

2. Next, form the conditional Poisson probabilities:

$$P'_i = \hat{P}_i / (1 - \hat{P}_0) \quad i = 1, 2, \dots$$

where

$$\hat{P}_i = \hat{\mu}^i e^{-\hat{\mu}} / i! \quad i = 0, 1, \dots$$

and then form the expected frequencies:

$$\hat{f}_i = m' P'_i \quad i = 1, 2, \dots$$

Each \hat{f}_i is the correctly conditioned expected sighting frequency because $\Sigma \hat{f}_i = \Sigma f_i = m'$ and $\Sigma i \hat{f}_i = \Sigma i f_i = m$.

3. Finally, grouping classes as necessary, form the usual G or χ^2 statistic for testing the fit of the distribution (Sokal and Rohlf 1981: 714–715). The statistic is judged against the χ^2 distribution with $a - 2$ degrees of freedom, where a is the number of classes after grouping. There must be >2 sighting classes to form the test.

A TERRESTRIAL FURBEARER ESTIMATOR BASED ON PROBABILITY SAMPLING

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Abstract: I used probability sampling results to develop a new method of estimating furbearer abundance based on observing animal tracks in the snow. This method requires that good snow conditions be present during the course of the study and that all animal tracks intersected during the sampling process are observed. Good snow conditions are defined to be fresh snow of sufficient depth so that presnowstorm and postsnowstorm animal tracks can be distinguished. Two general sampling designs are presented: the first assumes that animal tracks can be observed and followed to both the animal's location at the end of the snowstorm and to its present location; the second assumes that the number of different animals encountered along a set of transects can be determined and that it is possible to get movement data from a random sample of radio-collared animals. Using the first technique, I estimated 9.69 ± 1.97 (SE) wolverines (*Gulo gulo*) for a 1,871-km² area of southcentral Alaska. Using the second sampling design, I estimated 15.09 ± 4.34 lynxes (*Felis lynx*) for a 285-km² area of the Kenai Peninsula, Alaska.

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Large terrestrial furbearers, such as lynx, bobcat (*Felis rufus*), wolf (*Canis lupus*), wolverine, and coyote (*C. latrans*) occur at low densities, are secretive, and are often nocturnal. Increases in trapping pressure and loss of habitat have resulted in increased demands to monitor furbearer population levels.

Previous methods used to monitor furbearer population levels include mark-recapture experiments (Humphrey and Zinn 1982, Smith et al. 1984, Hallett et al. 1991), howling responses (Harrington and Mech 1982), trapnight indexes (Wood and Odum 1964), track counts (Linhart and Knowlton 1975, Roughton and Sweeny 1982, Conner et al. 1983, Van Dyke et al. 1986, DiStefano 1987), pack counts (Gasaway et al. 1983, Peterson et al. 1984, Fuller and Snow 1988, Fuller 1989), mail surveys of trappers (Lemke

and Thompson 1960, Slough et al. 1987), and total trapper harvest reports (Keith 1963, Hamilton and Fox 1987, Melchior et al. 1987, Novak 1987, Slough et al. 1987). In the past, these methods have proven difficult to implement or have given unsatisfactory results. Mark-recapture experiments are not appropriate (White et al. 1982) due to small population sizes and low capture probabilities. Howling responses provide an index of the number of wolf packs, but are biased toward large packs, are affected by topography and weather, and cannot be used accurately to estimate total wolf abundance (Harrington and Mech 1982). Track count indexes can be confounded by changes in movement patterns (Ward and Krebs 1985). Wolf pack counts assume all the wolves are counted (Gasaway et al. 1983, Peterson et al. 1984) or use adjustment

factors to account for missed lone wolves (Fuller and Snow 1988, Fuller 1989), and precision estimates are not available. Mail surveys provide, at best, an index to animal abundance (Brand and Keith 1979) and can be difficult to interpret. Trapper harvest reports tend to be confounded with socioeconomic conditions (Gilpin 1973, Weinstein 1977, Winterhalder 1980).

Hayashi (1978, 1980) and Hayashi et al. (1979) used snow tracks to estimate hare (*Lepus brachyurus angustidens*) population size in northern Japan. Hayashi (1978) generated population estimates by dividing the estimated average distance moved by an individual into the estimated distance moved by the population. Several methods can be used to estimate the average distance moved by an individual and the population (Hayashi 1978, Hayashi et al. 1979), all of which involve sampling subareas. Hayashi (1980) used a probability sampling scheme modeled after the Buffon needle problem to generate a population estimate. This estimate is based on the probability of observing animal tracks in the snow from an aerial survey, which is assumed to be constant for all animals. Reid et al. (1987) used counts of river otter (*Lutra canadensis*) tracks in snow, in small sample units, to obtain a population estimate.

