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Author(s): HARRY P. ANDREASSEN, HEGE GUNDERSEN, TORSTEIN STORAAS

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THE EFFECT OF SCENT-MARKING, FOREST CLEARING, AND SUPPLEMENTAL FEEDING ON MOOSE–TRAIN COLLISIONS

HARRY P. ANDREASSEN, Hedmark University College, Department of Forestry and Wildlife Management, Evenstad, N-2480 Koppang, Norway

HEGE GUNDERSEN,¹ Hedmark University College, Department of Forestry and Wildlife Management, Evenstad, N-2480 Koppang, and Centre for Ecological and Evolutionary Synthesis, University of Oslo, Oslo, Norway

TORSTEIN STORAAS, Hedmark University College, Department of Forestry and Wildlife Management, Evenstad, N-2480 Koppang, Norway

Abstract: We analyzed how the application of scent-marking, forest clearing, and supplemental feeding correlated with the number of moose (*Alces alces*)–train collisions along the most vulnerable railroad stretch in Norway. Data on 1,045 collisions has been compiled for 18 years since 1985, and remedial actions have occurred during various periods since 1990. We used sections of the rail line where remedies had never been applied as control sections to estimate the expected number of collisions per year and per km. In this way, we took into account the yearly variation in the number of accidents by using the difference between the actual number of accidents and the expected number of accidents as our response variable. We compared the difference between periods when remedies were applied to periods without any remedy. We found a general 46% decrease in the number of accidents during years with a remedy compared to what would have been expected the same years without any remedy. Forest clearing and supplemental feeding seem to be reliable ways of reducing the number of collisions. Scent was only applied for short distances in a few years, and the beneficial effects we observed were questionable. We conclude that mitigative efforts may substantially reduce accidental mortality in moose populations if applied for long distances. We discuss the economics of game-vehicle collisions by performing a simple calculation to visualize the need for a bio-economic approach to the problem.

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Key words: *Alces alces* L., forest clearing, moose–vehicle accidents, scent-marking, supplemental feeding.

Human development in past decades has been followed by a considerable increase in ungulate–vehicle accidents. The high socioeconomic cost of ungulate–vehicle collisions (Jaren et al. 1991) and the unpredictable effects on population development (Peterson and Danell 1992) have motivated many attempts to identify effective mitigative techniques. Bruinderink and Hazebroek (1996) and Romin and Bissonette (1996) summarized the effectiveness of various remedial actions in reducing ungulate–vehicle accidents and concluded that techniques based on sound, light, or scent-marking were ineffectual. However, forest clearing along roads with heavy traffic had some positive effect, and fences significantly reduced the number of accidents. Romin and Bissonette (1996) also suggested that supplemental feeding could reduce accidents, but the lack of data precluded any conclusive recommendations regarding feed. Fences have proven to be the most effective way of hindering ungulate–vehicle accidents. However, because fences disrupt habitat connectivity with unknown impact on the ecological community, there is a need to explore the efficiency of other techniques.

In Norway, the moose is responsible for the majority of the ungulate–vehicle accidents (Gundersen et al. 1998), and the Norwegian National Rail Administration has registered a steady increase in moose–train collisions from approximately 50 accidents yearly in the 1950s up to 1,000 yearly accidents in early 1990s (Andreassen et al. 1997, Statistics Norway 2003). In North America, moose mortality on highways and railways is a recurrent management problem (Child 1983, Child et al. 1991, Modafferi 1991). One of the most severely affected areas in Norway is a section of the Rørosbanen railroad (Gundersen et al. 1998, Gundersen and Andreassen 1998) where collisions occur mainly during winter; more specifically, they occur during long winters with deep snow when a high proportion of the moose population in the surrounding area migrates to winter ranges close to the railroad (Gundersen et al. 1998). Due to the severe problems associated with the moose–train collisions in this specific area, several attempts have been made to introduce various mitigative techniques, such as fencing, forest clearing, scent-marking, and the use of moose feeding stations.

We analyzed the effect of forest clearing, scent-marking, and feeding stations in reducing the number of winter collisions along a stretch of the Røros-

¹ Corresponding author e-mail: hege.gundersen@bio.uio.no

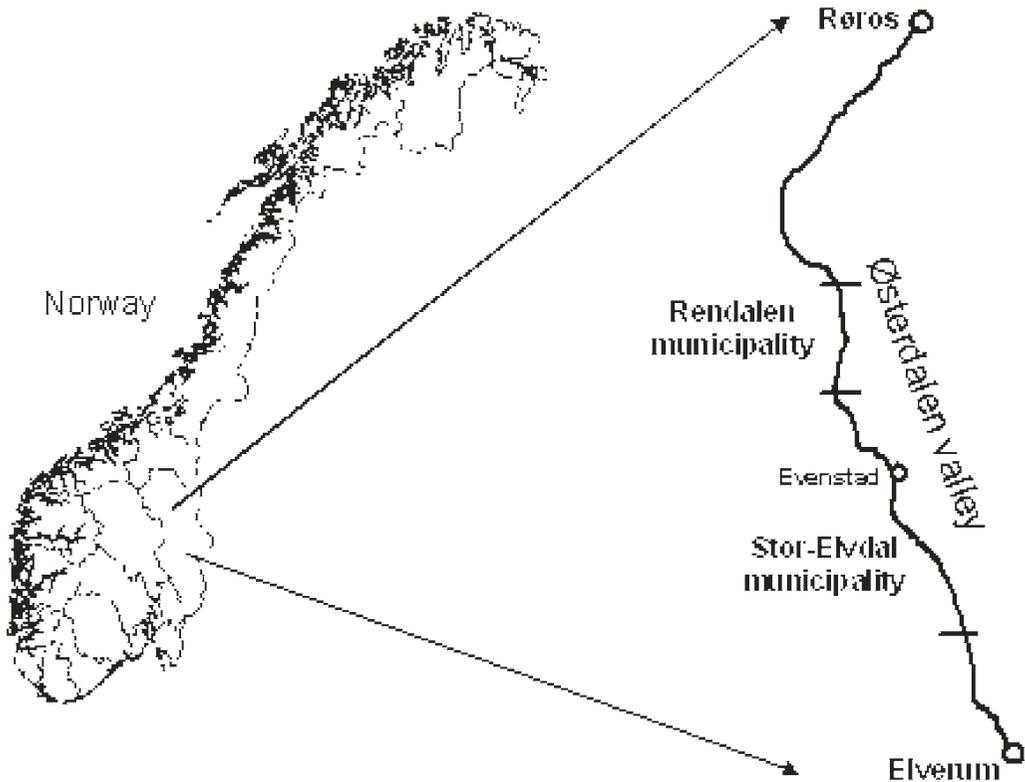


Fig. 1. The location of the Rørosbanen railroad and the 100-km section of the rail-line through Rendalen and Stor-Elvdal municipalities in Hedmark County, Norway, 2003.

banen railroad. These mitigative techniques were all replicated at several sites along the railroad in various years. To consider the yearly variation in the number of accidents, we estimated the expected number of accidents from control sections that were never treated. Hence, we used the difference between the actual number of collisions and the expected number of collisions as our response variable, and we compared years with and without any remedy. We also devised a simple calculation to estimate the economics of mitigative techniques.

STUDY AREA

We analyzed data on moose–train collisions from the most vulnerable stretch along Rørosbanen railroad line located in Stor-Elvdal and Rendalen municipalities, southeast Norway (Gundersen et al. 1998, Fig. 1). The railroad within these 2 municipalities was 100 km long (defined as 200- to 300-km rail-line from Oslo) and ran along the bottom of 1 of the main north-south valleys called Østerdalen. The valley is surrounded by hills of boreal forest, dominated by Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*), and inter-

spersed with a few boreal deciduous species such as birch (*Betula* spp.). Thirty-eight percent of the moose population migrates down to the highly trafficked valley as soon as snow starts to accumulate in the hills during winter (usually around Nov–Dec; Gundersen et al. 1998, Gundersen 2003).

METHODS

Source of Moose–Train Collision Data

We collected data on moose killed by trains from The Norwegian State Railroad (NSB), The Norwegian National Rail Administration, and from the local Wildlife Committees of Stor-Elvdal and Rendalen municipalities from 1 July 1985 until 1 April 2003. Each record of a moose–train collision included time and position to the nearest 100 m along the 100-km railroad section. We obtained daily average temperatures and snow depths from the Evenstad meteorological station (61°24'N, 11°7'E).

Remedial Actions

Various remedial actions have been applied within the study area through the initiative of

NSB, The Norwegian National Rail Administration, landowners in Stor-Elvdal and Rendalen municipalities, and Hedmark University College Division of Forestry and Wildlife Management. Ten 0.5-km lengths were treated with scent in 1994–1995 and 1995–1996, respectively. Two feeding stations (6.0 and 8.0-km long) were established in 1994, and 1 station (4.0-km long) was established in 1995. Eight forest clearings (0.9 to 14 km long) were established from 1990 to 2002. Thirty-one sites were subjected to treatment.

Fences are assumed to be the best way to reduce ungulate-vehicle accidents (Bruinderink and Hazebroek 1996, Romin and Bissonette 1996), as they may act as a complete barrier to moose movement. Previous studies show that fencing reduces ungulate-vehicle accidents by as much as 60–100% (Lehtimäki 1981, Ludwig and Bremicker 1983, McDonald 1991, Gleason and Jenks 1993, Cleverger et al. 2001). However, in some instances, the number of accidents might actually increase at the ends of fences when animals enter the traffic artery and become trapped between the fences (Lehtimäki 1981, Cleverger et al. 2001). Fences can also trap animals that penetrate or climb over the fence. In 1995, a 1-km, wire-mesh fence was erected, and it eliminated collisions with moose except for 1 at a fence end. Because we had only 1 fenced length, and since it was nearly completely effective, we excluded this 1-km-long stretch from further analyses and instead analyzed other, more subtle, remedies.

Scent-Marking.—Scent is supposed to make ungulates more alert and aware of dangers, hence making them more vigilant when the scent is combined with sound and light from vehicles. However Lutz (1994) found that game stopped reacting to the scent after 2 days. A commonly used scent is Duftzaun® (HAGOPUR® GmbH, Landsberg am Lech, Germany), which consists of components from bears (*Ursus arctos*), wolves (*Canis lupus*), lynx (*Lynx lynx*) and humans. In our study, Duftzaun® scent was placed along the railroad during the winters of 1994–1995 and 1995–1996. Ten sections, each 500 m long, were chosen each winter. Duftzaun® was sprayed on trees and bamboo canes at 5-m intervals on along the railway. One treatment lasted for about 3–4 months, so only 1 spraying was needed each winter. The spraying was applied during the first days when accumulated snow exceeded 20 cm (i.e., late Nov 1994–1995 and early Jan 1995–1996).

Forest Clearing.—Clearing of vegetation along trafficked arteries has been suggested to reduce

ungulate-vehicle accidents (Jaren et al. 1991, Gleason and Jenks 1993, Romin and Bissonette 1996, but see Rea 2003). It is recommended that trees and shrubs available for moose should be removed within 20–60 m from the track. Clearing of forest and browse was applied on 8 occasions along our study area. These sections were completely cleared of vegetation higher than 30 cm, so they were completely devoid of food and cover during winter conditions when they were covered by snow. Such clearings were maintained by repeated cutting of vegetation every year since.

Feeding.—Supplemental feeding seems to be an effective way to change moose movements, either by reducing migratory distances, or by making animals stay in certain locations (Carbaugh et al. 1975, Miller and Litvaitis 1992, Gundersen et al. 2005). Wood and Wolfe (1988) tested the efficacy of intercept feeding and found a reduction in the number of mule deer (*Odocoileus hemionus*)–vehicle collisions in 5 of 6 tests, although only 2 were significant. In our study, landowners initiated supplemental winter feeding of moose in 4 side-valleys used by moose during migration towards the winter range. Feeding stations were established by the landowners as an attempt to reduce traffic accidents in the area. Two of these side-valleys do, however, end up at the same location along the railroad (1 from the eastern and 1 from the western side). Hence, we analyzed 3 sections along the railroad for the effect of feeding on the number of collisions. The supplemental food consisted of baled and silaged graminoids and/or herbs of varying breeds and combinations, usually oat (*Avena sativa*) and canola (*Brassica napus*). One bale of silage weighs about 600 kg, and on average, 5.3 bales (range 1–36) were used at each feeding station each winter. All stations were placed near snow free roads with low human activity so that the food supplementation could easily be performed by car. The feeding period lasted from when the snow accumulated in the hillsides, usually in November, until the snow melted or summer migration began in April–May.

Analyses

We transformed the observed number of collisions per year in a remedied site by dividing the number of collisions with the length (km) of the site. This yielded the observed number of collisions per year (t) and km for each site (O_i, t).

Previously, we showed that 83% of the yearly variation in moose–train collisions in the area may be explained by the duration of the winter (Gunder-

sen et al. 1998). Hence, we cannot simply compare the number of accidents during years when the remedy was applied with periods when it was not applied, as this may be confounded with winter conditions. To take into account the annual variation, we lumped all stretches that had never been allocated for a remedy, hereafter termed control section, and estimated the expected number of moose collisions per km every year (E_t) by adding all moose collisions along control sections divided by 48.8 km (i.e., the total length of control section). The equivalent length where a remedy had been applied, hereafter termed remedy sections, was 51.2 km.

To compare the various remedial techniques, we employed a general linear mixed model with poisson error, log link, and $\ln(E_t)$ as an offset using the SAS macro GLIMMIX (Littell et al. 1996). Hence, the predicted estimates of the model were the yearly deviations between the observed and expected number of collisions. Due to the log-transformations, the actual estimates were $\ln(O_{i,t}) - \ln(E_t)$ that, when back-transformed, gave the value of 1 if there was no difference between the actual and expected number of collisions (i.e., $O_{i,t}/E_t = 1$), >1 if there were more collisions than expected, and <1 if there were fewer collisions than expected. We treated the 31 sites subject to remedies as random factors in the analyses to take into account innate variations within each section that was treated with a remedy for >1 year (i.e., forest clearing and supplemental feeding).

Within the remedy sections, we knew the observed number of collisions for years with and years without the application of the remedy. We included type of remedy and application (coded as yes and no) in the model as a between- and within-subject effect, respectively, with site as the subject defined as a random factor. Any difference in the effectiveness of various remedies was then found in a significant interaction between remedy and application, while the general effect of applying a remedy was found in a significant effect of the main factor application. Hence, a significant effect of application appeared when the $O_{i,t}/E_t$ differed between periods with and without the application of the remedy.

RESULTS

Effect of Remedies

We selected only the moose-train collisions that occurred during the winter from November to March (i.e., 86% of the total number of collisions registered)

since feeding and scent-marking was performed only during winter. The mean number of collisions each winter was 0.58 (SE = 0.08) moose/km. Of the 1,045 collisions in the analysis, 672 (64%) were located within remedy sections in at least 1 year. Hence, since 64% of the collisions were located inside 51.2% of the railroad (total length of remedy sections), remedial actions were allocated within areas with high risk of collisions.

Except for 1 site treated with scent, all other 30 remedy sites showed a decrease in the number of accidents during application of the remedy compared to the control sections. Although this trend was not statistically significant (effect of application: $F_{1,30} = 3.54$, $P = 0.071$), there was an average reduction of 46% (95% CL: -5, 73) in the number of accidents during the application of remedies. Within the remedy sections there were 2.5 times more moose killed (i.e., odds ratio, 95% CL: 1.8, 3.5) per km and year compared to control sections before the initiation of the remedy. During the application of the remedy, the numbers of killed moose approached the numbers in control sections (i.e., odds ratio: 1.3; 95% CL: 0.8, 2.3). There was no difference in the efficiency of various remedial actions (interaction effect of remedy * application: $F_{2,28} = 0.34$, $P = 0.715$).

A closer examination into each of the 3 remedial actions we analyzed separately showed that in areas cleared of forest there was a 49% reduction in collisions (95% CL: 10%, 71%; $F_{1,14} = 5.66$, $P = 0.032$), in food supplemented areas a 40% reduction in collisions (95% CL: 17%, 57%; $F_{1,4} = 9.55$, $P = 0.037$), and in scent-marked areas a 85% reduction in collisions (95% CL: -8%, 100%; $F_{1,38} = 0.84$, $P = 0.366$). However, the large variation in the effectiveness of scent meant that this remedy was not statistically significant (Fig. 2).

If the overall number of accidents decreased over time, the remedies may have only seemed effective because they were in the later years of the study. However, while the number of moose killed per km in remedy sections remained constant through time, it tended to increase in control sections (Fig. 3).

At some sections of the railway, various applications were carried out simultaneously. We tested whether 2 remedies were more effective than only 1 remedy by comparing sections cleared of forest or supplemented with food with sections with both clearing and supplementation. Due to the high variation in the effect of scent applied over short distances over few years, we did not test the effect

of including scent as a second remedy. Two remedies applied simultaneously did not reduce the number of collisions significantly compared to areas with only 1 remedy (reduction of 5%; 95% CL: -61%, 44%; $F_{1,15} = 0.04$, $P = 0.849$).

Quantifying the Reduction

Because most remedial actions are expensive, they may be more readily adopted if the application is effective and quantifiable. We illustrated the economic benefit of remedies using an example with forest clearing and supplemental feeding (Table 1). We limited the costs to the maintenance of remedies and the benefits to the value of moose meat (i.e., the predominant economic benefit of hunting in Norway).

We assumed an average winter with 58 moose-train collisions. As 2.5 times more moose were killed per km along remedy sections than elsewhere before the application of remedies, we expected 42 moose to be killed yearly along the 51.2 km of remedy sections.

If feed was applied to 18 km of the study area, a 40% reduction in moose collisions compared to expected collisions suggests that 5.9 moose were saved yearly due to feeding. If clearing was applied to 18 km of the railway, a 49% reduction in moose collisions due to clearing suggests that 7.2 moose were saved yearly. If this much meat was sold, the net benefit would be US\$8,260 and US\$10,080 due to feed and clearing, respectively.

Supplemental feeding in the study area costs on average US\$18,000 a year (applied to 18 km), while maintenance of clearings cost approximately US\$9,000 a year (US\$500 per km; Storaas et al. 2001). We found that forest clearings are profitable, while feed yields a deficit (Table 1). However, initially clearing a forest costs approximately US\$5,500 per km, and the cost and benefit do not necessarily accrue to the same person or agency.

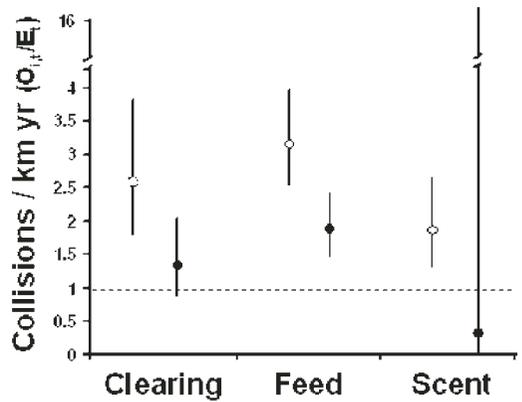


Fig. 2. The effect of various remedial actions against moose-train accidents in Rendalen and Stor-Elvdal municipalities, Hedmark County, Norway, Jul 1990–Apr 2003. The estimates are the back-transformed deviations between the observed (O) and expected (E) numbers, (i.e., $O_{i,t}/E_t$). A value of 1 indicates that the number of collisions was as expected that year, according to the yearly variation. Black and white markers represent periods with and without the application of remedies, respectively.

DISCUSSION

Our analyses showed that remedial actions were allocated to high-risk sections where the number of accidents in general was higher than control sections. Within remedial sites, however, there was

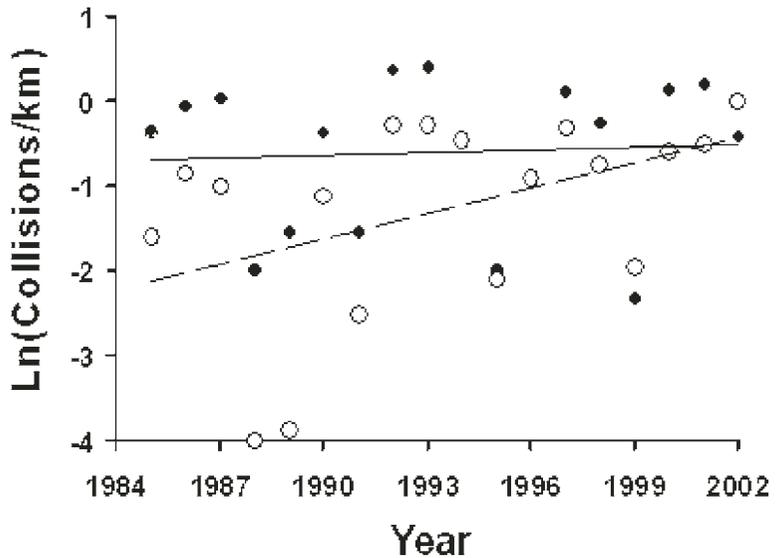


Fig. 3. Number of moose-train collisions per year in control sections (open circles) and sites allocated to remedies (black circles) in Rendalen and Stor-Elvdal municipalities, Hedmark County, Norway, from July 1990 through April 2003. Note that the site-specific deviation between these 2 was the response in our analyses. The linear predictor was positive in control sections (dotted line: $F_{1,16} = 5.42$, $p = 0.033$) and constant in remedy sections (continuous line: $F_{1,16} = 0.18$; $p = 0.676$). Removing the 2 outlying years with very few expected number of collisions (1988 and 1989) did not have any substantial effect on the analysis.

