A POPULATION ESTIMATOR BASED ON NETWORK SAMPLING OF TRACKS IN THE SNOW

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Abstract: We developed a technique to use stratified network sampling to sample animal tracks in the snow and to obtain to population estimates. This method requires sufficient snow conditions to allow animals to leave continuous tracks and a recent snowstorm or windstorm for delineation of fresh (poststorm) tracks. Additional requirements are that no fresh tracks in aerially surveyed sample units are completely missed, that these tracks can be followed to identify all sample units containing them, and size of the group that made these tracks can be correctly enumerated. Using this technique, we estimated gray wolf (*Canis lupus*) population density to be 8.16 ± 0.91 wolves/1,000 km^2 in a 31,373-km^2 game management unit in Interior Alaska. This sample design also allowed us to obtain population estimates and confidence intervals for those portions of the Koyukuk and northern Innoko national wildlife refuges (NWR) within the study area. Using concurrently collected radiotelemetry on 9 wolf packs, we did not detect any violations of assumptions.

JOURNAL OF WILDLIFE MANAGEMENT 62(3):968–977

Key words: aerial survey, *Canis lupus,* furbearer, gray wolf, large scale, network sampling, population estimation, probability sampling, snow, tracks.

Estimates of population size for terrestrial species that are secretive and occur at low densities (i.e., lynx [*Felis lynx*], wolverine [*Gulo gulo*], mountain lions [*Felis concolor*], and wolves) are difficult to obtain. Population enumeration of large predators such as wolves and mountain lions has become important to the understanding and management of predator–ungulate systems (Hornocker 1970, Gasaway et al. 1983, Ballard et al. 1987, Gasaway et al. 1992, Lindzey et al. 1994). Likewise, concern about habitat loss and exploitation rates of large furbearers such as lynx and wolverine has increased the need for accurate population estimates (Van Zyll de Jong 1975, Magoun 1985, Bailey et al. 1986, Whitman et al. 1986, Poole 1994)

Previous efforts to estimate population size for these species include mark–resight estimators (Hein and Andelt 1995), howling responses (Harrington and Mech 1982), counts of wolf packs (Mech 1966, Peterson 1977, Stephenson 1978, Gasaway et al. 1983), home range density (Mech 1973, Fuller 1982, Mech 1982, Peterson et al. 1984, Ballard et al. 1987, Fuller and Snow 1988, Fuller 1989), animal counts (Babb and Kennedy 1989), and model-based estimates (Fuller et al. 1992). Hayashi (1980) presented an estimator modeled after the Buffon needle problem, which assumes the probability of observing an animal's track in the snow is constant. Reid et al. (1987) used counts of river otter (*Lutra canadensis*) tracks in the snow to obtain population estimates. Transect–intercept-probability sampling (TIPS) of animal tracks in the snow (Becker 1991) has been used to estimate population size of wolves (Becker and Gardner 1990, Carroll 1994, Ballard et al. 1995), wolverines (Becker 1991, Becker and Gardner 1992), and mountain lions (Van Sickle and Lindzey 1991).

Except for estimates of wolf population size (Stephenson 1978, Gasaway et al. 1983, Ballard et al. 1987, Fuller et al. 1992, Carroll 1994), the above population estimates are for medium-sized study areas (approx 5,000 km^2; Peterson et al. 1984, Becker and Gardner 1992, Van Sickle and Lindzey 1991) or small study areas (<5,000 km^2; Babb and Kennedy 1989, Hein and Andelt 1995). Otis (1994) identified the need for population estimators for large-scale areas. He also noted that estimation techniques break down when populations are scarce, and that additional problems arise if the distribution patterns are fragmented, movements are dynamic, or both. Ballard et al. (1987) calculated

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gray wolf home range size and average pack size to obtain a wolf population estimate within a 7,262-km^2 study area. Gasaway et al. (1983) estimated wolf population size for a 15,300-km^2 area by counting all wolves, counting wolf tracks after a snowfall, or both. Neither of these wolf estimators can quantify the amount of uncertainty associated with the estimate, and use of radiocollared animals can be too expensive for routine population assessment. Fuller et al. (1992) used a modeling approach based on reported wolf range, average density of wolf packs, average size of wolf packs, an assumption of the percentage of single wolves, and an estimate of the prey base to obtain an estimate of wolf population size in a 53,100-km^2 area of northern Minnesota. This approach did not account for all the variation associated with the estimate, because variance of some parameters could not be obtained. Carroll (1994) used the TIPS estimator to obtain a fairly precise estimate (CV = 15.7%) of wolf population size in a 10,378-km^2 area in Arctic Alaska. Other wolf estimates using the TIPS estimator were for smaller areas (approx 5,000-km^2) and were less precise (CV = 24–80%; Becker and Gardner 1990, Ballard et al. 1995).