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PROPOSED TECHNIQUE

Probability (Horvitz and Thompson 1952) and line-intercept sampling (McDonald 1980, Kaiser 1983) are used in 2 different applications to obtain population estimates based on animal tracks observed in the snow. The former assumes that animal tracks can be followed to both the animal's present location and its location at the end of the snowstorm, whereas the latter assumes that a random sample of the population can be fitted with radio collars and that the number of different animals intersecting ran-

domly selected transects in the study area can be determined.

General Sample Design Requirements.

Using the probability of observing animal tracks, after a snowstorm, to generate a population estimate requires that all animals move during the course of the study; all animal tracks, of the species of interest, are readily recognizable; all animal tracks are continuous; animal movements are independent of the sampling process; pre- and postsnowstorm tracks can be distinguished; all animal tracks that cross sampled transects are observed; the study area is rectangular in shape; and all the transects are oriented perpendicular to a specified reference axis (x -axis).

Wind conditions after the snowstorm should be moderate, so that fresh tracks are not blown away. The condition that animal tracks be continuous can be relaxed if a 1-to-1 correspondence can be established between the track segments and animals in the population of interest. If possible, the x -axis should be oriented parallel to animal movement patterns to maximize the probability of encountering animals. I have assumed that transects are selected with a replicated systematic sample design. Replication of the sampling scheme is needed to obtain variance estimates (Kaiser 1983).

General line-intercept sampling results (Kaiser 1983) can be used to eliminate the last 2 assumptions, and as a result, unbiased estimates can be obtained for irregularly shaped study areas with random angled transects of unequal length.

Technique Involving Animal Tracking

Sample Design.—The initial assumption is that animal tracks can be observed and followed from the ground such as for marten (*Martes americana*) in Newfoundland (Bateman 1986) and marten and fisher (*Martes pennanti*) in Manitoba (Raine 1983) or from a slow moving airplane or helicopter. An additional assumption is that the animal can be tracked both to its present location and to its location at the end of the snowstorm. The distance the animal traverses parallel to the x -axis is determined from this information (Fig. 1).

The following notation is used: S_i is the i th systematic sample; T_v is the population total; p_v

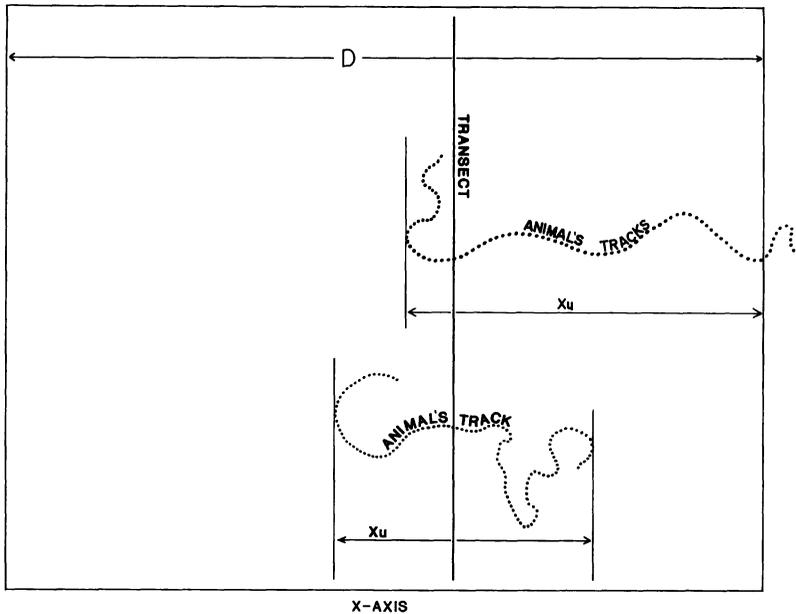


Fig. 1. Illustration of how X_u , the distance traveled parallel to the x -axis, is calculated. The length of the x -axis is denoted by D .

is the probability that the u th animal is contained in the sample; X_u is the x -axis distance traversed, parallel to the x -axis, by the u th animal (max. minus min. x -axis coordinate for the u th animal); and D is the length of the x -axis.

