Note: 1 km/sq-km = 1.61 mi/sq-mi

Management and Conservation Article

Correlates of Mortality in an Exploited Wolf Population

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ABSTRACT We investigated the influence of habitat use on risk of death from hunting and trapping of 55 radiocollared gray wolves (*Canis lupus*) from an exploited insular population in Southeast Alaska, USA. We compared mortality rates for resident and nonresident wolves and used Cox proportional hazards regression to relate habitat composition within 100-m circular buffers around radiolocations to risk of death of resident and nonresident wolves. In addition, we included covariates representing distances to roads, logged stands, and lakes and streams in those analyses. We also compiled harvest data from 31 harvest units within the study area to compare densities of roads and distances from human settlements with rates of harvest. During our study 39 wolves died, of which 18 were harvested legally, 16 were killed illegally, and 5 died from natural causes. Legal and illegal harvest accounted for >87% of the mortality of radiocollared resident and nonresident wolves. Mean annual survival was 0.54 (SE = 0.17) for all wolves. Annual survival was 0.65 (SE = 0.17) for resident wolves and 0.34 (SE = 0.17) for nonresidents. Very few (19%) nonresident wolves survived to colonize vacant territories or join existing wolf packs. Roads, muskegs, and distances from lakes and streams were covariates positively associated with death of resident wolves. Clear-cuts were positively associated with risk of death of nonresident wolves. Rate of harvest increased with density of roads; however, road densities >0.9 km/km^2 had little additional effect on harvest rates. Harvest rates decreased with ocean distances from nearest towns or settlements. Roads clearly increased risk of death for wolves from hunting and trapping and contributed to unsustainable rates of harvest. Wildlife managers should consider effects of roads and other habitat features on harvest of wolves when developing harvest recommendations. They should expect substantial illegal harvest where wolf habitat is accessible to humans. Moreover, high rates of mortality of nonresident wolves exposed to legal and illegal harvest may reduce or delay successful dispersal, potentially affecting linkages between small disjunct wolf populations or population segments. We conclude that a combination of conservative harvest regulations and large roadless reserves likely are the most effective measures for conserving wolves where risks from human-caused mortality are high. (JOURNAL OF WILDLIFE MANAGEMENT 72(7):1540–1549; 2008)

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Prince of Wales Island and neighboring cluster of smaller islands in Southeast Alaska, USA, support a population of 250–350 wolves (*Canis lupus*) that are genetically isolated from other wolves in the region (Person et al. 1996, Weckworth et al. 2005). Most of the land area is within the Tongass National Forest, and many watersheds have been extensively logged and are accessible by road. Changes in vegetation from post-logging forest succession (Alaback 1982) likely will reduce numbers of deer (*Odocoileus hemionus sitkensis*; Wallmo and Schoen 1980, Schoen et al. 1988), the principal prey of wolves (Person et al. 1996, Kohira and Rexstad 1997, Person 2001). As deer population declines, deer hunters will perceive wolves as competitors and likely seek to reduce their population by legal and illegal means (Person et al. 1996, Person 2001). Legal harvest annually removes 25–30% of the wolf population; however, this estimate does not include illegal take, which has not been previously estimated. The extensive road system on Prince of Wales and adjacent islands could be a key factor influencing legal and illegal harvests; therefore, it is important to understand and evaluate effects of roads, and other habitat factors that may facilitate harvest, on mortality of wolves.

Where wolves and humans coexist, humans generally overwhelm all other sources of mortality, particularly where humans can access wolf habitat via roads or other means (Ballard et al. 1987, Fuller 1989, Mech 1989). Numerous authors have examined relations between roads and presence or absence of wolves (Thiel 1985, Mech et al. 1988, Mech 1989, Thurber et al. 1994, Mladenoff et al. 1995), or wolf activity (Whittington et al. 2005). Those studies generally assumed that roads affect wolf populations by interfering with movements and activity, increasing mortality from traffic accidents, or facilitating unsustainable harvest by legal and illegal means. Few of those studies have examined direct effects of roads on risks of mortality of individual wolves or have evaluated those effects within the context of probabilistic analyses that ultimately may be used to assess risks of habitat change for the fitness of wolves and viability of populations. Moreover, habitat characteristics other than roads may influence risks of death and fitness. For example, in Southeast Alaska, wolves are easily observed in open habitats such as grassy meadows, young clear-cuts, and muskeg heaths. Consequently, use of those habitats by wolves may increase risks of death from legal and illegal hunting, particularly in areas accessible to humans.

The strategy for the conservation of wolves within the Tongass National Forest relies on a system of old-growth forest reserves, each at least partially supporting ≥1 wolf packs and linked to wolves in other reserves by dispersal (U.S. Forest Service 1997). Survival of dispersing and other nonresident wolves within the matrix of managed lands between reserves may be critical to long-term population viability, particularly in heavily logged and roaded landscapes. Nonresident wolves generally move through unfamiliar territory, potentially making them more vulnerable than residents to hunters and trappers, and to other wolves (Fuller et al. 2003). In areas that are accessible to humans

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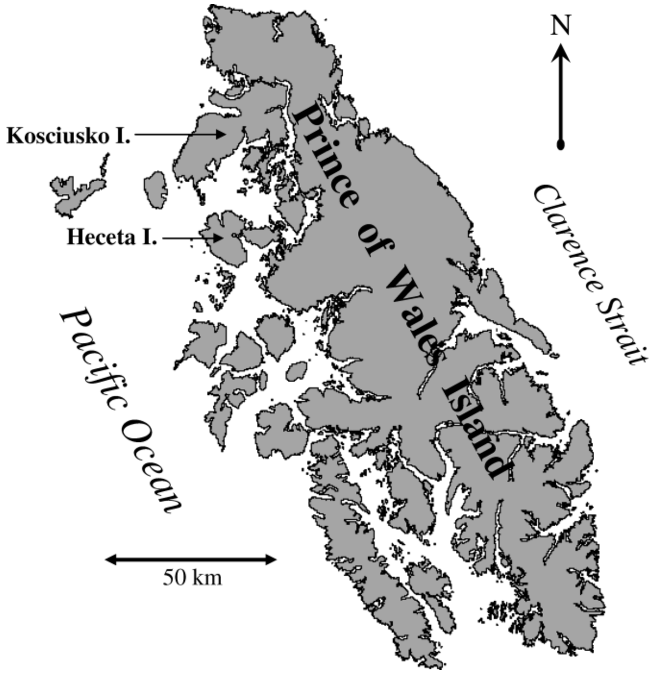

Figure 1. Prince of Wales and adjacent islands in Southeast Alaska, USA. We captured and monitored radiocollared wolves on Prince of Wales, Kosciusko, and Heceta islands, 1993–2004.

and where harvest levels are high such as Prince of Wales Island, rates of mortality of nonresident wolves could exceed those of residents. Similar to resident wolves, roads and open habitats could influence mortality of nonresidents. High rates of mortality of dispersing wolves could affect colonization of vacant territories, sever links between disjunct wolf population segments, and reduce levels of gene flow.

