Snowmobile Activity and Glucocorticoid Stress Responses in Wolves and Elk

SCOTT CREEL,*‡ JENNIFER E. FOX,† AMANDA HARDY,* JENNIFER SANDS,* BOB GARROTT,* AND ROLF O. PETERSON†

*Department of Ecology, 310 Lewis Hall, Montana State University, Bozeman, MT 59717, U.S.A.
†School of Forestry and Wood Products, Michigan Technological University, Houghton, MI 49931-1295, U.S.A.

Abstract: *The effect of human activities on animal populations is widely debated, particularly since a recent decision by the U.S. Department of the Interior to ban snowmobiles from national parks. Immunoassays of fecal glucocorticoid levels provide a sensitive and noninvasive method of measuring the physiological stress responses of wildlife to disturbances. We tested for associations between snowmobile activity and glucocorticoid levels in an elk (*Cervus elaphus*) population in Yellowstone National Park and wolf (*Canis lupus*) populations in Yellowstone, Voyageurs, and Isle Royale national parks. For wolves, comparisons among populations and years showed that fecal glucocorticoid levels were higher in areas and times of heavy snowmobile use. For elk, day-to-day variation in fecal glucocorticoid levels paralleled variation in the number of snowmobiles after we controlled for the effects of weather and age. Also for elk, glucocorticoid concentrations were higher in response to snowmobiles than to wheeled vehicles after we controlled for the effects of age, weather, and number of vehicles. Despite these stress responses, there was no evidence that current levels of snowmobile activity are affecting the population dynamics of either species in these locations.*

Actividad de Vehículos para Nieve y Respuestas de Stress Glucocorticoide en Lobos y Alces

Resumen: *El efecto de actividades humanas sobre poblaciones animales es ampliamente debatido, particularmente desde una reciente decisión del Departamento del Interior de EE.UU. de prohibir los vehículos para nieve en los Parques Nacionales. Inmunoensayos de los niveles glucocorticoides fecales proporcionan un método sensible y no invasivo para medir respuestas de stress fisiológico de fauna silvestre a disturbios. Probamos las asociación entre la actividad de vehículos de nieve y niveles de glucocorticoides en una población de alces (*Cervus elaphus*) en el Parque Nacional Yellowstone y en poblaciones de lobos (*Canis lupus*) en los parques nacionales Yellowstone, Voyageurs e Isle Royale. Para lobos, las comparaciones entre poblaciones y años mostraron que los niveles de glucocorticoides fecales son mayores en áreas y tiempos de intenso uso de vehículos para nieve. Para alces, la variación diaria de los niveles de glucocorticoides fecales fue paralela a la variación en el número de vehículos para nieve después de controlar para efectos del clima y la edad. También para alces, las concentraciones de glucocorticoides fueron mayores en respuesta a los vehículos para nieve que en respuesta a vehículos de ruedas después de controlar para los efectos de la edad, el clima y el número de vehículos. A pesar de estas respuestas al stress, no hubo evidencia de que los niveles de actividad de vehículos para nieve afecten la dinámica poblacional de ninguna de las especies en estas localidades.*

Introduction

Management policies for protected areas must address the effects of human activities on the animal populations they are designed to protect. Policies must also account for public access to protected areas, balancing a trade-off between access and human effects. On 27 April 2000, the U.S. Department of the Interior announced a ban on snowmobile activity in the national park system, a decision now under debate by biologists, politicians, the snowmobile industry, and the general public.

‡email screel@montana.edu
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Resolution of this debate depends in part on quantitative tests of the effects of snowmobile activity on animals. Behavioral studies have demonstrated varying degrees of avoidance of snowmobiles by white-tailed deer (*Odocoileus virginianus*; Dorrance et al. 1975; Richens & Lavigne 1978; Eckstein et al. 1979), mule deer (*Odocoileus hemionus*; Freddy et al. 1986), reindeer (*Rangifer tarandus*; Tyler 1991), and moose (*Alces alces*; Colescott & Gillingham 1998). Other studies have measured short-term physiological responses to nearby human disturbance, such as elevated heart rates measured via radiotelemetry in bighorn sheep (*Ovis canadensis*) and white-tailed deer (MacArthur et al. 1979, 1982; Moen et al. 1982), but these immediate behavioral and physiological responses do not directly shed light on the possibility of prolonged responses to human activity, or on variables that are closely linked to fitness.

