SHORT COMMUNICATION

Spatiotemporal analysis of wolverine *Gulo gulo* harvest in Alaska

Howard N. Golden, Aaron M. Christ & Elizabeth K. Solomon

Understanding changes in spatial and temporal patterns of harvest is vital for proper management of wolverine *Gulo gulo* populations. In Alaska, wolverines occupy nearly all areas of the state and are classified as furbearers and big game, with annual harvests averaging 545 (SD = 80) individuals since 1984. Because wolverine reproductive potential and survivorship are relatively low, it is important to understand spatial and temporal harvest dynamics to ensure populations are not overharvested. We analyzed the effects of geographic region, time period and number of harvesters on wolverine harvest using Poisson regression modeling. We also examined local harvest patterns for a portion of south-central Alaska where human population levels and concentrations of roadways differ substantially. Patterns of wolverine harvest during 1984-2003 indicated consistently higher harvest densities (wolverines/1,000 km^2) in the southern portion of Alaska. The Poisson regression model (goodness of fit: $\chi^2 = 1300$, df = 1288, P = 0.60) estimated mean annual harvest levels (wolverines/1,000 km^2) that were higher in South-central (0.35) than in Arctic/West (0.11; P = 0.009) and Interior (0.19; P = 0.001), but no other regional comparisons were significant. Geographic region, time period and number of harvesters were all significant covariates for describing wolverine harvest (P < 0.001 for each). Wolverine harvest densities at the local level indicated that areas with higher harvest densities were well distributed, but that areas with light or no reported harvest also were common and widespread. Our results also indicated that proximity to human population centers or roadways did not necessarily affect harvest densities at a local level. We reviewed the importance of areas with no or light harvest as potential refugia to maintain a sustainable harvest of wolverines.

Key words: Alaska, Gulo gulo, harvest, refugia, spatiotemporal analysis, wolverine

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Harvest of wolverines *Gulo gulo* is permitted across much of their circumboreal range, with the exception of some populations existing along the margins of that range (Banci 1994) or those currently threatened or in danger of extinction (COSEWIC 2003). In a global environment of expanding human population growth that is encroaching into wolverine habitat, understanding changes in spatial and temporal patterns of harvest is vital for proper management of wolverine populations. This is especially important where conflicts may exist with livestock industries (Landa et al. 2000), or where habitat fragmentation has created metapopulations of wolverines that require more vigilant management (McCullough 1996). Considering their low reproductive potential (Persson et al. 2006) and survivorship (Krebs et al. 2004) compared with most other furbearers or large carnivores, it is important to closely monitor harvest wherever it occurs. This is particularly true if, as suggested by Krebs et al. (2004), human-caused mortality may be mostly additive to natural mortality in most circumstances where wolverine harvest occurs.