Table 1. A breakdown of the economics of remedies, assuming the number of moose killed per km in the remedy sections before application of a remedy. We calculated the costs and benefits based on 18 km, as this was the length applied with feed. Income per moose was limited to meat value.

Description	Supplemental feeding	Forest clearing
Background numbers		
Moose killed / km and year	0.82	0.82
Length of application (km)	18.0	18.0
Costs of remedy (per km) ^a	1,000	500
Efficiency of remedy	40%	49%
Number of moose saved ^b	5.9	7.2
Economic calculations		
Cost per year (US\$)	18,000	9,000
Total income (US\$) ^c	8,260	10,080
Total Profit (US\$)	-9,740	1,080
Profit per km (US\$)	-541	60

^a Costs associated to supplemental feeding are actual values (K. Nicolaysen, Stor-Elvdal Landowner Organization, personal communication), while cost of forest clearing and meat income (US\$1,400 per moose) are approximate values (Storaas et al. 2001).

^b The number of moose saved is the product of moose killed, length of application, and efficiency of remedy.

^c Total income is the product of income per moose and number of moose saved.

a reduction in number of accidents compared to control sections. Remedies prevented the general increase in collisions that we observed in control sections. We are confident that the reduced collision rate was due to the applied remedies since the beneficial reduction in collisions took place in 30 out of the 31 analyzed sites.

Scent-marking showed the highest average effect (85%) on reducing the number of collisions. In an experimental study, Lutz (1994) was not able to show that Duftzaun[®] reduced the number of ungulate-vehicle accidents in the long term. The high variation in our estimates of the success of scent might be due to the remedy being applied only in 500-m long distances. Such short distances yield small and accidental numbers of collisions and thus high variation. Scent-marking is, however, a method that might be worth pursuing if applied over longer distances or in combination with other treatments, such as forest clearing.

Forest clearing was applied for various distances along the train track, and its beneficial effect in reducing collisions was similar to what was found previously for moose-train collisions in Norway (Jaren et al. 1991). Forest clearings not only hinder the animal from browsing near the road/railroad but also reduce the time spent near roads or rail-lines since the animals move straight across the clearing (Jaren et al. 1991). Furthermore, forest

clearings increases the visibility of moose for the locomotive conductor (or car-driver; Bashore et al. 1985).

Supplemental feeding of ungulates has frequently been applied as an emergency measure during hard winters (Cederlund 1982, Ozoga and Verme 1982, Baker and Hobbs 1985, Boyce 1989, Aagnes and Mathiesen 1995, Ouellet et al. 2001) and reduced the number of mule deer-vehicle collisions (Wood and Wolfe 1988). Our results suggest that feeding stations located at the side-valleys that guide moose to their winter range in Østerdalen might reduce collisions along the outlet of the valley. This might occur because fewer moose migrate all the way to the winter range, or they postpone their migration and thus spend a shorter time in the risky areas. However, feeding might only have a beneficial effect in certain areas characterized, for instance, by migration. The use of feeding stations by moose and its effectiveness at reducing forest damage has been described elsewhere (Gundersen et al. 2005). Hence, feeding stations might actually alter moose behavior in ways that are beneficial for industrial forestry and moose-vehicle accidents. The effect of feeding stations probably depends strongly on their location. Consequently, knowledge about the spatial distribution of local moose population is crucial. More studies on the allocation of feeding stations are needed.

The 3 methods applied were not instituted with a predetermined experimental design but rather as a practical experiment to reduce collisions. However, the application of several different treatments within the same general area provided an opportunity to compare the effect of various techniques. Complications arose, however, due to the yearly variation in winter conditions associated with the number of accidents. For this reason, we analyzed the yearly difference in the number of accidents within remedy sections (observed) and the number of accidents in control sections (expected). Furthermore, the number of collisions was highly site-specific (Gundersen et al. 1998) which hampers the comparison between remedies applied in different sites. However, the replicates (3–20) of each remedy may reduce some of the temporal site-specific factors that might confound the analyses, whereas the constant innate factors of site are taken into account as a random factor.

Other remedies have been suggested and applied in an attempt to reduce ungulate-vehicle accidents (see Bruinderink and Hazebroek 1996, Romin and Bissonette 1996, and Putman 1997 for reviews). For a remedy to have any effect it must

prompt the animal to run away or otherwise change its behavior. Fencing is presumably the most effective way to prevent ungulate-vehicle accidents (e.g., Falk et al. 1978, Ludwig and Bremicker 1983), but its application is limited because it is expensive (Reed et al. 1982). The main problem with erecting a fence, however, is that it interferes drastically with the animals' normal movement patterns. Well-built bypasses, under, over, or at ground level limit the interference with the animals' movements (Reed et al. 1975, Reed 1981, Lehnert and Bissonette 1997), but they increase the economic costs considerably (Reed et al. 1982).

Our results suggest that remedies to reduce ungulate-vehicle accidents are generally beneficial, but they do not completely eliminate collisions. The reduction of such accidental mortality gives wildlife managers more predictable estimates of the population size when, for instance, planning hunting quotas. Reducing accidents might have substantial economic benefits (Jaren et al. 1991). There seems to be a net economic benefit of remedies according to our simple calculation; however, a more detailed and long-term, bio-economic analysis is needed. For instance, forest clearing is expensive to initiate, but it has a low maintenance cost and may be beneficial over the long-term. The long-term economic profit of remedies that we analyzed should be compared to the building of fences and bypasses that can be comparatively costly. A bio-economic approach should preferably include a cost-benefit analysis at the level of landowners, local community, and national society. This is important since collisions mean not only a loss of meat and hunting revenue at the local level but also more widespread costs such as personal stress and injuries.

MANAGEMENT IMPLICATIONS

Due to temporal and spatial differences in the application of the remedies, we can not strongly recommend 1 remedial action over another. Although scent-marking showed the best average effect, it was highly variable and the technique was questioned by Lutz (1994). Supplemental feeding seemed to be beneficial, but it is expensive on a yearly basis. Forest clearing may be more economical from a long-term perspective because initial cutting is the main expense. Whatever remedial action is chosen, we expect the best results when it is applied over long distances because the high-risk areas change considerably from year to year and may be unpredictable (Gundersen et al. 1998).

However, the selected mitigation also has to depend on the impact on the whole ecological com-

munity. For instance, forest clearing may affect the mobility of species that need cover to move safely, and feed increases browsing considerably close to feeding stations (Gundersen et al. 2005) with unknown consequences for the forest community or the economic consequences for the landowner.

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Trains kill more than 800 antelope and deer on Montana tracks this winter

March 06, 2011 1:26 pm • By the Associated Press

GREAT FALLS - Hundreds of pronghorn antelope and deer have been killed by trains in Montana this winter after herds gathered on tracks to escape deep snows, a state wildlife official says.

Mark Sullivan, of Fish, Wildlife & Parks, said that a train recently killed about 270 pronghorn antelope near Vandalia in northeastern Montana, and 18 deer were found dead on the tracks by a grain elevator near Chinook.

Many antelope not killed by the impact had been destroyed by Blaine County authorities.

"To hunt and shoot animals is just different than shooting wounded animals like that," Blaine County Undersheriff Pat Pyette told the Great Falls Tribune. "You're close to it. You can look into their eyes. We see a lot of things, but (the deputy) was sick to his stomach after that."

Sullivan said hundreds of animals have been hit on Montana's Hi-Line.

"This is an exceptional winter on the Hi-Line," he said. "The numbers are getting close to 800 animals reported, and I'm sure there are a fair number of animals killed by trains that we don't know about."

Burlington Northern Santa Fe spokesman Gus Melonas said because of the deep snow, the company this year is working with state officials to track deer and antelope deaths. He said the company has always worked with Glacier National park to track the number of moose and bears killed by trains.

"The trains are designed to blow away the light snow, so to those animals it's clear ground for them," Melonas said. "Because of the weather, the animals migrated to the path of least resistance, and that's the railroad, unfortunately."

He said railroad truck drivers are called in to scare animals away from tracks when train operators spot a large herd. Also, he said, the company is trying not to leave grain and corn that might attract deer and antelope to the tracks.

The winter in general has been tough on wildlife, Sullivan said, and a prediction of a cold and snowy March has wildlife managers concerned.

"These animals have been fighting winter since November," he said. "How the spring is will have a lot to do with how many animals make it out alive."

Craig Miller, a biologist with the Bureau of Land Management, has tracked pronghorn migration for the last four years. He said he has lately spotted scattered groups of animals rather than the herds of hundreds he saw at the start of the winter.

"Perhaps they've broken into smaller groups, but I have a feeling that winter kill is going to be pretty high," he said.

Wildlife managers plan flights in April to count deer, and in July will count antelope when the animals return to summer feeding grounds. The number of hunting licenses will be set based on those numbers.

"I'm sure we'll be dropping our license numbers a fair amount so the animals can rebuild," Sullivan said.

RELATIONSHIP OF REDUCED TRAIN SPEED ON MOOSE-TRAIN COLLISIONS IN ALASKA

Earl F. Becker¹ and Carl A. Grauvogel²

¹Alaska Department of Fish & Game, 333 Raspberry Road, Anchorage, AK 99518; ²P.O. Box 1062, Palmer, AK 99645.

ABSTRACT: An experiment to test the effect of track site, train speed, direction of train travel, and train run (first versus second round trip of the day), on moose-train collision mortality along the Alaska Railroad in the lower Susitna River Valley of Alaska, was conducted in February 1988. Reduction of train speed from 79 kmph to 40 kmph did not result in a significant reduction in the number of moose hit by trains ($P = 0.439$), even though the probability of detecting a major reduction was substantial. Significantly more moose were hit in the northern test section than along the southern test section of track ($P = 0.096$) of the Alaska Railroad.

ALCES VOL. 27 (1991) pp.161-168

Collision with vehicles can be a major cause of moose (*Alces alces*) mortality especially where high speed highways transect heavily used moose winter range (Bangs *et al.* 1989). Collisions with trains are less widespread, but can become a major source of mortality in some areas. Muzzi and Bisset (1990) report that 40-50 moose per year are struck and killed by trains along a 225 km section of track in Ontario. Child (1983) estimated that annual moose mortality due to trains in the central interior of British Columbia range from hundreds to in excess of 1000 moose in winters of record snowfall. Similarly, the Alaska Railroad (ARR) has documented a mortality of 3054 moose in train collisions between May 1963 and April 1990, with an annual mortality ranging from 9 to 725 (Modafferi 1991a). During the winter of 1987-88, 173 moose were struck and killed by trains in Game Management Unit (GMU) 14B, a 5594 km² area in southcentral Alaska, in comparison to 43 by automobiles and 347 by hunters (Grauvogel 1990). The number of moose killed by trains in GMU 14B dropped to 87 during the winter of 1988-89 compared to 40 by automobiles and 140 by hunters (Grauvogel 1990). During the winter of 1989-90, record snowfalls resulted in a record 351 moose killed by trains and 47 by automobiles in GMU 14B, (Masteller pers. comm.) while hunters harvested 173 moose

(Morgan 1991). This mortality coupled with poor overwinter survival caused an estimated 35% reduction in the GMU 14B moose population (Abbott 1991) and a closure of the moose hunting season (Morgan, 1991).

The ARR originates at the coastal port of Seward and extends approximately 756 km north through southcentral and interior Alaska to Fairbanks. Most moose-train collisions occurs in GMU 14B between Wasilla, ARR milepost (MP) 160, and Chulitna (MP 273) where the right-of-way passes through an important moose winter range on the lower Susitna River floodplain and nearby nonriparian lowland habitat (Modafferi 1991a). The number of moose inhabiting this area and the duration of use depends primarily upon timing and quantity of snowfall and the persistence of snowcover (Modafferi 1988, 1991b). The greatest concentration of moose occurs when deep snow persists into late winter covering browse species at higher elevations (Rausch 1958, Modafferi 1988). The ARR and the Alaska Department of Fish and Game (ADF&G) discussed various options for reducing this moose-train collision mortality, including reducing train traffic, reducing train speeds, and increasing the frequency of snow plowing. Reduced train speed was identified as one of the most feasible options.

METHODS

The experiment was conducted on a 85.3 km section of ARR track between Talkeetna (MP 225) and Houston (MP 173) (Fig. 1) from February 16-23, 1988, when snow depths exceeded 76 cm. This area was selected because it had the highest incidence of reported moose mortality, due to collisions with trains, along the entire track (Modafferi 1991a). This section of track also parallels the lower Susitna River Valley, which is an area used as winter range by a population of moose from the east and a population of moose from the west of the Susitna River (Modafferi 1988, 1991b).

A stepwise regression analysis (Neter and Wasserman 1974) of the 1984-85 winter moose kill on the ARR in GMU 14B was conducted to determine if factors such as snow depth, snow fall, temperature, train frequency, train type (freight, passenger), train timing (day, night), and previous moose-train collision mortality were associated with high moose collision mortality. A square root transformation was used on the kill data (Snedecor and Cochran 1980). The experiment was initiated when factors identified by the above analysis were present.

A 2⁴ incomplete factorial repeated measures experimental design (Winer 1971:604-684, Milliken and Johnson 1984:80-84), was used to test the hypothesis that slower train speeds reduce the number of moose killed by trains. The train was run at 79 kmph (49 mph) along one-half of the test section of track between Talkeetna and Houston, and at 40 kmph (25 mph) along the other half. A speed of 79 kmph is the regular operating speed of trains and was used as the experimental control, whereas 40 kmph was the slowest speed which the ARR believed to be economically feasible for testing. To break the test section of track into 2 sites the Kashwitna River bridge, MP 199, was used as the halfway point (Fig. 1). On the return trip train speeds were reversed. A total of 2 round trips were run

each day, with the speed in the second run being the reverse of the first run. The experiment was conducted for 8 consecutive days with the speeds reversed for each site-direction-run combination of the previous day (Fig. 2). In addition to testing for a train speed

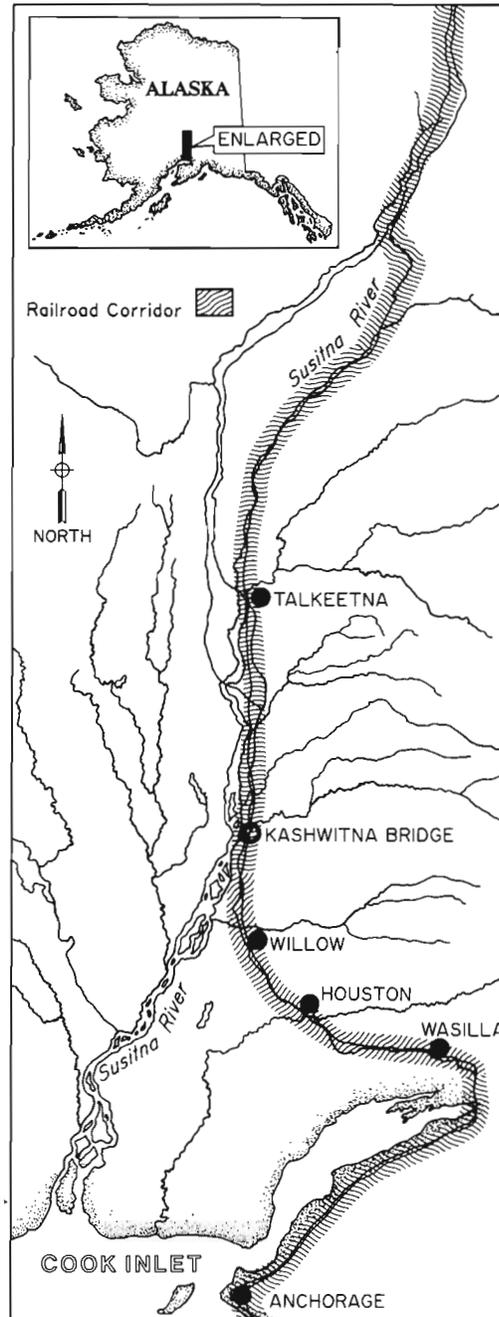


Fig. 1. The location of the Alaska Railroad rail line in the lower Susitna River valley, Alaska.

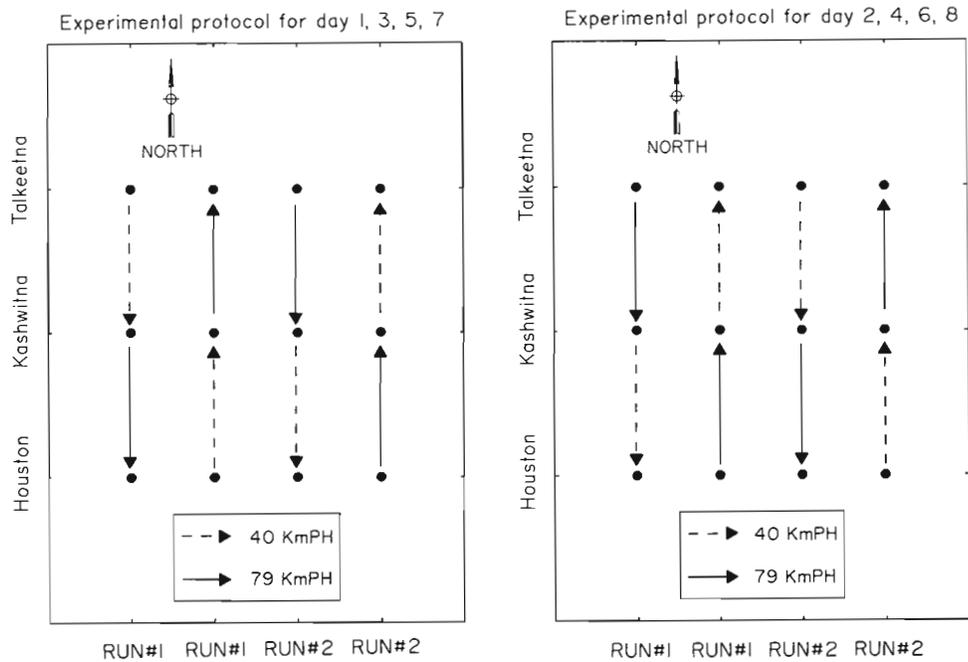


Fig. 2. Schematic of the 2⁴ repeated measures factorial design employed from 16-23 February, 1988, in the lower Susitna River valley, Alaska, to determine the effects of track site, train speed, direction, and run on moose-train collisions.

effect; site, train direction, train run, and 3 of 11 possible interactions: train speed by train direction, train speed by site, and train direction by site; were tested for. It was felt that the other interactions were not biologically meaningful.

Snow depth on the tracks was removed as a variable by wing-plowing the tracks 5.5 m off the center line. The ARR provided two 2,500 HP locomotives (model GP35 manufactured by General Motors), connected back to back, so that after each run the crew could move to the other locomotive for the return trip.

The study was terminated when the sample size (number of moose struck) was large enough to ensure that the power to detect a 2:1 difference in the number of moose hit by the 79 kmph vs 40 kmph train was near 80%, at $\alpha=0.20$. If reduced speeds resulted in fewer moose being struck, it was hoped that additional support could be obtained from the ARR to determine if the reduction was sig-

nificant at an alpha of 0.05 with a power of 80%. The site, train direction, and train run main effects and the 3 interactions listed above were tested at $\alpha=0.10$.

After the first day of the experiment, we modified the operational procedures to avoid killing moose. Instead of maintaining a steady 40 or 79 kmph, we instructed the train engineer to abruptly apply full braking when we were sure that continuing on at the designated speed would overtake the moose and kill it. Cows with calves were treated as one observation because the fate of the calf was dependent upon the behavior of the cow. Other than changing train speed, the engineer followed normal ARR operating procedures during the course of the study, these included using train whistles and lights to try to scare the moose off the tracks.

RESULTS

Regression Results

The regression model (Table 1) explained

Table 1. Linear regression coefficients for the square root of train moose kill in Alaska Game Management Unit 14 B for the winter of 1984-85.

Variable	Coefficient	
	Estimate	SE
Y-intercept	1.5074	0.1924
IMAV3SNF ^a	0.6942	0.1398
MAVPNOK ^b	-1.4447	0.2656
INTERACT ^c	-0.5391	0.2653
PREVKILL ^d	-0.2779	0.0919

- ^a- Denotes a moving average of the previous 3 days snow fall when ground snow is 91.44 cm or greater, otherwise 0 is used.
- ^b- Denotes the proportion of the previous 7 days in which 0 moose were killed.
- ^c- Denotes an interaction term between IMAV3SNF and MAVPNOK.
- ^d- Denotes the square root of the number of moose killed in the previous day.

a significant ($F_{4,132} = 29.389, P = 0.000$) amount of the variation in moose kill along the tracks. The following explanatory variables were included in the final model: a moving average of snow fall on the previous 3 days when snow depth ≥ 91.4 cm.

(IMAV3SNF), a moving average of the proportion of the previous 7 days in which 0 moose were killed (MAVPNOK), an interaction term between these 2 moving averages (INTERACT), and the square root of the number of moose killed on the previous day (PREVKILL). There was no positive serial correlation (Neter and Wasserman 1974) in the residuals (Durbin-Watson statistic = 2.021, $p-1 = 4, n = 137$). This model predicted that moose mortality due to collisions with trains would be high immediately following a snow-storm, when snow depths exceed 91 cm and the daily incidence of trains missing moose is low. The experiment was implemented when the above conditions were present.

