TRAIN MOOSE-KILL IN ALASKA: CHARACTERISTICS AND RELATIONSHIP WITH SNOWPACK DEPTH AND MOOSE DISTRIBUTION IN LOWER SUSITNA VALLEY

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ABSTRACT: Trends in moose (*Alces alces*) mortality (n = 3,054) due to train collisions along 756 km of railway in Alaska from 1963-90 are presented. Annual (May-April) mortality ranged from 9 to 725 moose. Winter (November-April) mortality varied from 7 to 705 moose, with more than 73% occurring from January through March. Mortality was greatest in sections of the railway transecting winter range. During the 1989-90 winter, 50 % (352 moose) of the train moose-kills occurred in a 64 km section of railway (8.5% of the railway length) in the lower Susitna Valley. There was a positive correlation among snowpack depth and train moose-kill, and moose numbers on winter range for the years when I studied the relationship. There was an inverse relationship between snowpack depth and moose density in alpine habitat, and between alpine density and train moose-kill for the years the relationship was studied. There was a relationship between the timing of deep snow and timing of moose occurrence on winter range, and timing of train moose-kill in two winters with greatly dissimilar patterns of snow accumulation. My results emphasize the importance of understanding moose movements in assessing and resolving the train-moose problem. Findings also identify the importance of alpine postrut concentration areas as a component of moose habitat.

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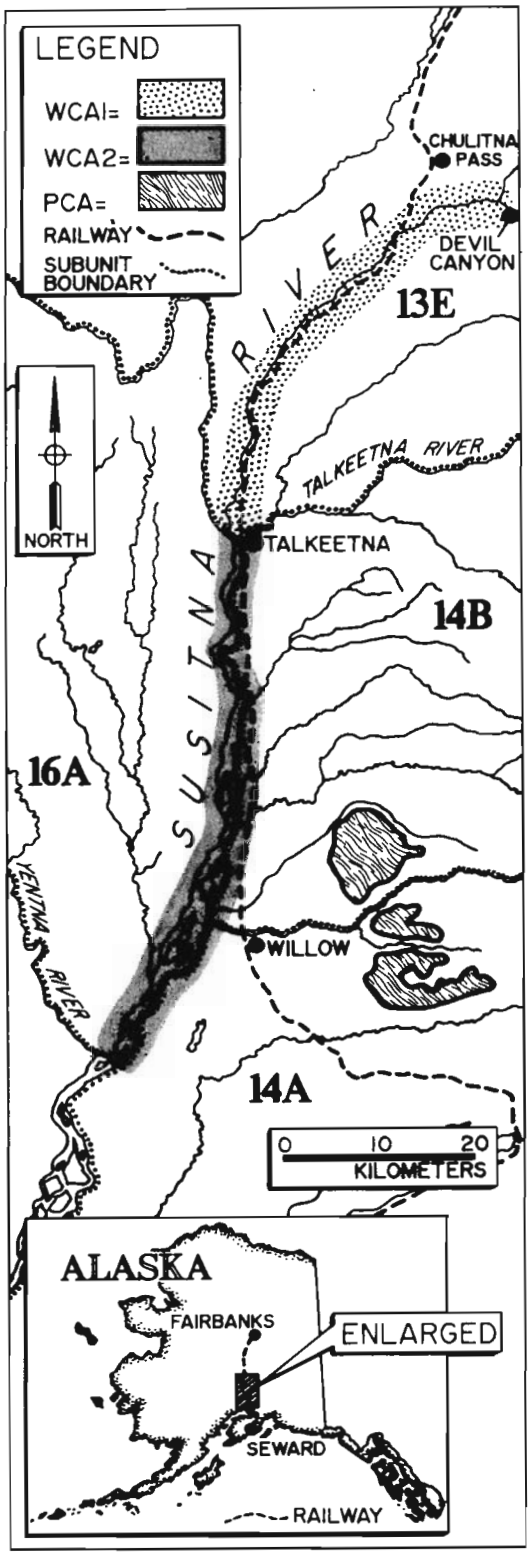
The Alaska railway passes through moose habitat in a 756 km route from Fairbanks, an interior location, to Seward, a marine port in south-central Alaska. Large numbers of moose are killed in train collisions during winter at specific locations in years with deep snow (Chatelain 1951, Rausch 1958). Losses of moose to train collisions are economically costly and socially unacceptable (Rausch 1958, Child 1983). The Alaska Railroad Corporation (ARC) and the Alaska Department of Fish and Game seek to mitigate train-moose conflicts. A first step in resolving the train-moose conflict is defining and understanding the nature of the problem.

The purpose of my study was to: (1) consolidate significant information on the train moose-kill, (2) describe characteristics of the train moose-kill and (3) explore relationships between snowpack depth, train moose-kill and moose distribution.

STUDY AREA

Railway

The Alaska Railroad railway goes between Seward (milemark = 0), a marine port on the east coast of the Kenai Peninsula in south-central Alaska, and Fairbanks (milemark = 470), a major city in the interior of the state (Fig. 1). The 756 km railway, passes through cities, towns, rural settlements, and vast expanses of unsettled land. The route traverses a variety of habitats including: coastal spruce-hemlock forests, closed spruce-hardwood forests, open low-growing spruce forests, shrub thickets and treeless bogs (Viereck and Little 1972). Elevation of the route changes from sea level in Seward to a high point of 700 m in Broad Pass (milemark = 297), on the south side of the Alaska Mountain Range, to 130 m at Fairbanks. The Alaska Mountain Range divides Alaska into interior and south-central geographical regions. In south-central Alaska, about 160 km of the railway runs near major lowland river drainages, extensive active floodplains and large tracts of



unmaintained old homestead land clearings. Forest vegetation along the route in the lower Susitna Valley include mixtures of old growth white spruce (*Picea glauca*), black spruce (*Picea mariana*), paper birch (*Betula papyrifera*), aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera*) and black cottonwood (*Populus trichocarpa*). Willows (*Salix* spp.), alders (*Alnus* spp.) and young deciduous tree species are particularly common at lower elevations in river drainages and in active floodplains. Early successional deciduous species dominate landscapes in settlements, unmaintained homesteads and the railway corridor where the ground surface has been disturbed by man. Willows and young deciduous tree species are preferred winter moose browse in south-central Alaska (Spencer and Chatelain 1953). Consequently, in winter, large numbers of migratory moose concentrate in locations along the railway in south-central Alaska where local conditions favor growth of early successional deciduous browse species.

Regional Conditions in Lower Susitna Valley

Winter climate in the lower Susitna Valley region is more variable and inclement away from the maritime influence of Cook Inlet and at higher elevations. Mean monthly temperatures vary from about 16 C in July to -13 C in January; maximum and minimum temperatures of 25 and -35 C are common. Total annual precipitation varies from about 40 cm in the south to over 86 cm in the north and west.

Fig. 1. Location of the 756 km railway between Seward (milemark 0) and Fairbanks (milemark 470) and the lower Susitna Valley study area in Alaska, showing game management subunits (14A, 14B, 16A and 13E), winter concentration areas (WCA1 and WCA2) and postrut concentration areas (PCA). Talkeetna and Willow were where snowpack depth was measured.

Snow accumulation varies with location, elevation, and site characteristics. Maximum snow depth can vary from <20 cm in the south to >200 cm in the north and west. Snow depth is generally deeper at higher elevations. Strong northerly winds often redistribute snow in exposed alpine sites and open floodplains. Snow accumulation in river channels varies depending on where and when ice forms over open water. Avalanches redistribute snow that accumulates on steep slopes.

Elevations within the region range from sea level to rugged mountain peaks well above 1500 m. Moose seldom use areas above 1100 m. Dominant habitat and canopy types in the region are characterized as: (1) floodplains dominated by willows, alders and poplars; (2) lowlands dominated by a mixture of wet bogs and closed or open mixed conifer-deciduous forests of paper birch, white spruce, black spruce, aspen; (3) mid-elevations dominated by mixed or pure stands of aspen, paper birch and white spruce; (4) higher elevations dominated by alder, willow, and birch shrub thickets (*Betula spp.*) or grasslands (*Calamagrostis spp.*); and (5) alpine tundras dominated by sedge (*Carex spp.*), ericaceous shrubs, prostrate willows, and dwarf herbs (Viereck and Little 1972).

METHODS

Train Moose-Kills

The ARC provided location and date for each moose-killed by the train on the railway between Seward and Fairbanks from October, 1963 through April, 1990. Accuracy in reporting train moose-kills in Alaska has greatly improved since 1980. Before which, numbers of were underreported (Rausch 1958). Data on train moose-kills before 1980 probably reflected month-to-month and year-to-year variations. Train moose-kill data for milemarks 0 to 470 were tabulated by year, season, month and location.

Train moose-kills were clustered in the section of the railway in the lower Susitna Valley. I explored relationships between snowpack depth, train moose-kill and moose distribution in a 145 km section of railway in the lower Susitna Valley from milemark 185 to 275. The high kill section of railway was divided into 2 segments. The train moose-kill on the segment extending from milemark 225 near Talkeetna to milemark 275 near Chulitna Pass was compared to moose counts in WCA1 and snowpack depth at Talkeetna. The train moose-kill on the segment extending from milemark 185 near Willow to milemark 225 was compared to moose counts in PCA and snowpack depth at Willow. The train moose-kill on the segment extending from milemark 185 to 275 was compared to moose counts in WCA1 + WCA2 and snowpack depth at Talkeetna.

Aerial Surveys

Numbers of moose were counted on aerial surveys in postrut concentration areas (postrut areas) and winter range in the lower Susitna Valley (Fig. 1). Survey areas were selected near railway sections with a high moose-kill.

Postrut areas (PCA) were located in the western foothills of the Talkeetna Mountains in Alaska Game Management Subunits 14A and 14B. This 240 km^2 area ranging in elevation from 600 to 1,200 m included 3 neighboring parcels of alpine habitat separated by lower elevation forested river drainages. This survey area was situated about 7 km east of the railway. In certain winters, moose were not found at higher elevations in the survey area. The area included portions of Bald Mountain Ridge, Moss Mountain and Willow Mountain.

Moose on winter range were surveyed in 2 areas of the Susitna River floodplain. One area was in Subunit 13E (WCA1); the other was in Subunit 16A (WCA2). The survey area in Subunit 13E was in the Susitna River floodplain between the Talkeetna River and Devil Canyon. This area encompassed 80 km of floodplain habitat ranging in elevation from 100 m at the Talkeetna River to 300 m at Devil

Canyon. Here, the floodplain was mostly <0.5 km wide with a scattering of islands. The railway from milemark 225-263 was mostly within 0.5 km of this survey area.

The survey area in Subunit 16A was located in the Susitna River floodplain between the Talkeetna River and the Yentna River. This area encompassed about 95 km of floodplain habitat ranging in elevation from 15 m at the Yentna River to 100 m at the Talkeetna River. In the survey area, the Susitna River floodplain was frequently >3 km wide where the river braids extensively around many small and large islands. The railway from milemark 185 to 225 was mostly within 2 km of this area.

Aerial surveys were conducted in winter, when snowcover was sufficient to observe moose, at 2- to 3-week intervals weather permitting. Surveys were conducted in WCA1 in 1981-85, WCA2 in 1982-84 and PCA in 1985-90. Survey flights were flown in Piper PA-18 aircraft at a search intensity of about 2.3 min per km^2. Low vegetative cover and good snow conditions in survey areas led to very high observability of moose.

Snowpack Depth

Snow depth data were obtained from Alaska Climatological Data Reports, U.S. Department of Commerce, NOAA, National Environmental Satellite, Data and Information Service, National Climate Data Center, Asheville, North Carolina. Snow depth data from Talkeetna were used as an index of snowpack depth in WCA1 and along the railway segment from milemark 225 to 275 in 1981-85, in WCA1+WCA2 and along the railway segment from milemark 185 to 275 in 1982-84, and along the railway segments from milemark 185 to 275 and milemark 225 to 275 in 1985-90. Snow depth data from Willow were used as an index of snowpack depth in PCA in 1985-90 and along the railway segment from milemark 185 to 225 in 1981-90. I presented the maximum snow depth recorded in each of 3, 10-day intervals (DIs) (1-10, 11-20 and 21-31 days) for each month. There were 21, DIs from October through April.

Snowpack depth was compared in relation to snowpack depth = 40 cm. Onset of fall-winter migrations of moose in Sweden (Sandegren *et al.* 1985) and Alaska (Van Ballenburghe 1977) were linked to snowpack depth of 42 and 40 cm, respectively.

Relationship Between Snowpack Depth, Moose Distribution and Train Moose-kill

To explore the relationship between snowpack depth, moose numbers on winter range, and train moose-kills, I used the Pearson correlation coefficient (Snedecor and Cochran 1980) to compare: (1) the maximum snowpack depth at Talkeetna (MSD-T) with the maximum number of moose counted in WCA1 (MMC-W) in 1981-85; (2) the MMC-W with the number of train moose-kills between milemarks 225 and 275 (TMK-T) in 1981-85; (3) the MSD-T with the TMK-T in 1981-85; and (4) the MSD-T with the TMK-T in 1981-90. Statistical significance was set at the 0.05 alpha level for all analyses in this papter.

To explore relationship between snowpack depth, moose numbers on winter range, and train moose-kills in 2 winters (1982-84) that differed greatly in the timing of snow accumulation, I used the Pearson correlation coefficient to compare: (1) the number of moose counted in WCA1 + WCA2 in each month (averaged by the number of counts per month) (AMC) with the number of train moose-kills between milemarks 185 and 275 in each month from November through March in the 1982-84 winters and (2) the AMC with the monthly maximum snowpack depth from November through March in the 1982-84 winters. I used a Chi-square analysis to compare the monthly number of train moose-kills between milemarks 185 and 275 from November through April in the winters, 1982-84. I used a Chi-square analysis with a Yates correction factor to compare the number of DIs with maximum snowpack depth <40 cm, and >40 cm in the 1982-83 and 1983-84

winters.

To explore the relationship between snowpack depth, moose numbers in postrut concentration areas and train moose-kills I used the Pearson correlation coefficient to compare: (1) the number of the DI when snowpack exceeded 40 cm at Willow (MIS-W) with the number of the DI when moose numbers in the PCA decreased by >75% in 1985-90; (2) the MIS-W with the number of train-moose kills between milemarks 185 and 225 (TMK-W) in 1985-90; (3) the number of the DI when moose numbers in the PCA decreased by >75% with the TMK-W in 1985-90; and (4) the maximum snowpack depth at Willow with the TMK-W in 1981-90.

RESULTS

Characteristics of the Train Moose-Kill

The ARC documented mortality of 3054 moose in train collisions in 756 km of railway between Seward and Fairbanks from May 1963 through April 1990. Numbers of train moose-kills ranged from 9 to 725 annually, May-April (Fig. 2). Numbers of train moose-kills ranged from 7 to 705 in winter. More than 93% of the train moose-kills were between Nov through Apr; 73.3% were in Jan through Mar (Fig. 3). Although only 3.5% and 4.4% of the annual train moose-kill occurred in November or April, it was 2.5-3.1 times greater than in any month from May through October.

In the 4 winters with the largest reported number of train moose-kills (1984-85 and 1987-90), kill locations were clusted in in Subunits 14A, 14B and 13E (Fig. 4). Kills were particularly numerous along a 193 km section of railway between milemarks 160 and 280 in the lower Susitna Valley. Other sections of the railway had few or no moose killed by trains. During the winters of 1984-85, and 1987-90, 204, 178, 88 and 352 moose were killed along a 64 km section of railway between milemarks 185 and 225. During these winters, 55, 56, 35 and 50 percent of the train moose-kills, respectively, occurred along 8.5

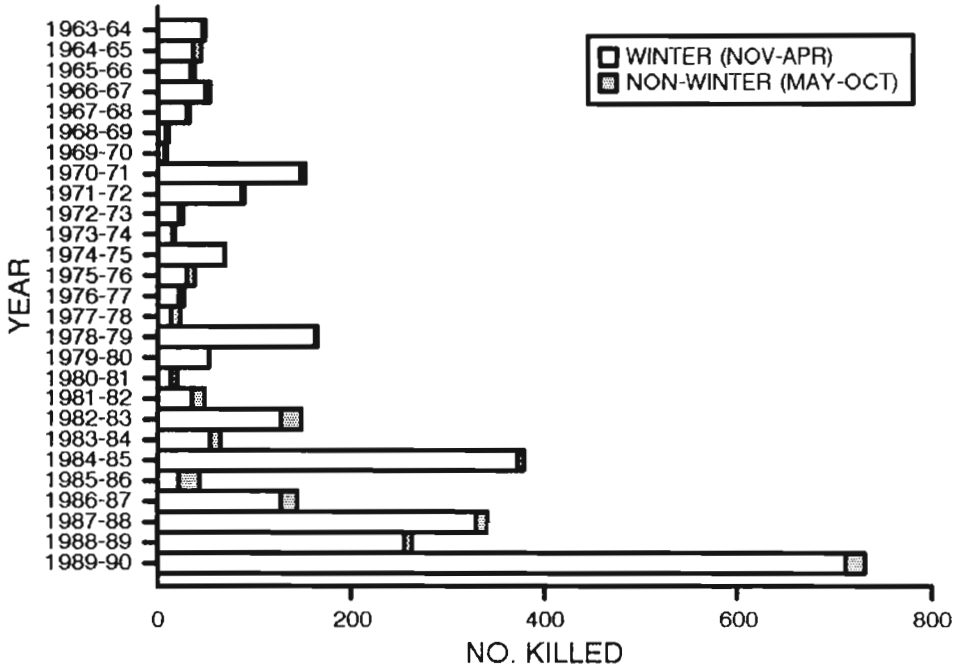


Fig. 2. Annual numbers of moose killed in train collisions May-April (n = 3054) and numbers killed in winter, November-April (n = 2851) and non-winter May-October (n = 203) in Alaska, 1963-90.

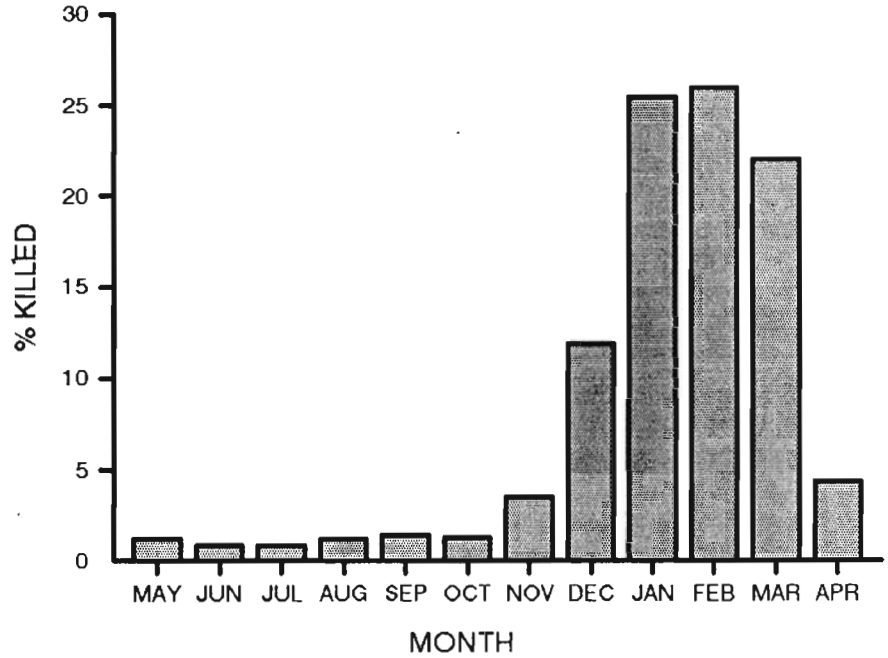


Fig. 3. Distribution of train moose-kills (n = 3054) by month in Alaska, 1963-90.

percent (64 km) of the railway.

Snowpack Depth, Moose Counts in Winter Concentration Areas, and Train Moose-Kills

Snowpack depth at Talkeetna, numbers of moose in winter concentration areas and numbers of train moose-kills varied greatly during 4 winters, 1981-85 (Fig. 5). Peak snowpack at Talkeetna, varied from 46 to 157 cm during these 4 winters. Snowpack generally increased from October through January, peaking in February or mid-March, and melting in late April. Thirty-four moose surveys were completed in WCA1 between November, 1981 and April, 1985, whereas 16 surveys were completed in WCA2 between November, 1982 and February, 1984. Thirty-seven surveys were conducted in PCA between October 1985 and March 1990.

The greatest number of moose counted in WCA1, in 34 surveys ranged from 36 to 132 during the 4 winters, 1981-85 (Fig. 5). Maximum numbers of moose counted was positively correlated with maximum snowpack depth during years 1981-85 (r=0.976,P=0.024, n=4). Thus the magnitude of moose meovement to winter range was related to snowpack depth.The fewest number of moose counted before and after the winter peak was 7 and 4, respectively. Moose numbers increased during November and December, peaking in January to mid-February, and then decreasing to low levels in March to mid-April. Numbers of train moose-kills between railway milemarks 225 and 275 ranged from 0-87 during the winters of 1981-85. There was a high non-significant positive correlation between train moose-kills and maximum moose counts during the winters 1981-85 (r=0.887,P=0.113, n=4). Train moose-kills were high when moose concentrated in winter areas near the railways.

Number of train moose-kills (1984-85) and the peak moose count was greatest when snowpack depth was greatest (Fig. 5). Train moose-kills (1981-82) and peak moose count was lowest when snowpack depth was lowest. There was a high non-significant positive correlation between greatest snowpack depth and train moose-kills during the 1981-85 win-

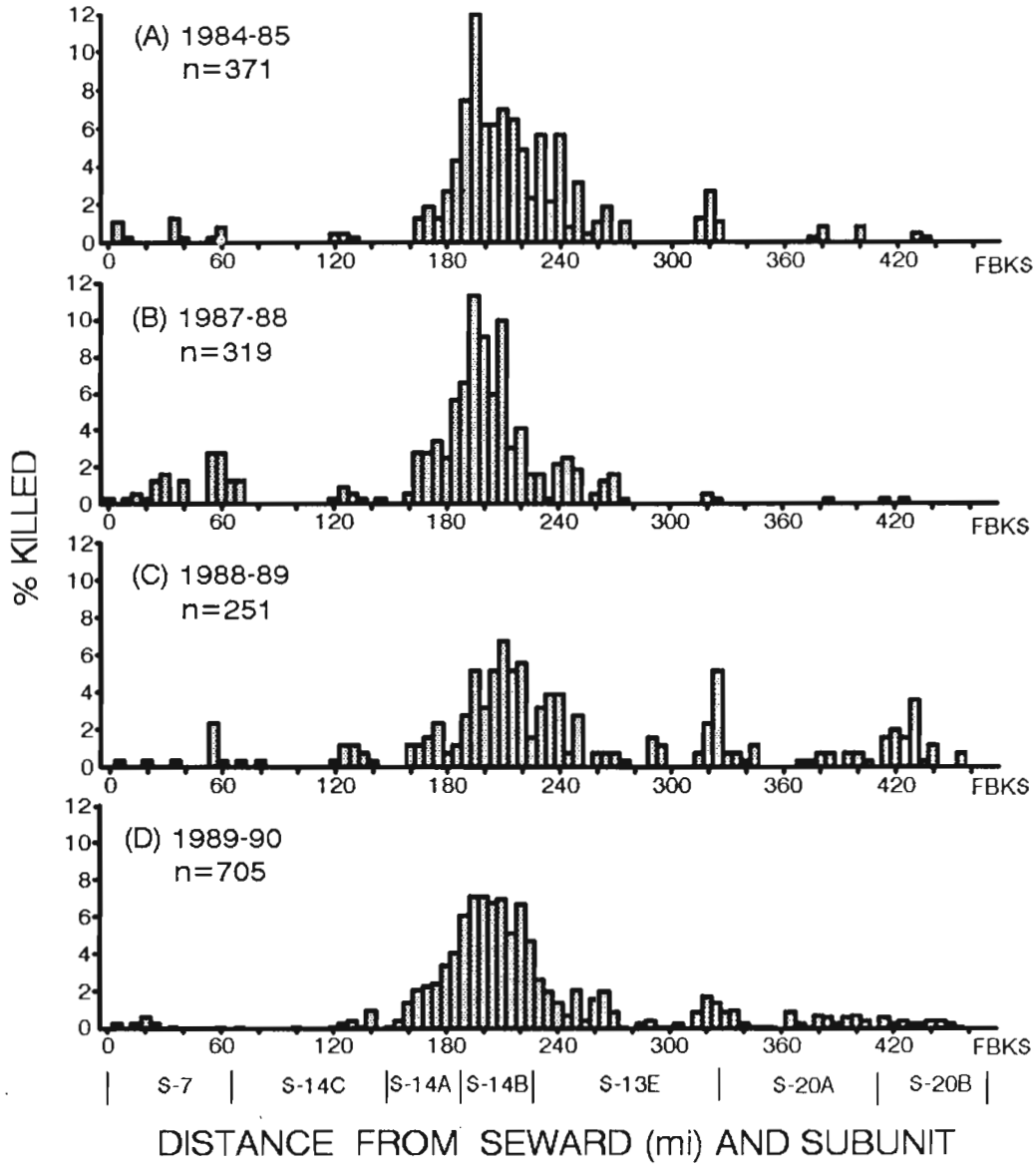


Fig. 4. Distribution of train moose-kills during winter, for 8-km sections along the railway from Seward (mi 0) to Fairbanks (mi 470), Alaska, during years, 1984, and 1987-89. Vertical lines below x-axis indicate milemark locations of Game Management Subunit (S-) boundaries. FBKS=Fairbanks.

ters (r=0.901,P=0.099,n=4). However, when the database was expanded including data from the 1985-90 winters, there was a significant positive correlation between snowpack depth and train moose-kills (r=0.962, P=0.0001, n=9). The train moose-kill was high when deep snow forced moose to migrate to winter concentration areas. Snowpack depth was bimodal in 1981-82, 1982-83 and 1984-85 (Fig. 5). Moose numbers in the WCA varied with this bimodal trend in snowpack depth (Fig. 5).

Snowpack depth, moose counts, and train moose-kills peaked earlier in 1982-83 than 1983-84 (Fig. 6). Snowpack depth increased from 23 to 81 cm between October and mid-January in 1982-83. During 1982-83, snowpack depth exceeded 40 cm by late Oc-

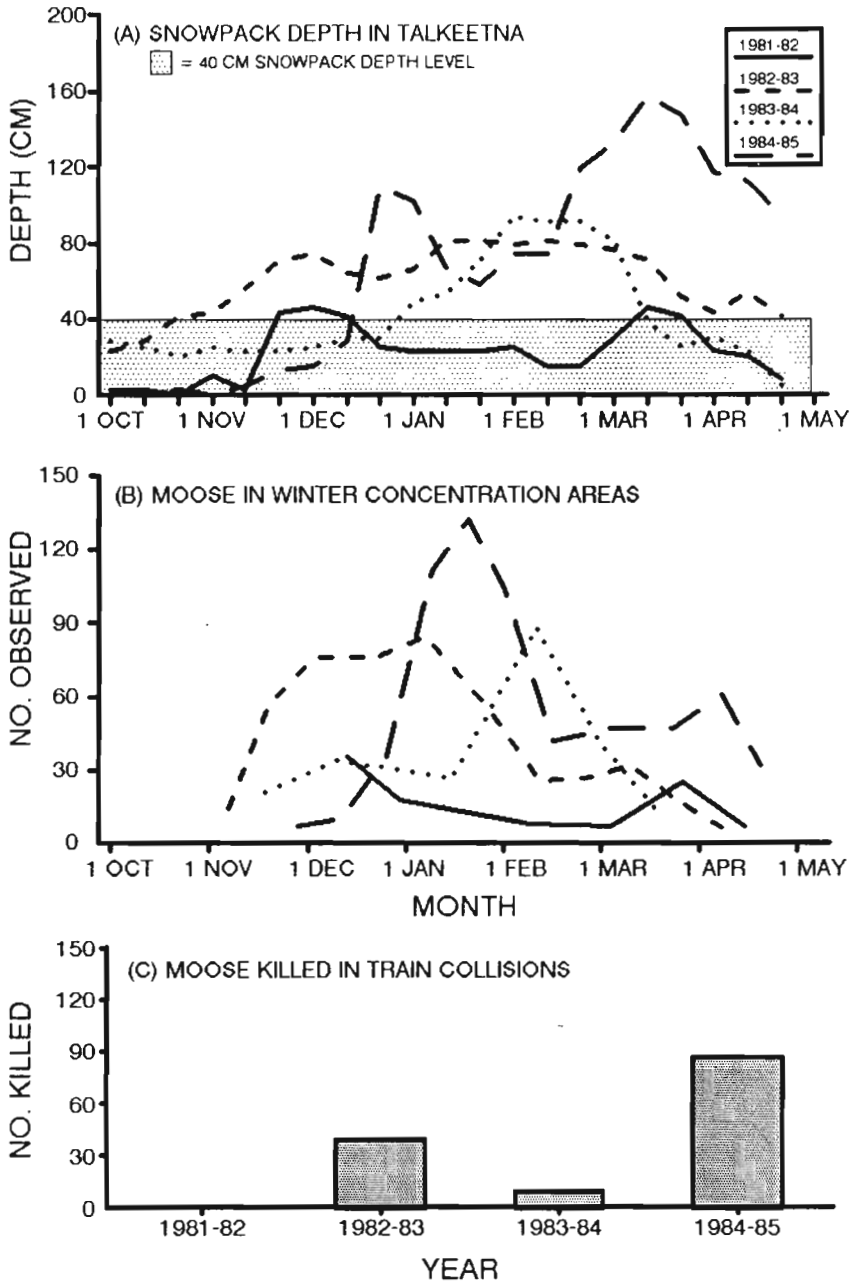


Fig. 5. Trimonthly maximum snowpack depth at Talkeetna (A), numbers of moose counted on aerial surveys in lowland winter concentration areas in the Susitna River floodplain between the Talkeetna River and Devil Canyon (B), and numbers of train moose-kills between railway milemarks 225 and 275, November-April (C), 1981-85, south-central Alaska. In other studies, onset of moose fall-winter migration coincided with snowpack depth = 40 cm.

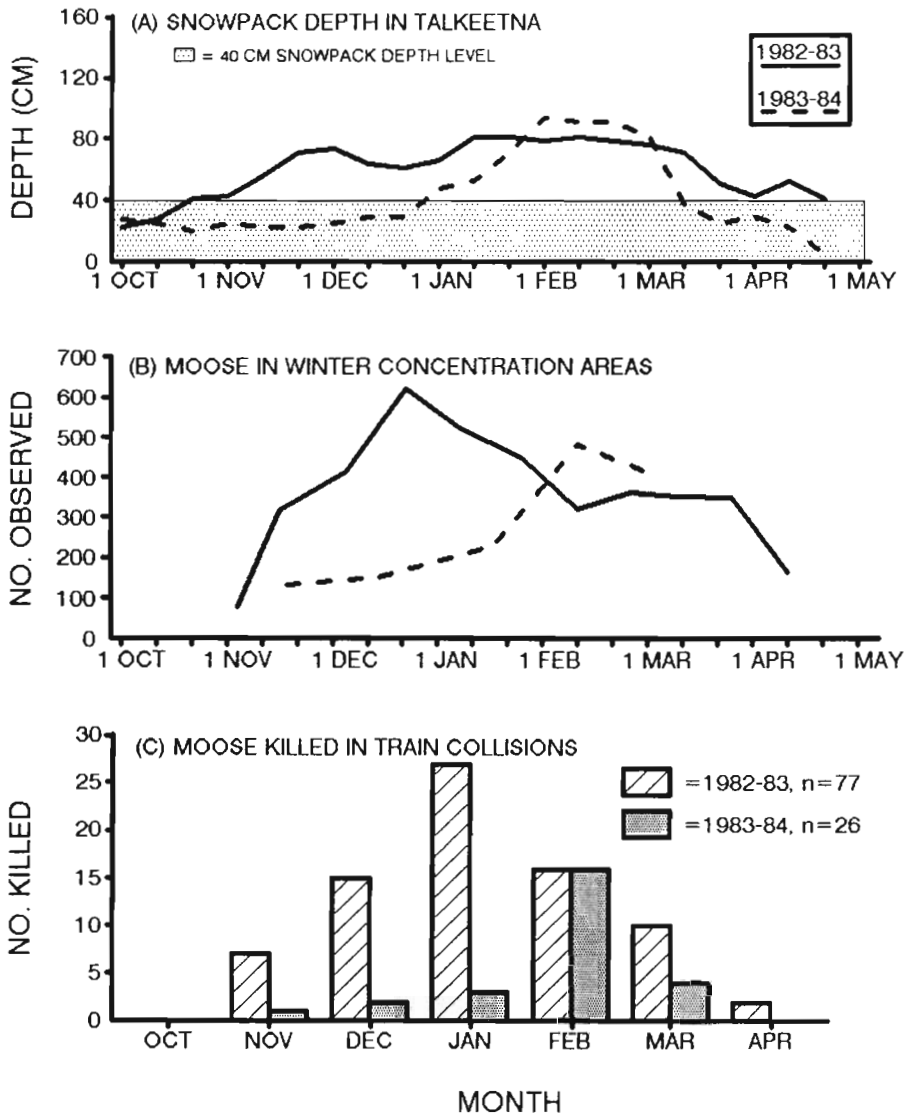


Fig. 6. Trimonthly maximum snowpack depth at Talkeetna (A), numbers of moose counted on aerial surveys in lowland winter concentration areas in the Susitna floodplain between the Yentna River and the Talkeetna River (B), and monthly number of train moose-kills between railway milemarks 185 and 275, October-April (C), 1982-84, south-central Alaska. In other studies,onset of moose fall-winter migration coincided with snowpack depth = 40 cm.

tober. In the 1983-84 winter, snowpack depth ranged from 5 to 94 cm. Snowpack depth exceeded 40 cm in early January, and peaked at 94 cm in early February. Snowpack depth exceeded 40 cm earlier and was >40 cm for a longer time in 1982-83 than 1983-84 ($X^2$12.22,df=1,P=0.005). Trends in numbers of moose counted in WCA1 + WCA2 differed between 1982-83 and 1983-84 (Fig. 6B). In 1982-83, numbers of moose ranged from 78 to 622 and peaked in late December, 1982. In 1983-84, numbers of moose ranged from 132 to 481, and peaked in early February. Monthly numbers of moose counted (AMC) were correlated with monthly maximum snowpack depth during November through March

(r=0.764, P=0.016,n=9). Monthly numbers of train moose-kills were different between the 1982-83 and 1983-84 winters (Fig. 6) (X^2=17.17,df=5, P=0.0042). In 1982-83, train moose-kills peaked in January and 64 percent occurred before February. In 1983-84, train moose-kills peaked in February and 78 percent occurred after January. Monthly numbers of train-moose-kills were positively correlated with monthly numbers of moose counted (AMC) (r=0.815, P=0.008,n=9). The timing of snowpack accumulation influenced the timing of moose movements to winter concentration areas, and the timing of train moose kills.

