A multiple mark and recapture estimate applied to polar bears

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The mark–recapture technique described in this paper estimates polar bear (*Ursus maritimus*) populations for all sample periods except the first sample period, incorporates an open population model, and is supported by ecological data from ringed seals and polar bears. The estimation procedure requires that survival rates are either known or estimated independently as part of the research program. Reasonably precise estimates will be produced if 10 to 20% of the population can be marked and sample sizes of 150 bears can be handled at any given sample period.

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La technique de marquage–recapture décrite ici a permis l'estimation des populations d'ours polaires (*Ursus maritimus*) pour toutes les périodes d'échantillonnage sauf la première; elle inclut un modèle de population ouverte et est corroborée par des données écologiques sur des phoques annelés et des ours polaires. Le processus d'estimation suppose que les taux de survie sont connus ou estimés par d'autres moyens. La technique permet des estimés précis lorsque 10 ou 20% de la population peut être marquée et elle permet de traiter des échantillons de 150 ours en n'importe quelle période d'échantillonnage.

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Introduction

Estimating the sizes of populations where the individuals do not concentrate at any time of the year, and in which the probability of sighting is always less than unity, presents unique problems. Historically, population estimates of polar bears have involved strip transects (Tovey and Scott 1957), sustainable kill estimates, or mark–recapture techniques (Stirling et al. 1975). Of the three, the latter seems the most cost effective, in that along with population estimates, mark–recapture programs provide information concerning movements, rates of growth, reproduction, and survival. The major disadvantage of strip-transect methods for estimating the sizes of such low-density populations is the large effort that is usually required to produce usably narrow confidence intervals on a population estimate (Eberhardt 1978). Another problem associated with strip transects is that the probability of sighting free-ranging polar bears with aerial surveys is both low and difficult to evaluate. Estimation based on sustainable kill data is fraught with untestable assumptions and poorly understood relationships between regulatory mechanisms and harvest strategies (DeMaster 1978).

Mark–recapture estimates of numbers of polar bears have usually incorporated closed population models (e.g., the Lincoln–Peterson estimate (Stirling et al. 1975)). The major problem with this approach is that it involves a compromise between sample size and the closed population assumption. If movements in and out of an area can be assumed to be negligible, then births and survival must be 0 and 1.0, respectively. The time interval during which there are no births or deaths in the population requires that the entire sampling procedure be accomplished within a few months at the longest, and therefore, unless polar bear densities are high, the sample sizes associated with tagging polar bears are unmanageably small (see Stirling et al. 1975).

The Lincoln–Peterson estimate can also be used in an open population model if births and immigration are negligible and marked and unmarked animals have the same rates of mortality and emigration. In this case, the estimate is for the population size midway through the initial marking period. However, situations where influx is negligible, while egress is assumed to be important, seem unlikely. Gilbert (1976) reported that influx and egress of polar bears through a study area in Alaska were important factors in influencing the population estimates.

The Seber–Jolly procedure (Seber 1973) is often used to avoid the assumptions of a closed population, but problems have arisen in estimating populations of polar bears with this method. Stirling et al. (1975) and Gilbert (1976) used this approach but found that the small number of recaptures in any one sample period caused each of their estimates of the population to be unreliable. One possible cause of this unreliability is that the Jolly–Seber technique uses the number of bears caught both before and after, but not at, period i, and these numbers tend to be extremely small and prone to error. In addition, population estimates could not be derived for the last sample period, thus reducing the value of a sample which was expensive to collect. Finally, Stirling et al. (1975) found that the estimated number of marks in the population at time i, $\hat{M}_i$, was occasionally an impossibly large number. This was either because one of the assumptions of the model was violated or because of random errors associated with small sample sizes. At this time it is impossible to determine which of these two factors is most important.

We derived the population estimate described in this paper as an alternative to current estimation procedures. We do not suggest that any one estimation technique for polar bears will be universally valid, but feel the following method is useful in some situations. One advantage of this technique, relative to the Seber–Jolly estimate, is that it is possible to estimate a population size for the most recent census period.

