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Low densities and wide-ranging behaviour make wolverines *Gulo gulo* difficult to monitor. We used quadrat sampling of tracks in snow to estimate wolverine populations. We conducted aerial surveys in upper Turnagain Arm and the Kenai Mountains (TAKM) in south-central Alaska and in Old Crow Flats (OCF) in northern Yukon during March 2004 following procedures for the sample-unit probability estimator (SUPE). This technique uses network sampling of tracks in snow in a stratified random system of quadrats or sample units. In TAKM, we sampled 87 (51%) out of 171 quadrats within a survey area of 4,340 km$^2$. The estimated density was 3.0 ($\pm$ 0.4 SE) wolverines/1,000 km$^2$ with a coefficient of variation (CV) of 12.0%. In OCF, we sampled 96 (71%) out of 135 quadrats within a survey area of 3,375 km$^2$. The estimated density was 9.7 ($\pm$ 0.6 SE) wolverines/1,000 km$^2$ with a CV of 6.5%. Our results indicated that the SUPE technique is an efficient method of obtaining precise estimates of wolverine population size under markedly different environmental conditions and population densities. We suggest that, where practical, it may be a less labour-intensive and more cost-effective technique for estimating wolverine abundance compared with techniques that do not use probability sampling of tracks.

Key words: Alaska, *Gulo gulo*, population estimation, sample-unit probability estimator, snow tracking, wolverine, Yukon
Wolverine *Gulo gulo* populations are difficult to monitor. They have low reproductive potential and usually occur at low densities relative to other furbearer species. The wolverine functions as a scavenger and predator throughout its circumboreal range, and it is considered a wilderness species and potential indicator of ecosystem health (Carroll et al. 2001). Wolverines are important to humans because of their valuable fur (Hash 1987), livestock depredation (Landa et al. 1999, Landa et al. 2000), and endangered species status over parts of their geographic range (COSEWIC 2003). These factors increase the potential sensitivity of wolverines to human use and disturbance and emphasize the need to monitor their population status (Banci et al. 2000). However, few techniques exist for estimating population abundance or trend.

Hornocker & Hash (1981), Magoun (1985) and Copeland (1996) estimated the abundance of wolverines in their study areas by monitoring the movements and calculating home-range sizes of radiocollared animals. Landa et al. (1998) monitored natal dens to estimate minimum population sizes, which required additional knowledge about sex ratio, age structure and proportion of breeding females. The above techniques can provide mean population estimates over one to several years, but their effectiveness may be limited when the survey area is large, available time and funds are restricted, and a measure of precision is desired.

An alternative technique for estimating population size is probability sampling of animal tracks in snow. Becker (1991) developed a technique for wolverines and wolves *Canis lupus* based on transect intercept probability sampling (TIPS), a line-intercept method in which systematically-arrayed linear transects of equal length are randomly selected. The linear transects are used to intercept and follow the entire length of an individual animal’s track-trail. Several assumptions regarding track deposition, sightability, and enumeration of individual animals must be met (Becker 1991). Aerial versions of this survey technique were used in two areas of south-central Alaska and resulted in density estimates of 4.7-5.2 wolverines/1,000 km² with coefficients of variation (CV) ranging within 13-20% (Becker 1991, Becker & Gardner 1992). Some problems in using the TIPS were: 1) meeting the assumption that all tracks present would be observed, especially in heavier canopy covers; 2) being able to maintain an accurate flight line in steep terrain; 3) completing the survey during a very short time frame considering the TIPS was designed to be completed in one day; and 4) CVs tended to be somewhat high, which limited the precision of the estimates (Becker et al. 2004).

To better meet survey assumptions and increase precision of the estimates while snow tracking, Becker et al. (1998) developed the sample-unit probability estimator (SUPE). This technique, initially designed for wolves, uses network sampling of tracks in snow in a stratified random system of quadrats or sample units. Although CVs from SUPE surveys of wolves conducted in several areas of Alaska and Canada ranged within 6.7-25%, most were under 15% and the surveys were easier to complete under more difficult conditions and across larger areas. SUPE surveys may also be conducted over more than one day because they are effective in handling partial surveys with incomplete snowfall (Becker et al. 2004). A major advantage of the SUPE is that it allows the pilot-observer team flexibility in how they survey a particular quad. For example, they can fly straight lines to cover a sample unit if the canopy cover is light but they can also fly in overlapping circles if canopy cover is relatively heavy. This ability increases the potential sightability of tracks, whether it is due to canopy cover or lighting conditions.