In the absence of adequate information on which to stratify, and assuming a tendency for animal home ranges not to overlap, a repeated systematic sampling of the transects should be close to the optimal sampling design. Under the above conditions, spreading the transects out over the study area should maximize the information gain, and it is reasonable to expect the variance within systematic samples (clusters) of parallel transects to be greater than the variance between systematic samples. Assuming a repeated systematic sample is used with equal length transects, then

$$\hat{T}_y = \sum_{u \in S_i} 1/p_u$$

is unbiased for T_y (Horvitz and Thompson 1952, McDonald 1980, Kaiser 1983), where $u \in S_i$ denotes the collection of animals that intercept transects from the i th systematic sample, i ($i = 1, 2, \dots, r$) indexes the systematic sample, r denotes the number of systematic samples that are conducted, q is the number of transects per systematic sample, and

$$p_u = \begin{cases} x_u/(D/q) & \text{for } x_u \leq (D/q) \\ 1 & \text{otherwise.} \end{cases} \quad (1)$$

Then,

$$\hat{T}_y = \sum_{i=1}^r \hat{T}_{y_i}/r \quad (2)$$

is an unbiased estimate of T_y , and an estimate of the variance of \hat{T}_y is:

$$\text{Var}(\hat{T}_y) = \left[\sum_{i=1}^r (\hat{T}_{y_i} - \hat{T}_y)^2 \right] / [r(r - 1)]. \quad (3)$$

Confidence intervals can be constructed based upon a t distribution with $r - 1$ degrees of freedom.

There are 2 ways the above results can be expanded to include observations on groups of animals. In the case where the location and the path of travel can be determined for every animal in the group, an inclusion probability (p_u) can be determined for each animal, and the calculations are done as before. In the case where animal tracks intersect and it is possible to observe all of the animals, but differences in travel route cannot be determined among individuals, the group of animals needs to be treated as a network (Thompson 1990), and a group inclusion probability must be calculated. An example

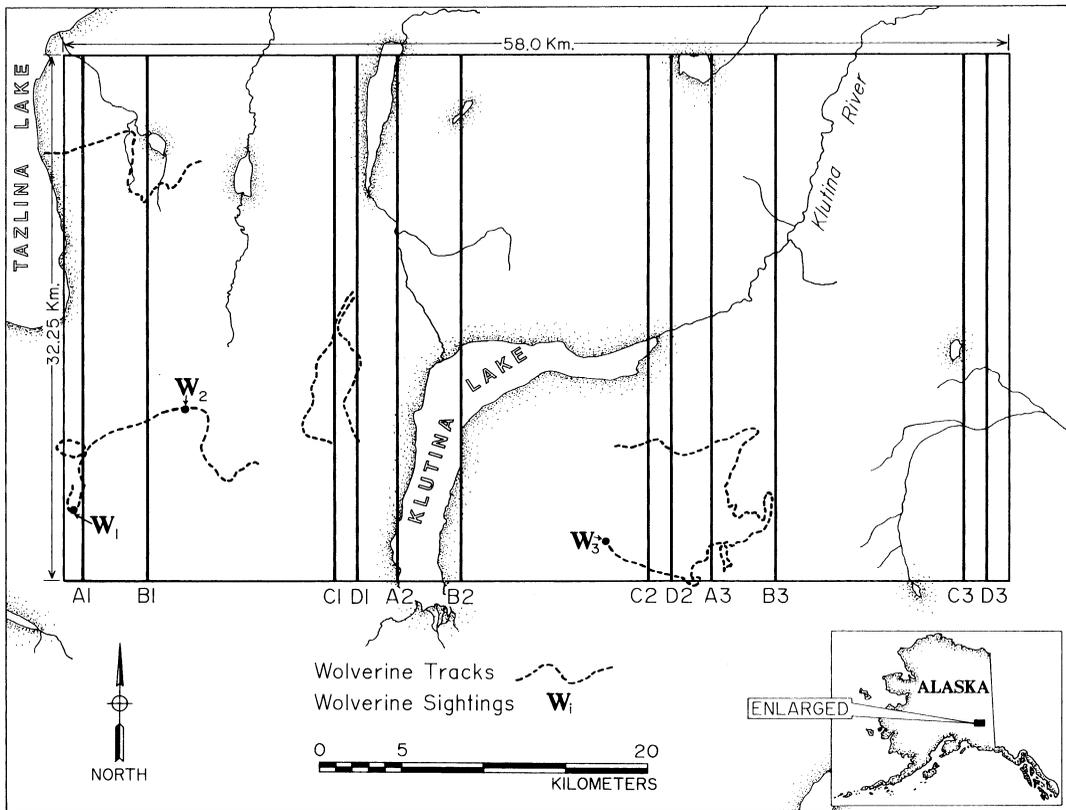


Fig. 2. Illustration of the systematic sample design used to estimate numbers of wolverine in a 1,871-km² area of the Chugach Mountains, Alaska, in March 1988. The 4 systematic samples are denoted by letters (A, B, C, D), and numeric values denote the transect location within the systematic sample.

