ATTACHMENT 3

REPRODUCTIVE SUCCESS OF ELK FOLLOWING DISTURBANCE BY HUMANS DURING CALVING SEASON

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Abstract: Restricting human activity in elk (*Cervus elaphus*) calving areas during calving season can be controversial because of increasing human uses of elk habitat, and little evidence exists to evaluate impacts of these activities on elk populations. We evaluated effects of human-induced disturbance on reproductive success of radiocollared adult female elk using a control–treatment study in central Colorado. Data were collected during 1 pretreatment year and 2 treatment years. Treatment elk were repeatedly approached and displaced by study personnel throughout a 3–4-week period of peak calving during both treatment years, while control elk did not receive treatment. We observed elk on alpine summer ranges in July and August on both areas to estimate the proportion of marked cows maintaining a calf. Calf/cow proportions for the control area remained stable, but those for the treatment area declined each year. Average number of disturbances/elk/year effectively modeled variation in calf/cow proportions, supporting treatment as the cause of declining calf/cow proportions. Average decrease in calf/cow proportion in the treatment group was 0.225. Modeling indicated that estimated annual population growth on both study areas was 7% without treatment application, given that existing human activities cause some unknown level of calving-season disturbance. With an average of 10 disturbances/cow above ambient levels, our model projected no growth. Our results support maintaining disturbance-free areas for elk during parturitional periods.

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Recently born elk calves are particularly susceptible to malnutrition and predation (Schlegel 1976, Taber et al. 1982:286, Bear 1989, Singer et al. 1997). Human-induced disturbance during calving season may exacerbate elk vulnerability, and restricting humans in parturitional habitats during calving season has been recommended to minimize impacts (Towry 1987). Seasonal closures may, however, conflict with human demands on these habitats, but little evidence exists to support or refute the need to protect elk from humans during calving season.

Previous studies have described displacement or alteration of elk spatial use patterns associated with activities such as vehicular traffic (Czech 1991, Cole et al. 1997), logging (Edge et al. 1985, Czech 1991), mining (Kuck et al. 1985, Johnson 1986), recreation (Berwick et al. 1986, Cassirer et al. 1992), and development (Berwick et al. 1986, Morrison et al. 1995). However, few studies have directly evaluated effects of calving-season disturbance on calf production. Johnson (1986) found no significant difference in reproduction (July calf:cow ratios) between elk using 3 surface-coal-mine areas and 3 control areas. Kuck et al. (1985) approached and displaced radiocollared calves in summer and reported no abandonment or mortality of collared calves, but small sample sizes provided low statistical power to detect an effect of disturbance on calf survival.

We hypothesized that human-induced disturbance of elk during calving season would reduce reproductive success (number of offspring of an individual surviving at a given time; Lincoln et al. 1998:261). We used control and treatment groups of elk to test our hypothesis by applying a disturbance treatment during calving season and comparing subsequent levels of reproductive success between groups.

STUDY AREA

Our study was conducted in 2 geographically contiguous areas in central Colorado, approximately 160 km west of Denver: Beaver Creek and Vail (Fig. 1). Elevations ranged from 2,250 m to 4,150 m at Beaver Creek, and 2,400 m to 4,000 m at Vail. Ecosystem types on both areas included alpine tundra, subalpine and montane forest, montane shrubland, and riparian (Fitzgerald et al. 1994). Additional study area descriptions were provided by de Vergie (1989), Morrison (1992), and Morrison et al. (1995).