Snowpack Depth, Moose Counts in Postrut Concentration Areas, and Train Moose-Kills

Snowpack depth at Willow, numbers of moose in postrut areas and numbers of train moose-kills varied among years 1985-90 (Fig. 7). Peak snowpack depth ranged from 43 to 234 cm. The greatest numbers of moose counted ranged from 626 to 938 moose, whereas the fewest number of moose counted before and after a winter peak was 42 and 12 moose, respectively. Numbers of moose counted in postrut concentration areas generally increased during October, peaked between late October and early December, and decreased from late December and mid-April.

In winter 1985-86, numbers of moose in postrut areas decreased by less than 50 percent between the peak count in early December and a count in late March. Snowpack depth first exceeded 40 cm in late March. In 1989-90, numbers of moose decreased precipitously in late October and early November, when 1989-90, snowpack depth first exceeded 40 cm in late October. Few moose were counted in late December, 1990, the year snowpack depth was greatest. During the winter of 1986-87, numbers of moose declined in December; snowpack exceeded 40 cm in early January. In the winters of 1987-89, moose numbers declined in mid-November to mid-December; snowpack depth exceeded 40 cm in late November.

The number of the DI when snowpack exceeded 40 cm was correlated positively with the number of the DI when numbers of moose counted in the PCA decreased to <75% of the peak count during the years 1985-90 (r=0.928, P=0.023,n=5). Moose dispersed from postrut concentration areas when snowpack exceeded 40 cm.

Numbers of train moose-kills between milemarks 185 and 225 ranged from 4 to 352 for the 1985-90 winters. Numbers of train moose-kills in winter were lowest in 1985-86, highest in 1989-90, and intermediate in 1986-89. Kills varied among the 3 winters with intermediate numbers of train moose-kills. Train moose-kills were twice as common in 1987-88 than 1988-89, and 2.4 times more numerous in 1988-89 than 1986-87. In 1986-87, snowpack depth exceeded 40 cm in early January, whereas in 1987-89 it exceeded 40 cm in late November. Snowpack depth in 1987-88 exceeded snowpack depth 1988-89 from mid-December through April. The numbers of the DI when snowpack exceeded 40 cm was not significantly correlated with the number of moose-kills 1985-90 (r=-0.793, P=0.109,n=5). The numbers of the DI when numbers of moose counted in the PCA were <75% of the peak count were not signficantly correlated with the numbers of moose-kills (r=-0.704,P=0.185,n=5). However, when the database was expanded including the 1981-85 winters, there was a significant positive correlation between maximum snowpack depth and train moose-kills ((r=0.815,P=0.007, n=9). The timing and depth of snow influenced dispersal of moose from postrut areas, and both correlated with train moose-kills. Maximum snowpack depth was an important factor influencing the number of train moose-kills. Perhaps, timing and magnitude of moose migrations from the PCA, which are influenced by snowpack depth, were weekly correlated with train moose-kills

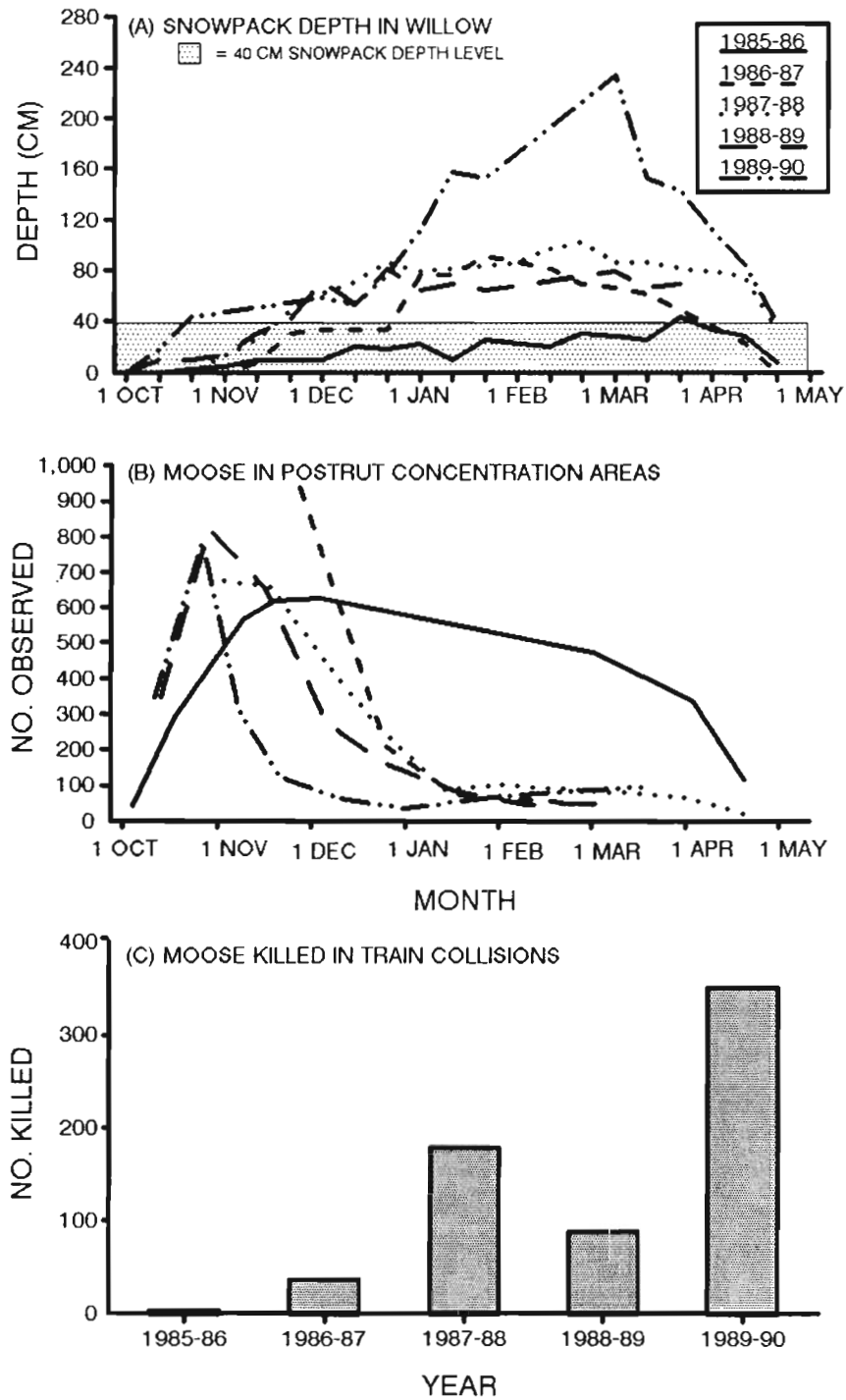


Fig. 7. Trimonthly maximum snowpack depth at Willow, numbers of moose counted on aerial surveys in alpine postrut concentration areas in the western foothills of the Talkeetna Mountains (B) and numbers of train moose-kills between railway milemarks 185 and 225, November-April (C), 1985-90, south-central Alaska. In other studies, onset of moose fall-winter migration coincided with snowpack depth = 40 cm.

because moose in the PCA migrate to winter range that is not near the railway.

DISCUSSION

A large number of moose were killed in train collisions in Alaska each year. This kill occurred mainly from November through April. Kills were clustered in certain segments of the railway, and more numerous in deep-snow winters. Kills were few in low-snow winters. These data agree with findings of others (Rausch 1958, Child 1983, Hatler 1983, Andersen *et al.* 1991). However, in southern Norway, <50% of the yearly train moose-kill occurred in winter (Jaren *et al.* 1991), and in Ontario and Manitoba, train-moose collisions were most frequent in June and July shortly after calving season (Child and Stuart 1987).

Train moose-kills increased when migratory moose moved to winter concentration areas near the railway. Kills were clustered in sections of the railway transecting migration routes and winter range. Kills were more numerous in deep-snow winters than in low-snow winters. In deep-snow winters, most moose in alpine postrut concentration areas dispersed to lowland winter range near the railway. In low-snow winters, many moose stayed in alpine habitat. The peak in train moose-kills occurred earlier in winter in an early-snow winter than in a late-snow winter because most moose migrated to winter range in response to snow accumulation. These findings were consistent with findings previously reported (Rausch 1958, Coady 1974, Van Ballenburghe 1977, Thompson *et al.* 1981, Child 1983, Sandegren *et al.* 1985). Although train moose-kills were numerous in deep-snow winters when large numbers of moose were near the railway, the additional affect of plowed snow along the railway likely affected behavior of moose increasing their vulnerability to train collisions (Rausch 1958, Child 1983, Hatler 1983, Andersen *et al.* 1991).

Loss of large numbers of moose in train collisions can have considerable consequences on management of local moose populations (Rausch 1958, Child 1983). More than 350 moose were killed in train collisions in Subunit 14B in the winter of 1989-90. However, in addition to moose resident in Subunit 14B, migratory moose from 2 neighboring Subunits were vulnerable to train collisions in Subunit 14B (R. Modafferi pers. comm.). Consequently, losses must be allocated among moose populations in 3 Subunits, and managers must understand movements of moose in the railway.

Plans to mitigate or resolve problems of train-moose collisions frequently include measures to manage habitat and moose populations along railways (Rausch 1958, Child 1983, Jaren *et al.* 1991). One option is to decrease numbers of moose near the railway. Forage along railways can be eliminated so moose are not attracted to the rail corridor. Habitat away from railways can be managed to attract moose and keep them distant from the rail corridor. Winter harvest quotas can be established near the railway. Fall harvest quotas can be increased in these Subunits overlapping the railway. However, findings in this study and another (R. Modafferi pers. comm.) suggest that these measures must be implemented at certain times and places to affect target moose populations.

In some moose management jurisdictions, railway corporations fail to provide wildlife managers with an accurate account of train moose-kills (Rausch 1958, Child and Stuart 1987). In Alaska, railway managers have cooperated with wildlife managers in collecting information on train-moose conflicts and in testing measures to help resolve the problem.

My findings indicate that moose distribution and numbers on winter range were related to snow accumulation throughout the winter. These findings agree with observations of Edwards and Ritcey (1956) who noted that

snow depth was a major factor influencing timing and extent of moose migrations and yearly differences in moose distribution. Van Ballenburghe (1977) found that snow conditions caused moose to break from traditional migratory patterns during a seasonal cycle. Crete (1980) showed that moose did not winter in the same forest stands during consecutive winters; snow conditions were not assessed. Modafferi (pers. comm.) indicated that some individual radio-marked moose in the lower Susitna Valley migrated differently and were located in different areas in a low-snow winter versus a series of average- to deep-snow winters. In contrast, Sweanor and Sandegren (1987) reported that moose fall-winter migration patterns were consistent each year. However, in all years of their study, snow depth exceeded 40 cm, the threshold snow depth that initiated onset of migrations in moose (Sandegren *et al.* 1985). In this study, timing, magnitude and extent of moose migrations were correlated with snowpack depth. My findings suggested that not all moose migrated in response to the same threshold of snowpack depth, and that snow depth influenced the final destination of migrations of moose.

There is considerable information on movements of moose to winter concentration areas and the importance of winter concentration areas to moose (Stevens 1970, Telfer 1970, Brassard *et al.* 1974, Coady 1974, LeResche 1974, Peek 1974, Van Ballenburghe 1977, Crete and Jordan 1982, Sandegen *et al.* 1985, Lavsund 1987, Danell and Bergstrom 1989, Hundertmark *et al.* 1990). There is less data available on movements of moose to postrut concentration areas and the importance of postrut areas in moose ecology (LeResche 1972, Lynch 1975, Thompson *et al.* 1981). Like winter concentration areas, importance of postrut concentration areas, is suggested by the traditional use by large numbers of moose. Moose left surrounding habitats to move to these postrut areas in early winter before deep snowpack forced them to move to winter range (Coady 1974, Telfer 1978). Thompson et al. (1981) suggested that quantity and quality of browse in moose early winter concentration areas was superior to browse in surrounding habitats. Weight and body condition of moose entering winter determines survival and influences productivity the following spring (Saether 1987, Schwartz *et al.* 1988). During the postrut period, moose increase food intake (Schwartz *et al.* 1984) and gain weight (Schwartz *et al.* 1987). Quality of range in these postrut concentration areas likely influenced moose movements to them.

My observations indicated moose winter range has two components, alpine postrut concentration areas and lowland winter concentration areas. Snowpack depth affected timing, duration and magnitude of moose use of each component. When deep snowpack occurred early, moose dispersed from postrut areas in November to winter ranges. During winters with low snowpack many moose stayed in alpine postrut concentration areas. This extended use of postrut areas reduced the impact of browsing on forage in lowland winter concentration areas. These findings suggest that moose postrut concentration areas were an intergral component of moose habitat that deserve protection and further study.

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Review

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The importance of invertebrates when considering the impacts of anthropogenic noise

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Anthropogenic noise is now recognized as a major global pollutant. Rapidly burgeoning research has identified impacts on individual behaviour and physiology through to community disruption. To date, however, there has been an almost exclusive focus on vertebrates. Not only does their central role in food webs and in fulfilling ecosystem services make imperative our understanding of how invertebrates are impacted by all aspects of environmental change, but also many of their inherent characteristics provide opportunities to overcome common issues with the current anthropogenic noise literature. Here, we begin by explaining why invertebrates are likely to be affected by anthropogenic noise, briefly reviewing their capacity for hearing and providing evidence that they are capable of evolutionary adaptation and behavioural plasticity in response to natural noise sources. We then discuss the importance of quantifying accurately and fully both auditory ability and noise content, emphasizing considerations of direct relevance to how invertebrates detect sounds. We showcase how studying invertebrates can help with the behavioural bias in the literature, the difficulties in drawing strong, ecologically valid conclusions and the need for studies on fitness impacts. Finally, we suggest avenues of future research using invertebrates that would advance our understanding of the impact of anthropogenic noise.

1. Introduction

The ever-expanding urban world has made anthropogenic (man-made) noise almost ubiquitous across the globe. Noise-generating human activities have increased considerably since the Industrial Revolution, leading to substantial changes in the acoustic landscape both on land and underwater. The prevalence of transportation networks, resource extraction and urban development in terrestrial environments is much greater today than in the past [1,2], while shipping, recreational boating, seismic exploration, sonar and pile-driving are widespread and occur with increasing frequency in aquatic environments [3]. Moreover, the sound generated by human activities is often very different from that arising from natural sources, both in terms of its prominent frequencies and in such acoustic characteristics as constancy, rise time, duty cycle and impulsiveness [4]. Anthropogenic noise therefore presents a very real, and often novel, challenge to animals including ourselves.

In humans, anthropogenic noise causes physiological, neurological and endocrinological problems, increased risk of coronary disease, cognitive impairment and sleep disruption [5,6]. These impacts can be severe and legislation is therefore in place to monitor and manage noise exposure in daily life [7]. Over the last decade, there has also been a growing awareness of the potential impact of anthropogenic noise on non-human animals, with studies on a number of different taxonomic groups demonstrating effects ranging from behavioural and physiological adjustments of individuals to changes at the population and community level [1,3,8–10]. Consequently, anthropogenic noise is now recognized as a major component of environmental change in the twenty-first century and a pollutant of international concern, featuring prominently on international directives and agendas (e.g. inclusion in the United States National Environment Policy Act

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and the European Commission Marine Strategy Framework Directive, and as a permanent item on the agenda of the International Maritime Organisation).

A comprehensive search of the peer-reviewed literature published on terrestrial species by the end of 2012 (see the electronic supplementary material) highlights a number of trends and issues (see also [11]); we focus here on terrestrial species for brevity, although similar conclusions can be made for aquatic organisms. One striking trend is that only two of the 83 papers considered an invertebrate species. Shieh *et al.* [12] compared the calling behaviour of the cicada *Cryptotympana takasagona* in noisy and quiet urban parks, finding positive correlations between noise levels and both call frequency and chorusing. Lampe *et al.* [13] found that male bow-winged grasshoppers (*Chorthippus biguttulus*) collected from noisy roadsides sang with a greater low-frequency component than males collected from paired quiet areas nearby. As male singing was recorded in the absence of noise stimuli in anechoic chambers, the differences are unlikely to be the consequence of behavioural plasticity, but instead may result from longer term adaptation. In both studies, modification of call frequency is presented as a mechanism for avoiding masking, although further investigation is needed to determine whether that is indeed achieved and whether the vocal adjustments generate associated costs [14].

The paucity of research on invertebrates does not reflect their general importance, the likelihood that anthropogenic noise will affect them or the potential for such investigations to advance our understanding of this issue. Invertebrates are hugely diverse, constituting the vast majority of species on the Earth and with a large proportion yet to be identified [15]. They are crucial components of food webs and fulfil many ecosystems services, such as pollination, decomposition and nutrient release [16]. Removal of invertebrate species can lead to changes in diversity and modification to ecosystem function [17]. Consequently, our understanding of community structure and resilience, as well as the pressing need for food security, makes it imperative that we study how invertebrates are impacted by environmental change [18], especially as it is clear that they are indeed vulnerable. For example, artificial light can alter invertebrate community composition [19], heavy metals can cause decreased immunity [20], slower development and reduced survival and fecundity [21], and climate change can result in shifts in geographical distribution, population size, phenology, behaviour and genetic composition [16]. As many invertebrates have a proven ability to hear, to use sound for a variety of reasons and to communicate acoustically [22], they are also likely to be affected by the noise introduced into the environment by the activities of humans. Moreover, many inherent characteristics of invertebrates (e.g. their relatively small sizes, short life cycles and ease of study in both laboratory and field conditions) provide the potential to overcome a number of the current issues that can hamper research into the impacts of anthropogenic noise (see [11] and below).

Here, we begin by explaining why invertebrates are likely to be affected by anthropogenic noise—we briefly review their capacity for hearing and provide evidence that they are capable of evolutionary adaptation and behavioural plasticity in response to natural noise sources, such as wind and the chorusing of other organisms. We then discuss the importance of quantifying accurately and fully both auditory ability and noise content, and emphasize considerations of direct relevance to how invertebrates detect sounds. We highlight some current issues identified by our review of the anthropogenic noise literature—a behavioural bias, the difficulty in drawing strong, ecologically valid conclusions, and a need for studies on fitness impacts—and consider whether studying invertebrates can help to resolve them. Finally, we suggest major avenues of future research relating to anthropogenic noise and how invertebrates can be used to advance our understanding of this pervasive global pollutant.

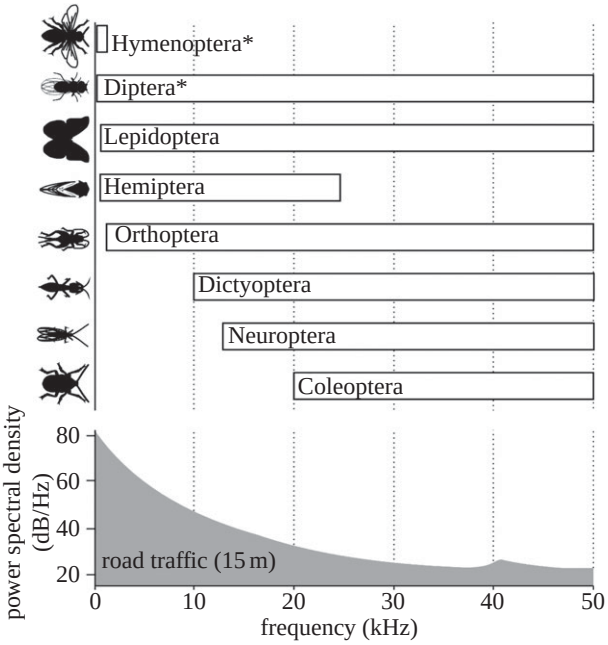

Figure 1. Approximate hearing ranges of insect orders and noise spectrum of road traffic recorded at 15 m. Noise spectra taken from Schaub *et al.* [28]. Asterisk indicates that species sensitive to particle velocity are also included.

2. Why invertebrates are likely to be affected by anthropogenic noise

There is a considerable body of work on the auditory capabilities of invertebrates and their responses to abiotic and biotic environmental noise, which combined suggest that they have the potential to be impacted by noise sources in an urban environment.

(a) Audition in invertebrates

Although audition is currently documented in detail in relatively few invertebrate species [22,23], the ability to detect sound has evolved multiple times in the insects alone, resulting in a diversity of auditory structures that can be found on nearly any segment of the body and with sensitivities anywhere between 10s of Hz to over 100 kHz [24,25]. Moreover, invertebrate species are known to produce sounds for a variety of reasons, in the same contexts as vertebrates: for example, aggression (e.g. *Drosophila*, Orthoptera, Coleoptera, Trichoptera; [22]), mate location, attraction and courtship (e.g. *Drosophila*, mosquitoes, Orthoptera, Hemiptera, Coleoptera; [22]), predator avoidance (e.g. Lepidoptera; [26]) and detection of parasite host species (e.g. tachinid flies; [27]). As many invertebrates rely on communication at frequencies below 10 kHz [24] and are capable of hearing within the main frequency spectrum of much anthropogenic noise (figure 1), their vulnerability to this pollutant is clear.

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The ability to hear typically refers to the detection of pressure waves; that is, oscillating compressions and rarefactions of the medium (usually air or water). Pressure waves are detected and produced by animals with tympanal ears: thin membranes coupled to mechanosensory cells that transduce the membrane vibration into electrical impulses. Humans, along with other vertebrates and many invertebrates, including the most conspicuously acoustic species, Orthoptera (crickets, katydids, grasshoppers) and cicadas, use tympanal ears [24]; recent work has demonstrated a remarkable example of convergent evolution between the ears of some insects and mammals [29]. As pressure waves dominate the sound field far from the source (greater than 1 wavelength (λ)), animals detecting sound pressure can communicate over considerable distances, but this also makes them vulnerable to noise originating further away. It is this component of sound that has been measured in all anthropogenic noise studies considering terrestrial animals to date.

There is a second distinct component to a sound wave, particle velocity, which comprises the oscillatory motion of particles back and forth within a propagating wave. As particle velocity is not detected by humans, it can be easy to overlook. However, many invertebrates detect this sound element using flagellar mechanosensory structures, such as hairs or antennae, that project into the oscillatory flow [25]. Particle velocity receivers sensitive to air-borne sound have been best characterized in two-winged flies (Diptera), where hair-like flagellar ears are sensitive to low frequencies (less than 1 kHz) [25,30,31]. The particle velocity component of sound attenuates rapidly and dominates only the sound field close to the source (less than 1 λ; for 10 Hz, $\lambda = 34$ m; for 1 kHz, $\lambda = 0.34$ m) [32]. Animals detecting just particle velocity may therefore be more robust than sound-pressure detectors to the impacts of anthropogenic noise. It must be noted, though, that the mechanosensory cells of both mosquitoes (*Toxorhynchites brevipalpis* [30]) and fruit flies (*Drosophila melanogaster* [31]), known to be sensitive to particle velocity, actively amplify quiet stimuli. This may effectively increase their sensitivity to distant sounds and, at the same time, their vulnerability to the effects of noise when compared with those species using a passive receiver system.

Vibrational communication through substrates, such as plants, spider webs and the ground, is also widespread in invertebrates [23]. While the sensory receivers for detecting substrate-borne vibrations are usually distinct from those of audition [22], acoustic stimuli can transmit into and be propagated in substrates, and hence acoustic noise also has the potential to impair vibratory communication. Recent work indicates that vibratory communication in the spider *Schizocosa ocreata*, for instance, is impacted by air-borne noise [33]. Vibratory communication is used in courtship in this species and when air-borne white noise (0–4 kHz) was played back, signal transmission and mating success in *S. ocreata* were decreased. The impact of anthropogenic noise on vibratory signals has received little direct attention (see [34] with an exception in Stephen's kangaroo rat (*Dipodomys stephensi*)) but as this modality is used by many different species both within and beyond the invertebrates, consideration of detrimental effects is important.

(b) Evidence for changes in response to noise

Many abiotic and biotic sound sources, such as wind, rain, running water and the choruses of other animals, can result in naturally noisy environments. To survive and reproduce in these conditions, invertebrates have evolved different mechanisms to cope with noise, incorporating adaptation over evolutionary time-scales and short-term behavioural plasticity.

Changes in auditory tuning mediated by both long-term physiological alterations and short-term behavioural modification are known in crickets and katydids. In noisy rainforests, where acoustic competition levels are high, the cricket *Paroecanthus podagrosus* has an auditory sensitivity that is relatively sharply tuned to conspecific song [35]. This contrasts with the broader auditory tuning of two species of European cricket, *Gryllus bimaculatus* and *Gryllus campestris*, which share their best frequency (the frequency of highest auditory sensitivity) with *P. podagrosus*, but live in quieter environments. The sharper tuning of *P. podagrosus* filters out background noise more effectively than in the broadly tuned species, but this may limit the detection of other environmental sounds that fall outside this narrow frequency range, for example those generated by approaching predators. Modifications in auditory tuning are also seen in the Australian bushcricket (*Sciarasaga quadrata* [36]). This species is able to close down the tracheal system, a system of air-filled tubes linking bilateral ears, to filter out much of the background noise generated by heterospecifics and tune the ear to the lower frequencies used by singing conspecific males. By maintaining a broad auditory sensitivity, these katydids may have a better ability to detect predators, while their flexible auditory response allows tuning into species-specific calls, and thus escape from acoustic competition.

There are also examples where species have evolved robust ways of communicating information even under noisy conditions. In bow-winged grasshoppers, calls include characteristics that allow attractiveness to be assessed even when subjected to high levels of white noise; noise does not appear to impair female choice in this species [37]. In other species, behavioural responses to noise are apparent, both in terms of sound production and recipient response. Römer *et al.* [38] found modifications to the temporal calling patterns in two sympatric katydid species, *Hemisaga dendiculata* and *Mygalopsis marki*, that almost completely overlap in call frequency, with *H. dendiculata* song suppressed in the presence of calling *M. marki*. In another species, *Mecopoda elongata*, which sings in choruses, levels of synchrony were reduced with increasing nocturnal rainforest noise [39]. Background noise can also induce changes in phonotaxis (the ability to move in an orientation with respect to a sound source). The playback of heterospecific calls or random noise interferes with female short-winged meadow katydid (*Conocephalus brevipennis*) movement towards conspecific male calls [40], while male grey bushcrickets (*Platycleis albopunctata*) move away from calling *M. marki* individuals, resulting in a separation of two sympatric species competing for acoustic space [41].

3. Receiver and noise source characterizations

To maximize the usefulness of research into the impact of anthropogenic noise, studies must suitably characterize the particular auditory receiver and noise source under consideration; it is common in the current literature to find that either or both are not done sufficiently to justify the conclusions drawn [11]. In this section, we highlight important general considerations in this regard (see also [10]), with particular

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reference to aspects of invertebrate sound detection that differ from most vertebrate hearing (see above).

(a) Auditory sensitivities

Determination of whether a given noise stimulus falls within the auditory capabilities of an organism is vital to assess correctly any apparent lack of effect. Characterization of invertebrate hearing should include appropriate consideration of pressure or particle velocity components of sound, as well as potential nonlinear auditory responses (where the sensory system does not respond linearly with input amplitude). Auditory nonlinearities have been demonstrated in mosquitoes [30], fruit flies [42] and the tree cricket *Oecanthus henryi* [43]; the latter represents the first evidence of nonlinear audition from a tympanal hearing insect. In these systems, the total sound level across frequencies can impact the sensitivity and tuning of the ear, indicating that even noise which does not overlap with the best frequency of the auditory system (frequency of highest sensitivity) may still generate signal masking and impede signal differentiation from the background.

Characterization of the mechanical properties of the ear and of auditory responses and physiological measurement of auditory thresholds are relatively simple to obtain in invertebrates owing to the peripheral location of many auditory structures and ease of access to auditory neurons [22]. This is true for invertebrates sensitive to pressure and particle velocity; for each of these types of receiver, there are good examples of auditory characterization at the mechanical and physiological level (see [29,31,42–44]). Moreover, neurophysiological methods have been developed to measure auditory thresholds both in the laboratory and the field in Orthoptera [45]. Natural habitats have sound fields that are far more complex than laboratory conditions, generating differences in the thresholds of what is perceived by the animal, which makes it important to put laboratory work into an ecologically relevant context.

(b) Noise quantification

To avoid erroneous conclusions, it is critical to quantify the noise source using tools that best reflect the auditory capabilities of the study animal. However, most readily available, and commonly used, audio equipment is designed for human aural sensitivities, and thus studies have often restricted recording and playback to frequencies audible to us (20 Hz–20 kHz) and employed recording filters that emulate human hearing (e.g. A-weighting filter (dBA)). While this approach has been deemed acceptable for birds, which hear in a similar frequency range to us and on which the majority of terrestrial work has so far been conducted, noise quantification ideally needs to cover broad bandwidths extending beyond audible frequencies using unweighted, flat-response recording equipment. A study by Schaub *et al.* [28] on bat foraging sets a robust standard for quantification of anthropogenic noise in a way relevant to the study species: they measured road traffic noise between 0 and 50 kHz with a flat-response microphone, showing the majority of energy concentrated below 5 kHz. Moreover, Schaub *et al.* quantified the number of vehicles, vehicle type and distance from the noise source; as the same type of noise source can produce highly variable sounds and the frequency content and amplitude are dependent on the distance from the source, including these factors adds valuable information. In general, studies should ideally report a range of relevant acoustic metrics (e.g. dB, weighting function, maximum power, integration time and order statistics); making high-quality audio recordings of the noise source being studied available for alternative spectral filtering and acoustic analysis would potentially represent the best practice and allow the greatest opportunity for comparative work and generalization (for further details see [10,46]).

For the study of some invertebrates, recording particle velocity or substrate vibration generated by anthropogenic noise, and mimicking these components in playbacks, should be a crucial element of the work. To date, there has been little attempt to quantify these components of terrestrial anthropogenic noise or their impact on animals sensitive to such stimuli (but see [34]), not least because the majority of studies have been conducted on organisms (i.e. vertebrates) for which these considerations are not important. The pressure component of a sound wave, the quantification of which is discussed above, can differ considerably from particle velocity [32] and measuring particle velocity or substrate vibration presents technological challenges. The majority of available microphones are pressure sensitive, but some do detect the pressure gradient, which combined with the use of integrating amplifiers output the particle velocity of a signal. These tools have been used successfully to record particle velocity in studies examining audition, communication and mate location in insects [42]. Likewise, the measurement of substrate vibration is frequently carried out in other contexts by employing accelerometers or non-contact laser Doppler vibrometry [33]. Thus, there is the capacity to measure these aspects of a noise source that are relevant to some invertebrate hearing.

4. Can invertebrates provide model systems to investigate the impact of anthropogenic noise?

Our review of the current anthropogenic noise literature has identified three key issues that we believe need resolving (see [11]): a behavioural bias, the difficulty in drawing strong, ecologically valid conclusions and a need to determine the effects on individual fitness. In this section, we outline these issues and then consider whether invertebrates can help with their resolution.

(a) Behavioural bias

The majority of studies (60 out of 83) investigating the impact of anthropogenic noise on terrestrial species have considered behavioural responses (see the electronic supplementary material). The most commonly researched behaviour is acoustic communication and particularly ways in which animals might minimize the risk that their auditory signals are masked; masking occurs when there is an increase in the threshold for detection or discrimination of one sound in the presence of another. Loss of clear and efficient transmission of acoustic information can create potential fitness costs, including those related to mate attraction and territory defence if song is masked, increased predation risk if detection of alarm calls is impaired and reduced reproductive success if parent–offspring or parent–parent communication is disrupted (see [14]). Consequently, anthropogenic noise has resulted in alterations to the vocal parameters (frequency, amplitude, rate and duration) or the timing of signalling in many birds

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and anurans, either through behavioural plasticity or evolutionary adaptation [14,47,48]. Some studies have also considered the impact of masking on adventitious signals [28,49]. For instance, greater mouse-eared bats (*Myotis myotis*), which listen for prey-generated sounds to locate food, avoid foraging when exposed to playback of road traffic noise and exhibit reduced foraging efficiency when noise is unavoidable. There is also some evidence that noise can mimic communicatory signals [34] and that vigilance behaviour is modified [50].

In contrast to behavioural adaptations, relatively little research has considered how anthropogenic noise impacts physiology ([8]; but see [51,52]), and there have been virtually no investigations with respect to development, neurobiology or genetics. Assessing how noise affects processes in addition to behaviour is vital for a full understanding of both proximate and ultimate impacts on fitness [8]. There is a long history of studying such fundamental processes in invertebrates in other contexts [53,54]. For example, by using genetic techniques and physiological and mechanical measurement, the molecular genetic and neural components required for an ear to receive and actively amplify sounds are being pieced together in *Drosophila* (see [53]). Moreover, there are good examples where invertebrate physiology, development and genetics have been studied with respect to global changes other than anthropogenic noise. For instance, considerable research has focused on the potential impacts of climate change on development in insects [55,56], as well as genetic effects in mosquitoes and fruit flies (for an overview see [57]). Physiological responses to climate change have also been measured in many invertebrates (for discussion see [58]). Such approaches should be equally applicable to studies examining the impact of anthropogenic noise.

(b) Difficulties in drawing strong, ecologically valid conclusions

Strong conclusions about the impact of anthropogenic noise are often not possible because suitable controls are lacking [11]. For example, roads are noisy, but they also have high levels of disturbance, chemical pollution and light, and provide an edge habitat. Studies comparing the responses of animals near a noisy road with those in a control area, either a quieter road or a site at a greater distance from the road, do not allow any differences to be conclusively attributed to noise. An experimental approach where noise is the only factor that differs is ideally required to tease out the direct effect of noise from potentially confounding factors.

Studies by Francis *et al.* [59] and Bayne *et al.* [60], for example, have highlighted that it is possible to provide strong evidence for the impact of noise using natural experiments: they have taken advantage of areas containing gas wells that either have or do not have noisy compressors to show that anthropogenic noise affects birds at both the species and community level. As the wells are comparable in both structure and surrounding habitat, and thus differ only in noise production, this system provides an excellent test of the impact of anthropogenic noise under field conditions. Such natural experimental situations may be rare, however, and manipulations are usually required. Careful controls are often the easiest in laboratory experiments, where more detailed data collection than in the wild is also potentially feasible [28,49,61], but care must be taken when extrapolating results to meaningful implications for free-ranging animals in natural conditions; the ecological validity of laboratory-based work can be questioned. Field experiments are becoming more common (e.g. [62,63]), but can be logistically more difficult, with the same level of control and detailed data collection harder to achieve than that in the laboratory, and characterization of some responses (e.g. neurological) particularly challenging. Studies that pair different types of work in different settings [48,64] offer the best solution, allowing the benefits of each approach to be used.