METHODS

Proposed Technique

In moderate to large areas, we propose using the probability of observing an animal track in the snow to obtain precise population estimates of low-density species whose tracks can be observed and followed from a small, low-flying airplane. These species include medium to large Felidae, large Mustelidae, Canidae, and other medium or large animals that occur at low density. To obtain our population estimate, we used a stratified, network sample design (Thompson 1992), which is a special form of probability sampling (Horvitz and Thompson 1952).

Assumptions.—The probability estimator used in the stratified-network sample design requires (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 postsnowstorm tracks can be distinguished; (6) postsnowstorm tracks in searched sample units (SUs) are not missed; (7) postsnowstorm tracks found in selected SUs can be followed (forwards and backwards) to determine, without error, all SUs containing those tracks; and (8) group size is correctly enumerated. Large study areas usually require several days to sample. Hence, to obtain an unbiased estimator in these instances, we assumed (1) animals did not move from unsampled to sampled areas wherein they left no fresh tracks in the unsampled areas, and (2) no animals are double-counted by moving from sampled to unsampled areas. If drifting snow or patchy, hard snow preclude continuous tracks, an unbiased estimate can be obtained if a 1-to-1 correspondence can be established between the track segments and the animals of interest that made them (Becker 1991).

Sample Design.—To implement the sample design, the study area must be partitioned into SUs, and the SUs are uniquely and exhaustively grouped into strata denoting the relative likelihood of observing a fresh track of the target species 24–36 hr after a snowstorm. The stratification is based upon knowledge of harvest patterns, abundance, and distribution of the target species, along with the location and abundance of its prey base. For example, in a 3-strata design, the high-stratum SUs are those in which observers regularly expect to see tracks of the target species, the low-stratum SUs are those in which it would be uncommon to see their tracks, and medium-stratum SUs are those with an intermediate track intensity. A simple random sample, without replacement, of SUs from each strata is selected for survey from a small, low-flying airplane with a pilot and biologist team experienced in tracking the target species.

The number of groups encountered in searched SUs determines the amount of information upon which the estimate is based. Size of study area and sampling intensity should be large enough to ensure ≥8 groups are encountered by the sample design. For example, assuming 3 strata are used, we recommend sampling intensities among the high, medium, and low strata of (1) 66, 40, and 20% when 8 groups are expected to be encountered; (2) 63, 37, and 18% when 18 groups are expected; and (3) 60, 35, and 16% when 28 groups are expected.

Observers use aircraft to search selected SUs for fresh tracks of the target species, usually starting 24 hr after a snowstorm. Fresh tracks are defined as tracks made since the last snowfall and new enough to follow by aircraft (usually <4 days old). Search intensity will depend upon overstory, lighting conditions, and amount of track deposition from other animals, but intensity should be sufficient to ensure meeting model assumptions. Sampling efficiency can be increased by sampling groups of selected and adjacent SUs as 1 large unit; the flight line may even overfly 1 or 2 nonselected SUs. Only animals whose tracks were observed in the selected SUs are included in the estimator.

The SU is usually a square between 1.4 and 41.4 km^2. The size of the SU depends upon the amount of information available for stratification, weighed with the fact search efficiency increases with a larger SU because of less time spent per area determining SU boundaries. Study area size will be limited by the ability to obtain good survey conditions over the entire region, and the ability to complete the sample design within a weather window that allows the sample design assumptions to be met.

When fresh tracks of the target species are found in a selected SU, they are backtracked to the point where they are no longer considered fresh, and then tracked forward to the animal(s). The number of individuals in the group (from the target species), the sample units that their fresh tracks intersected, the direction of travel, and distinguishing features about the individuals are recorded (e.g., pelt colors for wolves). If more than half of the track is out of the study area, the observation is not used in the estimate (population membership rule). If >1 group of fresh tracks intersect a SU, data should be recorded separately if the pilot–biologist team can separate the 2 groups along their entire set of tracks; otherwise they should treat them as 1 group. Once tracking has been completed, the remainder of the selected SUs should be searched for additional tracks.