Methods

The central problem in multiple mark–recapture censuses is to obtain a reliable estimate of the number of marked animals surviving in the population when a recapture is undertaken. The Jolly–Seber method considers M_i in the population at time i to be in two classes: the m_i recaptures at time i, and those not recaptured. If the subsequent sampling is random, on the average the same fraction of marked individuals will be subsequently recaptured whether they were marked and released at time i, or whether they were marks surviving from earlier captures. Equating these expected fractions leads to an estimate of M_i; but it is subject to a sampling error which may be large. The proposed technique, instead, estimates surviving marks each period by directly applying a survival rate to the previous number of marks. A survival rate is derived for the population by aging all captures and fitting a survival curve to the age structure.

The data were collected during a continuing tagging program on polar bears in the western Canadian Arctic from 1970 to 1978 (study area and methods are described in Stirling et al. (1975)).

Estimates of the population were then obtained from the mark–recapture series by:

[1] $\hat{N}_i = \hat{M}_i/\hat{p}_i$

where $\hat{N}_i$ = estimated population at time i; $\hat{M}_i$ = estimated marks in population before time i; and $\hat{p}_i$ = estimated fraction marked before time i; $\hat{p}_i$ is given by m_i/n_i where n_i = captures at

time i; and m_i = recaptures at time i. $\hat{M}_i$ is estimated by

[2] $\hat{M}_i = (\hat{M}_{i-1} + R_{i-1} - m_{i-1})\hat{\phi}$

where R_i = total marks released at time i. $R_i - m_i$ is thus new marks released at time i; and $\hat{M}_i + R_i - m_i$ is the total estimated marks after time i. Survival (ϕ) of these marks to the next capture time gives the estimated marks before that time.

The expected squared error of $\hat{M}_i$ is approximated by:

[3] $\mathrm{var}\,\hat{M}_i = \sum_{j=1}^{i-1} (R_{i-j} - m_{i-j})\hat{\phi}^j(1 - \hat{\phi}^j)$

$+ \left[\sum_{j=1}^{i-1} (R_{i-j} - m_{i-j}) \cdot j\hat{\phi}^{j-1} \right]^2 \mathrm{var}\,\hat{\phi}$

The first of these terms is the binomial variance due to the random survival of marks. The second is an approximation to that component of error variance of $\hat{M}_i$ which is due to error in the estimation of ϕ (Appendix A).[1] The variance of the population estimate can then be approximated thus:

[4] $\mathrm{var}\,\hat{N}_i = \mathrm{var}\,\hat{p}(\hat{M}_i^2/\hat{p}_i^4) + (\mathrm{var}\,\hat{M}_i)/\hat{p}_i^2$

where $\hat{p}_i$ and $\hat{M}_i$ are assumed uncorrelated as to error. The variance of $\hat{p}_i$ is given by

$\hat{p}_i(1 - \hat{p}_i)/(n_i - 1)$

(The derivation of estimated variances for $\hat{N}_i$ and $\hat{M}_i$ is given in Appendix A.)

The assumptions of this mark–recapture technique can be summarized as follows.

(1) The estimated annual survival rate, $\hat{\phi}$, and its variance, var $\hat{\phi}$, are constant throughout the entire study, are the same for marked and unmarked animals, and are known. Eberhardt (1977) suggests that for most long-lived marine mammals adult survival will be buffered from environmental variation and should remain relatively constant. Stirling et al. (1975) and Lentfer (1974) reported that polar bear populations in the eastern and western Beaufort Sea are distinct from each other with rates of exchange that are probably less than 5% per annum, so that movements in and out of the study area need not be considered. Therefore, changes in rates of annual survival should be solely responsible for changes in the numbers of tagged animals in the population. Survival rates for this population of polar bears were available from data independent of the mark–recapture estimates. All bears handled were aged by the removal and subsequent sectioning of a vestigial premolar (Stirling et al. 1975). An estimate of survival was calculated from the age distribution using an exponential decay curve, fitted by a log-linear regression. Using this method, annual survival (ϕ) was estimated to be 0.88. Comparison of the sex-specific annual survival rates calculated for different populations suggest that they are relatively constant between populations (Lentfer et al. 1977; Stirling et al. 1975). An error variance was deduced by considering a plausible range (0.76–1.0) to be 3.92 (2 × 1.96) standard errors. This gives var $\hat{\phi}$ = 0.00375.

