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Statistical methods for analysing responses of wildlife to human disturbance

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Summary

1. Off-road recreation is increasing rapidly in many areas of the world, and effects on wildlife can be highly detrimental. Consequently, we have developed methods for studying wildlife responses to off-road recreation with the use of new technologies that allow frequent and accurate monitoring of human–wildlife interactions. To illustrate these methods, we studied the response of Rocky Mountain elk *Cervus elaphus* L. to all-terrain vehicles (ATVs), one of the most prominent forms of summer recreation in North America. We studied elk because the species is not only of keen economic and social interest across North America and Europe but also exemplifies species that can be sensitive to human disturbance.

2. The study was part of a controlled landscape experiment where global positioning system (GPS)-equipped recreationists traversed an established 32-km route inside a 1453-ha elk-proof enclosure. Elk locations before and during the human disturbances were monitored using an automated telemetry system. The unique data set and study objectives led to our development of statistical methods for analysing the response of wildlife to human disturbance.

3. We developed a statistical method, referred to as a probabilistic flight response, which accounted for daily circadian rhythms in movement behaviour of elk, and related the probability of flight to distance to the disturbance and a number of environmental covariates. We also present methods for estimating spatially and temporally explicit movement vectors as a way of detecting and visualizing landscape-level movement patterns.

4. Using these methods, we observed that elk appeared to respond at relatively long distances (> 1000 m) to ATVs, and that the estimated probability of flight appeared to be higher when elk were closer to the ATV routes, even when the distance to an ATV was large.

5. *Synthesis and applications*. Our study quantifies the response of wildlife to human disturbance at a resolution well beyond previous work, and provides methods to improve our understanding of wildlife–human interactions related to management of wildlife and recreation. These methods may be used for any study involving accurate, frequent monitoring of animals and humans with the use of GPS or similar technologies now commonly available.

Key-words: non-parametric regression, off-road recreation, stochastic movement models, telemetry data, vector field

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Introduction

Off-road recreation is increasing rapidly in many areas of the world. In North America, the use of all-terrain vehicles (ATVs), for example, has increased sevenfold since 1972 (USDA Forest Service 2004), resulting in a variety of impacts that are not fully understood (Taylor & Knight 2003a,b). Consequently, understanding the behaviour of free-ranging wildlife like Rocky Mountain elk *Cervus elaphus* L. in response to recreation is a growing concern for habitat and wildlife managers.

A number of studies have described ungulate–human interactions, but the diversity of study designs and the predominant use of visual rather than radio-telemetry data has made it difficult to interpret these findings collectively (Taylor & Knight 2003a). The most intensive study of this kind is the work of Taylor & Knight (2003b), who observed bison *Bison bison*, pronghorn *Antilocapra americana* and mule deer *Odocoileus hemionus* responses to mountain bikers and hikers, and quantified animal response as a function of several explanatory variables. However, as in previous studies, the use of visual measurements may limit the detection of animal responses beyond the perceptive range of the observer, leading to underestimates of the 'area of influence' (Miller, Knight & Miller 2001) and the overall population response of animals to recreational activities. While the use of radio-telemetry technology can eliminate this potential bias in human disturbance studies (Phillips & Alldredge 2000; Conner, White & Freddy 2001), the logistics of implementing such landscape-scale experiments with both free-ranging animals and human telemetry is a significant challenge. Further, statistically modelling the data from an experiment with paired temporal streams of telemetry data is a complex spatiotemporal problem that is not covered by standard methodologies for analysing radio-telemetry data (White & Garrott 1990; Millspaugh & Marzluff 2001). More recent models to study animal movements assume diffusion or other theoretical frameworks that are difficult to adapt to empirical problems (Turchin 1996).