We studied survival and mortality of radiocollared wolves on Prince of Wales and adjacent islands during 1993–1995 and 1999–2004. We also analyzed wolf harvest data from our study area to look for relations between rates of harvest and variables such as density of roads and distances to human settlements. That analysis complemented our study of radiocollared wolves, and we intended it to provide useful information concerning effects of human access on wolf harvest, which could be used during land management planning. Our objectives were to compare rates of survival and sources of mortality between resident and nonresident wolves, determine if use of roads or open habitats such as muskegs, young clear-cuts, and meadows by resident and nonresident wolves affected risks of death from hunting and trapping, and determine if density of roads or other measures of access were significant predictors of rate of harvest.

STUDY AREA

Southeast Alaska comprises a narrow strip of mainland and a chain of islands, known as the Alexander Archipelago, which is oriented roughly parallel to the mainland. The archipelago consists of thousands of islands ranging in size from <0.01 km^2 to 6,700 km^2 with distances between islands and the mainland ranging from several meters to 15 km. The study area (9,344 km^2) encompassed Prince of Wales, Kosciusko, Heceta, and other adjacent islands (between 54°40′ and 56°20′ north and 132°00′ and 134°00′ west; Fig. 1). Prince of Wales Island was the third-largest in the United States (about 6,700 km^2) and contained the towns of Craig, Klawock, Hydaburg, and Thorne Bay, as well as several smaller villages and settlements. The topography included rugged mountains up to 1,160 m and long deep fiords. Habitat composition of the study area was about 48% old-growth coniferous forest, 24% open muskeg heath, and 21% clear-cuts or early seral forest. Approximately 196,000 ha were clear-cut–logged and >4,800 km of road were built. During our study, temperatures in January were typically >–1° C, temperatures in July >18° C, and annual precipitation ranged 279–505 cm. Snow accumulation was highly variable spatially and temporally, and depths ranged 0–76 cm.

The study area supported forests, dominated by Sitka spruce (*Picea sitchensis*) and western hemlock (*Tsuga heterophylla*), with lesser amounts of western redcedar (*Thuja plicata*), shore pine (*Pinus contorta*), and Alaska yellow cedar (*Chamaecyparis nootkatensis*). Alaback (1982) and Alaback and Juday (1989) described the understory characteristics, successional patterns, and ecology of those forests. Mammals that commonly occurred within the study area were Sitka black-tailed deer, black bears (*Ursus americanus*), beaver (*Castor canadensis*), river otters (*Lontra canadensis*), other mustelids, and several species of small rodents (MacDonald and Cook 1999). The study area contained many streams and rivers that supported abundant salmon (*Onchorynchus* spp.) populations.

Harvesting of wolves was regulated by the Federal Subsistence Board and the State of Alaska Board of Game. Regulations promulgated by the Federal Subsistence Board superseded state regulations on all federal lands, which constituted most of the study area. In game management unit 2 (GMU 2, so designated by the Alaska Department of Fish and Game), which included Prince of Wales Island, the state hunting season was 1 December–31 December with a bag limit of 5 wolves. The trapping season was 1 December–31 March with no bag limit. In 1997, a total harvest quota of 30% of the estimated autumn population was implemented because of concerns about excessive harvesting of wolves in the unit owing to extensive logging and road construction. The federal hunting season was 1 September–31 December with a 5-wolf bag limit and the federal trapping season was 15 November–15 March with no bag limit. Federal wildlife managers voluntarily conformed to the 30% harvest quota but were not required to do so by Federal regulations. State law required that hides of all wolves harvested during state or federal seasons be inspected by state-authorized fur sealers within 30 days after harvest.

METHODS

Capture, Handling, and Monitoring Wolves

We captured and radiocollared 55 wolves on Prince of Wales, Heceta, and Kosciusko Islands during March 1993–

August 2002. We captured wolves using padded or modified leghold traps and tranquilized them using Telazol (5–6 mg/kg; Wildlife Pharmaceuticals, Fort Dodge, CO) administered with a jab pole or blowgun. Capture and handling methods were described by Person (2001) and conformed to guidelines specified by the University of Alaska Fairbanks Institutional Animal Care and Use Committee and the American Society of Mammalogists (Animal Care and Use Committee 1998). Wolves were fitted with very high frequency radiocollars containing mortality sensors (Mod 500; Telonics, Mesa, AZ), which had battery lives of $\geq$36 months. All wolves were either dead or censored <39 months after capture. We recorded sex for each wolf and aged them as pups (<12 months old), yearlings ($\geq$12 months and <24 months), and adults ($\geq$24 months) using palpation of the epiphyseal process on the long bones of the front legs (Sullivan and Hagen 1956, Rausch 1967).

We monitored radiocollared wolves 2–6 times each month aerially and from the ground, obtaining a total of 2,356 radio locations. We determined ground locations by direct observation or by triangulation of $\geq$2 azimuths. During blind testing of observers using radiocollars at known locations, 90% of all estimated aerial and ground-based locations were <100 m from true locations. We overlaid radiolocations on geographically referenced ortho-photographs and assigned them coordinates (Universal Transverse Mercator Zone 8N, North American Datum 1927). We entered all locations into a Geographic Information System (GIS) database (Idrisi; Clark University, Worcester, MA) for analysis. We investigated mortality signals usually $\leq$2 days after detection. We determined causes of death by necropsies in the field. Most mortalities, however, were due to hunting and trapping and we obtained information concerning those deaths through the fur harvest sealing process mandated by state law. We identified illegal mortalities from evidence at the locations where we found the radiocollars or obtained during legal prosecutions of the perpetrators.