(2) Marked and unmarked animals have the same probability of capture. This assumes that marked animals are evenly mixed within the population. This was accomplished in the western Canadian Arctic by spreading the tagging effort as evenly as practical over the study area. The validity of this assumption is enhanced by the annual mixing that occurs when the polar bears in this area move north in early summer because of the retreat of the pack ice (Stirling et al. 1975). In this analysis, we considered all members of the population as independent individuals and

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[1]Appendix A is available, at a nominal charge, from the Depository of Unpublished Data, CISTI, National Research Council of Canada, Ottawa, Ont., Canada K1A 0S2.

TABLE 1. Data used to estimate polar bear population and subsequent estimates

					i			
	1	2	3	4	5	6	7	8
Year	1970–1971	1971–1972	1972–1973	1973–1974	1974–1975	1975–1976	1976–1977	1977–1978
n_i	32	48	109	109	189	63	36	40
m_i	0	1	4	9	35	13	10	6
R_i	32	46	107	108	187	63	36	38
$\hat{\rho}_i$	—	0.0208	0.0367	0.0826	0.1852	0.2063	0.2778	0.1500
$\hat{M}_i$	—	28.16	64.38	147.29	216.74	324.49	329.55	318.16
SD* $\hat{M}_i$	—	2.69	6.99	16.51	29.69	48.79	65.93	79.85
$\hat{N}_i$	—	1353.85	1754.22	1783.17	1170.30	1572.90	1186.29	2121.07
SD $\hat{N}_i$	—	1346.97	881.65	603.27	239.96	454.98	397.43	959.54
$\hat{M}_i + R_i - m_i$	32	73.16	167.38	246.29	368.74	374.49	355.55	350.16

*Standard deviation.

did not stratify the sample according to age or sex. We did this because stratification would make the sample sizes too small to be useful. Therefore, assumption 2 is not completely met in that marked family groups contain members that are not randomly mixed with the rest of the population. This problem only affects family groups with cubs of the year and yearlings, as most 2 year olds are weaned and become independent shortly after being captured with their mothers. Gilbert (1976) used the Seber–Jolly interval to estimate the number of groups in the population and then used average group size to derive a total population estimate. This has disadvantages in that sample sizes become extremely small and the variance associated with the average group size is difficult to incorporate into the variance estimate for the total population. Future analysis needs to be directed toward identifying how much of a problem this adds to the estimation procedure.

(3) Marked animals do not lose their marks and all marks are reported on recovery. The marking procedure for polar bears involves putting tags on each ear, and tattooing the inside of both upper lips. On recapture, any lost tags are replaced after the animal is reidentified from the lip tattoo. Therefore, tag loss is not thought to be a serious problem. In this analysis, returns of marked animals from Inuk hunters were not incorporated because of the biases introduced by only having marked animals reported, instead of the total kill. Therefore, problems associated with not identifying or misidentifying marked animals from hunter returns were avoided.

(4) All samples are instantaneous. Instantaneous in this sense is relative to the survival of the population members (Siniff et al. 1977). For polar bears, annual survival is high enough to make mortality negligible between the start and the end of each sampling period.