occurred during the March 1988 wolverine survey in which 2 wolverines waited out a snowstorm in different locations, traveled to the same carrion, and then went their separate ways (Fig. 2). Using the following notation, the above results can be extended for the second case: y_u is the number of animals in the u th group (for the above example $y_u = 2$); p_u is the probability that the u th group (network) is contained in the sample and is calculated using equation (1); and X_u is the x -axis distance traversed, parallel to the x -axis, by the u th group (max. minus min. x -axis coordinate for the u th group). Then,

$$\hat{T}_{y_i} = \sum_{u \in S_i} y_u / p_u \quad (4)$$

is unbiased for T_y (Horvitz and Thompson 1952, McDonald 1980, Kaiser 1983), where u now indexes groups instead of individuals. By applying equations (2) and (3), a population estimate and variance can be obtained.

The technique does not require closure, and as a result, animals can move in or out of the study area in the period between end of snow fall and termination of transect sampling. In such cases, if at least half of the animal's x -axis travel occurred within the study area, then X_u should be calculated from that part of the projection which is within the study area (Fig. 1), otherwise the animal is considered out of the study area.

Example.—A 1,870.5-km² study area (32.25 × 58 km) on the north side of the Chugach Mountains in southcentral Alaska was surveyed on 18 March 1988 for wolverine tracks. The study area consisted of about 60% alpine habitat, 20% open shrub/black spruce (*Picea mariana*) forest, and 20% moderately open black spruce forest. Three pilot/biologist teams conducted the survey in PA-18 Super Cubs. The pilots had extensive aerial tracking experience. All of the biologists were experienced aerial observers.

Table 1. Number of wolverines and group affiliation observed in a survey of the eastern Chugach Mountains of Alaska, March 1988.

Systematic sample	Transect id.					
	1		2		3	
	N	Group	N	Group	N	Group
A	3	g1, g2	0		1	g4
B	3	g1, g2	0		0	
C	2	g3	1	g4	0	
D	2	g3	1	g4	0	

The teams conducted the survey 12–18 hours after a snowstorm. Four systematic samples (A, B, C, D), each containing 3 32.25-km transects, were flown (Fig. 2); 6 wolverine tracks were observed (Table 1) and tracked to obtain the projected x -axis distance traversed.

Four of the transects were reflown with different pilot/biologist teams to determine if any wolverine tracks were unobserved in the first aerial pass. No additional wolverine tracks were observed on the second pass. Further evidence supporting the assumption that no tracks were missed includes: 3 different wolverine tracks crossed 2 transects and were observed both times, and another wolverine track crossed 5 transects and was observed every time. All of the wolverines associated with observed tracks were successfully located during tracking, with the exception of 2 animals whose tracks passed bare dark rocks that might have prevented the animals from being seen. Repeated circling where the tracks disappeared made it unlikely that the tracks reappeared but were unobserved.

Applying equation (4) (Tables 1 and 2), I obtained the following estimates: $\hat{T}_{yA} = 7.35$, $\hat{T}_{yB} = 5.36$, $\hat{T}_{yC} = 13.03$, $\hat{T}_{yD} = 13.03$. Then, $\hat{T}_y = 9.69$ wolverines, and $SE(\hat{T}_y) = 1.97$.

Technique Using Radio-Collared Animals

Sample Design.—In situations where it is unreasonable to assume that all animal tracks that intersect the transect can be accurately followed, the general sampling design is modified to record the number of individuals whose tracks intersect transects in each systematic sample. These data are used to obtain an estimate of the projected x -axis distance traversed by the population. Radio telemetry data are used to determine the average projected x -axis distance traversed by a group of radio-collared animals. The population estimate is based upon the ratio of 2 estimates; the estimated projected distance

Table 2. X -axis movement (km) and inclusion probabilities (p_u) for a wolverine survey of the eastern Chugach Mountains in Alaska, March 1988.

Group	y_u^a	X_u^b (km)	D^c (km)	P_u^d
1	1	8.75	58	0.453
2	2	12.25	58	0.634
3	2	3.50	58	0.181
4	1	9.75	58	0.504

^a y_u represents the number of animals in the u th group.