Treatment Effects

During the study a total of 29 moose were 'struck' by the train, of which 20 were 'paper strikes' and 9 were actual collisions. Of the 20 moose recorded as 'paper strikes', 8 came to within 3-7 m of being struck by the deaccelerating train, 2 were missed by a matter of centimeters, and one was bumped. One collision occurred during braking when the train blew a fuse, and as a result, the brakes failed and the moose was killed. The effect of reducing train speed was not significant ($P =$

Table 2. Analysis of variance for a 2⁴ incomplete factorial, repeated measures experiment on moose struck by trains in the lower Susitna River Valley, Alaska.

Source of Variation	MS	DJ	F	P-value
Train Speed (79,40)	0.0165	1	0.024	0.439 ^a
Direction (North, South)	0.141	1	0.214	0.646
Site (MP 215-199, 199-173)	1.891	1	2.882*	0.096
Run (First, Second)	0.016	1	0.024	0.878
Speed x Direction	0.141	1	0.214	0.646
Speed x Site	1.266	1	1.930	0.171
Direction x Site	1.266	1	1.930	0.171
Error	0.656	49		

^aSignificant at $\alpha = 0.20$
 $\alpha = 1$ sided test

0.439) (Table 2). Of the 29 moose struck, 14 (48.3%) were hit by the 40 kmph train and the remaining 15 (51.7%) by the 79 kmph train. The site effect was significant ($P = 0.096$); 20 moose were struck in the northern site, while 9 were struck in the southern site.

The power curve for this experiment (Figure 3) indicates that a true difference of 20:9 in the number of moose struck by the 79 versus 40 kmph trains would result in a significant test statistic 80% of the time. This experiment had a high probability (large power) to detect differences of 2:1 or greater in the number of moose struck by the 79 versus 40 kmph trains.

Moose Behavior

Most moose 'struck' by the train behaved similarly. When first observed moose were usually standing or walking on the railroad bed, often between the rails. Most animals retreated from the train and increased the speed of their escape. Some moose would trot at a slow to medium gait; others would run (sometimes 24-32 kmph) as the train approached. Nearly all moose ran down the center of the track. Because of faster train speeds, moose running on the track were overtaken by the train. Moose recorded as a 'paper' strike often continued to trot in front of the train, sometimes for distances of over 2 km. Moose exhibited a strong tendency to remain on the track when chased, even if exhausted. However, when the train stopped, moose generally left the track after moving 200m. Most moose that were encountered on the track, but not recorded as a 'strike', were crossing the track and apparently not affected by the approaching train.

Moose generally avoided crossing railroad bridges. In one instance a train had slowed down to 5 mph to avoid hitting a moose. The moose trotted up to an unplanked railroad bridge and then turned, and walked back toward the slowly approaching train. After a few minutes of indecision the moose exited the tracks.

DISCUSSION

The main goal of this experiment was to determine if slower train speed would reduce moose kill adequately to solve this pressing management problem. Moose kill reduction had to be substantial to justify the economic costs of using slower train speeds. A 2:1 reduction seemed to be the minimum size which would meet this criteria. A reduction of this magnitude would have reduced the 1987 train kill of moose in GMU 14B from 173 (Grauvogel 1990) to 87 moose.

In our opinion, every animal recorded as a 'paper strike' would have been killed if the braking order was not given. This opinion is supported by the fact that 1 moose was struck and killed during a temporary brake failure and the proximity of the train to the other moose at the time of braking. Additionally, moose which collided with the train and were killed did not exhibit a last second attempt to jump out off the track.

Our results demonstrate that slowing ARR trains to 40 kmph does not result in a significant (2:1) reduction in the moose hit by trains in the lower Susitna River Valley. Obviously there exists train speeds below 40 kmph which would result in lower moose mortality. These speeds were not considered in this experiment, because the ARR would not have been able to implement slower speeds due to economic considerations. These results are probably applicable to any railroad right-of-way where snow depths exceed 76 cm and snow density off the railroad bed hinders the ability of moose to run.

We found differences in the number of moose struck by trains at the 2 different sites, with the northern site having a significantly higher rate of strikes. Abandoned homesteads with early successional stages of birch, willow, and aspen are more common in the northern site. The site difference may have occurred because more moose were wintering at the northern site in the vicinity of the tracks.

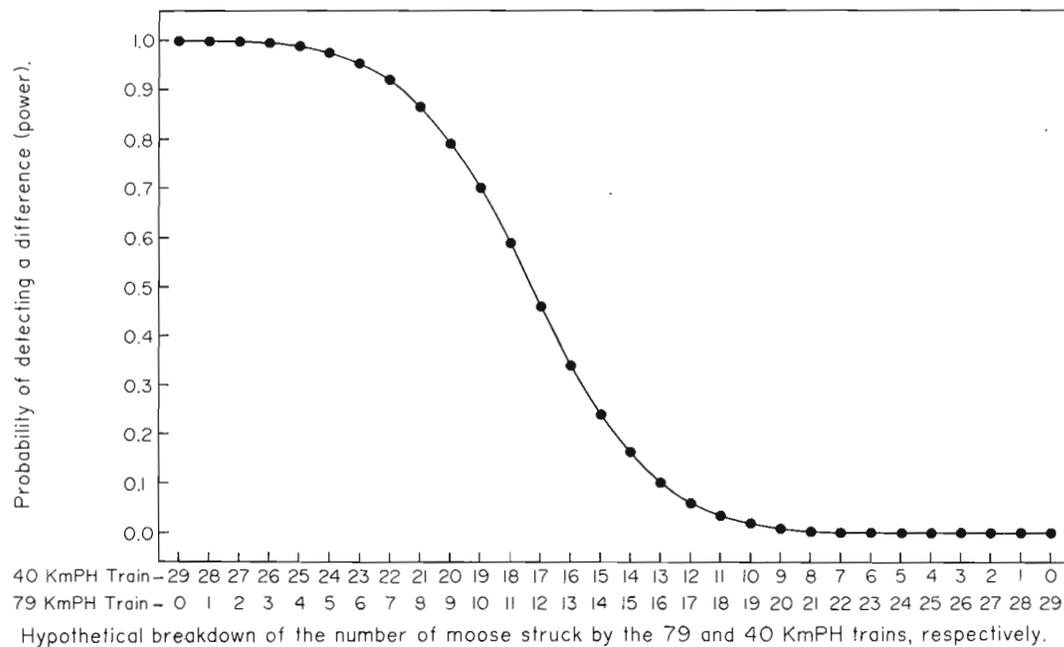


Fig. 3. Power curve for detecting if 40 kmph trains strike fewer moose than 79 kmph trains, at alpha = 0.2.

In order to obtain a more powerful test of the speed effect and separate the effects of potentially confounding factors, such as train direction, site, and run, the 2⁴ incomplete factorial design was used instead of a one-way ANOVA or chi-square analysis. This design can be thought of as a specialized ANOVA and has the same assumptions as an ANOVA (normality, independence, and constant variance) plus a sphericity assumption on the residuals of the repeated observations at a site within a given day (Winer, 1971). In this design, the site becomes the experimental unit with regard to testing for a train speed effect, and hence 8 observations about this effect were made every day and a total of 49 df were associated with the variance (MSE) (Table 2) used in testing for a speed effect.

Ideally, the sample size would have been sufficient for the experiment to have large power to detect 2:1 differences with an alpha of 0.05. The duration of the experiment and thus the sample size, was constricted by the high cost of running a special train at an

isolated location, and as a result, we had to choose between making a type I or II error (Ostle and Mensing 1982). In the context of this problem, it was much more important to identify a potential solution than to 'fail to detect' a difference due to inadequate sample size. If a significant difference was observed at $\alpha=0.20$, subsequent data could have been collected to reduce the probability of a type I error while still maintaining large power. Sequential testing of data is often used in clinical experiments (Anscombe 1963, Berry 1989), and could have been used to obtain valid experimental results if subsequent data were collected. The other comparisons were done with an alpha of 0.10 to increase the ability of the experiment to identify potential factors which are important sources of variation in the number of moose struck in this section of track. No follow up study of significant results for these factors (train direction, train run, and track site) was planned because of the expense and the inability to reduce these factors with regard to railroad operations.

Most of the struck moose were using the tracks as a trail or corridor to make north-south movements. The majority of these had sufficient time to exit the tracks, but they usually tried to out run the train. Child (1983) observed similar moose behavior in Canada. He hypothesized that fleeing from oncoming trains was part of a moose's anti-predator behavior.

Our study and Child's (1983), found that moose have a strong tendency to stay on the tracks when fleeing trains. In our study, snow depth was approximately 90 cm, and when a moose left the track it floundered. Child's (1983) moose anti-predator hypothesis coupled with moose floundering in deep snow off of the tracks would explain the reluctance of moose to leave the tracks.

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We express our gratitude to R. Modafferi and N. Steen for assisting in the data collection, and P. Shake, G. Beitinger, C. Brown, D. Lamb, and D. Reedy, for their expert operation of the train, cooperation, patience, and many helpful suggestions. K. Schneider, D. Reed, and S. Miller, provided constructive comments. We gratefully acknowledge the insightful review, comments and advice by K. Child and an anonymous reviewer. The Alaska Railroad provided the train and crew to run the experiment. Federal Aid in Wildlife Restoration and the Alaska Department of Fish and Game provided funding for this work.

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Grizzly Bear Mortality and Human Access in Banff and Yoho National Parks, 1971-98

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GRIZZLY BEAR MORTALITY AND HUMAN ACCESS IN BANFF AND YOHO NATIONAL PARKS, 1971–98

BRYON BENN, Faculty of Environmental Design, University of Calgary, 2400 University Drive, Calgary, AB T2N 1N4, Canada
STEPHEN HERRERO, Faculty of Environmental Design, University of Calgary, 2400 University Drive, Calgary, AB T2N 1N4, Canada, email: herrero@ucalgary.ca

Abstract: We conducted spatial and temporal analyses to examine the relationship between access, changing grizzly bear management strategies, and grizzly bear (*Ursus arctos*) mortality for 1971–98 in Banff and Yoho National Parks, Canada. We summarized mortality by cause of death, sex, age, and cohort. The annual number of grizzly bear deaths declined significantly between 1971–84 and 1985–98. However, the female portion of this mortality was 80% from 1985–98 compared to 50% during the earlier period. Human-related causes were the primary sources of recorded grizzly bear mortality in the study area (119 of 131 known mortalities). Control of problem bears accounted for 71% of 119 known human-caused mortalities, followed by highway and railway mortalities (19%), unknown cause of death (9%), and research (<1%). All 95 human-caused mortalities with known accurate locations were within 500 m of roads or 200 m of trails. Eighty percent of these mortalities occurred below 2000 m. Kills were concentrated at Banff townsite, Lake Louise, and along the Trans Canada Highway. Management of development, trail access, and human food and garbage are critical for managing grizzly bear mortality in the national parks. We present specific recommendations.

Ursus 13:213–221 (2002)

Key words: access, Banff National Park, Canada, development, grizzly bear, mortality, *Ursus arctos*, Yoho National Park, zone of influence

Grizzly bears in Banff and Yoho National Parks are part of a regional ecosystem in Canada called the Central Rockies Ecosystem (Fig. 1). The Central Rockies Ecosystem is experiencing intensive exploration and development of coal, oil, gas, and timber reserves. Cattle production, housing and highway development, and outdoor recreation are also increasing. Moreover, present attitudes toward the grizzly bear, a potentially dangerous animal (Herrero 1985) and competitor with humans for food and space (Mattson 1990), challenge human–grizzly bear coexistence. As a result, the grizzly bear is suffering from continuing habitat degradation and potentially unsustainable mortality rates in some regions of the Central Rockies Ecosystem (Herrero et al. 2000).

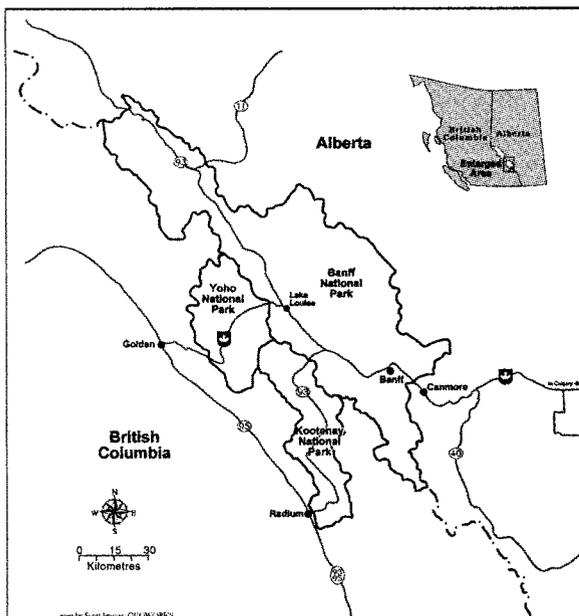


Fig. 1. The National Parks of the Central Rockies Ecosystem.

The national park portions of the Central Rockies Ecosystem continue to experience increases in human use, commercial development, and major transportation expansion with the doubling of the number of lanes of the Trans Canada Highway through Banff National Park (Banff-Bow Valley Study 1996). Grizzly bear hunting occurs on most provincial lands surrounding the parks. Interagency planning for effective land use at the regional scale (Herrero 1994), whereby bears can meet their energetic requirements and encounters between humans and bears can be reduced, may be the best option for reducing grizzly bear mortality (Mattson and Knight 1991).

Natural survival rates for adult grizzly bears in un hunted populations are high and consistent (Knight and Eberhardt 1985, McLellan 1990), whereas young bears die more frequently of natural causes such as intraspecific aggression (Stringham 1983), accidents (Nagy et al. 1983), and nutrition related causes (Nagy et al. 1983, Knight et al. 1988). However, tracking natural mortality is very difficult because habitat is often remote and heavily forested and carcasses are soon scavenged. Nonetheless, natural mortality is probably a minor cause of adult mortality (McLellan et al. 1999). Mortality data from North America show that human-caused mortality far outnumbers natural mortality (Craighead et al. 1988, McLellan 1990, Dood and Pac 1993, Gunson 1995). Historical (Storer and Tevis 1955, Noble 1972, McCrory and Herrero 1982) and recent works (McLellan and Shackleton 1988a, Mattson et al. 1996) consistently link the type and degree of human land use with grizzly bear mortality.

Sustainable total and harvest mortality rates for bears have been estimated in computer-simulated populations (Bunnell and Tait 1980, Harris 1986). However, the threshold mortality rate where grizzly bear populations begin to decline can rarely be determined precisely. The

determination of population numbers and vital rates for grizzly bears requires long term study, and the number of undetected mortalities is typically estimated by inference. McLellan et al. (1999) used unreported mortality of radiocollared bears from various western cordilleran studies to estimate the percentage of unreported human-caused mortality. They found that management agencies would have only detected 45–51% of human-caused mortality of radiocollared grizzly bears.

Roads are frequently implicated in contributing to increased grizzly bear mortality. They facilitate access for a host of human activities, increase the frequency of energetically costly flight responses, and increase vehicle related mortalities (Mattson et al. 1987, Nagy et al. 1989, Gibeau et al. 1996). As well, roadside vegetation may attract bears to roads, compounding the risk. At some undetermined level of human use, grizzlies, in particular established adult females, cease crossing major transportation corridors (Gibeau and Herrero 1998).

We analyzed grizzly bear mortality for Banff and Yoho National Parks for 1971–98. Results are discussed before and after changes in grizzly bear management strategies and relative to access.

STUDY AREA

The study area was Banff (6,836 km²) and Yoho national parks (1,313 km²) (Fig. 1). The vegetation and climate for the entire Central Rockies Ecosystem was described in Benn (1998). Major transportation corridors dissect both national parks. Approximately 58% (4,726 km²) of the study area is suitable grizzly bear habitat (<2,400 m), above which there is little grizzly bear foraging (Gibeau et al. 2001). Thus, grizzly bear habitat is restricted to major vegetated valley systems. Human use is also concentrated in these valleys. Zones of human influence around trails, roads, and other developments occupy about 25% of the suitable habitat (Gibeau et al. 2001). Grizzly bear population estimates for Banff National Park were 55–85 (G.W. Vroom, 1974, Grizzly and wolf observations, Banff National Park, Banff, Alberta, Canada) and 60–80 (Gibeau et al. 1996).

METHODS

Mortality and translocation databases for grizzly bears were supplied by Banff and Yoho National Parks for 1971–98. Additional mortality records came from other wildlife files provided by Parks Canada Western Region Office, annual warden and superintendent reports, a consultant's report (Millson 1978), and several graduate theses (Noble 1972, Taylor 1984). Mortalities included dead bears, bears

translocated to remote areas north and west of the parks that were not known to have returned, translocated bears that died in other jurisdictions, and bears placed in zoos. We used these mortality data to summarize mortality by cause, sex, age, and cohort.

Spatial Analyses

Locations of bear mortalities were referenced to the universal transverse Mercator (UTM) grid to the nearest 100 m and included a descriptor such as a river, creek, or cultural feature. Interviews were conducted with past and present wardens and wildlife managers to collect additional information about specific mortalities and their locations. We classified locations as accurate, reasonable, and estimate. Accurate locations had a UTM designation to ± 100 m and a geographic descriptor. Reasonable locations were within some stated distance from a known road, trail, drainage, or development. Mortalities with estimated locations were excluded.

Digital data containing human access information at a scale of 1:50,000 were supplied by Parks Canada. The road layer included railway lines and roads open to the public and negotiable by 2-wheel drive vehicle. The trail layer included roads closed to the public, utility corridors, and any other linear access features accessible by hiking, mountain biking, or horseback.

Access and mortality data were entered into a geographic information system, MapInfo 4.0 (MapInfo Corporation, Troy, New York, USA). Zones of influence (ZOI) of 500 m and 200 m were set around roads and trails, respectively, based on the judgment of the authors. Buffer widths of 500 m for motorized roads and 300 m for non-motorized trails were used in the cumulative effects model for grizzly bear in Yellowstone National Park (Mattson 1999). The Central Rockies Ecosystem has steeper and narrower valleys than Yellowstone, thus we are comfortable with 200 m for non-motorized trails in this forested mountain landscape. Road and trail buffers were combined into a single coverage and the area of overlap was only calculated once. Mortality locations in the area of overlap were analyzed as occurring within road buffers because roads were assumed to have a greater effect on mortality risk than trails.

Mortalities were tallied with respect to proximity to townsites and commercial tourist operations. We assumed that bears were attracted to these areas by the presence of food and garbage (Mattson et al. 1987, Weaver et al. 1987). This assumption was supported by limited data from mortality records and discussions with bear managers.

We recorded the elevation of 95 human-caused grizzly bear mortality locations and the elevations of some tourist destinations and park developments.

Temporal Analyses

We stratified mortality data into 2 periods to relate changes in mortality characteristics with changing patterns of human use and evolving management concerns and actions. We chose 1984–85 as the break, although no major changes occurred in any single year. Rather, a series of events in the early 1980s led to a progressive modification in management practices. These events included (1) the 1980 Whiskey Creek bear maulings in Banff National Park (A. Westhaver and A. Williams, 1980, Report of the superintendent's review team on the bear mauling incidents, Banff National Park, Resource Conservation and Interpretive Service, Banff, Alberta, Canada; Herrero 1985), which stimulated improved garbage management and increased efforts at communication and public education with respect to bears, (2) closure of the Banff landfill in 1981, and (3) commencement of fencing of the Trans Canada Highway from Banff's east park gate in 1983. Also, we recognized that it would take a few years for the bear population to adapt behaviorally to events such as the landfill closure. Finally, for ease of comparison, these periods were of equal length (1971–84, 1985–98). The Mann-Whitney *U*-test was used to test for differences in the annual number of grizzly bear deaths between periods, with $\alpha = 0.05$. The following hypotheses were tested:

- H_{01} : The annual number of grizzly bear mortalities in Banff and Yoho National Parks did not decline significantly from 1971–84 to 1985–98.
- H_{02} : The annual number of problem grizzly bear mortalities in Banff and Yoho National Parks did not decline significantly from 1971–84 to 1985–98.

Finally, we analyzed cause of death by seasons. We used 3 seasons of importance to bears (Apr–Jul = pre-berry, Jul–Oct = berry, Oct–Dec = post-berry).

RESULTS

We collected 108 and 11 records of human-caused mortality from Banff and Yoho National Parks, respectively. The average annual mortality was 4.3 grizzly bears/year, with peaks of 15 recorded deaths in 1972 and 13 in 1980 (Fig. 2).

Management actions and vehicle and train collisions accounted for 71% and 19%, respectively, of the 119 human-caused grizzly bear deaths. The remaining 10% included 1 research related incident and 11 deaths from unknown causes. In addition to mortalities recorded within Banff and Yoho National Parks, at least 7 research grizzlies known to use Banff and Yoho National Parks were killed in British Columbia and Alberta (M.L. Gibeau and S. Herrero, 1998, Eastern Slopes Grizzly Bear Project, Year 4–1997, Progress Report for the Eastern Slopes Grizzly Bear Project Steering Committee, Calgary, Alberta, Canada). We knew the sex and age of 83 dead grizzly bears (Table 1). Adult females and dependent young (cubs-of-the-year and yearlings) accounted for 65% of this total. Females accounted for 51% of all mortalities of known sex since 1971 (Table 1), and even after closure of the Banff landfill in 1981, 18 of 22 bear mortalities with sex known were female (Fig. 3). An additional 11 mortalities were unclassified as to sex during this time.