Surveys of large study areas should start at 1 location, preferably a corner, and work outward in a concentrated manner to complete a contiguous portion of the selected SUs within the study area. Sampling in this concentrated, expanding manner will help meet assumptions about not missing or double-counting animal(s) and will also allow an estimate of the completed portion of the study area to be obtained if poor weather conditions cause the premature discontinuation of the survey. New tracks that seem to originate from previously surveyed areas should be carefully investigated to ensure animals are not being double-counted. If weather conditions have caused a ≥1-day break in the survey, older tracks of the target species that are traveling from nonsampled SUs into previously sampled areas should be followed to determine if these animals are moving from unsampled to sampled areas wherein they have no probability of being included in the estimate.

The following notation is used: T_y is the population total, u and v index the animal group observations, y_u is the group size for the uth group, r is the number of groups whose tracks were in selected SUs, p_u is the inclusion probability (the probability that fresh tracks from the uth group are observed with this sample design), and p_{uv} is the joint inclusion probability (the probability that both the uth and vth animal groups are observed in this sample design). Based on results of standard probability sampling (Horvitz and Thompson 1952, Thompson 1992), the population estimate and variance are as follows:

$$\hat{T}_y = \sum_{u=1}^{r} \frac{y_u}{p_u}, \quad \text{and} \tag{1}$$

$$\hat{V}(\hat{T}_y) = \sum_{u=1}^{r} \frac{(1 - p_u)}{p_u^2} y_u^2 + 2 \sum_{u=1}^{r} \sum_{v=u+1}^{r} \left(\frac{1}{p_u p_v} - \frac{1}{p_{uv}} \right) y_u y_v. \tag{2}$$

In probability sampling, an observation (y_u) is weighted by the inverse of the inclusion probability ($1/p_u$), which, given equal group size, results in "unlikely" observations having a larger contribution to the population estimate than common observations.

Based on network sampling results, the inclusion probabilities are calculated as follows from (Thompson 1992):

$$p_u = 1 - \prod_{h=1}^{H} \binom{M_h - m_{hu}}{n_h} \bigg/ \binom{M_h}{n_h}, \quad \text{and} \tag{3}$$

$$p_{uv} = p_u + p_v - 1 + \prod_{h=1}^{H} \binom{M_h - m_{hu} - m_{hv} + m_{huv}}{n_h} \bigg/ \binom{M_h}{n_h}. \tag{4}$$

In these equations, Π denotes the multiplication operator, h indexes the number of strata, ($h = 1, 2, \ldots H$), M_h is the number of SUs in the hth stratum, n_h is the number of SUs searched in the hth stratum, m_{hu} is the number of SUs in the hth stratum that contain tracks from the uth group of animals, m_{hv} is the number of SUs in the hth stratum that contain tracks from the vth group of animals, and m_{huv} is the number of SUs that contain tracks from the uth and vth group of animals. The combinatorics notation $\binom{M_h}{n_h}$ denotes the number of ways to pick n_h things from M_h and is calculated as

$$\frac{M_h!}{(M_h - n_h)!n_h!},$$

where $n_h! = n_h(n_h - 1)(n_h - 2) \ldots (1)$, by definition, $0! = 1$. For example,

$$\binom{4}{3} = \frac{4 \times 3 \times 2 \times 1}{1 \times 3 \times 2 \times 1} = 4.$$

Assuming $H = 2,\ M_1 = 7,\ M_2 = 9,\ n_1 = 4,\ n_2 = 2,\ m_{1,1} = 2;\ m_{2,1} = 1;\ m_{1,2} = 3;\ m_{2,2} = 0;\ m_{1,1,2} = 2;\ m_{2,1,2} = 0$; then applying this data to Equation (3), we obtain:

$$p_1 = 1 - \left[\left[\left(\frac{5!}{1!\ 4!}\right) \Big/ \left(\frac{7!}{3!\ 4!}\right)\right]\left[\left(\frac{8!}{6!\ 2!}\right) \Big/ \left(\frac{9!}{7!\ 2!}\right)\right]\right]$$
$$= 1 - \left[\left(\frac{5}{35}\right)\left(\frac{28}{36}\right)\right] = 0.889.$$

Similarly, $p_2 = 0.971$ and the above data can be applied to Equation (4) to obtain $p_{1,2} = 0.882$. Confidence intervals can be constructed using a t-distribution with $r - 1$ degrees of freedom (Thompson 1992).

