISTIC procedure (SAS Institute 2002). Model AIC (Akaike information criterion) statistics were also output from which AIC_C values were computed.

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 $\beta_j x_i^*$ where (i) $x_i^* = x_i$ for the linear form, (ii) $x_i^* = \sqrt{x_i}$ for the moderated form, and (iii) $x_i^* = x_i$ 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 wildlife group size from 2 to 4 may reduce the odds of observing a movement response, while increasing the group size from 15 to 20 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 86 multinomial logit models for bison and elk, 36 models for swans, 12 models for bald eagles, and 6 models for coyotes 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 general form for each fitted logit model from the *a priori* model set having main and/or interaction effects is:

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

For the categorical variables year, on-road, habitat, and human activity, the x_i^* (or x_j^*) in each multinomial logits model were indicator variables corresponding to categorical levels of that variable. For a categorical variable or an interaction involving a categorical and a quantitative variable, the number of estimated parameters was one less than the number of categorical levels per logit. There was only one estimated parameter per logit for a quantitative variable or an interaction involving two quantitative variables.

For each model there were $3^6 = 729$ possible combinations of quantitative covariate effect forms because group size, distance from road, number of snowmobiles, number of coaches, interaction time, or cumulative visitation could each assume one of three forms. To address a problem of such high dimensionality, we used a sequential model selection process consistent with the *a priori* model and covariate form specifications (Borkowski et al. 2006, Appendix C). We began the process by fitting all *a priori* models with linear forms for the quantitative covariates and then selecting the “best” models for each species having the smallest AIC_C values. The number of “best”

models varied across species because they were based on cutoffs where large gaps in AIC_C values occurred. For example, the AIC_C values for the 24th and 25th best models for bison were 8.46 and 9.95, respectively, indicating that only the 24 best *a priori* models should be studied. For elk, however, the AIC_C values for the 32nd and 33rd best models were 10.57 and 11.10, respectively, indicating that the 32 best *a priori* models should be studied. We did not select fewer models because it was possible to observe a large improvement in an AIC_C value after covariate transformation. Thus, we advise observing the effect of covariate transformations on more than just the initial models differing in AIC from the best initial model by less than 2 units or by selecting a predetermined number of top models.

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. AIC_C values were calculated for these models. Similarly, the same linear effect was replaced with a threshold form and the 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 AIC_C value. Increments or decrements of 5 meters for distance from road, 1 animal for group size, 500 OSVs for cumulative visitation, 6 seconds for interaction time, and 1 vehicle for snowmobiles and coaches were used to select a threshold. The greatest improvements in AIC_C occurred with a group size threshold for bison, elk, and swans and an interaction time threshold for bald eagles and coyotes. There were also large improvements in AIC_C with a distance from road threshold for bison, bald eagles, and coyotes and a moderated form for swans.

Once AIC_C values corresponding to the best models for linear, moderated, and threshold forms of the first covariate were determined, variable forms yielding models with the best AIC_C values were selected and the sequential assessment process was repeated for the second quantitative covariate, yielding another set of AIC_C values. The variable forms yielding the models with the best AIC_C values were retained. This process was repeated until all quantitative covariates were examined with linear, moderated, and threshold forms. The final models were assessed to determine relationships between covariates, interactions, and the wildlife group responses. The covariates were examined in order of distance from road, group size, interaction time, cumulative visitation, and numbers of snowmobiles and coaches during this sequential process.

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 AIC_C value. We removed any model main effects or interactions that improved the current best AIC_C value. This step generally corresponded to the removal of main effects or interactions with large P -values. We also attempted to simplify models by combining 2 levels of a categorical covariate having similar parameter estimates. We replaced cumulative visitation with the quantitative covariate cumulative snow water equivalent because of a strong correlation between these covariates. We retained cumulative snow water equivalent if the current best AIC_C value was improved. In addition, we included the categorical covariate human group type (*gtype*) indicating whether OSVs were driven by staff or visitors.

Odds Ratios and Predicted Probabilities

Parsimonious post-hoc models consistent with the assessment results for the *a priori* models were used to generate predicted probability plots and odds ratios from the logit estimates. For covariate vectors x_1 and x_2 , the

odds of a wildlife group response requiring energy expenditure for vigilance and a wildlife group response requiring negligible or no energy expenditure under condition x_1 to that under condition x_2 is denoted

$OR_1(\mathbf{x}_1, \mathbf{x}_2) = \frac{\hat{\pi}_0(\mathbf{x}_1)/\hat{\pi}_2(\mathbf{x}_1)}{\hat{\pi}_0(\mathbf{x}_2)/\hat{\pi}_2(\mathbf{x}_2)}$. The odds of a wildlife group response requiring energy expenditure for

movement (M) and a wildlife group response requiring negligible or no energy expenditure under condition x_1 to

that under condition x_2 is denoted $OR_2(\mathbf{x}_1, \mathbf{x}_2) = \frac{\hat{\pi}_1(\mathbf{x}_1)/\hat{\pi}_2(\mathbf{x}_1)}{\hat{\pi}_1(\mathbf{x}_2)/\hat{\pi}_2(\mathbf{x}_2)}$. For each quantitative variable, x_1 and x_2 are

selected so the odds ratio was calculated for a one unit of measurement increase. For each categorical variable, x_1 and x_2 were selected so the odds ratio was calculated for a categorical change from its baseline (i.e., on the road for the on-road indicator, no response for human activity, and meadow for habitat). For quantitative covariate estimates, or interaction estimates between two quantitative covariates, the odds ratio (OR) associated with a one-unit increase were found by exponentiation of the parameter estimate (i.e., $OR = e^{\text{estimate}}$). We took the reciprocal ($1/OR$) to get the odds ratio associated with a one-unit decrease (i.e., $1/OR = 1/e^{\text{estimate}} = e^{-\text{estimate}}$). For categorical variable estimates, or for interaction estimates between quantitative and categorical covariates, the odds ratios were found by exponentiation of the difference in estimates between the effect of interest and the baseline (i.e., $OR = e^{\text{effect} - \text{baseline}}$ or $1/OR = e^{\text{baseline} - \text{effect}}$). The OR value represents the odds ratio for comparing an effect to the baseline while the $1/OR$ value represents the odds ratio for comparing a baseline to the effect. In all analyses, no response is the baseline group response.

Though odds ratios provide useful information regarding odds, they do not directly provide information regarding the probabilities associated with each response category. It is very useful for interpretation if patterns in the predicted probabilities $\hat{\pi}_0(\mathbf{x})$, $\hat{\pi}_1(\mathbf{x})$, and $\hat{\pi}_2(\mathbf{x})$ can be determined for different covariate x vectors because predicted response probabilities can be directly compared, while odds ratios comparisons are relative to a baseline response. Fortunately, for any x , estimates of the predicted probabilities $\hat{\pi}_0(\mathbf{x})$, $\hat{\pi}_1(\mathbf{x})$, and $\hat{\pi}_2(\mathbf{x})$ can be calculated from the predicted logits.

Because there were an infinite number of possible covariates conditions, scenarios for predicted response probabilities for bison, elk, and swans were calculated using the fitted logit models by judiciously selecting sets of covariate levels. The scenarios reflect varying levels of distance from road, group size, and cumulative number of OSVs at specific within-season dates, while allowing examination of all human activity and habitat effects on the bison or elk group response. The mean interaction times for the human activity categories were calculated from the data for each species and used as the values of interaction time in each scenario. For bison and elk, separate mean interaction times for each human activity category were calculated for both on-road indicator categories (i.e., animals on or off the road). Predicted probability plots were not generated for bald eagles and for coyote because of the small number of observations.