Of 85 problem wildlife mortalities, 64.7% were destroyed and 35.3% were handled for translocation purposes. Fifteen of the grizzlies handled died accidentally, and 15 were translocated. Five of the translocated bears were placed in the Calgary Zoo and 5 died in Alberta within 1–2 years of capture (1 shot legally, 2 shot illegally, 1 problem wildlife, 1 unknown cause).

Eleven family groups consisting of at least 6 cubs-of-the-year and 10 yearlings were destroyed or translocated

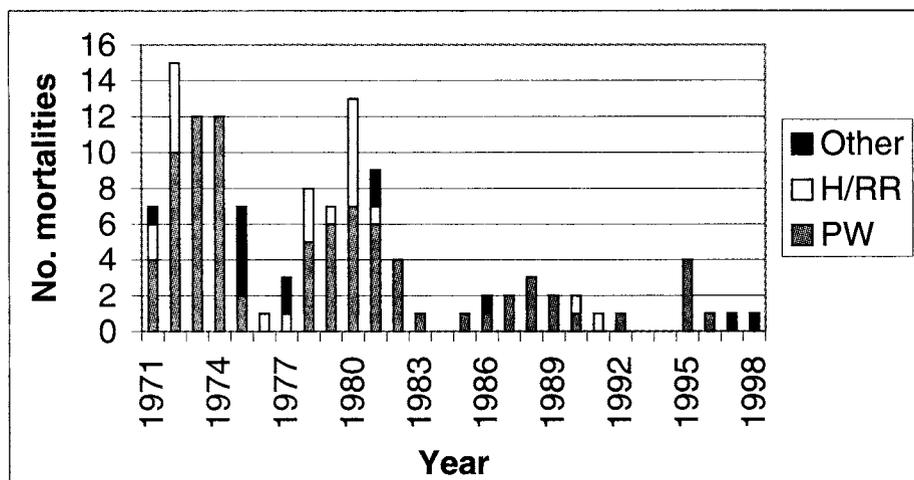


Fig. 2. Annual human-caused grizzly bear mortalities by type for Banff and Yoho National Parks, 1971–98, ($n = 119$). PW = problem wildlife, H/RR = highway/railway, Other = research or unknown.

Table 1. Percent grizzly bear mortality (number) by sex, age, and cohort for Banff and Yoho National Parks, 1971–98 (n = 119).

	Sex	Age	Cohort
male	33.9 (40)	adult	34.7 (41)
female	35.3 (42)	dependent	29.7 (35)
unknown	31.1 (37)	subadult	12.7 (16)
		unknown	22.9 (27)
			dependent
			adult female
			adult male
			subadult female
			subadult male
			unknown
			29.4 (35)
			16.0 (19)
			15.1 (18)
			7.6 (9)
			1.7 (2)
			30.3 (36)

from the ecosystem. This was considered a minimum number as 69% of 64 recorded problem wildlife mortalities were adult females (17) and dependent (cubs-of-the-year or yearlings) bears (27). Twenty-one records had no sex or age attached. Of 15 vehicle and train collisions where the cohort was known, adult males accounted for 47%, dependent bears 33%, and adult and subadult females 20%.

Spatial Analyses

All 95 human-caused grizzly bear mortalities, classified as having accurate or reasonable locations, occurred within zones of influence along roads and trails or around human settlements (Fig. 4). Mortality concentrations occurred at Banff and Lake Louise townsites and along the Trans Canada Highway (Table 2). A minimum of 59 mortalities throughout the analysis period was associated with the presence of human food and garbage.

Eighty percent of all known mortality locations were below 1,800 m. The remaining 20% occurred at 1,800–2,100 m (Fig. 5).

Temporal Analyses

We rejected both Hypotheses 1 and 2. The mean annual number of mortalities declined significantly from 1971–84 ($\bar{x} = 7.07$) to 1985–98 ($\bar{x} = 1.43$; $U = 164.5$, $P = 0.0010$). The mean annual number of problem wildlife mortalities also declined significantly from 1971–84 ($\bar{x} = 4.93$) to 1985–98 ($\bar{x} = 1.14$; $U = 151.0$, $P = 0.0066$).

Most mortalities in both periods were problem bears (67% during 1971–84; 80% during 1985–98). Although the number of problem bear deaths declined during 1985–98, the percentage of females increased from 50% to 80%. Adult females and dependent bears (cubs-of-the-year and yearlings) increased from 66% of the total mortality in the early period to 79% during period 2. Only 2 of 22 highway and railway mortalities occurred in the latter period.

We knew the date of death in 72 instances. More deaths (57%) occurred during the berry season (mid-Jul–late Sep) than during the pre-berry (35%) and post-berry (8%) seasons. Seventy-five percent and 58% of 48 dated mortalities of problem bears occurred during the peak tourist

Table 2. Types of developments and land uses where human-caused grizzly bear mortalities occurred in Banff and Yoho National Parks, 1971–98 (n = 95; some sites are tallied twice so total is >95).

Location of kill	No.	Detail of location
highway/railway	22	Trans Canada (16), Banff-Jasper (2), other (1), railway (3)
townsite	27	Lake Louise (15), Chateau Lake Louise (7), Banff (2), Field (3)
garbage dump/landfill	19	Banff (15), Lake Louise (4)
campground	16	
ski resort	8	Lake Louise (3), Norquay (3), Sunshine (2)
commercial lodge	11	
warden cabin	3	

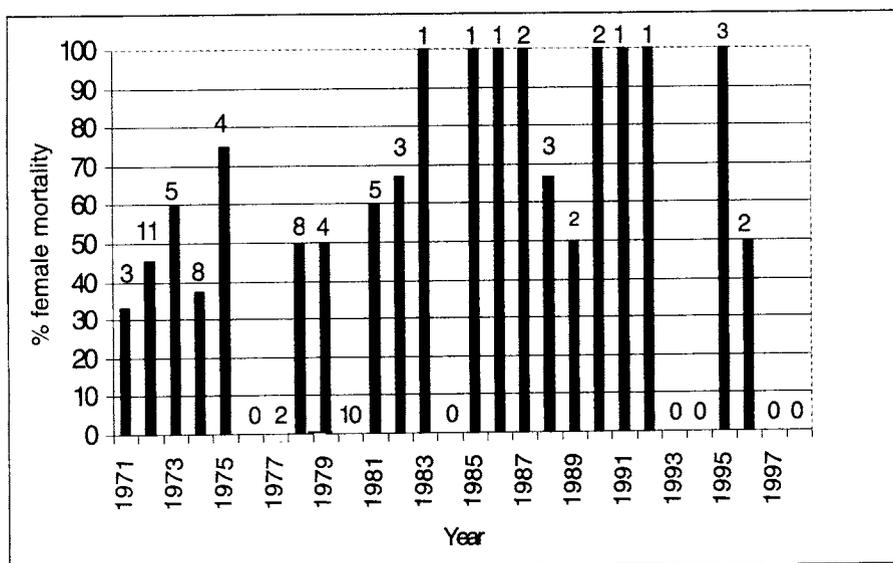


Fig. 3. Percent females in annual grizzly bear mortality. Numbers above the bars are the total mortalities with sex known for that year.

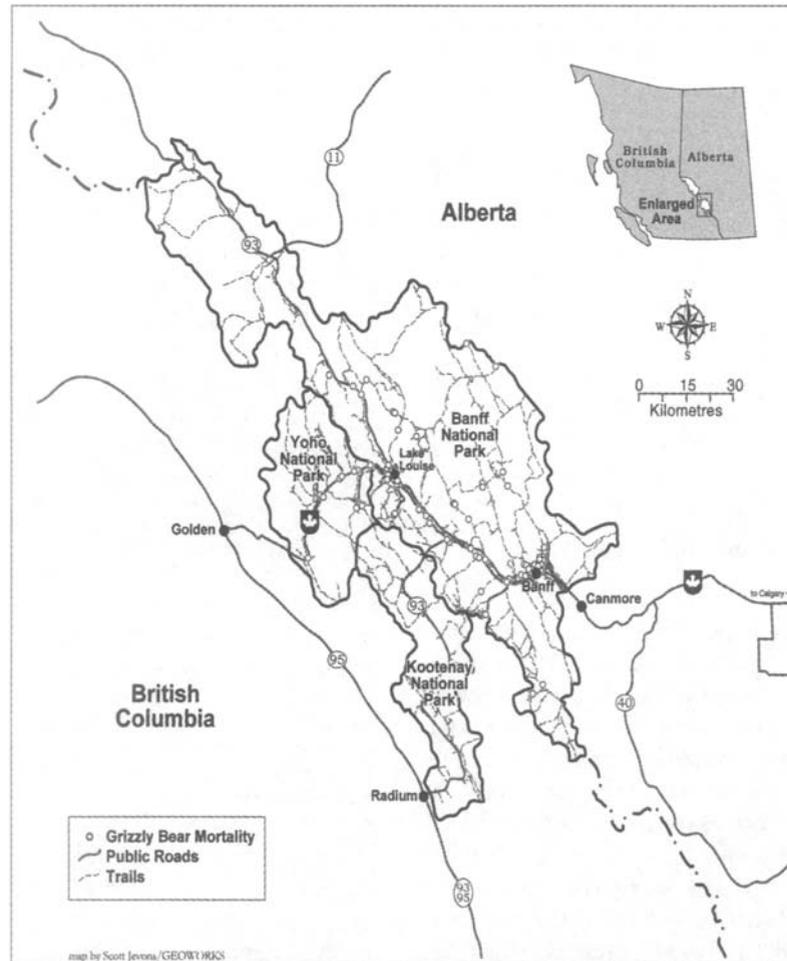


Fig. 4. Grizzly bear mortality locations in relation to roads and trails in Banff and Yoho National Parks, 1971–98.

season (late Jun–early Sep) and during the berry season, respectively.

DISCUSSION

The 119 recorded human-caused grizzly bear deaths in Banff and Yoho National Parks were considered to be the minimum number from 1971–98. Past and present wildlife managers suggested that there were probably more mortalities than were recorded, particularly during the 1970s (R. Kunelius, Banff National Park, Alberta, Canada, personal communication, 1998; M. Gibeau, Eastern Slopes Grizzly Bear Project, University of Calgary, Alberta, Canada, personal communication, 1998; D. Poll, Parks Canada, Western Region Office, Calgary, Alberta, Canada, personal communication, 1998). This large number of deaths caused by humans contrasts strongly with the adjacent and larger Jasper National Park, where in 1975–98 there were only 39 known grizzly bear mortalities (W. Bradford, Wildlife Warden, Jasper National Park, Alberta, Canada, personal communication, 1999).

Problem bear mortality was the most significant cause of death for this study. Management interventions helped reduce the total number of deaths (male and female) in 1985–98. However, the percent of female mortalities during this period increased from 50% to 80%, and the average annual female mortality was still higher than the total human-caused mortality target set based on the park's population estimate. This human-caused female mortality is the highest percent of total human-caused mortality reported for over 10 years for any grizzly bear population. As well, the human-caused mortality of dependent bears (cubs-of-the-year or yearlings) remained high throughout the study. These results may be explained by changing habitat use by specific cohorts over time. The higher male mortality in the early period was probably the result of more male bears feeding closer to people (in landfills and unsanitary campgrounds, Noble 1972). With the landfill closures and improved camper attitudes and garbage management, adult males may have selected habitats remote from human activity zones. Subadult grizzlies and adult females with young may have been more

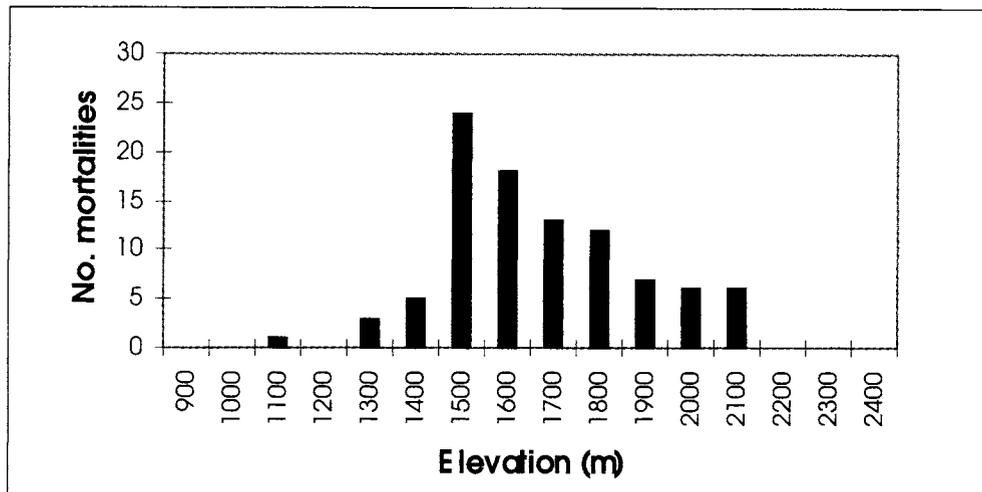


Fig. 5. Grizzly bear mortality locations by elevation in Banff and Yoho National Parks, 1971–98 ($n = 95$). Elevations of high human use areas in the parks: Banff, 1375 m; Castle Junction, 1430 m; Lake Louise, 1540 m; Chateau Lake Louise, 1740 m; Skoki Lodge, 2135 m; Moraine Lake Lodge, 1900 m; Lake O'Hara, 2000 m; Field, BC, 1250 m.

likely to use habitats near people, presumably to avoid adult males (Mattson et al. 1992, Gibeau et al. 1996). Thus, they may have been prone to habituation to humans and attraction to human food and garbage, increasing their mortality risk relative to males (Fig. 3) and their potential to be destroyed or translocated as problem animals (Mattson et al. 1987). This dynamic was previously described for the Yellowstone Ecosystem (Craighead et al. 1995).

The high accidental mortality of bears during management actions was the result of several points. All of these incidents occurred in the 1971–84 period. At this time, managers had less experience with tranquilizing drugs and handling techniques, and attitudes differed regarding animal welfare and grizzly bear conservation. We believe that all of these factors have improved in recent years.

Road mortality declined during 1985–98 even though traffic volumes increased. We have no definitive data to explain this; however, one likely cause is that the highway was fenced in stages to keep wildlife off the highway. Also, traffic became distributed over a 24-hour period and may have become so continuous as to act as a barrier to bears crossing unfenced portions of the corridor.

We found that grizzly bears died at low elevations and near human settlements and access. Roads, trails, and developments are almost always placed in valley bottoms, often fragmenting riparian habitats. Similarly, concentrations of kills at settlements and along roads and trails occurred throughout the Central Rockies Ecosystem (Benn 1998) and in other grizzly bear populations (Mattson et al. 1987, Nagy et al. 1989, Mace et al. 1996). Gibeau et al. (2001) showed that human use and developments reduced the amount of secure habitat for grizzly bears. Roads and trails improve access, and when placed in important seasonal habitats, increase the potential for nega-

tive bear–human encounters (McLellan and Shackleton 1988b). Increased access to the backcountry has been shown to alter bear behavior (McCullough 1982, Jope 1985), increase bear–human conflicts (Dalle-Molle and Van Horn 1989), increase the number of grizzly bear removals (Martinka 1982, Leonard et al. 1990), and displace certain cohorts, such as females with young (Mattson et al. 1987, Gilbert 1989).

The abrupt decline in grizzly bear mortality into the mid 1980s was correlated with closing the Banff landfill, improving garbage management, increasing public education regarding living and recreating in bear country, improving tolerance of grizzly bears, fencing of the Trans Canada Highway, and increasing use of aversive conditioning techniques over removals. However, the high mortality rate of the early period may have depressed the park's grizzly bear population. This effect could have continued through the 1985–98 period due to a lag effect and mortality concentrated in the female cohort. Closures of Yellowstone National Park landfills were followed by sharp declines in reproductive and survival rates (Craighead et al. 1974).

Finally, we found that a high proportion of mortalities occurred during the berry season. In mid-July to early October, grizzlies in the Central Rockies Ecosystem feed primarily on buffaloberry (*Shepherdia canadensis*) at lower elevation, often along roads and near people.

Human intolerance, inadequate management of access and food attractants, and a high rate of commercial development continue to be important contributing factors to grizzly bear mortality in Banff National Park. However, specific steps have been taken to reduce human-caused grizzly bear mortality. Recommendations by the Eastern Slopes Grizzly Bear Project to the Banff-Bow Valley Task Force (Gibeau et al. 1996) led to the implementation of

an annual human-caused mortality target of <1% of the estimated grizzly bear population. Also, habitat effectiveness targets aimed at supporting grizzly bear habitat use have been set for most carnivore management units. By implementing measures aimed at reducing potential conflicts between humans and grizzlies, human-caused grizzly bear mortality and the potential for human injury can be reduced.

There is an urgent need for these measures to be successful in the national parks and the rest of the Central Rockies Ecosystem. Because precise measurements of population demographic rates are only now becoming available, management of mortality must be conservative and management plans must consider adjacent jurisdictions in Alberta and British Columbia (Herrero et al. 1998). A recent population and habitat viability assessment workshop predicted both population and habitat declines for grizzly bears in the Central Rockies Ecosystem (Herrero et al. 2000). Because Banff and Yoho national parks are assumed to serve as core refugia for sensitive species such as grizzly bears, and because grizzly bear hunting exists on most of the land surrounding these national parks, human-caused mortality inside the parks must be minimal. Ecological integrity is the stated priority of the national parks (Banff National Park 1997), and the grizzly bear serves as the premier indicator of the health of the terrestrial ecosystem (Banff-Bow Valley Study 1996). Managing grizzly bear mortality at a level that prevents population decline is fundamental.

MANAGEMENT IMPLICATIONS

The following recommendations are based on the stated goal of Parks Canada to maintain a naturally regulated population and distribution of grizzly bears in the mountain national parks (Banff National Park 1997). These recommendations are offered as ways to prevent future increases in mortality, to reduce the unnecessary killing of grizzly bears, and to assist in the inter-jurisdictional management of grizzly bear mortality.

During the analysis period, a considerable number of grizzly bear deaths went unrecorded in official park databases, and the records were often incomplete. This has improved in recent years and must continue to improve.

There is some variation in the way mortality data are classified between jurisdictions in the Central Rockies Ecosystem. Park wildlife managers should work with managers from other jurisdictions to develop the same coding conventions and to clearly define the different causes of death.

Acquiring accurate mortality locations is necessary for understanding and managing mortality with respect to access, development, and use of the landscape. Mortality

needs to be monitored in the future to understand the effectiveness of management decisions. Additional information needs to be collected such as the distance a bear died from an access route or facility, the type of access route, the condition of the access route at the time of the mortality, the mode of travel of the person(s) responsible for the removal of the bear, presence of food attractants including natural foods, and what, if any, human behaviors played a role in the mortality.

Management of garbage and human and pet food continues to be a problem around Banff, Lake Louise, and in some campgrounds. Effective legislation and enforcement should be employed with respect to food and garbage handling. All backcountry users should be required to store food, garbage, and horse feed in bear-proof metal or seamless PVC containers, or effectively elevate attractants between trees or isolate camp within an effective portable electric fence.

To understand the effects that new management strategies and increases in human use of grizzly bear habitat have on grizzly bear mortality and population status, analyses should be repeated and reassessed in the future with more accurate population estimates.

The use of aversive conditioning programs on roadside- and campground-habituated bears, especially females, should be increased. On-site releases and aversive conditioning of many problem bears would reduce the costs and risks associated with translocating grizzlies.

Efforts should continue to inform the public about bear activity in high human use areas and to educate the public with respect to how to behave in bear country.

All of these recommendations will require adequate funding and administrative support.

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Are roads and railroads barriers to bumblebee movement in a temperate suburban conservation area?

Madhumita Bhattacharya^{a,*}, Richard B. Primack^a, Joel Gerwein^b

^aDepartment of Biology, Boston University, 5 Cummington Street, Boston, MA 02215, USA

^bBiology Department, University of Massachusetts, 100 Morrisey Boulevard, Boston, MA 02125, USA

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Abstract

We investigated how habitat fragmentation affects the movement of marked bumblebees between plant patches in a temperate conservation area in metropolitan Boston, Massachusetts. Our study was conducted on populations of sweet pepperbush (*Clethra alnifolia* L. f.) separated by a road and natural woodland, and buttonbush (*Cephalanthus occidentalis* L.) separated by a railroad. Bumblebees showed high site fidelity and only rarely crossed roads or railroads. When bees captured at one sweet pepperbush population were moved across a road to a new sweet pepperbush population and released, they returned to their original site, some within 20 min of their capture. When all inflorescences were removed from one sweet pepperbush patch, most bees moved to another sweet pepperbush population on the same side of the road. The results show that while bumblebees have the ability to cross a road and railroad, these human structures may restrict bumblebee movement and act to fragment plant populations because of the innate site fidelity displayed by foraging bees. Moreover, marked bees were almost never observed to move between populations unless they were displaced, or forced to seek additional forage sites. © 2002 Elsevier Science Ltd. All rights reserved.