The y_u/p_u term in Equation (1) is the contribution to the estimated population total for the uth group of animals. Their contribution to the variance of population estimate can be calculated as follows:

$$\hat{V}(\hat{T}_{yu}) = \frac{(1 - p_u)}{p_u^2} y_u^2 + \sum_{\substack{v=1 \\ v \neq u}}^{r} \left(\frac{1}{p_u p_v} - \frac{1}{p_{uv}}\right) y_u y_v, \quad (5)$$

and is useful for adjusting strata sample allocation for future surveys and determining the observation's influence on the variance.

By redefining y_u to be 1 for each group and then applying Equations (1) and (2), a point estimate and confidence interval for the number of groups can be obtained. Estimates of average group size can be obtained as follows:

$$\bar{Y} = \frac{\hat{T}_y}{\hat{T}_x}, \quad (6)$$

where $\hat{T}_y$ denotes a population estimate and $\hat{T}_x$ denotes an estimate of the number of groups. To our knowledge, there is no exact variance formula for a ratio based upon probability sampling using network sampling because there is not a 1-to-1 relationship between the object of interest and the SU; as a result, the number of groups in the population is unknown. An ad hoc vaiance estimate for such a ratio (e.g., Eq 6) can be obtained by substituting $\tilde{y}_u$ for y_u in Equation (2), where

$$\tilde{y}_u = y_u - \bar{y}, \quad (7)$$

and by dividing the resulting variance by $\hat{T}^2_x$. This ad hoc estimate is the variance estimate of a ratio obtained via probability sampling (Thompson 1992:70) with N (no. of SUs in the study area) replaced by an estimate of the number of groups ($\hat{T}_x$).

Field Methods

Study Area.—Game Management Unit (GMU) 21D, a 31,373-km^2 area intersected by the Yukon and Koyukuk rivers in Interior Alaska, was surveyed for wolf tracks on 8–17 March 1994. The GMU consisted of meandering rivers with numerous oxbows and lakes, and floodplains dominated by willow (*Salix* spp.). Dominant types of vegetation included alluvial mixed forest composed of white spruce (*Picea glauca*) and balsam popular (*Populus balsamifera*), and alluvial shrub composed of feltleaf willow (*Salix alaxensis*) and diamond leaf willow (*S. pulchra*). There was an open, lowland forest of black spruce (*P. mariana*) between uplands and riverine areas. Composition of uplands depended on edaphic conditions, but uplands were mostly black and white spruce mixed with paper birch (*Betula papyrifera*), but alpine tundra also occurred on tops of the higher hills.

Data Collection.—We conducted daily surveys with 2–4 pilot–biologist teams in a Piper PA-18 Super Cub aircraft and logged 46.5 hr either searching SUs or following wolf tracks. The majority of pilots and biologists had extensive aerial-tracking experience; the others had a moderate amount of experience. We assembled the teams to ensure that each team had at least 1 member with extensive tracking experience. We initiated the survey approximately 24 hr after a 4-cm snowfall on top of a good base (25–40 cm).

The GMU 21D was divided into 760 41.4-km^2 (6.4 × 6.4 km) SUs that were grouped into 144 high-, 259 medium-, and 357 low-strata