Invertebrates are amenable to a combined laboratory and field approach; they are small enough to be kept in large numbers in captivity and they can be manipulated in the wild. Römer *et al.* [38] provide an excellent example of this in their work with katydids, examining the influence of the acoustic environment on signal transmission. Investigating responses to masking by heterospecific noise, this study pairs both behavioural and neurophysiological measurements of auditory neurons in the field and laboratory settings, providing ecological validation for the laboratory work and technical controls for any confounding variables in the fieldwork. Further examples of experiments conducted in both the field and laboratory can be found in other orthopteran species. Schmidt & Römer [45] investigated neurophysiological detection thresholds for conspecific song in tropical crickets under noisy conditions, while studies of directional sensitivity in grasshopper audition [65] and katydid discrimination between background noise and calls of approaching predators [66] also used this paired laboratory and field approach.

(c) Need to evaluate effects of noise on individual fitness

Ultimately what is needed for successful policy-making and mitigation is consideration of how anthropogenic noise impacts individual survival and reproductive success, and consequently population and community structure. However, the vast majority of experimental studies to date have considered relatively short-term effects (see the electronic supplementary material), which do not necessarily have clear implications for fitness; at best, most of the current literature reports fitness proxies (see [11]). Some short-term effects (e.g. increased predation risk) can be translated relatively easily into ultimate consequences. However, others (e.g. foraging behaviour, signalling characteristics, movement patterns) need more careful consideration because animals may be able to compensate in quieter periods, the implications of the behavioural change are unclear or there may be costs associated with the noise-induced adjustment [14], and thus there may be no direct link between short-term effects and long-term consequences (see [67]). That is not to say changes in fitness do not result, but rather that the experiments required to determine them have rarely been carried out (but see [59,64,68,69]). A multi-year study by Francis *et al.* [59] demonstrated that some species might actually gain from additional noise if, for instance, potential predators avoid the area, and thus implications for individual fitness and community structure are not necessarily easy to predict.

As the life cycle of invertebrates is relatively short, it enables individual fitness and population viability to be assessed directly in a way that is logistically difficult in many vertebrates. Research into climate change provides good examples of how potential impacts of environmental modification on insects can be developed [70]. For example, an intergenerational

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study on the pitcher-plant mosquito (*Wyeomyia smithii*) has revealed large decreases in fitness in response to changes in photoperiod and climate over evolutionary time-scales [71]. In a tropical butterfly (*Bicyclus anynana*), resource availability and temperature were found to modify fitness-related traits, with implications for the impacts of climate change on this species [72].

It is also possible to use data on individual fitness consequences to parametrize theoretical models making predictions about outcomes at a population level. Such agent-based modelling has previously been applied to environmental resource management, and to ecological and conservation issues [73]. If modelling such as this can be introduced to anthropogenic noise research, individual-based fitness studies would be able to indicate conservation priorities without the immediate requirement for long-term data that are not likely to become available in the near future. However, validation of such models is a crucial element of the process, and this step is also feasible with short-lived invertebrate species: successive generations, with appropriate controls, could be bred under different noise conditions.

5. The future

In addition to the suggestions inherent in the previous sections, there are three main areas that we consider are in need of particular attention if research into anthropogenic noise is to move forward substantially. First, experimental studies to date have concentrated efforts on the impact of a single, acute noise exposure in isolation (e.g. [63,74]; but see [52,59,60,62]). While this is understandable from a logistical perspective, organisms in most natural situations are likely to experience either chronic or repeated exposure to noise, which might lead to changes in response through such processes as sensitization, habituation or tolerance [75]. Moreover, it is currently unclear precisely how the impacts of anthropogenic noise are affected by simultaneous exposure to such situations as high disturbance or light and chemical pollution; potential synergistic effects arising from the combination of noise with other stressors require investigation.

Second, the majority of (experimental) studies to date have tackled the simple, but important question: is there an immediate impact of noise? It is clear from the rapidly expanding literature that this is indeed the case across a range of taxa (see the electronic supplementary material). What is required now is consideration of additional issues that build on this knowledge. For example, what is the spatial scale of impact and the dose-dependent relationship between noise and responses? What characteristics of anthropogenic noises are most problematic; it is unlikely that it is simply the amplitude that matters, but do such aspects as predictability, rise time, and frequency range and modulation also play a key role? How quickly do animals recover to pre-exposure levels and do they show compensation for any noise-induced responses? How are different members of the same species affected by the same noise; are there, for example, age-, sex-, size- and condition-dependent responses?

Third, it is clear that the same noise may not affect different species in the same way. Such variation in impact could have consequences at the dyadic level (i.e. when two species interact). For example, if a predator is affected in a more detrimental manner than its prey [49], the reproductive success of the latter may be enhanced in noisy environments. There could also be consequences in terms of community structure. Francis *et al.* [59] have found, for instance, that the nest success of certain bird species increased at noisy treatment sites compared with a quiet control, owing to a decrease in the abundance of predators. To date, there have been relatively few attempts to consider how anthropogenic noise affects biodiversity *per se* (but see [59,60,76]) and findings are mixed and potentially taxon specific. For instance, Herrera-Montez & Aide [76] found that although avian biodiversity declined in noisy areas, anuran biodiversity was not significantly affected. Finally, recent work has provided, to our knowledge, the first evidence that anthropogenic noise could affect ecosystem services: Francis *et al.* [77] showed that noise could influence pollination and seed dispersal. Interactions at the community and ecosystem level are clearly more complex than when considering single species, but are crucial for a full understanding of the potential impact of anthropogenic noise.

Although the issues outlined above can potentially be addressed using vertebrates, intergenerational studies considering the impacts of chronic or repeated exposure, as well as the possibilities for recovery and compensation, are achievable within relatively short time-frames using invertebrates. Likewise, their small size and the relative ease of maintaining populations in the laboratory make it possible to examine the impacts of complex interactions with other stressors, dose- and condition-dependence and intrapopulation differences in response. Moreover, as invertebrates can be good bioindicators of impacts of environmental change [78], they offer an ideal opportunity to track the impact of anthropogenic noise on wildlife in natural habitats. Not only are invertebrates useful as models and indicators, but their ubiquity in ecosystems throughout the world makes it important to assess how noise is affecting them *per se* together with their interactions with other species within the ecosystem.

6. Conclusion

Anthropogenic noise is an issue of international concern and studies of its potential impacts are important and becoming more prevalent. For brevity, this review has focused on terrestrial species, but there is also increasing awareness of the effects of such noise in aquatic environments [3,9]. Little direct work has so far investigated how invertebrates, despite their probable vulnerability, are impacted (but see [12,13,79,80]). One potential reason for this is that regulators and policymakers are intrinsically more interested in how noise affects charismatic vertebrates. However, research on invertebrates is not only important (invertebrates are critical elements of all ecosystems, not least in providing the food for most vertebrates), but also has the potential both to assist with some of the current issues apparent in the literature and to drive the field forward, thus establishing the full impact of this global pollutant. Unlike, for example, climate change and ocean acidification, where studies are considering future predicted changes, anthropogenic noise is an issue in the present day. Advancing our knowledge of its impacts and developing mitigation measures is therefore of pressing importance, and we argue that the study of invertebrates, perhaps within the valuable framework recently outlined by Francis & Barber [10], can play a crucial, yet currently underused role.

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DISEASES AND MORTALITY IN FREE-RANGING BROWN BEAR (*URSUS ARCTOS*), GRAY WOLF (*CANIS LUPUS*), AND WOLVERINE (*GULO GULO*) IN SWEDEN

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ABSTRACT: Ninety-eight brown bears (*Ursus arctos*), 20 gray wolves (*Canis lupus*), and 27 wolverines (*Gulo gulo*), all free-ranging, were submitted to the National Veterinary Institute, Uppsala, Sweden, during 1987–2001 for investigation of diseases and causes of mortality. The most common cause of natural death in brown bears was infanticide. Infanticide also was observed in wolverines but not in wolves. Traumatic injuries, originating from road or railway accidents, were the most common cause of death in wolves and occurred occasionally in brown bears. Most wolverines were submitted as forensic cases in which illegal hunting/poaching was suspected. Sarcoptic mange was observed in several wolves but not in brown bears or wolverines. Sarcoptic mange most likely was acquired from infected red foxes (*Vulpes vulpes*) that were killed by wolves. Other parasites and infectious diseases were only found sporadically.

Key words: Brown bear, *Canis lupus,* diseases, forensic medicine, *Gulo gulo,* infanticide, mange, mortality, pathology, *Sarcoptes scabiei,* trauma, *Ursus arctos,* wolf, wolverine.

INTRODUCTION

Free-ranging populations of brown bear (*Ursus arctos*) and gray wolf (*Canis lupus*) have increased on the Scandinavian Peninsula during the last two decades, whereas wolverine (*Gulo gulo*) numbers have slowly declined. The brown bear population in Sweden was estimated at approximately 1,000 animals in the year 2001; the most recent estimate of the wolverine population was 250 animals (Anonymous, 1999). Approximately 25 yr ago, the wolf population included less than five individuals, but during the last 20 yr, it has increased to more than 100 animals (Anonymous, 1999). Sweden has a hunting season for brown bears, and approximately 50–60 are harvested annually. General county permits issued by the Swedish Environmental Protection Board regulate this hunting, and a limited number of permits are issued to each county. Permits to capture or kill wolverines (usually two–five animals) are issued by the Swedish Environmental Protection Board for protecting semidomestic herds of reindeer (*Rangifer tarandus*) in northern parts of Sweden. The wolf is almost completely protected by national legislation, and only a limited number of permits for killing individual problem wolves have been issued.

Brown bears, wolves, and wolverines that are found dead in nature, that die during research, or that are shot with permission from the Swedish Environmental Protection Board or county authorities are, according to Swedish legislation, the property of the Swedish state. Dead animals of these species must be reported to the local police and, thereafter, submitted to the National Veterinary Institute (NVI) or the Swedish Natural History Museum for examination and preservation. Because it is responsible for forensic cases, the NVI receives a majority of these animals when natural mortality because of disease is suspected and when the cause of death is not obvious. Animals that die in conjunction with wildlife research projects also are submitted to the NVI.

General knowledge about diseases and natural mortality among free-ranging bears, wolves, and wolverines in Sweden is

sparse, mainly because of the depressed populations during recent decades and limited submissions for diagnostic evaluation. This information is important, because excessive natural mortality can have negative impacts on management success for these species. With recent increases of large-predator populations in Sweden, increasing numbers of animals are available for diagnostic evaluation at the NVI every year. The present study summarizes diseases and causes of death of brown bears, wolves, and wolverines examined at the NVI from 1987 to 2001.

MATERIALS AND METHODS

Ninety-eight free-ranging brown bears, 20 wolves, and 27 wolverines examined at the NVI between 1987 and 2001 were included in the present study. Necropsies were conducted on all animals according to a standard protocol, with special attention given to forensic cases. For cases in which poaching was suspected, as well as in most forensic cases, the whole animal was radiographed to detect fragments of bullets or lead pellets. Animals were aged according to body size, weight, and dental development and were classified as juvenile (<1 yr), young (1–2 yr), or old (≥3 yr).

Specimens from liver, spleen, kidney, heart, and lung, as well as any tissue with signs of disease, were fixed in 10% neutral buffered formalin, sectioned at 4 μ, and examined histologically. When bacterial infections were suspected, liver and spleen or tissues with lesions were cultured for bacterial growth. In cases when parasitic infections were suspected, macroscopic examinations of the stomach, intestine, and lungs as well as fecal floatation and washing tissue through a sieve were used to recover parasites for identification. Samples of diaphragm or cheek muscle were routinely evaluated for *Trichinella* spp. by trichinoscopy or a digestion method (Roneus and Christensson, 1979).

RESULTS

Brown bear

Causes of mortality in brown bears are shown in Table 1. The most frequent cause of natural death was traumatic injury; 16 bears (16% of total submissions) were killed by other bears. All but one of these cases were young bears, and based on supporting observations from the field, these were classified as infanticide. Nine of these bears were less than 1 yr old, and six were 1–2 yr old. Eight were females, and seven were males. One bear was an adult female, and in this case, a male bear killed both cub and sow. Road accidents were the cause of mortality in five bears (5%). Three bears (3%), all younger than 1 yr, died from starvation.

TABLE 1. Causes of mortality in brown bears (*Ursus arctos*) examined at the National Veterinary Institute, Sweden, in the years 1987–2001.

Cause of mortality	No. of animals (%)
Killed by bear	16 (16)
Vehicular collision	5 (5)
Emaciation	3 (3)
Circulatory collapse	2 (2)
Septicemia	1 (1)
Forensic cases[a]	41 (42)
Euthanized[b]	12 (13)
Wildlife research[c]	9 (9)
Unknown	7 (7)
Total	98 (100)

[a] Killed by hunters in self-defense or suspected to be illegally shot
[b] Killed because either repeatedly killing domestic animals or appearing in villages and/or eating out of garbage bins or bee houses
[c] Died in conjunction with immobilization

Most forensic cases involved bears killed by hunters in self-defense during moose hunting. Seven bears were killed with special permission, because they were repeatedly appearing inside villages and/or eating from garbage bins.

Nine and 41 bears were examined for intestinal parasites and *Trichinella* spp., respectively. No parasites were detected.

Wolf

Causes of mortality in wolves are shown in Table 2. The most common cause of death in wolves (seven animals, 35% of total) was traumatic injuries associated with vehicular collisions.

One wolf, a young female, was killed as a result of a broken skull. Presumably, this injury was inflicted by a moose, as determined by supporting field evidence (observed tracks) that indicated a fight had

TABLE 2. Causes of mortality in wolves (*Canis lupus*) examined in the National Veterinary Institute, Sweden, in the years 1987–2001.

Cause of mortality	No. of animals (%)
Sarcoptic mange	4 (20)
Traffic collision	7 (35)
Killed by moose	1 (5)
Septicemia	1 (5)
Malformation	1 (5)
Forensic cases[a]	4 (20)
Euthanized[b]	1 (5)
Unknown	1 (5)
Total	20 (100)

[a] Killed by hunters in self-defense or suspected to be illegally shot
[b] Killed because either repeatedly killing domestic animals or appearing in villages and/or eating out of garbage bins or bee houses

taken place between a moose and wolves. Sarcoptic mange, most likely acquired from affected red foxes (*Vulpes vulpes*), was the primary mortality factor in four wolves. Three of the four cases of sarcoptic mange occurred in the year 2001 in a family group; one 1-yr-old animal and two 1.5-yr-old animals were affected. Septicemia, caused by *Pasteurella multocida,* was observed in one wolf.

Malformation of the spinal cord was observed in a 6-yr-old male with hemivertebra of the seventh thoracic vertebra. Increasingly debilitating clinical signs were observed by volunteers tracking this animal approximately 3 wk before it was killed. The animal was finally paralyzed in the hind legs and was incontinent.

One female was killed because of increasing interactions with male dogs. Concern existed that cross-breeding might occur, and she had repeatedly killed hunting dogs. Four wolves were examined as forensic cases, and all four animals were killed illegally (either shot or run over by snowmobile).

Seven animals were investigated for intestinal parasites and nine for *Trichinella* spp. Of these, one wolf was infected with *Taenia hydatigena* and another with *Uncinaria stenocephala.*

TABLE 3. Causes of mortality in wolverines (*Gulo gulo*) examined in the National Veterinary Institute, Sweden, in the years 1987–2001.

Cause of mortality	No. of animals (%)
Predator/other wolverine	11 (41)
Nephritis	1 (4)
Forensic cases[a]	9 (33)
Wildlife research[b]	3 (11)
Unknown	3 (11)
Total	27 (100)

[a] Killed by hunters in self-defense or suspected to be illegally shot
[b] Died in conjunction with immobilization

Wolverine

Causes of mortality in wolverines are shown in Table 3. The most common cause of death (11 animals, 41% of submissions) was traumatic injuries inflicted by other predators or wolverines. Other wolverines were identified as the source of this trauma in four cases; the source was uncertain in the remaining seven cases. Chronic nephritis was the primary cause of death in an old and emaciated male. Nine wolverines were examined as forensic cases, and all were found to have been either shot or killed in an illegal activity, such as being run over by a snowmobile and killed by a head trauma.

DISCUSSION

The present study was restricted to animals submitted to the NVI, and the results may not accurately represent all causes of natural mortality among these species in Sweden. For example, very young animals will be underrepresented in such submissions because of the den-related behavior of these species. These results, however, do provide information about causes of death associated with animals likely to be detected and reported by both the public and wildlife professionals. Many of the submitted animals were radiocollared as part of unrelated scientific studies. This was particularly true for wolves, because a large proportion of the existing population in Sweden is radiocollared and

most adults are found after death. This should provide very complete and accurate information regarding adult wolf mortality in the future.

Overall, the most common cause of death in brown bears, wolves, and wolverines was traumatic injuries, and in wolves, these injuries were associated with vehicles. This may reflect the natural habit of wolves to move long distances from forests in the west and north of Sweden into more populated and road-dense areas in the east and south. Only five brown bears (5%) and none of the wolverines died from vehicle-related injuries, reflecting that these animals live in sparsely populated mountain and forest areas in the north and west of Sweden; both areas have few major roads. This contrasts with the results reported for black bears (*Ursus americanus*) in Florida, USA, where accidents related to vehicles caused more than 50% of reported mortality (Dunbar et al., 1998). This difference may be explained by the fact that Florida has a road-dense area.

In brown bears and wolverines, intraspecies killing (infanticide) was the most common cause of natural mortality. Infanticide often could be verified with supportive field evidence of fighting, because animals were radiocollared or being tracked. Infanticide is believed to relate to limited resources, social pathology, parental manipulation, predation, and/or sexual selection (Hausfater and Hrdy, 1984), and it has been reported in a large number of animal species and humans (Hrdy, 1979; Hausfater and Hrdy, 1984; Dunn et al., 2002). Infanticide has been reported previously among brown bears in Sweden (Swenson et al., 1997). Intraspecific fighting among wolverines also has been reported previously in northern Scandinavia and was the most important cause of juvenile mortality (Person et al., 2003). Infanticide in brown bears probably is associated most commonly with territorial males (Swenson et al., 1997). As indicated by one observed case in which both an adult female and her cub were killed, such mortality also may occur in adults while presumably defending their young.

Several ongoing wildlife research programs in Sweden involve large predators, and a large number of the brown bears, wolves, and wolverines are currently fitted with radiocollars or intra-abdominal radiotransmitters. These animals are easily found when dead; this allows accurate estimates of illegal hunting, which unfortunately still occurs in Sweden (World Wildlife Fund Sweden, 2001).

Mortality caused by infectious diseases in free-ranging brown bears appears to be uncommon. Captive brown bears reportedly have died from Aujeszky's disease (Banks et al., 1999), but this disease has not been observed in free-ranging animals, even in areas where wild boar (*Sus scrofa*) are infected (Capua et al., 1997). Mortality caused by infectious diseases, with the exception of sarcoptic mange, also seems to be rare in free-ranging wolves in Sweden. We found one case of septicemia caused by *P. multocida* but no indications of mortality associated with any other infectious disease. Reports on infectious diseases in free-ranging wolves include canine parvovirus infection (Mech and Sagar, 1993; Johnson et al., 1994), rabies (Rupprecht et al., 2001), canine distemper (Johnson et al., 1994), and leptospirosis (Khan, 1991). Mortality among wolf pups has been reported as a possible result of canine parvovirus or canine distemper infection in wild wolf packs in the USA (Johnson et al., 1994; Mech et al., 1997). Both the presence and potential impact of viral infections in Swedish wolves are unknown, and to our knowledge, no serologic data are available. Because the causes of mortality among wolf pups in Sweden are also unknown, obtaining more information regarding viral or bacterial diseases that occur in the wolf population may be warranted. The potential impact of sarcoptic mange, which was found in several wolves of the present study, also deserves attention, especially given the social behavior of

this species and the potential for introduction by other domestic or wildlife species.

Information related to diseases and mortality in wolverines is sparse. Addison and Boles (1978) as well as Wilson and Zarnke (1985) reported on parasites in wolverines, and with the exception of a serologic survey of orthopoxviruses in carnivores in Scandinavia (Tryland et al., 1998), we could find no other reports of infectious diseases in wolverines.

Endoparasites were uncommon in all species included in the present study. This is in contrast to results for these species reported from North America (Addison and Boles, 1978; Phillips and Scheck, 1991) and Belarus (Shimalov and Shimalov, 2000), where endoparasites appear to occur more frequently. *Trichinella* spp. is reported in wolves from many parts of the world (Dick and Pozio, 2001) and in grizzly bears from Alaska (Zarnke et al., 1997). This parasite is quite common in red foxes in Sweden, and it has been found previously in large predators in Sweden (Mörner, 1992). The reason we did not detect *Trichinella* spp. in brown bears in the present study is not understood but may relate to food habits. Brown bears do not normally feed on red foxes or badgers (*Meles meles*) (Dahle, 1996; Sandegren and Swenson, 1997), which represent the main reservoirs of *Trichinella* spp. in Sweden. *Trichinella* spp. also was not found in 20 brown bears examined during the 1970s in Sweden (Roneus and Christensson, 1979) but was reported to be present in 9% of brown bears and 33% of the wolves examined in Finland from 1996 to 1998 (Oivanen et al., 2002). The high prevalence among wolves in Finland could be related to the high infection rate (38%) of *Trichinella* spp. in the raccoon dog (*Nyctereutes procyonides*), which is not present in Sweden (Oivanen et al., 2002). In Finland, the infection rates in brown bears and wolves were highest in the southwestern part of the country, where the raccoon dog is common.

Malformation of the spinal cords was observed in one 6-yr-old male wolf. This male is believed to have sired two litters. If hereditary, this malformation might be important in the future wolf population, as has been described in dogs (Kramer et al., 1982). However, no more cases of spinal cord malformations have been observed during the last 3 yr.

Swedish brown bear and wolf populations currently are increasing, and the animals generally are in good condition. The present report demonstrates that infectious diseases, possibly with the exception of sarcoptic mange in wolves, do not seem to be a factor that is negatively impacting these populations. Illegal killing and mortality associated with other human activity, however, are problems that could potentially impact future management of these species, especially in the case of the wolf population. The cause of the negative trend in wolverine numbers is unknown, but results suggest that it may relate to illegal killing.

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Sources and Patterns of Black Bear Mortality in Louisiana

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Abstract: Louisiana black bears *(Ursus americanus luteolus)* are protected under the Endangered Species Act and live in 3 isolated geographic areas thought to encompass nearly all breeding individuals for that subspecies. Management strategies to recover these bears continue to evolve without knowledge of any differences in demographic patterns among these populations. We summarized data on Louisiana black bear deaths to see if any evidence existed for differences in mortality patterns among the 3 subpopulations. Since June 1992, 34 of 75 (45±6 [SE]%) verified losses (72 deaths plus 3 live removals) were caused by vehicular collisions, including road kills (27), farm equipment (5), and train (2), which was the most common cause of death. Although this bear subspecies has been protected under the Endangered Species Act since 1992, at least 12 (16±4%) have been illegally shot. Nearly two-thirds of verified deaths have come from the coastal population, which is not believed to be as abundant as the population in northeast Louisiana. Also, mortalities in the coastal population were predominantly adult females, whereas subadult males dominated mortalities in northeast Louisiana. Given the frequency with which adult females have been lost from the coastal population, the geographic limits of suitable bear habitat, and increasing development, long-term viability of this population is precarious. Patterns of observed mortalities alone suggest that conservation agencies must develop area-specific management strategies for these 3 isolated populations.

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In the Coastal Plain of the southeastern United States, several relatively isolated black bear populations exist which differ by geographic extent and availability of

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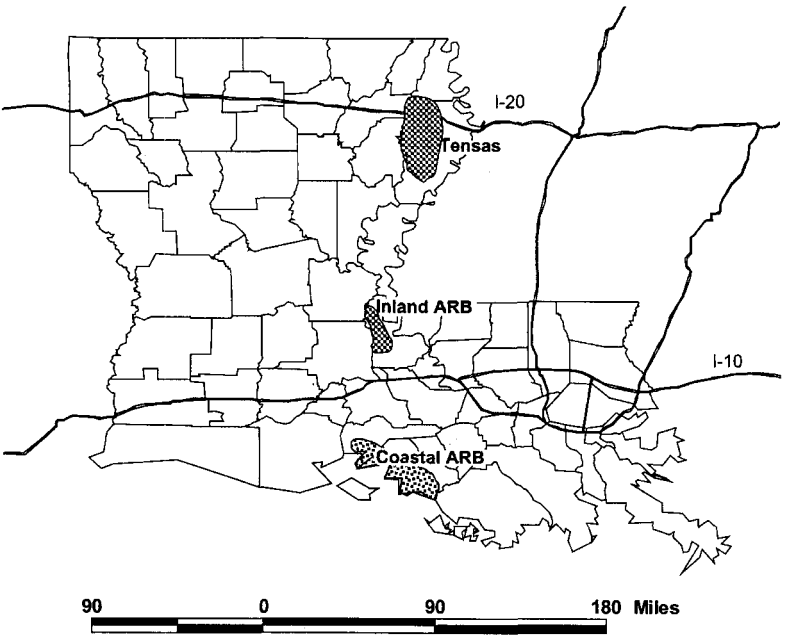

Figure 1. Louisiana black bear populations study areas designated for the analysis of mortality patterns.

habitat and are imperiled in the region primarily because of habitat loss (Wooding et al. 1994). Therefore, habitat enhancement and protection actions should dominate recovery or maintenance strategies offered for regional and state-wide bear populations. However, demographic patterns may affect short-term stability of local populations. Reproductive outputs vary within and among black bear populations, but this variability is generally thought to be a consequence of food availability and habitat quality (Pelton 1982, Bunnell and Tait 1981). Even if reproduction, which is generally difficult to monitor in unharvested bear populations, could be quickly enhanced through management, increased reproductive output does not always produce recruitment (Garshelis 1994). Conversely, differing mortality patterns may be a useful short-term indicator that new management emphases may benefit a local bear population. Evaluations of mortality patterns, in particular road kills, have been published for other coastal southeastern coastal plain bears, including North Carolina (Warburton et al. 1993), Florida (Wooding and Brady 1987) and the Great Dismal Swamp in Virginia (Hellgren and Vaughan 1989). We examined mortality sources and patterns for 3 relatively isolated black bear populations in Louisiana to determine if differences emerged among these populations or with other published reports that suggested differing management emphases were warranted.

Because all of Louisiana lies within the historic range of *U. a. luteolus* (Hall 1981), all Louisiana bears are protected by similarity of appearance and listed as threatened under the Endangered Species Act of 1973 (Fed. Reg. 57[4]:588:595).

Three relatively isolated geographic areas encompass all the known black bear breeding populations in Louisiana (Fig. 1). Probably the most numerous bear population located is in northeast Louisiana and is composed of 2 subpopulations with minimum interchange due to their separation by U.S. Interstate 20 (Pace et al. in press). The Inland Atchafalaya River population is considerably smaller than the other 2 populations (Pace et al. in press). All 3 populations have been subjects of continuous capture and tagging efforts since 1992 (Pace et al. in press) and researchers, together with the various responsible wildlife managment agencies, have placed a high priority on investigating and reporting bear deaths. However, no attempt had been made to summarize these data and assess their usefulness for setting management strategies.

We are grateful to many biologists, agents, mangers, technicians, and students who spent many field hours helping acquire these data. Research efforts have been supported by a wide array of public and private funding arrangements including considerable support from the U.S. Fish and Wildlife Service and the Louisiana Department of Wildlife and Fisheries. We are also grateful to an increasingly knowledgeable and responsive public in Louisiana who reported many of the otherwise unverifiable bear deaths or who otherwise aided our agencies' efforts. We thank D. Hightower, M. Vaughan, R. Wagner, and an anonymous referee for their reviews of our manuscript.

Methods

The 3 areas in Louisiana with occupied bear range are: 1) the Tensas River Basin (Tensas) on lands within, surrounding, and north of Tensas River National Wildlife Refuge (TRNWR), 2) the upper Atchafalaya River Basin (Inland ARB), especially the northwestern two-thirds of Point Coupee Parish, and 3) the coastal area west of the Atchafalaya River Delta (Coastal ARB), primarily south of U.S. Hwy. 90 in St. Mary and Iberia parishes. Considered part of the Tensas bear population, but north of and separated from TRNWR by U.S. Interstate 20 (I–20), are a number of bears living in small fragmented forest tracts owned by Deltic Timber Corporation. Tensas bears south of I-20 rarely encounter high-to-moderate traffic roads, whereas those north of I–20 are often forced to cross such roads to move among fragmented forest patches (Anderson 1997, Marchinton 1995). Road distribution and traffic volumes relative to bear habitat may be roughly comparable between Tensas north of I-20 and Inland ARB. In contrast, bear habitat in Coastal ARB is dissected by more well-traveled, paved, 2-lane roads. Row-crop agriculture is a common land use in all 3 geographic areas, but sugarcane farming is commonly practiced in Coastal ARB, occurs on the fringe of Inland ARB, and is absent in Tensas.

We pooled information from data bases held by 3 agencies to construct a list of verified bear mortalities. Verified mortalities were distinguished among reported mortalities by having filed reports demonstrating that agency personnel or bear researchers had examined the carcass. Dead bears were identified to study area, sex, age class (adult [>3], subadult, and cub of the year [<1]), whether or not the bear was tagged (ear tag and/or radio collar), probable cause of death, and date of death.

Dates of deaths varied in precision due to decomposition states of carcasses and were recorded as the first of the month if only month was reported.

We graphically explored data for patterns in timing of death (by year or month). We used loglinear models (Fienberg 1977) to examine associations between counts of deaths and sex, age (adult or subadult [included cubs of the year]), and area. Using a subset that excluded management and research-related losses, pooling among types of vehicular deaths and pooling other deaths, we used Fisher's exact test to examine if mortality counts by type (open situation vs. secluded situation) was independent of whether or not bears were tagged. This later test was performed to address whether or not inclusion of bears without radios would bias frequency of mortality causes toward vehicular deaths.

Results

Between 1 June 1992 and 31 May 2000, at least 75 bear (72) deaths plus live removals (3) occurred in Tensas (18), Inland ARB (8), and Coastal ARB (49) (Table 1). These 75 losses were attributed to road kills (27), unknown causes (15), shootings (12), management takes (8), sugarcane harvesting equipment (5), natural (4), research takes (2), and trains (2). Losses resulting from management actions included takes of 7 nuisance bears and 1 orphaned cub. Two management actions were live removals of nuisance bears from the population and their placement in zoos. The orphaned cub was moved from Coastal ARB to a rehabilitation center and later released at Tensas on 12 December 1997. It was radio-tagged at release and known to have left Tensas; its whereabouts are at present unknown. Management takes represented losses only to Coastal ARB (7) and Inland ARB (1). The 2 research takes were from deaths related to trapping efforts. Only 8 losses were observed for the Inland ARB population, and 4 of these were from illegal shooting. Mortalities were distributed somewhat uniformly among years (Fig. 2), but unevenly among months (Fig. 3). Relatively few deaths were

Table 1. Verified Louisiana black bear deaths (72) and live removals (3) from 3 areas arranged by probable source summed over years for the period 1 June 1992–31 May 2000.

Source	Coastal ARB	Inland ARB	Tensas	Total
Road kill	17		10	27
Poaching	6	4	2	12
Unknown	10	1	4	15
Management take[a]	7	1		8
Cane harvester	5		5	
Natural	2		2	4
Train	1	1		2
Research take	1	1		2
Totals	49	8	18	75

a. Includes 3 live removals. Two animals were placed in zoos. The third was moved from Coastal ARB to a rehabilitation center and later released at Tensas on 12 December 1997. It was radio tagged at release and known to have left Tensas; its whereabouts are at present unknown.

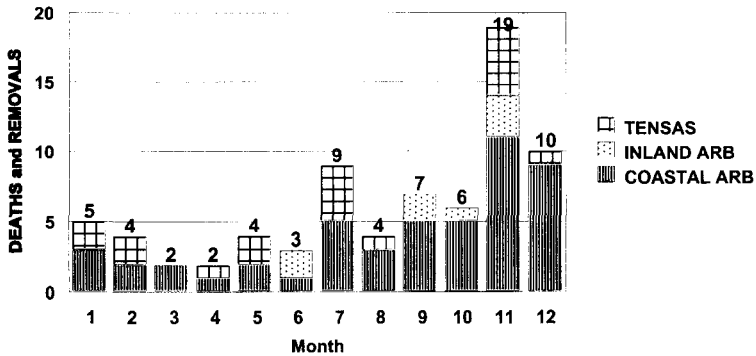

Figure 2. Verified bear deaths (72) and live removals (3) by year for the period 1 June 1992–31 May 2000 combined for 3 areas of Louisiana.

observed in the months of March through June (12±4%), whereas 25±5% occurred in November (Fig. 3). Road kills of males were nearly equal between January–June vs. July–December (6 vs. 8), whereas all 13 road kills of female bears occurred July–December (Fisher's exact test $P=0.016$). Mortality counts by source were nearly identical between sexes (all areas pooled) except for management takes (6M: 2F).

Despite small sample sizes, we had statistical evidence that mortalities ($N=65$), excluding research and management takes, were distributed disproportionately across areas by sex and age class (subadult and adult) ($\chi^2=9.18$, df=3, $P=0.03$). Adult female bears (42%) comprised the majority of deaths in Coastal ARB, whereas 9 of 18 Tensas bear deaths were subadult males (Table 2). During 8 years of observation, 8.5 times as many adult female bear deaths were recorded from Coastal ARB than Tensas. We observed 7 deaths of cubs of the year, all of which occurred in Coastal ARB.

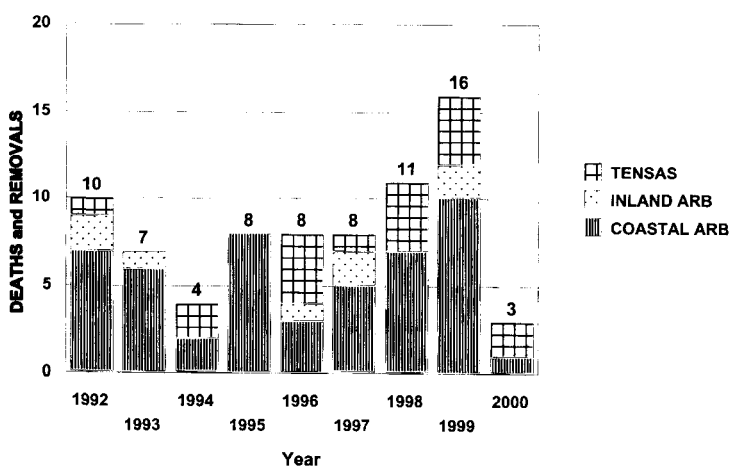

Figure 3. Verified bear deaths (72) and live removals (3) by month combined over the period 1 June 1992–31 May 2000 and over 3 areas of Louisiana.