Results

The estimates of population size (Table 1) suggest that the numbers of polar bears in the western Canadian Arctic declined markedly between the springs of 1974 and 1975, as previously reported by Stirling et al. (1975). Several independent sources of data support this suggestion. Between 1974 and 1975, the numbers of ringed seals dropped by 50% (Stirling et al. 1977) and their productivity by 90% (Smith and Stirling 1975, 1976). The natality rates of polar bears and the numbers of females accompanied by cubs of any age dropped by about 50 and 35% respectively between 1971–1973 and 1974–1975 (Stirling 1978). Finally, subadult male and female polar bears weighed significantly less in 1974 and 1975 than in 1971–1973 (Kingsley 1979). The environmental changes that began in the winter of 1973–1974 affected seal numbers and reproduction in the spring of 1974. Although the effects of the changes in seal distribution and abundance began to affect the survival of young bears and their weights immediately, the 1974 polar bear population estimate was taken too early in the year to detect the reduction in numbers that was so apparent by 1975.

Following the decline in numbers of both ringed seals and polar bears, the population of polar bears was expected to remain low for a period or to show. a gradual increase as seal numbers recovered. Aerial surveys of the distribution and abundance of ringed seals in 1976 and 1977 replicated the surveys of 1974 and 1975 but showed no increase in the population (Stirling, personal communication). However, the estimates of the polar bear population from 1976 through 1978 were erratic and their variances were sufficiently large that significant differences could not be established.

It is critical to evaluate why the technique was sufficiently sensitive to pinpoint the decline in 1974–1975 so accurately but gave inconsistent results in the subsequent 3 years. On inspection, it appears related to sample size. The samples in the 3 years leading up to 1974–1975 all exceeded 100 animals while those in the following 3 years were all much smaller. Another explanation is that ρ_i was inappropriately estimated because of problems in obtaining a representative sample. It is known that females with cubs of the year are underrepresented in the sample of captured bears (Stirling et al. 1975). It is also known that recaptures of family groups produce an upward bias in the estimation of ρ_i. In the light of the small sample sizes, this type of

TABLE 2. $(a)(R - m)\hat{\phi}^J(1 - \hat{\phi}^J)$ and the sum of such terms*; $(b) j\hat{\phi}^{J-1}(R - m)$ and the sum of such terms; and (c) data used to estimate variance of polar bear population estimate, and subsequent estimates

					i			
	1 (1970–1971)	2 (1971–1972)	3 (1972–1973)	4 (1973–1974)	5 (1974–1975)	6 (1975–1976)	7 (1976–1977)	8 (1977–1978)
		(a) $(R - m)\hat{\phi}^J(1 - \hat{\phi}^J)$ and the sum of such terms						
	(32)	3.38	5.59	6.95	7.68	7.98	7.96	7.73
		(45)	4.75	7.86	9.77	10.80	11.22	11.19
			(103)	10.88	17.99	22.36	24.73	25.67
				(99)	10.45	17.30	21.49	23.77
					(152)	16.05	26.56	32.99
						(50)	5.28	8.74
							(26)	2.75
$\sum_j (R - m)\phi^J(1 - \phi^J)$†		3.38	10.34	25.69	45.89	74.49	97.24	112.84
		(b) $j\hat{\phi}^{J-1}(R - m)$ and the sum of such terms						
	(32)	32.00	56.32	74.34	87.23	95.95	101.32	104.03
		(45)	45.00	79.20	104.54	122.66	134.93	142.49
			(103)	103.00	181.28	239.29	280.77	308.84
				(99)	99.00	174.24	230.00	269.86
					(152)	152.00	267.52	353.13
						(50)	50.00	88.00
							(26)	26.00
$\sum_j j\phi^{J-1}(R - m)$		32.00	101.32	256.54	472.05	784.14	1064.54	1292.35
$(\sum_j j\phi^{J-1}(R - m))^2$ var ϕ‡		3.84	38.50	246.80	835.62	2305.78	4249.67	6263.13
var $\hat{M}$		7.22	48.84	272.49	881.51	2380.27	4346.91	6375.97
		(c) Data used to estimate variance of polar bear population estimate, and subsequent estimates						
var $\hat{M}_i$	—	7.22	48.84	272.49	881.51	2 380.27	4 346.91	6 375.97
$(1/\hat{\rho}_i^2)$ var $\hat{M}_i$	—	16 688.24	36 261.31	39 938.38	25 700.72	55 927.80	56 326.94	283 376.44
$(\hat{M}_i^2/\hat{\rho}_i^4)$ var $\hat{\rho}_i$	—	1 797 651.34	741 035.16	323 995.23	31 881.92	151 084.80	101 625.08	637 347.54
var $\hat{N}_i$	—	1 814 340	777 300	363 930	57 580	207 010	157 950	920 720
Percentage of var $\hat{N}_i$ associated with $(1/\hat{\rho}_i^2)$ var $\hat{M}_i$	—	0.92	4.67	10.97	44.63	27.02	35.66	30.78