For each scenario, we evaluated the potential for habituation to cumulative OSV traffic by comparing response probabilities at the start of the winter season, on January 31, and on February 28. The respective cumulative OSVs for January 31 and February 28 were 15,330 and 29,532 in 2003, 10,657 and 19,529 in 2004, 8,691 and 17,069 in

2005, and 11,671 and 20,453 in 2006. Probability estimates were averaged over the four winter seasons. The responses of bison and elk during human/wildlife interactions were examined at distances of 50 meters and near the road (at 5 meters or on the road), and for group sizes of 4 and 8 bison or elk. The number of OSVs was set to 4 snowmobiles. For bison, the mean on-road and off-road interaction times for each level of human group activity, respectively, were 2.1 and 2.0 minutes for impede/hasten, 3.0 and 2.7 minutes for approach, 2.7 and 2.5 minutes for dismount, 2.4 and 2.1 minutes for stop but not dismount, and 1.1 and 0.7 minutes for no reaction. For elk, the mean on-road and off-road interaction times, respectively, were 3.1 and 3.9 minutes for approach, 4.3 and 3.8 minutes for dismount, 3.3 and 3.0 minutes for stop but not dismount, and 2.1 and 1.0 minutes for no reaction. The responses of swans during human/wildlife interactions were examined for two OSV cases (1 snowmobile or 1 coach) and group sizes of 1 and 7 swans. The mean interaction times for swans were 5.8 minutes for approach, 4.6 minutes for dismount, 2.9 minutes for stop but not dismount, and 0.9 minutes for no reaction. Because the only habitat for swans was aquatic, the covariate for habitat was replaced by distance from road in the predicted probability plots. Distances of 25, 50, 100, and 200 meters were considered in each plot, in addition to human group activity. Predicted probability plots were generated for each of the combinations.

Abundance, Demography, and Displacement of Wildlife

To evaluate if responses to human disturbance during winter adversely affected the demography of bison and elk, we obtained estimates of abundance, removals, calf ratios, and cause-specific mortality for bison and elk in central Yellowstone from Fuller (2006) and Garrott et al. (2006), respectively. Elk in the west-central portion of Yellowstone are non-migratory and, as a result, not subject to human harvests or management removals (Garrott et al. 2003). Thus, we regressed estimates of elk abundance directly on cumulative visitation each year during 1967-2006. Conversely, there were large, irregularly spaced management removals of central Yellowstone bison that significantly influenced their population trend during this period (Fuller 2006). We removed the effects of these culls from the population trend before considering the possible effects of other variables such as human visitation by calculating annual growth rates (r_t) as $r_t = \ln(\text{count}_t) - \ln(\text{count}_{t-1} - \text{removals}_{t-1})$. In other words, we used the number of bison remaining to reproduce at time $t-1$ after the removals to estimate r_t and regressed these growth rates on cumulative visitation each year during 1966-2006. We also regressed bison counts directly on cumulative visitation.

For elk in central Yellowstone, there is a significant negative relationship between spring calf:cow ratios, which are considered an index of annual recruitment, and the severity of snow pack conditions as indexed by cumulative snow water equivalent at the Madison Plateau SNOTEL site (April calf:cow ratio = $350 \times \exp(-\text{SWE}_{\text{ACC}} \times 0.00046)$, $R^2 = 0.91$, Garrott et al. 2003:41). Likewise, spring calf ratios for central Yellowstone bison are significantly and negatively related to cumulative snow water equivalent at the Canyon SNOTEL site (spring calf:cow ratio = $0.27 + (-0.000022 \times \text{SWE}_{\text{ACC}})$, $R^2 = 0.20$, Fuller 2006). We used these relationships to remove the effects of snow water equivalent from the spring calf ratios for bison and elk before considering the possible effects of cumulative visitation on calf survival. We calculated differences between predicted and observed calf ratios across the range of observed cumulative snow water equivalents and regressed these residuals, for which the effects of snow water equivalent were removed, on cumulative visitation. We also regressed calf ratios directly on cumulative visitation.

To evaluate if responses to human disturbance during winter adversely affected the demography of bald eagles and trumpeter swans, we regressed counts of nesting eagles, fledgling eagles, resident swans, and cygnets (McEneaney 2006) on cumulative visitation. We also monitored the distribution of swans in and near Yellowstone during winter 2003 by conducting weekly swan surveys on road segments along the Madison River, Firehole River, Yellowstone River, and Yellowstone Lake. Also, the Avian Ecology and Management Program in Yellowstone conducted aerial surveys for swans in and near Yellowstone each month during November through April.

RESULTS

The public OSV season lasted 72 days in 2003, 89 days in 2004, 72 days in 2005, and 82 days in 2006. The mean and standard deviation (SD) of daily OSVs entering the West Entrance Station were 320 ± 114 in 2003, 178 ± 59 in 2004, 156 ± 70 in 2005, and 181 ± 56 in 2006. Maximum daily numbers were 573 on February 20, 2003, 330 on February 15, 2004, 324 on February 23, 2005, and 338 on December 30, 2005 (winter 2005-06). Peak visitation typically occurred on weekends and holidays, while fewer vehicles entered the park on weekdays. Cumulative OSVs entering the West Entrance Station totaled 23,073 in 2003, 15,846 in 2004, 11,199 in 2005, and 14,856 in 2006. Peak snow water equivalents (centimeters) at the West Yellowstone SNOTEL site were 20.8 in 2003, 30.7 in 2004, 25.7 in 2005, and 36.1 in 2006. Thus, snow pack during our study was lower than the 37-year average of 26.6 centimeters in 2003 and above average in 2006 (Figure 1). Ambient temperatures were moderate in winters 2003-2006, with minimum daily temperatures during December through April ranging from -32 to 3°C at the Madison Plateau SNOTEL site and -41 to 3°C at the West Yellowstone SNOTEL site.

We observed 5,688 interactions between groups of wildlife and OSVs. Sixty-six percent of humans on OSVs that observed groups of wildlife showed no visible reaction and did not stop, 19% stopped to observe but remained on or inside their OSV, 8% stopped and dismounted their OSV, and 7% approached, impeded, or hastened the movement of bison, elk, or coyotes with the OSVs. For bison, 80% of responses to OSVs and associated human activities were characterized as no apparent response, 9% look/resume, 3% attention/alarm, 5% travel, 2% flight, and $<1\%$ defensive. For elk, 48% of responses were characterized as no response, 27% look/resume, 17% attention/alarm, 5% travel, 2% flight, and $<1\%$ defensive. For swans, 57% of responses were characterized as no response, 21% look/resume, 12% attention/alarm, 9% travel, and 1% flight. For bald eagles, 17% of responses were characterized as no response, 64% look/resume, 9% attention/alarm, 4% travel, and 6% flight. For coyotes, 39% of responses were characterized as no response, 29% look/resume, 8% attention/alarm, 14% travel, 9% flight, and 1% defensive.

For bison, the 2 best models resulting from the sequential model selection process had AIC_C values of 2,460 and 2,462, with Akaike model weights of $w_k = 0.45$ and 0.17. All other models had $\Delta\text{AIC}_C > 2.7$ (Table 1). The 6 best AIC_C -based models included year, group size, distance from road, on-road indicator, human activity, interaction time, number of snowmobiles and coaches, habitat, and cumulative visitation, with threshold values of 8 bison for group size, 85 meters for distance, 3.0 minutes for interaction time, 8 snowmobiles, 3 coaches, and 28,500 OSVs for cumulative visitation. The 6 best models also included the following interactions with Akaike predictor weights (w_p): *sppnum*dist* (1), *dist*hact* (0.69), *intxn*dist* (0.16), *intxn*sppnum* (1), *sppnum*hab* (0.22), and *year*cumvis* (0.97); though the *dist*hact* interaction was not statistically significant ($P = 0.15$). The estimated odds of responses

by bison decreased with increasing group size and with distance to road, but increased with increasing numbers of snowmobiles and coaches or when bison groups were on the road (Table 2). The odds of observing no response relative to a movement response were 17 times greater for each additional 10 animals in the group and 912 times greater for each 100-meter increase in distance from the road. However, the effect of increasing distance from roads at reducing the odds of a movement response decreased as bison groups got larger (*sppnum*dist*). The odds of observing a movement response were 1.1 times greater for each additional snowmobile, 1.5 times greater for each additional coach, 2 times greater when humans approached on foot, 7 times greater when OSVs impeded or hastened bison, 17 times greater when bison were on the road, and 17 and 1.6 times greater in aquatic or thermal habitat, respectively.