Table 2. Verified bear deaths (72) plus live removals (3) arranged by sex, age, and area, and summed over years for the period 1 June–31 May 2000.

	Male		Female		
Area	Subadult	Adult	Subadult	Adult	Total
Coastal ARB	11	10	7	17	49[a]
Tensas	9	5	2	2	18
Inland ARB	2	1	1	3	8[b]
Totals	22	16	10	22	75

a. Total includes 4 bears of unknown sex and/or age.

b. Total includes 1 bear of unknown age.

Over all, 35% of dead bears (excluding research and management takes) were wearing radio collars and the proportion was the same for Tensas and Coastal ARB. We had no statistical evidence to suggest that the proportion of bears wearing radio collars differed between deaths in relatively open settings (road kills, sugarcane harvesting equipment, and trains) and deaths in relatively secluded settings (shootings, natural, and unknown) (Fisher's exact test $P=0.426$). Neither did proportions differ for open-setting deaths among radio tagged, ear tagged only, and untagged bears (Fisher's exact test $P=0.294$). These results suggest that including unmarked bears did not strongly bias the observed distribution of deaths among causes of mortality.

Discussion

Based upon habitat availability, trapping success, and associated observations during 1988–1998, the expert opinions of biologists have remained constant and place the combined or statewide bear population at 200–300 animals (excluding cubs of the year), with the population distributed according to Tensas > Coastal ARB >> Inland ARB. At such low population abundance, moderate levels of anthropogenic mortality will depress bear population growth rates, especially if adult females constitute many of the deaths. Hence, the larger number of deaths observed and the high proportion of adult females lost from Coastal ARB and Inland ARB were especially disconcerting. An analysis of mark-recapture data gathered during 1992–2000 (R. M. Pace, La. Coop. Fish and Wildl. Unit, Baton Rouge, La., unpubl. data) provided evidence for lower adult female survival in Coastal ARB (75.8±8.6%) than in Inland ARB (94.0±8.2%) which was more indicative of an unexploited bear population (Bunnell and Tait 1981).

Road kills are a common source of non-hunting mortality in bear populations (Pelton 1982). Evaluations of road kills have been published for other coastal southeastern coastal plain bears, including North Carolina (Warburton et al. 1993), Florida (Wooding and Brady 1987), and the Great Dismal Swamp in Virginia (Hellgren and Vaughan 1989). In general, young males are the most common group of bears in road kill statistics (Wooding and Brady 1987, Warburton et al., 1993), especially during

summer. As in North Carolina and Florida, road kills of female bears were more common in fall, which is at least partly explained by female home range and habitat use shifts in fall (Hellgren and Vaughan 1989, Nyland 1995, Wagner 1995). In Coastal ARB, many bears use sugar cane fields in fall (Nyland 1995), which places them near roads more often during summer than winter.

We continue to be amazed by the number of illegal shootings of bears in Louisiana. Some of these undoubtedly occurred as the result of nuisance situations in rural settings. Some were linked to perpetrators ostensibly engaged in legal hunting, and for whatever reason decided to shoot a bear. Although agencies and non-governmental groups have been engaged in a public information campaign and nuisance abatement program for several years, these takes do not seem to have slowed.

We are somewhat surprised by our lack of evidence that the proportion of bears wearing radio collars was different among mortality causes. Because of the relatively dense understory and forbidding terrain of areas occupied by bears in Louisiana, it would be extremely difficult to locate bears that died from poaching, unknown, or natural causes without a radio tag on or near the carcass. We believe that our considerable ongoing efforts to trap, tag, and monitor bears coupled with aid from landowners interested in our work, led us to many dead but uncollared bears. Concomitantly, radio tags probably allowed us to find some bears that were struck by vehicles and wandered away from the road (open setting mortality) to secluded sites. The net result is that we believe our tabulation of mortality sources is less biased than a study without any radio-tagged animals, but may be somewhat biased relative to a study based solely on radio-tagged animals.

Management Recommendations

Antropogenic causes of mortality are taking a relatively large toll on the Coastal ARB population, both in terms of absolute numbers and because adult females represent a high proportion of the take. Similarly, female losses in Inland ARB are unacceptably high if that small population is to recover. Conversely, the mortality pattern observed in Tensas was predictable from life history and behavioral knowledge of black bears: young male bears tend to disperse and face greater hazards (Wooding and Maddrey 1994). The Coastal ARB population represents a challenge if management goals include the long term maintenance or enhancement of this population. Wildlife conservation agencies can do little to slow increasing human population growth and development in the area. The U.S. Fish and Wildlife Service has begun acquisition of land for a refuge featuring bears within Coastal ARB. Agencies have already joined with academic and non-governmental groups to work toward Louisiana black bear restoration (Bullock 1992), but the education and public awareness efforts need to be increased. Because poaching appears to be a relatively substantial cause of mortality in Coastal ARB and possibly Inland ARB, any increase in enforcement activities should be directed to those areas.

Management plans include repatriation of native bears to suitable vacant habitat within the historic range of Louisiana black bears (U.S. Fish and Wildl. Serv. 1995).

An effective method for repatriation appears to be winter translocation of female bears with their cubs of the year. Repatriation actions require selections of source populations from which adult females would be taken. Our mortality data represent the first comparative demographic information upon which to base a selection of a source population. In an analysis of mark recapture data spanning the same 8 years for Coastal ARB and Inland ARB, Pace (La. Coop. Fish and Wildl. Unit, Baton Rouge, unpubl. data) estimated annual survival of adult females at 75.8±8.6% and 94.0±8.2%, respectively. The already relatively low apparent survival and the disturbingly disproportionate number of mortalities of adult females in Coastal ARB seem to disqualify Coastal ARB as a potential source population until a more complete analysis of the impact of these removals on the long-term viability of this population can be completed.

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Keywords:
grizzly bear mortality, train-wildlife collisions, inhibit wildlife movement

Abstract:
Between 2000 and 2007, the Canadian Pacific Railway emerged as the leading human-related cause of grizzly bear mortality in Banff National Park. Seven grizzlies were struck by CPR trains, and none of the five cubs orphaned by these collisions survived within the park. Other wildlife also have been struck and killed. Spilled grain, track-side attractants, and preference of animals for open travel corridors are cited as contributing to these collisions. CPR’s rail lines bisect the Canadian Rockies and, along with other factors, inhibit wildlife movement and genetic connectivity. Ecologists and conservations seek to implement measures to ensure continued ecological connectivity across these man-made barriers. Railways have adopted various methods to reduce wildlife mortality, including more efficient sealing of grain cars, vacuum cars to recover spilled grain, and warnings that alert wildlife of approaching trains. Fencing and crossing structures, such as those assisting wildlife to cross highways, also are being considered. We discuss the causes of train-wildlife collisions, steps taken to reduce the number of collisions, propose further opportunities to reduce the likelihood of collisions.

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Trains, Grains, and Grizzly Bears: Reducing Wildlife Mortality on Railway Tracks in Banff National Park

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Abstract: Between 2000 and 2007, the Canadian Pacific Railway emerged as the leading human-related cause of grizzly bear mortality in Banff National Park. Seven grizzlies were struck by CPR trains, and none of the five cubs orphaned by these collisions survived within the park. Other wildlife also have been struck and killed. Spilled grain, track-side attractants, and preference of animals for open travel corridors are cited as contributing to these collisions. CPR's rail lines bisect the Canadian Rockies and, along with other factors, inhibit wildlife movement and genetic connectivity. Ecologists and conservations seek to implement measures to ensure continued ecological connectivity across these man-made barriers. Railways have adopted various methods to reduce wildlife mortality, including more efficient sealing of grain cars, vacuum cars to recover spilled grain, and warnings that alert wildlife of approaching trains. Fencing and crossing structures, such as those assisting wildlife to cross highways, also are being considered. We discuss the causes of train-wildlife collisions, steps taken to reduce the number of collisions, propose further opportunities to reduce the likelihood of collisions.

Introduction

Connectivity, at a range of scales, is critical to the survival of wildlife populations. In Banff National Park in the Rocky Mountains of western Canada, Canada's main east-west highway, a principal rail line, and other natural and man-made barriers divide wildlife populations. Measures have been taken to mitigate the busy traffic on the Trans-Canada Highway, including fencing to increase motorist safety and reduce wildlife mortality, and under- and over-passes to promote safe wildlife movement. Speed limits and access are reduced on other roadways to conserve wildlife.

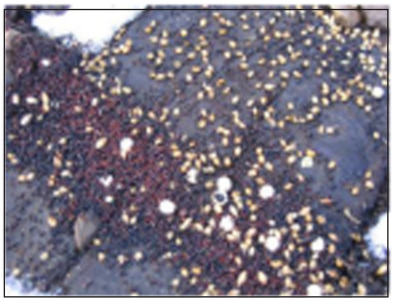
Since 2000, the Canadian Pacific Railway has emerged as "the number one known source of human-caused mortality" of grizzly bears in Banff National Park. Grizzlies and other animals are attracted to grain spilled from passing railway cars. Twelve grizzlies have been killed directly by trains or lost permanently to Banff National Park over the past seven years. This total includes four breeding age females and their seven cubs of the year. In 2006 alone, four black bears were killed. Necropsies by Parks Canada staff found grain in the stomachs of two of the black bears. More than a decade of efforts by the Railway has not meaningfully reduced the amount of grain on the tracks nor the number of animals struck and killed.

Spilled Grain

Grain spilled by rail cars has been identified by Parks Canada staff as the principal attraction that draws bears to their deaths between the rails in Canada's mountain parks. There are four major sources of spilled grain:

1. Derailments and other significant events that spill large amounts of grain;
2. Faulty, leaking, or improperly closed grain car discharge gates that spill small amounts of grain along the tracks, particularly along sections of tracks where cars are shaken in any way;
3. The temporary siding, stopping, or parking of grain trains, allowing leaking cars to spill larger amounts of grain in a single spot between the rails; and
4. The spillage of excess grain that has fallen onto flat surfaces of grain cars at the loading terminals and subsequently falls to the ground as the train moves along.

The Railway and government agencies respond promptly to derailments and larger spills, and usually take measures to prohibit bears and other wildlife from feeding on the spilled grain. Fencing, 24-hour human presence, Karelian bear dogs and other deterrents have been used until all grain has been cleaned. Similarly, minor spills from stopped or sided cars generally receive prompt attention, although some reported spills have remained on the tracks for more than 36 hours.



Smaller spills—with potentially more negative impacts on wild animals within Banff National Park—occur when small amounts of grain trickle along the tracks as loaded trains move west. Grain falls from hopper car discharge gates at the bottom of grain cars that are defective, worn or not closed properly. Of course, these are the same gates that spill larger amounts of grain when the cars move more slowly or with more jerky motions, or when the train is stopped.

The second source of trickled grain originates at terminals where grain hopper cars are loaded. Careless loading causes grain to fall outside of the hopper cars and collect on virtually every flat surface, including the tops of the cars and flat decks on either end of the cars. In turn, grain falls off these surfaces as trains move along. More than 10 cm of sprouting grain, spilled grain and detritus has been observed on hopper car end decks.

In 1990, the Canadian Pacific Railway introduced a specially designed self-powered vacuum truck to remove grain spilled on the tracks. The vacuum has proven effective on larger spills, but nearly useless on the constant streams of grain that trickles from leaking discharge gates and flat surfaces.

The Canadian Pacific Railway reports increased shipments of grain each year. Tracks were recently modified to accommodate even longer trains—up to two miles in length. So, there is increasing potential for grain spillage. Parks Canada wardens noted in 2006, “this is one of the heaviest years we’ve seen [for grain on the tracks].” Supervisors reported to the media, “our wardens are saying they’re seeing more grain on the tracks.”

It has been said that some leaking grain cars arrive at the Vancouver terminal completely empty. Grain can be found scattered along the tracks, heavier in locations where cars move more slowly or are jostled along the way. In some sections, spilled grain sprouts to a thick green carpet. The Farmer Rail car coalition estimates that up to Cdn $10 million worth of grain and pulse are spilled annually from leaking hopper cars hauled by the Canadian Pacific Railway.

The Canadian Pacific Railway leases bout 6,300 grain hopper cars that are owned by the Canadian federal government. These cars have been in service for 30 to 40 years, and carry a variety of discharge gate designs. New loading and unloading equipment used at terminals is more powerful, likely stressing older discharge gates. Most cars owned by the Railway are of newer design, compatible with powerful and high-speed terminal equipment. Anecdotal evidence suggests that some of the older designs may be the most troublesome—worn or damaged, and failing to close securely.

Grain and Dead Grizzlies

According to senior Parks Canada officials, “bears frequent the tracks because they get the reward of grain.” Dr. Stephen Herrero of the University of Calgary, one of Canada’s most respected grizzly bear experts, concluded that Canadian Pacific Railway trains “are the number one known source of human caused mortality” of grizzly bears in Banff National Park.

Between the spring of 2000 and mid-summer 2007, Canadian Pacific Railway trains struck and killed seven grizzly bears in Banff National Park alone. Four of these bears were breeding age females. None of the five orphaned cubs of the year survived in the park without their mothers. In 2006 alone, four black bears were struck and killed in Banff and Yoho national parks. Grain was found in the stomachs of two of the bears.

Bears and other wildlife are attracted to railway tracks for a variety of reasons—the promise of a meal between the rails, easy passage (particularly in the heavy snows of winter), and forage vegetation growing in open sunlight. In Canada’s Mountain Parks, grain has proven to be the most fatal attraction.

According to Edward Abbott, manager of resource conservation of Parks Canada’s Lake Louise, Yoho and Kootenay field unit, “bears frequent the tracks because they get the reward of grain. Over the years bears have a very good learning ability and they know where they get rewarded. And if they have been rewarded once, often they go back again just to check to make sure if there is anything there.”

We have observed and filmed a number of bears feeding between the rails and collected grain-filled bear scat along the tracks. More than a dozen bears have been seen in a single morning feeding at open railway tracks at Bath Creek Flats, near the border of Banff and Yoho national parks. When asked, some senior Parks Canada staff tell close friends and relatives that the best place to see grizzly bears in Banff National Park is along these tracks, as bears forage for grain. This is relatively open country, where the tracks offer no singular advantage of other forage or open travel. The bears are there because this is one of the very best dining areas along the “world’s longest bird feeder.”

Bears aren’t the only animals that seek grain and are killed between Canadian Pacific rails. According to Parks Canada figures, 564 elk, 9 moose, 51 deer were killed on CPR tracks between 1982 and 2001 in Banff and Yoho national parks. In turn, many of these carcasses attracted scavengers. During the same time period, 9 coyote and 9 wolves were killed by trains.

Management Responses by The Canadian Pacific Railway

The Railway conducted a wildlife mortality study in 1997. In 1999, the Canadian Pacific Railway, Parks Canada and other parties contributed to a seminal paper on railways and wildlife mortalities (Wells, P. et al. 1999, Wildlife mortalities on railways: monitoring methods and mitigation strategies. 11 pp. Unpublished.). The paper identified seven promising mitigation strategies: 1) concentrate mitigation strategies on identified problem areas; 2) instruct train crews to report wildlife incidents; 3) remove carcasses from right-of-way to reduce scavenging; 4) remove spilled attractants (e.g., grain) in a timely manner; 5) reduce chronic grain spills through car maintenance and loading/handling procedures; 6) reduce attractant vegetation on right-of-way; and, 7) share data among jurisdictions.

In the year this study was completed, the Canadian Pacific Railway put the industry's first vacuum truck into service, marking a major and innovative investment. The truck was designed to respond to reported spills and to clean spilled grain from the tracks. At the same time, the Railway instituted a program to train and encourage grain handlers at loading terminals. The intent was to reduce the amount of grain spilled on hopper car tops and end plates, and to ensure that discharge gates were fully closed and operating properly.

Prior to train departure, faulty discharge gates are to be noted and reported as "bad order cars." These cars are to be pulled from service and repaired. To date, the Canadian Pacific Railway has refused to release "bad order car" reports or to conduct public tests to document the spillage of grain or the effectiveness of its vacuum operations. And the Railway has declined to release the results of any tests it may have conducted.

The Railway has an agreement with Parks Canada to report grain spills and collisions with wildlife. Most reports are timely and adequate, but the process falls short on occasion. Parks Canada also agreed to allow the Railway to remove struck carcasses from the right-of-way onto park lands, reducing the likelihood that predators would be struck.

In a presentation to the American Association of Railroads in Urbana-Champaign, Illinois, USA in 2000, a representative of the Canadian Pacific Railway indicated that the company would carry out a number of measures to investigate and reduce the number of wildlife collisions, including trials of lights and sounds to alert wildlife, observations of wildlife behaviour, limited fencing, and programs to educate train crews and grain terminal operators. In addition, the Railway pointed to possible "future directions" including aversive conditioning, "science-based decision-making," "integrated research and planning" and crossing structures. The Railway has not reported any progress on these possible directions.

Under Canadian law, contracts and other agreements between government and private parties are governed by legal principles which consider the agreements as "privileged" in favour of the private party. As a result, the terms of the grain car lease, reports filed and other communications between the parties, and other documents are not—or in some cases, not easily—available to the public.

Media Responses by The Canadian Pacific Railway

Through most of this century, spokespersons for the Canadian Pacific Railway asserted the company was doing the best it could and that spilled grain was not a significant factor in the deaths of grizzly bears in the region. A sample of their responses, as recorded in local media, includes:

> "[The vacuum truck] does a good job of making the tracks as clean as possible so [the grain] is not evident. It has proven very effective." (August 5, 2004)
>
> "Look as a company at what we have tried to do to avoid contact with bears – we're trying our best." (Aug 25, 2005)
>
> "This is a bigger picture issue, not just a railway issue. It's the entire growth of human activity in that area. We're just one of the stakeholders. This is more of a community bear management issue." (Aug. 25, 2005)
>
> "But this is a bigger issue that just the railway..." (May 11, 2006)
>
> "I don't think grain is the issue here." (June 22, 2006)
>
> "We aren't a major contributor to bear mortality." (June 27, 2006)
>
> "We do have stringent measures in terms of our hopper maintenance and repair process that has been enhanced over the past year or two." (June 27, 2006)

The Big Breakthrough

On May 3, 2007, the Canadian Pacific Railway announced a new operating agreement with Canada's Ministry of Transport, Infrastructure and Community. The Railway's announcement read, in part (emphasis added):

> Under the agreement with Transport Canada, CP will, in addition to its normal maintenance practices, undertake over the next five years an extensive hopper car inspection and refurbishment program to ensure a quality fleet. **This will include the replacement of poor-performing discharge gates with technologically superior units as well as a general refurbishment program for the other gates on these cars.**

> "Canadian Pacific is pleased to have completed these extended negotiations with the federal government as it will ensure a secure hopper car supply for farmers and enhance operational fluidity," said Fred Green, President and CEO. **"This initiative will also strongly support our wildlife protection efforts by reducing grain and other wildlife attractants along our tracks."**

The refurbishment program on more than 6,300 hopper cars will take five years to complete at a cost of Cdn$20 million. The Railway expects to repair 70 percent of the cars by the end of 2010. The Canadian National Railway Company also agreed to invest Cdn$20 million in the 6,300 hopper cars it leases from the federal government.

Next Steps

Repairing leaking grain cars is a necessary—but not sufficient—step to reduce wildlife mortality on railway tracks. Animals will stray onto the tracks, even if grain is not present. And Banff's wild animals are habituated to finding grain on the tracks. As many as three generations of grizzly bears in Banff and Yoho national parks are accustomed to finding meals between the rails. For 15 years after open dumps were closed at Yellowstone National Park, bears returned looking for a meal. Additional steps will need to be taken as defective cars are repaired and as trains continue to move through Canada's premier national parks.

We suggest these steps to reduce wildlife collisions on CP Railway tracks:

1. Characterize sites where animals are struck, killed or frequently seen. The first step in understanding and reducing vehicle-wildlife collisions is to investigate the situations where animals are seen and struck. Was the incident on a straight or curved section? Does vegetation—particularly edible forage—grow close to the tracks? Is escape blocked by steep slopes, rivers, or embankments? Is there a known wildlife movement corridor in the vicinity?
2. Document wildlife incidents. Train crews should record location, time of day, weather conditions and speed of train. How far ahead of the train was the animal when spotted; what was it doing? How did the train crew respond (whistle, horn, lights, other)? How did the animal react and what was the outcome?
3. Test the effectiveness of lights to alert and deter bears and other wildlife. Train crews have reported that flashing lights appear to scare bears from the tracks.
4. Proceed as quickly as possible with the car repairs. "Bad order cars" should be pulled from service immediately. Measure the amounts of grain spilled at various locations to document the effectiveness of the repairs. In addition, measure the effectiveness of the vacuum truck.
5. Convene a workshop of wildlife managers, animal behaviour specialists, railway experts and others to address the causes and solutions to train-wildlife collisions.

While collisions with animals can have serious consequences for wildlife populations, relatively few trains strike wildlife on the tracks. To gather sufficient data for analysis, a larger data set likely will be needed. We suggest that the Canadian National Railway Company and the Burlington Northern Santa Fe Railway be engaged to contribute to the incident site characterizations and the collision incident reports.

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Invited Ideas

Fitness costs as well as benefits are important when considering responses to anthropogenic noise

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Trade-offs lie at the heart of behavioral ecology, with our ultimate understanding of many behaviors reliant on an assessment of both fitness benefits and costs. However, the rapidly expanding research literature on the impacts of anthropogenic noise (a recently recognized global pollutant) tends to focus on the benefits likely to be accrued by any resulting behavioral adaptations or plasticity. In particular, although studies investigating acoustic communication (the topic receiving the most attention to date) invariably discuss, and occasionally attempt to measure, the perceived benefits in terms of reduced masking that might arise from vocal adjustments by signalers, only rarely are the potential fitness costs even mentioned. The bias toward benefits prevents a full understanding of the consequences of anthropogenic noise, including the implications for population viability and community structure. Here, we argue for a greater consideration of fitness costs, outline a number of specific examples (reduced transmission distances, increased risk of predation/parasitism, altered energy budgets, loss of vital information), make suggestions about how to move forward, and showcase why a balanced view is as crucial in this field as any other aspect of behavioral ecology.

Key words: **acoustic communication, anthropogenic noise, costs and benefits, fitness, trade-offs, vocalizations.**

INTRODUCTION

Noise-generating human activities, such as urban development, transportation, and the exploitation of energy sources, increased considerably in the last century and have led to substantial changes in the acoustic landscape in both terrestrial and aquatic ecosystems (e.g., McDonald et al. 2006; Watts et al. 2007). A burgeoning number of studies have demonstrated that anthropogenic (man-made) noise can affect animals in various ways (see Tyack 2008; Barber et al. 2009; Slabbekoorn et al. 2010; Kight and Swaddle 2011); however, the topic receiving by far the greatest attention has been acoustic communication (Radford et al. 2012; Morley EL, Jones G, Radford AN, unpublished data). The possibility that signalers might alter their acoustic output as a consequence of anthropogenic noise has been suggested by correlational studies on a variety of taxa (e.g., birds: Slabbekoorn and Peet 2003; marine mammals: Parks et al. 2011; anurans: Vargas-Salinas and Amezquita 2013; fish: Picciulin et al. 2012; invertebrates: Lampe et al. 2012), with the strongest body of experimental evidence coming from avian research (e.g., Halfwerk, Bot, et al. 2011; Halfwerk, Holleman, et al. 2011; McLaughlin and Kunc 2013; Montague et al. 2013); here, we focus on bird vocalizations to illustrate our argument.

The most obvious way in which anthropogenic noise can disrupt acoustic communication is through masking, whereby there is an increase in the threshold for detection or discrimination of one sound in the presence of another (Brumm and Slabbekoorn 2005). Loss of clear and efficient transmission of acoustic information can create potential fitness costs, including those related to mate attraction and territory defense if song is masked (e.g., Halfwerk, Bot, et al. 2011), increased predation risk if detection of alarm calls is impaired (Lowry et al. 2012), and reduced reproductive success if parent–offspring or parent–parent communication is disrupted (Halfwerk et al. 2012; Leonard and Horn 2012). Consequently, adjustments resulting from both evolutionary adaptation (e.g., Luther and Baptista 2010) and behavioral plasticity (e.g., Gross et al. 2010) have been indicated in studies on a variety of avian species (Ortega 2012). For instance, evidence exists for anthropogenic noise–induced changes in vocal timing (Fuller et al. 2007), temporal structure (Halfwerk and Slabbekoorn 2009), amplitude (see Brumm and Zollinger 2011), frequency (see Slabbekoorn 2013), and complexity (Montague et al. 2013), and birds may also attempt to improve signal detection and discrimination by altering their choice of perch from which to vocalize (Halfwerk et al. 2012).

These vocal adjustments have often been described as adaptive in terms of a release from masking (Slabbekoorn and Ripmeester 2008), although there is some debate with respect to frequency

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shifts (Nemeth and Brumm 2010). More recent work has begun to test these perceived *benefits*, by calculating the increases in potential communication distances (e.g., Nemeth and Brumm 2009) and assessing reproductive output (Halfwerk, Bot, et al. 2011). Although direct evidence of fitness benefits remains scarce (Slabbekoorn 2013), less attention has been paid to the potential fitness *costs* arising from vocal adjustments made in response to anthropogenic noise. This issue was raised by Patricelli and Blickley (2006), but the majority of the 50 studies investigating the impacts of anthropogenic noise on bird vocal communication published since then (unpublished data) do not even mention the possibility of costs (see Nemeth and Brumm 2010; Halfwerk, Bot, et al. 2011; Halfwerk, Holleman, et al. 2011; Luther and Derryberry 2012; Proppe et al. 2012 for exceptions). We argue that both sides of the trade-off need careful consideration if the true effects of noise are to be determined.

POTENTIAL FITNESS COSTS

Vocal adjustments could result in many direct or indirect fitness costs; we highlight 4 general examples here.

Reduced transmission distances

Signals are shaped over time by the acoustic environment in which they are emitted, the "acoustic adaptation hypothesis" (Morton 1975). Changes in vocal parameters may therefore affect the level of attenuation and degradation, potentially reducing transmission through vegetation or into and out of a nest (Slabbekoorn 2004). As a specific example, high-frequency signals—favored in urban areas (e.g., Slabbekoorn and Peet 2003)—attenuate faster and are degraded more easily than low-frequency signals (Wiley and Richards 1982). Adjustments in the timing of when vocalizations are produced may also come at a cost to transmission distances. For instance, because sound transmits further and more reliably at dawn than at other times of the day, due to lower wind noise and fewer atmospheric fluctuations (e.g., Brown and Handford 2003), birds that shift their singing away from the dawn chorus may suffer by communicating to a more localized audience.

Increased risk of predation or parasitism

The alarm calls of small passerines are often suggested to utilize high frequencies because this renders the signaler more difficult to detect or locate by birds of prey (Marler 1955; Klump and Shalter 1984). Changes in frequency may therefore result in the caller being more at risk; ultimately, this could lead to selection for a reduction in alarm calling, with consequences for subsequent generations that learn to give and utilize alarm calls from experienced adults (Hollén and Radford 2009). For all vocalizations, an increase in amplitude and the duration of vocalizing will make the signaler more conspicuous and potentially more vulnerable to predators. Similarly, noise-driven changes in perch choice, such as vocalizing from higher or more exposed positions (see Halfwerk et al. 2012), could increase predation risk. More time spent vocalizing and louder sound production could also enhance the likelihood of brood parasitism if host vocal activity is used as a cue by parasites to locate nests (see Banks and Martin 2001).

Altered energy budgets

There is some evidence that it is metabolically costly to vocalize for longer (Gillooly and Ophir 2010), to produce high-amplitude songs compared with those of lower amplitude (Oberweger and Goller 2001), and to shift songs to higher frequencies (Lambrechts 1996). Although the energy required for such vocal adjustments may not be as great as first assumed (see Ward et al. 2004; Zollinger et al. 2011), there could be consequences for growth, survival, and reproductive success if compensation does not occur. Moreover, spending more time foraging to compensate for increased energy consumption may itself increase predation risk (Lima and Dill 1990), enhance the likelihood of foraging errors (see Purser and Radford 2011), and reduce opportunities for other important activities such as preening (Tieleman and Williams 2002). If insectivorous birds sing at dawn because prey are hardest to detect at times of low light intensities and reduced invertebrate activity (Kacelnik and Krebs 1983), then a diel shift in singing may also result in foraging at less optimum times.

Loss of vital information

The auditory sensitivity of a species is often tightly tuned to the frequencies used in communication (e.g., Okanoya and Dooling 1988), and thus the efficacy of perception by receivers may be impaired by noise-induced vocal changes. Moreover, because mate choice and male–male competition are often based on assessments of song characteristics, with higher quality indicated by such aspects as high amplitude (Brumm and Ritschard 2011; but see Nemeth et al. 2012), low frequency (Halfwerk, Bot, et al. 2011; but see Eens et al. 2012), broad bandwidth (Ballentine et al. 2004), and large repertoire size (Krebs et al. 1978), changes to acoustic structure and output could have direct consequences for reproductive success. Alterations in one song component in response to changes in the acoustic environment could also restrict the elaboration of other characteristics, which are preferred by females (Gross et al. 2010), thus indirectly impacting fitness. For instance, singing more loudly may compromise the ability to generate a high song rate and longer song duration (Wasserman and Cigliano 1991), whereas an increase in minimum frequency could constrain song complexity (Montague et al. 2013). Misjudging quality during mate choice may result in rejection of high-quality mates and less time spent raising the offspring, with impacts on their success, if a low-quality mate is selected (Halfwerk, Holleman, et al. 2011). In male–male competition, signalers may be attacked more often if perceived as less aggressive, and receivers may mistakenly attack males that are stronger or have a higher motivation to fight than anticipated (Ripmeester et al. 2007). Song matching may also be an important aggressive signal in male–male competition (Krebs et al. 1981), and a male that drops low-frequency songs from his repertoire may not possess the song types required to match conspecific rivals.

These fitness costs introduce a series of trade-offs for individuals. For example, although low-frequency songs might be favored by sexual selection, anthropogenic noise could exert a natural selection pressure for high-frequency songs; there may be a choice between being heard by many or being perceived as high quality by a few (Halfwerk, Bot, et al. 2011). The preference could be molded by the fundamental need of females to mate, with a signal that is heard being at a selective advantage compared with one that is not heard, even if the quality communicated is lower. Other methods of assessment could then be developed, or other existing signals relied on to a greater extent, to restore the element of choice in the future.

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POPULATION AND COMMUNITY CONSEQUENCES

All members of a population are unlikely to suffer the same costs associated with vocal adjustments. For instance, alterations that are energetically costly may be more easily borne by higher quality individuals (Zahavi 1975), which might give them further advantages in terms of female choice and male–male competition. However, if anthropogenic noise results in the loss of certain acoustic features that are used as honest indicators of quality, such as low-frequency song elements, then discrimination between different males becomes harder and lower quality males may be less easily dismissed. Ultimately, the exact nature of the cost will also depend on whether, and how quickly, a corresponding shift in assessment and preference by receivers occurs. Because females often have a preference for songs similar to those of their father or that were heard frequently during a learning period (Catchpole and Slater 2008), it is feasible that preference in this context at least could shift passively over a few generations simply through subadult experience.

In general, the effect of vocal adjustment on fitness will differ between species depending on 1) inherent vocal characteristics that vary the amount of adjustment needed, 2) the relevant sexual signals used that could be disrupted by adjustment, 3) the plasticity of song learning and corresponding plasticity in assessment, and 4) the inherent suitability of a species to persist in urban environments. For instance, there is a positive relationship between the existing vocal frequency range of a species and its response to noise (Hu and Cardoso 2010; Francis et al. 2011), and it is likely that naturally loud vocalizations also convey an advantage. Moreover, only a relatively small percentage of bird species are thought to be urban-adaptable (Johnston 2001). The different costs and benefits faced by different species in relation to anthropogenic noise will have consequences for community structure and functioning (Francis et al. 2009).

MOVING FORWARD

Ultimately, the assessment of fitness consequences requires measurement of reproductive success and survival. These are logistically challenging to determine, especially if the specific impact of a particular response, in this case vocal adjustments, is targeted. However, studies focusing on other, but related, questions have assessed such variables as pairing success (Habib et al. 2007; Gross et al. 2010), clutch size and fledging success (Francis et al. 2009; Halfwerk, Holleman, et al. 2011), and female fidelity (Halfwerk et al. 2012); care is needed to ensure that such effects are not the result of differential use of areas by individuals of different qualities (see Slabbekoorn 2013). Using playbacks at nests, or perhaps presentation of models, also offer opportunities to assess how different vocalizations affect predation or parasitism rates (see Haff and Magrath 2011).

If the fitness benefits and costs of responses to anthropogenic noise are to be determined, studies need to include several key elements (see also Slabbekoorn 2013). First, potential confounding factors must be ruled out; correlational work comparing, for instance, rural and urban areas or habitats at different distances from roads, cannot isolate noise as the reason for any differences found. Instead, naturally matched areas where only the noise differs (see Francis et al. 2009, 2011) or experimental manipulations (e.g., Halfwerk, Bot, et al. 2011; Halfwerk, Holleman, et al. 2011; McLaughlin and Kunc 2013; Montague et al. 2013) are required. Second, to assess cumulative effects and consider the possibility that responses change due to processes such as habituation, tolerance, and sensitization (Bejder et al. 2009), experiments over an extended period of time should ideally be conducted (e.g., Blickley et al. 2012), although they are more difficult to implement than short-term, acute exposures. Third, proper levels of replication are required; if strong conclusions are to be drawn about population-level consequences, then data from multiple sites, as well as multiple individuals, are needed (see Slabbekoorn 2013). In addition, to maximize the usefulness of studies investigating the impact of anthropogenic noise, the noise source should be characterized as fully as possible (reporting, for instance, dB, any weighting function, integration time and temporal variation, along with power spectra and spectrograms) and utilize equipment that best reflects the auditory capabilities of the study animal (see Schaub et al. 2009).

CONCLUSIONS

The human population is projected to increase by 2.3 billion between 2011 and 2050, with urban areas likely to absorb most of this growth (United Nations 2011). Noise pollution is thus both a pressing issue and one of ever-increasing concern. Ultimately, we need assessments of how anthropogenic noise affects individual fitness, population viability, and community structure. As with any aspect of behavioral ecology, this will only be possible if we consider both the benefits and costs arising from adjustments made in response to noise. Our aim is to stimulate a more balanced approach with respect to this trade-off; although we have illustrated our argument with reference to vocal signaling in birds, the principles apply across taxonomic groups and are relevant to all noise-induced behavioral changes.