Among other responses to physiological or behavioral stressors, the hypothalamic-pituitary-adrenal axis increases the secretion of glucocorticoids (GCs). Although GC responses are adaptive in the short term, chronically elevated GC levels produce an array of pathologies, including reproductive suppression, ulcers, muscle wasting, and immune suppression (Sapolsky 1992). Over the past decade, methods for non-invasive measurement of GC levels in urine or feces have been widely developed to investigate stress physiology in the wild (Wasser et al. 1988, 1997; Creel et al. 1991, 1996; Monfort et al. 1997; Palme et al. 1998). To assess physiological stress responses to snowmobiles, we measured GC concentrations in fecal samples collected noninvasively from elk (*Cervus elaphus*) in Yellowstone National Park and from wolves (*Canis lupus*) in Yellowstone, Voyageurs, and Isle Royale national parks.

Methods

We collected 125 fecal samples from 34 radiocollared adult female elk in Yellowstone National Park between November 1998 and May 1999. These elk are members of a nonmigratory population of 500–900 living in the Madison-Firehole-Gibbon area. The population has been under study since 1965, with radiotelemetry of known individuals since 1992 (Craighead et al. 1973; Aune 1981; Cole 1983; Eberhardt et al. 1998). In winter, elk are constrained mainly to low-elevation valleys, which in this case hold roads groomed for snowmobiling from West Yellowstone to Old Faithful. We collected 111 samples during the 89-day snowmobile season and 14 samples over 30 days immediately after the snowmobile season, during which wheeled vehicles used the roads. We collected samples by following tracks in the snow behind radiocollared individuals and collecting fresh fecal pellets, noting the time of day to statistically control for diurnal variation in GC secretion. We avoided driving the elk while tracking by using the radio signal to maintain distance. Because fecal concentrations reflect GC secretion 12 to 24 hours earlier (Millspaugh 1999), our methods should have had little or no effect on the GC values in the samples we collected.

Visitors were tallied by the Yellowstone National Park Visitor Services Office at the West Yellowstone entrance, through which most vehicles enter the study area. For our analyses, snowmobiles and snowcoaches were categorized together as oversnow vehicles; more than 98% of these were snowmobiles. Snowpack was measured as snow-water equivalent, determined by the mass of a snow column on a SNOTEL measuring device (www.wcc.nrcs.usda.gov/snotel/Montana/montana.html).

For wolves, our analysis was less fine-grained, but it complimented the data from elk by comparing larger areas over a longer period (2 years). We tested the hypothesis that GC levels would be higher in times and places with greater snowmobile activity by comparing wolf populations in two neighboring national parks: Isle Royale, which is closed to the public in winter, and Voyageurs, where snowmobiles are common. At Isle Royale, wolves were exposed to low-level surveys from one small, fixed-wing aircraft for 50 days each winter. During 1968–2000, one snowmobile was used daily at the research base during the survey period, but wolves rarely venture within 1 km of this site (Peterson 1995). In contrast, more than 110 miles of groomed trails and 28,000 ha of lake surface are accessible to snowmobiles in Voyageurs. Our data on snowmobile numbers in Voyageurs came from trail counters, which provided an index of visitor numbers rather than a total count. Total counts were not available because entrance points were not monitored and there are many trails.

We collected fecal samples for two consecutive winter seasons, 1998–1999 and 1999–2000, concentrating on the period when ice conditions were favorable for snowmobile use at Voyageurs and interior access was possible at both parks. Over two winters, we collected 178 samples from 9–10 different wolf packs at Voyageurs and 193 samples from three packs and several lone wolves at Isle Royale. We recorded scat locations in universal transverse mercator coordinates, pack identification, date, time of day, estimated time since excretion, temperature, and snow depth. Sex, rank, and individual identification of samples were unknown for most fecal samples (except from Yellowstone; see below). To avoid disturbing the animals, we collected samples only in their absence. We mixed each dropping, collected four or five separate subsamples, and combined subsamples in a 50-mL centrifuge tube (Creel et al. 1997*a*, 1997*b*).