Keywords: Habitat fragmentation; Bumblebees; *Bombus*; *Clethra alnifolia*; Anthropogenic barriers; Pollination

1. Introduction

Animal movement is important for the pollination and seed dispersal of plants. Fragmentation of habitats by roads, railroads, fields, buildings and other human activities can restrict animal movement (Mader, 1984; Didham et al., 1996; Forman and Alexander, 1998). If animals are unable to cross such barriers, they may not obtain sufficient nectar, pollen, and fruit resources to survive. Flowers may remain unvisited and fruits undispersed, leading to declines in gene flow (Oostermeijer et al., 1994; Westerbergh and Saura, 1994) and seed production and the eventual decline of plant populations (Jennersten, 1988; Lamont et al., 1993; Noderhaug, 1995; Steffan-Dewenter and Tschardtke, 1999).

Habitat fragmentation is becoming more of a danger to the persistence of plant populations due to an ever-increasing human population, and an increasing alteration of the natural environment (Saunders et al., 1991).

Despite the recognized impact of habitat fragmentation on plant–pollinator interactions (Aizen and Feinsinger, 1994a,b; Steffan-Dewenter and Tschardtke, 1999), few field studies have been conducted on how artificial barriers affect pollinator movement. Evidence from fragmented forests in Brazil suggests that some understory butterflies (Lovejoy et al., 1986) and euglossine bees (Powell and Powell, 1987) may not readily cross pastures. Yet it is generally unknown how roads constructed across a landscape affects pollinator movement.

Bumblebees in the genus *Bombus* and related genera are important pollinators of numerous temperate plant species (Heinrich, 1976, 1979a). Therefore, it is valuable to document how habitat fragmentation affects bumblebee movement and thus, plant gene flow. Bumblebees are known to be strong fliers, and are able to travel considerable distances (Heinrich, 1979a; Osborne et al., 1999); they are certainly capable of crossing a human-dominated landscape interwoven with barriers such as roads and railroads. But do landscape elements such roads or railroads restrict bumblebee movement in their normal foraging activities, or will bumblebees cross such features as they would any other intervening

* Corresponding author. Tel.: +1-617-353-5559/6989; fax: +1-617-353-6340.

E-mail address: mita@bu.edu (M. Bhattacharya).

space of natural habitat? If captured in one plant patch and released in another patch of the same species, will bumblebees cross a roadway or natural barrier to return to their original site or adopt the new patch as a foraging site? Will bumblebees forced to move from a site where all flowers have been removed, seek out replacement forage sites located across a road, or will they tend to relocate to new sites on the same side of the road as their original forage site? Such questions are critical to understanding the ability of pollinator and plant populations to persist in a fragmented landscape.

Bumblebees show high vagility and are known to display flower constancy and high site fidelity (Heinrich, 1976; Osborne and Williams, 2001). Therefore, it would be important to discern how habitat fragmentation superimposed on this behavior affects their foraging activity. We hypothesized that bees would be more likely to move between sites separated by natural habitat than sites separated by a road. To test this hypothesis we conducted a series of experiments using marked bumblebees in a suburban forest habitat.

2. Methods

2.1. Study location, plant species and bumblebee species

The study was conducted at the Webster conservation area (N 42° 19' 33.1", W 71° 10' 31.9"), a deciduous temperate woodland, located in Newton, Massachusetts. The study focused on a small (~1225 m²) wetland population of buttonbush (*Cephalanthus occidentalis* L., Rubiaceae) divided into two fragments (sites A and B) by a raised 14 m wide railroad bed, and scattered moist woodland populations of sweet pepperbush (*Clethra alnifolia* L. f., Clethraceae; Fig. 1) on either side of a 4-lane, 14 m wide road, the Hammond Pond Parkway. The four sweet pepperbush study populations are referred to as sites I, II, III and IV, with site I located on one side of the road and the remaining three sites on the other side of it (Fig. 1).

Buttonbush is a deciduous shrub that ranges in height from 1 to 4 m, and bears small white tubular flowers clustered on ball shaped inflorescences. Sweet pepperbush is a tall deciduous shrub that ranges in height from 1 to 3 m or more, with small white fragrant flowers borne on terminal racemes 5–15 cm long. Both shrub species are frequently visited by bumblebees, which are the primary pollinators of sweet pepperbush (Hemingson, 1986). In buttonbush, cross-pollination is known to enhance fruit set greatly compared to self-pollination (Imbert and Richards, 1993). The term 'bees' or 'bumblebees' referred to in this paper are worker bees of *Bombus impatiens* and *B. affinis*, and also include several (3–15%, depending on site and year) carpenter bees (*Xylocopa* species). For all observations and experiments,

counts of bumblebees reported include only those bees whose tag numbers could be read.

2.2. Mark and recapture of bees

In July 1997, 93 bees were captured on the buttonbush plants in both fragments (Table 1), cooled to make them passive and marked with Opalithplättchen or numbered plastic tags (Kearns and Inouye, 1993) glued to their thorax. Marked bees were returned to the shrub where they were originally captured within 10–20 min of capture. The area was surveyed for marked bees for 1–2 h on 6 days over a 2-week period.

In August of 1997, 137 bumblebees were marked at four sweet pepperbush sites designated "site I", "site II", "site III" and "site IV" (Fig. 1), with most bees captured from site I and site II (Table 1). Sites were separated from each other by a road or by intervening forest. The sites were observed for 0.5–1.5 h for 5–6 days over a 7–9 day period. In late July and early August of 1998, 137 bees were marked but only at sites I and II that are separated by the Hammond Pond road.

2.3. Bee displacement experiments

In late July of 1998 and early August of 1999, we captured bumblebees at the site I sweet pepperbush population, marked them, and then released them at site II located across the road. In 1999, we conducted a similar displacement of bees from site II to site I. Reciprocal displacements were also carried out between site II and site III located within the woods and separated by trees and shrubs (Table 2). After the displacement of bees, the original capture sites were monitored for a total time range of 205–570 min (depending on site) over a 4-day period to determine how many bees returned to their capture site. A Chi-Square test was performed to determine whether fewer bees returned to their original site when separated from it by a road than when separated by natural, woodland habitat.

2.4. Experiment where bees are forced to seek new forage sites

In mid August 2000, we marked 102 bees at the sweet pepperbush site II. After marking the bees, we removed all flowers from the plants at that site in order to force bees to seek additional forage sites. We hypothesized that bees would be more likely to move to replacement populations separated from site II by natural woods rather than seek populations located across a road. Nearby sweet pepperbush sites (I, III and IV) and a field with flowering purple loosestrife (*Lythrum salicaria* L., Lythraceae)—a major weed of wetlands in temperate North America—were monitored on 6 days over a 9 day

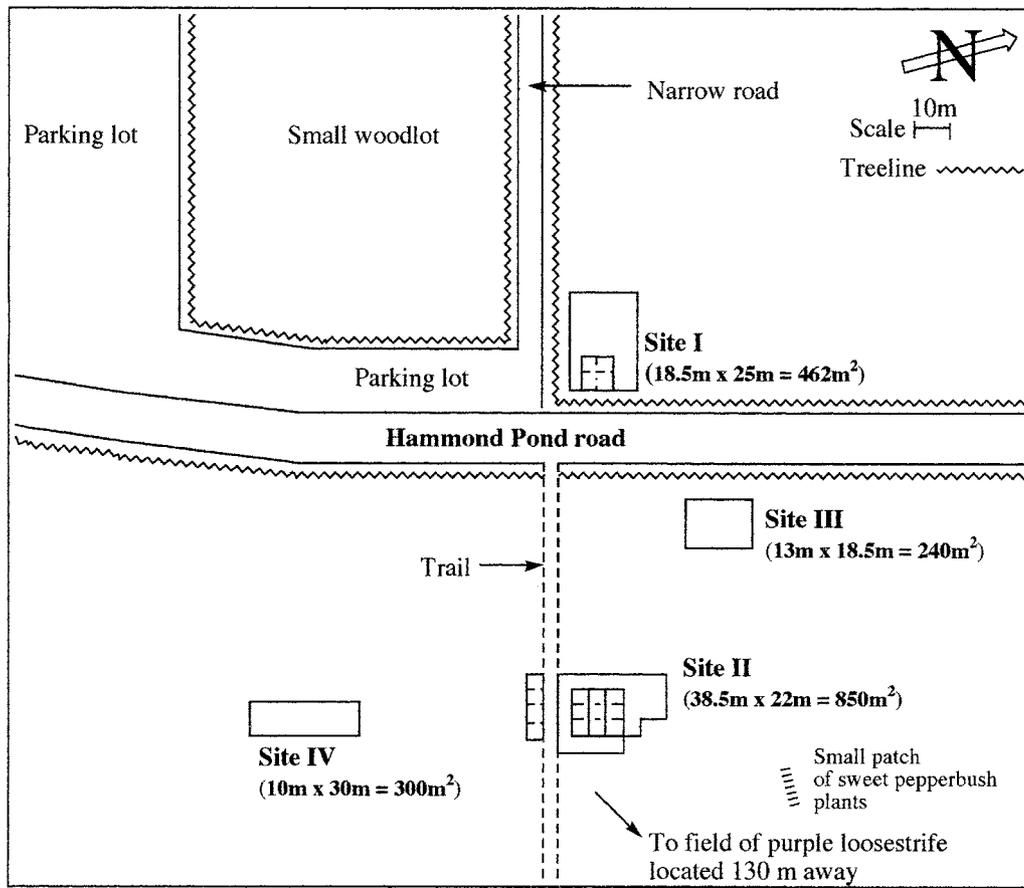


Fig. 1. Location and approximate area of sweet pepperbush populations (sites I–IV) in wetland patches in the Webster conservation reserve. Hatched areas at sites I and II show observation quadrats.

period for a total time range of 15–500 min (depending on site) for marked bees.

2.5. Site differences between sites I and II

Most of our experiments centered on the two bigger sweet pepperbush sites (I and II) separated by a road. Therefore, we decided to examine if these sites differed in aspects of inflorescence density that might determine bee visitation rates. Although fruit/seed set provide direct assessment of successful pollinator visits, we did not measure this, as fruit set is very high in sweet pepperbush (Jordan and Hartman, 1995). Since pollinator visitation is a function of plant density (Kunin, 1997), in 1998 we demarcated four quadrats (25 m² each) at site I and 11 quadrats of similar size at site II to census bees and record visitation rates of pollinating bees per quadrat at these sweet pepperbush sites (Fig. 1). Fewer quadrats were demarcated at site I because thick growth of the thorny greenbrier vine, (*Smilax rotundifolia* L., Liliaceae) hindered movement outside the marked quadrats. At site II, 11 quadrats were demarcated at the center of the population and to one side of the trail as fewer bees were seen at the peripheral plants of the population. Bees were censused on 8 days over a 12-day period from late

July to early August. Observation sessions lasted 5 min per quadrat. Inflorescence density (number of inflorescences present per quadrat) was also determined at both sites. A Mann–Whitney *U* test was conducted to compare both sites on inflorescence density per quadrat.

In 2000, we counted the number of inflorescences on randomly selected plants at sites I and II. Sweet pepperbush plants primarily propagate vegetatively through the regeneration of clonal sprouts (Jordan and Hartman, 1995); therefore in a given area several ramets could belong to the same genet. To avoid picking stems belonging to the same genet, we randomly selected 20 single stems separated by a distance of 2 m or more in the general area of the demarcated quadrats at sites I and II to represent single plants (Fig. 1). This was done prior to the flower removal experiment. A *t*-test (two tailed) for independent samples was performed to determine if the two sites differed for mean inflorescence count per plant. We also determined if the two sites differed in bee visitation rates. On each of these plants we further selected one inflorescence (of similar size and number of open flowers) and counted the number of bumblebee visits to it during a 5-min observation session. Bumblebee visits per inflorescence per 5-min observation session were monitored between 13:30–16:50 on 4

Table 1

Number of bees (*Bombus* and *Xylocopa*) marked and observed later at study sites (excludes bees from the displacement and flower removal experiments)

Site	Number of bees marked		Number of marked bees observed		Fraction of marked bees observed	
	1997	1998	1997	1998	1997	1998
<i>Buttonbush</i>						
A (north)	80	–	18	–	0.23	–
B (south)	13	–	0	–	0.00	–
Total	93		18		0.19	
<i>Sweet pepperbush</i>						
I	55	82	19	37	0.35	0.45
II	59	55	18	18	0.31	0.33
III	12	–	4	–	0.33	–
IV	11	–	1	–	0.09	–
Total	137	137	42	55	0.40	0.40

August and 9:50–13:05 on 5 August 2000 for site II, and between 13:45–17:05 on 5 August and 9:00–13:30 on 8 August 2000 for site I.

3. Results

3.1. Observation and movement of marked bees across barriers

Of the 367 bees marked at all sites in 1997 and 1998, 31% were observed again on subsequent days (Table 1). These recapture rates conform to other studies of marked bees (Kwak et al., 1991; Dramstad, 1996; Osborne and Williams, 2001).

Marked bees were almost exclusively observed at the patches where they were originally captured, marked and released. Only three bees were observed at sites other than where they were marked (Table 2). In 1997 at the buttonbush sites, two of the 80 bees marked on the north side of the railroad tracks (site A) were subsequently observed on the south side of the tracks (site B) foraging on purple loosestrife. Bees marked on the sweet pepperbush plants that year were only observed at the original sites where they had been marked over the course of several weeks. In 1998, the 137 bees marked at the sweet pepperbush sites also showed the same site fidelity with one exception. A single bee (W9) marked at site II was observed 130 m away at a large patch of purple loosestrife, separated by intervening forest (Fig. 1).

3.2. Bee displacement experiments

Twelve (48%) of the 25 bees caught at site I in 1998, marked, and released 20 min later at site II, were observed again (Table 2). One of these bees was later observed foraging at site II. The remaining 11 bees were

observed again only at site I, one of which was observed there only 20 minutes after being moved to site II.

In the 1999 experiments involving reciprocal displacement of bees between sites separated by a road (sites I and II) versus sites separated by natural forest (sites II and III), 36–59% of the displaced bees were observed again. Only two bees, one each from sites I and II were observed foraging at their site of release. The remaining 31 bees observed had crossed back to their original capture site. The reciprocal displacement between sites II and III showed a slightly greater tendency of bees to forage at the new site. One bee from site II continued to visit site III, while three bees from site III continued to visit site II. Of these three bees displaced from site III to site II, one bee (B37) was observed on subsequent days to forage at both its release and capture sites.

There was no significant difference between the effect of a road (separating site I and site II) or natural woodland (separating site II and site III) on bee movement between site of release and site of capture ($\chi^2 = 1.92$, $df = 1$, P -value > 0.05). However, the power of the test was low ($1 - \beta = 0.28$). Contrary to our prediction, our results show a trend, albeit non-significant, for fewer bees to travel back to their original site when the sites were separated by forest than when separated by a road.

3.3. Response of bees forced to seek new forage sites

Of the 102 bees marked at site II from where all flowers were subsequently removed, 12 bees were observed again (Table 2). Eleven of the 12 bees observed were seen on sweet pepperbush plants located at sites on the same side of the road as site II (Fig. 1). Of these, seven were seen at site IV, which is located 35 m away from site II. One bee was seen at site III where not more

Table 2
Bumblebee movements across anthropogenic barriers at the Webster conservation area (the number of bees marked at each site are denoted in parentheses)

Direction of bee movement		Year	Number of marked bees observed across barrier	Barrier (width m)	Fraction of recoveries to marked bees observed across barrier	Number of marked bees displaced to release site
From site:	To site:					
<i>Buttonbush</i>						
A (80)	B (13)	1997	2	Railroad (14 m)	0.11	–
<i>Sweet pepperbush</i>						
Site II (55)	Field (0)	1998	1	Natural forest (130 m)	0.02	–
<i>Bee displacement experiment</i>						
<i>Capture site</i>		<i>Release site</i>				
Site I (25)	Site II	1998	11	Road and Natural forest (14 + 70 m)	0.92 ^a	1
Site I (46)	Site II	1999	20	Road and Natural forest (14 + 70 m)	0.95	1
Site II (46)	Site I	1999	26	Road and Natural forest (14 + 70 m)	0.96	1
Site III (35)	Site II	1999	17	Natural forest (40 m)	0.85	3
Site II (33)	Site III	1999	11	Road and Natural forest (14 + 70 m)	0.92	1
<i>Flower removal experiment</i>						
<i>Capture and release site</i>		<i>Observation site</i>				
Site II (102)	Site I	2000	1	Natural forest (40 m)	0.08	–
Site II (102)	Site III	2000	1	Natural forest (40 m)	0.08	–
Site II (102)	Site IV	2000	7	Natural forest (35 m)	0.58 ^b	–
Site II (102)	Patch near site II	2000	1	Natural forest (20 m)	0.08	–
Site II (102)	Site II	2000	2	–	–	–

^a At this site, 11 of 12 (92%) marked bees observed had moved back to their original site.

^b Of the 12 marked bees observed from those tagged at site II, seven (58%) were observed at site IV after flower removal at site II.

than 2% of the plants were flowering that year, and one bee was seen at a small patch of plants adjacent to the flowerless site II. Only a single bee was observed across the road at site I (located 84m from site II), which was flowering strongly. Two of the marked bees were seen to return to site II where we had missed removing flowers from one plant.

3.4. Differences between site I and site II

Sweet pepperbush sites I and II did not differ significantly in the density of inflorescences, but site I had higher bee visitation rates compared to site II. In 1998, mean inflorescence density per quadrat between sweet pepperbush site I and site II (Table 3) did not differ significantly ($U=16$, $P=0.47$). However, site I had on average almost double the number of bee visits per quadrat compared to site II. Similarly, in 2000, mean inflorescence count per plant between sites I and II did not vary significantly ($t_{\text{stat}}=0.70$, $df=29$, $P\text{-value}=0.49$). However, overall bee visitation rates to inflorescences from morning to late afternoon over the course of 2 days in 2000, were significantly higher at site I compared to site II (Table 3).

4. Discussion

4.1. Artificial and natural barriers

Regardless of the distances (35–110 m) that separate sweet pepperbush patches, or the presence of a natural or artificial barrier between them, none of the bees marked at any of the sweet pepperbush sites were observed to move on their own among patches. The high site fidelity of foraging bees was particularly unexpected at site III, which had very few inflorescences in 1997, and is located only 37 and 40 m from the larger sites I and II, respectively (Fig. 1). These observations match similar reports, where no bees were observed to

cross a gap of 4–8 m separating two forage sectors within a patch (Comba, 1999). Rasmussen and Brødsgaard (1992), report 2.6% of bumblebees moved between patches separated by distances of 10–40 m, while Osborne and Williams (2001) report a slightly higher percentage of bumblebee movement (12–14%) between patch groups in an experimental area. We failed to observe inter-patch movement possibly because of the greater distances separating our study patches.

Bumblebees appear to be reluctant to cross barriers unless floral resources at their forage sites are declining or have been removed. We observed no instances of bee movement from one population of plants to another of the same species. The two bees that moved from but-tonbush site A to site B were leaving an area with declining floral resources and moving to an area with abundant purple loosestrife flowers. A bumblebee (W9), which moved from the sweet pepperbush site II to an open field, was also observed to be visiting purple loosestrife flowers (Table 2). These instances of bee movement to purple loosestrife may reflect the need for bees to seek new floral resources as their current forage plants finish flowering and they shift their “majoring” to other flowering plants (Heinrich, 1979b). The response of bees forced to seek replacement sites when flowers at their foraging site were removed, shows bees tend to move to new flower patches of the same species available nearby. They likely expend less energy in moving to nearby familiar forage flowers, compared to looking for new species of flowers and learning to work them. We observed fewer marked bees in this experiment (~12%), perhaps due to survey constraints spread over a much wider area. Since the flowers at site II were removed during the peak of flowering, the bees probably did not make the gradual transition from declining floral resources to a new species of flowering plants, and preferred to switch to nearby sweet pepperbush patches instead. Only one bee was observed at site I located across the road on one day, which shows bees are capable of crossing barriers to look for familiar forage plants.

Table 3

Mean (± 1 S.D.) visitation rates of marked and unmarked bumblebees on sweet pepperbush plants, and inflorescence counts per quadrat at sites I and II in 1998, and mean (± 1 S.D.) visitation rates of bumblebees and inflorescence count per plant in 2000

Sweet pepperbush sites	1998				2000				
	N^a	Bumblebee visitor		N^b	Inflorescence count per quadrat	N^a	Bumblebee visits per inflorescence	N^c	Inflorescence count per plant
		Unmarked	Marked						
I	156	4.52 \pm 2.85*	1.77 \pm 0.96*	4	403.75 \pm 230.85	93	2.68 \pm 2.58*	20	22.65 \pm 3.90
II	28	2.21 \pm 1.62*	0.43 \pm 0.57*	11	316.91 \pm 237.27	80	0.90 \pm 1.13*	20	28.55 \pm 7.49

^a Number of 5 min observation sessions.

^b Number of quadrats observed per site.

^c Number of plants per site.

* $P < 0.01$, t -test for independent samples.