In Alaska, wolverines are found throughout the mainland. They are classified by the state as furbearers and big game and are harvested under hunting and trapping regulations. Wolverine harvest seasons vary across the state. They range between September and March with a bag limit of one for hunting and between November and April with generally no bag limit for trapping. During 1984-2003, annual harvests in Alaska averaged 545 (SD= 80) individuals. The state requires anyone who harvests a wolverine to present the pelt for sealing with a locking metal tag and to report information on where, when and how the animal was taken. This information is recorded and managed in a statewide database. The reports indicate only successful harvests of those individuals who legally report their take. They do not indicate the number of individuals who tried to harvest wolverines nor the effort they may have spent in doing so.
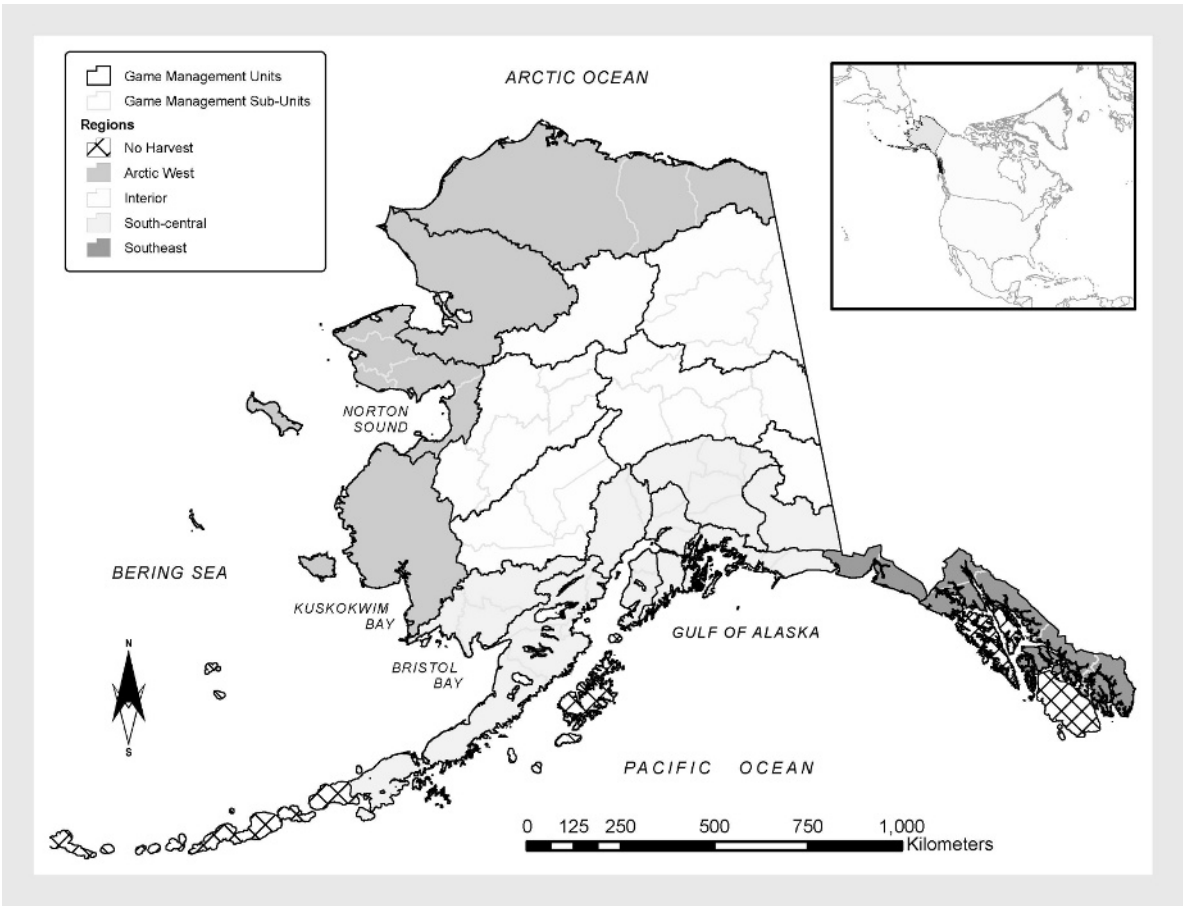

Figure 1. Regions, units and subunits used for game management in Alaska.

Alaska is partitioned into 26 game management units (GMUs), most of which are further partitioned into subunits (Fig. 1). A subunit is roughly based on topography and is generally the smallest area for which harvest regulations are applied. However, minor drainages of subunits are the smallest areas for which harvest is recorded. For administrative purposes, GMUs are combined into four regions that approximate the major ecological zones of the state: Arctic/West, Interior, South-central and Southeast (see Fig. 1).

For this paper, we examined spatial and temporal patterns of wolverine harvest in Alaska at regional and local levels. We analyzed the effects of geographic region, time and successful harvesters on harvest patterns across the state. We also examined local harvest relative to areas with no wolverine harvest, which could be considered refugia, and

the implications such areas may have on long-term management of wolverine harvest.

Material and methods

We summarized harvest data at the subunit level to illustrate spatial and temporal distributions of reported wolverine harvest among regions in Alaska in 5-year increments during 1984-2003 (i.e. 1984-1988, 1989-1993, 1994-1998 and 1999-2003). We calculated harvest densities (wolverines harvested/ 1,000 km^2) using mean annual counts of harvests along with areas of subunits. To make comparisons over time on an equivalent basis, we used a common scale over the four 5-year periods.