As part of a larger study to analyse the behavioural responses of Rocky Mountain elk and mule deer elk to summer recreational uses on national forests (Wisdom *et al*. 2004a), we describe statistical methods to measure the movements and flight responses of elk to ATVs. These methods were designed for analysis of typical animal movement data where combinations of measurement error, inherent randomness and daily circadian cycles may mask treatment effects. Plots of observed movement tracks for a large telemetry data set are difficult to interpret in terms of spatial patterns in velocity and other landscape-scale movement behaviours (Ager *et al*. 2004). Averages over all animals and all locations are not useful because movement patterns vary over space and time (Ager *et al*. 2004). Consequently, we developed a procedure for calculating smoothed vector plots that proved useful for visualizing general patterns of animal movement not easily detected from plots of observed movement arrows for individual animals. We estimated smooth movement vectors to understand better landscape movements of elk during control and treatment periods. We then built probabilistic flight response models to test the effect of variables such as topography, visibility and ATV proximity on elk movements. In previous work (Brillinger *et al*. 2001, 2002, 2004; Preisler *et al*. 2004) we studied effects of stationary features of the landscape (e.g. locations of roads) on animal movement using stochastic differential equations. In the present work we developed methods for studying response of wildlife to non-stationary disturbances, such as ATVs. Our work was focused on elk because the species is widely distributed across North America and Europe, is of keen economic and social interest to recreationists, and exemplifies those species that can be sensitive to human disturbance (Toweill & Thomas 2002).

Methods

STUDY AREA

Starkey Experimental Forest and Range covers 101 km^2 on the Wallowa Whitman National Forest, about 38 km south-west of La Grande, Oregon, USA. Starkey vegetation is a mosaic of bunchgrass meadows *Pseudorogneria* spp. and coniferous forest, the latter consisting primarily of Douglas fir *Pseudostuga menzesii*, ponderosa pine *Pinus ponderosa* and grand fir *Abies grandis*. Topography consists of gently rolling bench lands that are dissected by a network of drainages. In 1987 Starkey was enclosed with a 2·4-m tall woven-wire fence and further subdivided into several areas for studies on Rocky Mountain elk, mule deer and cattle (Rowland *et al*. 1997; Wisdom *et al*. 2004b). Elk and mule deer at Starkey are wild, hunted animals that are subjected to the same human activities and management as occurs across millions of hectares of public land in western North America (Rowland *et al*. 1997, 1998). The fenced study areas, however, provide needed experimental controls to measure behavioural, habitat and population responses of these species to human activities of interest, while minimizing confounding effects of other factors (Wisdom *et al*. 2004b). Data for our research was obtained from the 1453-ha west and east pastures of the Northeast Study Area.

ENVIRONMENTAL DATA

We selected a number of environmental variables as explanatory variables for the flight response model, based on previous work with elk at Starkey (Johnson *et al*. 2000; Rowland *et al*. 2000; Ager *et al*. 2003; Wisdom *et al*. 2004c) and plots of elk movements during the ATV treatments. Explanatory variables included slope, aspect, topographic convexity, altitude difference between the ATV and elk, visibility from the ATV route, forest canopy, distance to the ATV and distance to the ATV route. Topographic variables, including slope (per cent), altitudinal difference (metres) and aspect (radians), were calculated from US Geological Survey (USGS) 10 × 10-m grid of 145 197 pixels. Aspect (degrees) was linearized by summing the cosine and sine transformation of the original data to yield a measure that ranged from –1·0 to 1·0. A visibility index was calculated using the ArcGrid VISIBILITY command that measured the number of pixels on the 10 × 10-m gridded ATV route that were visible to each study area pixel. Topographic convexity (Ager *et al*. 2003) was calculated using the curvature function as implemented in ArcMap (ESRI, Redland, CA). Data on forest canopy closure was measured for 1029 forest stands in the area using stereoscopic photo-interpretation of 1 : 12 000 colour resource photos from year 2000. All derived explanatory variables were calculated in ArcGIS 8.2 (ESRI).

ATV TREATMENTS

ATVs were run daily, starting at 08.00 h, on a 32-km route through the study area for each of three 5-day treatment periods. The ATVs were run twice daily, starting at 08.00 and 13.00 h each day, at an approximate speed of 8–20 km h^{-1}. The treatment period lasted from 2 to 3 h and used two ATVs. Each 5-day period of ATV activity was followed by a 9-day control period, during which no human activities occurred in the study area. The experiment lasted from mid-April to October 2002, resulting in three replicates of each of the ATV and control periods (Wisdom *et al*. 2004a). There was no human entry beyond the ATV activities during the treatment or control periods. Locations of ATVs along the routes were generated at 1-s intervals, using Trimble model 3 c GPS units (Trimble, Sunnyvale, CA) carried in a backpack by one of the ATV operators. The accuracy of ATV locations was between 3 and 5 m (95% confidence bound).