For elk, the 3 best models resulting from the sequential model selection process had AIC_C values of 1,825, 1,825, and 1,826, with Akaike model weights of $w_k = 0.27, 0.22, \text{ and } 0.16$. All other models had $\Delta AIC_C > 2.0$ (Table 1). The 6 best AIC_C -based models included year, group size, distance from road, on-road indicator, human activity, interaction time, number of snowmobiles and coaches, habitat, and cumulative visitation, with a moderated form for distance and threshold values of 8 elk for group size, 5.7 minutes for interaction time, and 1 snow coach (Table 2). The 6 best models also included the following interactions with Akaike predictor weights (w_p): *sppnum*dist* (1), *sppnum*hact* (1), *intxn*dist* (0.80), *intxn*sppnum* (1), *sppnum*hab* (0.49), and *year*cumvis* (0.30). The estimated odds of responses by elk increased with increasing interaction time and when elk groups were on the road (Table 3). The odds of observing vigilance or movement responses relative to no response were 3-4 times greater for each 1-minute increase in interaction time. However, the effect of increasing interaction time at increasing the odds of a movement response decreased as elk groups got larger (*intxn*sppnum*) or the elk groups were farther from the road (*intxn*dist*). The odds of observing a movement response were 31 times greater when elk were on the road. The effects of human activities and habitat on elk were highly dependent on elk group size (*sppnum*hact*, *sppnum*hab*), with larger groups magnifying the odds of observing a vigilance or movement response when humans approached elk on foot or the habitat was aquatic or unburned forest. Conversely, the odds of observing a movement response decreased with larger groups in thermal habitat.

For trumpeter swans, the 2 best models resulting from the sequential model selection process had AIC_C values of 1,873 and 1,874, with Akaike model weights of $w_k = 0.30 \text{ and } 0.17$. All other models had $AIC_C > 2.1$ (Table 1). The 6 best AIC_C -based models included year, group size, distance from road, human activity, interaction time, number of snowmobiles and coaches, and cumulative visitation, with a moderated form for distance and threshold values of 7 swans for group size, 8.0 minutes for interaction time, and 1 snow coach. The 6 best models also included the following interactions with Akaike predictor weights (w_p): *dist*hact* (0.24), *intxn*dist* (0.59), *intxn*sppnum* (0.52), and *year*cumvis* (0.71). The estimated odds of responses by trumpeter swans decreased with increasing group size and distance to road, but increased with increasing interaction time and numbers of snowmobiles (Table 4). The odds of observing no response relative to movement responses were 6 times greater for each additional 10 birds in the group and 8 times greater for each 100-meter increase in distance from the road. The odds of observing a movement response were 1.2 times greater for each 1-minute increase in interaction time, 1.1 times greater for each additional snowmobile, and 3 times greater when humans approached on foot.

For bald eagles, the 2 best models resulting from the sequential model selection process had AIC_C values of 412 and 414, with Akaike model weights of $w_k = 0.61$ and 0.24. All other models had $\Delta AIC_C > 3.5$ (Table 1). The 6 best AIC_C -based models included year, group size, distance from road, human activity, interaction time, number of snowmobiles and coaches, habitat, and cumulative visitation, with a threshold values of 250 meters for distance, 1.4 minutes for interaction time, 18 snowmobiles, and 1 snow coach. The 6 best models also included the *intxn*dist* and *year*cumvis* effects, with Akaike predictor weights (w_p) of 0.85 and 0.01, respectively. The estimated odds of responses by bald eagles decreased with distance to road, but increased with numbers of snowmobiles (Table 5). The odds of observing no response relative to a movement response were 4 times greater for each 100-meter increase in distance from the road. The odds of observing a vigilance response were 60 times greater for each 1-minute increase in interaction time and 54 times greater when they were in burned forest than meadow habitat. The odds of observing a movement response were 1.3 times greater for each additional snowmobile and 5 times greater when humans approached on foot.

For coyotes, the best model was the general model with an AIC_C value of 275.5 and Akaike model weight of $w_k = 0.85$. All other models had $\Delta AIC_C > 4.2$ (Table 1). The 6 best AIC_C -based models included year, group size, distance from road, on-road indicator, human activity, interaction time, number of snowmobiles and coaches, and cumulative visitation, with threshold values of 2 coyotes for group size, 65 meters for distance, 1.1 minutes for interaction time, 7 snowmobiles, and 1 snow coach. The 6 best models also included the *intxn*dist* and *year*cumvis* effects, with Akaike predictor weights (w_p) of 0.05 and 0.10, respectively. The estimated odds of responses by coyotes decreased with distance to road, but increased with increasing interaction time and when humans approached on foot (Table 6). The odds of observing no response relative to a movement response were 163 times greater for each 100-meter increase in distance from the road. The odds of observing a movement response were 25 times greater for each 1-minute increase in interaction time and 10 times greater when humans approached.

There were no significant increases or decreases in the odds of movement responses for any wildlife species as cumulative OSV traffic increased through the winter. However, we observed significant decreases in the odds of vigilance responses by bison and swans as cumulative OSV traffic increased (Tables 2-6). The odds of observing a no response relative to a vigilance response by bison and swans were 1.04 and 1.08 times greater, respectively, for each additional 1,000 OSVs. In contrast, there was a significant increase in the odds of vigilance responses by elk as the cumulative number of OSVs increased through the winter. The odds of observing a vigilance response relative to no response by elk was 1.03 times greater for each additional 1,000 OSVs. The *cumvis*year* interaction indicated the effects of cumulative OSV traffic varied across winters for groups of bison and trumpeter swans. The odds of observing a movement response by bison as cumulative visitation increased were greater during winters 2003-2005 compared to winter 2006. In contrast, the odds of observing a movement response by swans decreased as cumulative visitation increased during winters 2003-2005 compared to winter 2006.

The post hoc exploratory analyses did not result in any improvement when cumulative visitation was replaced with cumulative snow water equivalent or human group type was added to the models. Also, the exploratory model for bison was the same as the *a priori* model (Appendices D and I). The best *a priori* model for elk ($AIC_C = 1824.7$) was improved by removing distance to road ($P = 0.14$), human activity ($P = 0.15$), number of snowmobiles ($P =$

0.70), and *sppnum*dist* ($P = 0.06$), and replacing group size ($P = 0.36$) and habitat ($P = 0.0004$) with *sppnum*hab* ($AIC_C = 1808.0$; Appendices E and J). The best *a priori* model for trumpeter swans ($AIC_C = 1872.7$) was improved by removing *sppnum*dist* ($P = 0.70$) and *dist*intxn* ($P = 0.26$; $AIC_C = 1866.6$; Appendices F and K). The best *a priori* model for bald eagles ($AIC_C = 412.4$) was improved by removing group size ($P = 0.31$; $AIC_C = 403.7$; Appendices G and L). The best *a priori* model for coyotes ($AIC_C = 275.5$) was improved by removing the group size ($P = 0.20$), on-road indicator ($P = 0.91$), snowmobile ($P = 0.25$), and coach ($P = 0.94$) covariates ($AIC_C = 249.7$; Appendices H and M).

Changes in predicted movement response probabilities of bison as visitation increased across winter for each human activity were: negligible in unburned forest, burned forest, and meadow habitats; decreased slightly in thermal habitats; and increased slightly in aquatic habitat or when bison were on the road and impeded or hastened by OSVs (Figures 2-5). Predicted vigilant response probabilities decreased across the winter for each covariate combination. For increasing bison group size, predicted movement probabilities increased slightly for all covariate combinations when distance was 50 meters. The largest increases occurred in aquatic habitats. When distance was reduced to 5 meters, however, predicted movement probabilities decreased slightly in thermal and burned forest habitats, while changes were negligible in aquatic and meadow habitats. These predictions were consistent with the significant *sppnum*dist* and *dist*hact* interaction estimates in the final bison model. Predicted vigilance response probabilities decreased with increasing group size for each covariate combination. For human activities, predicted movement probabilities were highest for all covariate combinations when OSVs impeded or hastened the bison group and lowest when humans did nothing. The probability profiles across human activity categories were similar in unburned forest, burned forest, and thermal habitats, while vigilance and movement response probabilities were smaller in meadow habitats.

Changes in predicted movement response probabilities of elk as visitation increased across winter for each human activity were negligible for all covariate combinations, while predicted vigilant response probabilities decreased across the winter (Figures 6-9). These predictions were consistent with the insignificant effect of cumulative visitation on the movement response logit and the significant positive cumulative visitation effect on the vigilance logit. There was a small decrease in both predicted movement and vigilance probabilities for all covariate combinations as distance of elk groups from the road increased. Predicted movement probabilities decreased slightly as elk group size increased in burned forest and thermal habitats, but were negligible in forest and meadow habitats. The only increases in predicted movement probabilities with increasing group size occurred in aquatic habitats and when humans approached elk on foot. These predictions are consistent with the significant *sppnum*hact* and *sppnum*hab* interaction estimates in the final elk model. Predicted vigilance response probabilities decreased with increasing group size for each covariate combination. Predicted movement probabilities were highest for all covariate combinations when humans approached elk and decreased as the level of human interaction decreased to dismount, stop but not dismount, and no reaction. Vigilance and movement probability profiles across human activities were similar for unburned forest, burned forest, and thermal habitats, but smaller in meadow habitats. For all covariate combinations, predicted movement probabilities were highest in aquatic habitats, followed by forest, meadow, burned forest, and thermal habitats.