4.2. *Bumblebee displacement*

The fact that bees return to their original site after being experimentally transported between sites show that roads and railroads are not insurmountable barriers to bumblebee movement. However, the very low numbers of bees that crossed these barriers without being experimentally transported (Table 2), underscores the high site fidelity of foraging bees (Heinrich, 1976; Bowers, 1985; Dramstad, 1996; Saville et al., 1997; Comba, 1999; Wesselingh et al., 2000; Osborne and Williams, 2001). Our observations confirm those of other studies where bumblebee pollinators mostly remain site constant regardless of the availability of equally rewarding (Osborne and Williams, 2001) or even richer forage patches nearby (Comba, 1999), and tend to visit closest neighboring plants within patches (Rasmussen and Brødsgaard, 1992; Comba, 1999). We did not measure wind direction or wind speed during bee displacement, although wind is known to influence bumblebee flights with longer flights downwind than upwind (Comba, 1999). However, as part of a current study conducted by the authors, bees displaced 100–500 m from their foraging site in winds of 4–8 mph from all directions were eventually able to find their way back to their forage sites, some within 10–15 min. Therefore, in our displacement experiments it is unlikely that bees were influenced significantly by winds.

Our observations suggests that although a railroad and a road are not impassable barriers to bumblebee movement, they may constrain or discourage bee movement by contributing to spatial cues that determine bee site-specific foraging behavior. This may explain the trend observed for higher numbers of displaced bees to remain at the release site to which they were moved, when capture and release sites were separated by a more homogeneous natural habitat (Table 2). In uniform habitats, bumblebees react with longer inter-plant flights and fewer backward turns, and can perceive environmental landmarks that break the uniformity of their forage patches (Plowright and Galen, 1985). When bees reach the edge of a patch most bees turn back and continue to forage (Rasmussen and Brødsgaard, 1992). Thus, a road or railroad that bisects a plant population may be a strong landmark possibly acts as a barrier, as site-specific bees may turn back from the road and restrict their foraging to only one fragment of the divided population.

Site fidelity was also underscored by the rapid return of displaced bees to their original sites. Feeding site fidelity was strong enough to propel these bees across a road back to their original forage site. Bees are known to follow a fixed flight path to return to their original forage sites (Heinrich, 1976; Thomson et al., 1987; Thomson, 1995; Wesselingh et al., 2000). Studies by Manning (1956) and Kunin (1997) show bees use spatial

cues to return to individual plants and flowers, often where they have obtained higher nectar rewards (Dreisig, 1995; Wesselingh et al., 2000). This suggests that bees are sensitive to site characteristics. However, the rapid return of bees to their capture site when released on the same species of plants at a different site, suggests site fidelity is a stronger cue in foraging behavior than flower constancy. Nevertheless, the few bees that did not return to their original site indicate that bees can adopt new patches as foraging sites. Perhaps these bees were young foragers with the flexibility of changing their traplines to adopt a new or richer forage site. The fraction (0.08–0.15) of displaced bees for sites II and III sweet pepperbush patches separated by forest was almost double that for sites I and II separated by a road (0.04–0.08; Table 2). Site quality—determined by size of forage area or inflorescence density—may play a role as suggested by the adoption of the larger site II by three bees displaced from the smaller site III to the larger site II. In contrast one displaced bee from site II adopted site III.

Although inflorescence density per quadrat or the number of inflorescence per plant did not significantly differ between the smaller site I and the larger site II, the rate of marked and unmarked bumblebee visits appear to be much higher at site I compared to site II (Table 3). We did not qualitatively or quantitatively measure nectar or pollen resources at the different sweet pepperbush sites. However, with fewer bees visiting inflorescences at site II compared to site I, flowers at site II were expected to have more nectar and pollen available. Therefore, bees displaced from site I to site II were expected to encounter less competition by exploitation or nectar removal, which should have facilitated their displacement to the more profitable site, and vice versa. This proved not to be the case. Thus patch size or profitability may not be the only qualities affecting bee displacement. For instance, the road could be a major landmark for “traplining” bees that facilitates in orientation and recognition of original forage sites.

4.3. *Response of bumblebees forced to seek new forage sites*

Bees can traverse roads in their quest for new forage plants but rarely do so when forage is available owing to their high site fidelity. This is demonstrated by the observation of a single marked bee at site I after being forced to move from site II. However, of the 12 marked bees observed after flowers were cut at site II, 11 were seen at sweet pepperbush patches occurring on the same side of the road as site II and separated from it by natural woods. The close proximity of site IV to site II may explain why seven of the 11 bees were seen at site IV, which is 35 m away from site II. In comparison, site I is located at 84 m from site II in addition to being separated

from it by a road (Fig. 1). Yet site I is larger than site IV and appeared to have more bee visitors (personal observation) compared to it. However, it has been suggested patch size may not have as strong an effect on pollinator visitation rate as does flower density (Kunin, 1997) or plant density (Comba, 1999). Although we didn't compare inflorescence or plant densities and bee visitation rates between sites I and IV, the number of bees visiting site I were much higher compared to site IV (personal observation). Indeed, site I continued to attract a higher number of bees compared to site IV, although it was near the end of its flowering. This could be due to the sunnier location of site I near the road or due to the higher production of nectar by the remaining flowers, either of which were not quantified in our study. Within site IV, marked bees from site II were invariably observed within the same forage area of the population over a number of days. This conforms to similar observations by Comba (1999). Indeed a section of the plants at site IV were flowering strongly but had very few bees perhaps because the plants were under constant shade. Our observations suggest that bees are more likely to remain on one side of a barrier if continuing resources are available there, and will seek new food sources when the original supply begins to decline.

While bumblebee movement may not be impeded by habitat fragmentation, habitat loss through activities such as road construction can definitely result in loss of potential nest sites for bees—an important issue that needs to be addressed in future studies on habitat fragmentation (Cane, 2001). Further studies on spatial distribution and variation in plant population genetic structure at the landscape level, along with detailed investigations of bumblebee flights and the sources of origin of pollen carried by bumblebees will help to clarify the effects of habitat fragmentation on pollinator movement.

5. Conclusions

Bumblebee pollinators are not restricted by barriers such as roads and railroads at the landscape level, where normal plant patchiness is comparable to habitat fragmentation by artificial barriers. High site fidelity displayed by bumblebees may further restrict their movement more than previously suspected because of this aspect of their foraging behavior. Although bumblebees are occasionally long-distance pollinators (Heinrich, 1979a), especially where flowers are sparse, they do not appear to travel between patches frequently where sizable patches of flowers are available. This applies even when patches are separated by natural habitat and the intervening distance is fairly short (30–40 m). When a natural population is divided into two sections by a road, field, or railroad, individual bumblebees

may tend to treat it as two separate populations and not readily cross the intervening area. This is particularly true where each smaller plant population is large enough to meet their foraging needs. Thus, division of plant patches by roads and other structures may further reduce the naturally low frequency of bumblebee movement between plant patches, leading to lower rates of visitation in small isolated populations. The result may have implications for decline in gene flow in fragmented populations of plant species that depend on bumblebee visitation.

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Experimental Evidence for the Effects of Chronic Anthropogenic Noise on Abundance of Greater Sage-Grouse at Leks

JESSICA L. BLICKLEY,*† DIANE BLACKWOOD,*‡ AND GAIL L. PATRICELLI*

*Department of Evolution and Ecology and Graduate Group in Ecology, 2320 Storer Hall, One Shields Avenue, University of California, Davis, CA 95616, U.S.A.

‡Florida Fish and Wildlife Conservation Commission, Fish and Wildlife Research Institute, St. Petersburg, FL, U.S.A.

Abstract: *Increasing evidence suggests that chronic noise from human activities negatively affects wild animals, but most studies have failed to separate the effects of chronic noise from confounding factors, such as habitat fragmentation. We played back recorded continuous and intermittent anthropogenic sounds associated with natural gas drilling and roads at leks of Greater Sage-Grouse (*Centrocercus urophasianus*). For 3 breeding seasons, we monitored sage grouse abundance at leks with and without noise. Peak male attendance (i.e., abundance) at leks experimentally treated with noise from natural gas drilling and roads decreased 29% and 73%, respectively, relative to paired controls. Decreases in abundance at leks treated with noise occurred in the first year of the study and continued throughout the experiment. Noise playback did not have a cumulative effect over time on peak male attendance. There was limited evidence for an effect of noise playback on peak female attendance at leks or male attendance the year after the experiment ended. Our results suggest that sage-grouse avoid leks with anthropogenic noise and that intermittent noise has a greater effect on attendance than continuous noise. Our results highlight the threat of anthropogenic noise to population viability for this and other sensitive species.*

Keywords: chronic noise, energy development, *Centrocercus urophasianus*, roads

Evidencia Experimental de los Efectos de Ruido Antropogénico Crónico sobre la Abundancia de *Centrocercus urophasianus* en Leks

Resumen: *El incremento de evidencias sugiere que el ruido crónico de actividades humanas afecta negativamente a los animales silvestres, pero la mayoría de los estudios no separan los efectos del ruido crónico de los factores de confusión, como la fragmentación del hábitat. Reprodujimos sonidos antropogénicos intermitentes y continuos asociados con la perforación de pozos de gas natural y caminos en leks de *Centrocercus urophasianus*. Durante 3 épocas reproductivas, monitoreamos la abundancia de *C. urophasianus* e leks con y sin ruido. La abundancia máxima de machos (i.e., abundancia) en leks tratados con ruido de la perforación de pozos de gas natural y caminos decreció 29% y 73% respectivamente en relación con los controles pareados. La disminución en abundancia en leks tratados con ruido ocurrió en el primer año del estudio y continuó a lo largo del experimento. La reproducción de ruido no tuvo efecto acumulativo en el tiempo sobre la abundancia máxima de machos. Hubo evidencia limitada para un efecto de la reproducción de ruido sobre la abundancia máxima de hembras en los leks o sobre la asistencia de machos el año después de que concluyó el experimento. Nuestros resultados sugieren que *C. urophasianus* evita leks con ruido antropogénico y que el ruido intermitente tiene un mayor efecto sobre la asistencia que el ruido continuo. Nuestros*

†Address for correspondence: J. Blickley, Department of Evolution and Ecology, 2320 Storer Hall, One Shields Ave, Davis, CA 95616, USA, email jlblickley@ucdavis.edu

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resultados resaltan amenaza del ruido antropogénico para la viabilidad poblacional de esta y otras especies sensibles.

Palabras Clave: *Centrocercus urophasianus*, desarrollo energético, ruido crónico, caminos

Introduction

Noise associated with human activity is widespread and expanding rapidly in aquatic and terrestrial environments, even across areas that are otherwise relatively unaffected by humans, but there is still much to learn about its effects on animals (Barber et al. 2009). Effects of noise on behavior of some marine organisms are well-documented (Richardson 1995). In terrestrial systems, the effects of noise have been studied less, but include behavioral change, physiological stress, and the masking of communication signals and predator sounds (Slabbekoorn & Ripmeester 2008; Barber et al. 2009). These effects of noise on individual animals may lead to population decreases if survival and reproduction of individuals in noisy habitats are lower than survival and reproduction of individuals in similar but quiet habitats (Patricelli & Blickley 2006; Warren et al. 2006; Slabbekoorn & Ripmeester 2008). Population declines may also result if animals avoid noisy areas, which may cause a decrease in the area available for foraging and reproduction.

There is evidence of variation among species in their sensitivity to noise. Noise sensitivity may also differ with the type of noise, which varies in amplitude, frequency, temporal pattern, and duration (Barber et al. 2009). Duration may be particularly critical; most anthropogenic noise is chronic and the effects of chronic noise may differ substantially from those of short-term noise in both severity and response type. For example, brief noise exposure may cause elevated heart rate and a startle response, whereas chronic noise may induce physiological stress and alter social interactions. Therefore, when assessing habitat quality for a given species, it is critical to understand the potential effects of the full spectrum of anthropogenic noise present in the species' range.

The effects of noise on wild animals are difficult to study because noise is typically accompanied by other environmental changes. Infrastructure that produces noise may be associated with fragmentation of land cover, visual disturbance, discharge of chemicals, or increased human activity. Each of these factors may affect the physiology, behavior, and spatial distribution of animals, which increases the difficulty of isolating the effects of the noise.

Controlled studies of noise effects on wild animals in terrestrial systems thus far have focused largely on birds. Recent studies have compared avian species richness, occupancy, and nesting success near natural gas wells oper-

ating with and without noise-producing compressors. In these studies, spatial variation in noise was used to control for confounding visual changes due to infrastructure (Habib et al. 2007; Bayne et al. 2008; Francis et al. 2009). Results of these studies show that continuous noise affects density and occupancy of a range of bird species and leads to decreases or increases in abundance of some species and has no effect on other species (Bayne et al. 2008; Francis et al. 2009; Francis et al. 2011). Results of these studies also show that noise affects demographic processes, such as reproduction, by reducing the pairing or nesting success of individuals (Habib et al. 2007; Francis et al. 2009).

Although these studies in areas near natural gas wells controlled for the effects of most types of disturbance besides noise, they could not address the effect of noise on naïve individuals in areas without natural gas wells and compressors. Furthermore, there have been no controlled experiments that address the effects of chronic but intermittent noise, such as traffic, which may be more difficult for species to habituate. Road noise may have large negative effects because it is widespread (affecting an estimated 20% of the United States) (Forman 2000) and observational studies indicate that noise may contribute to decreases in abundance of many species near roads (e.g., Forman & Deblinger 2000).

Noise playback experiments offer a way to isolate noise effects on populations from effects of other disturbances and to compare directly the effects of noise from different sources. Playback experiments have been used to study short-term behavioral responses to noise, such as effects of noise on calling rate of amphibians (Sun & Narins 2005; Lengagne 2008), heart rate of ungulates (Weisenberger et al. 1996), diving and foraging behavior of cetaceans (Tyack et al. 2011), and song structure of birds (Leonard & Horn 2008), but have not been used to study effects of chronic noise on wild animals because producing long-term noise over extensive areas is challenging. We conducted a playback experiment intended to isolate and quantify the effects of chronic noise on wild animals. We focused on the effects of noise from natural gas drilling on Greater Sage-Grouse (*Centrocercus urophasianus*).

Greater Sage-Grouse occur in the western United States and Canada and have long been a focus of sexual selection studies (Wiley 1973; Gibson 1989; Gibson 1996). Greater Sage-Grouse populations are decreasing in density and number across the species' range, largely due to extensive habitat loss (Connelly et al. 2004; Garton et al. 2010). The species is listed as endangered under Canada's

Species at Risk Act and is a candidate species for listing under the U.S. Endangered Species Act. Deep natural gas and coal-bed methane development have been expanded rapidly across the species' range since 2000 and substantial evidence suggests that these processes may contribute to observed decreases in the number of Greater Sage-Grouse (Holloran 2005; Walker et al. 2007; Holloran et al. 2010). Many factors associated with deep natural gas and coal-bed methane development are thought to lead to these decreases, including habitat loss, increased occurrence of West Nile Virus, and altered fire regimes due to the expansion of nonnative invasive species (Naugle et al. 2004; Walker et al. 2007; Copeland et al. 2009).

The noise created by energy development may also affect sage grouse by disrupting behavior, causing physiological stress, or masking biologically important sounds. During the breeding season (February–May), male sage grouse gather on communal breeding grounds called leks. Male attendance (number of male birds on the lek) at sage grouse leks downwind of deep natural gas development decreases up to 50% per year compared with attendance at other leks, which suggests noise or aerial spread of chemical pollution as factors contributing to these decreases (Holloran 2005).

We sought to test the hypothesis that lek attendance by male and female sage grouse is negatively affected by both chronic intermittent and continuous noise from energy development. To do so, we conducted a noise playback experiment in a population that is relatively unaffected by human activity. Over 3 breeding seasons (late February to early May), we played noise recorded from natural gas drilling rigs and traffic on gas-field access roads at sage grouse leks and compared attendance patterns on these leks to those on nearby control leks.

We conducted our experiment at leks because lekking sage grouse are highly concentrated in a predictable area, which makes them good subjects for a playback experiment. More importantly, sage grouse may be particularly responsive to noise during the breeding season, when energetic demands and predation risk are high (Vehrencamp et al. 1989; Boyko et al. 2004). Additionally, noise may mask sexual communication on the lek. Lekking males produce a complex visual and acoustic display (Supporting Information) and females use the acoustic component of the display to find lekking males and select a mate (Gibson 1989; Gibson 1996; Patricelli & Krakauer 2010). Furthermore, lek attendance is commonly used as a metric of relative abundance of sage grouse at the local and population level (Connelly et al. 2003; Holloran 2005; Walker et al. 2007). We used counts of lek attendance (lek counts) to assess local abundance relative to noise versus control treatments.

Methods

Study Site and Lek Monitoring

Our study area included 16 leks (Table 1 & Supporting Information) on public land in Fremont County, Wyoming, U.S.A. (42° 50', 108° 29'). Dominant vegetation in this region is big sagebrush (*Artemisia tridentata wyomingensis*) with a grass and forb understory. The primary land use is cattle ranching, and there are low levels of recreation and natural gas development.

We paired leks on the basis of similarity in previous male attendance and geographic location (Table 2 & Supporting Information). Within a pair, one lek was

Table 1. Pairing, treatment type, location, and baseline attendance for leks used in noise playback experiment.

Lek	Pair	Pair noise type	Noise or control	Years of playback	Baseline attendance*
Gustin	A	drilling	control	3	26
Preacher Reservoir	A	drilling	noise	3	49
North Sand Gulch	B	road	control	3	32
Lander Valley	B	road	noise	3	67
East Twin Creek	C	drilling	control	3	44
Coal Mine Gulch	C	drilling	noise	3	83
East Carr Springs	D	road	control	3	67
Carr Springs	D	road	noise	3	92
Powerline	E	drilling	control	2	49
Conant Creek North Monument	E	drilling	noise	2	44
Government Slide Draw	F	road	control	2	53
Nebo	F	road	noise	2	55
Nebo	G	drilling	control	2	18
Arrowhead West	G	drilling	noise	2	24
Onion Flats 1	H	road	control	2	41
Ballenger Draw	H	road	noise	2	38

*Baseline attendance is the average peak male attendance value (annual maximum number of males observed averaged across years) for that lek from 2002 to 2005.

Table 2. Mixed-effect candidate models used to assess change in peak attendance of male Greater Sage-Grouse at leks from pre-experiment baseline attendance during the natural gas drilling noise playback (2006–2008) and after the experiment (2009).

Model (year) ^a	K ^b	ΔAIC_c ^c	w _i ^d
Male experiment (2006–2008)			
treatment×type+season ^e	9	0	0.64
treatment×type ^e	7	1.8	0.26
treatment+experiment year	6	6.1	0.03
treatment+season	7	6.8	0.02
treatment	5	7.3	0.02
treatment×experiment year	7	8.0	0.01
treatment×type+treatment×season+experiment year	12	8.6	< 0.01
treatment×type+treatment×season	11	9.9	< 0.01
treatment×type+treatment×season+treatment×experiment year	13	10.0	< 0.01
treatment+type	6	10.4	< 0.01
treatment×season	9	16.2	< 0.01
null- random effects only	4	57.0	< 0.01
Male after experiment (2009)			
null, random effects only ^e	3	0.0	0.84
treatment	4	3.3	0.16

^aAll models contain pair as a random effect, and experiment (2006–2008) models also include year as a random effect. Covariates: treatment, lek treatment (noise or control) assigned to individual leks within a pair; type, pair noise treatment type (road or drilling assigned to pair); season, time of year (early [late February to 1 week prior to peak female attendance for that lek; female peak ranged from 15 March to 6 April], mid [1 week before and after female peak], and late [starting 1 week after female peak]); experiment year, years of experimental noise exposure.

^bNumber of parameters in the model.

^cDifference in AIC_c (Akaike's information criterion for small sample size) values from the model with lowest AIC_c .

^dAkaike weight.

^eModel with substantial support ($\Delta AIC_c < 2$).

randomly assigned to receive experimental noise treatment and the other lek was designated a control. We randomly assigned the experimental leks to receive playback of either drilling or road noise. In 2006, we counted attendance at 8 leks (2 treated with drilling noise, 2 treated with road noise, and 4 control). In both 2007 and 2008, we included an additional 8 leks for a total of 16 leks (4 treated with drilling noise, 4 treated with road noise, and 8 controls).

Throughout the breeding season, we counted males and females on leks with a spotting scope from a nearby point selected to maximize our visibility of the lek. We visited paired leks sequentially on the same days between 05:00 and 09:00, alternating the order in which each member of the pair was visited. We visited lek pairs every day during the breeding season in 2006 and, after expanding our sample size in 2007, every 2–4 days in 2007 and 2008. Peak estimates of male attendance from >4 visits are a highly repeatable measure of abundance at individual leks (Garton et al. 2010), so the lower frequency of visits in 2007 and 2008 was unlikely to have a substantial effect on estimates of peak male attendance. At a minimum, we conducted 2 counts per visit at 10- to 15-min intervals. The annual peak attendance was the highest daily attendance value at each lek for the season for males or females. For males we also calculated the peak attendance in 3 nonoverlapping date ranges: early (late February to 1 week prior to peak female attendance for that lek; female peak ranged from 15 March to

6 April), mid (1 week before and after female peak), and late (starting 1 week after female peak).

Noise Introduction

We recorded noise used for playback near natural gas drilling sites and gas-field access roads in a region of extensive deep natural gas development in Sublette County, Wyoming (Pinedale Anticline Gas Field and Jonah Gas Field). We recorded drilling noise in 2006 within 50 m of the source on a digital recorder (model PMD670, 44.1 kHz/16 bit; Marantz, Mahwah, New Jersey) with a shotgun microphone (model K6 with an ME60 capsule; Sennheiser, Old Lyme, Connecticut). We recorded road noise in 2005 with a handheld computer (iPAQ h5550 Pocket PC, 44.1 KHz/16 bit; Hewlett Packard, Palo Alto, California) and omnidirectional microphone (model K6 with an ME62 capsule; Sennheiser). Drilling noise is relatively continuous and road noise is intermittent (Supporting Information). Both types of noise are predominantly low frequency (<2 kHz).