TELEMETRY DATA

Elk locations were obtained from a loran-C telemetry system installed at Starkey in 1989 (Rowland *et al*. 1997). The telemetry system cycles through a set of radio-collars and attempts a location every 22 s, with a 60% success rate and a mean accuracy of 50 m (Johnson *et al*. 1998; Findholt *et al*. 2002). Data were collected from 12 female elk monitored from mid-April to October 2002. The radio-collared animals were part of a larger population of elk that inhabited the Northeast Study Area from spring to autumn of each year and constituted part of Starkey's wild, hunted populations of this species. The Northeast Study Area was divided into an east and west pasture by the same type of elk-proof fence that forms the outside boundaries. Seven of the radio-collared animals were released in the east pasture, where pre-calving elk density was approximately 12 animals km^{-2}. The other five radio-collared elk were released in the west pasture, where pre-calving elk density was approximately four animals km^{-2}. Elk were released in both areas 16 days before the treatments were initiated, and no human activity was allowed in the areas before treatments began. During each 5-day period of human activity, locations of individual elk were generated at approximately 10-min intervals (range 7–60 min) during daylight hours. During the 9-day control periods, animals were located approximately every 30 min (range 12–60 min).

ESTIMATING VELOCITY FIELDS

To estimate movement vectors, animals were labelled by $i = 1, \dots, I$; their locations were denoted by the vector $r_i(t_{ij}) = \{X_i(t_{ij}), Y_i(t_{ij})\}$ and were recorded at times t_{ij}, $j = 1, \dots, J_i$. The velocity vector $\{\Delta X_i(t_{ij}), \Delta Y_i(t_{ij})\}$ was the vector of step sizes per unit time in the easting and northing, respectively. Consider the observed step sizes for a unit time:

$$\Delta X_i(t_{ij}) = [X_i(t_{ij}) - X_i(t_{i(j-1)})]/[t_{ij} - t_{i(j-1)}],$$
$$\Delta Y_i(t_{ij}) = [Y_i(t_{ij}) - Y_i(t_{i(j-1)})]/[t_{ij} - t_{i(j-1)}] \qquad \text{eqn 1}$$

where $t_{i1} < t_{i2} < \dots < t_{ij}$. Average step sizes are likely to be different at different times of the day and different locations. For example, it might be expected that step sizes would be larger when animals were disturbed by humans or moving between foraging and resting habitat. A multidimensional, smoothing spline model can be used to smooth the step sizes as functions of location and time of day. To do this, we used the generalized additive model, GAM (Hastie & Tibshirani 1990), in R statistical software (Ihaka & Gentleman 1996; R Development Core Team 2004). The GAM routine in R uses penalized thin plate regression splines (Wood 2003) to perform multidimensional smoothing. The parameter that determines the amount of smoothing is selected automatically using cross-validation (Golub, Heath & Wahba 1979; Hastie, Tibshirani & Friedman 2001; Wood & Augustin 2002).

We smoothed the step sizes in the *x*- and *y*-directions separately. The latter is efficient if there is independence between the steps in the two directions. In the present data the correlation between the step sizes in the *x*- and *y*-directions was not biologically significant ($R = 0{\cdot}13$). Although we initially generated vector plots for all days within each treatment, examination of residuals (Fig. 1) led us to examine the plots for individual days and groups of days. Specifically, we fitted separate models for the first and last 2 days of each treatment replicate.

The predicted step sizes in the *x*- and *y*-directions for each location and time of day were used to generate arrow plots of the velocity vectors. Vector fields calculated from the discrete step sizes is one way of estimating the drift term in stochastic differential equations of motion (Brillinger *et al*. 2004; Preisler *et al*. 2004). In this study the estimated vector fields were used only as a visualization tool, summarizing the average movement vectors of animals over time. The estimated fields were not used in the next section on flight response models.