Changes in predicted movement response probabilities of trumpeter swans decreased from the start of winter to January 31st, but then increased slightly from January 31st to February 28th for all covariate combinations (Figures 10-13). Predicted vigilance response probabilities decreased through winter for all covariate combinations. Predicted movement and vigilance probabilities decreased for all covariate combinations as group size and distance from road increased. Predicted movement probabilities were highest and similar for all covariate combinations when humans approached on foot and decreased as the level of human interaction decreased to stop but not dismount and no reaction. The predicted movement probabilities were slightly higher for one snow coach compared to one snowmobile under all covariate combinations.

Abundance, Demography, and Displacement of Wildlife

Estimates of elk abundance were positively correlated with cumulative winter visitation during 1967-2006 ($R^2 = 0.21$, $df = 18$, $F = 4.5$, $P = 0.05$). Elk numbers fluctuated around a stable attractor of 500-550 elk during 1967-2002 despite a 20-fold increase in cumulative visitation (Figure 14). Numbers then decreased with cumulative visitation during 2002-2006; though this later relationship was likely due to the effects of restored wolves on elk population dynamics (Garrott et al. 2006). Elk calf ratios were positively correlated with cumulative visitation during 1992-2006 ($R^2 = 0.25$, $df = 14$, $F = 4.3$, $P = 0.06$). However, this relationship was not significant once the effects of snow water equivalent on calf ratios were removed ($R^2 = 0.02$, $df = 14$, $F = 0.3$, $P = 0.60$). Bison counts increased exponentially with cumulative visitation during 1966-1994 (Figure 15), but then decreased and varied irregularly after management removals increased during 1995-2006 ($R^2 = 0.63$, $df = 26$, $F = 41.8$, $P < 0.001$). Bison population growth rates, for which the effects of management culls were removed, were not significantly related to cumulative visitation during 1966-2006 ($R^2 = 0.01$, $df = 27$, $F = 0.1$, $P = 0.78$). Bison calf ratios were not significantly correlated with cumulative visitation ($R^2 = 0.01$, $df = 17$, $F = 0.2$, $P = 0.68$).

Numbers of nesting and fledgling bald eagles in Yellowstone increased incrementally during 1987-2005 (McEneaney 2006) and were not significantly correlated with cumulative visitation (Figure 16; $R^2 < 0.05$, $df = 18$, $F < 0.8$, $P > 0.40$). Numbers of resident adult/subadult and cygnet trumpeter swans decreased during 1961-2005 (McEneaney 2006) and were negatively correlated with cumulative visitation (Figure 17; adults: $R^2 = 0.37$, $df = 23$, $F = 13.0$, $P = 0.002$; cygnets: $R^2 = 0.13$, $df = 23$, $F = 3.1$, $P = 0.09$). Counts of trumpeter swans on the north and west shores of Yellowstone Lake and along the Yellowstone River peaked in late November 2002 at 496 swans, then decreased through late February 2003 as open water sections of the Yellowstone River diminished (Figure 18). Conversely, counts of trumpeter swans along the Madison and Firehole Rivers increased during late December 2002, peaked at 47 swans in mid-January 2003, and remained relatively high through early February. As winter progressed and open water areas in the park diminished, the proportion of the swan population counted within Yellowstone decreased compared to areas outside the park (Table 7).

DISCUSSION

Bald eagles, bison, coyotes, elk, and trumpeter swans 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 bison responding less frequently (20%) than swans (43%), elk (52%), coyotes (61%), or bald eagles (83%). This

difference was due to increased vigilance responses by swans (33%), elk (44%), coyotes (37%), and bald eagles (73%) compared to bison (12%). The frequency of higher-intensity movement responses was similar (8-10%) among bison, bald eagles, elk, and swans, but higher (24%) for coyotes. Similar to other studies, we found that the odds of a movement response significantly increased when humans stopped, dismounted, and approached wildlife on foot (Stalmaster and Kaiser 1998, Steidl and Anthony 2000, Papouchis et al. 2001, Gonzá'lez et al. 2006). Also, the likelihood and intensity of responses by these wildlife species increased significantly if animals were on or near roads, animal groups were smaller, interaction time increased, or numbers of snowmobiles and coaches increased. There were thresholds on the odds of eliciting a response by wildlife for several of these covariates. For example, the effects of group size at reducing the odds of a response reached a maximum at 7-8 animals for bison, elk, and swans. Conversely, the effects of interaction time at increasing the odds of a response were reached at quite different thresholds, including 1 minute for coyotes and eagles, 3 minutes for bison, 6 minutes for elk, and 8 minutes for swans. The odds of eliciting a movement response by wildlife were higher for coaches than snowmobiles, but the maximum effect was reached at a threshold of ≤ 3 coaches. In contrast, there was no threshold for elk and swans with each additional snowmobile and the threshold was 7-18 snowmobiles for bison, coyotes, and eagles.

Borkowski et al. (2006) sampled interactions between groups of bison and elk and OSVs in Yellowstone during 1999-2003 when visitation was 2-3 times higher than during 2004-2006. Similar to our study, they found elk responded 3 times more (52%) than bison (19%) during interactions with OSVs due to increased vigilance responses (elk: 44%; bison: 10%). In addition, the frequency of higher-intensity movement responses by bison and elk were similar (8-9%) and relatively low 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 meters.

The responses of bald eagles in our study (9% attention/alarm, 6% flight) were similar to those (3-17% alert/flight) of nesting eagle in Voyageurs National Park, Minnesota to watercraft passing within 800 meters of their nests (Grubb et al. 2002). However, Shea (1979) reported swans at Harriman State Park in Idaho had more pronounced reactions to human disturbance than swans in Yellowstone. Swans in Idaho took flight when approached by a person on skis or snowmobile and often moved several kilometers to another stretch of river (Shea 1979). Conversely, swans on the Yellowstone and Madison Rivers generally reacted to humans by swimming farther away while continuing to feed (Shea 1979). Several studies concluded eagle response rates were affected by distance, number of vehicles/event, interaction duration and rates, and time of day (Grubb et al. 2002, Gonzá'lez et al. 2006). Thus, buffer zones 400-800 meters wide, where watercraft or vehicles are not permitted to stop, have been recommended for sensitive foraging areas and nesting sites of eagles elsewhere (Stalmaster and Kaiser 1998,

Grubb et al. 2002, Gonzá'lez et al. 2006). During our study, however, there were few responses by eagles when the distance to OSVs and associated humans was >250 meters. Thus, the buffer zone that prohibits stopping within 400 meters of the eagle nest between West Yellowstone and Madison Junction has likely been somewhat effective at reducing disturbances to this pair. However, the majority of OSVs entering the park still drive approximately 55 meters from the nest and it is impossible for visitors to keep >250 meters from eagles in the Firehole and Madison drainages because, even at their widest points, the rivers are often <250 meters from the road.

The comparatively less frequent and lower intensity responses by the wildlife species we studied in Yellowstone suggest there is a certain level of habituation to OSVs and associated human activities. Also, we observed a decrease in the odds of vigilance responses by bison and swans as cumulative OSV traffic increased through the winter. Furthermore, the effect of increased cumulative visitation at increasing the odds of movement by bison was less in the high visitation year of 2003 (72,560 visitors) compared to relatively low visitation years of 2004-2006 (<49,000 visitors). 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 activity when the activity is controlled, predictable, and not harmful to the animals (Schultz and Bailey 1978, Thompson and Henderson 1998). Aune (1981) and Hardy (2001) concluded bison and elk habituated to the presence and patterns of human activity in Yellowstone. Also, Borkowski et al. (2006) reported the likelihood of an active response by bison during 1999-2004 in Yellowstone decreased within winters having the highest visitation, suggesting some further habituation to OSV recreation with increasing exposure to vehicles during the season. Shea (1979) reported swans wintering within 55 meters of the road along the Madison River, which had high snowmobile traffic, showed more tolerance to winter visitors than swans on the Yellowstone River where levels of traffic were lower. Likewise, Aune (1981) reported swans in Yellowstone appeared to habituate to moving snowmobiles, but often flew or swam away if vehicles stopped and/or humans approached on foot or skis. Several studies have reported the responses of eagles to recreation activities decreased over the course of a day or season (Stalmaster and Kaiser 1998, Steidl and Anthony 2000, Grubb et al. 2002, Gonzá'lez et al. 2006).

