

A spatial analysis of wolf harvest and harvest risk on Prince of Wales and associated islands, Southeast Alaska

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Abstract

We investigated associations between density of roads, land cover classes, and land and ocean distances to population centers with 3 metrics of harvest for gray wolves (*Canis lupus ligoni*) on Prince of Wales and adjacent smaller islands that constitute game management unit 2 (GMU 2) in Southeast Alaska. We used harvest data from fur sealing records obtained by the Alaska Department of Fish and Game (ADF&G) during 1985–2009, so our analyses only used legally reported harvest. Reported harvest was highest during 1985–1999, and we analyzed those data separately from harvest data obtained during 2000–2009, a period in which reported harvest was substantially lower.

Harvest rates were computed at the scale of average wolf pack home ranges (300 km²) and tabulated for 32 ADF&G wildlife analysis areas (WAA) within GMU 2. We averaged rates for each WAA and for the two time periods and used multiple linear regression to examine relations between those averaged rates and density of roads, proportion of WAAs composed of 10 land cover classes, and average land and ocean distances to towns and villages within GMU 2. We also included covariates representing the proportion of land within a WAA deferred from logging (nondevelopment land) and the proportion of land encompassed by medium and large old-growth forest reserves designated by the Tongass Land Management Plan (TLMP). In addition, we created binary variables indicating WAAs at risk of chronic unsustainable harvest (annual harvest rates ≥ 3 wolves/300 km² for ≥ 5 years between 1985 and 2009) and pack depletion (annual harvest rates ≥ 7 wolves/300 km² for ≥ 2 years between 1985 and 2009). Using logistic regression, we evaluated the effects of the same covariates used to predict harvest rates on risk of unsustainable harvest and pack depletion within WAAs. Annual reported harvest for GMU 2 averaged 75.7 wolves (SD = 31.9) during 1985–1999 and 48.5 wolves (SD = 21.1) during 2000–2009. Between 1985 and 2009, 19 WAAs met or exceeded our criteria for risk of chronic unsustainable harvest and 16 met the criteria for risk of pack depletion.

For WAAs on Prince of Wales Island, our regression models incorporating harvest data obtained during 1985–1999 indicated that density of roads and proportion of area composed of alpine terrain (surrogate for mountainous topography) were positively associated with mean harvest rates. For models incorporating 2000–2009 harvest data, land distance from towns and villages and proportion of WAAs composed of muskeg heath were negatively associated with mean harvest rate, whereas, proportion of WAAs composed of clearcuts >30 years old was positively associated with wolf harvest rate. Although density of roads did not enter any of the final models for these data, it was positively correlated ($r = 0.472$, $P = 0.02$) with harvest rate. Our logistic regression models suggested that density of roads and alpine terrain were positively associated with risk of chronic unsustainable harvest, whereas, muskeg and nondevelopment lands reduced that risk.

With respect to risk of pack depletion, road density and proportion of WAAs composed of nonfederal land (mostly clearcut) increased that risk, whereas, the proportion of area composed of nondevelopment lands reduced risk. For WAAs representing the smaller islands adjacent to

Prince of Wales Island and that are only accessible by boat or aircraft, we did not identify any significant covariates predicting harvest rates, unsustainable harvest, or pack depletion. We used our multiple linear regression and logistic regression models to predict relative changes in harvest rates and risks of unsustainable harvest and pack depletion owing to closures of roads planned by the U.S. Forest Service (USFS) that are intended to be fully implemented by 2015. Our results indicate that reductions of those harvest metrics likely will be modest despite extensive road closures. Based on our analyses, we suggest that Prince of Wales Island be considered a separate regulatory subunit within GMU 2 because, unlike the other islands in the unit, most of it is accessible by roads. Moreover, those roads link all of the principle population centers in the unit.

Wolf management in Southeast Alaska occurs at the scale of GMU (i.e., GMUs 1, 2, 3, and 5). Assessment of wolf viability or sustainability at scales at which ADF&G manages wolves was not undertaken as part of this work. Information presented in this report cannot in itself be used to assess either the viability or sustainability of overall wolf populations in GMU 2, including Prince of Wales Island.

Key words: *Canis lupus*, effects of roads, mortality, Prince of Wales Island, Southeast Alaska, Tongass National Forest, wolves, wolf harvest.

Introduction

Spatially explicit analyses of harvest data over time for gray wolves (*Canis lupus ligoni*) can be useful to management agencies and regulatory bodies such as the Alaska Department of Fish and Game (ADF&G), U.S. Forest Service (USFS), Alaska Board of Game (BOG), and Federal Subsistence Board. Results of the analyses may be useful in effectiveness monitoring of the Tongass Land Management Plan (TLMP, U.S. Forest Service 2008), which includes prescriptions for active forest and road density management. Moreover, analyzing harvest data spatially would be useful in modeling the potential effect of future road closures on harvest rates.

Wolves are difficult to monitor in Southeast Alaska because they rarely are seen in the thickly forested landscapes (Person et al. 1996). The only continuous time series of data for wolves are harvest data obtained during sealing of hides. State law requires that hides of all wolves harvested during state or federal seasons be inspected by state-authorized fur sealers. Although harvest reporting is mandatory, compliance with the sealing requirement may be an issue for some people. If wolf hides are not brought in for sealing, they will not be recorded in the harvest records. We also have no means to measure illegal harvest routinely. For these reasons, analyses of harvest data must take into account that they represent only a portion of human-caused mortality occurring in the population (Person and Russell 2008).

Prince of Wales Island and the neighboring cluster of smaller islands in southern Southeast Alaska are designated as game management unit 2 (GMU 2) by the ADF&G (Fig. 1). The unit supports a population of wolves that are genetically similar, but separated from other coastal wolves in Southeast Alaska and British Columbia (Weckworth et al. 2005). In addition, these wolves are genetically distinct from all other continental populations (Weckworth et al. 2005, Weckworth et al. 2011). During 1990–2003, the population ranged from 250–350 animals with highest numbers observed in the mid-1990s (Person et al. 1996, Person 2001, Person and Russell 2008). Hunters and trappers harvest wolves in GMU 2, which constitutes most of the annual mortality (Person and Russell 2008). Mean annual survivorship of a sample of 55 radiocollared wolves monitored between 1993–2004 was 0.65 for resident pack members and 0.34 for wolves that were not members of packs (Person and Russell 2008), values consistent with other wolf populations that are heavily harvested, but not subject to intensive predator-control activities (Ballard et al. 1987).

Wolf conservation on the Tongass National Forest relies on a suite of federal land management and state wildlife regulations. One key strategy for wolf conservation is the system of old-growth reserves, each at least partially supporting ≥ 1 wolf packs and linked to wolves in other reserves by dispersal (U.S. Forest Service 2008). In addition, TLMP encourages managers to consider options for maintaining habitat for deer sufficient to sustain viable populations of wolves, reducing human disturbance near known denning areas when pups are present, and managing the density of roads to reduce risks of excessive harvest. We examine effects of roads, distances to centers of population, and land cover types on rates of harvest of wolves within the 32 WAAs that constitute GMU 2 (Fig. 1). We follow similar analyses presented by Person and Russell (2008)