We classified wolves as resident pack members and nonresidents (Person 2001). Resident pack members had well-defined home ranges and associated closely with other pack members spatially and temporally. Nonresident wolves were those that dispersed or had settled but floated among several packs. Dispersers moved away from natal pack home ranges and did not return. Dispersers moved frequently and never remained >14 days in one place. Nonresidents that floated between packs were wolves that had settled following dispersal or were about to disperse. Nonresidents had well-defined home ranges that overlapped >1 resident pack home range and remained in those home ranges >14 days until they died, established a resident home range, or dispersed. We considered wolves that settled residents if we observed them interacting with other wolves on >2 occasions and they had well-defined home ranges that did not overlap those of neighboring packs. Some radiocollared wolves progressed through several social classes, beginning as resident pack members, becoming nonresidents when they dispersed, and finally establishing their own resident packs. We censored data for wolves as residents at the time they became nonresidents. After the transition, however, we included them as new individuals within the sample of nonresidents. If they eventually settled and became residents, we censored them at the time they settled and did not include them as new individuals in the sample of resident wolves. We believe that protocol was appropriate because all nonresident wolves survived as residents in packs located within our study area and it is difficult to conceive how including those wolves previously monitored as residents in our sample of nonresidents would bias estimates of survivorship of nonresident wolves or underestimate variances of any statistically derived parameters. It is unlikely that their experiences and characteristics would differ from any other independent representative sample of nonresidents. Nonetheless, not all resident wolves had been nonresidents and including wolves that successfully survived dispersal within the sample of resident wolves might bias our results; therefore, we censored them.

Classification of Habitat Features

We placed 100-m-radii circular buffers around radiolocations for wolves that we monitored. Habitat variables evaluated within 100-m buffers included habitat composition, average distance from roads, and average distance from lakes and streams. Habitat composition comprised 10 individual variables representing the proportions of buffers in each of 10 discrete vegetation classes and roads (Table 1). The proportion of a buffer composed of roads was analogous to a density of roads such that 1% was equivalent to about 15 m of road/ha. We did not classify roads by use or status. All roads were built originally to facilitate logging. Most roads were gravel and used primarily for logging and forestry activities but a small proportion (3.5%) were improved and paved in recent years. Most roads were open for highway vehicle use during at least a portion of our study but at any particular time about 25–50% were closed by gating, removing bridges and culverts, or were grown over. Unfortunately, the status of roads (including those grown over) frequently changed preventing us from reliably classifying them by levels of use over the duration of our study. Some roads were opened or closed for several months before we became aware of it. Moreover, closed roads often were used by snowmobiles in winter and all terrain vehicles (ATVs) year-round. Closed roads also facilitated hiking and frequently were used by hunters and trappers. In addition to logging and forestry-related activities, roads were used by anglers, hunters, trappers, subsistence harvesters, and recreational users. Vehicles using those roads included log trucks, logging equipment, small trucks, passenger automobiles, off-road vehicles, and bicycles. Very few roads were plowed in winter and snow frequently hindered use from December through February. Nonetheless, snow accumulations varied spatially and temporally and many roads remained open during winters with snow.

We compiled wolf harvest data from Alaska Department of Fish and Game fur sealing records for GMU 2. We

Table 1. Descriptions of vegetation classes that we used to evaluate habitat composition within 100-m-radii buffers surrounding radio locations of wolves monitored on Prince of Wales and adjacent islands, Southeast Alaska, USA, 1993–2004.

Vegetation	Description
Beach	Nonforested tide lands, open habitat consisting mostly of rocky, sandy, or muddy beaches. Any area within buffers that overlapped shoreline and ocean was considered to be beach or tideland.
Alpine	Nonforested, open habitat >600 m elevation; predominantly covered by rocks and herbaceous forbs.
Muskeg	Predominantly open heath or peat-land areas with sparse distribution of conifers.
Lake or stream	Fresh water lake or stream, often supporting salmon and other anadromous fish.
Open-canopy old-growth forest	Primarily uneven-aged hemlock–cedar forest <58.3 m^3/ha gross timber vol; thick understory vegetation.
Coarse-canopy old-growth forest	Primarily uneven-aged hemlock–spruce forest ≥58 m^3/ha gross timber vol; abundant understory vegetation.
Clear-cuts ≤10 yr	Even-aged clear-cuts ≤10 yr postlogging; canopy was completely removed, conifer regeneration was at seedling stage; moderate biomass of shrubs and forbs, abundant slash.
Clear-cuts 11–30 yr	Shrub-sapling–stage clear-cuts 11–30 yr postlogging; open canopy, conifer regeneration was at sapling stage, abundant understory vegetation.
Clear-cuts >30 yr	Pole-stage and saw-log–stage clear-cuts >31 yr postlogging; conifer regeneration >15-cm dbh, dense forest canopy prevented light from reaching forest floor; depauperate understory vegetation.
Meadow	Fresh or salt-water marsh or grassy meadows; nonforested open habitat composed mostly of sedges, grasses, and forbs; occasional scattered shrubs; mostly associated with estuaries.
Road	Paved and unpaved roadways.

included data collected between 1990 and 1999 but excluded information obtained after 1999. The GMU 2 wolf hunting and trapping season was closed prematurely in 1999 because the harvest quota was reached. Thereafter, reported harvest of wolves declined substantially and has remained lower than it was prior to 2000 (Fig. 2). We suspected that a substantial proportion of the harvest was not reported after 1999; therefore, recent harvest data may be unreliable. We tabulated harvest data by wildlife analysis areas (WAA), which were smaller administrative subunits ($\bar{x} = 292.9$ km^2, SD = 185.3 km^2) within GMU 2, and estimated average annual harvest rates/100 km^2 (Table 2). Calculating harvest rates enabled us to eliminate effects of differences in sizes of WAAs on harvest. We calculated density of all roads (i.e., open, closed, and overgrown roads) within WAAs. We