There are several characteristics of winter recreation in Yellowstone that likely facilitate behavioral habituation by wintering animals to OSV traffic (Aune 1981, Hardy 2001). All OSVs traveled through our study area in predictable ways, remaining confined to roads and typically without humans threatening or harassing wildlife. Few people ventured far from roads, established trails, or areas of concentrated human activities (e.g., warming huts, geyser basin trails). Also, the minimal risk of mortality associated with human presence may reduce avoidance responses by these species (Gill et al. 2001a). Hunting is illegal in the park (National Park Service Protective Act of 1894; 16 USC 1, 5§26) and few animals were hit and killed by OSVs each winter. Gunther et al. (1999) reported 10 bison, 3 elk, 2 coyotes, 1 red fox (*Vulpes vulpes*), and 1 pine marten (*Martes martes*) were killed by snowmobiles in Yellowstone during 1989-1998. For comparison, almost 600 mammals were killed within the same area by wheeled vehicles during these years. The road-kill attributed to wheeled vehicles was significantly greater than snowmobiles across all road segments after standardizing the data to account for open road days per vehicle type (Gunther et al. 1999). Likewise, 7 of 7 vehicle strikes that killed radio-collared elk, and 3 of 4 vehicle strikes that killed radio-

collared bison, in central Yellowstone during 1991-2006 occurred outside the winter recreation season (R. Garrott, Montana State University, and K. Aune, Montana Fish, Wildlife, and Parks, unpublished data).

However, there are complex species-specific differences and interactions among covariates that affect the degree of habituation by wildlife in Yellowstone and which complicate interpretation of recreation effects. For example, elk exhibited a significant increase in the odds of vigilance responses as OSV traffic increased through winter. Also, the effect of increased cumulative visitation at increasing the odds of movement by trumpeter swans was less in 2006 than 2003-2005, perhaps due to the reduced availability of ice-free areas during the hard winter of 2006. Animals can probably only habituate to particular types and levels of human disturbance up to some threshold (Steidl and Anthony 2000), above-which a change in the amount or type of disturbance may drastically alter the likelihood and intensity of their responses (Stalmaster and Newman 1978, White and Thurow 1985). Hence, winter recreational activities in Yellowstone should continue to be conducted in a predictable manner.

Similar to predation risk, an animal's decision of whether to move away from a disturbed area is influenced by factors such as the quality of the occupied site, the distance to and quality of other suitable sites, the relative risk of predation or competition at alternate sites, the investment the individual has made in a site (e.g., energy expenditure), and the individual's nutritional condition (Gill et al. 2001b). Animals should move away from disturbed sites if fitness costs of disturbance are high or, alternatively, fitness costs of disturbance are low, but there is a high availability of alternate habitat elsewhere for animals to relocate. For example, Stalmaster and Kaiser (1998) reported some bald eagles were displaced to secluded areas during disturbances along the Skagit River in Washington. However, there may be little change in numbers with increasing disturbance if there is little alternate habitat where animals can move (Gill et al. 2001b). There is some evidence animals were displaced away from roads with OSV traffic in Yellowstone. Aune (1981) and Hardy (2001) indicated elk were temporarily displaced about 60 meters from busy road segments (e.g., Madison to Old Faithful) as cumulative traffic increased, while Shea (1979) reported swans in Yellowstone often retreated from visitors that stopped by swimming away. Also, 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.

Human disturbance did not appear to be a primary factor influencing the distribution and movements of the wildlife species we studied, suggesting behavioral responses and apparent avoidance of humans in the vicinity of the road were apparently short-term changes that were later reversed. Bison, elk, and swans in Yellowstone used the same core winter ranges during the past three decades despite large winter-to-winter variability in cumulative exposure to OSVs (Craighead et al. 1973, Shea 1979, Aune 1981, Hardy 2001, Bruggeman 2006). Bruggeman (2006) found that factors influencing resource availability—including snow pack, population density, and drought—provided the primary impetus for variability in the distribution, movements, and foraging behavior of central Yellowstone bison during winter. Similarly, Messer (2003) reported the distribution of elk in central Yellowstone during winter was primarily influenced by snow mass and heterogeneity. During 2002-2006, a pair of bald eagles took up residence in a large tree nest located 55 meters from the road approximately 10 kilometers east of West Yellowstone (McEneaney 2006). Despite high OSV and wheeled-vehicle traffic, this pair maintained the territory

throughout the year and fledged 1-2 eaglets in 2002-2003 and 2005 (McEneaney 2006). Furthermore, the area located <100 meters from the road along the Madison River approximately 11 kilometers east of West Yellowstone has been a traditional nesting area for decades and at least 23 cygnets have fledged from this site since 1983, making it one of the more productive nesting areas in Yellowstone (McEneaney 2006).

While OSVs often elicited no observable movement responses by wildlife, recreational activities can also cause physiological responses such as elevated heart 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. Hardy (2001) 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. 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 different between winters. 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 to wildlife from interactions with OSVs in relation to their total daily energy expenditures because numerous assumptions are required and poorly defined parameter 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 5,000 to >100,000 riders during 1968-1994 (Gates et al. 2005). Counts of central Yellowstone bison increased exponentially over this same period from approximately 400 to 3,400 and annual survival of adult females was high and constant during 1995-2001 (Fuller 2006). Also, population estimates for central Yellowstone elk fluctuated around a dynamic equilibrium of

approximately 500-550 elk during 1968-2004 ($\lambda = 0.99-1.01$; Garrott et al. 2006). The annual survival of adult female elk in this population exceeded 90% and early winter calf ratios indicated healthy reproductive rates prior to the restoration of wolves in 1998 (Garrott et al. 2003). In addition, numbers of nesting bald eagles and fledglings in Yellowstone increased incrementally during 1987-2005 and a pair successfully nested and fledged young 55 meters from the most intensively used road segment for OSV traffic (McEneaney 2006). Thus, any adverse behavioral and energetic effects of OSV recreation to these 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.

The significant, negative correlation between swan counts and OSV traffic was likely spurious because numbers of swans decreased regionally throughout the Greater Yellowstone Area during the past several decades, including the productive Centennial Valley of Montana (Olliff et al. 1999, McEneaney 2006). Decreases in reproductive rates have been detected in eagles exposed to increased recreational activity (Stalmaster and Kaiser 1998, Steidl and Anthony 2000, Gonzales et al. 2006). However, it is unlikely that poor regional production by swans in Yellowstone resulted from winter recreation; especially when swans generally incubate eggs in May and hatch young in late June (Olliff et al. 1999) – which is well after the OSV recreation period. Also, as winter progresses and open water areas in the park diminish, the proportion of the swan population within Yellowstone decreases compared to areas outside the park. Thus, relatively few swans were exposed to motorized winter use in the park. Moreover, the area located <100 meters from the road along the Madison River approximately 11 kilometers east of West Yellowstone has been a traditional nesting area for decades and at least 23 cygnets have fledged from this site since 1983, making it one of the more productive nesting areas in Yellowstone (McEneaney 2006).

Resolution of the debate regarding winter recreation in Yellowstone depends, in part, on quantitative evaluations of the effects of OSVs on wildlife. If disturbances have serious fitness effects, then managers are justified in restricting access to wildlife areas. If human presence alters behavior but has no other effects, however, then such measures are not important from a conservation perspective and represent an unnecessary dissipation of effort and funds (Gill et al. 2001a). 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. The wildlife species we studied are acutely aware of their surroundings and any human activity in close proximity will 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 effects to park resources and values (National Park Service 2000).

Monitoring during 1999-2006 in Yellowstone documented the vast majority of winter visitors traveling on OSVs remained on groomed roads, behaved appropriately when viewing wildlife, and rarely approached wildlife except when animals were on or immediately adjacent to the road. These attributes have allowed wildlife 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 provides no evidence that levels and patterns of OSV traffic during the past 35 years adversely affected the demography or population dynamics of the wildlife we studied. Thus, we suggest regulations restricting the levels and travel routes of OSVs during recent years were effective at reducing disturbances to wildlife 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 monitoring. 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.