Recently, Becker et al. (2004) tested the hypothesis through simulation modeling that the TIPS would be a more precise estimator of wolverine populations than the SUPE. Simulations supported their hypothesis given the same budgetary constraints and sampling effort as used in the original TIPS survey. However, further simulations where sampling effort was increased to the level recommended for SUPE surveys indicated that the SUPE would be 24% more efficient (i.e. the CV was 24% lower) compared with an equivalent effort in the TIPS design. Becker et al. (2004) further suggested that the SUPE would be a more flexible technique in dealing with weather, flying in mountainous terrain, and variable canopy cover and track sightability issues.

Because of the apparent advantages of the SUPE, it was necessary to evaluate its ability to estimate wolverine populations under field conditions. We conducted SUPEs on wolverines in two contrasting areas: 1) a forested, mountainous peninsula in south-central Alaska and 2) a subarctic region of rolling hills and wetlands in northern Yukon. In this paper, we report the results of our evaluation of the SUPE technique in estimating wolverine populations.
Material and methods

Study areas
We surveyed wolverines in a 4,340-km$^2$ area of upper Turnagain Arm and northwestern Kenai Mountains (TAKM) in south-central Alaska and in a 3,375-km$^2$ area of the Old Crow Flats (OCF) in northern Yukon (Fig. 1). TAKM is located south of Anchorage and east of Cook Inlet on the northern edge of the Gulf of Alaska (60°30’N, 149°30’W). Turnagain Arm is an east-west fjord that separates the Kenai Peninsula from mainland Alaska. The OCF study area is contained within the Old Crow Basin in northern Yukon and is adjacent to the Alaska-Canada border (68°N, 140°W).

TAKM is characterized by steep, rugged mountains dissected by deep valleys and interspersed with glaciers and ice fields. Elevations range from sea level to 1990 m a.s.l. The northern maritime climate produces moderate temperatures and occasional mid-winter thaws. Coniferous and deciduous forests with light to moderately-heavy canopy cover dominate valley bottoms and alpine tundra covers most higher elevations (Viereck & Little 1972). Food sources for wolverines are abundant in the form of large ungulate carrion and smaller mammals and birds. The area is adjacent to two large urban centers and several smaller towns connected by two major highways, but much of the area is roadless and only accessible via hiking and cross-country ski trails, off-road vehicles, snowmachines, and light aircraft. Wolverines are harvested under hunting and trapping regulations administered by the Alaska Department of Fish and Game and several federal agencies.

Figure 1. Locations of the SUPE survey areas in Turnagain Arm/Kenai Mountains in south-central Alaska and the Old Crow Flats in northern Yukon, March 2004.
In OCF, the terrain drops gently from the surrounding mountain ranges into the Old Crow Flats. Higher elevations are 300-600 m a.s.l. and lowland areas mostly < 400 m a.s.l. OCF has a subarctic, continental climate characterized by long, cold winters with generally dry, loose snow conditions. Lowland vegetation is dominated by coniferous and deciduous forests with light to moderate canopy cover and upland vegetation consists mainly of tundra shrubs and grasses (Gray & Alt 2000). Important winter food resources for wolverines in OCF are caribou Rangifer tarandus carrion and small mammals and birds (Henry 2004). The nearest human population center is Old Crow, located 50-80 km south of OCF, and its 300 residents are predominantly members of the Vuntut Gwitchin First Nation (VGFN). OCF is a remote roadless area, accessible only by aircraft, by boat on the Old Crow River and its tributaries during early summer, or by snowmachines during the winter. Furbearers are harvested from a light to a moderate degree, and trapping activities are regulated by both the VGFN Government and the Yukon Territorial Government.