^b X_u represents the distance traveled parallel to the x -axis, i.e., the difference between the maximum and minimum x -axis coordinates.

^c D represents the length of the x -axis.

^d P_u represents the probability of a systematic sample intersecting the tracks of the u th group.

traversed by the population with regard to the x -axis is divided by the estimated average projected x -axis distance traversed by an individual. To estimate the x -axis distance traversed by the population, the following assumptions must be met: (1) systematic samples are constructed so that animal tracks intersecting 1 transect will not intersect other transects within the same systematic sample and (2) the number of different animals encountered in each systematic sample can be determined.

To estimate the average projected x -axis distance traversed by an individual of the population, animals are selected at random and fitted with radio collars. Their locations are plotted as often as possible for the period following the snowstorm to the completion of transect sampling. If continuous monitoring of radio collars to establish radio fixes is not feasible, then the radio-collared animals are tracked from where they bedded during the snowstorm to their location at the end of the survey. To obtain accurate movement information, this should be done as close to the end of transect sampling as possible. The x -axis distance traversed by each radio-collared animal is calculated either from radio fixes or from track locations plotted on a map of the study area. If a random sample of animals is not obtained, the selection of animals to be collared should mimic a simple random sample and reflect possible differences in movement patterns by sex and (or) age.

Additional notation used is: T_i is the total projected x -axis distance traversed by the population, n_i is the number of different animals encountered in the i th systematic sample, and μ_x is the average projected x -axis distance traversed by an individual of the population.

Assuming systematic sampling and $\max\{X_u\} \leq D/q$, and because $p_u = (x_u q/D)$, the estimator

Table 3. Number of individual lynx tracks observed in a survey of the Kenai National Wildlife Refuge, Alaska, March 1987.

Systematic sample	Transect			Total
	1	2	3	
A	0	1	2	3
B	0	4	0	4
C	1	1	1	3
D	0	1	1	2

$$\hat{T}_{xi} = \sum_{u \in S_i} x_u / p_u \quad (5)$$

is unbiased for T_x (Horvitz and Thompson 1952, McDonald 1980, Kaiser 1983). An unbiased estimate of T_x is

$$\hat{T}_x = \sum_{i=1}^r \hat{T}_{xi} / r \quad (6)$$

with variance

$$\text{Var}(\hat{T}_x) = \left[\sum_{i=1}^r (\hat{T}_{xi} - \hat{T}_x)^2 \right] / [r(r-1)] \quad (7)$$

An estimate of μ_x is

$$\hat{\mu}_x = \sum_{u \in S_R} x_u / n_R \quad (8)$$

where S_R denotes the sample of radio-collared animals, and n_R is the number of animals in that sample. The variance can be estimated by

$$\text{Var}(\hat{\mu}_x) = \left[\sum_{i=1}^{n_R} (x_u - \hat{\mu}_x)^2 \right] / [n_R(n_R - 1)] \quad (9)$$

Then,

$$\hat{T}_y = \hat{T}_x / \hat{\mu}_x \quad (10)$$

is an estimate of T_y with approximate variance

$$\text{Var}(\hat{T}_y) \approx (\hat{T}_x / \hat{\mu}_x)^2 \{ [\text{Var}(\hat{T}_x) / (\hat{T}_x)^2] + [\text{Var}(\hat{\mu}_x) / \hat{\mu}_x^2] \} \quad (11)$$

based upon a second-order Taylor-Series approximation and a covariance of zero between T_x and μ_x because the 2 variables are independently estimated (Mood et al. 1974). Confidence intervals can be constructed based on normal distribution assumptions. The bias of the point estimate is approximately

$$[\hat{T}_x / (\hat{\mu}_x)^3] \text{Var}(\hat{\mu}_x) = [\hat{T}_y / (\hat{\mu}_x)^2] \text{Var}(\hat{\mu}_x) \quad (12)$$

Example.—A 285-km² study area on the Kenai Peninsula in southcentral Alaska was surveyed for lynx tracks on 22 January 1987, about 24 hours after a snowstorm (Schwartz and Becker 1988). The survey consisted of 4 systematic

Table 4. X-axis movement (km) for 2 lynxes in the Kenai National Wildlife Refuge, Alaska, March 1987.