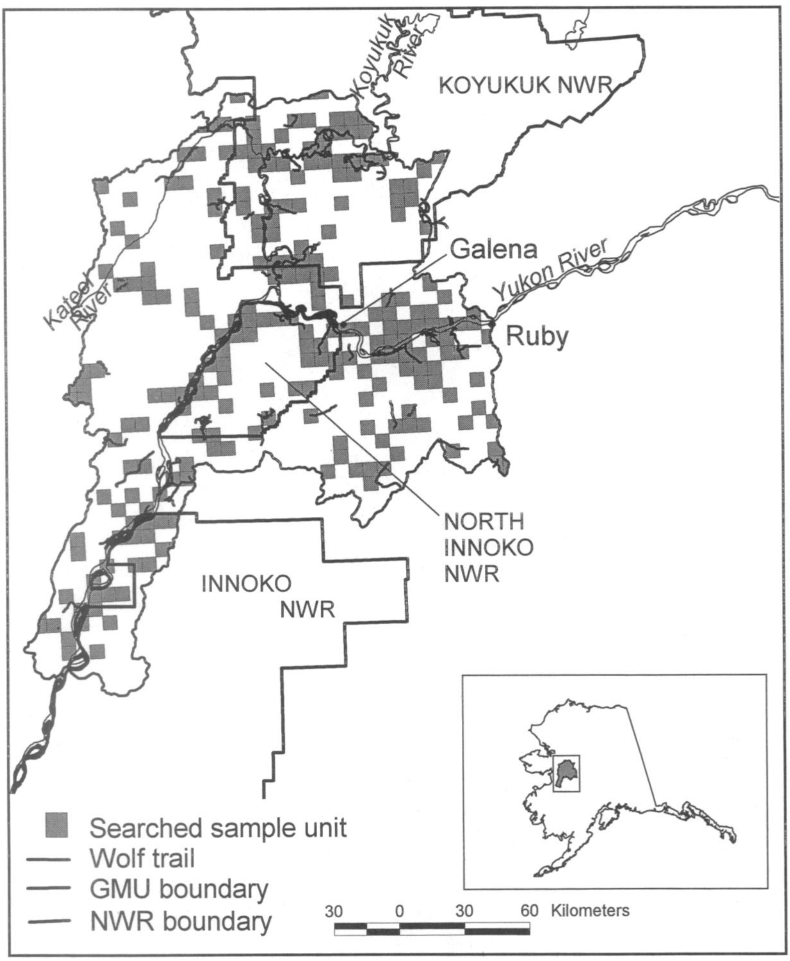

Fig. 1. Illustration of the stratified network-sample design used to estimate the number of wolves in a 31,373-km² game management unit in Interior Alaska during a 1994 March survey.

SUs. We sampled 66.7% of the high stratum, 32.8% of the medium stratum, and 14.3% of the low stratum, which resulted in a survey of 30.5% of the GMU (Fig. 1). The stratification was based upon historical records of wolf harvest locations and survey data, knowledge gleaned from local trappers, and winter distribution and abundance of moose (*Alces alces*). The stratification, coupled with our planned sampling intensity per strata, determined the final sample size. We varied search effort between 0.3 and 0.8 min/km^2 to avoid the likelihood of missing wolf tracks because of overstory, track deposition from other animals, and lighting conditions. We increased sampling efficiency by collectively searching groups of selected SUs in close proximity to each other. Our general search pattern was a series of perpendicular passes separated by approximately 1.5 km. We intensively searched kill sites and wolf travel routes such as rivers, streams, sloughs, hilltops, and lakes. We used presence of common ravens (*Corvus corax*) or other scavengers as an indicator that a kill site might be nearby. In SUs with heavy overstory, care was taken to closely examine sloughs and meadows for tracks, including open areas and possible travel routes outside the SU but adjacent to the SU border.

We followed fresh wolf tracks to the wolves and backwards to their previous location at the end of the snowstorm. We obtained inferences to pack size from track counts when conditions did not allow for a direct count of the pack (locations where the pack had dispersed into individual trails or sites where the pack laid down to rest). If a good count was not obtained, a pilot–biologist team would either land to examine tracks or search for the pack the next day. When tracking in a heavily forested or heavily tracked SU, we also searched nearby open areas such as lakes, sloughs, rivers, and meadows to ensure we correctly identified all SUs containing the fresh tracks.

To determine if model assumptions were reasonable, we located radiocollared packs (n = 9 packs, 14 wolves) near searched SUs at the end of the day. We used this information to determine if wolves were double-counted or had traveled undetected through searched SUs.

We obtained population estimates for GMU 21D and portions of Koyukuk and Innoko NWR within GMU 21D (10,236 km^2) by applying Equations 1–4 to the appropriate wolf observation and SU datasets. The GMU 21D dataset consisted of wolf data (u, y_u, m_{hu}, etc.) and SU information (N_h, M_h, etc.) from within GMU 21D, while the portions of Koyukuk and Innoko NWR within GMU 21D were derived from a subset of the above data and information. We applied the population membership rule to the appropriate wolf dataset to determine if the pack was a member of the population under investigation. We used Equation 5 to determine the contribution to the overall variance by pack. After all point estimates, we used a ± symbol to denote the standard error. We used Spearman's rank correlation statistic (Conover 1980) to test for correlation (α = 0.05) between pack size and their inclusion probability.