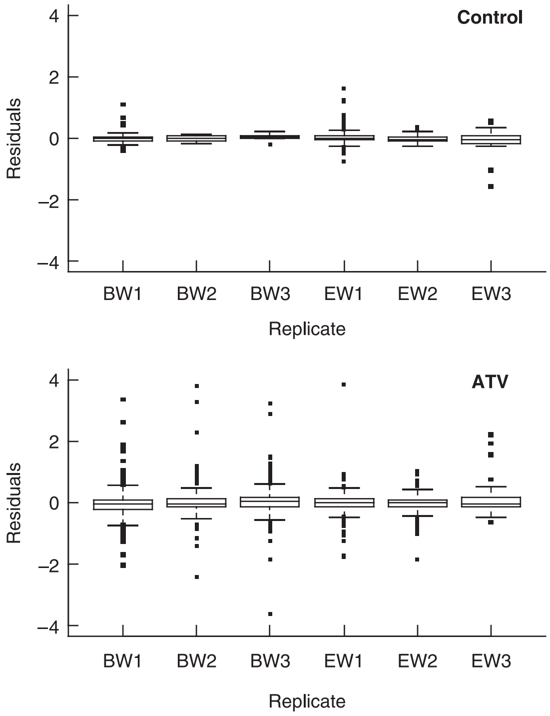

Fig. 1. Parallel box-plots of residuals in the *y*-direction vs. time since start of treatment. Residuals were produced by fitting three-dimensional splines to observed step sizes from control and ATV treatment days. Values were larger in the beginning (first 2 days) of each of the 3 weeks (BW1, BW2, BW3) of exposure to disturbance compared with the corresponding values at the end of the week (EW1, EW2, EW3). No such pattern was apparent in residuals for control days.

ESTIMATING FLIGHT RESPONSES TO HUMAN DISTURBANCE

Elk movements are characterized by daily cycles created by crepuscular transitions between foraging and resting habitat (Ager *et al*. 2003). Consequently, to characterize flight response to human disturbance one must first study elk movement patterns on days with no disturbance. In the present study, distributions of elk speeds for days with no disturbance were well approximated by the log-normal distribution with the mean modelled as a function of time-of-day. The estimated curve describing average elk speed over the course of a day showed two prominent peaks, one near 04.00 and another near 18.00 h (Fig. 2).

In addition to time-of-day, the elapsed time between consecutive observations had an effect on calculated elk speeds. To account for this phenomenon we included elapsed time as a covariate when modelling the mean elk speed. The curve in Fig. 2 is the estimated mean speed for 30 min elapsed time.

Given the above considerations, we defined a flight response as an observed speed greater than the upper 95 percentile of speeds observed during the control periods for the same hour of day, same elk, and adjusted for elapsed time. Specifically, let $S(h,d)$ be the logarithm of the speed of an elk at time h (h) calculated from two consecutive observations with elapsed time between observations equal to δ. We define a 0–1 random variable, with the value 1 indicating response, as follows:

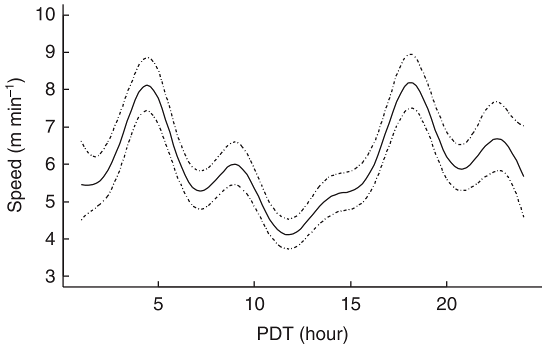

Fig. 2. Estimated speeds of elk (and approximate 95% confidence bounds) in the absence of human disturbance. The dawn and dusk velocity peaks are caused by crepuscular habitat transitions typical of elk and deer on summer range.

$$\begin{aligned} r(h) &= 1 \quad \text{if } S(h,\delta) > \hat{\mu}(h,\delta) + 1.645\hat{\sigma} \\ r(h) &= 0 \quad \text{otherwise} \end{aligned} \qquad \text{eqn 2}$$

where $\hat{\mu}$ and $\hat{\sigma}$ are the estimated mean and standard deviation of the logarithms of elk speed during non-disturbance days. With this model, the probability of an elk 'responding' during non-disturbance days is approximately 5%. As a result, if the estimated probability of flight when a disturbance is present was > 5%, then we assumed that the animal had reacted to the treatment (i.e. the human disturbance).

We used non-parametric logistic regression (Hastie & Tibshirani 1990) with spline functions to estimate the effects of distance to disturbance and other explanatory variables on the probability of flight. The advantage of using logistic regression with splines is that non-linear relationships (e.g. the circadian relationship seen in Fig. 2) between explanatory variables and the logit line may be estimated directly from the data. We used the following logistic model:

$$\text{logit}(p_{ij}) = \beta_o + \sum_k s(Z_{kij}) + e_i \qquad \text{eqn 3}$$

where p_{ij} is the probability of flight of the ith elk during the jth recorded observation, Z_{kij} are K explanatory variables, e_i is the random effect of the ith elk and $s()$ are spline smoothers (Green & Silverman 1994).