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Passerine Birds Breeding under Chronic Noise Experience Reduced Fitness

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Abstract

Background: Fitness in birds has been shown to be negatively associated with anthropogenic noise, but the underlying mechanisms remain obscure. It is however crucial to understand the mechanisms of how urban noise impinges on fitness to obtain a better understanding of the role of chronic noise in urban ecology. Here, we examine three hypotheses on how noise might reduce reproductive output in passerine birds: (H1) by impairing mate choice, (H2) by reducing territory quality and (H3) by impeding chick development.

Methodology/Principal Findings: We used long-term data from an island population of house sparrows, *Passer domesticus*, in which we can precisely estimate fitness. We found that nests in an area affected by the noise from large generators produced fewer young, of lower body mass, and fewer recruits, even when we corrected statistically for parental genetic quality using a cross-fostering set-up, supporting H3. Also, individual females provided their young with food less often when they bred in the noisy area compared to breeding attempts by the same females elsewhere. Furthermore, we show that females reacted flexibly to increased noise levels by adjusting their provisioning rate in the short term, which suggests that noise may be a causal factor that reduces reproductive output. We rejected H1 and H2 because nestbox occupancy, parental body mass, age and reproductive investment did not differ significantly between noisy and quiet areas.

Conclusions/Significance: Our results suggest a previously undescribed mechanism to explain how environmental noise can reduce fitness in passerine birds: by acoustically masking parent–offspring communication. More importantly, using a cross-fostering set-up, our results demonstrate that birds breeding in a noisy environment experience significant fitness costs. Chronic noise is omnipresent around human habitation and may produces similar fitness consequences in a wide range of urban bird species.

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Introduction

Anthropogenic noise can acoustically mask, and decrease, the efficacy of avian vocal communication. Warning calls, territorial defence and mating signals can be impaired, and this effect is often indicated by behavioural changes [1–6]. Communication impairment can have serious demographic consequences, as it has been shown to result in changes in bird abundance, community structure and predator–prey relationships [7–9]. More importantly, noise can also affect reproductive output. In a population of great tits (Parus major), for example, females laid smaller clutches in areas affected by traffic noise than in quieter areas; also, nests in noisy areas fledged fewer young [10]. The underlying mechanisms, however, remain unclear (but see [11]). Thus, while it is interesting to consider the effects of noise on specific behaviours, it is crucial to conservation efforts in urban environments to study the direct effects of environmental noise on reproductive success and recruitment [12].

Three, non-mutually exclusive, hypotheses have been suggested to explain why reproductive success is reduced in noisy areas [10]. H1, *impaired mate choice hypothesis*: Noise may interfere with the transmission of mate quality through bird song and a female's assessment of the quality of her mating partner may be impaired [10,11]. Under this hypothesis, females are expected to invest less, lay smaller clutches and solicit more extra-pair copulations when breeding in a noisy environment. H2, *reduced territory-quality hypothesis*: Noise may affect territory quality. If this is true, noisy areas are expected to be populated by less experienced or younger individuals of lower quality, or to be avoided in general [8,12,13]. H3, *impaired chick development hypothesis*: Noise can lead to poor chick development, by means of two different pathways. First, noise can induce physiological stress in chicks, which may lead to reduced growth [14]. Second, noise may mask acoustic communication between offspring and parents. Two potential mechanisms can operate: if chick begging is not audible, or is less audible, because it is acoustically masked by background noise, we expect chicks to increase the amplitude of their begging, or parents to provision less frequently [10]. Another possibility is that chicks may fail to notice their parents' arrival at the nestbox, resulting in them not begging for food [15].

These three hypotheses each predict reduced reproductive success in noisy environments. Here, we test these three hypotheses in an altricial passerine, the house sparrow (*Passer domesticus*). It is not usually possible to test for a within-individual effect of a noisy environment in a wild population, because this would usually require either the relocation of breeding individuals from a quiet to a noisy environment, and vice versa, or the experimental modification of the noise level around a group of breeding individuals [11]. The relocation of breeding birds is generally impractical. Changing the background noise level via loudspeakers would make it difficult to distinguish between the effects of the noise treatment *per se* and the effect of disturbance due to a change in the noise environment. Here, we take a different approach: we have a dataset of repeated measurements on individual sparrows who have bred in a noisy and three quiet environments, which, together with a cross-fostering set-up, allows us to statistically distinguish between among- and within-individual effects, as well as separating the effects of individual genetic quality and environmental noise. These data allow us to study the direct reactions of birds to the environmental noise that is part of their normal environment.

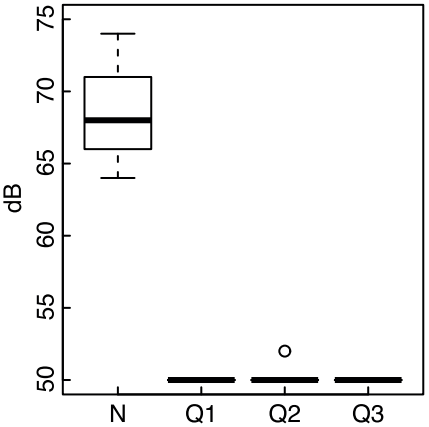

Figure 1. Mean noise levels at the four sites. Noise levels were assessed during the breeding season and measured at five random nestboxes at each site. We used a Silverline sound level meter, with A-weighting, with a range from 50–126 dB and an accuracy of ±2 dB.
doi:10.1371/journal.pone.0039200.g001

Methods

We used data from a long-term (2001–2008) study on a nestbox population of house sparrows on Lundy Island [16–21]. Low levels of migration to and from the island allow for accurate fitness and recruitment estimates; annual resighting probabilities of marked individuals are extraordinarily high (average 0.91, range: 0.72–1.00, [21]). The population has been systematically monitored since 2000; all nesting attempts are recorded from the moment the first egg is laid. Nearly all birds are individually marked as fledglings – therefore, we know their exact ages [17]. Cross-fostering of 2-day old hatchlings between nests has been routinely carried out between randomly chosen clutches of the same age, without changing clutch size, since 2000. Cross-fostering is a routine and systematic component of Lundy sparrow fieldwork and was not restricted to specific experiments (for more details on two small experiments please refer to [21] and references within). Birds were considered to have recruited into the breeding population if they started a brood.

Lundy Island is not connected to the power grid and electricity is generated on the island. Since March 2001, a set of generators (Cummins 6DTA5.9 and 6CTA8.3) has been run continuously between 06:00–12:00 h each day. These generators produce low-frequency noise that reverberates in the adjacent area (noisy environment, N), producing on average 68 dB(A) at the entrances of 29 nestboxes in the barn (Figs. 1, 2), as measured with a hand-held Silverline sound level meter. Another barn (quiet, Q1) harbours 46 boxes; 28 other nestboxes are attached to the outside of the buildings (Q2) and a further 27 nestboxes are located in a small wood (Q3). In Q1–Q3 the generator is only slightly audible. All areas but Q3 are similarly close to the main foraging area, the chicken run (Fig. 2).

The identities of parents at nestboxes were determined by visual identification of individual colour-ring combinations (viewed directly or with the help of video recordings), by catching parents at the nest box [17], and by using PIT-tags and corresponding nest-box antennae [21]. Since not all parents were caught at nestboxes the sample sizes for morphological measurements of parents differed from the sample sizes for parents of known age. Provisioning and incubation frequencies (measured as visits per hour), and incubation duration (in minutes) have been quantified since 2004 from video recordings (90 minutes long) taken at the nestboxes. The methodology is described in detail in [16]. Since sparrows are multi-brooded and, once in the breeding population, live on average for 3–4 years [17], we have repeated measures of provisioning by the same individuals within and between years, which allows us to test whether the same individuals changed their behaviour when they bred in the noisy area *vs* the quiet area. For the main analysis, we used provisioning frequencies collected at broods containing chicks that were 7 days old. We used Bayesian Markov-chain Monte Carlo (MCMC) methods to fit mixed models (BMM). We report effect sizes of the means of the posterior distribution. We considered fixed effects to be statistically significant if their 95% credibility interval (CI) did not include zero [22]. We used R 2.12.1 for statistical analyses.

Fitness Consequences of Noise

We first tested for the fitness consequences of being reared in a noisy location, independent of any potential mechanism. We only used cross-fostered chicks in this analysis. We compared the fate of chicks reared in the noisy environment, N (coded as 1), with those of birds breeding elsewhere, Q (all quiet areas pooled, coded as 0 = reference level). We used two binomial BMMs, with respectively survival from nestling to post-fledging and recruitment as the binomial response variables (survived = 1) and foster area (noisy versus quiet) as a fixed factor. We modelled year and natal area as random effects to correct for potential differences in parent quality. We modelled natal brood as a random effect to correct for chicks from the same nest being more alike than those from different nests.

Reproductive Investment (H1)

We tested if females invested differently in reproduction depending on whether or not they bred in the noisy environment. We tested for a difference in incubation visits and incubation time, whether broods in noisy areas contained fewer eggs and hatchlings, and whether the seasonal timing of breeding differed. We used data on genetic parentage [17] to test whether females breeding in the noisy area had more extra-pair offspring than those breeding in other areas.

Territory Quality (H2)

We tested whether sparrows avoided breeding in the noisy area by comparing annual occupancy rates between the areas. We then

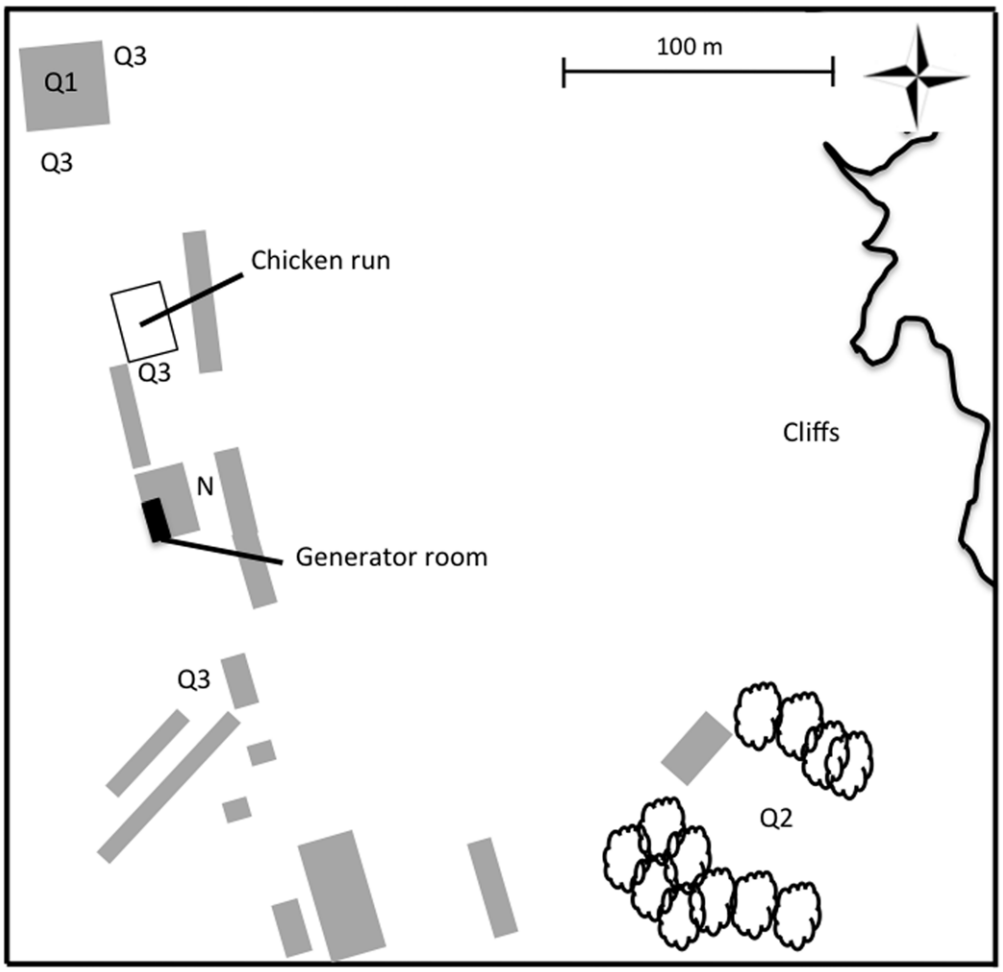

Figure 2. Locations of house sparrow nestboxes on Lundy Island. Grey boxes depict buildings.
doi:10.1371/journal.pone.0039200.g002

examined for the possibility that low-quality or less-experienced birds bred in noisy areas by comparing body mass and the age of parent birds breeding in different areas.

Chick Development (H3)

We first tested for the expectation that chicks that experienced noise grew more slowly, and tested for differences in body mass between fledglings from the noisy areas and elsewhere. We used only chicks that had been cross-fostered. We used a Gaussian BMM with brood, natal area and cohort as random effects to assess the effect of noise on chick body mass at day 12 after hatching. We corrected for time of day (morning or afternoon) as a fixed effect because chicks were lighter at the start of the morning before their parents started provisioning.

We then tested whether parents provided less to broods in a noisy environment than elsewhere. We carried out a cross-sectional analysis with Gaussian BMMs, where we compared the provisioning frequencies of sparrows breeding in the noisy environment with those breeding elsewhere in two models, one for each sex. We corrected for age of the parent and day of season by adding both variables as fixed effects to the model. Bird identity was modelled as a random effect on the intercept, as was year, to correct for annual variability. We then added identity of the partner as a random effect on the intercept, to correct for a potential bias resulting from the adjustments that individuals make, depending on the degree of parental investment by their partner [23].

Within-individual Effects of Noise on Provisioning

Using the same data, in which we have multiple records of individuals, we compared the provisioning by individual parents with those by the same individuals breeding in different areas (within-individual effects), using within-subject centring of variables in BMMs [24]. This model tests for the possibility that individual birds may display high provisioning frequencies when breeding in a quiet area, but low provisioning frequencies when breeding in a noisy area (either in the same or in subsequent years). We modelled the provisioning frequency of males and, respectively, females, as response variables. Our basic model structure was similar to the cross-sectional model, but did not include the non-significant effects of age, date of season, and identity of the partner. We added the number of chicks as a covariate, as individual birds may be able to flexibly adjust their provisioning frequency depending on the number of chicks they feed. We modelled bird identity as a random factor on the intercept, to account for potential heterogeneity among individuals. We used two new variables as fixed predictors: to eliminate any between-subject variation, we subtracted the mean location value (coded as: noisy $= 1$, quiet $= 0$) for each individual across all its broods from the value for the location of each individual brood.

Table 1. Results of a BMM with a logit link function modelling fledging and recruitment probability, of cross-fostered Lundy Island house sparrow chicks as response to noisy and quiet environments.

	Fledged		Recruited	
Effects	**Posterior mode**	**95% CI**	**Posterior mode**	**95% CI**
Fixed				
Intercept	1.02	0.48 – 1.39	−1.73	−2.30 – −1.08
Noisy environment	−0.55	−0.94 – −0.17	−0.49	−0.78 – −0.22
Random				
Brood	3.2	2.48–4.14	0.94	0.51–1.34
Natal location	0.01	0.00–0.12	0	0.00–0.02
Cohort	0.22	0.01–1.12	0.29	0.12–1.65
Residual	0	0.00–0.17	0.02	0.01–0.06

The quiet environment is the reference level. Statistically significant fixed effects are indicated in bold. N = 1474 chicks.
doi:10.1371/journal.pone.0039200.t001

That is, if a female bred once in the noisy environment and once elsewhere, it would get the value 0.5 for the datum when breeding in the noisy environment, and −0.5 for the other datum. This term estimates the within-subject variation component. We derived a second predictor variable to estimate the between-subject variation in provisioning, which is the mean area code for one individual [24].

To test whether within- and between-individual effects differed, we used a similar model, modelling the location (noisy or not) of each brood as a within-individual term and the mean location term from the first model, which represented the difference between the within- and between-individual effects. In both within-individual models, we also corrected for the number of hatchlings.

In order to test whether noise is the causal agent for the reduction of provisioning rate, we re-analysed the video recordings of two nests affected by the intermittent noise produced by a set of large industrial ventilators responsible for sucking in air to cool the power generators. When present, the noise level experienced at these separate nestboxes averaged 70 dB(A). The fans are turned on and off automatically as needed, at times of increased power consumption. Note that the nests are not affected by any airflow from these ventilators. We identified 22 video recordings of these nestboxes in which the ventilators either switched on or off; this was easily identified by listening to the audio track. The time when the fans went off or on was recorded. We calculated provisioning rate separately for the noisy and quiet sections of the videos, and tested whether birds responded directly to the noise levels. Provisioning frequency and fan use might be linked through a common correlate, such as outside temperature. In order to account for such a possibility, we used other videos taken at the same time, but at quiet nestboxes, as controls. This was possible because we usually used two or more cameras, and, therefore, matching videos were available for most cases. We partitioned the time in the same way as we partitioned the video data at the noisy locations. We then tested in the controls for a change in provisioning frequency during the times when the fans were on, even though those nests were not afflicted by the noise. For this analysis, we used data on provisioning frequencies across all chick ages to increase sample size.

This work was carried out under the permit from Natural England 20092529.

Results

Fitness Consequences of Noise

We compared the fate of cross-fostered house sparrow chicks reared in a noisy environment with those reared in other places (Figs 1, 2). Being reared in a noisy environment was associated with a significant drop in survival between hatching and fledging: When correcting for natal brood and area, the probability of fledging was 0.25 for nestlings reared in quiet environments (N = 1093) and 0.21 for chicks reared in the noisy environment (N = 381, Table 1, back-transformed coefficients from a binomial mixed linear model [23]). Chicks reared in the noisy environment also had a statistically significantly lower probability of recruiting into the population, compared to chicks from the other areas (Table 1, Fig. 3a).

Reproductive Investment (H1)

Broods in the noisy area did not differ from broods in quiet areas in the number of eggs (ANOVA with area (N, Q1–3) as a factor: $F_{3,1052} = 0.24$, $P = 0.87$), the number of hatchlings ($F_{3,967} = 1.12$, $P = 0.34$, Fig. 3b), or the laying date ($F_{3,1135} = 1.13$, $P = 0.34$). The number of incubation visits did not differ between noisy and quiet environments (Kruskal-Wallis test, Males: $\chi^2 = 1.13$, $df = 1$, $P = 0.29$, $N = 66$; Females: $\chi^2 = 2.06$, $df = 1$, $P = 0.15$, $N = 66$). Also, male and female house sparrows spent a similar amount of time incubating broods in the noisy environment as elsewhere (Males: $F_{1,65} = 0.02$, $P = 0.89$; Females: $F_{1,65} = 0.40$, $P = 0.53$). The proportion of clutches that contained extra-pair eggs did not differ between the noisy and the quiet environments (estimates from a binomial BMM with noisy or not as a fixed factor and year as a random effect: fixed effect: $b_{intercept} = -1.27$ (−5.46 to −0.45); $b_{noisy} = -0.54$ (−1.86 to 0.80), $u_{year} = 0.62$ (0.16 to 19.47), $e_{residual} = 0.22$ (0.08 to 39.12), $N = 953$ broods in 10 years). Also, the number of eggs per clutch sired by a male other than the social father did not differ among the four areas (Poisson BBM, fixed effect: $b_{intercept} = 0.10$ (0.05 to 0.16); $b_{noisy} = 0.002$ (−0.02 to 0.04), $u_{year} = 0.35$ (0.07 to 3.60), $e_{residual} = 0.48$ (0.33 to 0.79), $N = 953$ broods).

Territory Quality (H2)

Annual occupancy rates of nestboxes did not differ between the noisy area and elsewhere (ANOVA $F_{3,36} = 1.09$, $P = 0.37$). Body mass of sparrow parents was similar between quiet and noisy areas (females: $F_{3,584} = 0.15$, $P = 0.93$; males: $F_{3,520} = 0.98$, $P = 0.40$).

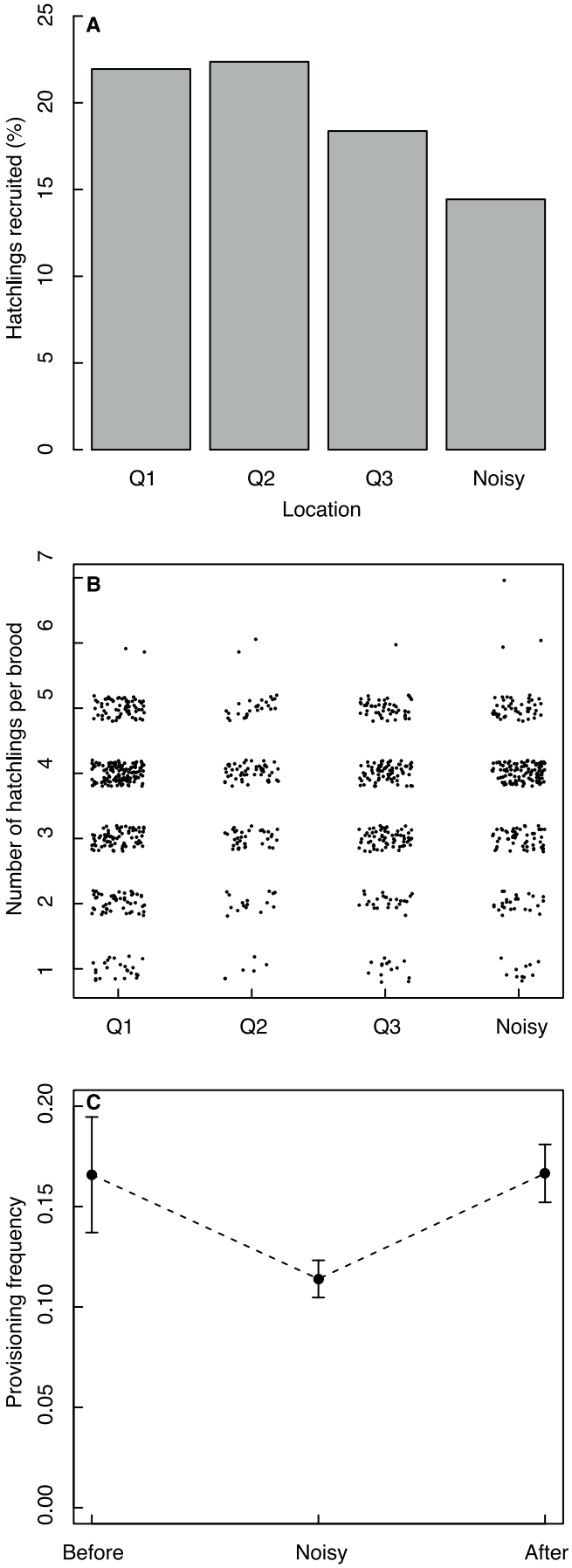

Figure 3. Reproductive success and provisioning frequency of Lundy island house sparrows breeding in nestboxes in the noisy area and elsewhere. (a) Percentage of house sparrow hatchlings that recruited to the breeding population, in relation to the environment in which they were raised (Q1–3 = quiet, N = noisy). These data are not corrected for natal brood and foster area. (b) Number of Lundy house sparrow hatchlings per brood in relation to brood area (jittered). (c) Provisioning frequency (visits per minute) within individual female house sparrows that bred in quiet environments before and after they bred, or both, in the noisy environment. *N* = 69 females switched between noisy and non-noisy locations between broods. Whiskers depict one standard error.
doi:10.1371/journal.pone.0039200.g003

Female age did not differ between noisy and quiet areas (Kruskal-Wallis test: $\chi^2 = 0.32$, $df = 1$, $P = 0.57$, $N = 962$) but males breeding at the noisy areas were older than those breeding elsewhere (Kruskal-Wallis test: $\chi^2 = 7.09$, $df = 1$, $P = 0.01$, $N = 954$).

Chick Development (H3)

We compared the fledging body mass of chicks reared in a noisy area with those reared elsewhere. We used the data from our cross-fostering experiment and corrected for the location of the natal brood. This was done to distinguish between the effect of low-quality parents, which might produce low-quality offspring, breeding more often in the noisy environment than elsewhere, from chicks suffering from being reared in the noisy environment. Chicks that were reared, but not necessarily born, in a noisy area had a significantly lower body mass when 12 days old than chicks reared in a quiet area (BMM, body mass at day 12 in grams: fixed effects: $b_{intercept} = 23.91$ (23.12 to 24.80); $b_{noisy} = -0.74$ (-1.39 to -0.02), $b_{time\ of\ day} = 1.58$ (0.77 to 2.24); random effects: $u_{brood} = 5.52$ (4.77 to 7.73), $u_{natal\ area} = 0.01$ (0 to 0.02), $u_{year} = 0.005$ (0 to 0.98), $e_{residual} = 7.49$ (6.82 to 8.55), $N = 922$).

Cross-sectional analysis. We then compared the provisioning frequencies of house sparrows breeding in the noisy environment with those of birds breeding elsewhere. Females, but not males, provisioned broods in the noisy environment significantly less often than in other areas (Table 2). Consistent with the previous observation that males are more repeatable in their parental care than females [16], we also found that males were individually more predictable caregivers than females (Table 2).

Within-individual effects of noise on provisioning. We used the same data to compare provisioning frequencies of individual parents breeding in the noisy area with the provisioning frequencies of the same individuals when they bred elsewhere (within-individual effects, see [24]). Individual females visited their broods less often per hour when breeding in the noisy environment (BMM parameter estimates (CI), fixed effects: $b_{intercept} = 6.52$, (4.93 to 8.01); $b_{within} = -1.09$ (-1.60 to -0.62); $b_{between} = -1.30$ (-2.41 to -0.29); $b_{clutchsize} = 0.40$ (0.02 to 0.78), random effects: $u_{ID} = 0.39$ (0 to 1.44), $u_{year} = 0.07$ (0–0.34), $e_{residual} = 16.61$ (14.3 to 19.46)). The within- and between-female effects of breeding in the noisy environment were not significantly different (BMM: fixed effects: $b_{intercept} = 7.86$ (6.10 to 9.56); $b_{within} = -2.59$ (-4.81 to -0.59); $b_{between\text{-}within} = 0.21$ (-1.09 to 1.35); $b_{clutchsize} = 0.39$ (-0.01 to 0.75). We did not find a similar effect of noisy location on provisioning frequency in male house sparrows (BMM, fixed effects: $b_{intercept} = 6.82$ (4.32 to 9.47); $b_{within} = -0.88$ (-3.95 to 2.13); $b_{between} = -0.10$ (-1.82 to 1.80); $b_{clutchsize} = 0.61$ (0.19 to 1.14), random effects: $u_{ID} = 4.69$ (1.84 to 8.20), $u_{year} = 0.71$ (0 to 3.37), $e_{residual} = 24.13$ (20.91 to 28.29)).

We then used a subset of data that consisted only of those females that changed, within and between years, from or to the noisy area, and tested whether their provisioning frequency changed. We retained the information on whether or not females had bred previously in a quiet area and moved into a noisy environment, or *vice versa*. The same females provisioned their young more frequently before and after moving to the noisy environment ($N = 96$ broods, Figure 3c, linear model with area as factor: $F_1 = 11.48$, $P<0.001$; clutchsize: $F_1 = 0.24$, $P = 0.63$).

Finally, we also tested whether sparrow females reacted by adjusting their provisioning rate in response to short-term noise. When the noise was present, female sparrows had a reduced provisioning rate within a single brood, and an increased provisioning rate when the noise-producing ventilators were off independent of the sequence of events (Fig 4, Table 3). We used data from video recordings of provisioning taken at quiet locations but at approximately the same time as controls, because the fans' running time might have been correlated with some external variable that also affected provisioning. However, we found no change in provisioning rates at quiet nestboxes during the times when the fans were on (Fig. 4, Table 3).

Discussion

House sparrows reared in a noisy environment experienced reduced parental provisioning, lower fledging mass, and lower fledging and recruiting success. Our results support the impaired chick development hypothesis (H3). We observed a reduced provisioning frequency in the noisy environment, which is suggestive evidence for a novel mechanism of how noise may affect fitness of passerines: by masking parent–offspring communication. Our study has one caveat: We had only one location that was subjected to constant noise with sufficient data to measure fitness, and we can therefore not exclude the possibility that some other variable we did not account for caused the drop in fitness in the noisy area. We, however, do not believe that this is the case because the noisy location is similarly close to the main feeding grounds as most other nest sites and, therefore, birds should not have had a harder time foraging. If another environmental factor, such as exhaust pollution, caused the lowered condition of chicks then we would have also expected to see a similar effect in the physical condition of adults breeding in that area, which we did not find. Similarly, if another factor had led to a change in the visitation rate by birds to their nests, we would also have expected a difference in incubation visits between the noisy and quiet areas, which again we did not find. Furthermore, all nestboxes in all areas were built following a standard model [25], reducing environmental variability. We have found earlier that house sparrows on Lundy are consistent in their within-individual reproductive output between years, which indicates that deviations from this constancy may be due to changes in the environment, not changes in the adult [17]. Finally, the observation that females respond flexibly to the presence of noise within short periods of time supports the idea that a change in feeding rate, as a response to noise, might be the cause for the low fitness in the noisy area.

We did not find support for the impaired mate choice hypothesis (H1): females did not decrease reproductive investment other than provisioning behaviour when breeding in the noisy area: clutch size, breeding date and incubation behaviour did not differ between the noisy and quiet areas. Clutches in the noisy area did not contain an increased rate of extra-pair offspring (contradicting [11]). It is possible that females decreased provisioning rate in response to a potentially perceived low mate-quality, if mate quality in house sparrows is mainly signalled by song displays. Little is known about how song quality affects female choice in house sparrows. However, if coitus, and the decision to mate with a certain individual, take place away from the nest [26] and outside of the noisy environment in our study, it is likely that most females have the chance to sample their mate's song quality in a quiet area, unbiased by the noise. Furthermore, if females assume her mate is of lower quality it would be more prudent to reduce primary reproductive investment, i.e. in clutch size rather than reducing parental care after investing in costly eggs. The similar rates of extra-pair offspring between nests in noisy and quiet areas additionally suggest that mating decisions of females were not affected by the noise. We therefore assume that, in our study, acoustic masking of the communication between the adults probably did not affect the reduced reproductive fitness in the noisy environment.

We found no support for the impaired territory quality hypothesis (H2): Sparrows did not avoid breeding in the noisy area. Surprisingly, we found that older males, but not females, were more likely to breed in the noisy environment. Older house sparrows have a larger black bib, which signals social dominance [18,27]. The apparent preference of older males for the noisy area is difficult to explain, although it must be noted that the effect size was relatively small (0.3 years difference). However, assuming that

Table 2. Results of a BMM modelling Lundy island house sparrow provisioning frequencies (visits/hour) on day 7 in quiet and noisy environments. Statistically significant fixed effects are indicated in bold.

	Female provisioning frequency		Male provisioning frequency	
Effects	**Posterior mode**	**95% CI**	**Posterior mode**	**95% CI**
Fixed				
Intercept	8.91	5.77–10.63	7.24	4.49–11.03
Noisy environment	−2.31	−3.20– −1.51	−0.85	−2.31–0.27
Laying date	0.009	−0.01–0.02	0.004	−0.01–0.02
Age of Mother	0.23	−0.12–0.56	0.14	−0.21–0.61
Age of Social Father	−0.16	−0.43–0.14	−0.16	−0.50–0.35
Random				
Mother ID	0	0.00–0.74	0.002	0.00–0.75

Females: $N = 422$, with observations on 147 individuals; males: $N = 420$, with observations on 138 individuals.
doi:10.1371/journal.pone.0039200.t002

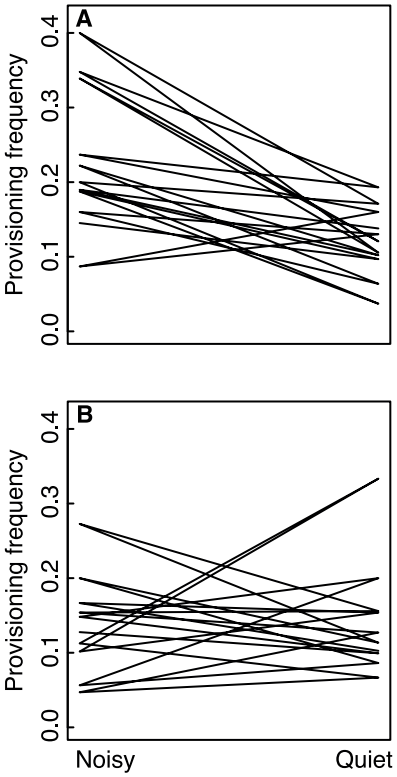

Figure 4. Frequency of provisioning (visits per minute) by female Lundy island house sparrows breeding in nestboxes affected by intermittent noise (top), and by those not affected by noise. Provisioning frequencies were calculated for the time period during which the noise was on and off in both groups. Lines represent changes in provisioning rate within individual females.
doi:10.1371/journal.pone.0039200.g004

older males are of higher quality, they would seem to consider the noisy area to be a desirable habitat.

Our results support the impaired chick development hypothesis (H3). Our study set-up does not allow us to distinguish between the effects of chronic stress and those of acoustic masking, and we discuss supporting evidence for or against both possible mechanisms. Chronic noise is known to induce stress-related changes along the hypothalamo–pituitary–adrenal axis [14], which might influence chick and parent physiology. We found twelve-day-old chicks to be of lower body mass when reared in the noisy environment, however, this seems as likely to be a consequence of the reduced provisioning frequency as a reaction to chronic stress. We found no evidence for an effect of stress in adults: body mass of adults did not differ between the noisy and quiet areas, which indicates that, at least for adults, the noise did not result in lowered condition due to stress. Stress could also affect adult behaviour and nest visitation rates. If this were the case, we would expect this stress response to similarly affect incubation behaviour, which was not the case. We cannot exclude that chronic noise and the associated stress has been the sole cause for the lowered chick condition, but given our results we consider it unlikely.

Provisioning rates were lower in the noisy environment than elsewhere. We have also shown that sparrow females respond flexibly to short-term, familiar environmental noise with an immediate reduction in provisioning frequency. The observation that sparrow females increase their provisioning rate during times with no noise is suggestive evidence for a causal mechanism to link provisioning behaviour with environmental noise. Parental birds

Table 3 Results of a BMM modelling Lundy island house sparrow female provisioning frequencies (visits/hour) at a location intermittently affected by noise and at control nestboxes during the same time periods (two-level factor with noise off as the reference level). Statistically significant fixed effects are indicated in bold.

Effects	Effect size	95% CI	Effect size	95% CI
	Intermittent noise		Control	
Fixed				
Intercept	13.73	10.54–16.60	8.27	5.44–10.90
Noise on	−6.54	−10.48–−2.61	0.25	−3.44–4.52
Random				
Bird ID	1.54	0.00–7.74	0.26	0.00–4.39
Residual	21.92	9.18–37.71	20.63	8.40–35.73

N_{noise} = 22 observation periods on five females, N_{quiet} = 20 observation periods on nine females.
doi:10.1371/journal.pone.0039200.t003

use the information communicated to them through begging from their chicks to adjust their provisioning frequency according to the chick's needs [28–33]. Offspring begging is an adaptive behaviour [33]; parent birds increase their provisioning rate when presented with increased begging [30]. Therefore, if noise masks begging vocalisations, parents will not respond appropriately. Another possibility is that offspring may not hear their parents arriving at the nestbox and therefore fail to beg for food [15].