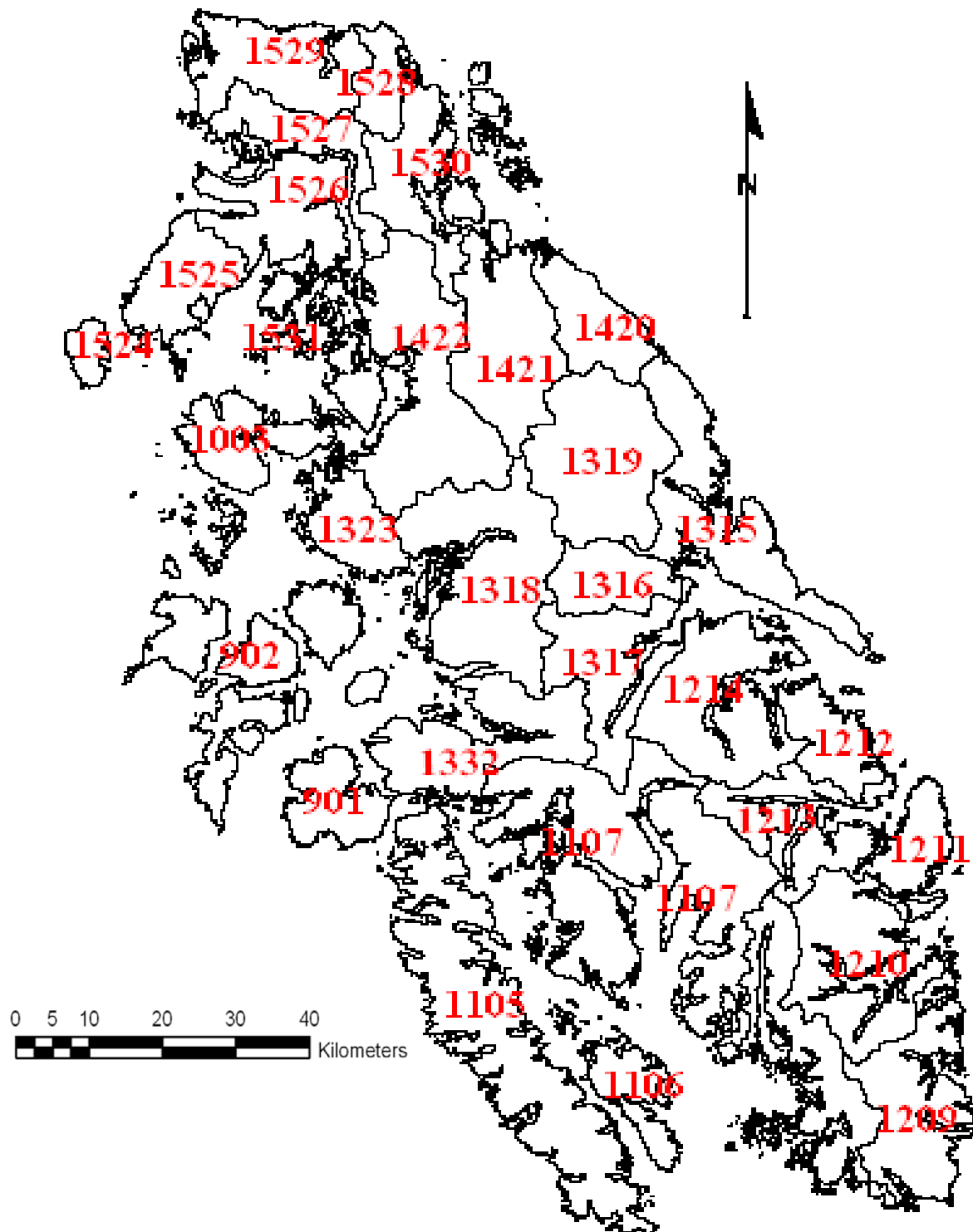


Figure 1. Map of Prince of Wales and adjacent islands (GMU 2) in Southeast Alaska showing boundaries of wildlife analysis areas (WAAs).

that identified density of roads and distances to towns and villages as key predictors of wolf harvest. Their work was based on harvest data obtained during 1990–1999, and we include those data in our analyses. However, we also include harvest data from 1985–1989 and 2000–2009 despite concerns expressed by Person and Russell (2008) about the possible lack of accurate reporting from the latter decade. We were interested in comparing the two periods (one [1985–1999] with relatively high rates of reported harvest and the other [2000–2009] with much lower rates) to see which covariates were influential during both periods and which covariates differed between periods. We evaluated 3 metrics of harvest and their relations with variables such as density of roads, distances to population centers, and land cover classes within WAAs. We calculated mean rates of harvest for each WAA based on sealing records. We used our models to predict those three harvest metrics for WAAs after 2015, when a large proportion of existing roads are scheduled to be closed to vehicular use. We expect that those road closures will reduce concerns about high harvest rates and risks of unsustainable harvest. Wolf management in Southeast Alaska occurs at the scale of GMU (i.e., GMU's 1, 2, 3, and 5). Assessment of wolf viability or sustainability was not undertaken as part of this work.

Study Area

Southeastern Alaska comprises a narrow strip of mainland and a chain of islands, known as the Alexander Archipelago that is oriented roughly parallel to the mainland. The archipelago consists of thousands of islands ranging in size from <0.01 to 6,700 km² with distances between islands and the mainland ranging from several meters to 15 km. The study area (GMU 2, 9,344 km²) 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 is the third largest in the United States (about 6,700 km²) and contains 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% clearcuts or early seral forest. Approximately 196,000 ha have been clearcut logged and >4,800 km of road have been 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 at lower elevations.

The temperate rainforests of the study area are dominated by Sitka spruce (*Picea sitchensis*) and western hemlock (*Tsuga heterophylla*), with lesser amounts of western red cedar (*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 (*Onchorhynchus* spp.) populations. Most of the land area (92%) is federal land managed by the USFS (U.S. Forest Service 1997).

Regulatory History and Background

Harvesting of wolves in GMU 2 is regulated by the State of Alaska, Board of Game (BOG) and, by the Federal Subsistence Board (FSB) for federally-qualified subsistence users on federal lands. This dual management system began in 1990 when the federal government assumed management of subsistence use of fish and wildlife resources on federal public lands. Because of this change in management authority, FSB regulations supersede state regulations on federal lands for federally qualified users. Because GMU 2 is mostly federal lands, most of the wolf harvest is by federally qualified users. The ability of the state to manage wolf harvest in GMU 2 is dependent on cooperative management with the FSB.

Currently, the BOG and the FSB regulate wolf harvest as both a big game animal (hunting) and a furbearer (trapping). Until 1993, wolf hunting and trapping seasons under state regulations were consistent across Southeast Alaska with the hunting season open all year and the trapping season lasting from 10 November to 30 April with no bag limit. In 1993, the BOG established separate hunting and trapping seasons for GMU 2. The state hunting season for GMU 2 was 1 August to 30 April with a bag limit of 5 wolves, and the trapping season was from 1 December to 31 March with no bag limit. The federal subsistence hunting and trapping seasons in 1993 mirrored that of the state, and the two entities retained similar seasons and bag limits through 2000. In 2001, the state and federal seasons began to diverge with the federal seasons beginning earlier in each case, and this divergent approach to hunting and trapping seasons has been retained since.

In 1997, the BOG instituted a number of changes in GMU 2 because it was concerned about excessive harvesting of wolves. The board adopted a harvest quota for wolves in GMU 2 of 25% of the estimated autumn population (Alaska Department of Fish and Game 2003). It also shortened the state hunting season to 1 December to 31 March, and shortened the state trapping season to 1 December until 31 March. Bag limits remained unchanged in both cases. Because some residents of GMU 2 were concerned that the wolf harvest quota was too conservative, the BOG in 2000 raised the harvest quota for wolves in GMU 2 to 30% of the estimated autumn population (Alaska Department of Fish and Game 2003). In addition, federal wildlife managers committed to consulting with ADF&G and the chair on the Southeast Alaska Regional Subsistence Advisory Council before closing the season under federal regulation. Since 1997, the federal wolf hunting seasons have varied; opening as early as 1 September to as late as 1 December and closing as early as 15 March to 31 March. The federal wolf trapping seasons have also varied; opening on 15 November to 1 December and closing on 15 March to 31 March.

Sealing records indicate that reported harvest peaked during 1990–1999 and declined thereafter with a high of 136 wolves in 1996 and a low of 18 in 2009 (Fig. 2). Person and Russell (2008) showed that illegal and unreported take are common and reported harvest was likely an underestimate of the true take. In 1999, ADF&G closed the trapping season early because the harvest guideline was reached before the normal closing date. Subsequently, annual reported harvest declined substantially in the following decade, particularly during 2004–2009. However, mortality from human take of radiocollared wolves in central Prince of Wales Island remained high during 2000–2004 despite a large decline in reported harvest across GMU 2 (Person and

Russell 2008). Person and Russell (2008) concluded that after the 1999 season was closed by emergency order, hunters and trappers were less cooperative with respect to sealing wolves and that harvest data after 1999 were less accurate compared with data obtained prior to that date.

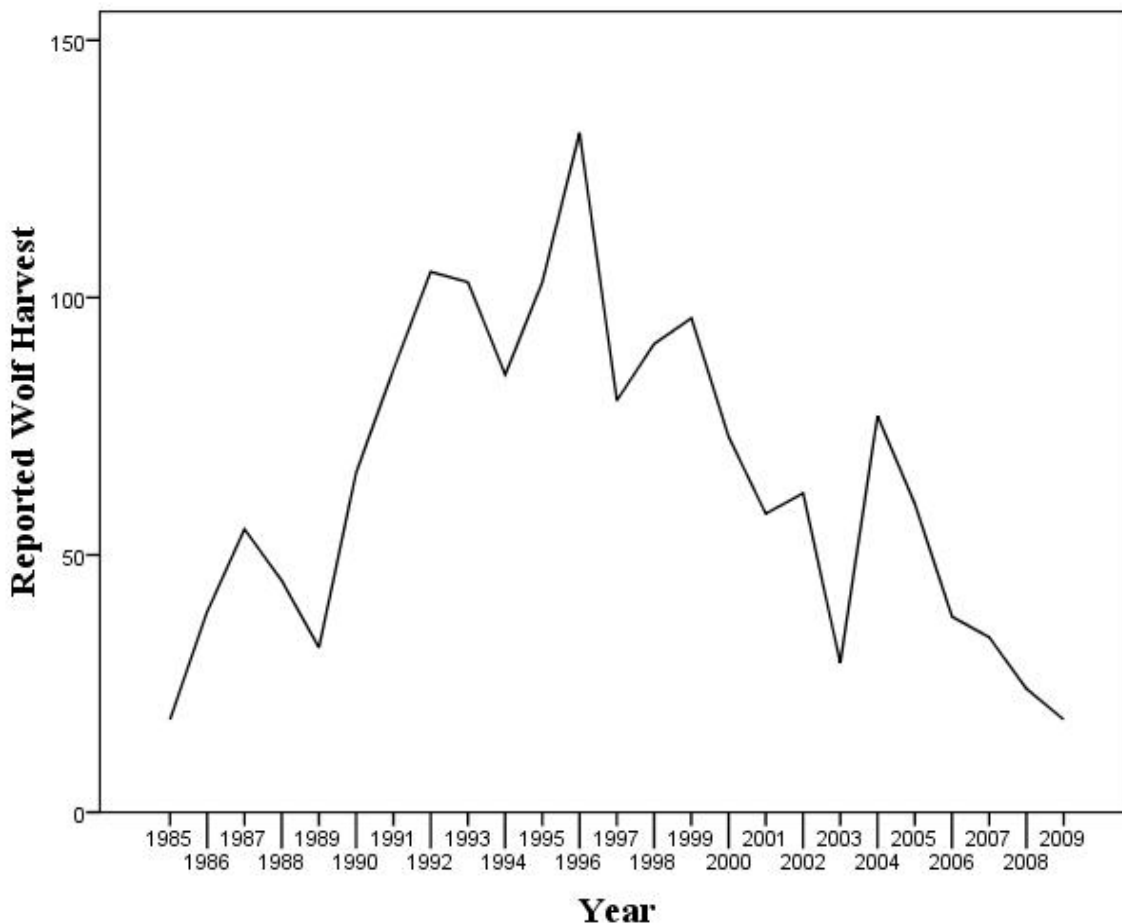


Figure 2. Reported wolf harvest in GMU 2, Southeast Alaska, 1985–2009.