Sex	X_u^a (km)	D^b (km)
F	7.35	88.50
M	4.38	88.50

^a X_u represents the distance traveled parallel to the x-axis, i.e., the difference between the maximum and minimum x-axis coordinates.
^b D represents the length of the x-axis.

samples, each containing 3 2.33-km transects, and 12 individual lynx tracks were counted (Table 3). Initially, there were 5 radio-collared lynxes in the study area; unfortunately 2 of these animals left by early January and a third was illegally trapped during the survey. The x-axis movement data (Table 4) were collected using radio-telemetry observations and ground tracking at the completion of the survey.

Applying equation (5) to our samples (Table 3), I obtained the following estimates: $\hat{T}_{xA} = 88.50$, $\hat{T}_{xB} = 118.00$, $\hat{T}_{xC} = 88.50$, and $\hat{T}_{xD} = 59.00$ km. From equations (6) and (7), $\hat{T}_x = 88.50$ km and $\text{Var}(\hat{T}_x) = 145.04$ km², respectively. Equations (8) and (9) applied to the radio-telemetry data (Table 4) yield $\hat{\mu}_x = 5.865$ km and $\text{Var}(\hat{\mu}_x) = 2.205$ km², respectively. A population estimate of 15.09 ± 4.34 lynxes was obtained from equations (10) and (11), respectively. I estimated the bias to be 0.97 lynx, or 6.88% of the population estimate.

Based on telemetry locations of the radio-collared lynxes, both animals crossed a transect and were observed during the course of the survey.

DISCUSSION

Wolverines and lynxes encountered in my study differed in movement patterns and habitat use, yet apparently, reasonable population estimates were obtained. The precision of the reported estimates would have decreased if the sampling effort allocated to checking model assumptions, by resampling, had been used to sample new transects.

Technique Involving Animal Tracking.—The rule to handle nonclosure of animal tracks is necessary to obtain accurate estimates. Estimates that ignore this rule will estimate the number of animals using the area for the period between end of snowstorm and termination of sampling, rather than provide a “snapshot” of the number present at a point in time. By spec-

ifying that at least half of an animal's x -axis movements have to be within the study area to be considered a member of the population, the potential for extremely small inclusion probabilities has been dramatically reduced, and as a result, the stability of the estimator increases.

If aerial sampling is used to track animals, the pilots and observers should be highly qualified at observing and identifying tracks from an airplane or helicopter. Use of unqualified pilots or observers will probably result in some tracks being missed and the population underestimated by an unknown amount. To help ensure that no tracks are missed, the aerial sampling technique should only be applied in relatively open habitats. Sampling with helicopters versus airplanes might reduce the possibility of missing tracks. Upon completion of transect sampling, aerial searches of areas missed by transects and likely to contain tracks could be conducted; observed tracks would be followed to determine if they intersect transects and went undetected. Additional ground sampling or using radio-collared animals would also help determine if all tracks that intersect the transect are observed.

My estimator differs from Hayashi (1980) in that the probability of observing an animal is allowed to differ among individuals. In some species, such as wolverine, there may be substantial differences in movements by individual and by sex (Whitman et al. 1986). Study site conditions and the movement behavior of the study species will dictate which set of assumptions can be met, and thus, which estimator is preferable.

Technique Using Radio-Collared Animals.—The biggest problem with the use of radio-collared animals to obtain x -axis movement is logistical; it is not easy to catch and maintain a sample of furbearers.

Although Hayashi (1978), Hayashi et al. (1979), and the method outlined in my paper all use the same ratio formulas to obtain population estimates, the estimators differ in how distances moved are defined. For wildlife studies in Alaska, it is easier to obtain my estimates of distance moved. The degree of access and the availability of trained observers will determine which method is preferable.

The bias of the ratio estimator (6.88%) used to obtain the lynx estimate was very small relative to the estimate and did not produce a distorted picture of lynx density. Through radio

fixes, a priori estimates of μ_x and $\text{Var}(\mu_x)$ could easily be obtained and used to estimate the percent bias. Because percent bias is the estimated bias divided by the population size, an estimate can be obtained by dividing equation (12) by T_v , or the estimated percent bias = $100\mu_x^{-2} \text{Var}(\mu_x)$.

General Considerations.—For fixed sampling effort, the precision of the estimates for both of my sample designs increases as inclusion probabilities (p_u) increase. The sampling process should attempt to maximize inclusion probabilities by orienting the x -axis parallel to major travel routes, such as valleys, and by allowing more time between the end of a snowstorm and the beginning of transect sampling. However, as the time since a snowstorm increases, the difficulty in meeting model assumptions also increases. The amount of difficulty will depend upon the degree of track degradation over time and the likelihood of other animal tracks obscuring tracks of the animal of interest.

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