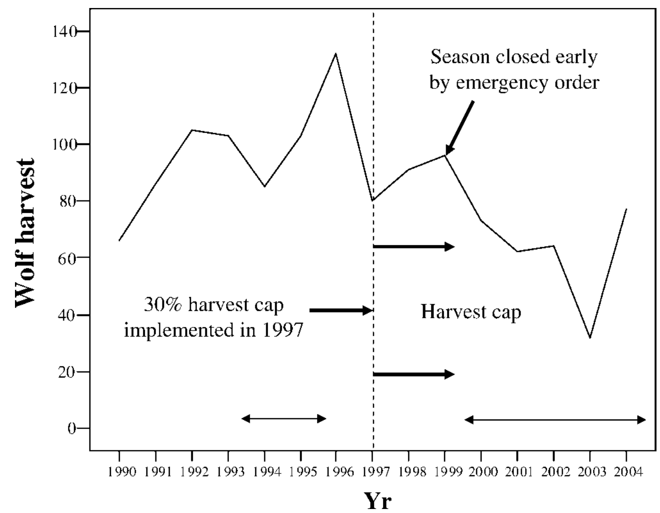

Figure 2. Wolf harvest 1990–2004 for game management unit 2, which included Prince of Wales and adjacent islands in Southeast Alaska, USA. A harvest quota was implemented in 1997 limiting harvest to 30% of the estimated wolf population in autumn. The wolf trapping season was closed prematurely in 1999 because the harvest quota was reached. Double-ended arrows indicate years in which we monitored radiocollared wolves.

estimated average land distances from 100 randomly selected points within WAAs to nearest villages or towns. If a WAA was not connected by road to the main road system on Prince of Wales Island, we estimated the average ocean distance from towns and villages to 100 randomly selected points along the shoreline of the WAA. Road density included roads on federal, state, and private lands that existed in 1995, which was the midpoint of the time-period covered by our harvest data.

We derived digital habitat maps used in our analyses from United States Forest Service GIS coverages for the Tongass National Forest. All data layers were current for the year 2005, and we were able to account for habitat changes during the course of our study. We conducted geographic analyses using IDRISI Andes raster GIS software. Raster cell resolution was 20 m.

Statistical Analyses

We captured and monitored wolves within the same portions of the study area during 2 discrete time periods (Mar 1993–Nov 1995 and Mar 1999–Nov 2004). We estimated survival and hazard functions for resident and nonresident wolves using the staggered entry Kaplan–Meier procedure (Pollock et al. 1989) for each of those monitoring periods. We used 2-week time intervals for our analyses because we occasionally had lapses up to 14 days between relocations of individual wolves owing to weather and logistical problems. We tested differences between survival functions for monitoring periods using log rank tests. We tested differences between survival functions for social, sex, and age classes using log rank tests stratified by monitoring period.

We evaluated relations between habitat use and mortality of wolves using Cox proportional hazards regression (Riggs and Pollock 1992, Hosmer and Lemeshow 2000). We

Table 2. Wolf harvest statistics for Prince of Wales and adjacent islands (game management unit 2) in Southeast Alaska, USA, 1990–1999. Data are shown by wildlife analysis areas (WAA).

WAA	Mean harvest 1990–1999	Mean road harvest 1990–1999	Area (km^2)	Road density (km/km^2)	Mean harvest rate (wolves/100 km^2)	Road harvest rate (wolves/100 km^2)
901	2.78	0.22	150.2	0.28	1.85	0.15
902	4.56	0.00	439.6	0.00	1.04	0.00
1003	2.00	0.11	182.3	1.13	1.10	0.06
1105	1.89	0.33	669.0	0.25	0.28	0.05
1106	1.33	1.00	129.6	1.40	1.03	0.77
1107	3.55	0.78	939.0	0.29	0.38	0.08
1108	0.67	0.00	404.6	0.00	0.17	0.00
1209	0.78	0.22	287.0	0.04	0.27	0.08
1210	0.67	0.00	368.6	0.03	0.18	0.00
1211	5.00	0.33	241.4	1.43	2.07	0.14
1212	0.44	0.00	143.1	0.00	0.31	0.00
1213	1.33	0.00	138.8	0.00	0.96	0.00
1214	5.78	3.78	394.1	0.79	1.47	0.96
1315	4.00	2.56	405.4	0.78	0.99	0.63
1316	1.89	0.00	163.4	0.01	1.16	0.00
1317	7.33	4.00	299.9	0.48	2.44	1.33
1318	6.78	5.11	506.8	0.93	1.34	1.01
1319	2.11	1.78	428.0	0.58	0.50	0.42
1323	0.33	0.11	157.8	0.12	0.20	0.07
1332	8.22	1.00	281.0	0.27	2.93	0.36
1420	3.44	3.44	196.6	0.92	1.75	1.75
1421	5.00	4.22	372.1	0.76	1.34	1.13
1422	6.88	6.63	492.8	1.02	1.40	1.35
1525	0.89	0.44	131.2	1.66	0.68	0.34
1526	2.78	0.22	277.6	0.11	1.00	0.08
1527	2.56	0.44	162.8	0.95	1.57	0.27
1528	0.22	0.11	112.5	0.31	0.20	0.10
1529	9.44	1.78	310.0	0.82	3.05	0.57
1530	2.11	1.22	253.4	0.95	0.83	0.48
1531	0.22	0.11	158.6	0.94	0.14	0.07