We analyzed the effects of geographic region, time period and number of successful wolverine
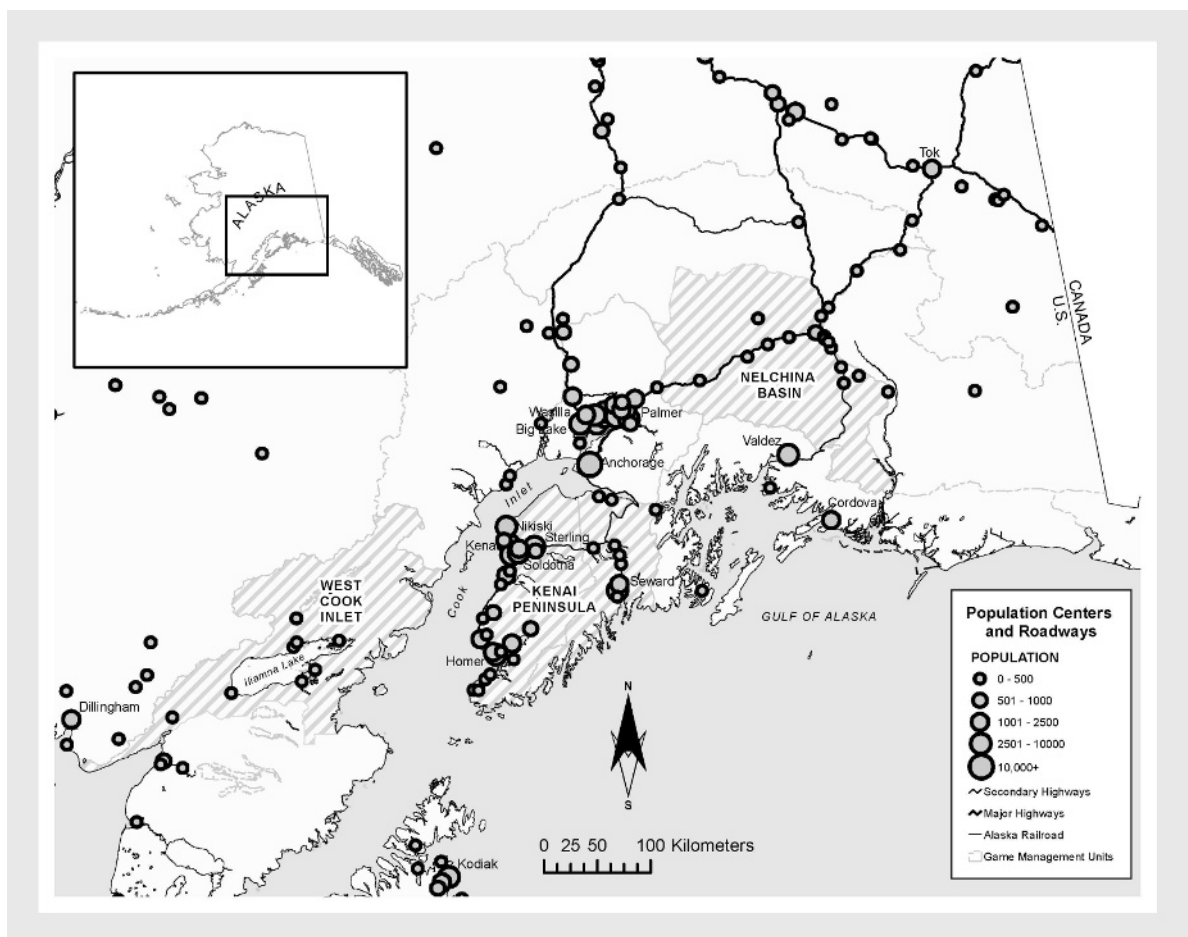

Figure 2. Distribution of human population centers and roadways within a portion of south-central Alaska, with the Kenai Peninsula, Nelchina Basin and West Cook Inlet highlighted for further comparison.

harvesters on wolverine harvest using Poisson regression (Fleiss et al. 2003) in the model:

$$\frac{\text{Count}}{\text{Area of subunit}} =$$

$$e^{\left(\alpha_{\text{region}} + \beta_{\text{region}} * \text{PERIOD} + \gamma_{\text{region}} * \text{HARVESTERS}\right)},$$

where, separately for each region, α = log of the base harvest over 20 years, β = log of the relative change between successive 5-year periods, and γ = log of the relative change for each additional successful harvester. For easier interpretation of model output, model coefficients were back-transformed to the scale of the harvest density. We used area of subunit as an offset (Fleiss et al. 2003), which allowed us to model the counts of different-sized subunits on an equivalent basis. We measured the significance of each effect at $\alpha = 0.05$. Models were estimated using Proc GLIMMIX in SAS 9.1 (SAS Institute, Inc., Cary, North Carolina, USA, 2002-2003).