We only found females to lower their provisioning rate in the noisy environment, not males. In house sparrows, males provide food to their young at a relatively constant rate while females are more flexible [16]. The most parsimonious explanation for the differences between the sexes is that males are unresponsive, while females may be more responsive to nuances in the chicks' begging vocalisations. We suggest that, in the noisy area on Lundy, female sparrows perceive they have less needy chicks because the acoustic communication with their chicks is intercepted by generator noise. The chicks of unresponsive parents are disadvantaged [29,32,33]. We suggest that acoustic masking of parent–offspring acoustic communication may be at least a partial explanation for the lowered parental provisioning in the noisy areas.

The strength of our study is that it suggests direct fitness consequences of chronic noise in wild birds. Fitness is generally difficult to measure in wild populations but, by using an island population, we can be relatively sure that the birds affected by noise had not simply dispersed. It is perhaps surprising that such a large fitness effect is found in house sparrows, a species thought to be well adapted to living in close association with humans, where chronic background noise is pervasive. Yet, insufficient reproductive output has been shown to be responsible for the decline of the sparrow from cities and rural areas [34]. Factors associated with urbanisation and food availability have been suggested as causes [35]. Our results point to the possibility that chronic noise might be a part of the explanation for the decline of the house sparrow in urban areas. Urban noise has been shown to interfere with acoustic communication between conspecifics in several bird species [9,36]. In order to assess which particular urban noises could be problematic we would need a comprehensive acoustic analysis of sound frequencies. The potential of urban noise to acoustically mask parent–offspring communication, as well as the physiological effects of urban noise, need to be investigated

experimentally in order to validate the extent of these effects, and to understand the conservation implications [12].

Acknowledgments

We are grateful to the Lundy Company and their staff for allowing us to work on Lundy, and for their invaluable support in the field. We thank N. Ockendon, D. Gillespie and M. Karlsson for field data collection. H. Dugdale, M. Hinsch, A. Liker, R. Radersma, I. Winney, and two anonymous referees provided helpful comments on an earlier version of the manuscript.

Author Contributions

Conceived and designed the experiments: JS SN IC TB. Performed the experiments: SN IC. Analyzed the data: JS. Contributed reagents/materials/analysis tools: TB SN. Wrote the paper: JS IC SN TB.

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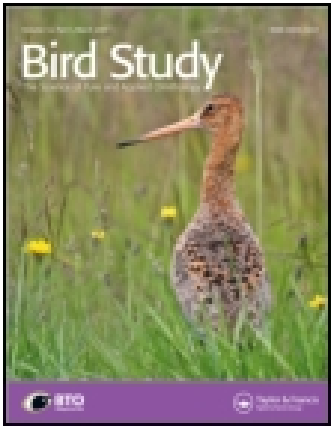

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Short Notes

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Avian casualties on railways

In their paper 'Casualties among Birds along a selected Road in Wiltshire' (*Bird Study*, 11:168-182), Dunthorn & Errington mention the possible existence of 'black spots' at which exceptional numbers of birds are killed by motor traffic. In an attempt to determine whether such spots occur on railways, I have engaged myself in a certain amount of correspondence and research. The primary question remains unanswered, but the general facts which have come to light should, I think, be put on record.

Howe (*Field Naturalist*, 3:9, 24) lists a total of 75 birds killed on a 2¼ mile stretch of line in Cumberland during 1957 and the first two months of 1958. In correspondence, Messrs. D. Holding and G. W. Follows inform me of 30 birds being found dead in recent years along the 1¾ mile stretch from Glazebury to Astley in south Lancashire, and Mr. D. G. Lawson tells me of 11 casualties along the three miles of line from Farington Junction to Euxton Junction in mid-Lancashire between January and the end of April, 1965.

All the above victims (116) were specifically identified but some additional birds too decomposed for recognition were found. Moreover, as Messrs. Holding and Follows point out, it is likely that a number of victims are thrown well clear of the track, and thus escape notice.

Of the 116, 41 were Owls (27 Tawny, 12 Barn, 1 Long-eared, 1 Little), from which it is clear that those birds are particularly vulnerable. Partridges (24) and Pheasants (9) were next in the casualty order.

A letter of enquiry printed in *Rail News*, February 1965, elicited five replies which, though rather generalised in content, confirm the existence of a regrettably high mortality of birds along the railway: three of the five writers particularly stress the vulnerability of Partridges and Pheasants. Also noteworthy is one writer's mention of a high accident-rate among feral domestic Pigeons alongside a viaduct near Kidderminster.

I thank the several correspondents upon whose information this present communication is based. Their letters have been deposited at the Alexander Library, where they may be consulted by anyone wishing to pursue the subject further.

K. G. Spencer,
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off Carr Road,
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Lancs.

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Lupinus nipomensis
(Nipomo Lupine)

5-Year Review:
Summary and Evaluation

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U.S. Fish and Wildlife Service
Ventura Fish and Wildlife Office
Ventura, California

October 2009

5-YEAR REVIEW

Lupinus nipomensis (Nipomo Lupine)

I. GENERAL INFORMATION

Purpose of 5-Year Review:

The U.S. Fish and Wildlife Service (Service) is required by section 4(c)(2) of the Endangered Species Act (Act) to conduct a status review of each listed species at least once every 5 years. The purpose of a 5-year review is to evaluate whether or not the species' status has changed since it was listed (or since the most recent 5-year review). Based on the 5-year review, we recommend whether the species should be removed from the list of endangered and threatened species, be changed in status from endangered to threatened, or be changed in status from threatened to endangered. Our original listing of a species as endangered or threatened is based on the existence of threats attributable to one or more of the five threat factors described in section 4(a)(1) of the Act, and we must consider these same five factors in any subsequent consideration of reclassification or delisting of a species. In the 5-year review, we consider the best available scientific and commercial data on the species, and focus on new information available since the species was listed or last reviewed. If we recommend a change in listing status based on the results of the 5-year review, we must propose to do so through a separate rule-making process defined in the Act that includes public review and comment.

Species Overview:

Lupinus nipomensis (Nipomo lupine) is a small annual plant in the pea family (Fabaceae). Historically and currently, the species is known only from the southwestern corner of San Luis Obispo County, California, scattered over an area of approximately 2 miles wide and 2 miles long (3.2 by 3.2 kilometers (km)) (Figure 1). It is restricted to sandy soils associated with the Callender Dune Sheet (Cooper 1967). For purposes of this review, we are considering the entire extent of the species to comprise one population; however, the California Natural Diversity Database (CNDDB) has divided the population into approximately 10 occurrences for tracking purposes. Over the last 4 years, the total number of individuals has fluctuated between approximately 139 and 771, depending on winter and spring climatic conditions (Land Conservancy of San Luis Obispo County (Conservancy) 2009). Over time, the species' habitat has been fragmented by State Highway 1 and oil refinery facilities, and bounded on the eastern side by development and agriculture. The small size of the populations and their proximity to a variety of human activities makes it vulnerable to stochastic extinction.

Methodology Used to Complete the Review:

This review was prepared by the Ventura Fish and Wildlife Office (VFWO), following the Region 8 guidance issued in March 2008. We used survey information from experts who have been monitoring various localities of this species, and the CNDDB maintained by the California Department of Fish and Game. The recovery plan and personal communications with experts were our primary sources of information used to update the species' status and threats. This 5-

year review contains updated information on the species' biology and threats, and an assessment of that information compared to that known at the time of listing or since the last 5-year review. We focus on current threats to the species that are attributable to the Act's five listing factors. The review synthesizes all this information to evaluate the listing status of the species and provide an indication of its progress towards recovery. Finally, based on this synthesis and the threats identified in the five-factor analysis, we recommend a prioritized list of conservation actions to be completed or initiated within the next 5 years.

Contact Information:

> **Lead Regional Office:** Diane Elam, Deputy Division Chief for Listing, Recovery, and Habitat Conservation Planning, and Jenness McBride, Fish and Wildlife Biologist, Region 8, Pacific Southwest; (916) 414-6464.
>
> **Lead Field Office:** Connie Rutherford, Listing and Recovery Program Coordinator for Plants; Ventura Fish and Wildlife Office; (805) 644-1766 x 306.

Federal Register (FR) Notice Citation Announcing Initiation of This Review: A notice announcing initiation of the 5-year review of this taxon and the opening of a 60-day period to receive information from the public was published in the Federal Register on March 25, 2009 (74 FR 12878). No information was received in relation to this species.

Listing History:

> **Original Listing**
> **FR Notice:** 65 FR 14888
> **Date of Final Listing Rule:** March 20, 2000
> **Entity Listed:** *Lupinus nipomensis* (species)
> **Classification:** Endangered
>
> **State Listing**
> *Lupinus nipomensis* was listed as endangered by the State of California in 1987.

Associated Rulemakings: N/A

Review History: N/A

Species' Recovery Priority Number at Start of 5-Year Review: The recovery priority number for *Lupinus nipomensis* is 5 according to the Service's 2008 Recovery Data Call for the Ventura Fish and Wildlife Office, based on a 1-18 ranking system where 1 is the highest-ranked recovery priority and 18 is the lowest (Endangered and Threatened Species Listing and Recovery Priority Guidelines, 48 FR 43098, September 21, 1983). This number indicates that the taxon is a species that faces a high degree of threat and has a low potential for recovery.

Recovery Plan or Outline: None

II. REVIEW ANALYSIS

Application of the 1996 Distinct Population Segment (DPS) Policy:

The Endangered Species Act defines species as including any subspecies of fish or wildlife or plants, and any distinct population segment (DPS) of any species of vertebrate wildlife. This definition limits listing as distinct population segments to vertebrate species of fish and wildlife. Because the species under review is a plant and the DPS policy is not applicable, the application of the DPS policy to the species' listing is not addressed further in this review.

Updated Information on Current Species Status, Biology, and Habitat:

Species Biology and Life History

Lupinus nipomensis is a small annual herb in the pea family (Fabaceae). The low-spreading individuals can reach 8 inches (20 centimeters) in height (Riggins 1993). Leaves are pinnately compound into five to seven leaflets. Up to 10 pinkish-purple flowers are borne on the ends of the inflorescences (flowering stems). Each flower produces a pod that contains three to four ovules (Riggins 1993), and one healthy plant can produce up to 10 inflorescences (Walters and Walters 1988). Potentially, seed production could reach on the order of 1,000 seeds; however, based on 2 years of sampling, observed seed production per plant ranged from 1 to over 200, with most plants producing less than 30 fruits (Walters and Walters 1988). Growth is indeterminate, with individuals aborting flowers on the central stems in favor of producing additional lateral branches and inflorescences when climatic conditions, particularly the timing of spring rains, are favorable (Walters and Walters 1988). Leaves and stems are succulent, and provide prolonged moisture for seed development. Flowers are self-compatible if manipulated; however, they may require insect visitation for full complements of seeds (Center for Plant Conservation (CPC) 2009). During their four-year study, no observations of pollinators were recorded by Walters and Walters (1988). While pollination ecology has not been specifically studied for *L. nipomensis*, other lupine taxa are known to be pollinated by butterflies and a variety of bee taxa, especially from the genera *Bombus*, *Osmia*, *Synhalonia*, and *Anthidium* (Moldenke 1976).

Distribution

According to records available through the CNDDB (2009) and the Consortium of California Herbaria (Consortium) (2009), all historical collections and unvouchered observations of *Lupinus nipomensis* are from one area in the southwestern corner of San Luis Obispo County. We estimate the total amount of potentially suitable habitat for *L. nipomensis* in contiguous portions of San Luis Obispo County is on the order of 1,000 acres (405 hectares (ha)), while the current footprint of the populations is on the order of 100 acres (40.5 ha).

At this time, *Lupinus nipomensis* is still known to be extant at one location in San Luis Obispo County, California (Appendix 1, figure 1). We consider all individuals at this site to comprise one population of approximately six occurrences (CNDDB 2009) or colonies scattered across a 2-mile (3.2-km) stretch of backdune habitat west of Highway 1 and between Black Lake Canyon to the north and Oso Flaco Lake to the south. All of the habitat for the species is privately

owned, most by Conoco-Phillips Oil Company (CPOC), and smaller portions are owned by Pacific Gas and Electric Company, the Conservancy, and other private landowners. A portion of the habitat is within a California Department of Transportation right-of-way.

Abundance, Population Trends

Early survey data from the 1980s is incomplete. The first effort to conduct an annual census was initiated in 1984 and focused on the three colonies that comprise the "Callender" occurrences (CNDDB #2 in Table 2 below); 273 *Lupinus nipomensis* individuals were counted in that year. A large number of individuals (886) were counted during 1985; this number included 83 individuals located near Jack Lake (CNDDB #1 in Table 2 below). A small number of individuals (77) were located in 1986; however, the latter did not represent a complete census of the Jack Lake occurrence (Walters and Walters 1988). By 1987, four additional occurrences had also been located.

No complete surveys or censuses were conducted between 1987 and 2004. Census data taken since 2004 is more complete, but difficult to reconcile with earlier census efforts due to differing mapping methods. In 2003, annual surveys were resumed by the Conservancy. Census data for 2004 and 2005 are considered to be inaccurate due to confusion in differentiating between *Lupinus nipomensis* and another small annual lupine that occurs in the area (Daniel Bohlman, restoration ecologist, Conservancy, pers. comm. 2009). The most accurate census data are from years 2006 through 2009 (See Figure 2). During this 4-year time period, the number of individuals ranged between a high of 771 and a low of 139, prior to mortality due to pocket gopher damage (Conservancy in litt. 2009). For the 3 years from 2007 through 2009, between 28 to 31 percent of *L. nipomensis* individuals were consumed by pocket gophers on Conoco-Phillips property (Conservancy in litt. 2009). Relative to numbers of individuals for other annual plant species, these numbers are extremely low (Keith 1998).

Figure 2: Conservancy census results for *Lupinus nipomensis* at selected locations.

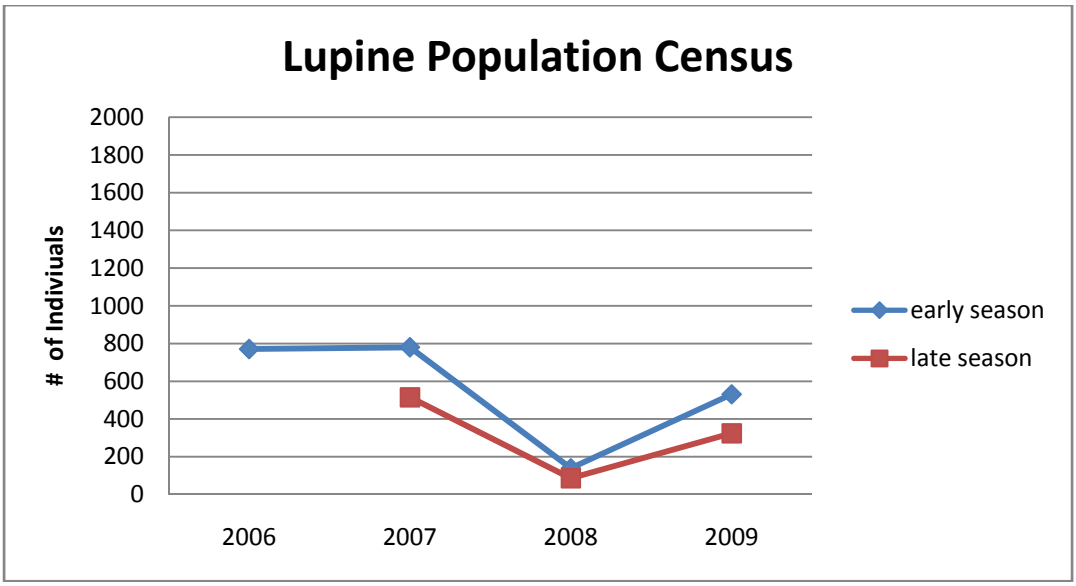

Table 1 below summarizes occurrence data from CNDDB; due to a difference in survey methodology, survey results from the Conservancy efforts (see Table 1) cannot be reconciled with CNDDB data, and therefore is not included in Table 1 below.

Table 1: Occurrence Records for *Lupinus nipomensis* Collated from the CNDDB (2009).

CNDDB #	Name (owner)	CNDDB Current trend	Year collected/observed	Pop size/Year surveyed	Reference
1	Southeast of Jack Lake (private)	presumed extant	Hoover #9365 (1965)	17 (1983) 83 (1985) 177 (1987) 276 (1988) 149 (1998)	CNDDB 2009
2	Callender switching station (CPOC and PG&E)	Presumed extant	Riggins #87204 (1987)	273 (1984) 803 (1985) 77 (1986) 317 (1987) 1035 (1988) 140 (2004)	CNDDB 2009
3	Near Black Lake and Highway 1 (Type locality) (Conservancy)	Presumed extirpated	Eastwood # 18929 (1940)	0 (1980) 0 (1981) 0 (1988)	CNDDB 2009
4	Southeast of main entrance of Unocal Oil Refinery (CPOC)	Presumed extant	--	50 (1987) 44 (1987) 636 (1988)	CNDDB 2009
7	0.8 mi SSW of jct of Highway 1and Willow Rd (private unknown)	Presumed extant	--	1300 (1988)	CNDDB 2009
8	Callender Dunes NE of Jack Lake (CPOC)	Presumed extant	--	80 (1998)	CNDDB 2009
9	Callender Dunes, 0.6 mi N of Jack Lake (CPOC)	Presumed extant	--	12 (1998)	CNDDB 2009

CNDDB identification # = element occurrence number assigned by the California Natural Diversity Database (CNDDB 2009).

Habitat or Ecosystem Conditions (e.g., amount and suitability)

Habitat for *Lupinus nipomensis* is comprised of stabilized back dunes supporting a central coastal dune scrub community. Dominant species include mock heather (*Ericameria ericoides*) and silver lupine (*Lupinus chamissonis*). Other frequent associated species include buckwheat (*Eriogonum parvifolium*), deerweed (*Lotus scoparius*), and horkelia (*Horkelia cuneata*), as well as a large variety of annual herbs interspersed in open areas between the shrubs (Howald 1988).

Walters and Walters (1988) described habitat for the species as either being of degraded quality due to disturbance (type 1) or better quality habitat that was less disturbed and more closely fits the description of coastal dune scrub above (type 2). The sites with disturbed or type 1 habitat are characterized by a lower diversity of species overall, a lower cover of shrubs, a higher percentage of bare sand, a higher cover of nonnative species, and, in most years, a lower density of *Lupinus nipomensis*. At some type 1 sites, the nonnative veldt grass (*Ehrharta calycina*) has become abundant and is crowding out native species.

Lupinus nipomensis needs open habitat to persist. Sandy soils along the coast typically undergo a certain amount of natural disturbance from coastal winds and from the activity of wildlife. However, over time, natural disturbance regimes have been altered by the planting of such species as European beach grass (*Ammophila arenaria*) and eucalyptus (*Eucalyptus* spp.), and

human-caused disturbances, such as off-highway vehicle use, have increased. Although high densities of *L. nipomensis* may occur in disturbed habitat in certain years, predation of both seeds and plants is also known to be greater in areas of higher density *L. nipomensis* (Walters and Walters 1988), resulting in lower seed production or mortality. As a result, the occurrence of higher numbers of individuals in disturbed sites does not necessarily equate to a benefit to the species.

Changes in Taxonomic Classification or Nomenclature
No changes in taxonomy or nomenclature have been made since the time of listing.

Genetics
No new studies concerning the genetics of this taxon have been conducted since the time of listing.

Species-specific Research and/or Grant-supported Activities
In 2004, the Service contributed half of the funds necessary to establish a national endowment for the species through the CPC; a private donor contributed the rest of the funds. The endowment addresses activities related to seed collection, viability testing, long-term storage, and propagation if needed. The Santa Barbara Botanic Garden is a member of the CPC and has been undertaking this work (CPC 2009). Wilken (in litt. 2009) tested two batches of seed for viability. Seed that was at least 15 years old and not stored according to standard storage protocols exhibited no germination, while 1-year old seed and stored according to standard storage protocols exhibited 60 percent germination. Wilken also tested for self-compatibility and found that 100 percent (six out of six) of the individuals developed seed.

Five-Factor Analysis

FACTOR A: Present or Threatened Destruction, Modification, or Curtailment of Habitat or Range

According to the California Department of Fish and Game (2005), three historical localities had been extirpated by the late 1990s. Plants have not been seen at the type locality, near Black Lake, since 1937; the location of the other two extirpated localities is unclear. All mapped occurrences, both historic and current, are found within the same small geographic area; therefore, we do not consider that there has been a reduction in the range of the species.

At the time of listing *Lupinus nipomensis* in 2000 (Service 2000), we discussed activities related to energy extraction and refinement (e.g., maintenance activities, hazardous waste cleanup) and development as threats to the species. Since the time of listing until the time of this review, we had not been aware that these activities have contributed to the alteration or loss of any habitat. However, during the course of this review, we became aware of a Notice of Preparation to expand refinery capabilities at the Conoco-Phillips plant (County of San Luis Obispo 2008). The Service has also recently received a notice regarding a proposal to construct a telecommunications facility less than 0.25 mile (0.4 km) away from EO #7 (C. Mehlberg, Service, in litt. 2009). The project proponent notes that the site was previously developed with agricultural fields; whether above-ground plants or a seed bank of *L. nipomensis* remains is

unknown. In addition, it appears that several housing developments have been constructed within a mile of *L. nipomensis* habitat over the past 5 years (Google Earth 2009). The presence of a larger human population in the adjacent area is likely to introduce additional direct and indirect effects (such as trampling from recreational use, spread of invasive horticultural species used in landscaping, and loss of pollinator habitat) on the species as time goes on.

At the time of listing, we did not discuss under Factor A the role of sheep grazing, cattle grazing, or the spread of invasive veldt grass in the modification of habitat for *Lupinus nipomensis*. We typically discuss grazing impacts under Factor C (predation) and E (trampling), and competition with nonnative species under Factor E. However, because both these activities can play a role in modifying habitat for *L. nipomensis*, we are including them in Factor A in this review. Sheep grazing was terminated in the area sometime in the mid-1980s (Conservancy 2001). Since the time of listing, the number of cattle grazed on the Conoco-Phillips property has been reduced. In addition, the cattle are grazed between July 1 and December 1 of each year (Bohlman, pers. comm. 2009); because the timing of grazing is not during the active growing and flowering period for *L. nipomensis*, we believe that the direct impacts of grazing from trampling are less than they were at the time of listing.

Veldt grass was described as "rampant" in the area at least 25 years ago (McLeod and Walters 1987); its presence can cause a shift from scrub habitat to grassland habitat (Bossard et al. 2000, California Invasive Plant Council 2009). Since 2000, the Conservancy has been actively removing veldt grass from *Lupinus nipomensis* habitat. While these efforts may have slowed the conversion to a monoculture of veldt grass, it is likely that the habitat will have to be managed in perpetuity to maintain the open patches that is required by *L. nipomensis*. The Conservancy conducted grazing trials in the late 1990s to determine if cattle grazing would be useful in reducing the biomass of veldt grass in advance of treating the veldt grass with herbicides. They found that, although cattle grazing may be useful to reduce veldt grass biomass, it may not be effective in reducing the number of tufts (frequency) due to their pernicious root systems (Bossard et al. 2000, Conservancy 2001). In addition, they found that native shrubs experienced substantial damage from cattle trampling, and that veldt grass increased in areas where cattle grazing was reduced. The Conservancy concluded that the benefits of using cattle for removal of veldt grass biomass were outweighed by damage to native shrubs (Conservancy 2001). Long-term effects of cattle grazing may include altering biodiversity within the habitat and are not completely understood at this point in time.

Conservation

Conoco-Phillips is the primary landowner of habitat where *Lupinus nipomensis* remains extant. In the late 1980s, they entered into an agreement with California Department of Parks and Recreation for the latter to manage Conoco-Phillips lands that border Oceano Dunes State Vehicular Recreation Area. The designation of this land as a buffer zone decreased the amount of illegal off-highway vehicle activity in the area (R. Glick, in litt. 2009). In addition, Conoco-Phillips is working cooperatively with the Conservancy to continue veldt grass removal and to annually census *L. nipomensis* colonies on their lands (Bohlman in litt. 2009). In 1997, the Conservancy acquired a parcel that includes Black Lake and the surrounding area, which was the type locality for *L. nipomensis*. Although habitat is not currently suitable to support *L. nipomensis* due to heavy vegetation cover, it could possibly do so in the future. The

Conservancy has actively been managing for veldt grass, both on their own lands and in partnership with adjacent landowners.

In summary, oil refinery activities appear to be less of a threat than at the time of listing, but a proposal to expand refinery operations in the near future may alter or destroy suitable habitat for *Lupinus nipomensis.* Urban development activities may become more of a threat in the future with human population growth in the area. Overall, habitat is being more closely managed, and has resulted in several parcels falling under more protective management, including a reduction of illegal off-highway vehicle use, and the removal of veldt grass from *L. nipomensis* habitat. Little opportunity for population expansion is available adjacent to the existing populations because habitat has already been converted to other uses, including roads, facilities, agriculture, and housing. However, there may be some opportunity to enhance habitat at existing population sites. The presence of veldt grass continues to be the greatest long-term threat to *L. nipomensis* and its habitat.

FACTOR B: Overutilization for Commercial, Recreational, Scientific, or Educational Purposes

Overutilization for commercial, recreational, scientific, or educational purposes was not known to be a factor in the 2000 final listing rule (65 FR 14888). Overutilization for any purpose does not appear to be a threat at this time.

FACTOR C: Disease or Predation

Disease was not considered a threat at the time of listing in 2000. At that time, we identified that pocket gophers (*Thomomys bottae*) had consumed entire colonies of *Lupinus nipomensis*, as reported by Walters and Walters (1988). While pocket gophers are known to harvest seeds of many species in general (Martin et al. 1951), it is more likely that they consume the roots, stems, and leaves of *L. nipomensis*, and that seeds die prior to full maturation. However, seed that are able to complete maturation despite being excised from the plant may find suitable germination sites in the vacated gopher mounds the following winter season (Walters and Walters 1988). In addition, our listing rule stated that the presence of veldt grass increases the food source for pocket gophers and thus potentially increases their numbers and their potential harm to *L. nipomensis* (Walters and Walters 1988). Survey results for the 3 years from 2007 through 2009 indicate that from 28 to 31 percent of *L. nipomensis* individuals are consumed by pocket gophers on Conoco-Phillips property (Conservancy in litt. 2009); therefore, we continue to believe that pocket gophers continue to be a threat to the species.

Our listing rule stated that a variety of insects were variously foraging on the seeds, stems, or leaves of *L. nipomensis* and reducing its reproductive potential; insects include an anthomyid fly (*Hylemya lupini* Coquillette), the common painted lady butterfly (*Vanessa cardui*), a noctuid moth (family Pyridae), and a lupine blue butterfly (*Plebejus lupini monticola*). No data have been gathered to determine the extent of these threats on the long-term persistence of *L. nipomensis*.

At the time of listing, we were not aware of, and did not discuss, the potential impacts of cattle grazing on *Lupinus nipomensis*. In the early 2000s, the Conservancy worked with Conoco-Phillips to reduce the number of cattle grazed on their lands (Service in litt. 2005). In addition, the timing of grazing is such that it does not occur when *L. nipomensis* is growing and flowering. Therefore, we believe the effects of grazing due to consumption are small to none (see Factor A for a discussion of the effects of grazing on habitat).

FACTOR D: Inadequacy of Existing Regulatory Mechanisms

At the time of listing, regulatory mechanisms thought to have some potential to protect *Lupinus nipomensis* included: (1) listing under the California Endangered Species Act (CESA); (2) the California Environmental Quality Act (CEQA) and the National Environmental Policy Act (NEPA); (3) the California Coastal Act; and (4) local land use laws, regulations, and policies. The listing rule (65 FR 14888) provides an analysis of the level of protection that was anticipated from those regulatory mechanisms. For the most part, this analysis appears to remain valid. However, there may also be future federal and state involvement through the Environmental Protection Agency, the Water Quality Control Board, and the Air Quality Control Board, due to their regulatory authority over air quality, water quality, and hazardous waste management associated with oil refinery activities. In addition, the Federal Communications Commission may have regulatory authority over the installation and permitting of telecommunications facilities.

Lupinus nipomensis was listed as endangered by the State of California in 1987. As such, projects that would affect *L. nipomensis* are subject to CESA and CEQA requirements. Protection of listed species through CEQA is dependent upon the discretion of the lead agency involved. To the best of our knowledge, no projects have evaluated impacts to the species pursuant to CESA and CEQA since the species was listed. A Notice of Preparation was recently circulated by the County of San Luis Obispo for a proposed project to increase refinery capabilities by the Conoco-Phillips refinery by 12.5 percent (County of San Luis Obispo 2008). The project may include installation of a new pipeline from the refinery north to the San Francisco Bay area; if so, the pipeline would potentially alter or destroy habitat for *L. nipomensis.* This project would likely be subject to both state and federal agency regulations.

In summary, although there are both state and federal regulatory mechanisms that would potentially apply to projects within *Lupinus nipomensis* habitat, none of them have been invoked since the time of listing. We believe that pending and future projects will be subject to available regulatory mechanisms.

FACTOR E: Other Natural or Manmade Factors Affecting Its Continued Existence

At the time of listing, we discussed competition with nonnative species and stochastic extinction due to small size of populations and numbers as threats to *Lupinus nipomensis.* An analysis of these threats is contained in the final rule and appears to remain currently valid.

<u>Nonnative Species</u>
In general, invasion of this habitat by nonnative species (particularly veldt grass (see Bossard et

al. 2000)) is a threat to populations of native species because individuals cannot compete well for light, water, and resources (D'Antonio and Vitousek 1992). The expansion of veldt grass in *Lupinus nipomensis* habitat and its effects on the species were discussed in Factor A.

Stochastic Extinction

We continue to believe that the existence of less than 10 occurrences and the small number of individuals in the occurrences (Figure 1 and Table 1) place *Lupinus nipomensis* at risk of extinction from stochastic events. The conservation biology literature commonly notes the vulnerability of taxa known from one or very few locations and/or from small and highly variable populations (e.g., Shaffer 1981, 1987; Groom et al. 2006; Primack 2006). In particular, although the plants are apparently self-compatible and capable of self-fertilization, the small size of the population makes it difficult for this species to persist while sustaining the impacts of habitat alteration that favors nonnative plant species and the potential loss of pollinator habitat.

Climate Change

At the time of listing, we did not discuss the potential effects of climate change on the long-term persistence of *Lupinus nipomensis*. Current climate change predictions for terrestrial areas in the Northern Hemisphere indicate warmer air temperatures, more intense precipitation events, and increased summer continental drying (Field et al. 1999, Cayan et al. 2005, Intergovernmental Panel on Climate Change 2007). Recently, the potential impacts of climate change on the flora of California were discussed by Loarie et al. (2008). Based on modeling, they predicted that species' distributions will shift in response to climate change, specifically that the species will "move" or disperse to higher elevations and northward, depending on the ability of each species to do so. Species diversity will also shift in response to these changes with a general trend of increasing diversity shifting towards the coast and northwards with these areas becoming de facto future refugia. However, predictions of climatic conditions for smaller sub-regions such as California remain uncertain. It is unknown at this time if climate change in California will result in a warmer trend with localized drying, higher precipitation events, or other effects.

While we recognize that climate change is an important issue with potential effects to listed species and their habitats, we lack adequate information to make accurate predictions regarding its effects to *Lupinus nipomensis* at this time.

III. RECOVERY CRITERIA

Recovery plans provide guidance to the Service, States, and other partners on ways to minimize threats to listed species and on criteria that may be used to determine when recovery is achieved. There are many paths to accomplishing recovery of a species and recovery may be achieved without fully meeting all recovery plan criteria. For example, one or more criteria may have been exceeded while other criteria may not have been accomplished. In that instance, we may determine that, over all, the threats have been minimized sufficiently, and the species is robust enough, to reclassify the species from endangered to threatened or perhaps to delist it. In other cases, new recovery opportunities unknown at the time the recovery plan was finalized may be more appropriate. Likewise, new information may change the extent that criteria need to be met for recognizing recovery of the species. Overall, recovery is a dynamic process requiring

adaptive management, and assessing a species' degree of recovery is likewise an adaptive process that may, or may not, fully follow the guidance provided in a recovery plan. We focus our evaluation of species status in this 5-year review on progress that has been made toward recovery since the species was listed (or since the most recent 5-year review) by eliminating or reducing the threats discussed in the five-factor analysis. In that context, progress towards fulfilling recovery criteria serves to indicate the extent to which threat factors have been reduced or eliminated.

A recovery plan for *Lupinus nipomensis* has not yet been developed; therefore no recovery criteria exist.

IV. SYNTHESIS

The status of *Lupinus nipomensis* does not appear to have changed substantially since the time of listing in 2000. Conservation measures have been undertaken to improve management of the habitat on several parcels. The Conservancy in partnership with adjacent landowners has been working to reduce the amount of veldt grass within *L. nipomensis* habitat. They have also been instrumental in carrying out an annual census of the species. Nevertheless, alteration of habitat due to the presence of veldt grass is a primary continuing threat to the species.

The most reliable census information from years 2006 through 2009 indicates that the total numbers of individuals of *Lupinus nipomensis* is very low and fluctuates annually. Pocket gopher predation has removed approximately 30 percent of the plants censused between 2007 and 2009. In addition, seed studies to date indicate that viable seed is being produced; however, germination rates in the wild appear to be lower than those in greenhouse studies. The combination of low numbers of individuals and the concentration of all occurrences in a small geographic area make this species vulnerable to stochastic extinction. We conclude that this taxon continues to be in danger of extinction throughout its currently known range and therefore meets the definition of endangered under the Federal Endangered Species Act; no status change is recommended at this time.

V. RESULTS

Recommended Classification:

____ Downlist to Threatened
____ Uplist to Endangered
____ Delist (indicate reasons for delisting per 50 CFR 424.11):
    ____ *Extinction*
    ____ *Recovery*
    ____ *Original data for classification in error*
__X__ No Change

New Recovery Priority Number and Brief Rationale: N/A

VI. RECOMMENDATIONS FOR FUTURE ACTIONS

1. Complete a Recovery Outline and Species Action Plan for *Lupinus nipomensis* as a first step in preparing a recovery plan for the species.

2. Work with Conoco-Phillips and California Department of Transportation to ensure that management of their lands and rights-of-way is consistent with the long-term persistence of *Lupinus nipomensis* at those sites. In addition, work with the County of San Luis Obispo to ensure that consideration is given to *L. nipomensis* during projects review and implementation.