Portions of the Interstate-70 corridor are

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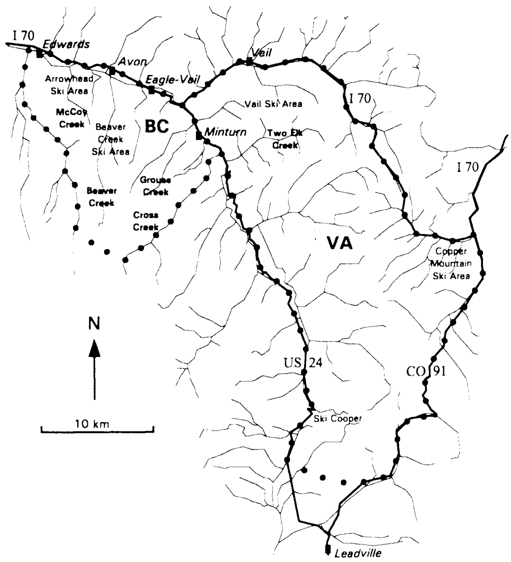

Fig. 1. Location of Beaver Creek (BC) and Vail (VA) study areas in central Colorado. Approximate boundaries of study areas shown by dotted lines.

heavily developed along the northern perimeter of both areas. Edwards, Avon, and Eagle–Vail occur north of the Beaver Creek study area along Interstate 70. Although shown as points (Fig. 1), these communities extend along the valley floor in a nearly continuous strip from about 2 km west of the intersection of Interstate 70 and U.S. Highway 24, westward beyond Edwards. Similarly, the town of Vail covers an approximately 12-km strip along Interstate 70 on the north boundary of the Vail study area. Minturn lies between Beaver Creek and Vail study areas along U.S. Highway 24 from Grouse Creek to Cross Creek. Both areas contain ski resorts: Copper Mountain, Vail, and Ski Cooper on the Vail study area, and Beaver Creek and Arrowhead on the Beaver Creek study area. Copper Mountain, Vail, and Beaver Creek Ski Areas are year-around resorts. National Forest lands within both study areas are popular destinations for recreationists engaged in backcountry activities. Because of land management policies in effect prior to, and throughout, our study the Two Elk Creek drainage, upper sections of McCoy Creek, and parts of the Beaver Creek drainage were closed to public access in May and June to protect elk during calving.

Beaver Creek and Vail study areas were well suited for use as treatment and control areas because of ecological and land use similarities, and both contained large, extensively studied elk herds. de Vergie (1989) reported that most elk on Beaver Creek and Vail occupied either one or the other area, and rarely crossed U.S. Highway 24, implying that Beaver Creek and Vail elk herds were sufficiently segregated to afford a treatment–control experimental opportunity. Cows captured on winter ranges in de Vergie's (1989) study used open alpine areas during summer, which would facilitate daily observation of marked cows for our study.

METHODS

We maintained samples of marked adult female elk on Beaver Creek and Vail study areas from 1995 to 1997 (71–85 elk/area/yr), and applied a disturbance treatment to marked elk within the Beaver Creek study area during the peak calving period in 1996 and 1997. No treatment was applied to Beaver Creek elk in 1995 or to Vail elk in all 3 years. We ascertained presence or absence of a calf for individual marked adult cows by visual observation in July and August to estimate annual proportions of marked cows maintaining a calf on each area (calf/cow proportion). We compared treatment–control differences in calf/cow proportions for 1 year of pretreatment data and 2 years of treatment data to estimate effects of disturbance.

Capturing and Marking Adult Female Elk

We used helicopter net-gunning to capture a representative sample of adult female elk at specified locations spread across both study areas (Phillips 1998). Elk were fitted with frequency-specific transmitters on neck collars containing 2 plastic identification sleeves marked with unique alpha-numeric codes of 76-mm-high black characters on a white background (Freddy 1993). Elk were also marked with unique combinations of colored plastic livestock ear tags (76 mm × 76 mm).

Disturbance Treatments on Beaver Creek Study Area

We applied a treatment of simulated recreational hiking to radiocollared elk on the Beaver Creek area by approaching a radiocollared animal until she was displaced. The rationale behind our disturbance treatment was that a small number of people targeting a specific sample of animals (through the use of telemetry equipment) could create an effect equal to a greater number of recreationists hiking through the area.

Based on estimated parturition and conception dates for elk in Colorado (Bear 1989, Freddy 1989, Byrne 1990), and a median gestation period of 255 days (Bubenik 1982:171), we expected that 80–90% of calves would be born from 26 May to 19 June. These dates bounded our treatment period in 1996, but to increase treatment efficacy, we expanded the treatment period by 7 days in 1997 to 19 May through 19 June.