Finally, we measured winter GC levels of wolves (n = 161 samples) in the northern range of Yellowstone National Park. In winter, the northern range is closed to snowmobiles but open to wheeled vehicles (unlike the Yellowstone elk study area) and has a level of disturbance intermediate between those of Isle Royale and Voyageurs. Fecal samples were collected from a mixture of known and unknown individuals in three packs between 17 January 1999 and 18 July 1999. We observed individuals of known rank and sex with spotting scopes from distances of 1–2 km and collected samples after the wolves moved away. We noted the time of defecation and the time of collection to statistically control for diurnal fluctuation in GC levels and breakdown of GCs prior to collection. (Because of low ambient temperatures, no breakdown was detectable on the time scale of this study.)

Extractions and Radioimmunoassays

Fecal samples were usually frozen or partially frozen when collected. All samples were frozen in the field and stored at −80° C until extraction. For both species, feces were weighed, fully dried in a rotary evaporator without heat, then reweighed to determine water content. We boiled 0.2 g of dried feces in ethanol for 20 minutes, then centrifuged them at 1500 rpm for 10 minutes. Centrifuge pellets were weighed to determine the amount of indigestible matter before discarding. (In comparison to ungulate droppings, the composition of carnivore scats is highly variable.) Supernatants were decanted, dried under air, rinsed with 2–3 mL ethanol, redried, and reconstituted in 1 mL absolute methanol. For wolf samples, tubes were placed in an ultrasonic glass cleaner for 10 seconds and centrifuged after the ethanol rinse to free particles adhering to tube walls. Fecal extracts in methanol were stored at −80° C. Of this extract, 25 or 50 μL was taken to assay, diluted as necessary with phosphate-buffered saline. Assay results were expressed as ng GC/g dry feces.

In statistical analyses, we tested water content and (for wolves) the proportion of indigestible matter as methodological covariates. Together, these variables control for variation in the diet and for water absorbed or evaporated after defecation. Because we collected samples primarily in winter, samples were normally frozen or partially frozen when we collected them, with little apparent absorption of water or dessication.

For elk, we measured GCs with a previously validated double-antibody ^{125}I-corticosterone assay from ICN Biomedicals (Millspaugh 1999). This antibody cross reacts little with other steroids (maximum 0.1% for testosterone). Serial dilution of standards and fecal extracts yielded parallel changes in antibody binding for seven points to 128-fold dilution. Recovery of cortisol (25 μL at 25–500 ng/mL) added to fecal extracts was 98% ± 9% ($t = 10.57$, $p < 0.001$, $r^2 = 0.92$). The intra-assay coefficient of variation was 2.86, and interassay CVs were 7.84 and 10.36 for high and low concentration controls, respectively. Sensitivity was 12.5 pg/tube.

For wolves, we measured GCs with a coated-tube ^{125}I-cortisol assay from Diagnostic Products Corporation, with little cross-reactivity to other steroids (maximum 0.2% for progesterone). Serial dilution of standards and fecal extracts yielded parallel changes in antibody binding for six points to 10-fold dilution. Recovery of cortisol (25 μL at 5–500 ng/mL) added to fecal extracts was 107% ± 2% ($t = 55.9$, $p < 0.001$, $r^2 = 0.998$). Intra- and interassay coefficients of variation were 5.8% and 10.4%. Sensitivity was 10 pg/tube.

Statistical Analysis

All statistical analyses were performed with STATISTICA (StatSoft 1999), including tests of assumptions for parametric tests. To avoid pseudoreplication, we used a nested analysis of variance (ANOVA) with data from individually known elk and Yellowstone wolves that were resampled, which showed that fecal samples could be considered statistically independent units of analysis (Steel & Torrie 1980). We conducted a multiple-regression analysis on the elk data to determine the effects on GCs of age, snow depth, mean daily temperature, visitor numbers, and water content of the feces. For wolves, we used factorial ANOVA to determine the effects on GCs of the different sites/visitor-use conditions, years, time since defecation, average daily temperature, water content, and percent indigestible material of the feces. Variances were compared with Bartlett's test, and GC values were log-transformed when necessary.