*Entries in parentheses are $(R_i - m_i)$. Succeeding entries on the same line are $(R_i - M_i)\phi^J(1 - \phi^J)$ for successive values of j.
†$\phi = 0.88$.
‡var $\phi = 0.00357$.

problem could be responsible for the erratic estimate of population size.

In an effort to reduce the variance associated with the estimated population, an analysis of the relative contribution to the total variation of various components of the variance estimate was conducted (Table 2). The fraction of the total variation of $\hat{N}_i$ that was associated with the term $(1/\hat{\rho}_i^2)$ var $\hat{M}_i$ ranged between 0.01 and 0.45. Thus most of the error variance of $\hat{N}_i$ was contributed by the term $(\hat{M}_i^2/\hat{\rho}_i^4)$ var $\hat{\rho}_i$. Noting that

$$[5] \quad \hat{M}_i = \hat{\rho}_i \hat{N}_i$$

the var $\hat{N}_i$, when rewritten to incorporate Eq. 5, becomes

$$[6] \quad \text{var } \hat{N}_i = (\hat{N}_i^2 \text{ var } \hat{\rho}_i + \text{var } \hat{M}_i)/\hat{\rho}^2,$$

with the term $\hat{N}_i^2$ var $\hat{\rho}_i$ predominating. Assuming that var $\hat{N}_i$ is negligible compared with $\hat{N}_i^2$ var $\hat{\rho}_i$, Eq. 6 can be rewritten as

$$[7] \quad \text{var } \hat{N}_i = [\hat{N}_i^2(1 - \hat{\rho}_i)]/[(n_i - 1)\hat{\rho}_i]$$

Equation 7 is useful in predicting the standard error of an estimated $\hat{N}_i$ for a particular sample size. Assuming that $\hat{N}_i$ equals 1500 and $\hat{\rho}_i$ equals either 0.1 or 0.2, the precision of the estimate for N_i increases very rapidly as sample sizes initially increase (Fig. 1). However, the precision of the estimate does not increase as rapidly after sample size reaches 200. This analysis suggests that with the population estimation technique described in this paper, relatively imprecise estimates will be produced with sample sizes of less than 50, given that the proportion of marked animals in the population is between 0.1 and 0.2. Sample sizes of 150 will produce a much more precise estimate, but the cost of such a sample may be prohibitive. If research needs demand a particular level of confidence, cost needs to be taken into consideration. However, samples of less than 50 should probably be discouraged regardless and sample sizes of 150 or more should be encouraged if possible.