We examined goodness of fit tests for a model that included an interaction between year and number of successful wolverine harvesters. However, there was conflicting evidence under G^2 and Akaike (AIC) and Bayesian (BIC) information criteria as to whether the additional parameter cost sufficiently increased the model fit. Arctic/West, South-central and Southeast showed no significant interactions ($P = 0.10$, 0.39 and 0.08, respectively). Interior had a statistically significant coefficient estimate ($P = 0.02$), but it was probably biologically negligible because the interaction indicated < 1% increase in harvest density per unit of time and harvester. We attributed this result to a large sample size rather than some very minute underlying interaction in the Interior region. The results pointed to at best one region with a very small interaction and at worst no worthwhile improvement in model fit for increased model complexity. Therefore, we chose the more parsimonious model without the interaction between year and number of harvesters.
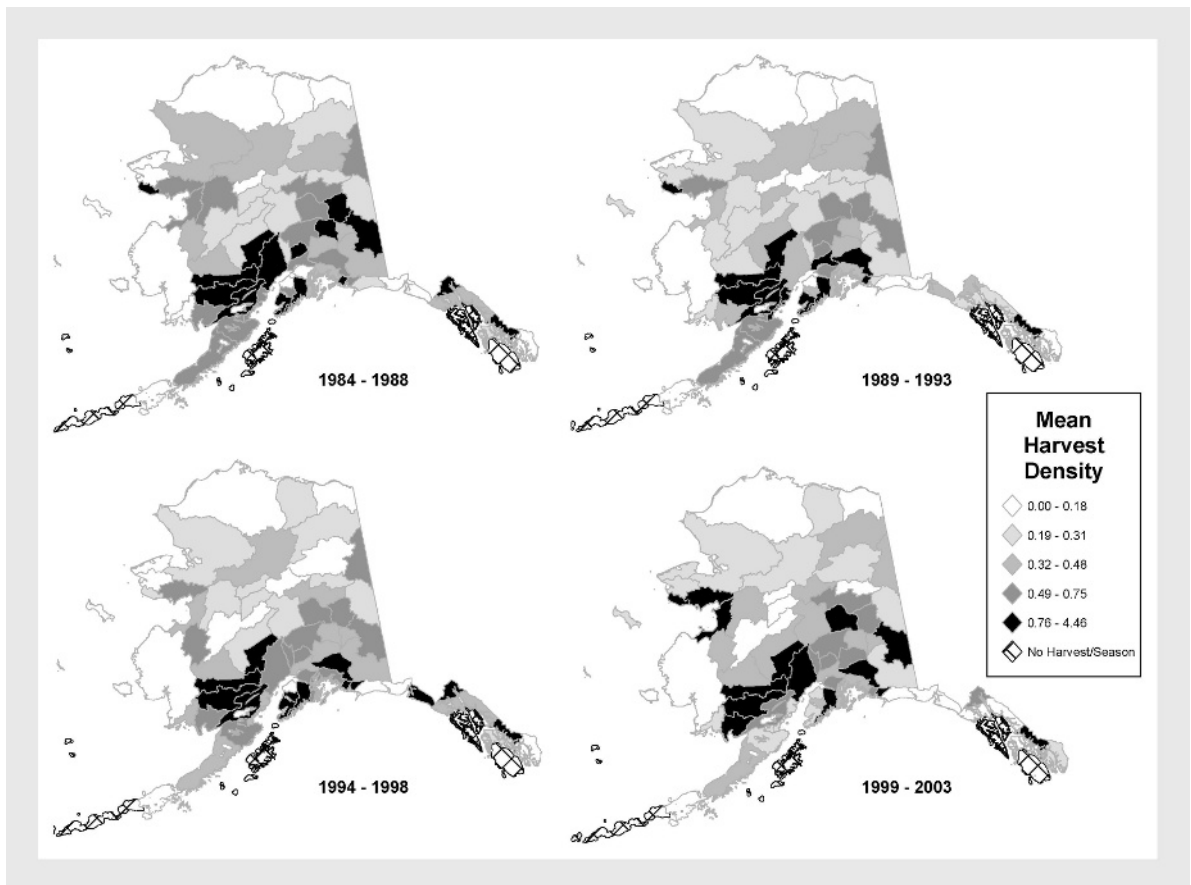

Figure 3. Wolverine harvest density (wolverines harvested/1,000 km^2) by subunit in Alaska averaged over four 5-year increments during 1984-2003. For uniformity, harvest density levels were standardized over the entire 20-year period.