Methods

HARVEST METRICS

Scale

Wolf management occurs in Southeast Alaska at the scale of GMU (i.e., GMU's 1, 2, 3, and 5). These scales also correspond with like numbered Federal Subsistence Units. The U.S. Forest Service places an emphasis on the biogeographic province to maintain viable and well-distributed populations of wolves within the Tongass National Forest (U.S. Forest Service 1997). Within GMU 2, 4 biogeographic provinces have been established. While ADF&G manages wolves at a larger scale, there is a benefit in looking at local areas (e.g., WAAs or combinations of multiple

WAAs) to understand population variability within the broader landscape. This noted, the analysis presented in this report cannot in itself be used to assess either the viability or sustainability of overall wolf populations in GMU 2, including Prince of Wales Island.

We used wolf harvest data from hide sealing records collected during 1985–2009 of only legally taken wolves. Every legally taken wolf needs to be sealed by a representative of ADF&G. During sealing, the locations of harvested wolves are recorded using ADF&G’s internal geographical coding units, wildlife analysis areas (WAA), multi-watershed areas that range from 112.5–939.0 km² within GMU 2. We considered WAAs the appropriate scale of analyses because they are the smallest geographic units for which the spatial locations of harvested wolves are accurately recorded. In addition, the mean size (292.5 km²) of WAAs in GMU 2 approximates the mean area of wolf pack home ranges (≈ 300 km² [Person 2001, ADF&G unpublished data]). Therefore, harvest rates within a WAA roughly can be interpreted as harvest mortality affecting a single wolf pack, which is useful for evaluating the potential impacts of harvest on the wolf population. Certainly, >1 wolf pack may intersect WAA boundaries, however, those boundary issues can be alleviated somewhat by considering results from our analyses among groups of neighboring WAAs rather than individual areas. For example, a WAA with high rates of wolf harvest surrounded by areas with low rates may simply indicate that the movements of packs occupying the adjacent areas intersect that WAA. Thus, the effect on population of the rate of harvest in the WAA is diluted because it represents harvest of wolves from a much bigger area and population segment. Clearly, that circumstance would be of less concern than high rates of harvest within groups of adjacent WAAs.

Data

We calculated the mean number of wolves reported harvested annually for each WAA during 1985–1999 and again during 2000–2009. We then divided the mean number of wolves killed by humans and reported annually by the area of the WAA to calculate a harvest density. Next, we multiplied that density by the mean area of wolf pack home ranges (300 km²) to estimate a harvest rate at the scale of individual wolf packs. We used those harvest rates as dependent variables to relate to road density, distances from towns and villages, and land cover classes within WAAs.

Definitions

Unsustainable harvest mortality

During autumn, pack sizes average 7–8 wolves in GMU 2 (Person 2001, Person and Russell 2008). We also expect that 1–2 nonresident wolves inhabit an area the size of a wolf pack home range for a total number of 9–10 wolves expected within a 300-km² area. Person and Russell (2008) reported that 38% total annual mortality may be close to the limit of what wolves can sustain in GMU 2 without declining, and they demonstrated that legal and illegal harvest overwhelmed all other sources of mortality. The existing regulatory harvest guideline assumes that a reported harvest of 30% of the autumn population is the upper limit of sustainable harvest. Therefore, we assumed that an annual reported harvest rate ≥ 3 wolves/300 km² (30–33% of

wolves within 300 km²) indicated unsustainable harvest mortality within a WAA. We acknowledge our 30% harvest rate threshold allows only a 5–8% buffer for illegal and unreported take, which Person and Russell (2008) indicated could be much higher in some areas. We identified WAAs that had unsustainable annual harvests ≥ 5 times during the entire 25-year reporting period (1985–2009) and assigned them to a group representing WAAs with chronically unsustainable harvests.

Pack depletion

We assumed that a harvest of ≥ 7 wolves out of an average pack 7–8 wolves in a WAA risked causing pack depletion. We identified WAAs in which annual harvest rates were ≥ 7 wolves at least twice during the reporting period. Those WAAs were assigned to a group representing areas in which risk of pack depletion and turnover was high.

CLASSIFICATION OF ROADS, DISTANCE MEASURES, AND HABITATS WITHIN WAAs

We obtained data for roads from USFS GIS databases that included roads on federal, state, and private lands. For our retrospective analyses of harvest rates during the periods 1985–1999 and for 2000–2009, we did not classify roads by use or status. All roads were originally built to facilitate logging. Most roads were gravel surfaced 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, however; at any time about 25% were closed by gating, removing bridges and culverts, or were grown over.

Unfortunately for our retrospective analyses, the status of roads (including those grown over) frequently changed, preventing us from reliably classifying them by levels of use during the period covered by our analyses, which is why we chose to use the total densities of roads within WAAs rather than try to distinguish open from closed roads. Many roads were open for much of their length with only a portion of the length closed. Moreover, closed roads and road segments often were used by snowmobiles in winter and all terrain vehicles (ATVs) year round. They 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 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 their use from December through February. Nonetheless, snow accumulations varied spatially and temporally and many roads remained open during winters with snow.

We divided total length of roads in WAAs by the areas of the WAAs to calculate road densities. For the period 1985–1999, we used the density of roads within WAAs measured during 1998. For the period 2000–2009, we used density of roads in 2008. We included all roads on federal, state, and private lands in our analyses.

The USFS intends to close many roads on federal lands to vehicular use by 2015 and data concerning those future closures were available allowing us to calculate densities of open and

closed roads after 2015 (U.S. Forest Service 2009, Table 1). For our analysis of future wolf vulnerability, we classified roads as open to vehicular travel if use of highway and off-road vehicles (including ATV's, trail bikes, and snowmobiles) was allowed. Some roads will be gated but most will be closed by having culverts and bridges removed. About 51% of existing roads on federal lands will be open for vehicular use in 2015 with closures ranging 0%–80% by WAAs. Similar data concerning road closures on state and private lands are not available; therefore, we assumed the proportion of roads closed would mirror that on federal lands (49%). Although, lands owned by Alaska Native corporations typically are closed to the public, wolves are hunted and trapped by corporate shareholders and those given permission to access corporate lands.

Brinkman (2007) surveyed deer hunters on Prince of Wales Island and reported that the median distance that hunters were willing to walk from their vehicles to hunt deer was about 2.4 km (1.5 miles). Brinkman (2007) also stated that many hunters interviewed preferred to hike and hunt closed roads because they believed deer were more abundant along them. We assumed wolf hunters and trappers behaved similarly and that they would be willing to walk at least 1 km on closed roads to pursue wolves. Indeed, use of roads by wolves increases as vehicle traffic decreases (Thurber et al. 1994); thus, the probability of harvesting a wolf may be higher on closed roads. To account for that effect, we included the first 1-km segment of any closed road from the point where it connected to an open road in our open road density estimates for 2015. Thus, we considered it an effective road density in 2015.

We estimated mean overland distances (km) from 100 randomly selected points within each WAA on Prince of Wales Island to all of the permanent villages and towns on the island that were accessible by road. We computed distances to the towns and villages of Coffman Cove, Craig, Hollis, Hydaburg, Kasaan, Klawock, Naukati, Port Protection, Thorne Bay, and Whale Pass. For all WAAs not on Prince of Wales Island or those inaccessible by road, we estimated the mean ocean distance (km) from towns and villages to 100 randomly selected points along the shoreline of the WAA. We computed water distances to the same towns listed above but also included Edna Bay on Kosciusko Island and Point Baker on Prince of Wales Island.

We recognized 10 land cover classes within WAAs (Table 2). The total area of each land cover class within a WAA was divided by the total area of the WAA and then multiplied by 100 to calculate percent cover. Percent cover for each habitat was then used as a potential covariate in our models. Habitat classes were derived using the existing vegetation and managed stands GIS data layers from the USFS GIS database for GMU 2 (Table 2). In addition, we calculated the percentage of each WAA composed of nondevelopment lands, which included old-growth reserves designated by TLMP, wilderness and other congressionally protected lands, stream buffers, beach buffers, and all habitat classes not containing commercially valuable timber. We also calculated the percent of each WAA composed of medium and large old-growth reserves and considered those values as potential covariates of wolf harvest. Geographic analyses were conducted using IDRISI Kilimanjaro raster GIS software (Clark Labs, Worcester MA.). The raster cell resolution was 20 m.

Table 1. Road densities (km/km²) within WAAs on Prince of Wales and adjacent islands (GMU 2) in Southeast Alaska. Density of all roads in 2009, density of roads remaining open for motorized vehicular use after 2015, and effective density of roads after 2015 are shown.