Survey design
We designed surveys in TAKM and OCF following the recommended procedures for conducting a SUPE (Becker et al. 2004). That is, for each survey area we first established a network of quadrats that were systematically spaced rectangles approximately 25 km² in size (see Fig. 1). This network was a single contiguous area in TAKM, but, due to incomplete map coverage for OCF, the network of quadrats had to be arranged in four large blocks. We labeled each quadrat, or sample unit (SU), with an alphanumeric code for identification. We then used past knowledge of abundance, habitat use, harvest patterns and distribution of wolverines and their prey to stratify SUs according to their relative likelihood of containing wolverine tracks. The purpose of the stratification was to allow proportionately more sampling effort in higher strata and less effort in lower strata, thereby improving the precision of the estimate. We divided each area into high and medium-low strata and used a simple random sample without replacement to select SUs to survey. We followed the sampling fractions recommended by Becker et al. (1998), which were based on wolf estimates, of at least 60% for the high stratum and 16-35% for the medium-low stratum.

The SUPE design requires meeting the following eight assumptions, listed by Becker et al. (1998: 969): "(1) all animals of interest move during the course of the study; (2) their tracks are readily recognizable from a small, low-flying aircraft; (3) tracks are continuous; (4) movements are independent of the sampling process; (5) pre- and post-snowstorm tracks can be distinguished; (6) post-snowstorm tracks in the searched sample units (SUs) are not missed; (7) post-snowstorm tracks found in selected SUs can be followed (forward and backward) to determine, without error, all SUs containing those tracks; and (8) group size is correctly enumerated." If a study area is too large to be surveyed in one day, two additional assumptions are required: "(1) animals do not move from unsampled to sampled areas and they leave no fresh tracks in the unsampled areas; and (2) no animals are double counted by moving from sampled to unsampled areas" (Becker et al. 1998: 969).

To help meet these assumptions, Becker et al. (2004) recommended starting wolverine surveys within 12-24 hours after a snowstorm and to try to complete the survey within 2-3 days. This time frame allows fresh tracks to accumulate but limits the amount of time for wolverines to circle back to a hole or den site, where multiple tracks may be confused for more than one wolverine. In cases of confusion, a track trail must be treated as belonging to a single individual. Weather conditions may sometimes require a break of several days between surveys of a particular area. Should this happen, the survey after the break still must follow a fresh snowfall within the above time frame. Teams must make sure they count only fresh tracks, distinguishable from old tracks (which may linger in forested areas) by their lack of sharp, crisp edges, and more diffuse appearance (Becker et al. 2004).

It is essential for successful surveys that at least one member of each pilot-observer team be not only an experienced aerial observer but also very skilled in track identification. One advantage of following tracks forward and backward is that it usually becomes apparent quickly whether or not a particular track was actually made by a wolverine. However, even experienced observers may not be able to make a positive species identification from the air. In this case, either the team must land to examine the track more closely or it must not be counted in the survey.
**Sampling procedures**

We flew the surveys with Super Cub (The New Piper Aircraft, Inc., Vero Beach, FL) or similar aircraft because of their ability for low-level, maneuverable flight. We conducted surveys in March 2004, which was the first opportunity of that winter in both TAKM and OCF when snow and light conditions were suitable and the pilot-observer teams were available. Survey conditions were good in both areas. Snow depths were sufficient to cover low shrubs completely and there were fresh snowfalls of several cm 1-2 days before surveys commenced with clear skies and light wind during surveys. We surveyed selected sample units in TAKM on 6 and 17 March 2004, using five pilot-observer teams on the first day and two teams on the second day for a total flight time of 32.5 hours. We flew the OCF survey on 16-18 and 21-22 March 2004, using two pilot-observer teams during the first period and one team during the second period for a total flight time of 55 hours. Poor snow or flying conditions prevented us from completing the surveys in either area on consecutive days and the sizes of both areas required more than one day to conduct the surveys.

To ensure no wolverines were missed or double counted between survey days, we flew SUs as a contiguous block each day with no gaps in our coverage. We began each survey period within 24 hours after fresh snowfalls had ended. Each team was assigned 10-15 SUs to survey in a day. Teams were spaced out and kept in close radio communication for safety. Aircraft flew 90-130 km/hour at altitudes of 35-150 m above ground level as we searched for tracks along ridges, hillsides, and valley bottoms. We searched all portions of a selected SU until we were confident no fresh wolverine tracks were missed and that the model assumptions were met. Survey time per SU was 5-20 minutes depending upon sightability conditions (e.g. density of vegetation, canopy cover and lighting) and topography. We documented snow age (days) and condition, light quality and habitat type. We also assigned a general rating for overall survey conditions, which could range from poor to excellent.