Results

Elk

In the Madison-Firehole-Gibbon elk herd at Yellowstone, GC levels increased with age (partial regression, $t_{120} = 2.64$, $p = 0.009$) and with deeper snow ($t_{120} = 2.14$, $p = 0.034$). For the multiple regression, $F_{4,120} = 11.079$, $p < 0.001$, and $R^2 = 0.25$. Potential covariates not in the final regression model included mean daily temperature and water content of the feces (see Methods).

After we controlled for the effects of age and snow depth, GC levels were significantly higher during the snowmobile season than during the wheeled-vehicle season ($t_{120} = 3.72$, $p = 0.0003$, also controlling for daily number of vehicles). During the snowmobile season, elk GC levels increased significantly as the daily number of snowmobiles in the area increased (Fig. 1, $t_{120} = 2.58$, $p = 0.011$). Total over-snow vehicles included 44,274 snowmobiles and 768 snowcoaches over

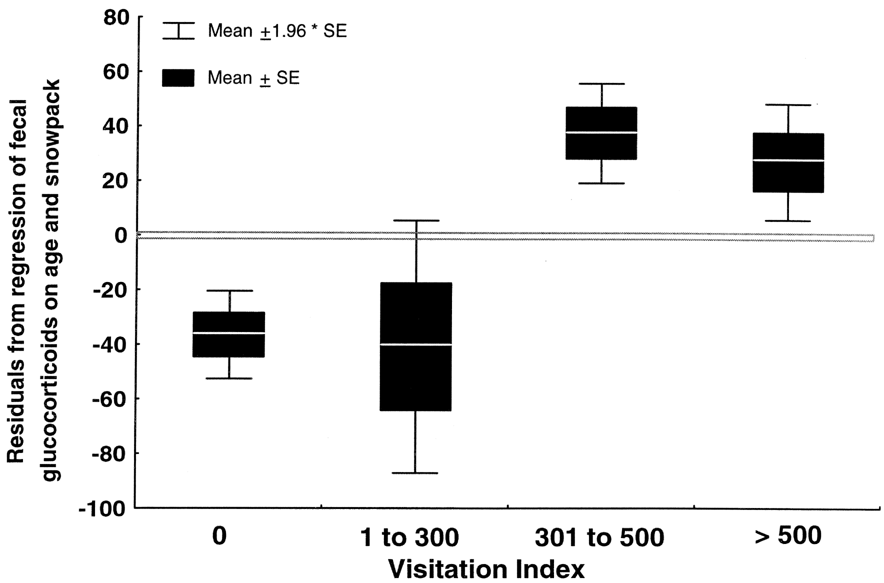

Figure 1. Fecal glucocorticoid (GC) concentrations of adult female elk in the Madison-Firehole-Gibbon region of Yellowstone National Park as a function of the daily number of snowmobiles entering the area. Because age and snow pack affected GC concentrations, the ordinate shows residuals from the regression of GC on age and snow-water equivalents. Visitation index gives the number of snowmobiles entering the area via West Yellowstone (see methods).

the 89-day winter season (maximum daily total, 1168; minimum daily total, 144; mean daily total, 514). The wheeled-vehicle season included 11,514 wheeled vehicles over a 30-day period (maximum daily total, 732; minimum daily total, 134; mean daily total, 384). In our analysis, "snowmobiles" includes snowcoaches, which constituted <2% of all over-snow vehicles.

To summarize, snowmobiles provoked a stronger physiological stress response in elk than wheeled vehicles did, and stress responses paralleled changes in the number of visitors. The comparison of snowmobiles to wheeled vehicles should be treated with caution. First, our sample of days with wheeled traffic is small. Second, we collected samples for the wheeled-vehicle period as winter was changing to spring, when changes in food availability and quality and a redistribution of elk away from valley-bottom roads was occurring.