RESULTS

We observed 37 groups containing 173 wolves whose tracks intersected at least 1 searched SU (Table 1) and were considered members of the GMU 21D population. Group size ranged from 1 to 14 wolves, and inclusion probabilities ranged from 0.143 to 1.000. The inclusion probabilities were not correlated with pack size (r_{35} = 0.23, P = 0.180; Fig. 2). Applying Equations (1) and (2) to data in Table 1 resulted in a population estimate of 256 ± 28.4 wolves (90% CI = 208–303), or a density of 8.2 ± 0.9 wolves/1,000 km^2 (90% CI = 6.6–9.7).

Packs 35 and 36 were responsible for a large proportion (37%) of the variance of the population estimate. Examination of Equation (5) and Figures 2 and 3 indicated that the moderate inclusion probabilities of these packs, coupled with moderate to large pack size, resulted in their large contribution to the total variance.

By applying Equations (1) and (2) to packs of size 1, we obtained an estimate of 16.4 ± 9.1 single wolves in GMU 21D during this period, which is 6.4% of the estimated population total. We followed Ballard et al. (1987) and defined a wolf pack as a group of ≥2 wolves. By restricting the dataset to wolf packs and applying Equations (1) and (2), we obtained an estimate of 240 ± 27 wolves in packs. Replacing y_u with 1 for this dataset and applying Equations (1) and (2) resulted in an estimate of 49.3 ± 6.1 packs. Applying Equation (6) to the above estimates resulted in an estimated average pack size of 4.9 ± 0.3 wolves.

No violations of the sample design assumptions were noted, based on concurrently obtained locations of 9 radiocollared wolf packs (14 radiocollared wolves). Seven (11 radiocollared wolves) of the 9 packs were observed during the survey, since their tracks were found within selected SUs. After they were found, we obtained follow-up radiolocations of these packs, which indicated they were not double-counted. Of the 2 packs not found, 1 (2 radiocollared wolves) spent the entire survey period out of the study area (GMU 21D); the other pack (1 radiocollared wolf) was located within GMU 21D in a nonselected SU at the time the survey was conducted near their location.

We observed 14 groups that contained 76 wolves and whose tracks intersected at least 1 searched SU and were considered members of the GMU 21D-NWR population. Group size ranged from 1 to 14 wolves, and inclusion probabilities ranged from 0.694 to 1.000. Applying Equations (1) and (2) to the wolf data, we estimated the NWR population to be 89 ± 12 wolves (90% CI = 76–108), or a density of 8.7 ± 1.2 wolves/1,000 km^2 (90% CI = 7.4–10.6).

DISCUSSION

In theory, it is possible to obtain a negative variance from Equation (2) (Sarndal et al. 1992, Thompson 1992), but this possibility is considered remote with moderate to large sample sizes (Sarndal et al. 1992:48). Thompson (1992:50) provided an alternative formula that is nonnegative and tends to overestimate the true variance. Avoiding extremely small inclusion probabilities (<0.05) also can help avoid obtaining a negative estimate with Equation (2). We used a sampling fraction of 0.10–0.20 for the

Table 1. Observed wolf pack size (y_u), number of sample units containing tracks (m_{hu}), inclusion probability (p_u), contribution to the population estimate (y_u/p_u), and contribution to the variance [$\hat{V}$ ($\hat{T}_{yu}$)], by pack, for a March 1994 wolf survey in Alaska Game Management Unit 21D.

