ANURSUS: A POPULATION ANALYSIS SYSTEM FOR POLAR BEARS (Ursus maritimus)

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Abstract: ANURSUS estimates the mean and standard error of polar bear (Ursus maritimus) population parameters (i.e., cub survival rate, litter survival rate, subadult and adult survival rates, litter production rate, litter size, and mating and reproductive intervals) from age specific observations of litter size and family group status. The parameterization for recruitment estimates is unconventional so that the 3-year reproduction cycle of polar bears may be correctly described (Taylor et al. 1987).

Previous estimates of annual polar bear cub survival rate considered only the loss of individual cubs; they did not consider abandonment of single cub litters or loss of entire litters. We provide an estimation procedure that accommodates all sources of cub mortality for arctic polar bear populations. Data required for the procedure include the female age structure; number of females with offspring; presence or absence of cubs-of-the-year, yearlings, or 2-year-olds; and observed litter size.

The average age of 1st reproduction may be calculated by weighting each age by its probability of 1st reproduction and determining the weighted average. The probability of 1st reproduction at age x is determined from age specific litter production rates and the standing age distribution. The average age is for all females in the population during the census period.

The mean interval between producing litters (litter recruitment interval) and the mean interval between mating availability (mating interval) are different for polar bears. The reciprocals of the 2 intervals, mean litter recruitment rate and mean mating rate, are useful to compare populations but should not be used for population projections. In addition to litter recruitment interval and mating interval, 2 measures of the expected number of litter recruitment events are also defined.

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In 1978 the International Union for Conservation of Nature and Natural Resources (I.U.C.N.) Polar Bear Specialists' Group recognized the need to standardize analyses of polar bear population data. Traditional life table methods were evaluated but they required assumptions that did not correspond to polar bear life history biology. Therefore, new approaches were suggested, evaluated, and modified. The result of this process was a series of algorithms termed ANURSUS. ANURSUS has been coded in FORTRAN and is a series of interrelated subroutines and programs which are available on request.

Our primary goal was to obtain an estimate of population growth rate (λ) and a measure of sustainable harvest. A secondary goal was to develop summary statistics to facilitate comparisons among polar bear populations. Additionally, the multi-annual polar bear reproduction cycle parameters are summarized as mean annual rates to facilitate comparisons between populations in which adult females breed annually. This paper also describes the ANURSUS results. To illustrate the type of data required and estimates produced, we analyzed an example data set. Because the alogrithms correctly correspond to polar bear life history, the discussion is mainly concerned with the assumptions and possible sources of bias in the data.

The ANURSUS approach has 3 main components. The 1st is a modified Fisher-Ford (Fisher and Ford 1947) procedure to obtain population estimates and survival rates from mark-recapture data. The 2nd component is a procedure for estimating the reproduction parameter rates. A parameterization consistent with the 3-year reproduction cycle was necessary to develop meaningful estimates of reproduction rates. The final component is a set of projection models that restate the estimates of vital rates, population numbers, and age structure observations as summary parameters. These parameters include population growth rate, sustainable harvest rate, average age at 1st reproduction, mean annual recruitment rate, and the average number of recruits produced per adult female.

The calculation procedures have been organized so the derivation of a parameter precedes its use in calculations for other parameters. The projection model (Taylor et al., in press) requires a measure of survival rate; however, estimates of the parameters relating to recruitment may be made with reference to the standing age distribution. This standing age approach is explained in the 1st section.

The ANURSUS analysis procedure requires that there are no age, sex, or family status biases in the observations. The time of census is spring, after the females have emerged from maternity dens with cubs, and during the mating season.

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STANDING AGE DISTRIBUTIONS

The ANURSUS analysis procedures are for standing, rather than cohort, age distributions. The standing age frequency curve cannot be analyzed directly for age specific survival rate unless the population growth rate is known (Caughley 1966, 1977). When the population is not at stable age distribution, the ratio of the number of individuals of age x at time t ($N_{x,t}$) to the number of age x+1 at time t ($N_{x+1,t}$) depends on age specific survival rate (p_x), population growth rate (λ), and the magnitude of deviation from stable-age distribution.

Any standing age distribution gives a measure of the relationship between $N_{x,t}$ and $N_{x+1,t}$. We term this measure the Phi (ϕ) schedule, where Phi of age x (ϕ_x) is $N_{x+1,t}/N_{x,t}$. At stable age distribution $\phi_x = p_x/\lambda$ and at stationary ($\lambda = 1.0$) age distributions $\phi_x = p_x$. Several techniques are available for estimating ϕ for populations with a constant ϕ_x schedule. The Chapman-Robson (1960) method is superior because it provides an unbiased, minimum variance estimator (Barlow 1982). We assume that ϕ_x is constant for the adult (age 3+ years) age strata (DeMaster et al. 1980, Lentfer et al. 1980, Furnell and Schweinsburg 1984).