stratified analyses of resident wolves by wolf packs because we often radiocollared >1 wolf from individual packs and their behavior likely was not independent of other pack members. Stratification allowed estimation of baseline hazard functions for each pack separately but enabled estimation of covariates across packs (Prentice and Gloeckler 1978). Nonresident wolves behaved independently of other nonresident wolves and did not require data to be stratified. We averaged habitat variables tabulated within buffers around radiolocations over all locations for each wolf. Thus, we created an average buffer for each wolf that represented the history of habitat use by that animal. We were not concerned with habitat features at the location of death. Although that information may be of some importance, we were interested in how habitat use over time differed between wolves that lived compared to those that died. Cox regression assumes that hazard functions for groups of individuals compared in an analysis are proportional and that covariates do not confound proportionality in some time-dependent fashion. We tested those assumptions by comparing survival and hazard functions of wolves grouped by age, sex, and social class and calculating Schoenfeld residuals (Hess 1995) to reveal any time-dependent effects of model covariates. We also included variables representing year and season of capture to address potential effects of our staggered-entry design on proportional-hazards models (Riggs and Pollock 1992). We screened variables for strong correlations ($-0.7 \geq r \geq 0.7$) with other covariates prior to model selection. If we detected strong correlations, we dropped covariates with the weakest relations to the outcome variables from the models. We used Akaike's Information Criterion for small samples (AIC_c) to select the best multivariate models (Burnham and Anderson 1998). We only considered a model viable if the difference (Δ) between its AIC_c score and that of the best model in the model selection set was <4.0. We calculated AIC weights (w_i) for comparisons of all viable models.

We calculated risk ratios for each covariate in the best subset models. Risk ratios estimate changes in relative risk of death for incremental changes in magnitudes of predictor variables (Riggs and Pollock 1992); hence, risk ratios represent effect sizes of the independent contributions to risk of death made by each covariate. We compared effect sizes among variables by calculating risk ratios for a 10% increase within the range of observed values for each covariate.

We used multiple linear regression to relate total rate of harvest within WAAs to density of roads, and average land and ocean distances from towns or villages. Approximately half of wolves killed were taken by harvesters using boats rather than vehicles on roads. Therefore, we also regressed the same covariates against harvest rates of wolves killed from roads only. We included ocean distance in those analyses because some hunters and trappers harvesting

Table 3. Habitat correlates of mortality for resident wolves on Prince of Wales and adjacent islands in Southeast Alaska, USA, 1993–2004. Results are for Cox proportional hazards regression (stratified by wolf pack) of habitat characteristics within 100-m buffers around radiolocations. Only the best subset of models and their Akaike's Information Criterion scores (AIC_c) are included. Also shown are the AIC weights (w_i) for comparison of models shown.

Covariate	β[a]	SE[b]	P[c]	RR[d]	Δ10%[e]
Model 1					
% muskeg	0.046	0.027	0.090	1.555	0.3 ha
% roads	0.434	0.213	0.042	1.612	17.3 m
Distance from lakes and streams	0.018	0.008	0.023	2.446	207.6 m
Model 2					
% roads	0.337	0.179	0.059	1.449	17.3 m
Distance from lakes and streams	0.016	0.007	0.019	2.215	207.6 m
Model 1: AIC_c = 34.048; w_i = 0.551					
Model 2: AIC_c = 34.462; w_i = 0.448					

[a] Coeff. of covariate in Cox regression model.
[b] SE of coeff.
[c] P-value of coeff.
[d] Risk Ratio: odds ratio evaluated for 10% increase in covariate. RR = 1.0 indicates no effect.
[e] 10% increase within 100-m buffers expressed in areal units used to calculate risk ratios.

wolves on remote islands used ATVs and other vehicles on roads on those islands, and ocean distances from towns and villages influenced the probability that vehicles would be transported to the islands. We screened variables and selected multiple linear regression models using the same procedures described for our Cox regression analyses.

RESULTS

We captured and monitored 24 males and 31 females. Of those, we monitored 32 as juveniles, 15 as yearlings, and 33 as adults (total >55 because we monitored some wolves for >1 age classes). We monitored 43 resident pack members and 31 nonresident wolves (some wolves transitioned through both social classes). During our study 39 (70.9%) of 55 wolves radiocollared died. Hunters and trappers killed 18 wolves legally, 16 were killed illegally, and 5 died from natural causes (killed by other wolves, disease, or starvation). Thus, 87.1% of wolves that died were killed by humans. Most wolves killed illegally were shot (13) out of season or killed during legal seasons but not reported. The proportion of mortality due to each cause was similar between social classes ($\chi^2_3 = 2.79$, $P = 0.425$), age classes ($\chi^2_6 = 5.07$, $P = 0.535$), and sexes ($\chi^2_3 = 0.189$, $P = 0.979$). No juvenile wolves were captured as neonates; therefore, we were examining post-weaning survival of pups and not survival from birth. Of 12 packs we monitored, 4 were eliminated by hunting and trapping. Of the territories of those packs, 2 remained vacant for 2 years before dispersing wolves occupied them and one was recolonized by dispersers after 1 year. The other territory was absorbed by a neighboring pack within 1 year.

Annual survival rate for all wolves radiocollared during the first monitoring period averaged 0.45 (SE = 0.17) and 0.62 (SE = 0.16) during the second period. Survival functions from each monitoring period were not different for resident (log rank $\chi^2_1 = 0.934$, $P = 0.334$) and nonresident wolves (log rank $\chi^2_1 = 0.390$, $P = 0.533$). Average annual rate of survival for all wolves was 0.54 (SE = 0.17); however, all pups included in that estimate were >4 months old. Therefore, actual survival within the wolf population sampled may have been lower. Average annual rates of mortality owing to legal harvest, illegal harvest, and natural mortality were 0.23 (SE = 0.12), 0.19 (SE = 0.11), and 0.04 (SE = 0.05), respectively.

Survival functions did not differ between age classes (log rank $\chi^2_2 = 1.11$, $P = 0.605$) or sexes (log rank $\chi^2_1 = 0.032$, $P = 0.858$) but survival functions for nonresident wolves differed from resident pack members (log rank $\chi^2_1 = 8.27$, $P = 0.004$). Average annual survival rate for resident wolves was 0.65 (SE = 0.17) and 0.34 (SE = 0.17) for nonresidents. Survival rate of resident wolves at 104 weeks and 156 weeks was 0.45 (SE = 0.17) and 0.34 (SE = 0.17), respectively. Unless they settled, no nonresident wolves lived >86 weeks after radiocollaring or commencing extraterritorial or dispersal movements. Of 31 monitored, only 6 (19%) nonresident wolves settled, of which 3 were known to reproduce before being killed and 2 were shot before they could breed a second time. Surviving nonresidents settled in <34 weeks after beginning dispersal and half of those settled in <18 weeks. The single exception was a wolf that was still dispersing when our study ended. All wolves that survived dispersal from known natal packs settled within 30 km of their natal-pack home ranges.