Wolves

For wolves in Voyageurs and Isle Royale, factorial ANOVA (Fig. 2a) showed that GC levels were higher in Voyageurs than in Isle Royale ($F_{1,367} = 19.32, p = 0.001$) and higher in 1998–1999 than in 1999–2000 ($F_{1,367} = 6.64, p = 0.0104$). There was a strong interaction between year and location ($F_{1,367} = 5.66, p = 0.017$), driven by a change between years in the GC levels of wolves in Voyageurs. Within Voyageurs, a 37% decline from 1998–1999 to 1999–2000 in the number of snowmobiles (Fig. 2b; 23,922 vs. 15,011 visitors) was accompanied exactly by a 37% decline in mean GC levels (means: 1784 ± 170.2 vs. 1129 ± 145.4 ng GC/g dry feces, $t_{175} = 2.91, p = 0.004$).

Because fecal samples were not from known individuals in Isle Royale or Voyageurs, we could not directly test if fecal samples were statistically independent. With similar sample sizes and more-frequent resampling of individuals, nested ANOVA of the Yellowstone wolf data showed that fecal samples were formally independent (Steel & Torrie 1980). We considered as covariates mean daily temperature, time from defecation to collection, water content, and proportion indigestible, none of which had a detectable effect on GC levels in this ANOVA. Overall, the GC levels of wolves were substantially higher at locations and times with more snowmobile usage, although variables other than snowmobile activity (such as diet) also differed between these populations. Moreover, snowmobiling was lighter in 1999–2000 because there was less snow (69.09 cm total in 1999–2000 compared with 166.37 cm in 1998–1999). If snowpack affected GC levels in wolves by mechanisms unrelated to human activity, low snow years would be expected to increase GC levels because ungulate prey remain in better condition and probably less vulnerable to wolves when the snowpack is low (Garrott et al. 1996; and see results above for the effect of snowpack on elk GC levels). As expected under the disturbance hypothesis, mean GC levels in wolves of northern-range Yellowstone were intermediate (Yellowstone; 1201.9 ± 157.5 ng CG/g dry feces; Voyageurs, 1468.0 ± 114.2; Isle Royale, 872.0 ± 73.1) in an area with human disturbance intermediate between that of Voyageurs and Isle Royale.

Discussion

Data from two species in three national parks show that stress-hormone levels correlate with snowmobile usage on both short (daily) and long (annual) time scales. It is

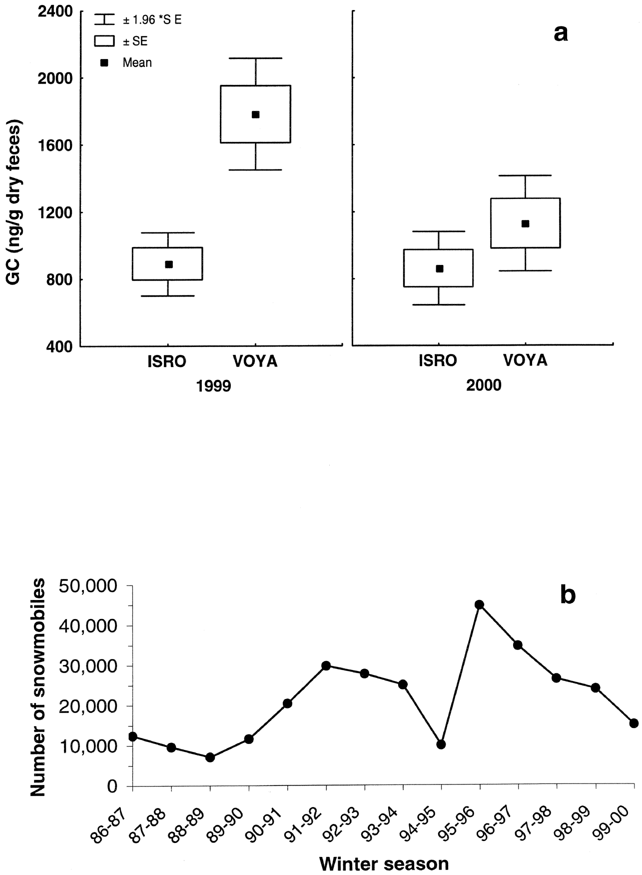

Figure 2. (a) Fecal glucocorticoid (GC) concentrations of wolves in Isle Royale (ISRO) and Voyageurs (VOYA) national parks in the winters of 1998–1999 (left) and 1999–2000 (right). (b) Index of snowmobile usage in Voyageurs National Park.