WAA	All roads 2009	Open roads 2015	Effective 2015
901	0.45	0.18	0.37
902	0.02	0.01	0.01
1003	1.37	0.46	1.08
1104	0	0	0
1105	0.14	0.06	0.06
1106	1.53	0.64	0.64
1107	0.34	0.15	0.19
1108	0	0	0
1209	0.02	0.02	0.02
1210	0.04	0.02	0.02
1211	1.06	0.46	0.54
1212	0	0	0
1213	0.15	0.06	0.06
1214	0.87	0.40	0.59
1315	1.20	0.45	0.78
1316	0.01	0	0
1317	0.71	0.28	0.57
1318	1.14	0.53	0.64
1319	0.70	0.24	0.49
1323	0.21	0.10	0.16
1332	0.46	0.16	0.30
1420	1.05	0.50	0.88
1421	0.83	0.29	0.70
1422	1.16	0.44	1.04
1524	0	0	0
1525	1.81	0.62	1.36
1526	0.11	0.02	0.03
1527	0.97	0.34	0.71
1528	0.35	0.14	0.26
1529	0.88	0.34	0.70
1530	1.11	0.44	0.99
1531	1.01	0.32	0.79

Table 2. Descriptions of land cover classes on Prince of Wales and adjacent islands, Southeast Alaska, USA.

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	Open heath or peatland areas and unproductive forestlands.
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 volume; thick understory vegetation.
Coarse-canopy old-growth forest	Primarily uneven aged hemlock-spruce forest ≥58 m ³ /ha gross timber volume; abundant understory vegetation.
Clearcuts ≤10 years of age	Even-aged clearcuts ≤10 years post logging; canopy was completely removed, conifer regeneration was at seedling stage; moderate biomass of shrubs and forbs, abundant slash.
Clearcuts 11–30 years of age	Shrub-sapling stage clearcuts 11–30 years post logging; open canopy, conifer regeneration was at sapling stage, abundant shrub and forb biomass during snow-free months.
Clearcuts >30 years of age	Pole-stage and saw log stage clearcuts 31+ years post logging; conifer regeneration >15 cm dbh, dense forest canopy prevented light from reaching forest floor; depauperate understory vegetation.
Nonfederal lands	State and privately owned parcels most of which are composed of clearcuts <30 years old.

STATISTICAL ANALYSES

We separated data into 2 groups for analysis representing WAAs on Prince of Wales Island and those on the smaller outlying islands within GMU 2. We did that because modes of access are very different for each group. Prince of Wales Island has an extensive interconnected road system linking the largest population centers in the unit. The other islands have roads but only Kosciusko Island has a small permanent human settlement and access from any major town requires a boat or aircraft. As stated previously, we analyzed harvest rates for 2 separate time periods (1985–1999 and 2000–2009), so that we could compare results during a period in which there were high levels of reported harvest and another period in which those levels were lower. When evaluating probabilities of chronic unsustainable harvest and pack depletion, we only considered the complete time series of data (1985–2009).

We used multiple linear regression (SPSS 2009) to relate mean rates of harvest within WAAs to density of roads, mean land and ocean distances from towns or villages, and land cover types. To stabilize variance, we square root transformed harvest rates. We then screened potential covariates for correlations with transformed harvest rates and eliminated from consideration those with $r < 0.5$. We tested models containing all combinations of the remaining covariates using AIC_c criteria and considered all models with $\Delta \leq 4$ as potential candidates (Burnham and Anderson 1998). However, because our sample size of WAAs was 32, we constrained model combinations to $k \leq 4$ to avoid saturation. If the best candidate model (Burnham and Anderson 1998) had AIC weight (w) < 0.8 , we model averaged all viable candidate models with $w \geq 0.1$ to derive the best model. We derived models for probability of unsustainable harvest and risk of pack depletion using multiple logistic regression (Hosmer and Lemeshow 2000, SPSS 2009). We compared all potential covariates individually with the outcome variables using univariate Mann-Whitney tests and only selected variables with P -values ≤ 0.2 . Those variables were then considered in all combinations with $k \leq 4$ and candidate models selected using AIC_c criteria as described previously. Model averaging, when necessary, was done as before.

We used our best candidate models derived from harvest rates observed during 1985 to 1999 and 2000 to 2009 to predict levels of harvest within WAAs after 2015. The model derived from harvest data during 1985 to 1999 generally predicted higher harvest rates compared with predicted values using the 2000 to 2009 model. We also used our models of risk of unsustainable harvest and pack depletion to predict those metrics after 2015. We used density of open roads (plus the first 1-km segment of closed roads that intersect open roads) as input rather than density of all roads to evaluate the potential changes in harvest metrics when a large proportion of roads are closed to vehicular use after full implementation of USFS plans to close roads.

Results

WOLF HARVEST RATES

The mean total reported annual harvest in GMU 2 during 1985 to 1999 was 75.7 wolves (SD = 31.9) and ranged from a minimum of 18 wolves in 1985 to a maximum of 136 during 1996. The average rate of harvest within WAAs was 2.4 wolves/300 km² (SD = 1.9) and ranged from a minimum of zero in WAA 1524 during most years to a maximum of 33 wolves/300 km² in WAA 1529 during 1992. Mean harvest rates ranged from 0 wolves/300 km² in WAA 1524 to 6.3 wolves/300 km² in WAA 1529 (Table 3). Hunters and trappers using boats to access wolf habitat killed most wolves (59%), but 41% of wolves reported were taken by those using roads. During 2000 to 2009, the mean total harvest reported was 48.5 wolves (SD = 21.1) and ranged from a minimum of 18 wolves to a maximum of 77. The mean harvest rate for the period was 1.5 wolves/300 km² (SD = 1.5) with minimum of zero occurring during all years in WAA 1209 and a maximum of 18.9 wolves/300 km² in WAA 1531 during 2002. Mean harvest rates ranged from 0 wolves/300 km² in WAA 1209 to 6.6 wolves/300 km² in WAA 901 (Table 3). The proportion of reported harvest taken along roads was 41%, the same as during the previous period.

We identified a single valid candidate model predicting harvest rate for WAAs on Prince of Wales Island that was based on harvest data from 1985–1999 (Table 4). Density of roads and proportion of WAAs composed of alpine habitat were positively associated with harvest rates. Road density had the largest effect. Indeed, if percent alpine habitat was zero, the model would predict unsustainable rates of harvest (>3 wolves/300 km²) when density of roads exceeded 1.2 km/km² (2.0 mi/mi²). We did not identify any significant covariates of harvest rates for WAAs associated with the smaller islands adjacent to Prince of Wales Island. We expected ocean distance to be a significant predictor, but that was not the case. Consequently, the best predictor for harvest is simply the mean harvest rate for each WAA over the period.

For harvest data obtained during 2000–2009, we identified 2 models predicting harvest rates for WAAs on Prince of Wales Island (Table 4). In the best model, harvest rates were negatively related to land distances from towns, and percent of area composed of muskeg. Harvest was positively related to percent of area composed of clearcuts ≥ 30 years post logging. Although road density was not included in the best subset of models, it was positively correlated with harvest rate ($r = 0.472$, $P = 0.02$). We did not identify any valid models predicting harvest rates of wolves in the WAAs on the smaller islands in GMU 2.

UNSUSTAINABLE HARVEST AND PACK DEPLETION

Twenty-nine of 32 WAAs in GMU 2 had harvest rates ≥ 3 wolves/300 km² at least once during 1985–2009 (Table 5). Annually, the number of WAAs with harvest rates ≥ 3 wolves/300 km² peaked during 1993–1999 and then declined after 1999, the year in which the trapping season was closed early. There were 19 WAAs with chronically unsustainable harvest based on our definition of that harvest metric (≥ 3 wolves/km² for ≥ 5 years, Fig. 3). Five WAAs (901, 902, 1317, 1332, and 1420) had unsustainable rates during ≥ 10 years. The annual number of WAAs

Table 3. Mean wolf harvest rates for wildlife analysis areas on Prince of Wales and adjacent islands (GMU 2) in Southeast Alaska, USA during 1985–1999 and 2000–2009. Also shown is the proportion of harvest taken by hunters and trappers using roads.

WAA	1985–1999 rate (wolves/300 km ²)	% Road	2000–2009 rate (wolves/300 km ²)	% Road
901	4.5	5.9	6.6	0.0
902	2.6	1.8	3.5	0.0
1003	2.1	5.3	3.3	25.0
1105	0.8	8.0	1.4	26.7
1106	3.7	75.0	0.2	0.0
1107	1.0	19.2	1.7	13.0
1108	0.4	0.0	0.2	0.0
1209	0.5	0.0	0	0.0
1210	0.5	0.0	0.1	0.0
1211	5.6	6.0	1.1	55.6
1212	0.4	0.0	0.2	0.0
1213	2.3	0.0	0.4	0.0
1214	3.2	58.1	0.7	66.7
1315	2.9	45.8	2.0	37.0
1316	2.1	5.9	3.1	5.9
1317	5.5	51.2	2.3	65.2
1318	3.6	70.0	1.4	100.0
1319	1.6	91.4	1.3	100.0
1323	0.4	33.3	1.5	62.5
1332	6.8	8.3	3.8	7.7
1420	3.9	84.2	4.3	82.1
1421	2.9	81.5	0.5	100.0
1422	2.8	88.2	1.8	96.6
1524	0.0	0.0	0.3	0.0
1525	2.1	50.0	1.1	80.0
1526	2.5	5.9	0.7	33.0
1527	3.6	93.1	0.6	33.0
1528	1.4	25.0	0.5	50.0
1529	6.3	23.5	1.6	75.0
1530	2.1	50.0	1.9	81.3
1531	0.5	0.0	0.5	0.0
Mean	2.4		1.5	
SD	1.9		1.5	

with harvest rates ≥ 7 wolves/300 km² peaked during 1992–1999 and thereafter declined. Twenty-two WAAs had rates of harvest for at least 1 year during the period between 1985 and 2009 that could have resulted in pack turnover or pack depletion (harvest rate ≥ 7 wolves/ 300 km², Table 5). We observed 16 WAAs in which harvest rates equaled or exceeded our definition of high risk of pack depletion (harvest rate ≥ 7 wolves/300 km² for ≥ 2 years, Fig. 4). Six of those WAAs (901, 1211, 1316, 1317, 1332, and 1420) risked pack depletion ≥ 5 times.