Table 1. Poisson regression model effects (95% CI) by geographic region for base harvest rate, 5-year harvest periods, and number of successful harvesters of wolverines in Alaska during 1984-2003.

| Region | Mean annual harvest (wolverines/1,000 km²)[1] | Percent increase or decrease per unit | |
		5-year period[2]	Harvesters
Southeast	0.22 (0.11, 0.41)	6 (-4, 17)	28 (20, 37)
South-central	0.35 (0.27, 0.44)	-2 (-5, 1)	9 (8, 10)
Interior	0.19 (0.14, 0.24)	7 (3, 10)	10 (9, 12)
Arctic/West	0.11 (0.05, 0.24)	16 (6, 27)	8 (5, 10)

[1] Annual average harvest over entire 20-year study period.
[2] Unit of measure is a 5-year period, i.e. 1984-1988, 1989-1993, 1994-1998, and 1999-2003.

We examined local harvest patterns at the minor drainage level for a portion of south-central Alaska where concentrations of human population and roadways differ substantially. We averaged annual harvest densities (wolverines harvested/1,000 km²) for the period 1999-2003 to illustrate harvest patterns at the minor drainage scale. Because approximately 20% of the reported harvest was not recorded to a specific minor drainage within a subunit, we did not attempt to model spatial and temporal effects among these smaller areas. We also calculated annual harvest density and measured the percent area without wolverine harvest, which could be considered refugia, among select
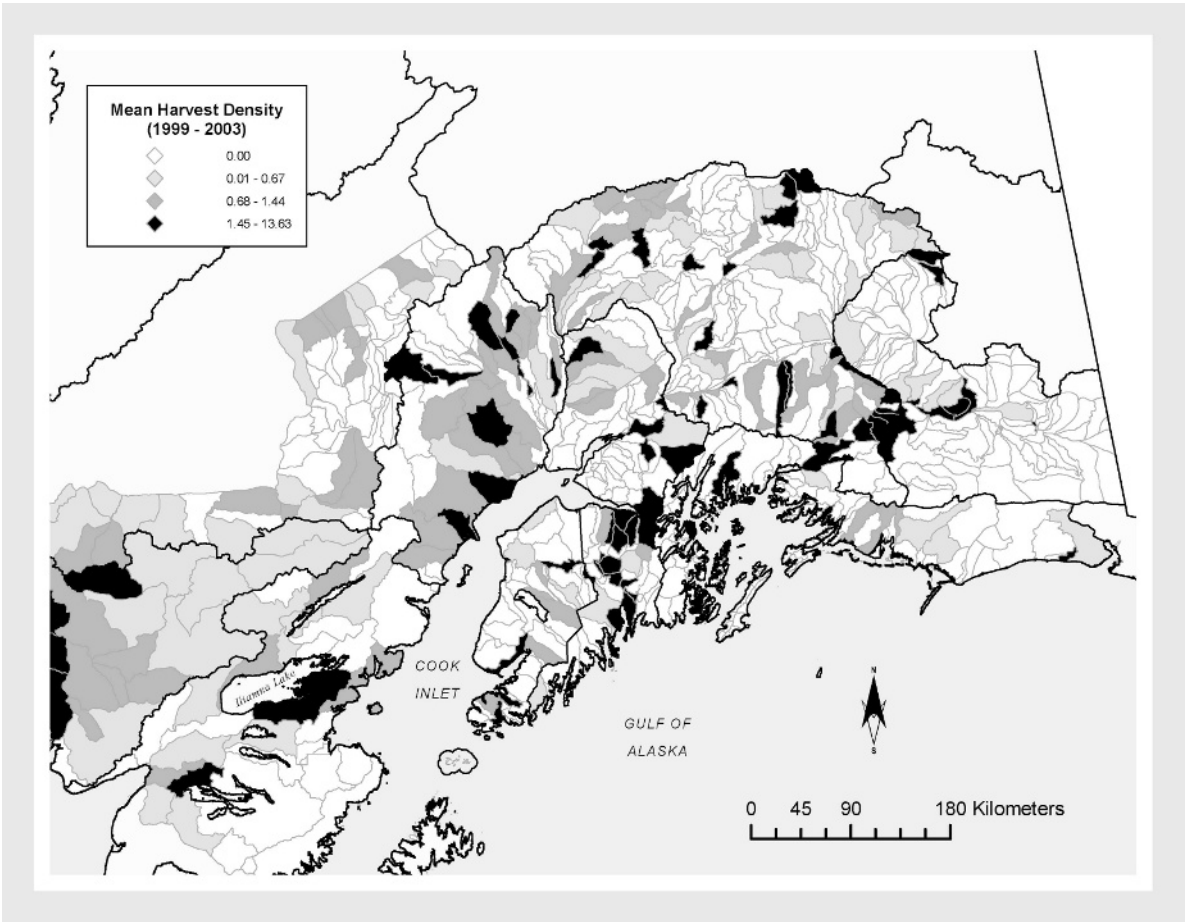