The analysis of the various sources of variance (Table 2) also shows a progressive increase in var

TABLE 3. Comparison of population estimates from Lincoln–Peterson and Seber–Jolly models

|	1 (1970–1971)	2 (1971–1972)	3 (1972–1973)	4 (1973–1974)	5 (1974–1975)	6 (1975–1976)	7 (1976–1977)	8 (1977–1978)
				Lincoln–Peterson estimates				
M_i	0	32	77	180	279	431	481	507
$\hat{N}_i$	—	1538	2098	2179	1506	2089	1731	3380
				Seber–Jolly estimates				
r_i	8	17	16	26	11	0	0	—
z_i	0	7	20	27	18	16	6	0
$\hat{M}_i$	0	20	138*	121	341*	—	—	—
$\hat{p}_i$	0	0.0208	0.0367	0.0826	0.1852	0.2063	0.2778	0.1500
$\hat{N}_i$	—	962	3760	1465	1841	—	—	—
$\hat{\phi}_i$	0.62	2.12	0.50	1.55	—	—	—	—

*M_i is larger than maximum M_i possible.
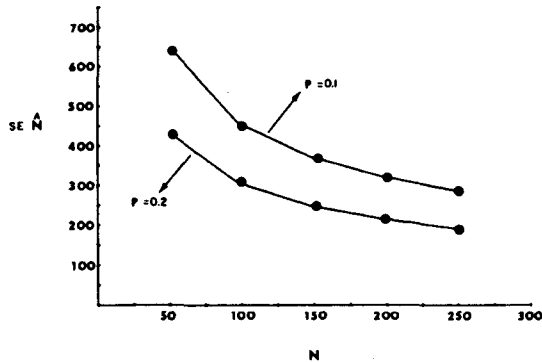
FIG. 1. Sample size versus standard error of population estimate. p, proportion of population that is marked; n, sample size; SE $\hat{N}$, standard deviation of the population estimate.

$\hat{M}_i$. The components of variation due to var $\hat{M}_i$ form an increasing fraction of the error variance of $\hat{N}$, and this suggests that this estimation procedure will have to be truncated when this source of variation starts to predominate in the error variances of $\hat{N}_i$. Presumably, this could be avoided if a Seber–Jolly estimate of $\hat{M}_i$ could be made at some point during the study. However, so far, the principal contribution to the error of $\hat{N}_i$ is associated with the var $\hat{p}_i$. Therefore, the most effective way of increasing the precision of the estimate of N_i is to increase the proportion of marked animals in the population or to increase the number of animals that are captured in each sample period.

Discussion

The crux of this technique is the incorporation of additional independent information in the estimation of the number of marks in the population at time i. In this case, survival estimates allow for the estimation of M_i in an open population. The survival rate is estimated from age structure data and necessarily assumes that (1) the growth rate of the population is incorporated into the survival estimate (Payne 1977), (2) the survival rate is constant, and (3) the age structure of the population is stationary. The estimation of M_i also assumes that emigration of marked animals is negligible or at least absorbed in the survival estimate. One advantage with incorporating additional information into the population model is that the model need not be as general and can therefore be more efficient in estimating specific parameters of the population.

A comparison of Lincoln–Peterson and Seber–Jolly population estimates (Table 3) with the estimates produced in this paper suggests that assumptions of the Lincoln–Peterson and Seber–Jolly models are unavoidably violated. The closed population assumption of the Lincoln–Peterson model produces an estimated number of marks that is necessarily biasing $\hat{N}_i$ upwards. This is because the estimated number of marks in the population ($\hat{M}$) at time i assumes that none of the animals previously marked have suffered any mortality. Therefore, $\hat{M}_i/\hat{p}_i$ will tend to be too large.

The Seber–Jolly estimates (Table 3) are known to be unreliable because two of the four estimates of $\hat{M}_i$ are larger than the maximum number of marks that could exist. This is reflected in survival rates that are greater than 1.0 for these 2 years. Specifically which assumption of the Seber–Jolly model is violated is not clear. Sample sizes in specific years may be responsible for overestimating M_i. It may also be that r_i/R_i may not equal $Z_i/(\hat{M}_i - m_i)$ (this is necessarily assumed with Seber–Jolly estimate of $\hat{M}_i$: see Seber 1973, p. 196). However, the reasons why these two ratios would not be equal have not been identified as yet.

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