Table 4. Results of multiple linear regression of square root transformed mean wolf harvest rates on habitat variables within WAAs on Prince of Wales Island ($N = 22$) in GMU 2. Two groups of models were derived, one for harvest rates reported during 1985–1999 and the second for rates reported during 2000–2009. Variables considered were road density (road dens), ocean and land distances to towns and villages (land dist), and land cover classes (%alp, %musk, and %CC30) (see Table 2). Only the best candidate models are shown ($\Delta \leq 4.0$). Shown are coefficients (β), AIC_c scores, AIC weights (w), r^2 values of regression models, and model-averaged coefficients.

Harvest rates 1985–1999							
Model ¹	Constant	β (road dens)	β (% alp)		AIC_c	w	r^2
1	0.552	0.964	0.624		-49.87	0.999	0.79
Harvest rates 2000–2009							
Model ²	Constant	β (land dist)	β (%musk)	β (%CC30)	AIC_c	w	r^2
1	1.372	-0.016	-0.005	0.034	-45.8	0.62	0.59
2	1.297	-0.019	0	0.035	-44.82	0.38	0.59
AVG	1.344	-0.017	-0.003	0.035			

¹ road dens = road density and % alp = % % of area in alpine habitat.

² land dist = land distance to towns, %musk = % of area in muskeg habitat, and %CC30 = % of area in clearcuts >30 years of age.

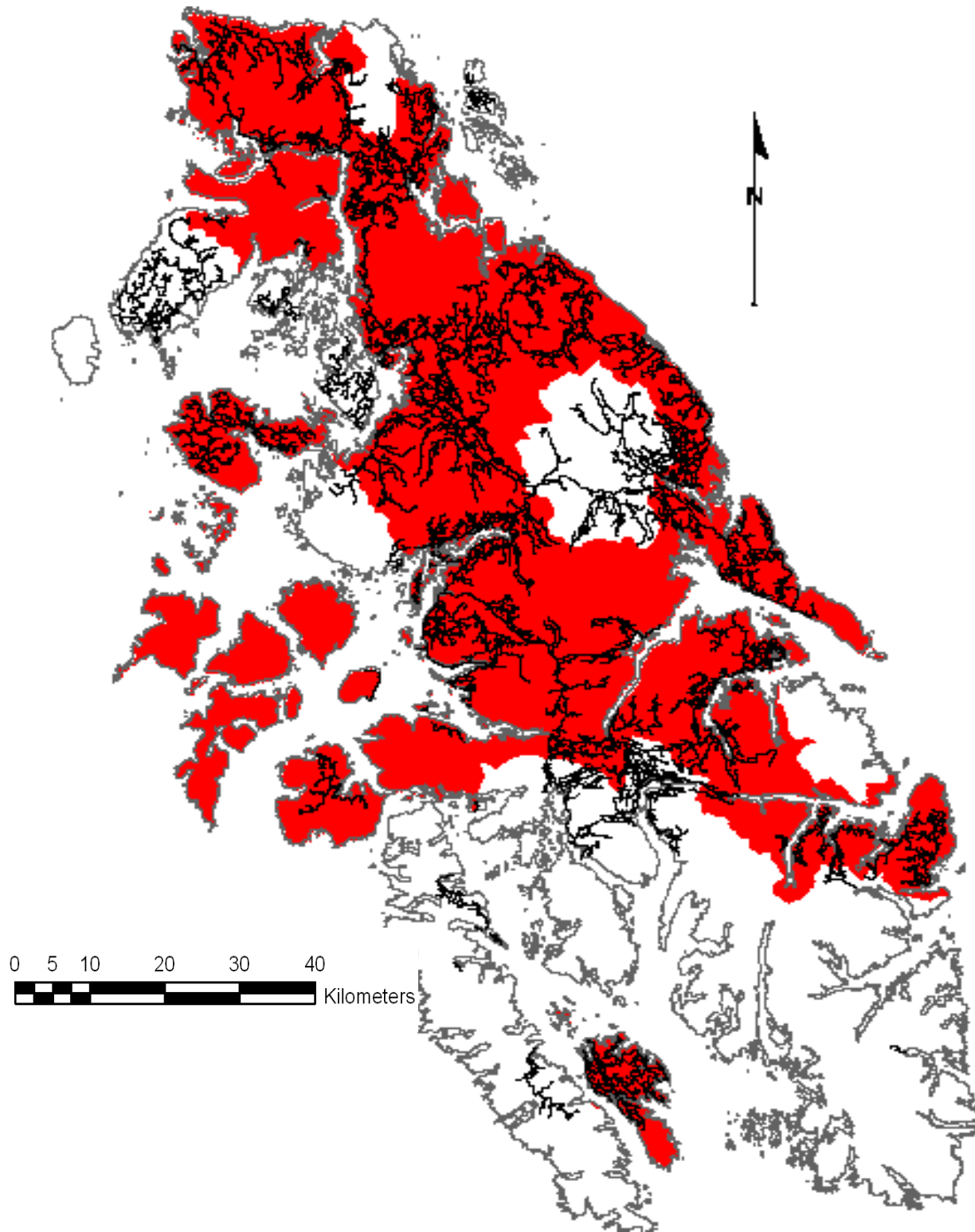


Figure 3. Wildlife analysis areas (shown in red) in GMU 2 in which reported wolf harvest rate exceeded 3 wolves/300 km² for 5 or more years during 1985–2009.

Table 5. Number of years in which wolf harvest rates within WAAs in GMU 2 were ≥ 3 wolves/300 km² (unsustainable harvest) and were ≥ 7 wolves/300 km² (pack depletion) between 1985 and 2009.

WAA	≥ 3 wolves/300 km ² Years	≥ 7 wolves/300 km ² Years
901	11	8
902	10	3
1003	9	3
1104	0	0
1105	2	0
1106	6	2
1107	2	1
1108	1	0
1209	1	0
1210	0	0
1211	9	5
1212	1	0
1213	5	1
1214	9	2
1315	7	2
1316	9	5
1317	11	5
1318	6	2
1319	2	0
1323	4	0
1332	13	8
1420	14	5
1421	5	2
1422	7	1
1524	0	0
1525	3	1
1526	5	3
1527	6	3
1528	2	0
1529	8	3
1530	7	1
1531	3	1

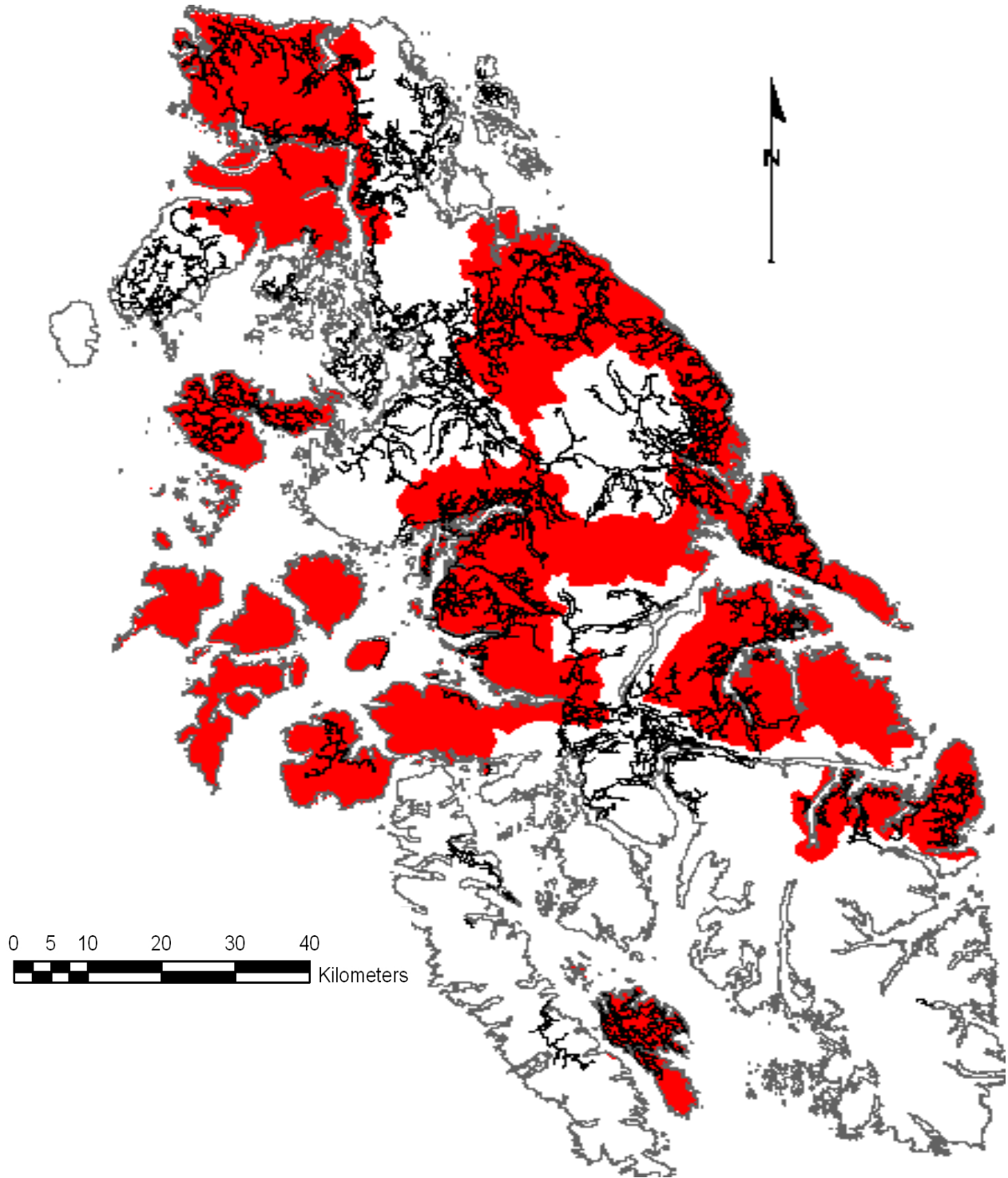


Figure 4. Wildlife analysis areas (shown in red) in GMU 2 in which reported wolf harvest rate exceeded 7 wolves/300 km² for 2 or more years during 1985–2009.