Once a fresh track or track-trail was found, we followed it forward to its end and attempted to enumerate the number of wolverines from direct observation or from the number of separate tracks in a trail. We then backtracked the trail to its beginning, which may have been a resting hole or den site or where it was obscured from the last snowfall. We recorded Global Positioning System (GPS) coordinates of the beginning and ending points of the tracks and carefully recorded the entire track line to determine the selected SU where the track was first found and all other quadrats it passed through. This mapping effort helped ensure that tracks identified from a previous day’s survey, which crossed into the new day’s survey area, were not recorded again. We observed the rule that if a track went outside the boundary of the survey area we followed it to its end to determine the proportion of the track within the study area (Becker et al. 2004). This proportion was then used to calculate the proportion of the track group size (i.e. number of wolverines) to be used in the total population estimate for the survey area. Because we followed this boundary rule, the arrangement of sample units in OCF into four large blocks was not a problem in estimating abundance for the entire survey area.

**Data analysis**

We used data pooled from each survey day in the program SUPEPOP, which is available at ftp://ftp3.adfg.state.ak.us/MISC/PROGRAMS/SUPEPOP/, to calculate the population size for the area. This site also contains detailed descriptions of the program, population estimation procedures, data entry protocol, and results output. Calculations used in SUPEPOP were based on formulas presented in Becker et al. (1998). SUPEPOP uses the number of independent track groups observed in each stratum, the number of sample units each track group passes through, and the original sampling fraction of quadrats per stratum to estimate a population size and variance for each survey area. Population estimates (± SE) were generated with confidence intervals (CI) at the 80 and 90% levels, which we viewed as reasonable levels of precision for wolverine population estimates. We also calculated density estimates and CVs, which indicated survey efficiency.

**Results**

Snow, weather and lighting conditions ranged from fair to excellent on all survey days in TAKM and OCF. No teams reported problems finding or following tracks, except one track in TAKM that had been obscured by wind and could not be backtracked. It was excluded from the analysis because it was likely an old track prior to the most recent
snowfall. None of the teams for either survey area reported finding wolverine tracks that appeared to have moved from a sample unit that had already been surveyed to an adjacent SU that was surveyed the following day.

In TAKM we sampled 87 (51%) out of 171 quadrats within the 4,340-km² survey area at sampling fractions of 66% in the high stratum and 32% in the medium-low stratum (Fig. 2, Table 1). Average flight time spent per selected SU surveyed was 22 minutes. We observed 11 individual wolverine tracks among 10 track groups (see Fig. 2). Track groups remained within the boundaries of the survey area and were found at all elevational levels in

Table 1. Sample unit distribution and sample effort allocation for SUPE surveys of wolverines in upper Turnagain Arm/Kenai Mountains (TAKM) in south-central Alaska and Old Crow Flats (OCF) in northern Yukon, March 2004.

<table>
<thead>
<tr>
<th>Area &amp; Strata</th>
<th>Total quadrats</th>
<th>Sample units</th>
<th>Sampling %</th>
</tr>
</thead>
<tbody>
<tr>
<td>TAKM</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>High</td>
<td>94</td>
<td>62</td>
<td>66</td>
</tr>
<tr>
<td>Medium-low</td>
<td>77</td>
<td>25</td>
<td>32</td>
</tr>
<tr>
<td>Total</td>
<td>171</td>
<td>87</td>
<td>51</td>
</tr>
<tr>
<td>OCF</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>High</td>
<td>114</td>
<td>82</td>
<td>72</td>
</tr>
<tr>
<td>Medium-low</td>
<td>21</td>
<td>14</td>
<td>67</td>
</tr>
<tr>
<td>Total</td>
<td>135</td>
<td>96</td>
<td>71</td>
</tr>
</tbody>
</table>
both forested and tundra habitat types. The estimated population size within the survey area was 12.8 (± 1.5) wolverines with lower and upper 80% (± 16.6%) CIs of 11.0 and 14.9, respectively (Table 2). For the lower CI, we used the number of wolverines actually observed because it was higher than the calculated value of 10.7. The estimated density for the survey area was 3.0 (± 0.4) wolverines/1,000 km² (see Table 2). The CV for the estimates was 12.0%.