We used twice-weekly aerial telemetry to locate elk during the treatment period and to allocate treatment effort. Up to 9 technicians using telemetry receivers were assigned to areas of high elk densities for 24 days in 1996 and 30 days in 1997. We documented each disturbance by recording animal identification, time, location, and visual and telemetry evidence demonstrating that the target animal had been treated. We concluded that a treatment occurred when nearby elk were seen or heard running away, telemetry evidence supported the proximity of the target animal at time of treatment, and posttreatment telemetry evidence demonstrated a fading signal in the same direction that elk were seen or heard to move (Phillips 1998).

Estimating Calf Status of Marked Elk

We observed marked adult female elk on Beaver Creek and Vail study areas each year during July and August to determine presence or absence of a calf. Observations were generally made from dawn to 1000 hr, and 1600 hr to dark at points that provided extensive views of alpine summer range where risk of disturbing elk was minimal. We recorded length of time that each marked cow was continuously visible and monitored. We documented time and duration of nursing and licking bouts, along with other types of interactions between cows and calves. Individual observation periods generally occurred over several days, were at numerous locations, and varied from several seconds to several hours, depending on animal movements, vegetation cover, terrain, and weather.

Calf status (CS) was determined for as many marked elk as possible, where CS1 denotes presence of a calf and CS0 denotes absence of a calf. Twinning occurs in elk but is generally <1% (Bubenik 1982:170, Taber et al. 1982: 280). Our use of a binary response variable for calf status implies 1 calf or no calf. If twinning rates were unusually high, bias could result from interpreting calf/cow proportions as the number of calves/cow, rather than the proportion of cows maintaining a calf (or calves). We could not determine presence of twins for marked cows because calves were not individually identifiable, but we did not observe any marked cows nurse 2 calves simultaneously or different calves, sequentially. We believe that calf/cow proportions can be interpreted as the number of calves/cow with negligible risk of bias from cows maintaining 2 calves. Our July–August calf/cow proportions are, therefore, conceptually similar to the summer calf production rate of Singer et al. (1997).

We concluded that a maternal bond existed between cow and calf if the cow nursed a calf for ≥10 sec, or if a cow exhibited "strong calf association", including licking bouts with a calf or traveling as a unit (Phillips 1998). Implicit here was an assumption that such behaviors are rare between cows and calves not maternally related (Geist 1982). Female red deer (*Cervus elaphus*) with calves infrequently allow a strange calf to nurse, but usually drive them away (Lowe 1966). We commonly observed cows reject nursing attempts by calves, although some calves were persistent in their attempts. These interactions were characterized by aggressive or avoidance behaviors by the cow toward the calf, similar to those described by Altmann (1952). Strong calf association was more subjective than nursing, but provided reliable CS1 evidence. We were looking for a distinctive attentiveness between cow and calf, especially when alarmed, that was not present in casual calf–cow interactions. Usually, most cows that exhibited strong calf association were later seen nursing a calf.

Concluding that a cow did not have a calf was not definitive because it was impossible to continuously observe individuals long enough to conclude CS0 with certainty. We obtained CS0 evidence (actually a lack of CS1 evidence) by accumulating blocks of uninterrupted observation time (several sec to several hr), within which a particular cow did not associate with calves. Observation data from summer 1995, comprised of discrete blocks of continuous observation time, indicated that approximately 95% of CS1 cows were detected within 350 min of cumulative observation time, and that longer observations provided rapidly diminishing returns (Phillips 1998). Cows that showed no strong calf association were included in analysis as CS0 only if total cumulative observation time was ≥350 min. Use of an arbitrary cutoff time introduces bias from excluding individuals with <350 min of observation time and no strong calf association. To balance this bias, we constrained evidence of calf association to occur within 350 min to classify an individual as CS1, i.e., cows were classified as CS0 if CS1 evidence was observed after 350 min of total observation time, but not within 350 min of observation. Only 8 CS0 classifications (2% of all classified individuals) resulted from this constraint.