Survival and hazard functions for resident wolves differed from nonresidents; therefore, we analyzed data for each group separately. We combined age classes and sexes, however, because survival and hazards functions did not differ by age or sex. We plotted Schoenfeld residuals and detected no time-dependent effects on the proportional hazards assumption. Further, no variables representing season or year of capture were significant predictors in any of the models indicating that our staggered-entry design did not confound Cox regression analyses.

For mortality of resident wolves from hunting and trapping, we could not distinguish clearly between 2 models (Table 3). Percent roads and distance from lakes and streams were positively related to risk of death in both models. A 10% (17.3 m) increase in roads within 100-m buffers increased risk of death 61% in model 1 and 45% in model 2. Distance from lakes and streams was also influential, increasing risk of death 145% in model 1 and 122% in model 2 for every 10% (207.6 m) increase in distance. Model 1 also indicated that muskegs were positively associated with death, increasing risk 56% for a 10% (0.3 ha) increase in muskegs within 100-m buffers. The coefficient for roads increased almost 30% from its value in model 2 when muskeg was included in the model suggesting a potential interaction between covariates. Adding an interaction term, however, did not substantially

Table 4. Habitat correlates of mortality for nonresident wolves on Prince of Wales and adjacent islands in Southeast Alaska, USA, 1993–2004. Results are for Cox proportional hazards regression of habitat characteristics within 100-m buffers around radiolocations. Only the best subset of models and their Akaike's Information Criterion scores (AIC_c) are included. Also shown are the AIC weights (w_i) for comparison of models shown.

Covariate	β[a]	SE[b]	P[c]	RR[d]	Δ10%[e]
Model 1					
% meadows	0.552	0.333	0.098	1.180	0.02 ha
% clear-cut >30 yr old	0.042	0.016	0.008	1.478	0.30 ha
% clear-cut <10 yr old	0.031	0.013	0.016	1.363	0.06 ha
Model 2					
% clear-cut >30 yr old	0.039	0.015	0.012	1.437	0.30 ha
% clear-cut <10 yr old	0.028	0.012	0.025	1.323	0.06 ha
Model 3					
% clear-cut >30 yr old	0.031	0.015	0.032	1.334	0.30 ha
Model 1: $AIC_c = 75.104$; $w_i = 0.339$					
Model 2: $AIC_c = 74.646$; $w_i = 0.426$					
Model 3: $AIC_c = 75.836$; $w_i = 0.235$					

[a] Coeff. of covariate in Cox regression model.
[b] SE of coeff.
[c] P-value of coeff.
[d] Risk Ratio: odds ratio evaluated for 10% increase in covariate.
[e] 10% increase within 100-m buffers expressed in areal units used to calculate risk ratios.

improve model fit when compared to the other simpler models (interaction term $P = 0.238$, $\Delta = 1.278$, $w_i = 0.161$), although Δ for the model still fell within our criteria for viable models. Wolves that died tended to have higher proportions of both muskeg and roads within 100-m buffers than those that survived.

We identified 3 plausible Cox proportional hazards models for nonresident wolves (Table 4). All models indicated that clear-cuts >30 years old were positively associated with risk of death and 2 models indicated clear-cuts <10 years old were positively associated with death. Old clear-cuts increased risk of death >30% in all models for a 10% (0.3 ha) increase in that covariate. Young clear-cuts also increased risk of death >30% in models 1 and 2 for a 10% (0.06 ha) increase in that covariate. Model 1 also included meadows but the effect was modest with a 10% (0.02 ha) increase in meadows only increasing risk of death 18%.

Roads, Distance, and Wolf Harvest

The average reported annual harvest in GMU 2 during 1990–1999 was 95.0 wolves (SD = 17.8) and the average rate of harvest within WAAs was 1.1 wolves/100 km^2 (SD = 0.82). Most wolves (57%) were killed by hunters and trappers using boats to access wolf habitat. Density of roads within WAAs averaged 0.56 km/km^2. Average number of wolves killed from roads annually in GMU 2 was 40.9 (SD = 17.7) and average harvest rate from roads within WAAs was 0.4 wolves/100km^2 (SD = 0.49). We square-root–transformed average wolf-harvest rates because residuals from the untransformed models strongly deviated from normal.

The best model predicting average total rate of harvest for

Table 5. Results of multiple linear regression of average total wolf harvest within wildlife analysis areas in game management unit 2 in Southeast Alaska, USA, versus density of roads, average land distance to nearest town or village, and average ocean distance to nearest town or village. Harvest data were from fur sealing records from 1990 to 1999 and we square-root–transformed them to stabilize variance. Shown are Akaike's Information Criterion scores (AIC_c), differences from lowest score (Δ), AIC weights (w_i), and r^2 values for the regression models. We included only models with Δ values ≤4.0.

Model	AIC_c	Δ	w_i	r^2
Road density, ocean distance	−58.46	0.00	0.502	0.271
Ocean distance	−58.45	0.01	0.498	0.258

Best models:

$$\text{Harvest rate} = [1.010 - 0.005(\text{ocean distance}) + 0.207(\text{road density})]^2$$

$$\text{Harvest rate} = [1.146 - 0.006(\text{ocean distance})]^2$$

WAAs indicated that it increased with density of roads but decreased with greater ocean distance from towns and villages (Table 5). Nonetheless, a second model that excluded density of roads but included ocean distance fit the data nearly as well. The influence of roads on harvest was obscured partially because most wolves were killed by harvesters using boats. None of the viable models included land distance from towns and villages. The values for adjusted r^2 were low indicating that a large proportion of the variance in average total harvest rate was not explained by density of roads or ocean distances.