The explanatory variables used in the model were distance between an elk and the ATV; altitude difference between the elk and the ATV; percentage canopy cover at the location of the elk; distance between elk and nearest ATV route; number of visible route pixels at the elk location; time since the beginning of the first treatment encounter; whether the elk had a calf or not; and whether the elk was in the east or west pasture. The random elk effect was included to account for correlations between observations on the same elk over time. All estimations were done in the statistical package R with the glmmPQL and GAM modules. The glmmPQL module allows the fitting of generalized linear mixed models using penalized quasi-likelihood (Schall 1991; Wolfinger & O'Connell 1993; Venables & Ripley 2002). In order to incorporate non-linear smoothing functions, e.g. splines, in the glmmPQL model, we first determined the basis function for each of the explanatory variables using the bs() function in R. Once the basis functions are determined they can be included linearly in other linear regression routines, e.g. glmmPQL in R or glimmix or nlmix in SAS (SAS 2003). The model with non-linear functions (equation 3) was compared with another with only linear effects using the Akaike information criteria (Hastie, Tibshirani & Friedman 2001) and by studying plots of the estimated spline functions. Estimates of the spline functions are given by the partial effects plots produced by the GAM module.

The final model, including only the highly significant variables ($P < 0{\cdot}01$), was estimated by GAM using two-dimensional splines to account for an interaction between the explanatory variables distance to ATV and distance to nearest route. We estimated the standard errors using jack-knife procedures to account for the between-elk variability. We calculated the jackknife standard errors by dropping one elk at a time from the data. Next we estimated uncertainties by calculating the variability in the response probabilities produced by the subsets of the data (Efron & Tibshirani 1993).

Results

MOVEMENT VECTORS

Estimated vector fields describing general patterns of elk movement during control periods showed that on average elk moved little during morning hours and movement direction appeared mostly either random or heading away from the fences. An overall test for circular uniformity was rejected ($z = 6{\cdot}99$, P-value $< 0{\cdot}001$; Zar 1999). Movement patterns were best seen in the plots of the smoothed arrows and plots of elk locations in the eastern/larger region where most of the collared elk were located (Fig. 3). Observed elk locations between 09.30 and 12.00 h appeared distributed throughout the study areas, suggesting little or no selection for specific locations within the area.

The estimated vector fields at the corresponding hours during ATV days (Fig. 4) showed stronger directional patterns than those during control days (test of circular uniformity was rejected, with $z = 9{\cdot}1$, $P \ll 0{\cdot}001$). The patterns were particularly strong during the first 2 treatment days in all three replicates. Almost all observed elk in the east pasture appeared to be moving to 'hiding' places near or against the fence in the north and north-east areas of the pasture. During days 4 and 5 of treatment, the movement vectors remained larger than those for the control days but elk appeared to have either habituated, or found close refugia, rather than fleeing to far corners of the pasture as observed in the first 2 days of each treatment period. Plots of residuals from fitted movement vectors supported this finding, showing larger residual values in the first 2 days of the week compared with the last 2 days, particularly for the step sizes in the y-direction (Fig. 1). These temporal differences in residuals were not observed in data for the control periods fitted in the same way. In the above example only morning hour telemetry data were used because they were a good example for demonstrating the statistical techniques. Movement patterns of elk in the afternoon hours were different from those in the morning (less movement observed; Fig. 2). Consequently, the results described above do not extend to other hours of the day.

RESPONSE TO HUMAN DISTURBANCE

Three variables, distance of elk to ATV riders, distance to nearest ATV route and the pasture, appeared to have significant effects on the probability of flight (P-value <