Analysis of Calf-status and Treatment-effort Data

We used a generalized linear mixed model approach, incorporated in the GLIMMIX macro of SAS Version 6.12 (Littell et al. 1996), to analyze calf-status and treatment-effort data. Error type was specified as binomial, and we used the logit link function to linearize the dependent variable and to scale estimates of calf/cow proportions between 0 and 1. The form of the general model was

$$\text{logit}(R_{ijk}) = m + \text{area}_i + \text{year}_j + (\text{area} \times \text{year})_{ij} + \text{indv(area)}_{ik},$$

where $\text{logit}(R_{ijk}) = \log_e[R_{ijk}/(1 - R_{ijk})]$; R_{ijk} = probability that a specific individual k, given area i and year j, maintained a calf during the July–August observation period; m = intercept; area_i = fixed effect of the i^{th} area, $i = 1, 2$ (Beaver Creek and Vail, respectively); year_j = fixed effect of the j^{th} year, $j = 1, 2, 3$ (1995, 1996, and 1997, respectively); $(\text{area} \times \text{year})_{ij} = ij^{th}$ area-by-year interaction fixed effect; and indv(area)_{ik} = random effect of the k^{th} marked elk, nested within the i^{th} area, $k = 1, 2 \ldots 184$.

Individual marked elk, sampled from the larger population of interest (all elk on Beaver Creek and Vail study areas), were the unit of analysis and were treated as a random-effects term. Modeling individuals as a random effect allowed for partitioning overall variance of calf-status data into components. With a separate estimate of the indv(area) variance component, $\hat{\sigma}^2_I$, the remaining variance is partitioned among fixed effects. Fixed effects are more appropriately interpreted when also accounting for random effects. Significance of $\hat{\sigma}^2_I$ was evaluated with a likelihood-ratio test between the general model and a reduced model without indv(area) (Lebreton et al. 1992:80).

We used deviance divided by degrees of freedom (DEV/df) as a general index for goodness of fit and overdispersion. We also used DEV as a goodness-of-fit statistic approximately distributed χ^2_{df} with df = $n - p$, where n = number of observations and p = number of independent fixed-effects parameters in the model (Littell et al. 1996:432,445). The GLIMMIX macro uses the residual estimate as an extra dispersion (ED) scale parameter to indicate if the observed conditional variance of the errors is different than theory. Overdispersion is indicated when ED > 1 and underdispersion when ED < 1. By default, GLIMMIX adjusts the analysis for ED, but ED can be set to 1.0 to prevent this adjustment.

Estimated annual calf/cow proportions for each study area (area-by-year $\hat{R}_{ij}$) and 95% confidence limits were obtained from back transformations of logit-scale area-by-year means and 95% confidence limits using the inverse logit link function (Littell et al. 1996:431). The area × year interaction effect and contrasts of annual differences between Beaver Creek and Vail area-by-year calf/cow proportions were examined for evidence of treatment effect. Our research hypothesis was that treatment-group $\hat{R}_{ij}$ (that is, $\hat{R}_{12}$ and $\hat{R}_{13}$) would decline relative to control values, after accounting for pretreatment differences. The contrast used to test the null hypothesis of no treatment effect was

$$[(R_{12} - R_{22}) + (R_{13} - R_{23})]/2 - (R_{11} - R_{21}) = 0$$

(average treatment effect).

This contrast states that the average difference between treatment and control calf/cow proportions during treatment years was the same as for the pretreatment year. Substitution of corresponding $\hat{R}_{ij}$ for each R_{ij} in the contrast provides an estimate of the average treatment effect adjusted for pretreatment difference between Beaver Creek and Vail. A negative estimate corresponds with reduced average calf/cow proportions for the treatment group during 1996 and 1997.