Prompted by the ambiguous relation between roads and harvest rates indicated in the previous analysis, we plotted rate of harvest of wolves taken only from roads against road density, which indicated that a linear relation between those variables existed at densities of roads ≤0.9 km/km^2 (Fig. 3). At greater road density, variance in harvest rate expanded dramatically and the linear relation disappeared. We regressed covariates against square-root–transformed harvest rate for WAAs with road density ≤0.9 km/km^2 (Table 6). The best model included road density only and explained a

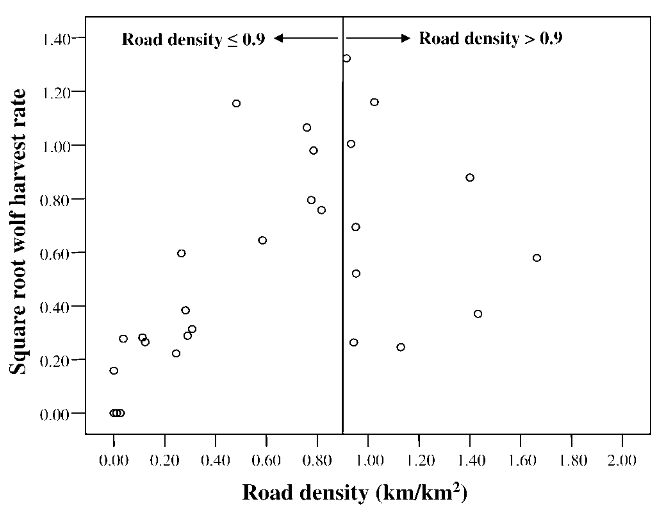

Figure 3. Relation between density of roads and mean wolf harvest rates (wolves harvested/100 km^2) during 1990–1999 for wildlife analysis areas in game management unit 2 in Southeast Alaska, USA. We square-root–transformed harvest rates to stabilize variance.

Table 6. Results of multiple linear regression of average wolf harvest from roads within wildlife analysis areas (WAA) in game management unit 2 in Southeast Alaska, USA, versus density of roads, average land distance to nearest town or village, and average ocean distance to nearest town or village. Harvest data were from fur sealing records from 1990 to 1999 and we square-root–transformed them to stabilize variance. We conducted separate analyses for WAAs with densities of roads $\leq$0.9 km/km^2 and for those with road densities >0.9 km/km^2. Shown are Akaike's Information Criterion scores (AIC$_c$), differences from lowest score (Δ), AIC weights (w_i), and r^2 values for the regression models. We included only models with Δ values $\leq$4.0.

Model	AIC$_c$	Δ	w_i	r^2
Road density $\leq$0.9 km/km^2				
Road density, land distance	−60.53	3.20	0.137	0.778
Road density, ocean distance	−61.10	2.63	0.182	0.771
Road density	−63.73	0.00	0.680	0.800
Road density >0.9 km/km^2				
Road density, ocean distance	−13.57	3.72	0.134	0.476
Ocean distance	−17.29	0.00	0.866	0.489
Best model road density $\leq$0.9 km/km^2:				
Harvest rate = [0.073 + 1.126(road density)]^2				
Best model road density >0.9 km/km^2:				
Harvest rate = [0.952 − 0.009(ocean distance)]^2				

large proportion of the variance in rates of harvest. We repeated that analysis for WAAs with densities of roads >0.9 km/km^2, which indicated that only ocean distance was a significant predictor of harvest rate (Table 6).

DISCUSSION

Our study area provided an excellent opportunity to evaluate direct effects of roads and other habitat features on mortality of an exploited wolf population. The closed, insular nature of the population enabled us to monitor the fates of all radiocollared wolves including nonresidents. Overall rate of mortality (0.46) for wolves in our study was comparable to other areas in Alaska where wolves were heavily exploited. For example, Ballard et al. (1987) and Gasaway et al. (1983) estimated annual mortality rates to be 0.45 and 0.58 for heavily harvested wolf populations in south-central and interior Alaska, respectively. Wolf populations declined during both of those studies. In our study area, the wolf population declined significantly during 1993–1995 (Person et al. 1996). Annual mortality of radiocollared wolves averaged 55% during that period. Although not statistically different, average annual mortality was lower (38%) for wolves monitored during 1999–2004. Nonetheless, wolf population still declined during 1999–2002 (Alaska Department of Fish and Game 2003). Therefore, total annual mortality >38% likely was unsustainable. That result was consistent with an analysis of demographic studies of wolves in North America reported by Fuller et al. (2003), which indicated annual mortality rates >0.34 generally resulted in population declines.

Survival of resident wolves (65%) was lower than estimates reported from other studies that distinguished between resident and nonresident wolves. Survival of resident wolves was higher on the Kenai Peninsula (73%; Peterson et al. 1984) and Copper River Delta in Alaska (81%; Carnes 2004). Both of those populations experienced light harvests. Fuller (1989) estimated survival of resident wolves $\geq$5 months old to be 67% for a protected population in north-central Minnesota, USA, a value only slightly higher than ours. Despite legal protection, humans accounted for $\geq$76% of all mortality of those resident wolves compared to 90% in our study. Nonetheless, total mortality of resident wolves was similar indicating that harvest may partially compensate for other sources of mortality (Fuller et al. 2003).

Dispersing and other nonresident wolves had a low average annual rate of survival (0.34) compared with resident wolves. Indeed, for dispersing wolves only, annual survival was 16% with most killed by hunters and trappers before settling. Few published studies distinguish between residents and nonresidents when estimating survival. Peterson et al. (1984) reported an average annual survival rate of 0.38 for dispersing wolves on the Kenai Peninsula, Alaska. Annual survival for all nonresident wolves was 52% in the Copper River Delta of Alaska (Carnes 2004) and 52% in north-central Minnesota (Fuller 1989). Theoretically, territory vacancies created by harvests could provide opportunities for nonresidents to settle and pair (Hayes et al. 1991). For example, Ballard et al. (1987) reported that $\geq$42% of dispersing wolves settled and were pair-bonded or accepted into packs in an area where wolves were previously harvested heavily. Nonetheless, rates of successful dispersal may be 20–40% higher where no legal harvesting occurs (Gese and Mech 1991). In most studies where harvesting wolves was legal, nonresident wolves had higher mortality than resident pack members (Peterson et al. 1984, Carnes 2004) and where wolves were protected there was little difference (Fuller 1989, Boyd and Pletscher 1999). Pletscher et al. (1997) reported lower survival of dispersing wolves in a protected population in Montana; however, many dispersers in that study moved into Canada where they were legally harvested. In all studies, humans were the primary sources of mortality of nonresident wolves. We believe that under conditions in which wolves are easily accessible to hunters and trappers, nonresident survival may be low, reducing the probability of settling and potentially delaying recolonization. Indeed, 3 of 4 territories containing radiocollared wolves that became vacant owing to harvest remained unoccupied for >1 year despite the existence of neighboring wolf packs. Although those territories eventually were recolonized, survival of the new occupants was very low and only half successfully reproduced within their new territories before being killed. Of those, most were killed before breeding a second time. All of those territories had extensive road systems or were easily accessible by boat.