Figure 4. Distribution of wolverine harvest density (wolverines harvested/1,000 km²) by minor drainage in a portion of south-central Alaska averaged over a 5-year period, i.e. 1999-2003. For uniformity, harvest density levels were standardized over the entire 5-year period.

game management subunits in three geographic areas over a 20-year period, i.e. 1984-2003. The areas, which were roughly equivalent in size but with different levels of human activity and access, were 1) the Kenai Peninsula (21,748 km^2), 2) the Nelchina Basin (26,399 km^2), and 3) West Cook Inlet (23,892 km^2; Fig. 2).

Results

Patterns of wolverine harvest during 1984-2003 indicated consistently higher harvest densities (wolverines/1,000 km^2) in the southern portion of Alaska (Fig. 3). The Poisson regression model (goodness of fit: $\chi^2 = 1300$, df = 1288, P = 0.60) estimated mean annual harvest levels (wolverines/1,000 km^2) that were higher in South-central (0.35) than in Arctic/West (0.11; P = 0.009) and Interior (0.19; P = 0.001), but no other regional comparisons were significant (Table 1). Recall results in Table 1 are not the coefficients from the regression, but rather the coefficients back-transformed to the scale of the harvest count. Geographic region, time period and number of harvesters were all significant covariates for describing wolverine harvest (P < 0.001 for each). Arctic/West had a much larger variance that needed to be accounted for in the model; therefore, we allowed for a different variance for this region than for the other regions. Mean harvest density increased by 16% over time in Arctic/West but was fairly stable among the other regions (see Table 1). The effect of successful wolverine harvesters in Southeast was nearly three times the levels found in other regions.

The pattern of wolverine harvest density (wolverines/1,000 km^2) at the minor drainage level averaged over a 5-year period, i.e. 1999-2003, indicated that areas with higher harvest density were well distributed and that areas with light or no reported harvest were common and widespread (Fig. 4). Although many of the minor drainages with higher harvest densities occurred near human population centers and along roadways, there also were many that were not on the road network (see Fig. 2). Human population and roadway infrastructure levels were relatively high for the Kenai Peninsula, moderate for the Nelchina Basin, and low for West Cook Inlet (see Fig. 2).

Trends in annual harvest densities for the Kenai Peninsula, Nelchina Basin and West Cook Inlet were inversely related to trends in percent area with-