Level of treatment effort represents a potential mechanism (magnitude of disturbance) to explain variation in the data, especially interaction effects. We determined the average number of treatments/individual for each area-by-year group and used these values as individual-specific covariates ("group-average" covariate). We replaced the area × year interaction in the general model with a term for the group-average covariate. This approach modeled the linear relationship between group-average number of treatments/cow and average calf/cow proportions, among area-by-year groups. We assessed efficacy of the group-average covariate relative to the interaction term using an analysis-of-deviance F-test and degrees of freedom appropriate when considering area-by-year groups, rather than individuals, as units of analysis (Skalski et al. 1993). An F-test was more appropriate than a likelihood-ratio test for this approach because it explicitly accounted for small denominator degrees of freedom resulting from the reduced sample size of 6 area-by-year cells. The structure of the F-statistic was

$$F = [(DEV_{red} - DEV_{cov})/(df_{red} - df_{cov})] \div [(DEV_{cov} - DEV_{gen})/(df_{cov} - df_{gen})],$$

where DEV_{red} = deviance of the reduced model containing m, area, year, and indv(area); DEV_{cov} = deviance of the model containing m, area, year, treatment effort covariate, and indv(area); DEV_{gen} = deviance of the general model; df_{red} = degrees of freedom for the reduced model; df_{cov} = degrees of freedom for the covariate model; and df_{gen} = degrees of freedom for the general model.

This F-test did not evaluate whether the covariate explained a significant amount of deviance when added to the reduced model. Rather, it tested how well the covariate served as a surrogate for the interaction term. The null hypothesis was that the covariate did not adequately substitute for the interaction in accounting for variation in area-by-year calf/cow proportions. We also computed the percentage of deviance explained by the covariate relative to the interaction term by

$$(DEV_{red} - DEV_{cov})/(DEV_{red} - DEV_{gen}) \times 100.$$

Modeling Population Dynamics with Effects of Calving-season Disturbance

We explored the potential impact on population growth of various levels of disturbance, by incorporating the group-average covariate model as a predictor of prehunt calf/cow proportions in a density-independent population-dynamics model for elk. We parameterized the model using information from our study and others conducted in Colorado, and from Colorado Division of Wildlife 1986–95 harvest data (Phillips and Alldredge 1999). Because Beaver Creek and Vail study areas are popular with recreationists, and because large areas of each were open to human access during our study, some unknown level of disturbance probably occurred that was not caused by our treatment effort. Inclusion of the covariate model within the population model reflects potential changes in population growth if calving-season disturbances increase relative to levels that existed for non-treatment elk during our study.

RESULTS

We documented 407 and 691 reliable treatment events on the Beaver Creek study area in 1996 and 1997, respectively. Average numbers of treatments/Beaver Creek individual were 5.4 in 1996, and 8.3 in 1997. We estimated calf status for >75% of marked cows/area throughout the study. Final sample sizes for calf status of marked cows were 59, 61, and 73 for Beaver Creek, and 54, 62, and 70 for Vail in 1995, 1996, and 1997, respectively.

We first fitted the general model without controlling the ED-scale parameter to evaluate lack of fit and overdispersion. Values of DEV (417.3, df = 372, P = 0.052), DEV/df (1.12), and ED scale (0.89) provided little evidence of lack of fit or overdispersion, so we set ED scale = 1.0 for further analysis.

A significant component of overall variation in probability of having a calf was explained by the random effects of individual elk (indv(area) likelihood-ratio test $\chi^2_1 = 47.9$, $P < 0.001$), and the random effects term was retained in the model. The GLIMMIX macro provides estimates of random-effects variance components in the logit scale, only: $\hat{\sigma}^2_I = 0.300$, SE = 0.241, 95% CI = 0.098–3.866.

Differences between Beaver Creek and Vail calf/cow proportions were not the same for each year of the study (area × year interaction, $\chi^2_2 = 14.0$, $P < 0.001$). After adjusting for pretreatment differences, estimated average treatment effect was −0.225 (contrast $F_{1,191} = 3.94$, $P = 0.024$), indicating that average calf production was 0.225 calves/cow lower for treatment elk than for control elk in 1996 and 1997. Final estimates of annual area-specific calf/cow proportions were obtained using the general model (Table 1). Confidence intervals are asymmetric because the transformation from logit scale to biological scale is nonlinear.