CUB SURVIVAL

Arctic polar bears remain with their mother for about 2.5 years and are weaned in the spring of their 3rd year. Throughout most of their range, the litter size of cubs-of-the-year (aged 0.5 years) rarely exceeds 2. Exceptions occur in the subarctic Hudson Bay population where some polar bears produce litters every other year and about 10% have litters of 3 (Ramsay and Stirling 1982).

We assume the maximum litter size of cubs is 2 (DeMaster and Stirling 1981, 1983). We also assume reproduction rates plateau at maturity (Caughley 1977) so that litter size does not vary systematically with age, although an age-specific procedure can be written. For brevity, we present a procedure that estimates mean values for all age classes pooled.

During the period of maternal care, polar bear young may die as a result of: 1) death of their mother (and subsequent death of accompanying cubs and yearlings); 2) incidents affecting individual cubs and yearlings; 3) incidents affecting whole litters, but not the mother; and 4) incidents related specifically to the loss of single cub litters (e.g., abandonment).

DeMaster and Stirling (1983) gave a procedure to estimate individual cub mortality (Type 2) given that the female survives but mistakenly assumed that only Types 1 and 2 mortality occur (Larsen 1985). The following estimation procedure explicitly accounts for all 4 types of cub mortality.

Individual cub mortality (Type 2) will affect mean litter size, whereas mortality due to the mother's death (Type 1) and loss of the entire litter (Type 3) will not. When only surviving litters are considered, litter size is either 1 or 2. This binomial parameterization allows us to determine the proportions of 1- and 2-cub litters from mean litter size. The expected proportions depend on the mean litter size of cubs and individual cub survival rate (DeMaster and Stirling 1983). Figure 1 depicts the probability contingencies given that at least 1 of the littermates survive.

If the average litter size of yearlings is less than the average litter size of cubs, a single cub survival rate in both 1- and 2-cub litters is assumed (Model 1). If the average litter size of yearlings is greater

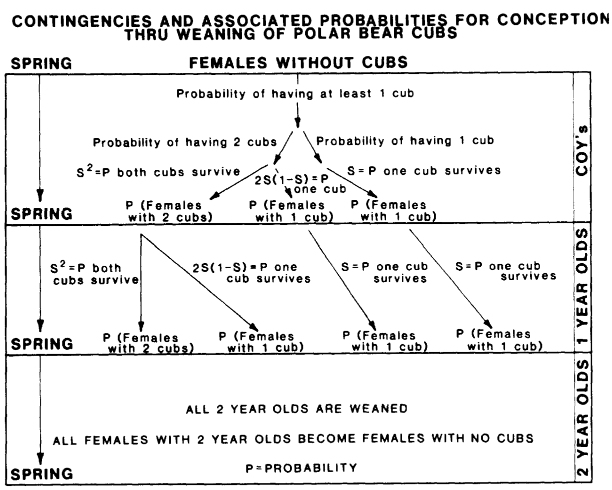

Fig. 1. Survival and mortality contingencies with associated probabilities for polar bear cub litters.

than the average litter size of cubs, separate survival rates are calculated for cubs in 1- and 2-cub litters (Model 2). Litter size can only increase if cubs in single cub litters experience a higher mortality than cubs in 2-cub litters.

The following terminology is employed in the 2 models:

$P1C$ = proportion of cub litters with 1 cub,
$P2C$ = proportion of cub litters with 2 cubs,
$S1$ = annual survival rate of cubs in 1-cub litters,
$S2$ = annual survival rate of cubs in 2-cub litters,
$P1Y$ = proportion of single yearling litters,
$P2Y$ = proportion of double yearling litters,
S = annual survival rate of cubs when survival rate is not different between 1- and 2-cub litters,
$\overline{C}$ = mean litter size of cubs,
$\overline{Y}$ = mean litter size of yearlings.