Our results demonstrated that roads had an important direct influence on mortality of resident wolves from hunting and trapping. In addition, distance to lakes and streams and use of muskegs were important risk factors. Lakeshores and stream banks were habitats commonly used by wolves (Person 2001) that often were not easily accessible to humans during winter when trapping seasons were open. Further, those habitats generally were forested, making it difficult to observe and shoot wolves. Risk of death increased as wolves used habitats further from the relative safety of streams corridors and lakeshores. That relation may be different in places where consistent snowfall and cold temperatures enable hunters to access frozen lakes and streams by snowmobiles or aircraft. Under those circumstances, wolves may be vulnerable when traveling on or near lakes and streams. In most of Southeast Alaska, however, freezing conditions are intermittent and uncommon except at higher elevations. Wolves frequently used muskegs for resting, hunting, and traveling (Person 2001). Muskegs adjacent to or bisected by roads represented risky habitat for wolves because they were accessible to people and wolves were visible. Combinations of road access and open habitats likely present dangerous conditions for wolves throughout their range.

Although roads were not directly linked with risk of death for nonresident wolves, clear-cuts were associated closely with roads and increased risk of death from hunting and trapping. Clear-cuts also were habitats avoided by resident wolves (Person 2001), which may have increased the frequency of their use by nonresidents, placing them at risk. Nonetheless, we suspect that risks associated with clear-cuts mostly were because roads enabled humans to access those habitats. Use of meadows increased risk of death for nonresident wolves. Most meadows were grasslands associated with estuaries. Wolf trappers working from boats commonly set traps under shallow water in tide pools at baited sites within estuaries.

Road density was an important predictor of harvest. Nonetheless, that relation deteriorated at road densities >0.9 km/km^2, which probably represented a threshold beyond which further increases in road density had little detectable effect on rates of harvest. The large variance in reported harvest from roads within WAAs with road densities >0.9 km/km^2 may result from unsustainable mortality. Indeed, the 4 packs eliminated during our study were located in areas in which road densities exceeded that threshold. Our model for harvest rates from roads predicts a harvest of 1.2 wolves/100 km^2 at a road density of 0.9 km/km^2, which would equate to a harvest rate of 3.5 wolves within an area the size of wolf pack home ranges (300 km^2) in our study area (Person 2001; D. K. Person, Alaska Department of Fish and Game, unpublished data). Average pack size in autumn was 8 wolves and we would expect an additional 1–2 nonresident wolves within that area (Person 2001). Therefore, that harvest rate could represent about 35–39% of the autumn population. Additional wolves would likely be killed illegally, by harvesters using boats and by natural causes. Therefore, total mortality could greatly exceed 38% of the autumn wolf population and be unsustainable at that density of roads.

Our model predicting harvest rates from roads enabled us to evaluate the road density guideline included in the management plan (TLMP) for the Tongass National Forest, which specifies that densities of roads open to use by motor vehicles should not exceed 0.43 km/km^2 in areas where there are concerns about high rates of wolf harvest (U.S. Forest Service 1997). On average, density of open roads on federal lands represents about 53% of all roads (L. Kramer, United States Forest Service, unpublished data); therefore, the guideline equates to a total road density of 0.81 km/km^2. Our model predicts a harvest rate of 2.9 wolves/300 km^2 (90% CI $= 2.1$–3.7) for a density of roads equal to 0.81 km/km^2, which would represent 29–32% mortality based on the average number of wolves within a territory in autumn. Although likely within sustainable limits, that mortality does not include additional wolves killed by hunters and trappers using boats, illegal harvest, and natural mortality. Depending on circumstances, total mortality could be $>50\%$ higher. Therefore, the TLMP guideline entails considerable risk of facilitating chronic unsustainable mortality.

The status of roads as open or closed to motorized vehicle use likely had an important influence on mortality of wolves from hunting and trapping. We suspect that (had we been able to differentiate between open and closed roads) our results would have indicated that mortality was more strongly associated with open roads. Nonetheless, hunters and trappers frequently used closed and overgrown roads in our study area because they believed wolf activity was higher, a perception supported by Thurber et al. (1994). Moreover, barriers used to close roads often were bypassed by people riding ATVs, trail bikes, and snowmobiles.

Fuller et al. (2003) summarized studies that examined relations between roads and presence or absence of wolves and concluded that human tolerance of wolves was a strong mitigating factor enabling wolves to exist where road density and human access were very high. We concur with that conclusion. Nonetheless, human tolerance for wolves may become strained if people perceive wolves as competitors for game and subsistence foods or threats to livestock and pets. Under those circumstances, legal and illegal killing of wolves may make the persistence of wolf populations or population segments much more sensitive to density of roads and human activity.

MANAGEMENT IMPLICATIONS

We observed high rates of illegal harvest indicating that reported harvest substantially underestimated mortality due to hunting and trapping. Regulatory changes in seasons and bag limits can play an important role influencing harvest levels; nonetheless, harvest regulations are unlikely to have much effect on rates of illegal harvest. Where roads and other features facilitate access by humans, wildlife managers should expect high rates of illegal harvest of wolves. In addition, high rates of mortality of nonresident wolves exposed to legal and illegal harvest may reduce or delay successful dispersal, potentially affecting linkages between small disjunct wolf populations or population segments occupying fragmented landscapes. Therefore, we conclude that a combination of conservative harvest regulations and large roadless reserves likely are the most effective measures for conserving wolves where risks from human-caused mortality are high.

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