Average number of disturbances/elk/year did a good job of explaining the declining trend in Beaver Creek calf/cow proportions (Fig. 2). The

Table 1. Estimates of July–August calf/cow proportions[a] for samples of marked adult female elk on Beaver Creek (BC) and Vail (VA) study areas, Colorado, 1995–97.

		Biological scale[b]		Logit scale[c]	
Year	Area	Mean	CI	Mean	SE
1995[d]	BC	0.646	0.512–0.761	0.6035	0.2822
	VA	0.627	0.486–0.750	0.5194	0.2924
1996	BC[e]	0.524	0.394–0.651	0.0972	0.2670
	VA	0.631	0.500–0.746	0.5368	0.2730
1997	BC[e]	0.398	0.288–0.519	−0.4147	0.2487
	VA	0.703	0.582–0.802	0.8637	0.2698

[a] Proportion of marked cows maintaining a calf, or calves/cow assuming a negligible rate of twinning.
[b] Mean calf/cow proportion, and 95% CI back-transformed from logit scale to biological scale (0–1 calves/cow), using the inverse logit link function (Littell et al. 1996:431).
[c] Logit-scale mean and SE provided for CI computation using 1-sided Student's t-statistic and 191 df.
[d] Pretreatment year.
[e] Disturbance treatment applied to Beaver Creek elk in 1996–97.

group-average covariate representing treatment effort (5.4 and 8.3 treatments/Beaver Creek cow in 1996 and 1997, respectively, and 0 treatments/cow for all other area-by-year cells) was 95% as effective as the area × year interaction at explaining deviance in our data, but due to small sample size (n = 6 area-by-year cells) and low degrees of freedom, it appeared that the covariate term did not adequately substitute for the interaction term ($F_{1,1} = 17.226$, $P = 0.075$). Removal of nonsignificant area and year main effects provided more parsimonious covariate and reduced models, indicating that the covariate term adequately substituted for main-effects and interaction terms ($F_{1,4} = 10.962$, $P = 0.015$). The final model relating calf/cow proportions and treatment effort was

$$\text{logit}(\hat{R}) = 0.6485 - 0.1211 \times T,$$

where T = group-specific average number of treatments/cow for each year, and standard errors were 0.1410 and 0.0319 for intercept and slope, respectively.

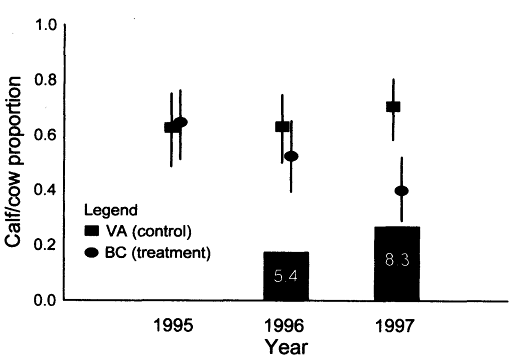

Fig. 2. Calf/cow proportions and 95% CI for Beaver Creek (BC) and Vail (VA) study areas (symbols), and average number of reliable BC disturbance treatments/marked cow (histogram). No treatments were applied in 1995.

Population modeling using a calf/cow proportion of 0.657 (treatment-effort covariate model output for 0 disturbances) indicated an annual growth rate of 7%. This growth rate includes the effect of some unknown level of disturbance of Beaver Creek and Vail elk from existing levels of human activity during calving season, but not treatment disturbance. Adding 10 calving-season disturbances/cow to ambient disturbance levels produced no growth (at 0.363 calves/cow), and >10 disturbances caused population decline. Although our model is approximate, it suggests that 1997 treatment levels were nearly high enough to curtail population growth (1% annual population growth at 8.3 disturbances/cow).