3. In partnership with Santa Barbara Botanic Garden, continue with research on seed characteristics, particularly to determine the extent of the soil seed bank present, and whether there is a difference in seed viability between those produced from self-fertilization and those produced by cross-pollination to determine if lack of pollinators is a concern.

4. In partnership with Santa Barbara Botanic Garden and the Conservancy, experiment with establishment of new populations in other coastal dune scrub habitat in coastal San Luis Obispo County.

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U.S. FISH AND WILDLIFE SERVICE
5-YEAR REVIEW of *Lupinus nipomensis* (Nipomo lupine)

Current Classification: Endangered

Recommendation Resulting from the 5-Year Review:

____ Downlist to Threatened
____ Uplist to Endangered
____ Delist
__X_ No change needed

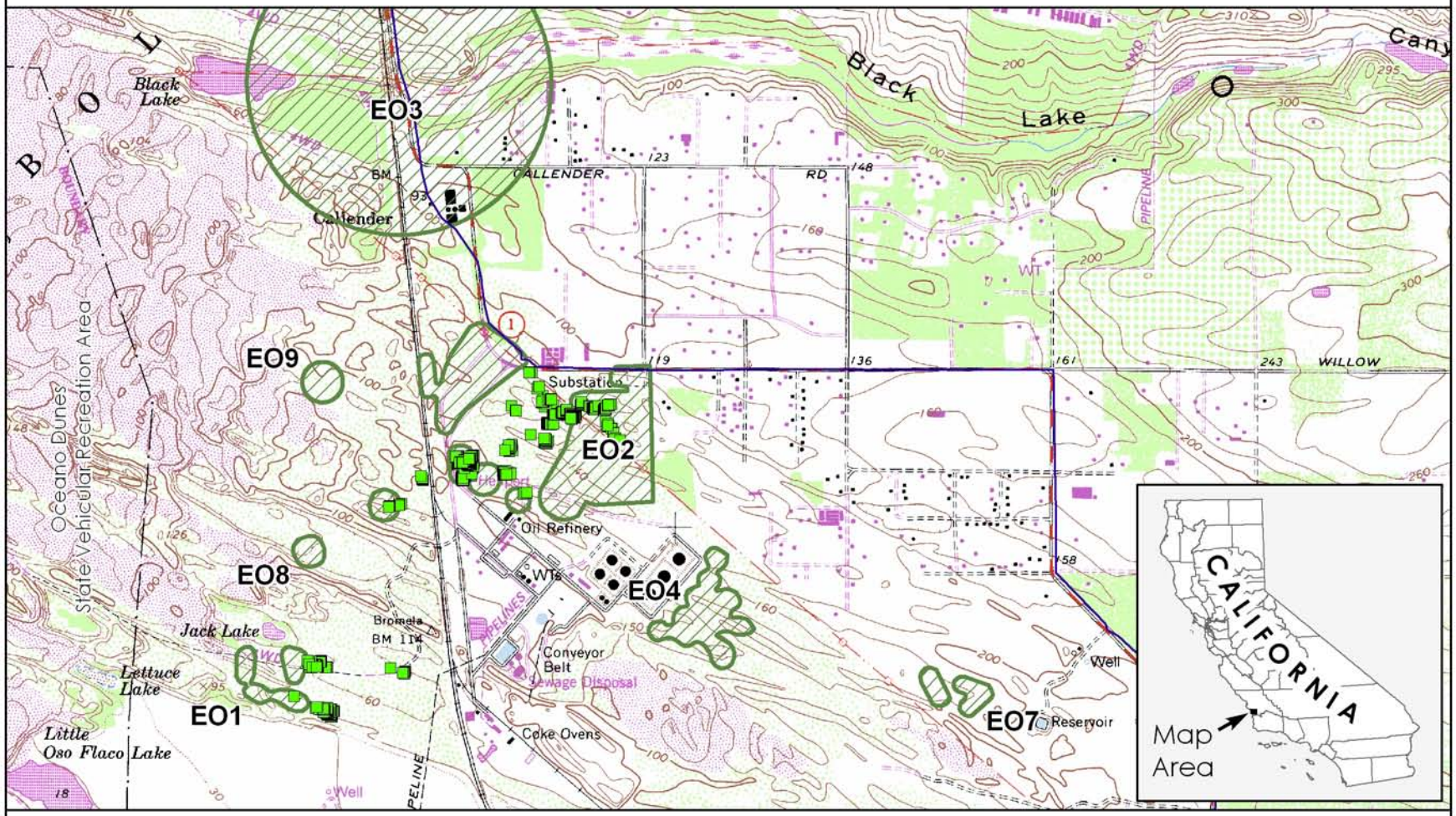
Review Conducted By: Connie Rutherford

FIELD OFFICE APPROVAL:

Field Supervisor, U.S. Fish and Wildlife Service

Approve Diane K Noda Date 10/19/09

Appendix 1: Figure 1. Distribution of *Lupinus nipomensis* (Nipomo lupine), San Luis Obispo County, California



0 0.5 1 Kilometers

Prepared for the 5-year Review

Nipomo Lupine Records

- Conservancy Records 2007-2009
- CNDDB 2009 records

U.S. Fish & Wildlife Service
Ventura Fish & Wildlife Office
September, 2009

Year of death	Sex of bear	Cause Specific	Inside/outside recovery zone		bears killed
2013	F	train	inside	1984	1
2013	F	train	outside	1985	1
2011	M	train	outside	1986	1
2011	M	train	outside	1987	0
2011	M	train	outside	1988	0
2009	M	train	inside	1989	2
2009	M	train	outside	1990	5
2008	F	train	inside	1991	0
2007	M	train	outside	1992	1
2007	F	train	outside	1993	0
2007	M	train	outside	1994	0
2007	M	train	inside	1995	2
2007	M	train	outside	1996	2
2006	F	train	inside	1997	3
2006	M	train	inside	1998	1
2006	M	train	inside	1999	5
2004	F	train	inside	2000	0
2004	M	train	inside	2001	4
2003	M	train	inside	2002	1
2003	F	train	inside	2003	3
2003	F	train	inside	2004	2
2002	M	train	inside	2005	0
2001	F	train	inside	2006	3
2001	M	train	inside	2007	5
2001	F	train	inside	2008	1
2001	F	train	inside	2009	2
1999	F	train	inside	2010	0
1999	M	train	inside	2011	3
1999	M	train	inside	2012	0
1999	M	train	outside	2013	2
1999	M	train	outside		
1998	F	train	inside	total	50
1997	M	train	inside		
1997	F	train	inside		
1997	F	train	inside		
1996	M	train	inside		
1996	M	train	inside		
1995	F	train	inside		
1995	M	train	inside		
1992	M	train	outside		
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1990	M	train	inside		
1990	M	train	inside		
1990	F	train	inside		
1990	F	train	inside		
1989	M	train	inside		
1989	F	train	inside		
1986	M	train	inside		
1985	F	train	inside		

1984	M	train	inside

data received on Sept 17, 2014
sent by Grizzly Bear Recovery Coordinator, USFWS, at request of Chris Servheen
University Hall, Room 309, University of Montana, Missoula, MT 59812
Office: 406-243-4903
grizz@umontana.edu

for NCDE population

Van Why, K.R., and M.J. Chamberlain. 2003. Mortality of black bears, *Ursus americanus*, associated with elevated train trestles. Canadian Field-Naturalist 2003:113-115.

Abstract:

The Louisiana Black Bear (Ursus americanus luteolus), a threatened species in the United States, inhabits the Tensas and Atchafalaya River Basins of Louisiana. These basins contain three breeding populations, but dispersal among the populations is limited due to habitat fragmentation and a lack of corridors. Highways and railroads bisect the few available corridors. and mortalities occur as a result of collisions with vehicles. Waterways and flood control structures used as travel corridors by bears are crossed by road and rail bridges creating the potential for additional mortalities. We documented two mortalities associated with elevated railroad spans. Both occurred along the same span of track located within the Morganza Spillway in Pointe Coupee Parish, Louisiana, and both mortalities were a result of the bear falling from the span or being struck by a train while crossing the trestle.

BioOne RESEARCH EVOLVED

EFFECTS OF TRANSPORTATION INFRASTRUCTURE ON GRIZZLY BEARS IN NORTHWESTERN MONTANA

Author(s): JOHN S. WALLER and CHRISTOPHER SERVHEEN
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EFFECTS OF TRANSPORTATION INFRASTRUCTURE ON GRIZZLY BEARS IN NORTHWESTERN MONTANA

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Abstract: Highways and railroads have come under increasing scrutiny as potential agents of population and habitat fragmentation for many mammalian species, including grizzly bears (*Ursus arctos*). Using Global Positioning System (GPS) technology and aerial Very High Frequency (VHF) telemetry, we evaluated the nature and extent of trans-highway movements of 42 grizzly bears along the U.S. Highway 2 (US-2) corridor in northwest Montana, USA, 1998–2001, and we related them to highway and railroad traffic volumes and other corridor attributes. We employed highway and railroad traffic counters to continuously monitor traffic volumes. We found that 52% of the sampled population crossed highways at least once during the study but that crossing frequency was negatively exponentially related to highway traffic volume. We found that grizzly bears strongly avoided areas within 500 m of the highway and that highway crossing locations were clustered at a spatial scale of 1.5 km. Most highway crossings occurred at night when highway traffic volume was lowest but when railroad traffic was highest. Highway crossing locations were flatter, closer to cover in open habitat types, and within grassland or deciduous forest vegetation types. Nighttime traffic volumes were low, averaging about 10 vehicles/hr, allowing bears to cross. However, we project that US-2 may become a significant barrier to bear movement in ~30 years if the observed trend of increasing traffic volume continues.

JOURNAL OF WILDLIFE MANAGEMENT 69(3):985–1000; 2005

Key words: connectivity, Global Positioning System, GPS, grizzly bear, highways, Montana, railroads, roads, transportation, *Ursus arctos*.

The grizzly bear was once common throughout much of the western United States from the Canadian–American border south to the present-day Mexican–American border (Rausch 1963). However, expanding human populations have severely reduced many grizzly bear populations, particularly in the southern portions of their range (Servheen 1999, Mattson and Merrill 2002). Grizzly bears in the United States now occur in only 5 ecosystems within the states of Idaho, Montana, Wyoming, and Washington (Servheen 1990). The extent of grizzly bear movement between these ecosystems is probably minimal, and no natural movement between ecosystems has been documented (Kasworm et al. 1998).

The Grizzly Bear Recovery Plan recommends establishment and maintenance of linkage zones between these 5 ecosystems (U.S. Fish and Wildlife Service 1993) to maintain genetic diversity within each population and to lessen the impacts of demographic and environmental stochasticity (Wilcox 1980). Consequences of reduced population size, isolation, and subsequent inbreeding and demographic vulnerability have been widely discussed (Wright 1931, Soulé 1980, Gilpin and Soulé 1986, Lande 1988, Mills and Smouse 1994, Lande 1995, Paetkau et al. 1998).

Highways and/or railroads currently bisect all 5 grizzly bear ecosystems. Negative effects of transportation corridors have been documented for numerous wildlife species including woodchucks (*Marmota monax*; Woodward 1990), sandhill cranes (*Grus canadensis*; Dwyer and Tanner 1992), ravens (*Corvus corax*; Knight and Kawashima 1993), passerines (Reijnen and Foppen 1994), deer (*Odocoileus* spp.; Romin and Bissonette 1996), and bumblebees (*Bombus* spp.; Bhattacharya et al. 2003); indeed, the negative effects of highways on wildlife have been noted for over 75 years (Stoner 1925, Forman et al. 2002). However, data for grizzly bears are limited.

Previous research on the effects of roads on grizzly bears has been largely confined to tertiary and/or unimproved road systems occurring within forests managed for timber harvest (Archibald et al. 1987, McLellan and Shackleton 1988, Kasworm and Manley 1990, Mace et al. 1996) or within national parks (Mattson et al. 1987). All have shown displacement due to roads. Previously published works from 2 areas specifically addressed the impacts of high-volume highways on brown bears. Chruszcz et al. (2003) found that traffic volume affected crossings on high-volume highways in Banff National Park, Alberta, Canada, and Kaczensky et al. (2003) found a similar situation in Slovenia.

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Our objective was to describe the effects of a high-speed highway and its associated transportation corridor on the movement and habitat-use patterns of resident grizzly bears. Specifically, we studied whether grizzly bears avoided areas near the highway, if resident grizzly bears used specific crossing areas to traverse highways, and whether or not these locations differed from non-crossing areas. We also studied whether or not any existing temporal patterns of highway crossings were related to highway and railroad traffic levels.

STUDY AREA

Our 2730 km^2 study area consisted of 4 fifth-order watersheds located along Montana Highway 49 (MT-49) and US-2, approximately between Essex and East Glacier, Montana. The most northern east-west highway in the contiguous United States, US-2 was a 2-lane highway separating Glacier National Park to the north from the Bob Marshall Wilderness complex to the south. The western portion of the highway lay within the valley bottom of the Middle Fork of the Flathead River and Bear Creek valley until it crossed the Continental Divide at Marias Pass (elevation 1610 m). East of Marias Pass, US-2 dropped into the prairie biome, paralleling the South Fork of the Two Medicine River and crossing the western boundary of the Blackfeet Indian Reservation (BIR).

Another paved 2-lane highway, MT-49, joined US-2 from the north at East Glacier. Carrying primarily local and tourist traffic, it wound through the Rocky Mountain foothills near the eastern edge of Glacier National Park to its terminus with U.S. Highway 89 at Kiowa Junction, Montana. Only small portions of MT-49 lay within the study area.

A major railroad line paralleled US-2 for its entire length within the study area. This railroad line was a primary freight corridor between Chicago, Illinois, and Seattle, Washington, and it was also the primary means of transporting grains from eastern Montana and North Dakota to markets on the West Coast.

Small concentrations of homes, businesses, ranches, and small communities existed within the US-2 corridor, but the majority of the area was undeveloped federal land, (36% of the area lay within the boundaries of Glacier National Park). U.S. Forest Service lands were managed primarily for recreation, timber harvest, and grazing. Tribal lands were managed primarily for cattle grazing.

Topography associated with US-2 varied from flat valley bottoms to steep mountainsides. Dominant vegetation was primarily coniferous forest in the western portions of the study area, where a Pacific maritime climate predominated. Open grass/forb/deciduous tree communities were more common in the east where the climate was continental. The collision of these 2 climatic regimes often resulted in unsettled weather conditions. Riparian areas paralleled the highway for much of its length within the study area. Avalanche chutes were preferred grizzly bear foraging areas (Waller and Mace 1997, McLellan and Hovey 2001) and occurred in numerous locations, often close to the highway.

We chose this particular study area for several important attributes. First, grizzly bears occupied areas on both sides of US-2, and anecdotal observations and preliminary data showed that they crossed this portion of US-2. Second, the level of development within the corridor was significant but not so great as to preclude observations of grizzly bear crossing patterns; and third, we could access areas in which to capture grizzly bears.

METHODS

Capture and Telemetry

To obtain a representative sample of grizzly bears residing within the highway corridor, we placed trap sites as equidistantly as possible along both sides of US-2 within the study area. We captured grizzly bears with Aldridge snares or culvert traps using standard techniques (Johnson and Pelton 1980, Jonkel 1993), or, on the BIR, we fired tranquilizer darts at grizzly bears from tree stands placed over livestock carcasses (Jonkel 1993). All trapping occurred during the months of June and July 1998–2001. We equipped all grizzly bears captured in 1998 with a Telonics model 500RM VHF telemetry transmitter (Telonics Inc., Mesa, Arizona, USA) to assess the extent of highway crossing by resident grizzly bears before beginning full field efforts.

In past research efforts, conclusions concerning specific road segments and their influence zones were limited by existing radiotelemetry technology. Rugged topography often limited ground tracking, and close aerial tracking was limited by frequent periods of inclement weather, restriction to daylight hours, and the high cost of flight time. Further, intensive aerial telemetry in mountainous terrain was dangerous to researchers. Recent incorporation of GPS technology into wildlife telemetry collar systems helped overcome aerial VHF telemetry obstacles. Therefore, during 1999 and 2000, we fitted captured female grizzly bears weighing ≥91 kg with a Telonics Generation IIRM

store-on-board GPS collar. During 2001, the final year of fieldwork, we collared male and female grizzly bears. We fitted grizzly bears weighing <91 kg with an ear-tag transmitter (Advanced Telemetry Systems, Isanti, Minnesota, USA).

Our GPS collars obtained a position once every hr, 24 hr per day, and location information was stored within the collar. The GPS collars could obtain either 2-dimensional (2D) or 3-dimensional (3D) positions. The 2D positions are obtained using 3 GPS satellites and 3D positions require ≥4 satellites and generally give a more accurate position. We chose the hourly location rate as a reasonable compromise between battery life and spatial specificity. We estimated battery life would be about 120 days, which was sufficient to provide GPS positions between time of trapping and denning. Because the collar needed to be retrieved and downloaded to obtain the accumulated information, we equipped all collars with a VHF beacon and a programmable breakaway device. The VHF beacon operated concurrently with the GPS unit, and through variable pulse rates, provided information about GPS system status and/or animal mortality. We located all transmitters 2 times per week from fixed-wing aircraft, as weather conditions allowed, to keep track of animals and provide timely cause-specific mortality information. After we retrieved GPS collars and downloaded their information to a computer, we differentially corrected positions using Trimble Pathfinder Office™ (Trimble Navigation Ltd., Sunnyvale, California, USA), and proprietary software developed by Telonics Incorporated.

Traffic Monitoring

We installed Peek Trafficomp II™ pneumatic vehicle counters (Peek Traffic Corporation, Palmetto, Florida, USA) on US-2 at each end of the study area (approximately 35 km apart). The counters operated June through mid-October during 1999–2001. We configured the counters to tally the number of vehicles passing over the counter sensors each hr of a 24-hr day in each lane (east and west-bound lanes). Having counters at each end of the study area provided system redundancy in case 1 of the counters became inoperative and allowed calculation of local vs. through traffic. Because the counters counted axles, we developed a correction factor for multi-axle vehicles by tallying axles and classifying vehicle types during 11 30- to 60-min observation periods. We then compared these actual counts to those collected by the counter to derive a ratio estimate of the true number of vehicles. We then compared this estimate to the statewide correction factor used by the Montana Department of Transportation (MDOT).

We collected railroad traffic data by downloading automatic train counters through modem access provided by the Burlington-Northern Santa Fe railroad. The counters recorded date, time, direction, length, and speed of all trains crossing the counters. We used counters located just west and east of the study area boundaries. We measured differences in railroad traffic between months and between day and night.

Environmental Variables

We collected hourly weather data during 1999–2001 from remote weather stations operated by MDOT located just west of the study area at Essex and 50 km southeast of the study area at Pendroy, Montana. The Essex weather data were most representative of weather conditions west of the Continental Divide while the Pendroy weather data were more representative of conditions east of the Continental Divide. Weather data included temperature, wind speed, wind direction, and presence, type, and rate of precipitation.

We grouped all GPS positions into dawn, day, evening, and night categories based upon day length. Dawn and evening were the periods between civil twilight and sunrise or sunset. Civil twilight was the period between sunrise or sunset and when the sun was 6 degrees below the horizon. Day was the period between sunrise and sunset, and night was the period between the end of evening twilight and the beginning of morning twilight. We calculated sunrise, sunset, and twilight periods for East Glacier, Montana using Sun.exe (http://www.sunrisesunset.com).

We obtained digital cover-type maps from the U.S. Forest Service and imported them into our computerized Geographic Information System (GIS). The Wildlife Spatial Analysis Lab at the University of Montana produced these maps by classifying Thematic Mapper satellite imagery (Redmond et al. 1998). The Flathead National Forest made further refinements based on potential vegetation types and recent wildfires. The minimum mapping unit for these maps was 2.5 ha. We simplified the map by combining similar vegetation types, thus reducing the number of cover types from 25 to 8. The 8 cover types were rock (barren/nonvegetated), grassland, shrubland, riparian, deciduous forest, mixed forest, conifer forest, and water.

We obtained grizzly bear habitat quality maps from the U.S. Forest Service, constructed during

cumulative effects modeling efforts for the Northern Continental Divide Ecosystem (NCDE; Mace et al. 1999). Mapped habitat quality values were most strongly influenced by elevation and greenness. Greenness was a measure of herbaceous phytomass and was strongly related to grizzly bear habitat selection (Mace et al. 1999, Stevens 2002).

We constructed digital maps of US-2 and the railroad within the study area by digitizing these features on U.S. Geological Survey (USGS) orthophoto quadrangles with 1-m resolution. We obtained hydrological and 10-m digital elevation data from the USGS. We represented terrain ruggedness along US-2 by calculating the standard deviation of elevation within a 1-km moving circle. The U.S. Forest Service, as part of its cumulative effects modeling efforts, classified campgrounds, housing, and other types of human developments into low, moderate, or high-impact categories based upon a Delphi consideration of their perceived impacts on grizzly bears. We obtained these digital maps of human impact points from the U.S. Forest Service, and we then created maps displaying the distance from each of these development categories. We created a distance-to-cover map by digitizing the border of roadside vegetation from USGS orthophoto quadrangles.

We constructed a road density layer by running a moving circle procedure on digital road maps that we obtained from the U.S. Forest Service and from U.S. Census Bureau TIGER files. The moving circle (or focal-sum) process assigned the number of 30-m road cells within a 1-km circle to the center cell. The circle thus moved across the map assigning a value to every cell (Mace et al. 1996). We used ArcView GIS version 3.2 (Environmental Systems Research Institute, Redlands, California, USA) for all GIS analyses.

Data Analysis

We tabulated observed highway crossing events and examined differences in crossing frequency between sex and age classes, season, and time of day. We regressed crossing frequency on traffic volume and evaluated fit using Kolmogorov-Smirnov and chi-square tests. We compared observed highway crossing frequencies to that expected for each grizzly bear with a GPS collar and that crossed US-2 or MT-49. We calculated expected crossing frequencies by generating 100 random walks within each individual bear's 100% minimum convex polygon (MCP) home range (Serrouya 2000). The random walks used the observed distances applied in random directions, thus preserving realistic rates of movement. We arbitrarily selected the 100% MCP (Burt 1943) as a reasonable means to limit the random walks to the areas in which the grizzly bears actually lived. We then calculated the mean number of times the random walks crossed US-2 along with the ± 95% confidence intervals. We considered observed crossing frequencies outside ±95% confidence intervals statistically significant. We generated the home range polygons and random walks using the Animal Movement extension for ArcView GIS (Hooge and Eichenlaub 1997).

We recognized that highway crossing patterns may be proportional to temporal patterns of activity. We compared mean movement distances and rates between highway crossings and non-crossings by individual and tested for significance ($P \leq 0.05$) using the Kruskal-Wallis test (Sokal and Rohlf 1995). We performed this test using mean 24-hr movement rates and mean movement rates calculated for only those hours in which crossings occurred.

To establish a putative distance over which grizzly bears modified their behavior patterns in response to road traffic, we created distance isopleths around US-2 and MT-49 from zero to 1,000 m in 100-m increments. We did not explicitly include the railroad because it generally ran closely parallel with US-2. The mean distance between the railroad and US-2 within the study area was 239 m and ranged from <30 m to 1.7 km (±95% 151–328 m). We assumed that any disturbance associated with the railroad would be additive to that of US-2 and be reflected in isopleth selectivity. We quantified the use and availability of each isopleth by each of the 11 GPS-collared grizzly bears that came within 1 km of US-2 or MT-49 by creating selection ratios (Manly et al. 1993:65). We combined selection ratios over all animals for an estimate of the population selection ratio using equation 4.40 from Manly et al. (1993). We estimated the variance of the population selection ratio as recommended by Manly et al. (1993:38, 67). We tested the selectivity of individual animals by calculating a chi-square statistic with I-1 degrees of freedom, where I was the number of categories. We tested overall selection by summing these statistics over all *j* animals and testing with n(I-1) degrees of freedom (Manly et al. 1993:66). We then identified the putative disturbance zone using a Friedman non-parametric ANOVA on ranks (White and Garrott 1990) followed by post hoc, multiple comparisons (Conover 1980).

To assess the spatial clustering of highway crossing locations or the lack thereof, we modified the method derived by O'Driscoll (1998) and Cle-

venger et al. (2003). First, we assumed that the crossing location occurred at the intersection of the highway and a line connecting the subsequent locations on either side of the highway. Given that locations were 1-hr apart, we felt confident that bears crossed the highway reasonably close to that point.

Using all the n intersections as crossing locations, we then calculated the distance between each crossing point i and its nearest neighbor j, along that portion of the highway where crossings occurred (i.e., the highway segment between the most distant crossing points). We then binned the accumulated distances into arbitrary 1-km distance classes, or scales, ranging from 500 m to 38 km. We then summed the number of nearest-neighbor distances in each bin to yield a form of Ripley's K-statistic (Ripley 1981). Because we pooled observations of highway crossings among individual bears, these statistics reflect the spatial distribution of crossing points of those individuals that crossed highways most often.

In order to assess significance of the K-statistics, we drew a random sample of points along the highway of size n, (simulated crossing locations), and then computed K-statistics for each of 100 iterations. We displayed results as plots of $L(t)$, the observed number of crossings minus the simulated mean, against distance. Values of $L(t) > 0$ indicated clustering and values <0 indicated dispersion. We deemed values of $L(t)$ outside the upper or lower 95th percentile significant (O'Driscoll 1998). We then used the scale distance with the first significant level of clustering as the basis for modeling potential crossing areas. We referred to this scale distance as the patch length or maximal cluster scale, and it was independent of clustering intensity, and was represented by the height of the distribution.

Modeling

We used logistic regression to estimate the probability of bears crossing US-2 as a function of landscape factors that we believed might explain the observed clustering of crossing locations. These factors were: distance to water, distance to cover, cover type, change in elevation adjacent to the roadway, road density, distance to low, moderate, or high human impact points, and habitat quality. We tested each factor at both the base map scale (30-m raster map) and at the generalized maximal cluster scale identified above. We calculated factor values at the maximal cluster scale by computing the average (for continuous data) or modal (for categorical data) values within a moving circle with a diameter equal to the maximal cluster scale. We tested each factor for univariate significance with unbalanced, 1-way ANOVA (continuous data) or χ^2-tests computed from the marginal frequencies of $2 \times k$ contingency tables (categorical data). We tested all factors for multicollinearity prior to logistic regression analysis (Menard 1995). We then included all these factors into a full log-linear model. We estimated model parameters using maximum likelihood techniques where the dichotomous response variables were used (1) or available (zero; Manly et al. 1993). During the moving circle procedure on cover type, the values for the rarest types (i.e., rock, riparian, and water) dropped out. We created 0/1 indicator variables for each of the 5 remaining cover types. For the categorical variable cover type, we held out mixed forest as the standard indicator variable against which others varied. We iteratively removed nonsignificant model parameters based on χ^2-tests of Wald statistics (Hosmer and Lemeshow 1989). We used Akaike's Information Criterion (AIC) to select the most parsimonious model describing grizzly bear crossing areas. We then derived 95% confidence intervals for each parameter estimate by creating a separate model for each $n - 1$ sample of individuals (jackknifing). In this manner, we were able to assess the influence of individual animals on model stability and variability.

RESULTS

Capture and Telemetry

We captured 43 different grizzly bears in 51 capture events (13 adult males, 11 subadult males, 10 adult females, 9 subadult females). We deployed 22 VHF radios on 19 individuals (3 individuals had VHF radios replaced) and 23 GPS collars on 23 individuals. Eight individuals fitted with GPS collars were also given VHF ear-tag transmitters to allow relocation after the GPS collar released (Table 1).

We collected 912 aerial telemetry locations in 242 hrs of flight time during 1998–2001 and 20,944 GPS positions during 1999–2001. Four of the 9 GPS collars deployed in 1999 and 2000 functioned properly. One collar failed due to a fault in the antenna power supply, and 4 failed to initialize properly. We recovered 10 of 14 GPS collars deployed in 2001, and 2 of the 10 failed prematurely. We did not recover 4 GPS collars due to failure of the automatic release mechanism. Success rate over all hourly GPS position attempts was 72% for 2D and 3D locations combined and 39% for 3D only. Accuracy of differentially corrected locations was expressed as 95% circular-error probable (CEP),

Table 1. Identification of grizzly bears captured and collared along US Highway 2 in northwest Montana, USA, 1998–2001, dates of capture, and type of collar used.

Sex-age code/ID[a]	Date of first capture	Collar type[b]	Radio days[c] VHF/GPS[d]	Highway crossings[e] VHF/GPS	Days per crossing[f] VHF/GPS
m2	6 Jun 1998	VHF/GPS	504/0	30/0	17/0
F5	10 Jun 1998	VHF	526	2	263
M6	11 Jun 1998	VHF/GPS	87/18	0/0	
M7	12 Jun 1998	VHF	67	0	
F8	14 Jun 1998	VHF	563	27	21
f9	14 Jun 1998	VHF	666	23	29
F11	14 Jun 1998	VHF	191	7	27
M12	14 Jun 1998	VHF/GPSe	54/26	2/2	27/13
M13	16 Jun 1998	VHF	42	0	
F921	11 Jun 1999	GPSe	239/140	0/0	
F14	12 Jun 1999	GPSe	321/115	0/0	
f922	18 Jun 1999	GPSe	479/140	0/0	
f20	1 Jul 1999	VHF	127	6	21
F24	15 Jun 2000	GPS	121/0	10/0	12/
F26	16 Jun 2000	GPS	59/0	0/0	
m286	22 Jun 2000	GPSe	0/0	0/0	
f293	13 Jul 2000	GPSe	176/100	0/0	
F218	28 Apr 2001	GPSe	180/0	7/0	26/
m34	4 Jun 2001	GPS	104/134	2/8	52/17
M365	6 Jun 2001	GPS	0/17	0/0	
M36	7 Jun 2001	GPS	110/138	0/0	
f37	7 Jun 2001	GPS	105/132	0/10	/13
M925	7 Jun 2001	GPS			
f367	8 Jun 2001	GPS	127/0	0/0	
M181	8 Jun 2001	GPS			
M274	1 Jun 2001	GPSe			
m926	11 Jun 2001	VHF			
M38	15 Jun 2001	GPS	104/124	1/5	104/25
m40	17 Jun 2001	VHF	127	10	13
F224	18 Jun 2001	GPS	0/15	0/7	/2
F42	20 Jun 2001	GPS	27/41	0/0	
m289	5 Jul 2001	GPS	94/86	4/18	23/5

[a] Sex-Age/ID codes: m = subadult male, M = adult male, f = subadult female, F = adult female.
[b] Some individuals wore both GPS and VHF collars at different times, and GPS collars contained a VHF beacon. Bears fitted with a GPS collar and an eartag transmitter are designated GPSe.
[c] Radio days are the number of days between first and last relocations.
[d] Abbreviations: GPS (Global Positioning System), VHF (Very High Frequency) telemetry.
[e] Highway crossings are the number of times successive relocations were on opposite sides of US-2 and/or MT-49, documented with VHF and GPS telemetry.
[f] Days per crossing are crossings/radio days for VHF and GPS telemetry.

which was the distance from the true location encompassing 95% of the positions. Our CEP was 22.4 m for 3D locations and 67.7 m for 2D locations (Graves 2002).

Traffic Monitoring

Our traffic counters recorded over 6,000 hr of traffic from 1999–2001. During 8.5 hr of counter testing, the counters accurately recorded the number of axle crossings (±1%) for 1,063 vehicles, but they overestimated the number of vehicles because every 2 axles counted as 1 vehicle. We estimated the actual number of vehicles to be 84% of the recorded vehicle counts. The standard statewide correction used by MDOT was 82% for principal rural highways.

Traffic patterns on US-2 showed strong daily and seasonal patterns (Fig. 1). Traffic counts peaked during late afternoon then dropped to near zero during pre-dawn hours. Average bi-directional hourly traffic at the west counter was 77 cars/hr (range 0–318), and mean daily traffic was 1,806 vehicles (range 220–3,338). Counts at the east counter were higher: 87 vehicles/hr (range 0–398) and 2,066 vehicles/day (range 17–4,289). Mean hourly counts by year in a given lane never differed by more than 9 vehicles at either location. Traffic counts peaked during the month of July then decreased monotonically through October. We estimated that approximately 30% of the east-bound and 24% of the west-bound traffic was local.

We collected 4,135 hrs of train counts at the west train counter during 1999–2001 and 1,141 hrs at the east counter during 1999–2000. Work and maintenance trains were generally shorter than 21 cars, while freight trains averaged 75 cars. We found that train length (both types included) was consistently higher during early morning and late evening hours than during midday and that rail traffic did not vary substantially between years. Mean bidirectional rail traffic was 1.2 trains/hr and ranged from 0–3.75 trains/hr (Fig. 2). Average rail traffic was slightly higher in October (1.53 trains/hr) than in July–September (1.19–1.34 trains/hr). We also found that rail traffic was higher ($\bar{x}$ = 1.5 trains/hr vs. 1.2 trains/hr) during hours of darkness, particularly the pre-dawn hours, than during the daylight or evening hours. Train speed averaged

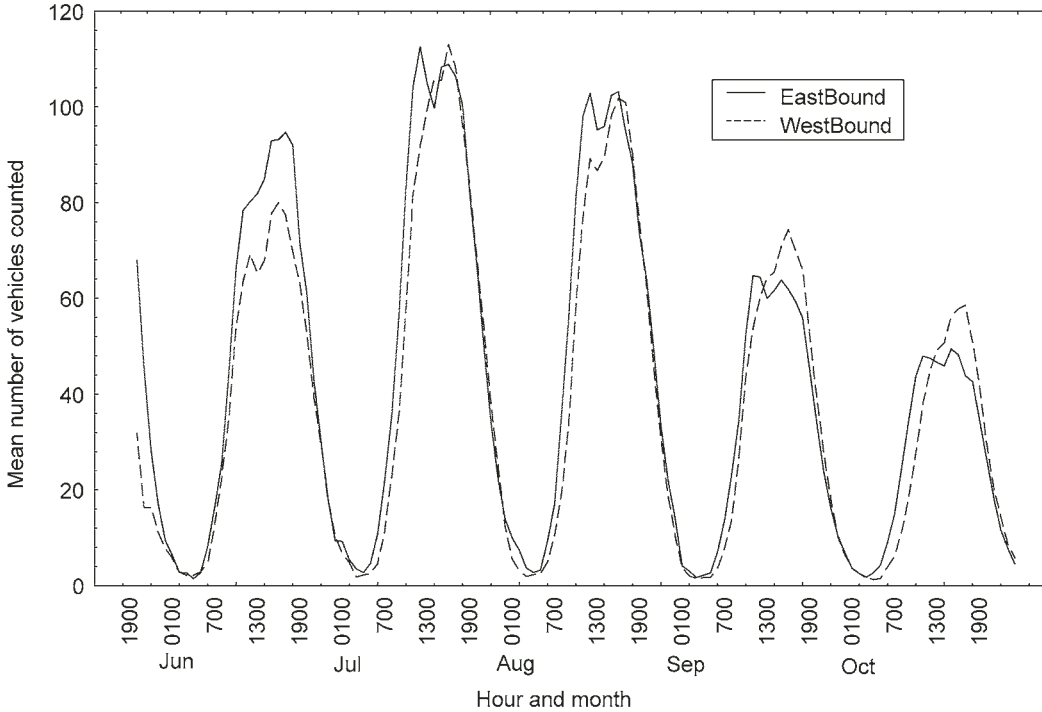

Fig. 1. Corrected bi-directional mean vehicles by hour and month at the west traffic counter on U.S. Highway 2, northwest Montana, USA, 1999–2001.