For areas on Prince of Wales Island, we identified 3 viable candidate models predicting probability of chronic unsustainable harvest (Table 6). In the best model, model-averaged probability of chronic unsustainable harvest was strongly associated with density of roads and proportion of an area composed of alpine habitat. It was negatively associated with proportion of WAAs composed of muskeg habitat and nondevelopment lands. We compared effect sizes of covariates by calculating odds ratios for increases of covariates equal to 1/10 of their observed ranges. For road density, an increase of 0.2 km/km² (0.3 mi/mi²) resulted in a 167% increase in risk of chronic unsustainable harvest. For percent alpine, a 0.2% increase in area increased risk 75%. A 9% increase in percent nondevelopment lands reduced risk 9% and a 5.2% increase in percent muskeg reduced risk 11%. Road density and percent alpine habitat were the most influential variables. We found no valid models for chronic unsustainable harvest for WAAs on adjacent to Prince of Wales Island.

We found 4 valid candidate models predicting high risk of pack depletion (Table 7). The best model (model averaged) indicated that density of roads was positively associated with risk of pack depletion but the effect was modest. Indeed, a 0.2 km increase in road density only increased risk 23%. Proportion of WAAs composed of nonfederal lands (mostly young and shrub-sapling stage clearcuts) had a weak positive relation to pack depletion. A 1.9% increase in area increased risk 11%. In addition, the proportion of nondevelopment lands within a WAA decreased risk of pack depletion but the effect was small with a 9% increase in area reducing risk 4%. Finally, we found no valid models for risk of pack depletion for WAAs on islands adjacent to Prince of Wales Island.

HARVEST METRICS AFTER 2015

We predicted mean rates of harvest for WAAs after road closures are completed in 2015 using the best model derived from the 1985–1999 harvest data and again using the best model derived from 2000–2009 harvest data (Table 8). The 1985–1999 model generally (not always) predicted higher rates of harvest than the second model. We did not identify any valid models predicting harvest in WAAs on the smaller islands adjacent to Prince of Wales Island. Therefore, for those areas we simply predicted mean rates after 2015 to be the same as they were during 1985–1999 and 2000–2009. We predict that nine WAAs will have mean harvest rates ≥ 3 wolves/300 km² after 2015 based on the 1985–1999 model and 8 WAAs using the 2000–2009 model. Four WAAs (901, 1317, 1420, and 1422) are predicted by both models to have such high levels after 2015. The mean predicted harvest rate for GMU 2 was 2.7 wolves/300 km² (SD = 2.2) based on the 1985–1999 model and 1.8 wolves/300 km² (SD = 1.5) based on the 2000–2009 model. Both models suggest that rates of harvest may be high in many WAAs despite closures of roads by 2015. Nonetheless, some WAAs, such as 1211, 1315, 1318, could have substantial reductions in harvest rates.

We did not identify any valid models predicting risk of chronic unsustainable harvest or pack depletion in WAAs on the smaller islands adjacent to Prince of Wales Island. Therefore, for those areas we used the observed values for 1985–2009 as our predictions for 2015 (Table 9). For all WAAs in GMU 2, we predict that 13 WAAs will have high probabilities (>0.75) of chronic

Table 6. Results of multiple logistic regression of probability of chronic unsustainable wolf harvest against habitat variables within WAAs on Prince of Wales Island ($N = 22$) in GMU 2 during 1985–2009. Variables considered were road density, ocean and land distances to towns and villages, and land cover classes (see Table 2). Only the best candidate models are shown ($\Delta \leq 4.0$). Shown are coefficients (β), AIC_c scores, AIC weights (w), and P -value of Hosmer and Lemeshow (2000) goodness of fit statistics (HL) for candidate models and model-averaged coefficients.

Model ¹	β_0	$\beta(\text{road dens})$	$\beta(\%alp)$	$\beta(\%musk)$	$\beta(\%nondev)$	AIC_c	w	HL
1	-4.787	5.535	3.75	0	0	19.404	0.660	0.440
2	-1.711	4.549	0	0	0	21.651	0.214	0.625
3	5.430	0	2.941	-0.179	-0.076	22.717	0.126	0.778
AVG	-2.841	4.627	2.517	-0.023	-0.010			

¹ road dens = road density and % alp = % of area in alpine habitat, % musk = % of area in muskeg habitat, %nondev = % of land cover in nondevelopment status.

Table 7. Results of multiple logistic regression of probability of high risk of pack depletion against habitat variables within WAAs on Prince of Wales Island ($N = 22$) in GMU 2 during 1985–2009. Variables considered were road density, ocean and land distances to towns and villages, and land cover classes (see Table 2). Only the best candidate models are shown ($\Delta \leq 4.0$). Shown are coefficients (β), AIC_c scores, AIC weights (w), and P -value of Hosmer and Lemeshow (2000) goodness of fit statistics (HL) for candidate models and model-averaged coefficients.

Model ¹	β_0	$\beta(\text{road dens})$	$\beta(\text{nondev})$	$\beta(\%nonfed)$	AIC_c	w	HL
1	-0.561	0	0	0.125	31.764	0.317	0.142
2	-1.135	1.871	0	0	31.835	0.306	0.258
3	-1.470	1.625	0	0.104	32.339	0.238	0.758
4	0.981	0	-0.030	0	33.407	0.139	0.212
AVG	-0.739	0.959	-0.004	0.054			

¹ road dens = road density, %nondev = % of land cover in nondevelopment status, and %nonfed = % of land cover in nonfederal status.

Table 8. Predicted mean wolf harvest rates for wildlife analysis areas on Prince of Wales and adjacent islands (GMU 2) in Southeast Alaska, USA. Predictions for 2009 and after 2015 are shown using models derived from 1985–1999 and 2000–2009 harvest data. Values for 2009 are model predictions not the actual observed values shown in Table 3. Therefore, we are comparing predictions based on expected changes in the values of model covariates.

WAA	1985–1999 Model			2000–2009 Model		
	Harvest rate (wolves/300 km ²)			Harvest rate (wolves/300 km ²)		
	2009	2015	Δ%	2009	2015	Δ%
901	4.5	4.5	0.0	6.6	6.6	0.0
902	2.6	2.6	0.0	3.5	3.5	0.0
1003	2.1	2.1	0.0	3.3	3.3	0.0
1104	0.0	0.0	0.0	0.0	0.0	0.0
1105	0.8	0.8	0.0	1.4	1.4	0.0
1106	3.7	3.7	0.0	0.2	0.2	0.0
1107	2.0	1.6	-20.0	1.5	1.5	0.0
1108	0.6	0.6	0.0	0.2	0.2	0.0
1209	0.4	0.4	0.0	0.0	0.0	0.0
1210	0.4	0.3	-25.0	0.3	0.2	-33.0
1211	2.7	1.3	-52.0	0.6	0.6	0.0
1212	0.5	0.5	0.0	0.6	0.6	0.0
1213	2.6	2.3	-12.0	0.6	0.6	0.0
1214	3.7	2.8	-24.0	1.5	1.5	0.0
1315	3.1	1.9	-39.0	2.5	3.0	20.0
1316	1.8	1.7	-6.0	1.3	1.2	-8.0
1317	6.9	6.2	-10.0	3.3	3.3	0.0
1318	6.3	4.1	-35.0	1.4	1.3	-7.0
1323	0.6	0.5	-17.0	0.9	0.9	0.0
1332	4.6	4.0	-13.0	1.2	1.4	13.0
1420	5.0	4.3	-14.0	2.6	3.5	36.0
1421	2.7	2.3	-15.0	1.2	2.2	83.0
1422	4.4	3.9	-11.0	1.8	3.9	117.0
1524	0.0	0.0	0.0	0.3	0.3	0.0
1525	2.1	2.1	0.0	1.1	1.1	0.0
1526	2.5	2.5	0.0	0.7	0.7	0.0
1527	4.2	3.2	-11.0	1.2	2.3	92.0
1528	1.9	1.7	-11.0	1.2	1.4	17.0
1529	4.4	3.7	-16.0	1.4	2.6	63.0
1530	2.7	2.3	-15.0	2.2	3.9	77.0
1531	0.5	0.5	0.0	2.5	2.5	0.0
Mean	2.9	2.4	-17.0	1.3	1.7	31.0
SD	1.9	1.5		0.8	1.2	

Table 9. Predicted probabilities of chronic unsustainable harvest and high risk of pack depletion for wildlife analysis areas on Prince of Wales and adjacent islands (GMU 2) in Southeast Alaska, USA. Predictions for 2009 and after 2015 are shown using models derived from 1985–2009 harvest data.