We played noise on experimental leks from 2 to 4 rock-shaped outdoor speakers (300 W Outdoor Rock Speakers; TIC Corporation, City of Industry, California) hooked to a car amplifier (Xtant1.1; Xtant Technologies, Phoenix, Arizona) and an MP3 player (Sansa m240; SanDisk, Milpitas, California). The playback system was powered with 12 V batteries that we changed every 1–3 days when no birds were present. We placed the speakers

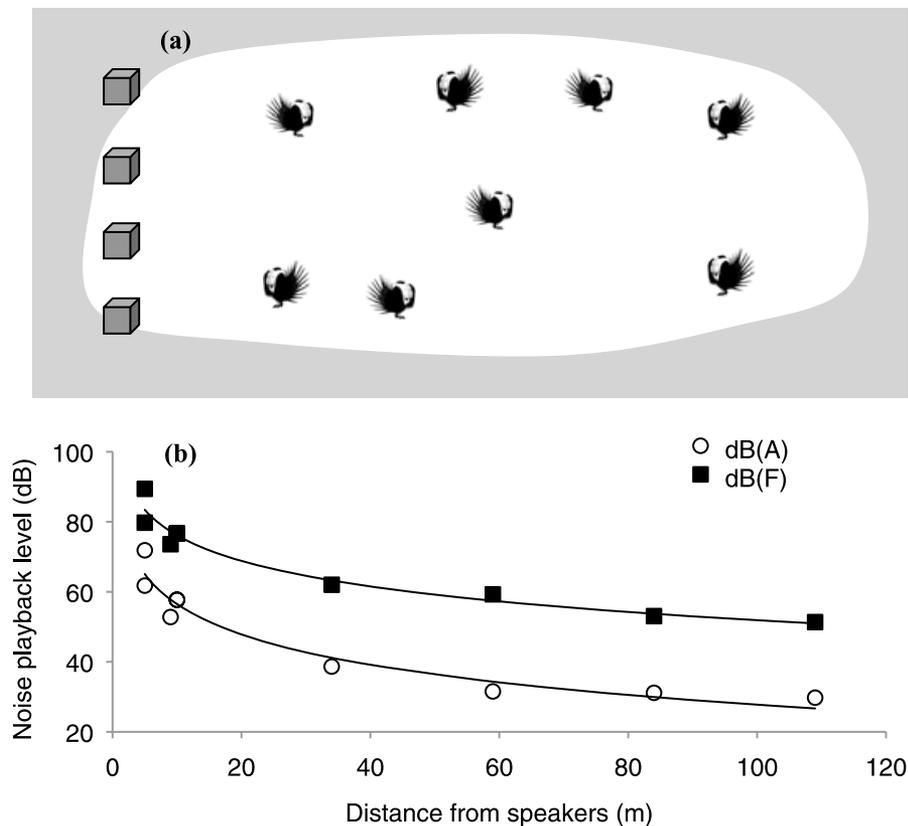


Figure 1. (a) Placement of speakers (on noise-treated leks) or dummy speakers (on control leks) (boxes) at Greater Sage-Grouse leks. (b) Mean maximum noise level (unweighted decibels, dB[F], and A-weighted decibels, dB[A], measured in L_{max} [highest root-mean-square sound pressure level within the measurement period]) at Greater Sage-Grouse leks measured on transects at 25-m intervals from the line of speakers on a typical lek treated with road noise. Playback levels of natural gas drilling noise (measured in L_{eq}) followed the same pattern. Ambient levels of noise at control leks ranged from 30 to 35 dB(A).

in a straight line across one end of the lek (Fig. 1a). In 2006 we placed 3 speakers at leks treated with drilling noise and 2 speakers at leks treated with road noise. In 2007 and 2008, we increased the number of speakers, placing 4 at each noise-treated lek to increase the area in which noise was present on the lek. At control leks, we placed dummy speakers of similar size and color to playback speakers (68-L plastic tubs). Within each lek pair, dummy and real speakers were placed in similar configurations. To control for playback-related disturbance, the leks in each pair were visited an equal number of times during the morning for counts of birds and in the afternoon for battery changes.

We played drilling noise and road noise on leks at 70 dB(F) sound pressure level (unweighted decibels) measured 16 m directly in front of the speakers (Fig. 1 & Supporting Information). This is similar to noise levels measured approximately 400 m from drilling rigs and main access roads in Pinedale (J. L. Blickley and G. L. Patricelli, unpublished data). Four hundred meters (0.25 miles) is the minimum surface disturbance buffer around leks at this location (BLM 2008). We calibrated and measured noise playback levels with a hand-held meter that provides sound-pressure levels (System 824; Larson-Davis, Depew, New York) when wind was <9.65 k/h. On drilling-noise-treated leks, where noise was continuous, we calibrated the noise playback level by measuring the average sound level (L_{eq} [equivalent continuous sound

level]) over 30 s. On leks treated with road noise, where the amplitude of the noise varied during playback to simulate the passing of vehicles, we calibrated the playback level by measuring the maximum sound level (L_{max} [highest root-mean-square sound pressure level within the measurement period]).

For leks treated with drilling noise, recordings from 3 drilling sites were spliced into a 13-min mp3 file that played on continuous repeat. On leks treated with road noise, we randomly interspersed mp3 recordings of 56 semitrailers and 61 light trucks with 170 thirty-second silent files to simulate average levels of traffic on an access road (Holloran 2005). Noise playback on experimental leks continued throughout April in 2006, from mid February or early March through late April in 2007, and from late February through late April in 2008. We played back noise on leks 24 hours/day because noise from deep natural gas drilling and vehicular traffic is present at all times. This experimental protocol was reviewed and approved by the Animal Care and Use Committee at University of California, Davis (protocol 16435).

To measure noise levels across experimental leks, we measured the average amplitude (15 s L_{eq}) of white-noise played at 1–5 points along transects that extended across the lek at 25-m intervals roughly parallel to the line of speakers. We calibrated white-noise measurements by measuring the noise level of both the white noise and either a representative clip of drilling noise or a semitrailer

10 m directly in front of each speaker. To minimize disturbance, we took propagation measurements during the day. Daytime ambient noise levels are typically 5–10 dBA higher than those in the early morning (J. L. Blickley and G. L. Patricelli, unpublished data) and are likely higher than those heard by birds at a lek.

After the experiment, we counted individuals on all leks 2–6 times from 1 March through 30 April 2009. In 2009 we continued to play noise on 2 experimental leks as part of a related experiment, so we did not include these lek pairs in our analysis of postexperiment male attendance at a lek.

Response Variables and Baseline Attendance Levels

Sage grouse leks are highly variable in size and, even within pairs, our leks varied up to 50% in size. To facilitate comparison of changes in attendance on leks of different sizes, we calculated the attendance relative to attendance levels before treatment (i.e., baseline attendance levels). We obtained male baseline abundance from the Wyoming Game and Fish Department. We used the standard lek-count protocol (Connelly et al. 2003) to count birds at leks approximately 3 times/breeding season. Due to the small number of counts in pre-experiment years, we calculated male baseline attendance by averaging the annual peak male attendance at each individual lek over 4 years (2002–2005). We assessed changes in early-, mid-, and late-season peak male attendance from this 4-year baseline attendance. Female attendance was highly variable throughout the season with a short (1–3 day) peak in attendance at each lek. Due to the limited number of annual counts, female counts from 2002 to 2005 were not reliable estimates of peak female attendance and could not be used as baseline attendance levels. Because we introduced noise to experimental leks after the peak in female attendance in 2006, we used maximum female counts from 2006 as a baseline for each of the 8 leks monitored that year. We assessed changes in annual peak female attendance from this 1-year baseline attendance. The 8 leks added to the experiment in 2007 were not included in statistical analyses of female attendance due to the lack of a baseline.

Statistical Analyses

We used an information-theoretic approach to evaluate the support for alternative candidate models (Table 2). All candidate models were linear mixed-effect models that assessed the relation between covariates and the proportional difference in annual and within-season peak attendance and baseline attendance (both males and female) (Tables 2 & 3). We ranked models on the basis of differences in Akaike's information criterion for small sample sizes (ΔAIC_c) (Burnham & Anderson 2002). Akaike weights (w_i) were computed for each model on the basis of ΔAIC_c scores. We calculated model-averaged variable

Table 3. Mixed-effect candidate models used to assess change in peak annual attendance of female Greater Sage-Grouse at leks from pre-experiment baseline attendance in 2006 during noise playback.

Model ^a	K ^b	ΔAIC_c ^c	w_i ^d
Null, random effects only ^e	4	0	0.71
Treatment ^e	5	1.9	0.27
Treatment+experiment year	6	8	0.01
Treatment×experiment year	7	14	<0.001

^aAll models contained pair and year as random effects. Due to the small sample size (4 pairs), pair type variable (road versus drilling) was not included in the model set. Covariates: treatment, lek treatment (noise or control assigned to individual leks within a pair); experiment year, years of experimental noise exposure.

^bNumber of parameters in the model.

^cDifference in AIC_c (Akaike's information criterion for small sample size) values from the most strongly supported (lowest AIC_c) model.

^dAkaike weight.

^eModel with substantial support ($\Delta AIC_c < 2$).

coefficients, unconditional 95% CI, and variable importance (weight across models) for variables contained in models that were strongly supported ($\Delta AIC_c < 2$). All statistical analyses were performed in R (version 2.12.1) (R Development Team 2010).

The detection probability for males and females is likely to vary across a season and among leks (Walsh et al. 2004). We sought to minimize sources of error and maximize detection by conducting frequent counts from locations with a clear view of the lek and by implementing a paired treatment design (each noise lek is compared with a similar control lek, monitored by the same observer on the same days). To ensure that detection probability did not differ among noise and control leks, we corrected our data for detection probability. First, we used detection error rates, estimated as difference between the maximum count and the count immediately before or after the maximum count within a day (for both males and females), and then we applied the bounded-count method (for males only; Walsh et al. 2004). With the multiple-count estimator, estimates of detection between noise and control leks did not differ (males: $t = 1.02$, $df = 6$, $p = 0.35$; females: $t = 0.21$, $df = 3$, $p = 0.84$). We analyzed both corrected and uncorrected counts and found that neither correction qualitatively changed our results; therefore, results are presented for uncorrected counts.

Results

Male Attendance

Peak male attendance at both types of noise leks decreased more than attendance at paired control leks, but the decreases varied by noise type. In the most strongly supported models of the candidate set ($w_i = 0.90$, all

Table 4. Model-averaged parameter direction and effect sizes and variable importance for all variables present in strongly supported models ($\Delta AIC_c < 2$ in Table 2) of changes in peak attendance of male greater sage-grouse at leks from baseline attendance during experimental noise playback.

Variable	Percent effect size (SE)	Variable importance*
Intercept	31 (22)	1.0
Treatment, noise	-29 (7)	0.91
Type, road	33 (22)	0.91
Treatment, noise*type, road	-40 (10)	0.91
Season, mid	18 (6)	0.66
Season, late	23 (6)	

*Variable importance is the summed weight of all models containing that variable.

other models $\Delta AIC_c > 6.1$) (Table 2), there was an interaction of the effects of experimental treatment (control versus noise) and noise type (drilling versus road) on annual peak male attendance. At leks treated with road noise, decreases in annual peak male attendance were greater (73%), relative to paired controls, than at drilling noise leks (29%). As indicated by the effect size for the main effect of pair type, attendance at control leks paired with road noise leks was 33% greater relative to the baseline than control leks paired with drilling noise leks (Table 4). However, changes in attendance were compared within a pair to control for such differences. Male attendance increased over the course of a season, with 18% and 23% increases in peak male attendance in mid and late season from the early-season peaks, but seasonal increases were similar across noise and control leks (Table 4 & Fig. 2b).

There was no evidence that the effect of noise on attendance changed as years of exposure to noise increased. The models with substantial support did not contain a main effect of years of exposure or an interaction of years of exposure and treatment type (control versus noise) (Table 2). In spite of decreases in attendance throughout the experiment, peak male attendance exceeded baseline attendance on all leks in 2006, 13 leks in 2007, and 11 leks in 2008 (Table 4 & Fig. 2c). There was an increase in sage grouse abundance regionally in 2006 (Fig. 3).

After the experiment (2009), attendance at leks we experimentally exposed to drilling and road noise was lower relative to paired controls (Table 2). The model that included the treatment variable showed an effect size of -30% (across road and drilling noise leks) but had only moderate support ($\Delta AIC_c = 3.3$) relative to the null model.

Female Attendance

Peak female attendance at leks treated with noise in 2007 and 2008 decreased from the 2006 baseline, relative to control leks (Table 3). The most strongly sup-

ported model in the set was the null model; however, the model that included noise treatment was highly supported ($\Delta AIC_c < 2$). The effect size of noise treatment on female attendance was -48% (10% SE), which is similar to the effect of noise on male attendance averaged across both noise types (51%).

Discussion

Results of previous studies show abundance of Greater Sage-Grouse decreases when natural gas and coal-bed methane fields are developed (Holloran 2005; Walker et al. 2007; Doherty et al. 2008). Our results suggest that chronic noise may contribute to these decreases. Peak male attendance relative to the baseline was lower on noise leks than paired control leks, and the decrease was larger at road noise leks (73% decrease in abundance compared with paired controls) than drilling noise leks (29%; Fig. 3). These decreases were immediate and sustained. The effects of noise occurred in the first year of the study and were observed throughout the experiment, although patterns of male attendance within a season were similar at noise and control leks. Differences in male attendance between noise and control leks in the year after the experiment were not supported in the top models, which suggests attendance rebounded after noise ceased. However, the sample size for this analysis was small, and the effect size (30% average decreases in male attendance for both noise types) suggests a residual effect of noise.

There are 2 mechanisms by which noise may reduce male attendance. First, males on noise leks may have had higher mortality than males on control leks. Noise playback was not loud enough to cause direct injury to individuals, but mortality could be increased indirectly by noise playback if the sounds of predators (coyotes [*Canis latrans*] or Golden Eagles [*Aquila chrysaetos*]) were masked by noise. However, on-lek predation events were rare. We observed ≤ 1 predation event per lek per season during the experiment (observations of sage-grouse carcasses or feathers at a lek [J. L. Blickley, personal observation]). The cumulative effect of rare predation events would lead to a gradual decrease in attendance, rather than the rapid and sustained decrease we observed. Furthermore, experimental noise was likely too localized to substantially affect off-lek predation because noise levels decreased exponentially as distance to the speakers increased (Fig. 1b). To date, increased predation risk of adults due to anthropogenic noise has not been demonstrated in any species, but some species increase vigilance when exposed to noise, leaving less time for feeding, displaying, and other important behaviors (Quinn et al. 2006; Rabin et al. 2006). Noise may also affect off-lek mortality indirectly. For example, noise-stressed males may be more susceptible to disease due to a suppressed

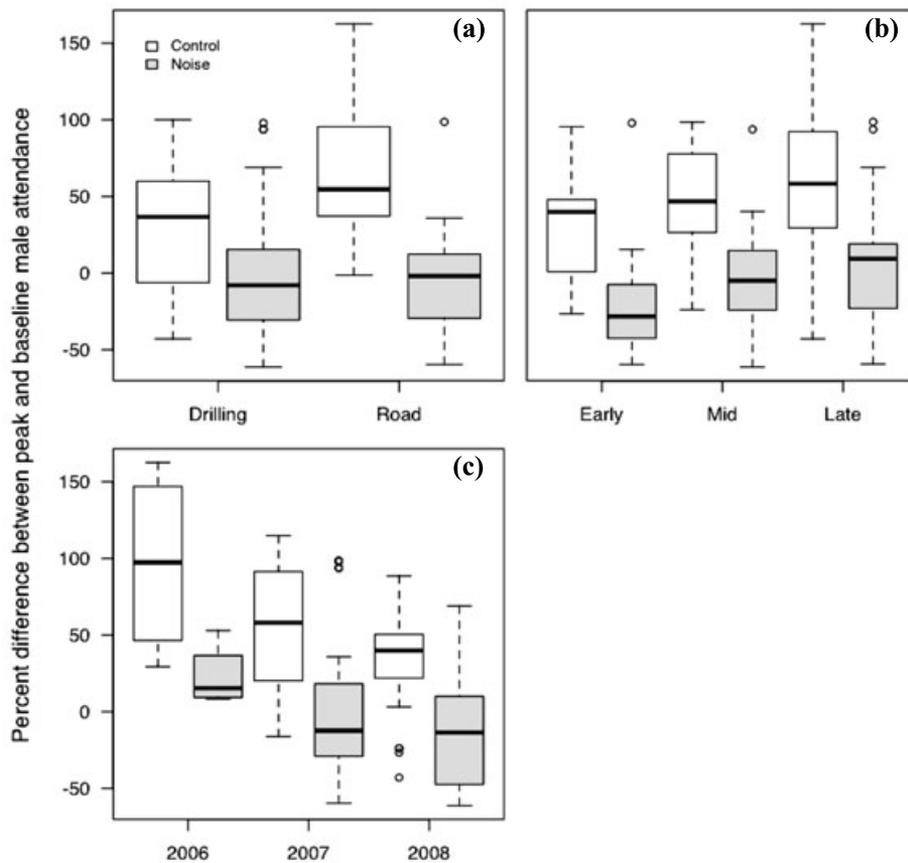


Figure 2. Percent difference between baseline attendance (i.e., abundance before experiments) of male Greater Sage-Grouse and (a) peak male attendance on control leks and leks treated with noise from natural gas drilling and road noise, (b) peak male attendance in the early (late February to 1 week prior to peak female attendance for that lek), mid (1 week before and after female peak [female peak ranged from 15 March to 6 April]), and late (starting 1 week after female peak) breeding season; on control leks and leks treated with noise, and (c) peak male attendance at control leks and leks treated with noise in experimental years 2006, 2007, and 2008 in Fremont County, Wyoming (U.S.A.) (horizontal lines, median value; box ends, upper and lower quartiles, whiskers, maximum and minimum values). Data are observed values, not model output.

immune response (Jankowski et al. 2010). Although long-term stress from noise is unlikely to be the primary cause of the rapid decreases in attendance we observed here, it may have been a contributing factor over the course of the experiment. Furthermore, in areas of dense industrial development, where noise is widespread, noise effects on mortality may be more likely.

Alternatively, noise may lower male attendance through displacement, which would occur if adult or juvenile males avoid leks with anthropogenic noise. Such behavioral shifts are consistent with the rapid decreases in attendance we observed. Adult male sage grouse typically exhibit high lek fidelity (Schroeder & Robb 2003) and visit leks regularly throughout the season, whereas juvenile males visit multiple leks and their attendance peaks late in the season (Kaiser 2006). If juveniles or adults avoid noise by visiting noisy leks less frequently

or moving to quieter leks, overall attendance on noisy leks could be reduced. We could not reliably differentiate between juveniles and adults, so we do not know the relative proportion of adults and juveniles observed. Consistent with displacement due to noise avoidance, radio-collared juvenile males avoid leks near deep natural gas developments in Pinedale, Wyoming, which has resulted in decreases in attendance at leks in close proximity to development and increased attendance at nearby leks with less human activity (Kaiser 2006; Holloran et al. 2010). Reduced recruitment of juvenile males is unlikely to be the only driver of the patterns we observed because we did not observe larger decreases in lek attendance on noise-treated leks later in the season, when juvenile attendance peaks. Rather, we found immediate decreases in attendance early in the season when playback began (Fig. 2b), at which time there are few juveniles on the lek. This

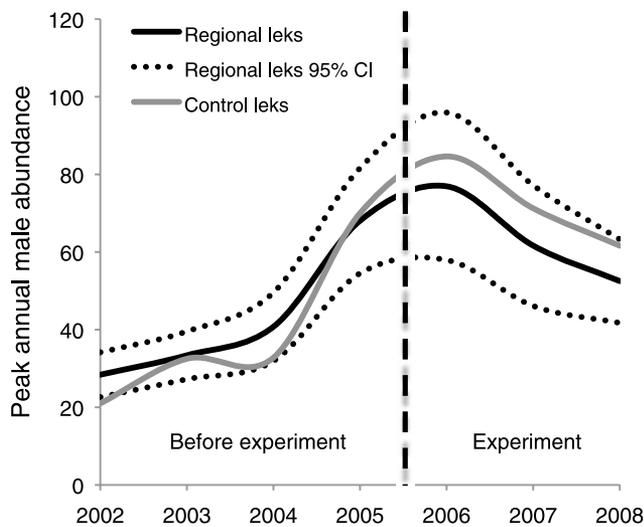


Figure 3. Maximum abundance of male Greater Sage-Grouse from 2002 to 2008 at control leks ($n = 8$) (no anthropogenic sound played) and other leks in the region that were not part of the experiment (regional leks) ($n = 38$).

is consistent with both adult and juvenile noise avoidance. We did not find evidence for a cumulative negative effect of noise on lek attendance, although cumulative effects may have been masked by regional population declines after 2006, a year of unusually high abundance (Fig. 3).