RECOMMENDATIONS

- Continue to conduct winter recreational activities in a predictable manner with OSV traffic levels at or below those observed during the last 3 years of our study (i.e., <50,000 over-snow visitors).
- Convey information about factors that increase the likelihood of responses by wildlife (e.g., humans dismount and approach animals, animals on or near roads, longer interaction times, larger groups of snowmobiles and coaches) to guides so that they may take actions to minimize wildlife disturbance by visitors under their control.
- Collect additional data over subsequent winters for bald eagles and coyotes to increase sample sizes and statistical power for detecting effects not included in the models. The absence of potential group size effects in the exploratory models for bald eagles and coyotes does not prove this covariate was insignificant regarding responses due to the small number of observations. It is possible the statistical tests were not powerful enough to detect true effects that were smaller in magnitude.
- Continue to collect data on the proportions of wildlife group responses that fall into each of the possible response category so that a finer analysis of the response structure within groups and their relation to study covariates can be analyzed. This type of data was not available for the first two years of this study (2003-2004), but is available for the last two years (2005-2006). Many of the potential main effects and interaction effects did not appear in our current models, suggesting either (a) the effects were not truly significant, (b) sizes of the effects were too small to be detected as significant given the variability in the data, or (c) some effects did not appear in the final models as an artifact of the response that was analyzed (i.e., most common response occurring in a wildlife group).
- Use telemetry and/or ground distribution data for bison and elk in Firehole, Madison, and Gibbon drainages to investigate the prediction that selection of habitats increases with increasing distance away from open roads

and, also, intensity of OSV traffic, during the winter use season (Rowland et al. 2004, Wisdom et al. 2005). These analyses should consider potential individual heterogeneity in responses of bison and elk to human recreation to evaluate if some animals live closer to the road corridor (i.e., habituation), while others avoid the road corridor (Papouchis et al. 2001).

- Use data on the pregnancy and survival rates of bison and elk to investigate if responses to human disturbance during winter adversely affected these rates. We also recommend examining indices of nutrition (e.g., allantoin:creatinine; Garrott et al. 1998) for elk, from which the effects of snow water equivalent have been removed, to investigate if responses to human disturbance during winter adversely affected the quantity and/or quality of diet.

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Table 1. Model selection results for the top 6 *a priori* models for bison, elk, trumpeter swans, bald eagles, and coyotes. Each model for a given species contains the base model and the terms indicated. Abbreviations are: *year* (year of study); *dist* (distance from road in meters); *sppnum* (group size); *onroad* (on or off road indicator); *hact* (human activity); *intxn* (interaction time in minutes); *sb* (number of snowmobiles); *coach* (number of coaches); *cumvis* (cumulative daily number of over-snow vehicles); *hab* (habitat); T (variable threshold); K (number of model parameters); ΔAICc (AIC corrected for small sample size); and w_k (AIC model weight).

Bison	Model = <i>year</i> + <i>sppnum</i> (T = 8) + <i>dist</i> (T = 85 m) + <i>onroad</i> + <i>hact</i> + <i>intxn</i> (T = 3.0) + <i>sb</i>(T = 8) + <i>coach</i> (T = 3) + <i>sppnum</i>*<i>dist</i>	K	ΔAICc	w_k
1	<i>hab</i> + <i>cumvis</i> (T = 28500) + <i>dist</i> * <i>hact</i> + <i>intxn</i> * <i>sppnum</i> + <i>year</i> * <i>cumvis</i>	56	0.00	0.45
2	<i>hab</i> + <i>cumvis</i> (T = 28500) + <i>intxn</i> * <i>sppnum</i> + <i>year</i> * <i>cumvis</i>	48	1.98	0.1
3	<i>hab</i> + <i>cumvis</i> (T = 28500) + <i>dist</i> * <i>hact</i> + <i>intxn</i> * <i>sppnum</i> + <i>sppnum</i> * <i>hab</i> + <i>year</i> * <i>cumvis</i>	64	2.71	0.1
4	<i>hab</i> + <i>cumvis</i> (T = 28500) + <i>dist</i> * <i>hact</i> + <i>intxn</i> * <i>dist</i> + <i>intxn</i> * <i>sppnum</i> + <i>year</i> * <i>cumvis</i>	58	3.31	0.0
5	<i>hab</i> + <i>cumvis</i> (T = 28500) + <i>intxn</i> * <i>sppnum</i> + <i>sppnum</i> * <i>hab</i> + <i>year</i> * <i>cumvis</i>	56	3.64	0.07
6	<i>hab</i> + <i>cumvis</i> (T = 28500) + <i>intxn</i> * <i>dist</i> + <i>intxn</i> * <i>sppnum</i> + <i>year</i> * <i>cumvis</i>	50	4.81	0.04
Elk	Model = <i>year</i> + <i>sppnum</i> (T = 8) + $\sqrt{\text{dist}}$ + <i>onroad</i> + <i>hact</i> + <i>intxn</i> (T = 5.7) + <i>sb</i> + <i>coach</i> (T = 1) + <i>sppnum</i>*<i>dist</i>	K	ΔAICc	w_k
1	<i>hab</i> + <i>cumvis</i> + <i>sppnum</i> * <i>hact</i> + <i>intxn</i> * <i>dist</i> + <i>intxn</i> * <i>sppnum</i>	48	0.00	0.27
2	<i>hab</i> + <i>cumvis</i> + <i>sppnum</i> * <i>hact</i> + <i>intxn</i> * <i>dist</i> + <i>intxn</i> * <i>sppnum</i> + <i>sppnum</i> * <i>hab</i> + <i>year</i> * <i>cumvis</i>	56	0.39	0.22
3	<i>hab</i> + <i>cumvis</i> + <i>sppnum</i> * <i>hact</i> + <i>intxn</i> * <i>dist</i> + <i>intxn</i> * <i>sppnum</i> + <i>year</i> * <i>cumvis</i>	54	1.08	0.16
4	<i>hab</i> + <i>cumvis</i> + <i>sppnum</i> * <i>hact</i> + <i>intxn</i> * <i>dist</i> + <i>intxn</i> * <i>sppnum</i> + <i>sppnum</i> * <i>hab</i> + <i>year</i> * <i>cumvis</i>	62	2.08	0.10
5	<i>hab</i> + <i>cumvis</i> + <i>sppnum</i> * <i>hact</i> + <i>intxn</i> * <i>sppnum</i> + <i>sppnum</i> * <i>hab</i>	54	2.81	0.67
6	<i>hab</i> + <i>cumvis</i> + <i>sppnum</i> * <i>hact</i> + <i>intxn</i> * <i>sppnum</i>	46	2.95	0.06
Swan	Model = <i>year</i> + <i>sppnum</i> (T = 7) + $\sqrt{\text{dist}}$ + <i>hact</i> + <i>intxn</i> (T = 8.0) + <i>sb</i> + <i>coach</i> (T = 1) + <i>sppnum</i>*<i>dist</i>	K	ΔAICc	w_k
1	<i>cumvis</i> + <i>intxn</i> * <i>dist</i> + <i>year</i> * <i>cumvis</i>	36	0.00	0.30
2	<i>cumvis</i> + <i>intxn</i> * <i>sppnum</i> + <i>year</i> * <i>cumvis</i>	36	1.14	0.17
3	<i>cumvis</i> + <i>dist</i> * <i>hact</i> + <i>intxn</i> * <i>sppnum</i> + <i>year</i> * <i>cumvis</i>	42	2.14	0.10
4	<i>cumvis</i> + <i>intxn</i> * <i>dist</i>	30	2.22	0.10
5	<i>cumvis</i> + <i>intxn</i> * <i>dist</i> + <i>intxn</i> * <i>sppnum</i> + <i>year</i> * <i>cumvis</i>	38	2.56	0.08