DISCUSSION

Calf/cow proportions were similar on both study areas in the pretreatment year (1995) and remained relatively stable for Vail throughout our study. However, Beaver Creek calf/cow proportions declined steadily in 1996 and 1997, as would be expected if reproductive success were inversely related to treatment effort (Table 1, Fig. 2). Statistically significant area × year interaction and contrast of average treatment effect suggest the declining trend in Beaver Creek calf-cow proportions was not due to sampling variation, rather, that some factor(s) in the environment caused this decline.

Under our research hypothesis, the probability of a cow successfully raising a calf should be inversely related to the number of times she was disturbed by humans. A strong relationship would be expected assuming that all disturbance events were of equal intensity; all cows were similar in their ability to successfully raise a calf in the presence of disturbance; the true number of disturbances/cow was measured (or at least measured in proportion to their true occurrence); that numbers of cows were uniformly distributed with respect to number of disturbances/cow; and that a measurement of disturbance for a cow could serve as a measure (or index) of disturbance and survival probability for her calf. We believe that violations of these assumptions introduced error variation into the disturbance numbers we documented, rendering these data ineffective as individual-specific covariates. However, we believe that use of mean numbers of treatments/cow/group allowed many of these errors to "average out", providing a reliable index to treatment level. The group-average treatment-effort covariate substituted almost completely for the area × year interaction in the general model, meaning that average annual levels of treatment effort explained variation between area-by-year calf/cow proportions nearly as well as the most important term in the general model. Our results do not prove cause and effect, but they support treatment as a causal mechanism for decreased reproductive success on the Beaver Creek study area in 1996 and 1997.

Use of a control, acquisition of pretreatment data to contrast with treatment data, and implementation of a manipulative treatment effort are elements of our study design that strengthen a cause-and-effect conclusion. However, Hurlbert (1984) and Manly (1992) caution that when design is unreplicated and treatment not randomly allocated, as in our study, other factors may contribute to observed results.

To minimize the potential for inherently different levels of reproductive success for control and treatment elk, we selected adjacent study areas that were similar in ecological and land use characteristics. There was no reason to expect gross differences in elk population parameters between these areas and pretreatment calf/cow proportions were similar for both. We further attempted to minimize confounding effects by estimating calf/cow proportions in July and August to eliminate effects of hunting mortality, and by selecting adult elk for samples to minimize variability in reproductive success due to inclusion of yearlings (Freddy 1987:21,22).

We assumed that treatment activity during calving would not make elk more secretive and less observable during the observation period because all observations were temporally separated, and most were spatially separated, from treatments (Phillips 1998). Violation of this assumption would introduce unknown variance components in calf/cow proportion estimates, potentially affecting tests of main and interaction fixed effects. The contrast used to test for average treatment effect was based on within-year differences between calf/cow proportions, so nonconstant observability across years factored out if observability between Beaver Creek and Vail remained similar within years.

We tested for differences between year-specific cumulative distributions of 2 measures of observability for Beaver Creek and Vail: total observation time/marked cow, and total observation time required to determine a cow had a calf, and compared annual group-total observation time and percentage of marked cows classified for calf status between Beaver Creek and Vail study areas. We found no evidence that observability of marked cows, or interactions with their calves, decreased in response to treatment (Phillips 1998).

Additional evidence suggested that the low Beaver Creek calf/cow proportion in 1997 resulted from increased calf mortality rather than reduced observability. On Beaver Creek, 2, 3, and 10 marked cows, and on Vail, 1, 0, and 0 marked cows were observed nursing yearlings (but not calves) in 1995, 1996, and 1997, respectively (Phillips 1998). Potential hypotheses explaining yearling nursings include: a nonpregnant female may continue to nurse a calf through winter and the following summer (Darling 1936, 1937; Lowe 1966), and a cow that loses her calf may continue to lactate and resume nursing her previous calf (Altmann 1952, 1963).