Female attendance at leks treated with noise was lower than that on control leks; however, the null model and the model that included noise treatment were both highly supported, providing only moderate support for the effects on noise on attendance. For this model, the overall estimated effect of noise on female attendance (-48%) was similar to that of the effect of noise on male attendance. Due to the high variability of female daily maximum attendance throughout the season and small sample size for this analysis (female attendance data available for only 4 of the 8 lek pairs), our statistical power to detect differences in female attendance was limited and effect sizes may not be representative of actual noise effects.

Our results suggest that males and possibly females avoid leks exposed to anthropogenic noise. A potential cause of avoidance is the masking of communication. Masked communication is hypothesized to cause decreases in abundance of some animal species in urban and other noisy areas. For example, bird species with low-frequency vocalizations are more likely to have low abundance or be absent from natural gas developments, roads, and urban areas than species with high-frequency vocalizations, which suggests that masking is the mechanism associated with differences in abundance (Rheindt 2003; Francis et al. 2009; Hu & Cardoso 2010). Sage-grouse may

be particularly vulnerable to masked communication because their low-frequency vocalizations are likely to be masked by most sources of anthropogenic noise, including the noises we played in our experiment (Supporting Information). This may be particularly important for females if they cannot use acoustic cues to find leks or assess displaying males in noisy areas.

Alternatively, individuals may avoid noisy sites if noise is annoying or stressful, particularly if this noise is associated with danger (Wright et al. 2007). Intermittent road noise was associated with lower relative lek attendance than continuous drilling noise, in spite of the overall higher mean noise levels and greater masking potential at leks treated with drilling noise (Supporting Information). Due to the presence of roads in our study area, sage grouse may have associated road noise with potentially dangerous vehicular traffic and thus avoided traffic-noise leks more than drilling-noise leks. Alternatively, the pattern of decrease may indicate that an irregular noise is more disturbing to sage grouse than a relatively continuous noise. Regardless, our results suggest that average noise level alone is not a good predictor of the effects of noise (Slabbekoorn & Ripmeester 2008) and that species can respond differently to different types of noise.

Our results cannot be used to estimate the quantitative contribution of noise alone to observed decreases in Greater Sage-Grouse abundance at energy development sites because our experimental design may have led us to underestimate or overestimate the magnitude of these effects. Decreases in abundance due to noise could be overestimated in our study if adults and juveniles are displaced from noise leks and move to nearby control leks, which would have increased the difference in abundance between paired leks. Similar displacement occurs in areas of energy development, but over a much larger extent than is likely to have occurred in response to localized playbacks in our experiment (Holloran et al. 2010).

In contrast, we could have underestimated noise effects if there were synergistic effects of noise and other disturbances associated with energy development. For example, birds with increased stress levels due to poor forage quality may have lower tolerance for noise-induced stress, or vice versa. Noise in our experiment was localized to the immediate lek area and only played during the breeding season, so we cannot quantify the effects of noise on wintering, nesting, or foraging birds. Noise at energy development sites is less seasonal and more widespread than noise introduced in this study and may thus affect birds at all life stages and have a potentially greater effect on lek attendance. Leks do not represent discrete populations; therefore, local decreases in lek attendance do not necessarily reflect population-level decreases in abundance. However, at large energy development sites, similar displacement of Greater Sage-Grouse away from the ubiquitous noise may result in population-level declines due to spatially exten-

sive changes in land use or increases in dispersal-related and density-dependent sources of mortality (Aldridge & Boyce 2007). Enforcement and refinement of existing seasonal restrictions on human activity could potentially reduce these effects.

We focused on the effect of noise associated with deep natural gas and coal-bed methane development on sage grouse, but our results may increase broader understanding of the effects of noise on animals. Both intermittent and constant noise from energy development affected sage grouse. Other noise sources with similar frequency range and temporal pattern, such as wind turbines, oil-drilling rigs, and mines, may have comparable effects. Similar effects may also be associated with highways, off-road vehicles, and urbanization so that the potential for noise to have an effect is large.

We believe that noise should be investigated as one potential cause of population declines in other lekking North American grouse species that are exposed to similar anthropogenic development. Populations of many bird (van der Zande et al. 1980; Rheindt 2003; Ingelfinger & Anderson 2004) and mammal (Forman & Deblinger 2000; Sawyer et al. 2009) species have been shown to decrease in abundance in response to road, urban, and energy development, and noise produced by these activities may contribute to these decreases. Our results also demonstrate that wild animals may respond differently to chronic intermittent and continuous noise, a comparison that should be expanded to other species. Additionally, we think these results highlight that experimental noise playbacks may be useful in assessing the response of wild animals to chronic noise (Blickley & Patricelli 2010).

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Supporting Information

Spectrograms and power spectrums of drilling noise, road noise and male sage-grouse vocal display (Appendix S1), map of experimental and control leks (Appendix S2), and noise playback levels on experimental leks (Appendix S3) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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A preliminary report of amphibian mortality patterns on railways

KAROLINA A. BUDZIK¹, KRYSZTOF M. BUDZIK²

¹ Department of Comparative Anatomy, Institute of Zoology, Jagiellonian University Gronostajowa 9, 30-387 Kraków, Poland. Corresponding author. E-mail: coffee8b@gmail.com

² Institute of Botany, Jagiellonian University Kopernika 27, 31-501 Kraków, Poland

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Abstract. In contrast to road mortality, little is known about amphibian railroad mortality. The aim of this study was to quantify amphibian mortality along a railway line as well as to investigate the relationship between the availability of breeding sites in the surrounding habitats and the monthly variation of amphibian railway mortality. The study was conducted from April to July 2011 along 45 km of the railway line Kraków - Tarnów (Poland, Małopolska province). Three species were affected by railway mortality: *Bufo bufo*, *Rana temporaria* and *Pelophylax kl. esculentus*. Most dead individuals (77%) were adult common toads. The largest number (14) of amphibian breeding sites was located in the most heterogeneous habitats (woodland and rural areas), which coincides with the sectors of highest amphibian mortality (42% of all accidents). As in the case of roads, spring migration is the period of highest amphibian mortality (87% of all accidents) on railroads. Our findings suggest that railroad mortality depends on the agility of the species, associated primarily with the ability to overcome the rails.

Keywords. Habitat effect, seasonality effect, common toad, Poland.

One of the main consequences of urbanization is the construction of new communication

networks, e.g. linear infrastructures such as roads and railways. Roads are physical barriers to animal migration, which may have negative consequences both in terms of animal mortality and habitat fragmentation (Andrews and Gibbons, 2005) and, in turn, may lead to isolation of populations through reduced movement and gene flow (Gibbs, 1998; St. Clair, 2003). Among vertebrates, amphibians are the most affected by these threats (Stuart et al., 2004). Their requirement of aquatic habitats and reproduction-dependent seasonal migrations make them particularly vulnerable to the negative impact of road traffic (Hels and Buchwald, 2001; Hamer and McDonnell, 2008). Apart from roads, railways may also act as migratory barriers and thus negatively affect amphibian populations (Berthoud and Antoniazza, 1998; Ray et al., 2002). To date, the impact of railways on amphibians has not been established and, in contrast to the issue of amphibian road mortality (Carr and Fahrig,

2001; Mazerolle, 2004; Sirello, 2008; Sutherland et al., 2010), data on amphibian mortality due to the presence of railways are very scarce (Berthoud and Antoniazza, 1998; Vos et al., 2001; Reshetylo and Briggs, 2010). The aim of this study was to quantify amphibian mortality along a railway line and to investigate the effect of the surrounding habitat and the seasonal variation of railway mortality of amphibians. The study was conducted along 45 km of the line Podłęże - Biadoliny (direction Kraków - Tarnów, southern Poland) (Fig. 1). The railroad is constituted by two rail lines that split into several others where large stations occur. The track spacing is 1.435 m wide, and the height of the rail profile is 0.172 m. The substrate of the tracks is made of stones. The average daily number of trains running on this route in both directions is about 60. The trains run between 3:00 am and 23:00 pm. The average frequency of trains is 2-3 trains / h, increasing up to 3-4 trains / h from 14:00 to 20:00 (due to a lack of data, freight trains were not included). The study site included highly urbanized and agricultural

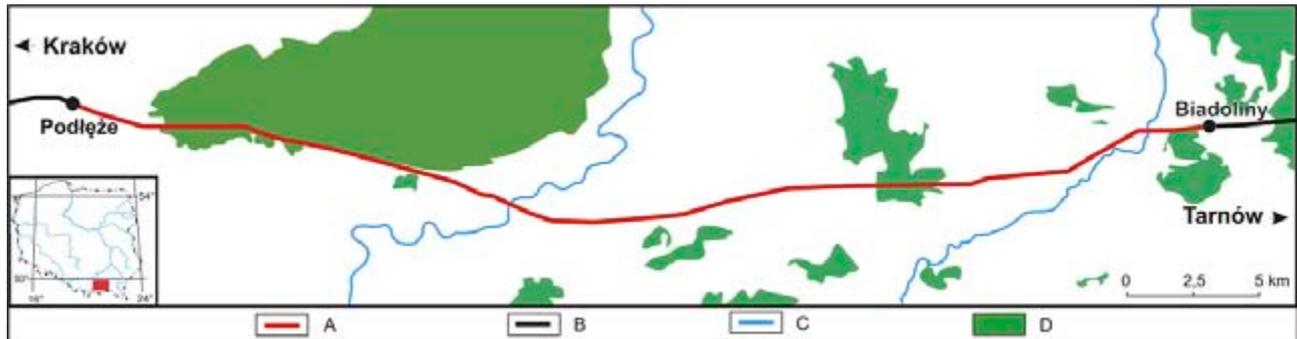


Fig. 1. Location of the surveyed transect in Poland. Legend: A - surveyed transect of railway line, B - further railway line, C - rivers, D - forests.

areas, grasslands and forests. Numerous ditches, oxbows and wetlands, as well as some larger water bodies, such as fish ponds, occur near the railway line and constitute potential breeding habitat for amphibians. The stretch was divided into 30 transects associated with different types of habitat. Five types of transects were established: 'woodland' transects with woodland on both sides of the railroad (six transects; total length: 11.35 km), 'woodland and rural areas' transects with woodland on one side of the railroad and rural areas on the other side (four transects; total length: 6.16 km), 'rural areas' transects with rural areas on both sides of the railroad (10 transects; total length: 14.74 km), 'open areas' transects with open, natural areas (eight transects; total length: 9.8 km) and 'urban areas' transects (two transects; total length: 3.25 km). The study was conducted from April to July 2011. In April and May each transect was monitored twice a month, while in June and July, once a month. All transects were surveyed on foot. The duration of each survey was 1 to 3 hours. The surveys were conducted from the morning until the evening (often three or four transects a day), usually in sunny and dry weather. All findings of dead amphibians were georeferenced, photographed, and information on amphibian species and age (juvenile or adult) were taken. This detailed information ensured that we avoided recounting of dead individuals, even though we did not remove dead amphibians from the rails. Additionally, the presence of dead reptiles was registered. A buffer zone of about 150 m on both sides of the railway was monitored for the presence of amphibians and potential reproductive sites at the same time as the railway mortality surveys. The inspections consisted of searching through all ditches, pools, puddles and water bodies, their edges and vicinities. The water reservoirs were also dipnetted. All individuals were released after identification in the field. The determination of amphibian presence was based on direct observations of adults

and juveniles, as well as on observations of spawn, larvae and male mating calls. All observed green frogs were classified as *Pelophylax* kl. *esculentus*. Chi square tests were used to assess differences in railroad mortality depending on habitat type and month. Additionally, differences in number of breeding sites in different habitat types were assessed. The analysis included only breeding sites of species affected by railroad mortality. Then, differences between pairs of habitat types in respect to railroad mortality and breeding site abundance were tested. Spearman's correlation was used to measure the association between the number of dead specimens found on the railroad for each species with the number of reproductive sites found in the buffer zone.

Within the study area we found the following species (the number of breeding sites is given in parentheses): the agile frog *Rana dalmatina* (23 sites), the common frog *R. temporaria* (7 sites), the moor frog *R. arvalis* (1 site), the green frogs *Pelophylax* kl. *esculentus* (43 sites), the European tree frog *Hyla arborea* (1 site), the fire-bellied toad *Bombina bombina* (10 sites), the common toad *Bufo bufo* (5 sites), the great crested newt *Triturus cristatus* (4 sites), and the smooth newt *Lissotriton vulgaris* (1 site). A total of 62 dead individuals of three species (*B. bufo*, *R. temporaria* and *P. kl. esculentus*) were found within the area of the railway tracks. Seven frog specimens were not identified. Most dead amphibians were adult common toads (77%), and a large proportion of dead frogs (73%) were juveniles. The transect differed in terms of amphibian mortality ($\chi^2 = 54.4$, $df = 4$, p -value < 0.001): the majority of the amphibian mortality occurred in woodland and rural areas (Fig. 2, Table 1). The buffer zone areas (habitat types) varied in terms of amphibian breeding site abundance ($\chi^2 = 10.8$, $df = 4$, p -value < 0.05). Most of the breeding sites (of amphibians affected by railroad mortality) were located in the 'woodland and rural areas' type (Table 2). The number of dead speci-

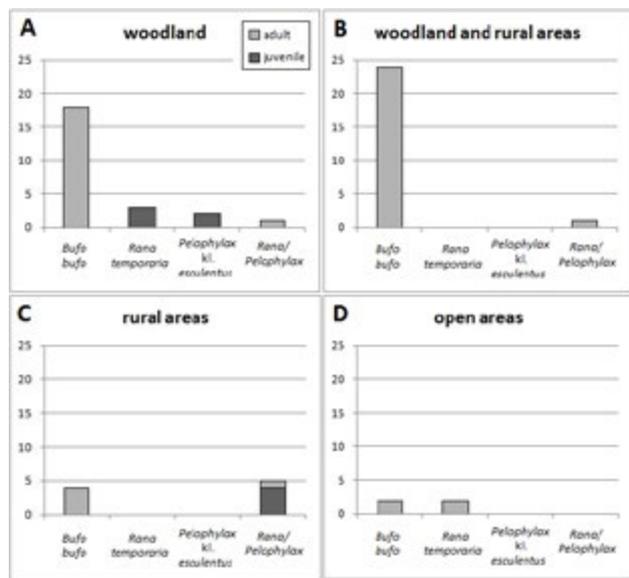


Fig. 2. Number of dead individuals (including their age) found in different types of habitat: woodland (A), woodland and rural areas (B), rural areas (C) and open areas (D).

mens and the number of reproductive sites occurring in the habitat types was not significantly correlated for any of the species. However, this association is present if all dead frogs (*Rana temporaria*, *Pelophylax kl. esculentus* and unspecified *Rana/Pelophylax*) are taken together ($R = 0.436$, p -value < 0.05). There is also a significant relationship between dead *B. bufo* and breeding sites abundance ($R = 0.458$, p -value < 0.001), if three breeding sites situated outside the buffer zone (up to 1.3 km in a straight line

from the tracks) (Budzik K. M., pers. inf.) are taken into account. The majority of dead amphibians were found at the beginning of the reproductive season ($\chi^2 = 128.2$, $df = 3$, p -value < 0.001 ; Fig. 3). Most dead amphibians found in April were spatially clustered, while in the following months the specimens were scattered. Many of the toads (58%) were found within the railroad tracks and their remains were fragmented. The remaining individuals, as well as other dead amphibians, were not mechanically damaged. All dead frogs were found outside of the railroad track. Additionally, in May we found one road-killed fire-bellied toad under one of the rail viaducts. We found six dead grass snakes (*Natrix natrix*), one of which was found near a dead common toad (Fig. 4).

To our knowledge, this study - despite being largely exploratory - reports the first empirical data on amphibian railway mortality. Our results show that railway mortality is a real threat for amphibians, an issue that requires deeper evaluation for conservation planning. The amphibians found in the study area are common in this region of Poland (Głowaciński and Rafiński, 2003). Furthermore, two of the three species affected by railroad mortality (*B. bufo*, *R. temporaria*), are among the most common European amphibians, for which there is evidence of great road-mortality (Orłowski, 2007; Bonardi et al., 2011; Matos et al., 2012). The high number of amphibians killed along woodland and rural areas is likely associated with the abundance of breeding sites in these types of habitats. However, the results predominantly relate to the common toad, therefore they are highly conditioned by this species, which typically inhabits heterogeneous habitats (Pavignano et al., 1990).

Table 1. Chi-square test comparing the railroad mortality between each pair of habitat types. “-” refers to low expected frequencies, test is not applicable.

	Woodland	Woodland and Rural	Rural	Open
Woodland and Rural	$\chi^2 = 5.4$, $df=1$, $p < 0.05$			
Rural	$\chi^2 = 11.5$, $df=1$, $p < 0.001$	$\chi^2 = 31.7$, $df=1$, $p < 0.001$		
Open	$\chi^2 = 11.5$, $df=1$, $p < 0.001$	$\chi^2 = 27.7$, $df=1$, $p < 0.001$	-	
Urban	$\chi^2 = 6.9$, $df=1$, $p < 0.01$	$\chi^2 = 13.2$, $df=1$, $p < 0.001$	-	-

Table 2. Chi-square test comparing the number of *B. bufo*, *R. temporaria*, and *P. kl. esculentus* breeding sites between each pair of habitat types. “-” refers to low expected frequencies, test is not applicable. NS: non significant p-value.

	Woodland	Woodland and Rural	Rural	Open
Woodland and Rural	$\chi^2 = 1.7$, $df=1$, NS			
Rural	$\chi^2 = 2.7$, $df=1$, NS	$\chi^2 = 8.4$, $df=1$, $p < 0.01$		
Open	$\chi^2 = 1.1$, $df=1$, NS	$\chi^2 = 4.8$, $df=1$, $p < 0.05$	-	
Urban	$\chi^2 = 1.3$, $df=1$, NS	$\chi^2 = 3.4$, $df=1$, NS	-	-

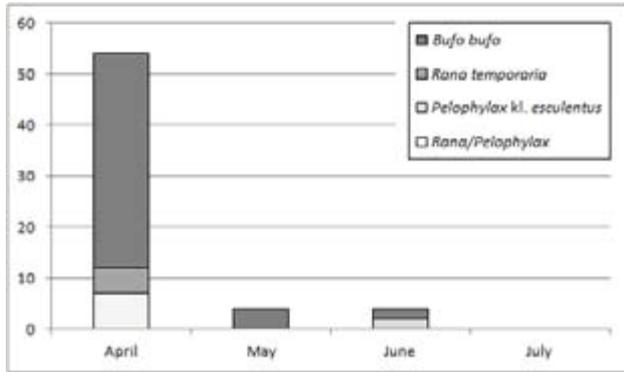


Fig. 3. Number of dead individuals found in each month of the survey.



Fig. 4. Dead common toad (*Bufo bufo*, arrow) on the tracks with dead grass snake (*Natrix natrix*). Photo by K.M. Budzik.

Most dead amphibians were spatially clustered in April but this result appears conditioned by the large number of common toads and their mass migrations to breeding sites. Toads were scattered after the breeding season, suggesting seasonal migrations towards feeding grounds. Additionally, as in the case of roads (Hels and Buchwald, 2001; Hamer and McDonnell, 2008), spring migration seems to be the period of highest amphibian mortality on railroad tracks. Undetermined frogs were probably representatives of the common frog or moor frog, which awakened from hibernation in April. The peak of green frog mortality in June may indicate dispersal in search of new habitats because of the gradual drying of habitat in ditches alongside the railroad tracks. The fragmentation of the remains of common toads clearly suggests that the direct cause of death was collision with a train. The short limbs of these animals reduce their ability of overcoming barriers such as rails. In addition, numerous studies have shown that amphibians are likely to remain immobile if

faced with an approaching light (Cornell and Hailman, 1984; Mazerolle et al., 2005). Thus, it is possible that common toad activity can be disturbed under train light, increasing the risk of mortality. The toads that were not damaged, but trapped inside the track, probably died of dehydration. Because dead frog individuals were not mechanically damaged, we suppose that they were probably hit by a train while trying to overcome the rails. The majority of dead frogs were juveniles. We suggest that most adults, able to hop farther and faster than the juveniles, may migrate more successfully. We did not find any dead individuals of the agile frog, the European tree frog, the fire-bellied toad or newts. As regards the latter, small-sized species may avoid the tracks because they are unable to cross them. To successfully migrate, their only option may be to avoid the rails and rather move along the viaducts: this suggestion is worthy of further investigation. However, this result may also be due to a sampling issue: on the one hand, small-sized amphibians dry up faster; on the other hand they may be crushed by a train; either way, this would make them very difficult to detect (Dodd et al., 2004; Mazerolle et al., 2005). There is also the possibility that small-sized amphibians may migrate through a gap under the railway. The agile frog and probably the other frogs seem to successfully cross the rails, probably thanks to their jumping ability. Railroad mortality seems to depend on physical features (such as body size, limb length) and may be associated with the agility of the species. In the case of roads, agility was related mainly to velocity of the individual (Schlupp and Podloucky, 1994; Hels and Buchwald, 2001), while in the case of railroad tracks, agility relates primarily to the ability to overcome obstacles. Due to its physical features, the common toad was more likely to become stranded at the rail, indicating that this species is more vulnerable to railway mortality. However, other species that do not cross the track because of their small body size may also be affected by the railroad, but at the level of gene flow (Reh, 1989; Vos et al., 2001) which represents a conservation issue that is worthy of further study.

Further investigations examining in detail the effect of individual physical features on amphibian railroad mortality, railway-related migration behavior of amphibians, as well as gene flow among amphibian populations isolated by railway line, are warranted.

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