6	<i>cumvis + intxn*sppnum</i>	30	2.77	0.08
Eagle	Model = <i>year + sppnum + dist (T = 250) + hact + intxn (T= 1.4) + sb (T = 18) + coach (T = 1)</i>	K	ΔAICc	w_k
1	<i>hab + intxn*dist + year*cumvis</i>	30	0.00	0.61
2	<i>hab + cumvis + intxn*dist</i>	32	1.89	0.24
3	<i>hab</i>	28	3.52	0.10
4	<i>hab + cumvis</i>	30	5.27	0.04
5	<i>hab + cumvis + intxn*dist + year*cumvis</i>	38	9.04	0.01
6	<i>hab + cumvis + year*cumvis</i>	36	12.31	0.00
Coyote	Model = <i>year + sppnum (T = 2) + dist (T = 65) + onroad + hact + intxn (T= 1.1) + sb (T = 7) + coach (T = 1)</i>	K	ΔAICc	w_k
1		26	0.00	0.85
2	<i>year*cumvis</i>	28	4.24	0.10
3	<i>intxn*dist</i>	28	5.75	0.05
4	<i>cumvis + intxn*dist</i>	30	10.13	0.01
5	<i>cumvis + year*cumvis</i>	34	18.66	0.00
6	<i>cumvis + intxn*dist + year*cumvis</i>	36	25.41	0.00

Table 2. Estimates, standard errors, and *P*-values for the movement logit and vigilance logit from the *a priori* model for bison best supported by the data. Abbreviations are: *year* (year of study); *dist* (distance of group from road); *sppnum* (group size); *onroad* (on or off road); *hact* (human activity); *intxn* (interaction time); *sb* (number of snowmobiles); *coach* (number of coaches); *hab* (habitat), *cumvis* (cumulative daily number of over-snow vehicles); IH (impeded/hastened animal movement); AP (approached animals on foot); D (dismounted or exited OSVs); S (stopped to observe animals); N (no visible reaction); ON (animals on the road); OFF (animals off the road); A (aquatic); BF (burned forest); F (unburned forest); TH (thermal); and M (meadow). For each categorical variable, results are presented relative to the baseline level (i.e., 2006 for *year*, N for *hact*, ON for *onroad*, and M for *hab*) and each estimate represents a departure from zero (i.e., no effect).

Effect	Movement logit			Vigilance logit		
	Estimate	SE	<i>P</i>	Estimate	SE	<i>P</i>
<i>intercept</i>	-0.23	0.63	0.776	0.82	0.42	0.055
<i>year</i> = 2003	2.20	0.42	<0.0001	0.74	0.25	0.003
= 2004	-0.08	0.40	0.839	-0.03	0.27	0.912
= 2005	-0.08	0.48	0.545	0.21	0.30	0.478
= 2006	-1.83	0.63	0.004	-0.92	0.31	0.003
<i>sppnum</i>	-2.9	0.72	<0.0001	1.53	0.54	0.004
<i>dist</i>	-6.82	2.61	0.009	-2.32	0.81	0.004
<i>hact</i> = IH	1.41	0.33	<.0001	1.12	0.31	<0.001
= AP	0.33	0.65	0.608	-0.53	0.49	0.282
= D	-1.47	0.50	0.003	0.08	0.30	0.782
= S	0.20	0.27	0.456	-0.07	0.22	0.738
= N	-0.47	0.30	0.112	-0.60	0.23	0.009
<i>intxn</i>	0.27	0.21	0.206	0.49	0.14	<0.001
<i>onroad</i> = OFF	-1.43	0.20	<0.0001	-0.50	0.12	<0.0001
= ON	1.43	0.20	<0.0001	0.50	0.12	<0.0001
<i>sb</i>	0.11	0.04	0.002	0.08	0.03	0.002
<i>coach</i>	0.41	0.15	0.009	0.32	0.12	0.009
<i>hab</i> = A	1.90	0.53	<0.001	1.28	0.34	<0.001
= BF	-0.37	0.27	0.161	-0.27	0.19	0.156
= F	-0.11	0.21	0.588	0.08	0.14	0.581
= TH	-0.47	0.24	0.047	-0.66	0.17	<0.0001
= M	-0.95	0.22	<0.0001	-0.43	0.14	0.002
<i>cumvis</i>	0.00	0.02	0.825	-0.04	0.01	0.001
<i>sppnum</i> * <i>dist</i>	4.85	1.25	<0.001	-0.74	0.72	0.305

<i>dist*hact</i> = IH	1.06	3.77	0.779	-2.10	2.47	0.395
= AP	-11.62	8.87	0.190	-0.11	1.29	0.935
= D	5.38	2.47	0.029	0.70	0.84	0.406
= S	2.59	2.39	0.279	0.85	0.75	0.256
= N	2.59	2.38	0.277	0.66	0.72	0.364
<i>intxn*sppnum</i>	0.01	0.32	0.966	-0.66	0.22	0.003
<i>cumvis*year</i> = 2003	-0.07	0.02	0.005	0.03	0.02	0.095
= 2004	0.07	0.03	0.786	-0.03	0.02	0.110
= 2005	0.03	0.04	0.496	-0.01	0.03	0.656
= 2006	0.03	0.04	0.399	0.02	0.02	0.392

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Table 3. Estimates, standard errors, and *P*-values for the movement logit and vigilance logit from the *a priori* model for elk best supported by the data. Abbreviations are: *year* (year of study); *dist* (distance of group from road); *sppnum* (group size); *onroad* (on or off road); *hact* (human activity); *intxn* (interaction time); *sb* (number of snowmobiles); *coach* (number of coaches); *hab* (habitat), *cumvis* (cumulative daily number of over-snow vehicles); AP (approached animals on foot); D (dismounted or exited OSVs); S (stopped to observe animals); N (no visible reaction); ON (animals on the road); OFF (animals off the road); A (aquatic); BF (burned forest); F (unburned forest); TH (thermal); and M (meadow). For each categorical variable, results are presented relative to the baseline level (i.e., 2006 for *year*, N for *hact*, ON for *onroad*, and M for *hab*) each estimate represents a departure from zero (i.e., no effect).

Effect	Movement logit			Vigilance logit		
	Estimate	SE	<i>P</i>	Estimate	SE	<i>P</i>
<i>Intercept</i>	-2.59	0.84	0.002	-0.73	0.55	0.185
<i>year</i> = 2003	0.41	0.31	0.193	0.37	0.16	0.019
= 2004	0.23	0.22	0.300	-0.03	0.11	0.741
= 2005	1.12	0.30	<0.001	0.63	0.15	<0.0001
= 2006	-1.76	0.36	<0.0001	-0.96	0.15	<0.0001
<i>sppnum</i>	2.03	1.53	0.184	0.94	0.93	0.310
<i>dist</i>	-1.18	0.73	0.108	0.19	0.32	0.559
<i>hact</i> = AP	0.69	0.64	0.283	0.42	0.53	0.422
= D	-0.83	0.77	0.281	0.31	0.51	0.548
= S	-0.64	0.50	0.201	-0.55	0.31	0.077
= N	0.78	0.49	0.111	-0.18	0.31	0.574
<i>intxn</i>	1.45	0.24	<0.0001	0.90	0.17	<0.0001
<i>onroad</i> = OFF	-1.29	0.36	<0.001	0.00	0.30	0.987
= ON	1.29	0.36	<0.001	-0.00	0.30	0.987
<i>sb</i>	0.00	0.02	0.862	-0.01	0.01	0.526
<i>coach</i>	0.63	0.33	0.054	-0.06	0.17	0.714
<i>hab</i> = A	0.62	0.31	0.043	0.44	0.15	0.003
= BF	-0.36	0.28	0.199	-0.09	0.12	0.452
= F	0.91	0.28	0.001	0.41	0.15	0.007
= TH	-1.25	0.51	0.015	-0.54	0.19	0.006
= M	0.08	0.33	0.818	-0.22	0.14	0.124
<i>cumvis</i>	0.03	0.02	0.224	0.03	0.01	0.007
<i>sppnum</i> * <i>dist</i>	0.87	1.20	0.467	-1.21	0.64	0.057
<i>sppnum</i> * <i>hact</i> = AP	0.65	1.11	0.556	-0.45	0.87	0.608

= D	1.90	1.32	0.150	-0.69	0.89	0.438
= S	1.23	0.94	0.192	1.43	0.57	0.012
= N	-3.78	1.08	<0.001	-0.29	0.59	0.622
<i>intxn*dist</i>	-0.28	0.18	0.127	-0.31	0.12	0.009
<i>intxn*sppnum</i>	-1.62	0.33	<0.0001	-0.74	0.21	<0.001

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Table 4. Estimates, standard errors, and *P*-values for the movement logit and vigilance logit from the *a priori* model for trumpeter swans best supported by the data. Abbreviations are: *year* (year of study); *dist* (distance of group from road); *sppnum* (group size); *hact* (human activity); *intxn* (interaction time); *sb* (number of snowmobiles); *coach* (number of coaches); *cumvis* (cumulative daily number of over-snow vehicles); AP (approached animals on foot); D (dismounted or exited OSVs); S (stopped to observe animals); and N (no visible reaction). For each categorical variable, results are presented relative to the baseline level (i.e., 2006 for *year* and N for *hact*) and each estimate represents a departure from zero (i.e., no effect).