In OCF, we sampled 96 (71%) out of 135 quadrats within the 3,375-km² survey area at sampling fractions of 72% in the high stratum and 67% in the medium-low stratum (Fig. 3, see Table 1). Average flight time spent per selected SU surveyed was 34 minutes. We observed 31 wolverine track groups

<table>
<thead>
<tr>
<th>Area &amp; Parameter</th>
<th>Estimate</th>
<th>SE</th>
<th>80% CI</th>
<th>+/-%</th>
<th>90% CI</th>
<th>+/-%</th>
</tr>
</thead>
<tbody>
<tr>
<td>TAKM Population size</td>
<td>12.8</td>
<td>1.5</td>
<td>11.0-14.9</td>
<td>16.6</td>
<td>11.0-15.6</td>
<td>22.1</td>
</tr>
<tr>
<td>Density</td>
<td>3.0</td>
<td>0.4</td>
<td>2.5-3.4</td>
<td>16.6</td>
<td>2.5-3.6</td>
<td>22.1</td>
</tr>
<tr>
<td>OCF Population size</td>
<td>32.9</td>
<td>2.1</td>
<td>30.1-35.7</td>
<td>8.5</td>
<td>29.2-36.5</td>
<td>11.0</td>
</tr>
<tr>
<td>Density</td>
<td>9.7</td>
<td>0.6</td>
<td>8.9-10.6</td>
<td>8.5</td>
<td>8.7-11.0</td>
<td>11.0</td>
</tr>
</tbody>
</table>

Figure 3. Distribution of high and medium-low strata, sample units surveyed, and wolverine track groups observed for the SUPE in Old Crow Flats in northern Yukon, March 2004.
that were all of single animals. Eight of those track groups were partially outside the survey area boundaries, consequently the remaining proportion inside equated to 28.7 wolverines (see Fig. 3). Most of the tracks were found in the forested drainages. The estimated population size within the survey area was 32.9 (± 2.1) wolverines with lower and upper 80% (± 8.5%) CIs of 30.1 and 35.7, respectively (see Table 2). The estimated density for the survey area was 9.7 (± 0.6) wolverines/1,000 km² (see Table 2). The CV for the estimates was 6.5%.

Discussion

Despite the 3-fold difference in estimated density between TAKM and OCF, the CVs of 12 and 6.5%, respectively, are the lowest reported for wolverines. The next lowest was the CV of 13% reported by Becker & Gardner (1992) for a wolverine estimate derived with the TIPS technique. Becker et al. (2004) suggested the goal should be CVs of ≤ 10%. The TAKM estimate of 3.0 wolverines/1,000 km² was relatively low compared with TIPS estimates of 4.7 and 5.2 wolverines/1,000 km² reported for other areas of south-central Alaska (Becker 1991, Becker & Gardner 1992). In contrast, the OCF estimate of 9.7 wolverines/1,000 km² was the highest reported estimate based on either TIPS or SUPE surveys. Other estimates of wolverine density (wolverines/1,000 km²) based on long-term radio-telemetry estimators were 15 in northwest Montana (Hornocker & Hash 1981), 7-21 in arctic Alaska (Magoun 1985), 5.6 in southern Yukon (Banci 1987), and 4-5 in central Idaho (Copeland 1996).

Probability sampling provides a scientifically robust population estimate but only for a short period of time and for the particular area surveyed. For example, all estimates of wolverine abundance using the SUPE or TIPS methods, including TAKM and OCF, were conducted in areas open to wolverine harvest and followed the hunting and trapping seasons when population sizes would likely be at their lowest annual level. In addition, these surveys were not designed to consider the potential influence of animal movement from adjacent areas. Each survey result should be considered a point estimate or ‘snapshot’ and, therefore, appropriate care should be taken in making temporal or spatial comparisons.