out wolverine harvest (Fig. 5). Harvest density reported for the Kenai Peninsula ranged within 0.3-1.5 wolverines/1,000 km^2. The range in percent area without harvest was high and remarkably stable at 73-96%, but the trend seemed loosely related to harvest density. Harvest density for the Nelchina Basin was less variable than for the Kenai Peninsula (range = 0.3-1.2 wolverines/1,000 km^2), but percent area without harvest was similarly high and quite stable at 72-95%. In addition, the trend of each measure in the Nelchina Basin seemed fairly closely related to the other. Harvest density for West Cook Inlet was the most variable of the three areas with a wider range (0.1-1.8 wolverines/1,000 km^2) and relatively dynamic amplitudes.
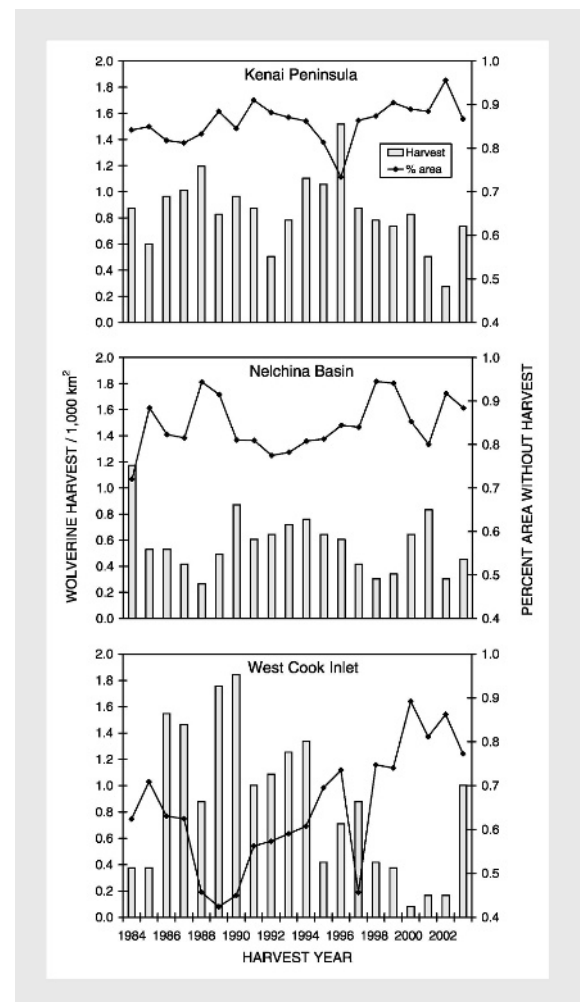

Figure 5. Wolverine harvest density (wolverines harvested/1,000 km^2) and percent area without harvest for the Kenai Peninsula, Nelchina Basin and West Cook Inlet in south-central Alaska during 1984-2003.

The range in percent area without harvest was lower than in the other two areas at 42-89%, but still seemed fairly well related to harvest density. The trend in percent area without harvest seemed to increase as harvest density decreased.

Discussion

Our results indicated that the density of wolverine harvest varied significantly over geographic region, time period and number of harvesters in Alaska. Although time had a greater effect in Arctic/West and harvesters had more effect in Southeast, it was clear that the highest wolverine harvests per unit area occurred in South-central (see Table 1). This was not unexpected considering that more than half of all Alaskans reside within a 100-km radius of Anchorage, the state's largest city. In fact, wolverine harvest densities generally followed human population density patterns among the four regions in the state. The increased effect of time on harvest in Arctic/West likely reflected actual higher harvest because compliance with reporting furbearer harvest in this region has remained fairly constant over time (S. Machida, Alaska Dep. Fish & Game, pers. comm.). The greater effect by successful harvesters in Southeast may have been due largely to the relatively small land area of that region and the concentration of wolverines in certain drainages that were easily accessible to harvesters by boat, road or snowmobile (N. Barten, Alaska Dep. Fish & Game, pers. comm.).

Although lightly versus heavily harvested areas were discernable at the subunit level (see Fig. 3), they were much clearer relative to roads and cities (see Fig. 2) at the minor drainage level (see Fig. 4). Harvest seemed to be concentrated in more specific areas, which left many other areas available as possible refugia. Our results indicated proximity to human population centers or roadways did not necessarily affect harvest densities at a local level. For example, the Kenai Peninsula had most human infrastructure of the three areas, but did not have higher harvest density than West Cook Inlet (see Fig. 5), where access is mainly by aircraft and snowmobile (see Figs. 2 and 4). The Kenai Peninsula also had higher and more consistent levels in percent area without wolverine harvest than West Cook Inlet (see Fig. 5), indicating substantial potential refugia for wolverines there despite human activity levels (see Figs. 2 and 4).

The advantage of areas like West Cook Inlet and the Nelchina Basin is that each is bordered by additional potential refugia that may provide sources for immigration into harvested areas (see Figs. 2 and 4). The Kenai Peninsula must rely on immigration from refugia within its own boundaries or via the isthmus to mainland Alaska (see Fig. 2 and 4). Such restriction was reflected in results of mitochondrial DNA analysis that indicated wolverines on the Kenai Peninsula have lower haplotype and nucleotide diversity than mainland wolverines but not enough to be considered a different subspecies (Tomasik & Cook 2005).