[a]Pack identification	y_u	$m_{\text{high}, u}$	$m_{\text{medium}, u}$	$m_{\text{low}, u}$	p_u	(y_u/p_u) wolves	$\hat{V}$ ($\hat{T}_{yu}$)
1	2	7	0	0	1.000	2.00	0.00
2	10	2	2	0	0.951	10.52	4.97
3	1	0	0	1	0.143	7.00	35.70
4	7	3	3	1	0.991	7.07	0.36
5	14	1	1	1	0.808	17.33	55.29
6	4	0	0	3	0.371	10.78	65.14
7	6	0	3	0	0.699	8.59	20.11
8	4	0	0	3	0.371	10.78	65.14
9[a]	5	2	0	0	0.890	5.62	3.14
10	6	3	0	0	0.965	6.22	1.20
11[a]	7	6	0	0	0.999	7.01	0.05
12	3	0	0	4	0.462	6.50	17.99
13	3	2	1	1	0.937	3.20	0.46
14	3	3	3	0	0.984	3.03	0.05
15	2	1	1	0	0.776	2.58	1.15
16	2	0	4	0	0.799	2.50	0.73
17	4	2	0	0	0.890	4.49	1.95
18	2	0	0	2	0.266	7.53	35.36
19	7	3	1	0	0.976	7.17	1.06
20	6	0	2	0	0.550	10.92	50.50
21	4	3	1	0	0.976	4.10	0.30
22	2	1	0	1	0.714	2.80	1.79
23[a]	5	3	2	0	0.984	5.08	0.75
24	2	2	1	0	0.926	2.16	0.22
25	3	0	0	3	0.371	8.08	34.89
26	5	5	0	0	0.996	5.02	0.07
27	1	2	1	0	0.926	1.08	0.02
28	6	0	2	4	0.758	7.92	12.51
29	1	1	1	0	0.776	1.29	0.20
30	7	2	0	0	0.890	7.86	6.33
31	4	3	2	0	0.984	4.07	0.19
32	8	0	3	0	0.699	11.45	36.80
33	5	1	5	0	0.955	5.23	0.91
34[a]	7	1	1	0	0.776	9.02	17.55
35	5	0	1	0	0.328	15.24	151.16
36	9	0	1	2	0.507	17.76	147.29
37	1	0	0	1	0.143	7.00	35.70

[a] Packs 9 and 11 traveled though the same high sample unit (SU; e.g. $m_{\text{high } 9, 11} = 1$). Packs 23 and 34 traveled though the same high SU (e.g. $m_{\text{high } 23, 34} = 1$).

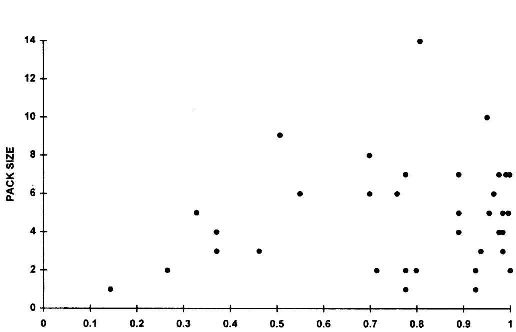

Fig. 2. Wolf pack size versus inclusion probability for a March 1994 survey in GMU 21D, Alaska.

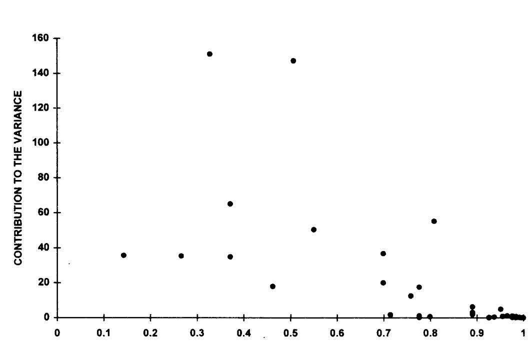

Fig. 3. Wolf Pack inclusion probability versus contribution to the variance for a March 1994 survey in GMU 21D, Alaska.

low stratum in this and 11 other applications (9 wolf and 2 wolverine surveys) of this procedure and did not encounter this problem.

Application of Equation (2) to data with grouped animals, (e.g., wolves) often results in a variance dominated by a few observations. The contribution to the variance becomes larger as group size increases or the inclusion probability decreases. This trade-off is nonlinear, and the differences in the contribution to the variance can be quite dramatic. Examination of Figures 1 and 2 indicates a 232% difference in the contribution to the variance between packs 6 and 35 (y_6 = 4 wolves, P_6 = 0.371, $V(\hat{T}_{y6})$ = 65.1; y_{35} = 5 wolves, P_{35} = 0.328, $V(\hat{T}_{y35})$ = 151.2; Table 1). With grouped data, the most efficient design has the inclusion probability proportional to group size (Sarndal et al. 1992), but this design requires prior knowledge that is generally unavailable. Prior knowledge on the general location of exceptionally large groups (e.g., wolf packs >12) can be handled by a priori assigning 1–2 additional SUs into strategic locations within the high stratum. The placement should account for the SU stratification in the area and any knowledge about secondary travel routes.