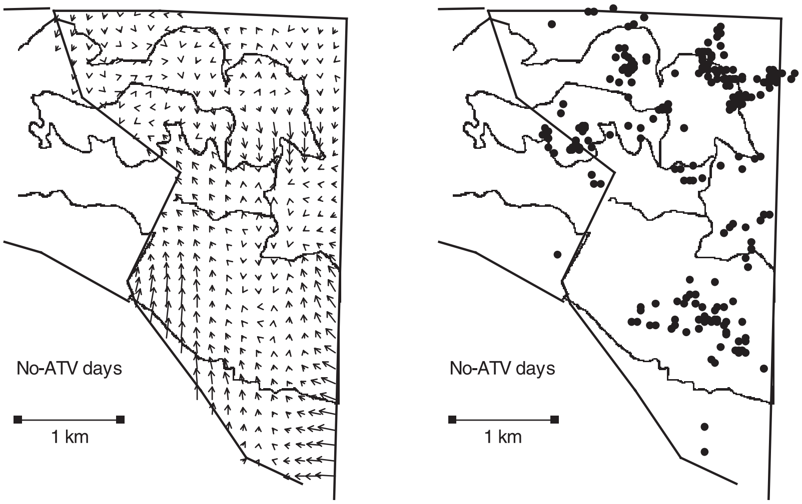

Fig. 3. Estimated velocity field (left panel) at 08.30 h and observed locations of elk (right panel) after 09.00 h in the absence of human disturbance. Except for some movements away from the fence in the southern part of the pasture there is little indication of spatial movement patterns.

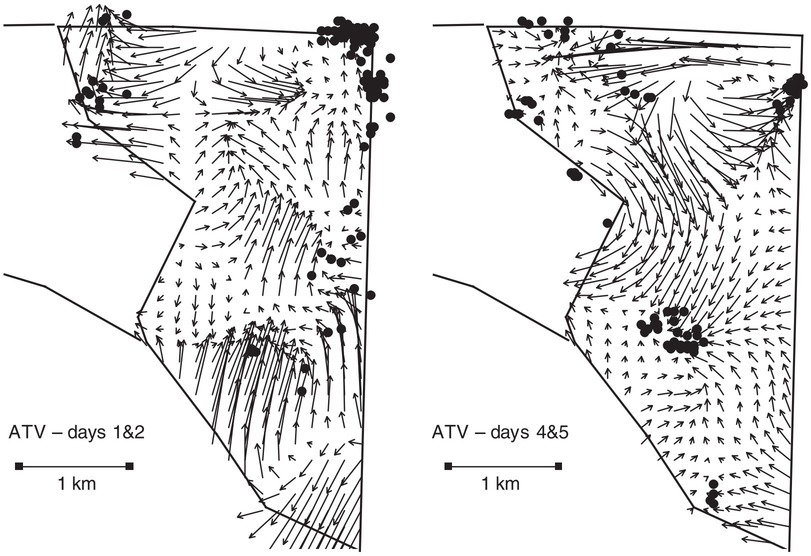

Fig. 4. Estimated velocity field at 08.30 h and observed locations of elk after 09.00 h in the presence of ATVs. Arrows describe movement patterns of elk at 08.30 h and the dots show observed locations of elk after 09.00 hours. Strong patterns of movements to refugia are apparent in both figures. In the first two days of exposure elk appear to move to a relatively remote hiding area not visible from the ATV route (north-eastern corner). However, after 3 days of exposure the elk appear to use other hiding areas that require less overall movement (see Fig. 2).

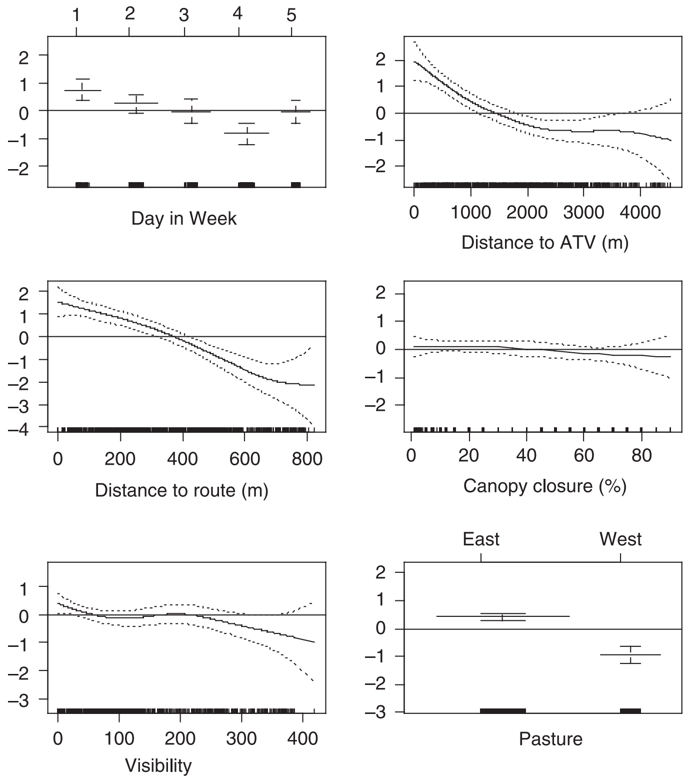

Fig. 5. Estimated partial effects (solid) and 95% confidence bounds (dashed) of explanatory variables on probability of flight. The effects are in logit scale and standardized to have mean zero. A variable does not have a 'significant' effect if the horizontal line at zero is almost completely within the confidence bounds.