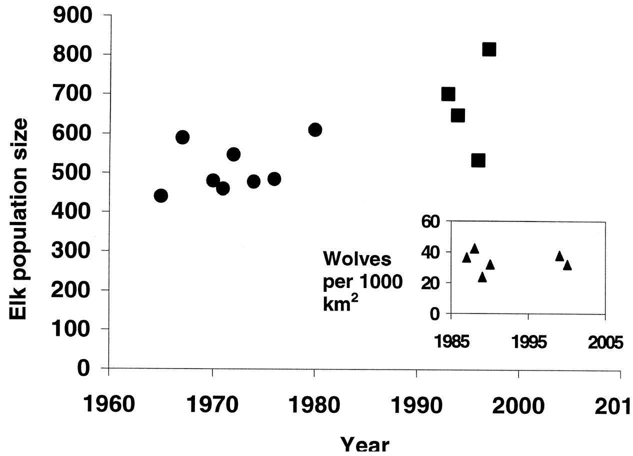

Figure 3. Population size for the Madison-Firehole elk herd, 1965–1999. Population counts from 1965 to 1980, which ranged from 436 to 612 (Aune 1981; Cole 1983; Craighead et al. 1973; Eberhardt et al. 1998), were slightly lower than the population estimates obtained during a study by R. A. Garrott from 1993–1997 (mean = 679). The earlier data (circles) are simple total counts of animals observed during ground and/or aerial surveys, whereas the recent data (squares) are estimates based on aerial mark-recapture methods. The apparent increase is attributable to changes in methods. The inset shows the density of wolves (number/1000 km^2) with ranges wholly or partially within Voyageurs National Park.

well established that chronic GC elevation can suppress several important physiological systems, including several aspects of immune function and the activity of the hypothalamic-pituitary-gonadal axis (Munck et al. 1984; Sapolsky 1992), but we did not examine these effects directly. It is thus logical to ask whether the elevations of GCs we observed are currently having negative effects on population dynamics or demography.

For elk in the Madison Firehole region of Yellowstone, the annual survival of adult females exceeds 90%, cow-calf ratios show healthy recruitment of juveniles, and population size has been relatively constant over the past 35 years (Fig. 3a). This suggests that the population is able to compensate for the physiological effects of increased snowmobile activity over that period. For wolves in Voyageurs, estimates of population size also show no tendency to decrease (Fig. 3b). In addition, wolves in Voyageurs have been observed using snowmobile tracks in heavier snow conditions because the compacted surface created by the snow machines makes traveling easier. Thus, wolves in Voyageurs might benefit from snowmobile "tracks," at least in the absence of actual machine activity (similar to the routine use of trails and roads by many other carnivores).

What message can be drawn from these data for wildlife policy in the national parks? At one extreme, it could be argued that in the absence of a measurable decline in population size, human activities could be considered benign. At the other extreme, one could argue that human activities that induce physiological stress responses should be curtailed. We take an intermediate view, that GC levels provide a sensitive method of measuring stresses engendered by human activities prior to demographic responses or changes in population size. A large body of research on captive mammals and humans shows that large, prolonged GC elevations typically reduce survival and reproduction (Munck et al. 1984; Sapolsky 1992). Although data on fitness effects of GC elevations in the wild are currently limited, the clear expectation from lab studies is that fitness effects will increase as a stressor becomes more severe or more prolonged (e.g., Blanchard et al. 1995). Figures 1 and 2 show that, averaged across an entire winter, the mean GC concentrations we observed were considerably below the levels expected during peaks of snowmobile activity, both among and within years. For example, the overall mean GC level for Yellowstone elk was well below the mean for periods with 700–800 snowmobiles per day, and snowmobile usage in Voyageurs was substantially lower in both years of this study than in some recent years (Fig. 2b). Consequently, one cannot conclude from our data that there are no fitness costs associated with current or recent levels of human activity.

We suggest that noninvasive GC measurements can be used as a simple and efficient method of detecting and monitoring human effects on animal populations, even incipient effects. For elk and wolves in three national parks, this method detects a clear physiological stress response induced by the current level of snowmobile activity. In this case and for other species of concern, such data can be used to inform decisions about the management of interactions between humans and wildlife.

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