Prolonged lactation of nonpregnant cows has been documented for mild maritime climates, but we found no evidence documenting this behavior in harsher continental climates (typified by our study areas) where earlier weaning of calves may be expected due to greater physiological stress in winter (Smith 1974). The relatively low yearling nursing rates for marked cows in all area-by-year groups, except Beaver Creek 1997, suggest that most elk on our study areas did not routinely nurse calves through winter and the following summer. Under hypothesis 1, increased yearling nursings observed on Beaver Creek in 1997 would result from lower conception rates in 1996. Hunting pressure, potentially a disruptive factor during the rut, probably was not greater in 1996 than 1995 because hunting mortalities of marked elk did not increase in 1996 (4 marked Beaver Creek cows in both years). We have no reason to believe that conception rates in Beaver Creek were different for 1995 and 1996, and therefore, no reason to expect increased rates of prolonged lactation by nonpregnant cows from 1996 to 1997. There is reason to expect an increase in calf mortality rate because 1997 was the year we applied the strongest disturbance treatment. Observed rates of yearling nursing may, therefore, indicate increased calf mortality on Beaver Creek in 1997, consistent with arguments that we documented declining calf/cow proportions instead of declining elk observability.

By targeting adult cows for treatment, we probably also disturbed their calves, and it is likely that we disturbed more calves than we saw. We occasionally observed lone calves without seeing any nearby adult elk. Some calves exhibited classic "hider" behavior (Lent 1974: 22–27, Geist 1982:237) but others stood and ran. Some that ran appeared neither comfortable nor competent in that activity. Although we did not touch calves or remain near them for more than a few minutes, such encounters probably increased calf energy requirements and risk of detection by predators, because disturbed calves move greater distances than undisturbed calves (Kuck et al. 1985).

We did not evaluate mechanisms for calf mortality, but studies reporting causes of mortality of radiocollared neonatal elk calves implicate predation as the primary proximate factor. Bear (1989) reported that coyotes (*Canis latrans*) were the main predators on calves of all ages. Black bears (*Ursus americanus*) were the main predators of neonatal calves in a 3-year study in northcentral Idaho (Schlegel 1976), and grizzly bears (*Ursus arctos*) and coyotes were the main predators of calves in summer during 1987–90 in Yellowstone National Park (Singer et al. 1997). We commonly saw and heard coyotes on the Beaver Creek study area during the treatment period, once observed a mountain lion (*Felis concolor*), and saw black bears on several occasions. We also found 2 elk calves killed by black bears on the Beaver Creek study area. We speculate that predation may have been the primary proximate factor in reducing calf/cow proportions on Beaver Creek during treatment years. Disturbance may have increased vulnerability to predation either through increased calf movement, nutritional stress, desertion, or a combination of these factors.

MANAGEMENT IMPLICATIONS

Our study demonstrates the potential magnitude of impact to elk populations from high levels of recreational activity during calving season if people are dispersed across calving areas. However, large numbers of recreationists, traveling randomly and covering long distances, would be necessary to produce levels of disturbance similar to our treatment effort. Most of our treatments occurred away from recreational trails, and off-trail recreation on the Beaver Creek study area during calving season appeared to be minimal in both 1996 and 1997, even though large areas used by elk during calving season were open to the public. It appeared that elk and humans (other than project personnel) were spatially segregated, suggesting that elk avoid areas of human activity.

Our study did not specifically address the effects of trail-based recreational disturbance on elk. Effects of trail density and location, activity type, and trail-user volume on elk populations should be studied. Until such studies are done, however, maintaining low trail densities in traditional calving areas and selective use of calving-season closures seem justified to ensure that adequate areas of calving habitat remain undisturbed.

To ignore potential effects of human-induced disturbance of elk during calving season is to risk declining reproductive success in elk populations. If elk are left inadequate calving-season habitat and can no longer escape disturbance, either from over development of backcountry access corridors or from high levels of off-trail activity, then populations may decline. It is difficult to predict whether a declining population will eventually stabilize or become extirpated; even more difficult to curtail human activities once they become traditional, or to recover wildlife habitats once they are lost. To ensure a future for elk, it is prudent to plan for recreational developments that minimally impact populations.

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