WAA	Chronic unsustainable harvest		High risk pack depletion	
	Probability		Probability	
	2009	2015	2009	2015
901	1.00	1.00	1.00	1.00
902	1.00	1.00	1.00	1.00
1003	1.00	1.00	1.00	1.00
1104	0.00	0.00	0.00	0.00
1105	0.00	0.00	0.00	0.00
1106	1.00	1.00	1.00	1.00
1107	0.48	0.31	0.63	0.60
1108	0.02	0.02	0.28	0.28
1209	0.01	0.01	0.28	0.28
1210	0.02	0.02	0.31	0.31
1211	0.84	0.32	0.69	0.57
1212	0.02	0.02	0.30	0.30
1213	0.58	0.48	0.33	0.31
1214	0.93	0.78	0.73	0.67
1315	0.94	0.69	0.80	0.72
1316	0.29	0.28	0.28	0.28
1317	0.99	0.99	0.50	0.47
1318	1.00	0.95	0.70	0.59
1319	0.87	0.72	0.43	0.38
1323	0.04	0.03	0.34	0.33
1332	0.95	0.89	0.66	0.62
1420	0.99	0.97	0.55	0.52
1421	0.80	0.69	0.47	0.44
1422	0.97	0.95	0.56	0.53
1524	0.00	0.00	0.00	0.00
1525	0.00	0.00	0.00	0.00
1526	1.00	1.00	1.00	1.00
1527	0.97	0.89	0.56	0.50
1528	0.44	0.34	0.35	0.33
1529	0.97	0.94	0.52	0.48
1530	0.86	0.77	0.56	0.53
1531	0.00	0.00	0.00	0.00

unsustainable harvest in 2015 and that 3 will have moderate risk (>0.5 and ≤ 0.75). With respect to pack depletion, we predict that 5 WAAs will have high probability of risk, 9 will have moderate risk, and the rest low risk ($0 \geq$ and ≤ 0.5).

Discussion

Mean rates of reported wolf harvest in GMU 2 were often high throughout 1985–1999 (Fig. 5). Rates declined substantially after 2000 possibly owing to higher fuel costs for hunters and trappers and a shift to other means of earning revenue (i.e., trapping of furbearers such as American martens (*Martes americana*) and river otters, commercial fishing, etc.). In addition, low harvest rates during the latter half of 2000–2009 may reflect a decline in wolf population numbers during the period. The decline in wolf harvests may have been exacerbated by noncompliance with reporting requirements.

Boundaries of WAAs do not spatially coincide with wolf pack home ranges, thus some WAAs may overlap several packs resulting in harvest rates that are exceedingly high in one WAA but much lower in a neighboring area. For example, a high harvest during 1992 in WAA 1529 likely was because the WAA overlapped portions of the home ranges of several wolf packs. Indeed, a simultaneously low harvest reported for neighboring WAA 1528 probably occurred because most wolves killed from packs occupying that WAA were taken from the road system and shoreline along the eastern edge of WAA 1529. High harvests in WAA 1420 near Coffman Cove involved a pack (monitored using radiocollared wolves) that occupied most of 1420 and the northern portion of 1315, and a second pack that is mostly within WAA 1421 north of Sweetwater Lake. However, trappers were able to harvest wolves from both groups along the road system in WAA 1420.

Evaluating effects of harvest mortality on wolf population using WAAs as the spatial units is not ideal; however, they are the smallest unit by which harvest data are reliably tabulated. Therefore, we urge caution about inferring the sustainability of harvest or wolf viability for any particular WAA without considering neighboring areas. We are particularly interested in how populations at a larger scale might be affected when neighboring clusters of WAAs experience high or unsustainable rates of harvest over time. For example, there is a continuous ring of WAAs with moderate to high rates of wolf harvest from WAA 1422 in the north to 1332 in the south and stretching east to WAAs 1315 and 1420 (Fig. 5). Consistent with our models of harvest rates, that area largely coincides with high densities of roads and proximity to the most populous towns on Prince of Wales Island. As indicated by our models of unsustainable harvest and pack depletion, the spatial distribution of WAAs with chronically unsustainable harvests and high risks of pack depletion also tend to reflect the distribution of roads on Prince of Wales Island (Fig. 3 and 4). Although most wolves harvested in GMU 2 were taken by hunters and trappers working from boats, the number of wolves taken along roads was sufficiently high to cause density of roads to be a key variable influencing rates of harvest (Person et al. 1996, Person 2001, Person and Russell 2008) on Prince of Wales Island. Person and Russell (2008) demonstrated that roads significantly increased risk of death of individual radiocollared wolves from hunting and trapping, thereby establishing the causal link between roads and harvest rates. Other authors

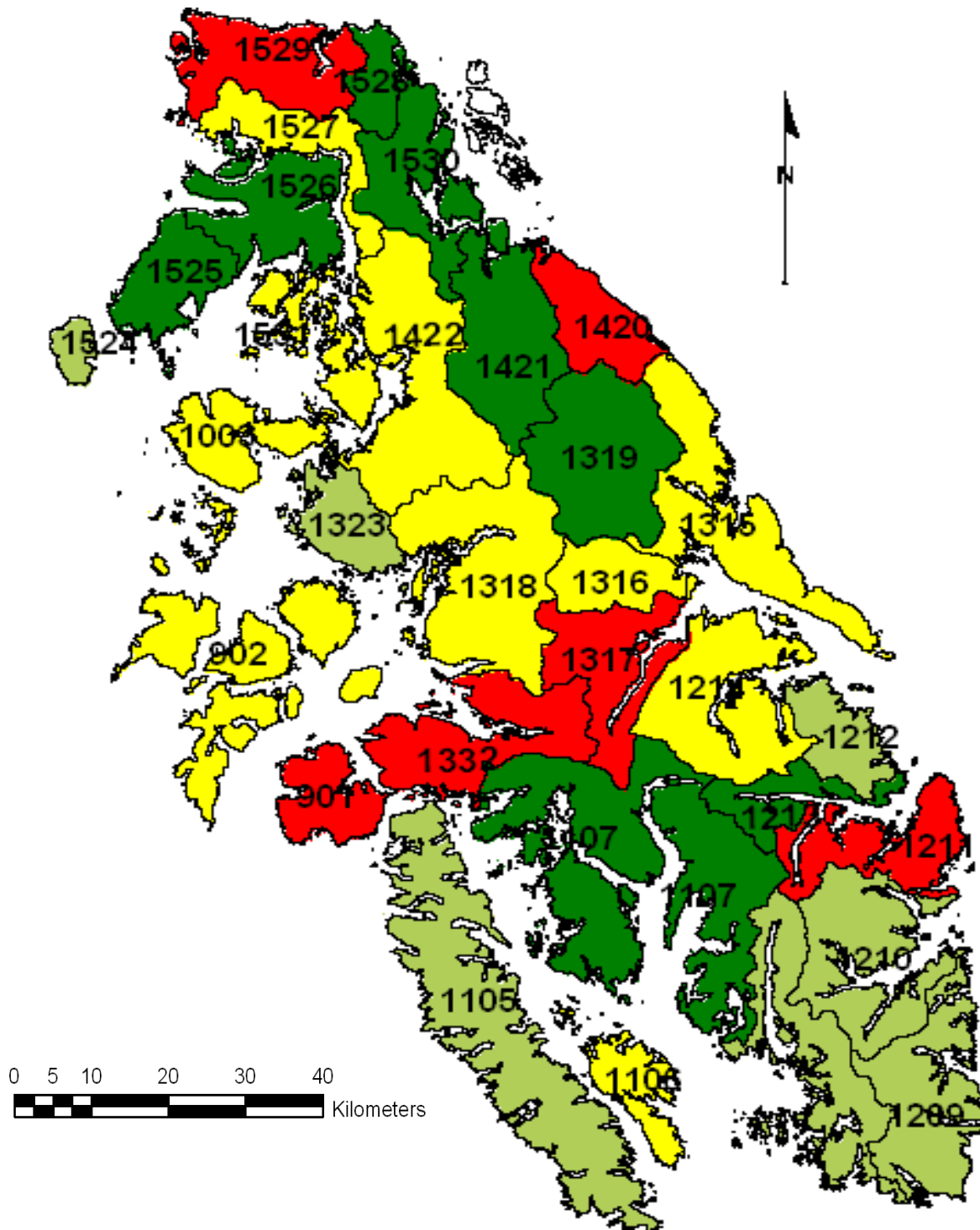


Figure 5. Mean wolf harvest rates for WAAs in GMU 2 in Southeast Alaska during 1985–2009. Harvest rates are averaged over the entire 25-year reporting period. Light green areas indicate mean harvest rate <1 wolf/300 km², medium green areas indicate harvest rates 1–1.9 wolves/300 km², yellow areas indicate harvest rates 2.0–2.9 wolves/300 km², and red areas indicate harvest rates ≥ 3.0 wolves/300 km².

noted negative effects of roads on occupancy by wolves (Thiel 1985, Mech et al. 1988, Mech 1989, Mladenoff et al. 1995). Wydeven et al. (2001) concluded roads were a key habitat feature influencing the suitability of habitat for re-colonizing wolf populations in the Great Lakes region of the United States. However, Person (2001) and Person and Russell (2008) documented relatively high abundance of wolves in areas with densities of roads much higher than levels other authors considered threshold values limiting occupancy. Clearly, roadbeds are not the wildlife management issue relative to wolf mortality in GMU 2, rather it is the access roads afford to hunters and trappers. In this respect, wolves in GMU 2 are not unique. The effects of road access on levels of legal and illegal harvest are documented for a number of wildlife species in North America. For example, road density was determined to be a key factor contributing to unsustainable harvest levels of grizzly bears (*Ursus arctos*) in southern British Columbia (McLellan and Shackleton 1988) and northwestern Montana (Mace et al. 1996). In Idaho, elk (*Cervus elaphus*) harvest was positively related to road density but negatively associated with the percent of successful hunters (Gratson and Whitman 2000).