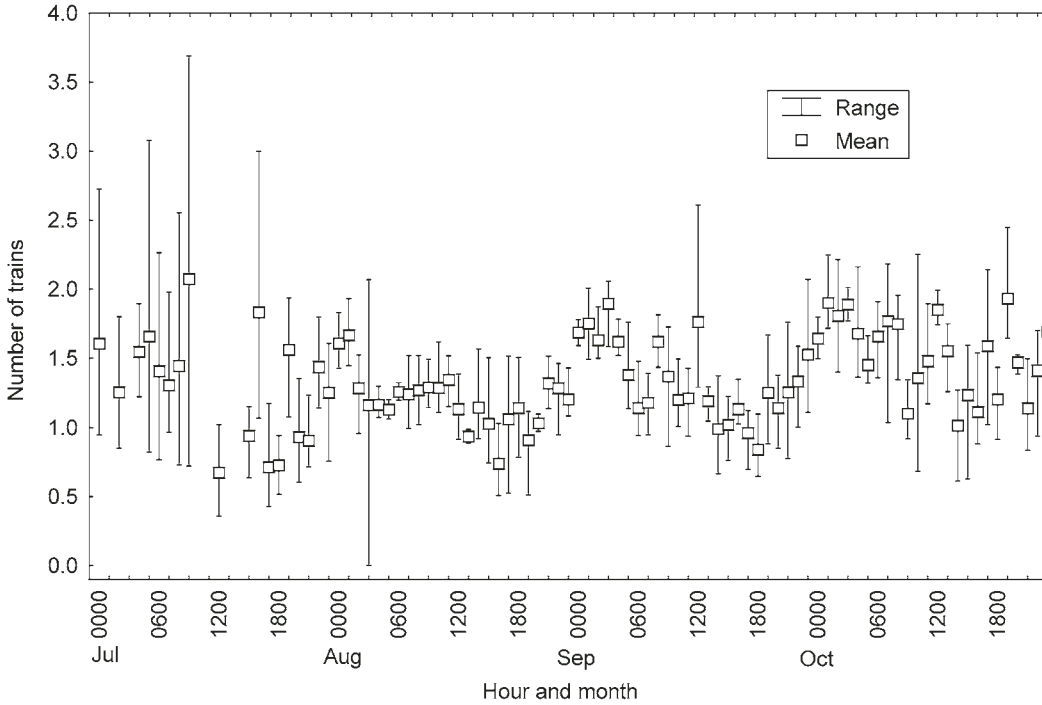

Fig. 2. Range and mean number of trains by hour and month tallied at the west train counter in the U.S. Highway 2 study area, northwest Montana, USA, 1999–2001.

Table 2. Observed total number of highway crossings, crossings of U.S. Highway 2 and the Burlington Northern–Santa Fe railroad (R.R.), and number of observed crossings of both US Highway 2 and the R.R. by Global Positioning System (GPS)-marked grizzly bears compared to that expected in 100 random walks, northwest Montana, USA, 1999–2001.

Bear ID	No. of GPS locations	Observed no. of highway crossings	No. crossings over US-2	Observed no. of R.R. crossings	No. of US-2 crossings also crossing R.R.	No. of highway crossings in 100 random walks					
						$\bar{x}$	–95%	+95%	Minimum	Maximum	SD
F224	236	7	3	5	3	8.5	7.4	9.5	0	26	5.3
m289	1176	18	15	11	6	33.9	31.2	36.5	8	64	13.4
f37	3161	10	10	9	8	53.5	48.5	58.5	6	155	25.4
m34	3216	8	4	6	4	26.6	22.1	31.1	0	87	22.8
M38	2972	5	5	6	5	34.1	29.8	38.5	1	77	21.8
M12	124	2	2	2	2	6.4	5.2	7.6	0	26	6.2

Table 3. Selection ratios, χ^2 values, and their significance for 11 grizzly bears along U.S. Highway 2, northwest Montana, USA, 1999–2001. Selection ratios are the proportions of used/proportion of available road distance categories. Road Distance Categories are 100-m increments beginning with 0–100 m (category zero) through 900–1,000 m (category 9).

Bear ID	Road distance category										χ^2	*P*
	0	1	2	3	4	5	6	7	8	9		
F14	0	3.898	0.375	0.910	0.688	0.492	0.913	1.202	1.647	1.089	25.420	0.002
F42	0.377	0.729	1.298	1.701	1.059	1.453	1.161	1.001	0.640	0.347	23.870	0.004
F224	1.040	1.240	1.268	1.592	0.836	1.846	0.338	0.769	0.759	0.335	10.370	0.321
F921	0.616	0.158	0.538	2.449	0.257	1.386	0.636	0.809	1.555	1.452	16.22	0.062
F922	0	0	0	0.092	0.227	2.088	2.106	2.012	1.464	0.724	168.630	0.001
F37	0.234	0.524	0.573	1.619	1.154	1.048	1.154	0.637	1.086	2.153	123.890	0.001
M6	0	0	0.965	0	0	2.720	1.999	0.657	1.544	0.304	9.570	0.386
M12	0.394	0	0	0	1.260	2.159	0.454	2.205	0.436	3.203	14.090	0.119
M38	0.203	0.150	0.419	0.414	0.283	1.465	3.202	0.732	1.693	1.566	51.480	0.001
m34	0.080	0.546	0.780	1.929	0.999	1.009	1.094	0.977	1.571	1.285	79.610	0.001
m289	3.912	1.003	0.656	0.407	0.202	0.043	0.225	0.990	0.900	1.143	114.410	0.001
Pooled	0.633	0.541	0.620	1.268	0.794	1.128	1.205	1.041	1.273	1.284	637.580	0.001
SE	0.441	0.096	0.100	0.256	0.152	0.035	0.031	0.031	0.016	0.074		
–95%	0.231	0.353	0.422	0.767	0.497	0.761	0.861	0.697	1.025	0.749		
+95%	1.527	0.729	0.818	1.769	1.091	1.495	1.549	1.385	1.521	1.819		

about 56 kph at the west counter, while westbound speeds at the east counter were slower (40 kph) because of the increasing grade towards Marias pass. Average train speed was greater during pre-dawn hours and peaked noticeably (~60 kph) at 0800 and 2000 hr.

Grizzly Bear Movements

We tracked 25 grizzly bears with aerial telemetry, and 13 of these crossed US-2 at least once (52%), for a total of 131 crossings (Table 1). We documented 39 crossings of US-2 by 6 of the 14 bears with GPS collars from which we obtained data. Of these 6 individuals, 3 also made an additional 11 crossings of adjacent MT-49. For those bears for which we had concurrent GPS and VHF crossing data, aerial VHF telemetry captured only 7 of 33 crossings (21%). Based on GPS data, subadult males and subadult females crossed highways the most (8 and 23 days between crossings, respectively), while adult females and adult males crossed the least (61 and 46 days between crossings, respectively). Adult females that crossed highways during monitoring did not do so when accompanied by cubs of the year ($n = 2$) but did so when accompanied by yearlings or 2-year-olds ($n = 2$).

All bears with GPS crossing data crossed highways less than expected when compared to random moves of equal length (Table 2). Because US-2 closely paralleled the railroad tracks for most of its length within the study area, in most cases, bears that crossed US-2 also crossed the railroad tracks during the same move (Table 2). One exception, bear m289, frequented a large riparian area between the railroad tracks and the highway.

Most (85%) crossings of US-2 were made at night and when highway traffic volumes could be expected to be low (Fig. 3). Actual mean traffic volume during crossings was 30 vehicles/hr and ranged from 2–98 vehicles/hr (±95%; 20–40 vehicles/hr). Crossing frequency declined exponentially with increasing traffic volume (Fig. 4), and model fit was quite good (Kolmogorov-Smirnov d = 0.112, $P < 0.001$; $\chi^2 = 0.342$, df = 2, $P = 0.843$). All

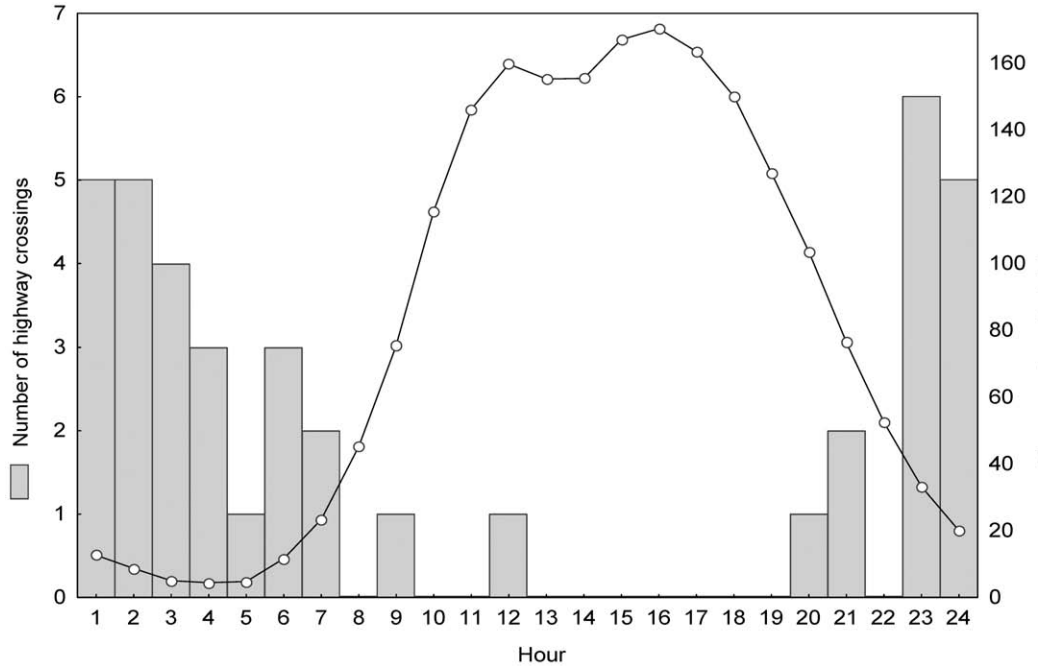

Fig. 3. Frequency of U.S. Highway 2 crossings by grizzly bears during 2001 plotted against mean traffic volume by hour, northwest Montana, USA.

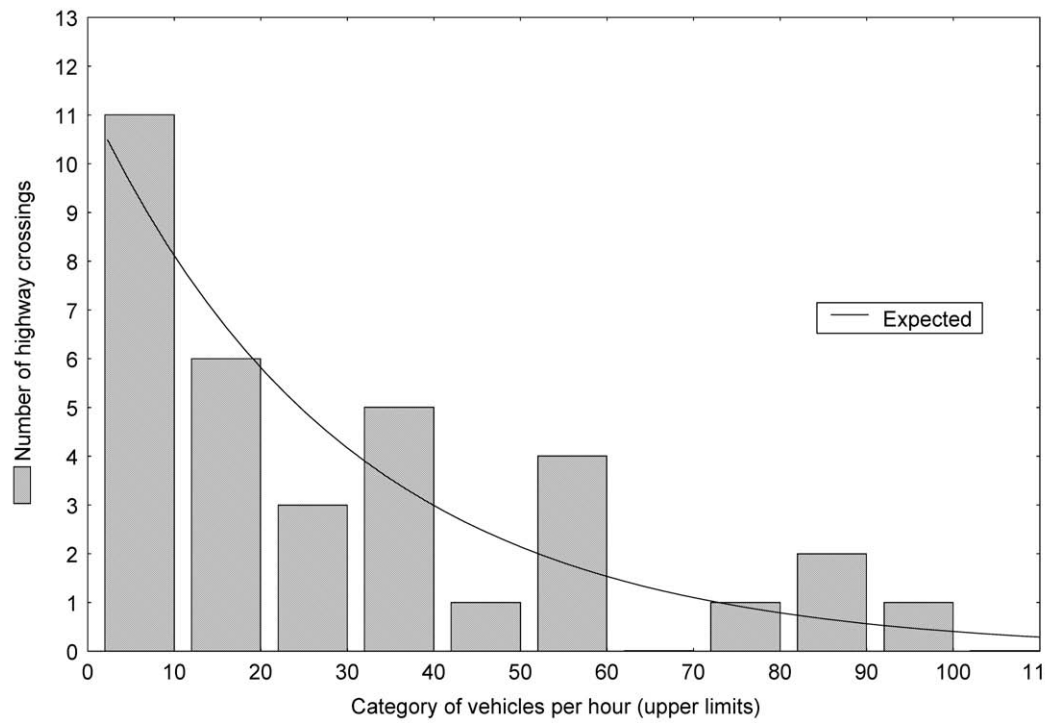

Fig. 4. Observed grizzly bear crossings of U.S. Highway 2 fitted to an exponential distribution with traffic volume categories, northwest Montana, USA, 1999-2001.

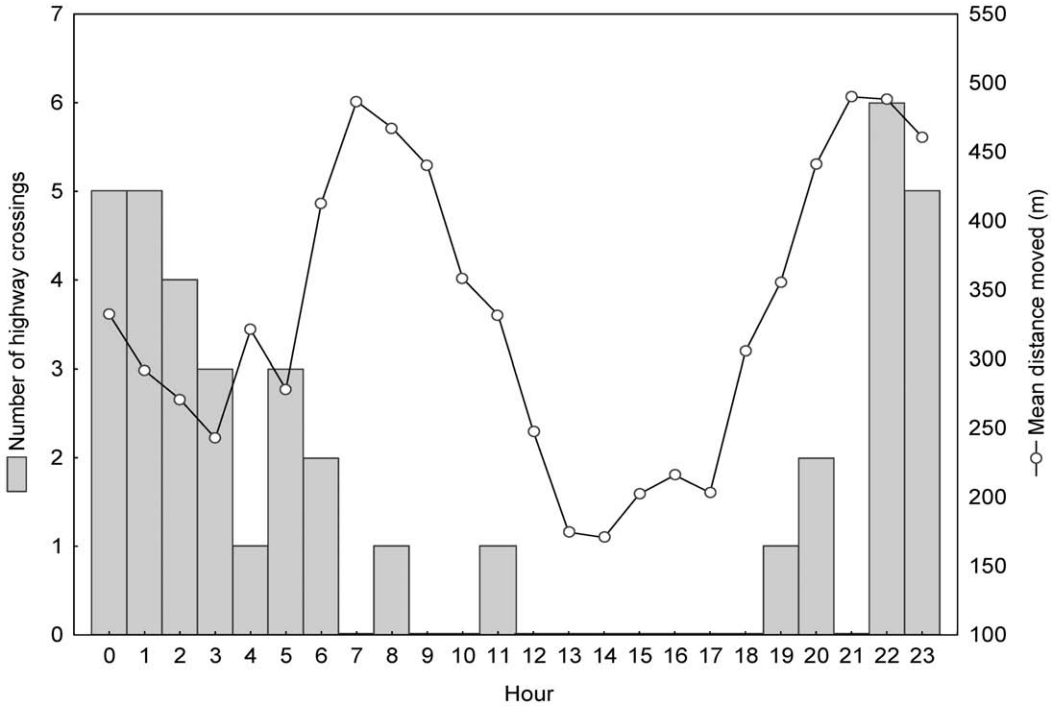

Fig. 5. Frequency of observed grizzly bear crossings of U.S. Highway 2 during 2001 plotted against mean grizzly bear movement distance by hour, northwest Montana, USA.

but 1 of the bears with GPS collars showed strong crepuscular activity patterns regardless of their distance from highways. The exception was an adult female (F14) with a diurnal activity pattern that occupied a tightly constricted home range within Glacier National Park. Morning highway crossings occurred before the morning period of peak bear activity, which was 0600–1100 hr. However, evening highway crossings occurred during the peak of evening bear activity, 1900–2300 hr (Fig. 5). None of the crossings recorded with GPS occurred during periods of precipitation. However, during 2001, precipitation was recorded on only 7 and 16 days at the Pendroy and Essex weather stations, respectively. There did not appear to be any seasonal patterns of crossing frequency.

Only 4 of the 39 recorded crossings of US-2 occurred between fixes >1 hr apart. For 4 of 6 GPS-marked bears that crossed highways, mean sequential movement distances and movement rates were significantly greater when crossing highways than when not crossing highways. Differences were significant considering both mean 24-hr movements (676 m further and 700 m/hr faster) and movements only during those hours when highway crossings occurred (543 m further and 573 m/hr faster).

Eleven of the 14 GPS-marked bears ventured within 1 km of US-2 or MT-49. Based on their selection ratio statistics, most were highly selective of distance isopleths (Table 3). However, 1 individual (m289) was unique in having selectivity for isopleths closer to highways. This subadult male spent large amounts of time within a riparian area close to US-2. The variability introduced by this animal resulted in the Friedman ANOVA failing to detect selectivity ($P = 0.370$). With m289 excluded, ANOVA results were significant ($P = 0.034$). We observed increasing selectivity for distance isopleths to an apparent asymptote within the 500–600-m category (Fig. 6). Based on post hoc multiple comparisons, inspection of the matrix of rank differences between isopleths, and groupings of similar categories based on significant differences, we chose distance isopleths 1–5 (0–500 m) as the disturbance area surrounding the highway and railroad.

Most (64%) of the observed crossings of US-2 were made by 2 subadult bears, f37 and m289. These crossings of US-2, when pooled with those of 4 other GPS-marked bears, were significantly clustered out to a scale distance of nearly 9 km, with an exception at the 3–4 km bin. Crossings were significantly dispersed at scales from 15 km

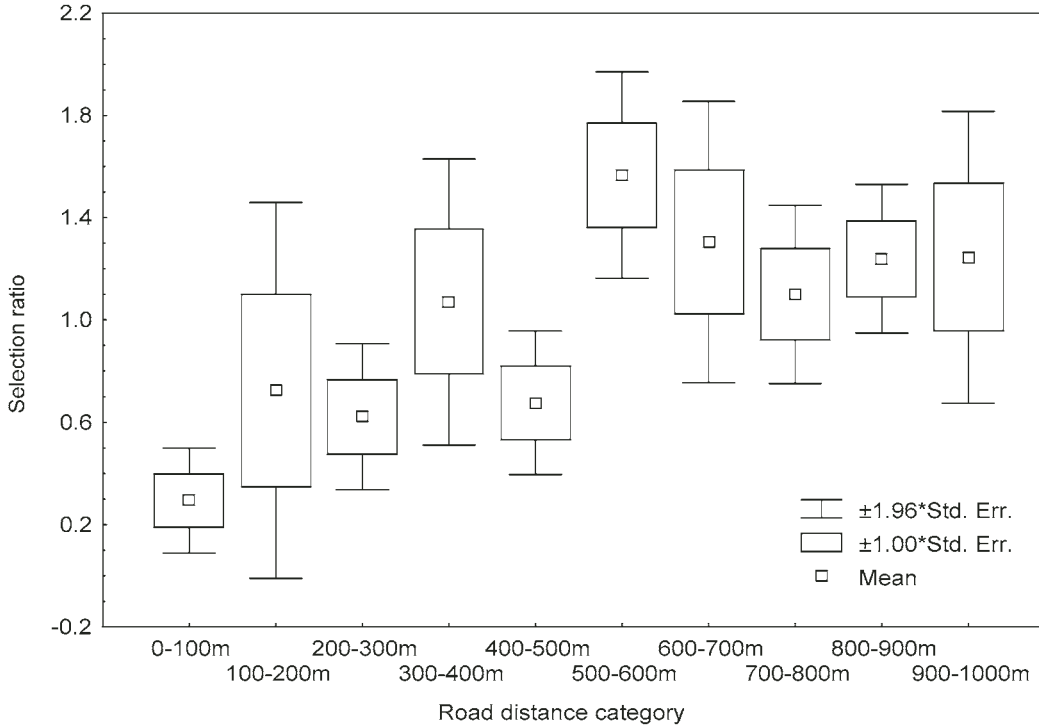

Fig. 6. Selection ratios for 10 grizzly bears (m289 excluded) along U.S. Highway 2, northwest Montana, USA, 1999–2001. Mean and standard errors of selection ratios calculated for each 100-m distance isopleth away from the highway. Values >1.0 indicate selection, and values <1.0 indicate avoidance.

to 26 km (Fig. 7). The strongest clustering we observed was at the 1–2 and 5–6-km scales. Although the clustering intensity was somewhat higher at the 5–6-km scale, we selected the 1–2-km scale for modeling in order to maximize spatial specificity and because the first significant cluster represented the patch length (O'Driscoll 1998). As a result, we used a moving circle radius of 750 m (1/2 patch length) to calculate maximal cluster values in the habitat models.

Modeling

In univariate tests, only distance to cover lacked significance. The other factors attained significance ($P \leq 0.05$) at either the base scale or maximal cluster scale. Significance levels were at least as great at the maximal cluster scale. The only categorical factor, cover type, was also significant at both scales. All but the conifer forest cover type contributed significantly to the total chi-square. We found no significant multicollinearity among the factors ($r \leq 0.51$). The full model was significant, but it contained many nonsignificant terms and unstable standard errors ($-2LL = 279.40$, $\chi^2 = 53.15$, df = 12, $P \leq 0.001$, AIC = 305.40). The low, moderate, and high point distance terms dropped out of the full model, as did distance to water, road density and habitat quality. Our final, most parsimonious model ($-2LL = 287.92$, $\chi^2 = 44.58$, df = 6, P 0.001, AIC = 301.92) consisted of only 3 parameters: elevation SD, distance-to-cover, and cover type (Table 4). Distance-to-cover assumed significance in multivariate models because of its interaction with cover type. Crossing areas in grassland or shrub cover types were significantly closer to cover than crossing areas in forested cover types. Based on the sign and strength of parameter estimates, crossing areas used by grizzly bears appeared to be flatter, closer to cover in open cover types, and more likely to be within grassland cover types (Table 4). Thirty-eight percent of the observed crossings of US-2 were made by m289, so as expected, this individual had the largest effect on model parameter estimates. Exclusion of this individual resulted in a much higher attraction for grassland, shrubland, and conifer habitats and strong avoidance of the deciduous forest cover type, relative to the mixed-forest cover type.

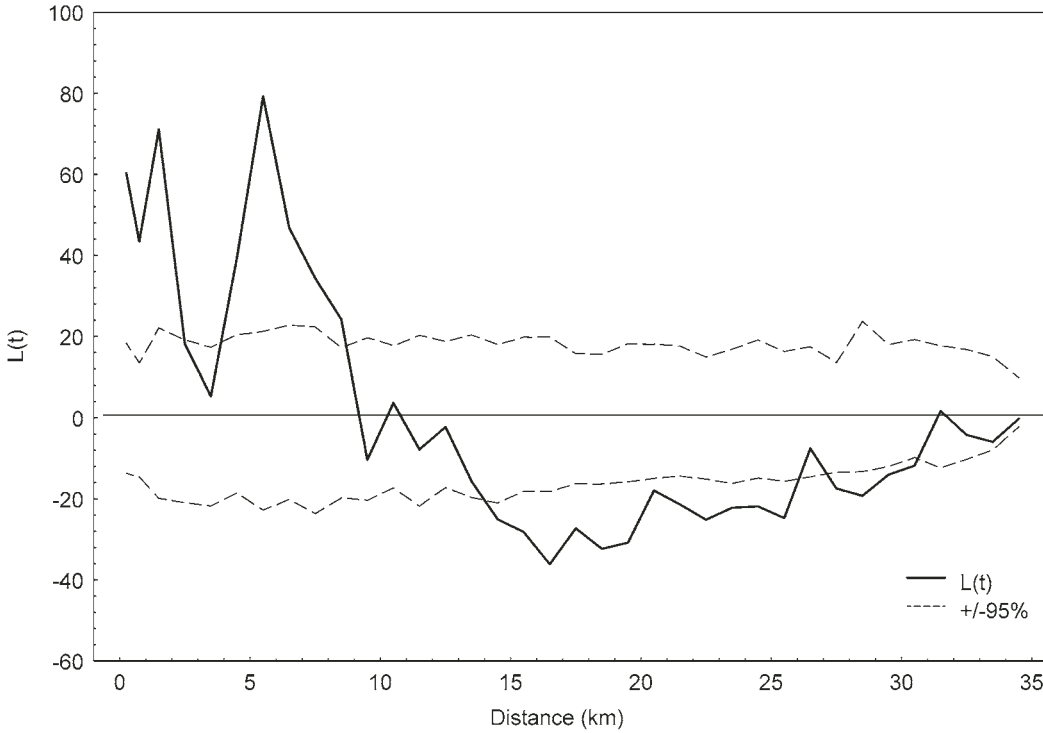

Fig. 7. Plot of L(t) against distance, where L(t) is the difference between the observed number of highway crossings by grizzly bears during 2001 and the simulated mean, northwest Montana, USA. Values of L(t) >0 indicate clustering, values <0 indicate dispersion. We deemed values above or below the 95th percentile significant.

DISCUSSION

We showed that grizzly bears' highway crossings were relatively frequent and successful; nearly half of our sampled population successfully traversed US-2. However, we also presented evidence that US-2 affected grizzly bear movement patterns. All our study animals crossed US-2 significantly less than expected under a random movement hypothesis. Our grizzly bears crossed more often at night, even when outside their normal periods of activity. And when they did cross, they moved farther and faster than normal. Grizzly bears were apparently choosing to cross when they were less likely to encounter highway traffic. Hourly mean traffic during crossings was half that of normal daytime traffic levels. This result suggests that there was a threshold of acceptable traffic level and/or that perceived vulnerability encouraged night crossings. Adult female grizzly bears appeared to be the most sensitive to traffic, especially when accompanied by cubs, whereas subadults and males appeared the least sensitive. This finding somewhat contradicts that of Chruszcz et al. (2003), who found that adult males were less likely to cross low-volume highways than females were.

Chruszcz et al. (2003) found that traffic volume was the single greatest determinate of road crossings and that grizzly bears were reluctant to cross

Table 4. Mean maximum likelihood estimates, their 95% confidence intervals, minimum and maximum values, and *t* statistics for a model describing locations where grizzly bears crossed U.S. Highway 2, northwest Montana, USA, 2001.

	0	– 95%	+ 95%	Minimum	Maximum	SE	*t*	*P*
Constant	–0.962	–2.643	0.720	–4.185	0.0534	0.654	–1.470	0.130
Elevation	–0.144	–0.207	–0.082	–0.195	–0.030	0.024	–5.991	0.001
Distance-to-cover	–0.021	–0.025	–0.016	–0.026	–0.016	0.002	–11.687	0.001
Grassland	1.772	0.441	3.102	0.537	4.175	0.517	3.423	0.008
Shrubland	0.181	–0.961	1.322	–0.888	2.289	0.444	0.407	0.348
Deciduous forest	–2.698	–12.449	7.053	–21.663	1.203	3.793	–0.711	0.288
Conifer forest	–0.277	–1.635	1.081	–2.198	1.879	0.528	–0.525	0.327

roads with high traffic volume. It is difficult to compare our study to that by Chruszcz et al. (2003) because of fundamental differences in methodology. However, Chruszcz et al. (2003) observed that only 11 individuals of 74 crossed the Trans-Canada highway during 12 years of research. Gibeau (2000) observed that traffic volumes on the Trans-Canada highway in Banff National Park can exceed 20,000 vehicles/day, but did not measure temporal changes in traffic volume. In Slovenia, Kaczensky et al. (2003) found similar effects of a 4-lane highway with an estimated traffic volume of 7,500 vehicles/day. In the US-2 corridor, peak traffic volumes are only a tenth that of the Trans-Canada highway and a fourth that observed in Slovenia.

Our study, when considered with the work of Gibeau (2000), Chruszcz et al. (2003), and Kaczensky et al. (2003), indicates the existence of a threshold traffic volume beyond which highways become significant barriers to grizzly bear movement. We hypothesize that this threshold occurs near 100 vehicles/hr (Fig. 4). We believe that connectivity was maintained across US-2 because hourly traffic volumes decreased dramatically at night, sometimes reaching zero vehicles/hr.

In our study area, grizzly bears had to contend with both a highway and a railroad. While grizzly bears appeared to make behavioral adjustments to temporal patterns of highway traffic volume, they were faced with a different situation along the railroad. During hours of low highway traffic, when grizzly bears were choosing to cross US-2, railroad traffic was high. Trains were more frequent, longer, and faster at night than during daylight hours. Furthermore, rail traffic was greater during fall when bears were in hyperphagia. This situation arose for a number of reasons. First, most track maintenance work was accomplished during daylight hours; thus, freight traffic was often curtailed during the day to allow track work to proceed. Second, arrival times for freight trains depended partially on their departure time. Freight trains loaded on the Pacific coast (approx 800 km to the west) during the day left in the evening and arrived in our study area at night the next day, 24–36 hr later. The result was that grizzly bears had to contend with high railroad traffic when highway traffic was lowest. We observed greater grizzly bear mortality caused by trains than that caused by cars on the highway. Between 1980 and 2002, 29 grizzly bears were killed on the 109-km section of railroad track between West Glacier and Browning, Montana, and 23 of these deaths occurred within our study area. During this same period, 2 grizzly bears were killed by vehicles in the study area (C. Servheen, U.S. Fish and Wildlife Service, unpublished data). During our study, 2 radio-marked grizzly bears were struck and killed by trains, and none were killed on the highway within the study area. Historically, grizzly bears have been attracted to the railroad by grain that leaked from cars along the tracks or that accumulated at sites of repeated derailments, and grizzly bears have been struck and killed by trains at these sites. Since the mid 1990s, BNSF has been largely successful in cleaning up and reducing the occurrence of grain spills, however, grizzly bears continue to be killed along this section of railroad. Our GPS data did not show any concentrated relocations on the railroad tracks that suggested the presence of an attractant. This research suggests that the coincidence of high rail traffic volume, low highway traffic volume, and natural grizzly bear movement patterns may be partially responsible for the observed patterns of mortality.

Collar-borne GPS technology greatly improved our ability to assess the extent of highway crossings by grizzly bears. With traditional bi-weekly aerial telemetry, we missed 79% of the highway crossings. Global Positioning System technology also allowed us to examine fine scale avoidance of the highway corridor. Mattson et al. (1987) found avoidance of roads to 500 m for grizzly bears in Yellowstone National Park using aerial relocation data collected between 1974 and 1983. Kasworm and Manley (1990) found road avoidance occurring in a 274–915-m zone in the Cabinet/Yaak ecosystem. Since that time, other authors have used 500 m as an assumed zone of influence (Mace et al. 1996). We also showed avoidance of areas within 500 m of US-2, supporting the contention that 500 m is a representative zone of influence around high-use roads. Conversely, Chruszcz et al. (2003) showed a preference for areas within 1,000 m of low-volume highways. However, our findings were based on more intensive telemetry (hourly vs. weekly) on a smaller number of individuals (11 vs. 24) over a shorter period (3 yrs vs. 12 yrs), and at a finer scale (100 m vs. 200 m). Furthermore, such an analysis does not consider the distribution of habitats within the zones. Changes in topography can drastically alter the distribution of preferred habitats among the zones. Chruszcz et al. (2003) suggest that the extreme topography within Banff National Park constricts bears to zones closer to roads than in other areas.

Spatial patterns of highway mortality suggest that many species utilize specific crossing areas

and that the use of crossing areas can be expected to change seasonally as resource needs change (Bellis and Graves 1971). One of our goals was to identify crossing areas and describe their attributes. We were able to show that grizzly bear highway crossing locations were spatially clustered, and we were then able to model the attributes of these locations. However, we are not convinced that terrain, distance to cover, and cover type were the only factors affecting where grizzly bears cross highways. Other factors that we could not model include large-scale topographic position, bear density, and relative position of different age/sex classes. Chruszcz et al. (2003) found similar relationships, but they also found that habitat quality influenced crossings of high-volume highways. Our qualitative assessment is that the large scale attributes of US-2 provided for habitat connectivity. These attributes were low traffic levels, narrow road width, limited human developments, and expansive pristine habitats on either side of the highway.

The highway corridor we studied was the converse of that typically conceptualized in the literature—a narrow strip of habitat in a matrix of human development (Simberloff et al. 1992, Beier 1995, Forman 1995, Beier and Noss 1998). Rather, our corridor was a narrow strip of human development in a matrix of wild land. Such configurations have been termed fracture zones (Servheen et al. 1998). This fracture zone has the potential to act as a population sink or trap because high-quality spring habitats along the highway will tend to bring grizzly bears into close proximity to traffic and human activity. Also, population pressure may cause subdominant grizzly bear sex/age classes, seeking to avoid conspecifics, to place themselves within these fracture zones (Mattson et al. 1987, Allen and Sargeant 1993). We observed that situation here, where a subadult male spent a large amount of time in close proximity to US-2 and other developments. Judging from our capture success within the corridor, the area continues to provide resources for a resident bear population, and even if the area is a population sink, the result may be more grizzly bears and continued connectivity (Pulliam 1988). This suggests that we can continue to maintain large scale habitat connectivity for grizzly bears despite limited development (Boone and Hunter 1996).

MANAGEMENT IMPLICATIONS

Within our study area, mean hourly traffic levels doubled since 1987 from 41.2 vehicles/hr to 77–91 vehicles/hr (Pedvillano and Wright 1987). Continued population growth in Montana's intermontane valleys will undoubtedly perpetuate this trend. Thus, in the future we may expect the US-2 corridor to become an agent of fragmentation requiring mitigative action. Such actions may range from radar-activated warning signs to bridges or tunnels specifically designed for wildlife passage. Currently, mean traffic volume during the time grizzly bears cross US-2 the most (2300–0700 hr) is 10.9 vehicles/hr (range 0–67, SD = 9.5). If highways become impermeable at 100 vehicles/hr, then we expect US-2 to become impassable to grizzly bears in 30 yrs if the current traffic trends continue. Obviously, unforeseen developments could change this estimate. During our study, there was a proposal to widen US-2 into a 4-lane divided highway to encourage local economic development. While the economic benefits of such a project are debatable, the effects on grizzly bears appear predictable. Planning for wildlife passage now may offset some of the financial burden of providing wildlife crossing structures when they become a necessity. These results should help planners anticipate when mitigative action is required and provide insights as to where such actions should occur.

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