0·001). Relationships between explanatory variables and probability of flight (logit-scale) were best seen in plots of the estimated partial effects (Fig. 5). Probability of flight appeared to decrease linearly as the distance to nearest ATV route increased (Fig. 5). Similarly, the effect of distance to ATV appeared to decrease linearly up to approximately 1 km, after which the effect appeared to level off. AIC value was smaller for a model with non-linear effects, confirming the significance of the non-linear term seen in Fig. 6.

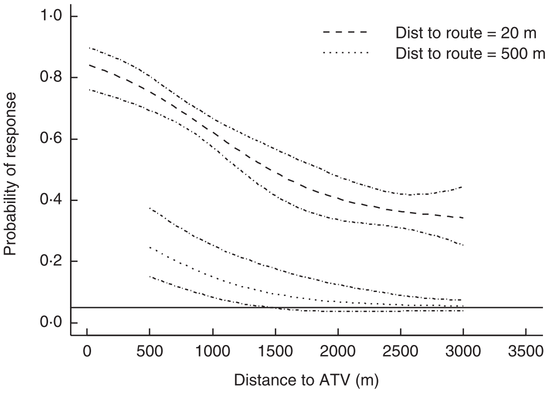

Fig. 6. Estimated probabilities of flight response by elk as a function of distance to ATV and distance to closest ATV route (Dist to route). The bounds around the estimated probabilities are approximate point-wise 95% limits. The horizontal line at 5% response is the level below which responses are similar to those on control days. When elk are close to routes (20 m) the probability of flight is higher, even when the ATV is far away (e.g. 1000 m). The response appears to drop dramatically when there are no routes closer than 500 m.

Responses in the east pasture, where elk density was higher, appeared larger on average than those in the west (Fig. 5). The observed pasture effect may have been a surrogate for some topographic differences not captured by the variables in the model.

Of the three time variables (time of day, day in week and treatment week), only day in week appeared to have a significant effect (P-value = 0·014). All other variables did not appear to have significant effects on probability of flight (P-value > 0·1).

A model that included only the three highly significant variables (P-value < 0·001) indicated that probabilities of response could be as high as 80% when there was an ATV route nearby (20 m) and the ATV was within 100 m of the elk (Fig. 6). The estimated odds of an elk responding to an ATV at 500 m was 7–13 (95% limits of odds ratio) times larger when the nearest ATV route was 20 m vs. 500 m. We found that when elk were near an ATV route there appeared to be significant responses to ATVs travelling even at distances as far as 2 km. Response of elk to ATVs appeared to be significantly smaller when the distance to nearest ATV route was large (> 500 m).

Discussion

Our work at Starkey is the first experiment of its kind where telemetry data were used to monitor the landscape-level response of a large ungulate to humans in a controlled experiment over time. Previous studies (Taylor & Knight 2003a, table 1a) used direct observations to quantify the response rather than telemetry. Consequently, the responses of animals outside the perceptive range of the observer go undetected without the use of telemetry. For instance, we detected a small but significant response when the ATV was 3000 m from elk, well beyond the observational range of the observers in forested habitats. Thus, direct observation could lead to a downward bias of the estimate of the 'area of influence' (Miller, Knight & Miller 2001) associated with recreation.

Despite the advantages of using telemetry to study wildlife response to humans, detecting and quantifying flight distance and distance moved from two sets (observer and animal) of sequential x,y coordinates still requires significant data interpretation. Response parameters such as alert distance (*sensu* Taylor & Knight 2003a,b) would also require monitoring of heart pulse rate in addition to animal locations. Automated methods for estimating other kinds of responses from radio-telemetry data (Taylor & Knight 2003a,b) have yet to be formalized in the literature.