The relatively low estimate of wolverines in TAKM may be due in part to the sampling effort used there. In TAKM, we achieved the recommended sampling fraction at 66% for the high stratum and 32% for the medium-low stratum (see Table 1). Although OCF was slightly smaller than TAKM, we knew less about wolverine distribution and, therefore, sampled more heavily at 72% for the high stratum and 67% for the medium-low stratum (see Table 1). Based on CVs of our surveys, it appears we slightly undersampled quadrats in TAKM and probably sampled more than necessary in OCF. Most of the variance in the estimates for both areas was due to observations of individual wolverine tracks in only single SUs in the high strata.

Using simulations in SUPEPOP, we tested the effects of modifying sampling effort in TAKM while maintaining the original wolverine observations. Our simulations indicated that an increase in sampling fraction effort from 66 to 70% in the high stratum and from 32 to 50% in the medium-low stratum would lead to a 10% increase in overall sample effort that would reduce the CV by 2%.

Our results indicated that modifying sampling fractions could increase the efficiency of future surveys without a substantial increase in effort or cost. In addition, increasing sampling fractions to higher levels than recommended by Becker et al. (2004) could result in very precise estimates and provide valuable baseline data on wolverine populations. Based on these results, we recommend sampling fractions for wolverine SUPE surveys of 65-70% of SU's in high strata and 45-50% in medium-low strata. Restratiﬁng areas for future surveys probably would be beneﬁcial as well. Some portions of TAKM that we stratified as high, such as the northwest quarter of the area, actually contained relatively few track groups. In OCF, we found that most of the wolverine track groups were within the drainages.

As suggested by simulations conducted by Becker et al. (2004), these SUPE surveys were efficient in obtaining precise estimates of wolverine population size under markedly different environmental conditions and population densities. TAKM was challenging to fly because of its rugged terrain, the extra time required to search for tracks in the sometimes dense canopy cover, and the often stormy weather typical of the Kenai Peninsula in late winter. OCF, on the other hand, had nearly ideal survey conditions with relatively gentle terrain, light canopy cover, and mild weather. Aerial surveys required approximately 50% more time to
complete in OCF (34 minutes/SU) than in TAKM (22 minutes/SU) but about half as much survey time per wolverine group found (106 vs 195 minutes). This was probably a function mainly of the sampling efforts used and densities observed, which required more time for following tracks in OCF.

The SUPE design allows observers to evaluate fairly effectively how well the assumptions are being met while conducting the survey. If proper care is taken in survey sampling, it is usually apparent if one or more of the assumptions is being violated. We detected no violation of the 10 assumptions employed in our surveys with the possible exception of one: that "all animals of interest move during the course of the study" (Becker et al. 1998: 969). Our first opportunity to conduct surveys was in March, due in part to the suitability of snow and light conditions which are often most favourable in Alaska and northern Canada in late winter. However, the peak of parturition for reproductively active females occurs from mid-February through March in Alaska and Yukon (Rausch & Pearson 1972). Consequently, some adult females may not have been active outside their dens between the end of snowfall and the start of our aerial surveys. This would have made them unavailable for sampling and bias our estimate downward. However, parturient females often move among multiple dens and continue to forage long distances with denning young (Magoun 1985, Magoun & Copeland 1998). Testing the accuracy of the SUPE design, using radio-marked wolverines or double-sampling, may provide suitable correction factors if more accurate estimates of population size are needed or if comparisons of SUPE estimates between early winter and late winter are desired.

An advantage of probability sampling as used in the SUPE technique is its scientific design, which is repeatable and provides an estimate with a measure of precision. A disadvantage is that to be effective across large areas SUPE surveys must be aerially based. This can be costly and may be limited by poor sightability conditions, such as thick forest canopy cover, or by other environmental factors like snow conditions, weather and lighting. We have found that pilot or observer availability can sometimes be the most important limiting factor in conducting the surveys. These and other factors need to be assessed carefully for each survey to meet the assumptions of the sample design (Becker et al. 1998, Becker et al. 2004). From our experiences, we suggest that where practical the SUPE design may be a less labour-intensive and more cost-effective technique for estimating wolverine abundance compared with techniques that do not use probability sampling of tracks.

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