The ability to obtain estimates of density within subareas may be extremely useful in a situation with multiple federal and state land owners or managers. Additional biological insights can be obtained when comparing density estimates of subareas to other biological data collected from these areas (e.g., wolf–moose ratios); however, the SUPE estimates are a snapshot in time of a potentially dynamic parameter. For example, snapshots of wolf pack size will vary as packs split-up and rejoin, wolves disperse, and the breeding season begins.

We conducted the wolf survey in March, when pack size can be dynamic because of packs dispersing and recombining, breeding pairs separating, and young wolves beginning to disperse (Ballard et al. 1987). In addition, the typically large daily range that wolves exhibit limits ability to exactly predict SUs that would contain the pack on the survey day. Our sample unit probability estimator (SUPE) overcame these difficulties by substituting a stratification requirement on the likelihood of an SU containing fresh tracks rather than the conventional sampling requirement that the SU contain the wolves.

The dynamic nature of wolf movements, pack size, and location, including resting on kills, presents a worst-case scenario for an estimator. The age of the track varies with the number of days since fresh snow, high winds, or both, which makes track lengths and inclusion probabilities dynamic. The presence of a new food source (e.g., fresh moose kill) may temporarily reduce daily wolf movements wherein travel of some packs could be restricted to a single SU containing the kill. Observers can overcome these difficulties and inferences can be made about a large study area and subareas within that area by using probability sampling. For species trackable in the snow, probability sampling addresses many of the problems that Otis (1992) identified. The difficulty in use of probability sampling is finding a way to determine the probability that an observation is contained in the sample for the given sample design. The use of an animal's tracks in the snow is a way to obtain this probability. A limitation of the SUPE method is it requires good piloting skills to fly a small aircraft slow and low to the ground, as well as good tracking skills by both the pilot and observer to find, identify, and follow tracks of the target species.

When movement of the target species relative to the study area is hard to predict, this design can be used with 1 stratum, although alternative probability estimators such as TIPS may be a more efficient design (Becker 1991). We hypothesize that the best ad hoc answer to which estimator is more efficient is to determine the type of flight pattern that would most efficiently find these tracks. The TIPS design is probably more efficient if a linear flight pattern is thought the best way to find an animal's tracks (e.g., wolverine), whereas circular search patterns in certain habitat types (e.g., riparian habitat for wolves feeding on winter moose concentrations) suggest that a SUPE design would be more efficient. One major advantage of the SUPE design is the assumption of not missing tracks in searched SUs (assumption 6) is easier to meet than the TIPS assumption that no tracks intersecting the transect are missed. Because the SUPE search flight often overflies the track several times. All the TIPS surveys we are aware of have been done in a 1-day period; hence, the design would probably have to be modified for a survey of several days. In future work, we hope to examine the relative efficiency of these 2 estimators in different sampling situations.

A computer program (SUPEPOP) to analyze

SUPE data can be obtained at the following website address: ftp://ftpr3.adfg.state.ak.us or the Region III, Alaska Department of Fish and Game FTP site 146.63.246.240 with account = Anonymous and password = E-mail address. The self-extracting zipifile (SUPEPOPI) containing the program can be found in the program subdirectory.

ACKNOWLEDGMENTS

We are indebted to H. J. Griese and M. A. Masteller for their support, fieldwork, and helpful suggestions during the early development of the estimator. K. W. Pitcher, D. A. Anderson, K. P. Taylor, and F. D. Stearns provided invaluable support and helped obtain funding. R. A. Nunnley helped with map preparation, and R. A. DeLong wrote the SUPEPOP program. T. H. Spraker, L. B. Saperstein, and P. N. Simon, Jr. were aerial observers, while C. B. McMahon, M. J. Meekins, P. A. Liedberg, and C. B. Brown expertly piloted our survey planes and helped collect data. M. R. Marshall, R. A. Strauch, and D. L. Spencer assisted with cartography. Pittman-Robertson funds provided to the Alaska Department of Fish and Game and U.S. Fish and Wildlife Service National Wildlife Refuge funds supported this study. We thank Associate Editor L. L. McDonald and 2 referees for their helpful comments and suggestions that have improved the manuscript.

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Received 16 December 1996.
Accepted 1 May 1997.
Associate Editor: McDonald.