Our methods introduce several approaches to analysing animal movements. Smoothing spatially and temporally explicit velocity vectors over all animals using spline functions allowed the detection of movement patterns that otherwise might not have been seen. The incorporation of both time and space into the smoothing makes it particularly well suited for analysing landscape movement patterns for ungulates and other animals that have strong, daily cycles of activity patterns and movements. Application of these methods to data from other studies at Starkey has shown the methods have general utility to a number of problems related to describing and understanding animal movement patterns (Ager *et al.* 2004; Preisler *et al.* 2004). We also considered background circadian cycles of movement in the flight response model, which is an important factor for species such as elk that have pronounced crepuscular movements and habitat shifts (Ager *et al.* 2003).

Our examination of a number of covariates indicated that distance to the actual disturbance, the ATV, and distance to potential route of disturbance were the most important variables among those in the model. Previous work at Starkey (Johnson *et al.* 2000; Wisdom *et al.* 2004a) showed that distance to road has a stronger effect in resource selection functions when the respective road has a higher traffic rate. Both the current study and previous work (Recarte, Vinvent & Hewison 1998; Taylor & Knight 2003b; Wisdom *et al.* 2004c) show a heightened response to motorized traffic when animals are closer to the road. This behavioural mechanism can produce the spatial distributions previously reported for Starkey and elsewhere for elk (Ager *et al.* 2003, 2004). Whether there is an additional effect where the flight distance decreases with increasing traffic rate, however, is not known. In any event, it appears that elk in this study perceive roads or trails as the location of a predictable source of human disturbance.

A number of studies have demonstrated that direct approaches to wildlife elicit a different response other than a tangential encounter (Moen, Whitemore & Buxton 1982). Although recreationists in this study did not stop and approach wildlife, many direct or near-direct encounters occurred when animals were on roads and trails and thus in the direct path of the humans. We view the difference between a tangential and direct approach as a gradient of encounter angles that is incorporated into our response model via the use of perpendicular distance to road and distance to ATVs. The increased response at closer distances to roads (Fig. 6) shows the incremental change in response as the angle of encounter decreases.

The telemetry data also showed that a significant number of animals appear to find close refugia from passing ATV, although we did not consider these a response in our models (Fig. 6). By viewing both ATV and elk telemetry in 'movie' software written for the study we examined close elk–ATV encounters to try and understand why many of the encounters do not result in flight of the animals. The movies confirmed that a significant number of animals appear to 'freeze' while ATV pass very close (e.g. 50–100 m). While our response model did not show a significant effect of the visibility variable, the arrow diagrams seem to suggest the possibility that elk are using topography and vegetation to escape detection at close distances to roads. We suggest that this behaviour is a form of passive response and can also be incorporated into the flight response model as velocities lower than the 95% confidence interval during the control periods. We did not attempt this in the present study because the location error in the telemetry data sampled at high frequencies imparts an upward bias to velocity estimates for stationary animals (Ager *et al*. 2003). Future work will include more accurate GPS data and perhaps make it possible to estimate the probabilities of both passive and active responses.

The replication of treatments over successive days (5) and treatment periods (three), combined with 9-day control periods between treatments, made it possible to examine the longer-term response of elk to human disturbance. The data showed that over successive days of treatment, elk appear to adjust their distributions so that they are located closer to areas that are not visible from roads. However, during the 9 days of rest in-between treatments, the animals appeared to return to their pre-treatment distributions.

The eventual goal of this work is to measure animal energy expenditures associated with different types and intensities of recreational disturbances (Freddy, Bronaugh & Fowler 1986). Given a flight response model such as the one presented here, and one that estimates distance moved, energy expenditures can be modelled as well as the impact on foraging time. The parameters may be used in a simulation model to examine the effects of varying animal population levels, recreationists and changes in routes. Ultimately these results may be used to understand better the impacts of recreational activities on animal growth, survival and reproduction.

Importantly, our study quantifies responses of wildlife to human disturbance at a resolution well beyond previous work, and provides methods for obtaining information of keen interest to managers of wildlife and recreation (Béchet, Giroux & Gauthier 2004; Kramer-Schadt *et al*. 2004; Malo, Suarez, & Diez 2004). Our methods appear useful for studies that collect accurate and frequent locations of animals and humans with the use of GPS or similar technologies now commonly available in most areas of the world.

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Supplementary material

The following supplementary material is available as part of the online article (full text) from http://w.w.w.blackwell-synergy.com.

Figure S1. Location of the Starkey Experimental Forest and Range in north-east Oregon, western USA, and the Northeast Study Area where our research was conducted.