Model 1: Non-Differential Mortality

If $S2 = S1$ (i.e., average cub litter size > average yearling litter size):

$$P2Y = \frac{P2C \times S^2}{P2C \times S^2 + P2C \times 2 \times (S\text{-}S^2) + S \times P1C}$$

therefore,

$$S = \frac{(P2Y \times P2C \times 2) + (P2Y \times P1C)}{[P2C \times (1 + 2 \times P2Y)] - (P2C \times P2Y)}$$

$$= \frac{(\overline{Y} - 1) \times \overline{C}}{(\overline{C} - 1) \times \overline{Y}}.$$

Model 2: Differential Mortality

$S1 < S2$ [i.e., average cub litter size < average yearling litter size]

$$P2Y = \frac{P2C \times S2^2}{P2C \times S2^2 + P2C \times 2 \times (S2 - S^2) + P1C \times S1},$$

$$S1 = \frac{P2C \times S2^2 - (P2C \times P2Y) \times (2 \times S2\text{-}S2^2)}{P2Y \times P1C}.$$

This equation gives the relationship of $S1$ to $S2$ when mean litter size increases with age. The maximum value of $S1$ is at $S2 = 1.0$, whereas the minimum value of $S2$ is at $S1 = 0.0$. Without an independent estimate of $S1$ or $S2$, a point estimate of either parameter is not possible using the change in litter size method. Additionally, the relationship between $S1$ and $S2$ is nonlinear so the ratio of these parameters is not constant.

Individual survival rates are calculated for yearlings in the same manner as for cubs. Once the individual survival rates of cubs and yearlings have been calculated, the litter survival rates (LSR) of cubs and yearlings may be estimated.

The number of females at age x with cubs that are observed with at least 1 yearling at age x+1 is a function of ϕ_x, the fraction of cub litters in which at least 1 cub survives (based on individual cub survival rates), and the whole litter survival rate (LSR). Assuming that increased mortality of cubs in single cub litters does not occur (i.e., $S1 = S2 = S$), the ratio of females with cub litters to females with yearling litters is:

$$\frac{F \text{ with cubs}_x}{F \text{ with yr1}_{x+1}}$$

$$= \frac{1}{[P2C \times (2S - S^2) + P1C \times S] \times \phi \times LSR \text{ (cubs)}},$$

LSR (cubs)

$$= \frac{F \text{ with } yr1_{x+1}}{F \text{ with } cubs_x \times [P2C \times (2S - S^2) + P1C \times S] \times \phi}.$$

Litter survival rate for yearlings is calculated by comparing the ratio of females with yearlings at age x to females with 2-year-olds at age x+1. The age specific rates for both cubs and yearlings may be averaged if the litter survival rate is the same for all ages. Because data for this calculation are taken from the standing age structure, ϕ_x is the appropriate value to relate number at age x to number at age x+1. However, when the total cub survival rate is calculated for use in a projection model, the actual female survival rate p_x or (FSR) should be used. The effect of litter survival rate and female survival rate on total cub survival rate is independent of the proportions of 1- and 2-cub litters:

YSR = total young survival rate,
YSR (cubs) = $[P2C \times (2 \times S2\text{-}S2^2) + P1C \times S1] \times FSR \times LSR(\text{cubs})$,
YSR (yrl) (when $S1 = S2$) = $[P2C \times (2 \times S\text{-}S2) + P1C \times S] \times FSR \times LSR(\text{yrl})$.

LITTER RECRUITMENT RATES FOR FEMALES AVAILABLE TO MATE

Females with cubs and yearlings typically do not mate (Ramsay and Stirling 1986). Females available for mating include females with 2-year-olds and females with no offspring. The mating season is from mid-spring to early summer. Our measure of litter recruitment rate for available females (*LRAF*) is the fraction of females available to mate at age x that would be observed with litters at age x+1, if all of them survived:

$$LRAF_x = \frac{N_{x+1,t\ (\text{with cubs})}}{N_{x,t\ (\text{available})} \times \phi}.$$

LRAF also may be calculated by comparing the number of females with yearlings (age = x+2) to the number of females available at age x. This procedure must include the possibility of a female producing but losing a litter of cubs (DeMaster and Stirling 1983, Larsen 1985). The following terms allow the fraction of females with cubs that survive but lose their litters to be written explicitly:

Ratio = ratio of females with yearlings at x+2 to females with cubs at x+1 given that the mother survived and excluding loss of litters as a unit. This ratio is calculated from the mortality contingencies associated with the transition from cubs to yearlings.
$= [S2^2 + 2 \times S2 \times (1\text{-}S2)] \times P2C + S1 \times P1C$
$= P2C \times (2 \times S2\text{-}S2^2) + P1C \times S1.$

Age specific *LRAF* may be calculated using the following formulas:

Age Specific Litter Recruitment Rate of Females with Cubs:

$$LRAF_x = \frac{\text{females with cubs aged } 0.5_{x+1} \times \phi^{-1}}{\text{females available}_x}.$$

Age Specific Litter Recruitment Rate of Available Females with Yearlings:

$$LRAF_x = \frac{\text{females w/yrl}_{x+2} \times \text{Ratio}^{-1} \times \phi^{-2} \times LSR(\text{cubs})^{-1}}{\text{females available}_x}.$$

The 3rd "averaged" estimate reduces the variability of the numerator (Stirling et al. 1980, Furnell and Schweinsburg 1984). This estimate assumes that neither females with cubs nor females with yearlings are undersampled. The estimate combines the previous 2 estimates as follows:

$Q = \text{females w/cubs}_{x+1} \times \phi^{-1}$,
$T = \text{females w/yrl}_{x+2} \times \phi^{-2} \times \text{Ratio}^{-1} \times LSR(\text{cubs})^{-1}$,

$$LRAF_x = \frac{Q + T}{2 \times \text{females available}_x}.$$

An additional estimate using females with cubs, females with yearlings, and females with 2-year-olds can be derived in the same manner.

AVERAGE AGE OF 1ST REPRODUCTION

The average age of 1st reproduction (i.e., average age of 1st litter production) of a specific cohort may not be the same as the average age of 1st reproduction of the female population. The reason for this disparity is that selective harvest, population growth rate, and variability in vital rates alter the age structure, thus altering the proportion of females at age x from that of a horizontal or cohort age distribution. Our estimate of the average age of 1st reproduction is for the observed population of females.

An approach to this problem was suggested by DeMaster (1981), however, his approach was specific to stationary populations that mate annually. We calculate the average age of 1st reproduction by determining the weighted mean of all possible ages of 1st reproduction. The weighting factor is the number of females that first produce litters at that age. For polar bears, the probability of first producing a litter at age x is a function of subadult litter recruitment rate, *LRAF*, and ϕ. To determine the weighting factor we define the following quantities:

A_x = females available for reproduction at age x that have not produced a litter previously,

R_x = females that produce a litter for the 1st time at age x,
b = earliest age of reproductive maturity (i.e., available for mating),
b+1 = earliest age of litter production.

For all ages x greater than b:

$$A_x = A_b \times \prod_{i=b}^{x} [(1.0\text{-}LRAF_{i-1} \times \phi_{i-1}],$$

$$R_x = A_{x-1} \times LRAF_{x-1}.$$

The weighted average age of 1st reproduction ($\overline{R}$) is calculated as the weighted mean:

$$\overline{R} = \sum_{x=b+1}^{w} (R_x \times x) / \sum_{x=b+1}^{w} R_x$$

where w is the final age class. The observed age specific litter recruitment rate of subadults should be used rather than *LRAF* for the subadult age classes.

PROJECTION OF MEAN REPRODUCTION INTERVALS

Factors influencing how often a female polar bear is available to mate and how often a litter is produced include litter size, female survival, cub survival, and litter recruitment rate. Our measures of mating and litter recruitment intervals are for cohorts of mature females starting at the age of reproductive maturity. The probability of litter recruitment intervals of 2 years, 3 years, 4 years, and so forth, is determined and each interval is weighted by its associated probability. The weighted mean is termed the mean litter interval. Similarly, the probability of mating intervals of 1, 2, or 3 years is determined and each interval is weighted by its associated probability. The weighted mean is termed the mean mating interval.

The reciprocal of litter recruitment interval is termed reproduction rate and the reciprocal of mating interval is termed mating rate (Stirling et al. 1980, Lentfer et al. 1980, DeMaster and Stirling 1981). Caughley (1977) cautions against using the product of litter recruitment rate and litter size as an estimate of annual recruitment rate.

The probabilities of the various litter recruitment and mating intervals are only for surviving females because we include adult female mortality in our definition of these intervals. Thus, our weighting factors (probabilities) for various intervals do not sum to 1. The difference between the sum of probabilities for various intervals and 1 is equal to the probability that a given female will die before she again mates or produces a 2nd litter.

The parameters used are consistent with those already defined The only exception is the use of annual mortality rate (p_x). This quantity is assumed to be available from mark-recapture studies or long-term telemetry programs. We distinguish between ϕ_x, which is available from the observed or standing age structure, and p_x which is not:

$$p_x = (N_{x+1,t+1}/N_{x,t})$$
$$= p \text{ (i.e., assume constant survival rate).}$$

The contingencies and associated probabilities for the transition from cubs to yearlings are illustrated in Figure 1. The transition from yearlings to 2-year-olds is academic in this instance because females with 2-year-olds are presumed available for mating. The availability for mating of a female that has lost her yearlings is assumed to be the same as that for a female with 2-year-olds or with no cubs.