Alpine habitat was positively associated with harvest rates and risks of chronic unsustainable harvest. We believe the proportion of alpine habitat within WAAs was simply a surrogate for mountainous topography. Wolves spend most of their time within habitats at lower elevations (Person 2001), particularly during winter when the trapping season is open. In mountainous terrain, narrow valley bottoms and beach fringes may concentrate wolf activity. Also, logging roads often follow along valley bottoms in mountainous terrain. If those areas are accessible to trappers, they likely increase risks that wolves are harvested and elevate harvest rates. The proportion of clearcuts >30 years after logging also increased harvest rates, however, that was likely related to road access. Wolves generally avoid stem exclusion second growth, particularly if stands are precommercially thinned (Person 2001), and they may prefer to travel along roads when moving through that habitat. Consequently, they may be at greater risk of harvest. Nonfederal lands, most of which are logged, increase harvest risks, a relation that is likely also a function of roads on those lands.

The primary habitat components reducing harvest were proportion of WAAs composed of muskegs (including unproductive forest), and nondevelopment lands. Both of those variables were negatively correlated with density of roads (muskeg and road density, $r = -0.743$, $P < 0.001$; nondevelopment lands and road density, $r = -0.624$, $P = 0.002$). Person and Russell (2008) reported that muskegs increased risk of death of radiocollared wolves presumably because they were more easily detected by hunters in open habitat. They also suggested that the risk was amplified when muskegs intersected roads. Nonetheless, at the spatial scale of WAAs, muskegs are associated with lower densities of roads and thus lower rates of harvest. For example, the large, mostly roadless, old-growth habitat reserves located in Honker Divide, by Sarkar and Salmon Lakes, and within the South Prince of Wales Wilderness Area contain very large patches of muskeg and unproductive forest lands. Similarly, nondevelopment lands by default have fewer roads and thus restrict access to some hunters and trappers. The other key factor reducing wolf harvest was land distance from towns and villages, which is probably a reflection of convenience.

We did not identify any valid models for our harvest metrics within WAAs on the smaller islands adjacent to Prince of Wales Island. We were surprised that ocean distance was not a significant covariate similar to land distance for WAAs on Prince of Wales Island because those islands are only accessible by boat or aircraft. However, the logistical dynamics associated with wolf hunters and trappers on the smaller islands differ greatly from those harvesting wolves on Prince of Wales Island. For example, several key trappers are commercial fishers who normally ply the waters surrounding those islands during winter trolling seasons for salmon. They often simultaneously harvest wolves as a sideline and unless fuel costs or market conditions restrict their fishing, ocean distances have little effect on wolf harvest. Moreover, Alaska and federal subsistence regulations do not currently require traps or snares to be checked within a specific time period. Consequently, fishers and others who trap wolves on the islands surrounding Prince of Wales Island do not need to visit their traplines very frequently, which may further reduce the effects of ocean distances on harvest.

Closing roads to vehicular access should significantly reduce mortality from human causes within WAAs that are accessed primarily by highway and off-road vehicles. Indeed, road closures have been effective in reducing harvest levels of other species in North America such as elk (Gratson and Whitman 2000). Hence, we predicted that the high proportion of roads for which vehicle use will be restricted after 2015 would reduce rates of harvest, risks of unsustainable harvest, and pack depletion. Comparing predictions of our models for habitat conditions in 2009 (assuming all existing roads are open) with model predictions for conditions after 2015 indicated only modest changes in rates and probabilities of risk.

Since the model for harvest rates derived from 2000–2009 harvest data does not include road density as a covariate, road closures would have no influence on model predictions. However, road density was significantly correlated with harvest rates but the effect was probably subsumed within the covariate for older clearcuts. In contrast, the model derived from harvest rates obtained during 1985–1999 is overtly influenced by road density. As anticipated, predicted rates of harvest were lower after 2015, but the change was much less than we expected given the proportion of roads to be closed. Indeed, the average change per WAA was only 0.5 wolves/300 km² (-17%). With respect to probabilities of chronic unsustainable harvest, only WAA 1211 shifted from high to low risk and WAAs 1213, 1315, 1319, and 1421 changed from high risk to moderate risk. Only WAA 1529 went from high risk of pack depletion to low risk and WAA 1315 shifted from high to moderate risk. The reason for the modest reductions is that our effective density of roads after 2015 included 1-km segments of closed roads from the point where they connect to roads that are open. If all existing roads on federal land are considered open in 2009, the average federal road density within WAAs is 0.60 km/km². After 2015, the effective road density on federal lands will be 0.44 km/km² or 73% of the density in 2009. On further examination, we placed a 1-km buffer only around open roads after 2015 and did the same for all existing roads in 2009. The buffer around open roads after 2015 encompasses about 71% of the area within the buffer around all roads in 2009. Based on our analysis, scheduled road closures will not reduce access to landscapes commensurate with the proportion of roads to be closed to vehicle use.

Other options exist to reduce wolf mortality in GMU 2. One option would include changes to hunting and trapping regulations through state and federal regulatory processes. A second option would be to increase law enforcement presence to help ensure regulations are being followed.

Limitations of our Analyses

We previously discussed some of the limitations of using WAAs as the spatial units of analyses, which is a key weakness because their boundaries are arbitrary with respect to the biology of wolves. We also stress that our analyses focus only on one source of mortality and do not constitute an assessment of wolf population viability or sustainability in GMU 2, including Prince of Wales Island. We do not consider other sources of mortality, including illegal harvest or population recruitment, both of which are required for wolf viability assessments. Nonetheless, our metrics for unsustainable harvest and pack depletion are based on demographic data obtained from radiocollared wolves in GMU 2 (Person 2001, Person and Russell 2008, Person and Russell 2009). Therefore, we are confident that the metrics represent reasonable thresholds of reported harvest beyond which we expect wolf numbers within WAAs to decline, particularly if those levels persist simultaneously within clusters of neighboring WAAs. However, while individual WAAs may have unsustainable harvest rate information, in itself it cannot be used to assess either viability or sustainability for overall wolf populations in GMU 2, including Prince of Wales Island.

The risks of high rates of harvest and pack depletion within groups of WAAs to demographic viability and genetic diversity are unknown. A panel of experts was convened by the USFS in 1996 to evaluate the conservation strategy for wolves incorporated within the Tongass Land Management Plan, and they suggested that wolf viability might not be at risk despite local depletion from harvest. However, they were considering populations at the regional scale and not individual GMUs (Iverson 1997).

Illegal take and unreported harvest are important issues that are discussed by Person and Russell (2008). Suffice to say, they can represent a substantial portion of total annual mortality of wolves. Therefore, WAAs with average reported harvest rates between 2–2.9 wolves/300 km² actually may exceed sustainable harvest limits due to illegal and unreported take. These WAAs should at very least be considered areas that are on the borderline between sustainable and unsustainable harvest. Again, because of boundary effects, it is best to consider harvest rates among clusters of WAAs rather than single areas. Finally, our model predictions are expectations useful for comparing changes over time and to highlight areas within GMU 2 where unsustainable harvest of wolves may persist despite widespread road closures. Our estimates of probabilities of chronic unsustainable harvest and risk of pack depletion represent relative risks of those conditions, not absolute probabilities. There are many factors that affect wolf harvest that we do not consider, such as regulatory changes, changes in the number of trappers and hunters, and increases in cost of fuel. We suggest that our models be used to establish relative rankings among WAAs with respect to potential concerns about harvest mortality, to examine the spatial arrangement of WAAs for which there may be concerns, and identify key habitat features that affect harvest levels. They should not be used as precise predictions of future harvest levels.

Management Implications

Our analyses and results will inform future habitat, road, and regulatory measures that will contribute towards sustainable wolf harvest in managed landscapes. Wolf harvest and land management regulations can only be effective within the context of the landscape. Therefore, it is important for land managers to work together with wildlife managers and the various public stakeholders such as hunters and trappers. Regulatory changes are valuable tools to manage harvest but can be difficult to implement on small geographic scales. However, our analyses strongly suggest that the roaded portion of central and northcentral Prince of Wales Island be considered for a regulatory regime separate from the rest of GMU 2. We believe harvest levels of wolves within the northcentral and central portions of Prince of Wales Island often were high and frequently unsustainable. Those areas encompass almost all of the major population centers on the island, and most are connected to those towns by roads. Hunters and trappers using roads take most wolves harvested in that portion of Prince of Wales Island.

The spatial arrangement of WAAs with high rates of harvest emphasizes the importance of providing core habitats of low road density. The Conservation Strategy of the Tongass National Forest Plan is intended to accomplish this via a reserve network that contains all non-development Land Use Designations (LUDs), including a system of small, medium, and large old-growth reserves, and implementation of standards and guidelines designed to maintain long-term sustainable wolf populations by integrating road management objectives with hunting and trapping regulations.

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