Wolverines, particularly juveniles, may disperse at high rates (as much as 69-100%) depending upon the availability of food and habitat resources (Vangen et al. 2001). Krebs et al. (2004: 500) suggested that "sustained harvest of wolverine populations likely is maintained by dispersal from untrapped refugia". Therefore, when examining harvest patterns, it is important to be able to identify potential refugia. Because this is difficult to do on a statewide or regional level, examination at a finer resolution is necessary.

Considering the relatively low survivorship and reproductive potential of wolverines (Krebs et al. 2004, Persson et al. 2006) and their tendency to disperse at fairly high rates (Vangen et al. 2001), a harvest system incorporating spatial controls may be beneficial (McCullough 1996). Krebs et al. (2004) suggested that for wolverine populations in the northern portion of their range in North America, where populations are continuous and harvest pressure is relatively light, naturally occurring refugia may be able to sustain harvest. However, they also suggested that tighter controls to conserve metapopulations may be needed in the southern extent of their range. Sæther et al. (2005) concluded that the viability of more vulnerable wolverine populations may be put at risk if the necessary restrictive measures are not followed. Magoun & Copeland (1998) suggested a system of spatial control should be used to minimize harvest in wolverine denning areas. Although temporal controls may exist for managing wolverine harvests, systems for monitoring potential refugia for wolverines also may be desirable across their range. This could be particularly important for those areas where harvest pressure and habitat encroachment by humans could limit the future ability of current *de facto* refugia to sustain harvestable populations.

References

Banci, V. 1994: Wolverine. - In: Ruggiero, L.F., Aubrey, K.B., Buskirk, S.W., Lyon, L.J. & Zielinski, W.J. (Eds.); The scientific basis for conserving forest carnivores: American marten, fisher, lynx, and wolverine in the western United States. U.S. Department of Agriculture, Forest Service, Fort Collins, Colorado, USA, pp. 99-127.

COSEWIC 2003: COSEWIC assessment and update status report on the wolverine Gulo gulo in Canada. - Committee on the Status of Endangered Wildlife in Canada, Ottawa, Ontario, Canada, 41 pp.

Fleiss, J.L., Levin, B. & Paik, M.C. 2003: Statistical methods for rates and proportions. 3rd edition. - John Wiley & Sons, Inc, Hoboken, New Jersey, USA, 760 pp.

Krebs, J., Lofroth, E., Copeland, J., Banci, V., Cooley, D., Golden, H., Magoun, A., Mulders, R. & Shults, B. 2004: Synthesis of survival rates and causes of mortality in North American wolverine. - Journal of Wildlife Management 68: 493-502.

Landa, A., Linnell, J.D.C., Lindén, M., Swenson, J.E., Røskaft, E. & Moksnes, A. 2000: Conservation of Scandinavian wolverines in ecological and political landscapes. - In: Griffiths, H.I. (Ed.); Mustelids in a modern world -management and conservation aspects of small carnivore: human interactions. Backhuys Publishers, Leiden, The Netherlands, pp. 1-20.

Magoun, A.J. & Copeland, J.P. 1998: Characteristics of wolverine reproductive sites. - Journal of Wildlife Management 62: 1313-1320.

McCullough, D.R. 1996: Spatially structured populations and harvest theory. - Journal of Wildlife Management 60: 1-9.

Persson, J., Landa, A., Andersen, R. & Segerström, P. 2006: Reproductive characteristics of female wolverines (Gulo gulo) in Scandinavia. - Journal of Mammalogy 87: 75-79.

Sæther, B-E., Engen, S., Persson, J., Brøseth, H., Landa, A. & Willebrand, T. 2005: Management strategies for the wolverine in Scandinavia. - Journal of Wildlife Management 69: 1001-1014.

Tomasik, E. & Cook, J.A. 2005: Mitochondrial phylogeography and conservation genetics of wolverine (Gulo gulo) of northwestern North America. - Journal of Mammalogy 86: 386-396.

Vangen, K.M., Persson, J., Landa, A., Andersen, R. & Segerström, P. 2001: Characteristics of dispersal in wolverines. - Canadian Journal of Zoology 79: 1641-1649.