Effect	Movement logit			Vigilance logit		
	Estimate	SE	<i>P</i>	Estimate	SE	<i>P</i>
<i>intercept</i>	0.64	1.03	0.534	2.40	0.65	<0.001
<i>year</i> = 2003	1.42	0.56	0.011	0.29	0.39	0.467
= 2004	0.73	0.77	0.343	1.46	0.48	0.002
= 2005	-2.01	0.97	0.038	0.05	0.45	0.917
= 2006	-0.14	0.64	0.824	-1.79	0.51	<0.001
<i>sppnum</i>	-3.10	1.73	0.073	-2.78	1.15	0.016
<i>dist</i>	-2.12	1.09	0.052	-2.50	0.65	<0.001
<i>hact</i> = AP	0.31	0.35	0.376	0.32	0.32	0.307
= D	0.38	0.28	0.180	-0.31	0.27	0.252
= S	0.10	0.22	0.668	0.23	0.18	0.210
= N	-0.78	0.23	<0.001	-0.24	0.18	0.201
<i>intxn</i>	0.38	0.15	0.013	-0.04	0.13	0.776
<i>sb</i>	0.08	0.03	0.012	0.07	0.02	0.004
<i>coach</i>	0.53	0.18	0.004	0.46	0.14	0.001
<i>cumvis</i>	-0.10	0.07	0.141	-0.08	0.04	0.062
<i>sppnum</i> * <i>dist</i>	1.58	2.12	0.455	0.78	1.42	0.580
<i>intxn</i> * <i>dist</i>	-0.22	0.18	0.211	0.08	0.14	0.578
<i>cumvis</i> * <i>year</i> = 2003	-0.10	0.09	0.252	0.01	0.06	0.928
= 2004	-0.08	0.12	0.497	-0.18	0.07	0.016
= 2005	0.39	0.15	0.010	0.08	0.07	0.268
= 2006	-0.20	0.11	0.062	0.09	0.08	0.240

Table 5. Estimates, standard errors, and *P*-values for the movement logit and vigilance logit from the *a priori* model for bald eagles best supported by the data. Abbreviations are: *year* (year of study); *dist* (distance of group from road); *sppnum* (group size); *hact* (human activity); *intxn* (interaction time); *sb* (number of snowmobiles); *coach* (number of coaches); *hab* (habitat); AP (approached animals on foot); D (dismounted or exited OSVs); S (stopped to observe animals); N (no visible reaction); BF (burned forest); F (unburned forest); and M (meadow). For each categorical variable, results are presented relative to the baseline level (i.e., 2006 for *year*, N for *hact*, and M for *hab*) and each estimate represents a departure from zero (i.e., no effect).

Effect	Movement logit			Vigilance logit		
	Estimate	SE	<i>P</i>	Estimate	SE	<i>P</i>
<i>intercept</i>	0.37	1.40	0.791	-3.11	1.31	0.017
<i>year</i> = 2003	1.04	0.45	0.022	0.05	0.38	0.895
= 2004	-0.24	0.51	0.633	0.77	0.34	0.023
= 2005	0.66	0.45	0.141	0.38	0.37	0.297
= 2006	-1.46	0.56	0.009	-1.20	0.35	<0.001
<i>sppnum</i>	-0.18	0.17	0.296	-0.43	0.33	0.190
<i>dist</i>	-1.21	0.72	0.094	0.67	0.55	0.229
<i>hact</i> = AP	0.80	0.85	0.346	-0.27	0.75	0.715
= D	0.13	0.55	0.812	-0.72	0.51	0.158
= S	-0.14	0.49	0.774	-0.32	0.42	0.444
= N	-0.79	0.66	0.232	1.32	0.54	0.014
<i>intxn</i>	0.19	1.27	0.883	4.40	1.17	<0.001
<i>sb</i>	0.23	0.08	0.003	0.19	0.07	0.005
<i>coach</i>	1.41	0.67	0.036	0.56	0.51	0.267
<i>hab</i> = BF	0.34	0.37	0.363	2.06	0.34	<0.0001
= F	-0.81	0.40	0.045	-0.39	.33	0.232
= M	0.47	0.49	0.338	-1.67	0.50	<0.001
<i>intxn*dist</i>	0.15	0.67	0.822	-1.37	0.59	0.019

Table 6. Estimates, standard errors, and *P*-values for the movement logit and vigilance logit from the *a priori* model for coyotes best supported by the data. Abbreviations are: *year* (year of study); *dist* (distance of group from road); *sppnum* (group size); *onroad* (on or off road); *hact* (human activity); *intxn* (interaction time); *sb* (number of snowmobiles); *coach* (number of coaches); AP (approached animals on foot); D (dismounted or exited OSVs); S (stopped to observe animals); and N (no visible reaction). For each categorical variable, results are presented relative to the baseline level (i.e., 2006 for *year*, N for *hact*, and ON for *onroad*) and each estimate represents a departure from zero (i.e., no effect).

Effect	Movement logit			Vigilance logit		
	Estimate	SE	<i>P</i>	Estimate	SE	<i>P</i>
<i>intercept</i>	-1.46	1.80	.417	-1.13	1.27	.376
<i>year</i> = 2003	.93	.68	.170	1.28	.49	.009
= 2004	-.48	.61	.429	-.32	.43	.454
= 2005	.41	.57	.479	.70	.39	.075
= 2006	-.86	.60	.153	-1.66	.49	<.001
<i>sppnum</i>	.72	.70	.302	-.49	.51	.339
<i>dist</i>	-6.22	1.96	.001	-1.78	1.57	.256
<i>hact</i> = AP	1.64	.90	.068	-.62	1.12	.581
= D	-.34	.73	.647	-.12	.62	.848
= S	-.39	.54	.467	.50	.51	.327
= N	-.92	.67	.174	.24	.56	.669
<i>intxn</i>	2.78	1.53	.070	2.31	.90	.010
<i>onroad</i> = OFF	.27	.63	.668	.10	.62	.872
= ON	-.27	.63	.668	-.10	.62	.872
<i>sb</i>	.05	.16	.764	.17	.11	.105
<i>coach</i>	.07	.91	.935	-.19	.69	.796

Table 7. Aerial survey counts of trumpeter swans in and near Yellowstone National Park, Wyoming, during winter 2003 (T. McEneaney, Yellowstone National Park, unpublished data).

Survey Date	Area	Adults	Cygnets	Total
November 29	YELLOWSTONE NATIONAL PARK	789	144	933
	Yellowstone River and Lake	413	83	496
	Madison and Firehole Rivers	12	3	15
	Other areas within the park	364	58	422
	OUTSIDE YELLOWSTONE	333	43	376
	Paradise Valley	Not Surveyed		
	Hebgen Lake	333	43	376
	Wyoming (e.g., Flagg Ranch, Snake River)	Not Surveyed		
January 28	YELLOWSTONE NATIONAL PARK	324	56	380
	Yellowstone River and Lake	247	33	280
	Madison and Firehole Rivers	22	13	35
	Other areas within the park	55	10	65
	OUTSIDE YELLOWSTONE	522	66	588
	Paradise Valley	Not Surveyed		
	Hebgen Lake	522	66	588
	Wyoming (e.g., Flagg Ranch, Snake River)	Not Surveyed		
February 11	YELLOWSTONE NATIONAL PARK	146	34	180
	Yellowstone River and Lake	98	23	121
	Madison and Firehole Rivers	13	4	17
	Other areas within the park	35	7	42
	OUTSIDE YELLOWSTONE	487	45	532
	Paradise Valley	23	5	28
	Hebgen Lake	462	40	502
	Wyoming (e.g., Flagg Ranch, Snake River)	2	0	2
April 8	YELLOWSTONE NATIONAL PARK	28	4	32
	Yellowstone River and Lake	17	3	20
	Madison and Firehole Rivers	0	0	0
	Other areas within the park	11	1	12
	OUTSIDE YELLOWSTONE	248	36	284
	Paradise Valley	Not Surveyed		
	Hebgen Lake	248	36	284
	Wyoming (e.g., Flagg Ranch, Snake River)	Not Surveyed		