Litter Recruitment Interval

We here define the intervals between the production of litters. All mortality is assumed to occur after mating but before the next census period (i.e., during winter). Thus, a female with cubs at age x cannot have cubs at age x+1 (Ramsay and Stirling, 1986).

A = fraction of females with cubs that lose their litters,
= $(1.0\text{-}S2)^2 \times P2C + (1.0\text{-}S1) \times P1C + [1.0\text{-}LSR(\text{cubs})]$,
1.0 - A = fraction of females that keep their cubs at least to yearlings,
I_t = fraction of females with reproduction interval of t years,
t = number of years,
I_1 = 0.0,
I_2 = $LRAF \times p^2 \times A$,
I_3 = $LRAF \times p^3 \times [(1.0\text{-}LRAF) \times A + (1.0\text{-}A)]$,

$$I_t = LRAF \times p^t \times [(1.0\text{-}LRAF)^{(t-2)} \times A + (1.0\text{-}LRAF)^{(t-3)} \times (1.0\text{-}A)],$$

$$ISUM = \sum_{t=1}^{w} I_t \times t.$$

$$FRSUM = \sum_{t=1}^{w} I_t.$$

$$\text{Mean reproduction interval} = \frac{ISUM}{FRSUM}.$$

Unweighted litter recruitment rate for adult females

$$= \frac{1}{\text{mean reproduction interval}}.$$

Fraction of reproducing females that have only 1 litter

$$= 1.0 - FRSUM.$$

Mating Interval

Adult females are not available to mate when they are encumbered with cubs or yearlings. Thus the maximum mating interval is 3 years.

M_t = fraction of females with mating interval of t years,

$$M_1 = p \times (1.0\text{-}LRAF),$$
$$M_2 = p^2 \times LRAF \times A,$$
$$M_3 = p^3 \text{ x } LRAF \times (1.0\text{-}A),$$
$$MSUM = \sum_{t=1}^{3} M_t \times t,$$
$$FMSUM = \sum_{t=1}^{3} M_t,$$

$$\text{Mean mating interval} = \frac{MSUM}{FMSUM},$$

Unweighted mating rate (mating availability rate)

$$= \frac{1.0}{\text{mean mating interval}}.$$

Interval from Availability to Production of 1st Litters

The mean intervals described here are from the time an adult female is available for mating to the time when the female appears with a litter of cubs:

Y_t = proportion of females with a 1st litter interval of t years,

$$Y_1 = p \times LRAF,$$
$$Y_2 = p^2 \times (1.0\text{-}LRAF) \times LRAF,$$
$$Y_3 = p^3 \times (1.0\text{-}LRAF)^2 \times LRAF,$$
$$Y_t = p^t \times (1.0\text{-}LRAF)^{(t-1)} \times LRAF,$$

$$YSUM = \sum_{t=1}^{w} Y_t \times t,$$

$$FYSUM = \sum_{t=1}^{w} Y_t.$$

The mean interval between availability and production of 1st litter is:

$$\frac{YSUM}{FYSUM}.$$

1.0 - *FYSUM* = Fraction of adult females available to mate that never produce another litter of cubs.

VARIANCE ESTIMATES

Polar bear population parameters vary from year to year (Stirling et al. 1975, 1978; Furnell and Schweinsburg 1984). We assume that the variability is not due to systematic causes such as an increasing per capita harvest rate or an approach to carrying capacity. Our estimates of variance utilize the nonparametric "jackknife" procedure (Arveson 1969). Application of this procedure is valid when the total data set may be stratified in a meaningful way; the ANURSUS procedure stratifies data by year.

Most rates are binomial parameters, however, the jackknife estimate is essentially the mean of the annual means. These annual means are normally distributed and the variance, standard deviation, and standard error (standard deviation of annual means) may be calculated for the years sampled.

AN EXAMPLE

Estimates of the previously described parameters and their variances (Table 1) were made using a pooled data set (Appendix A) collected in the Canadian arctic from 1970 to 1984 (I. Stirling, unpubl. data).

Although only 3 years are required to wean a litter of cubs and reproduce again, the estimate of litter recruitment interval suggests that the usual litter recruitment cycle is 3.72 years. The average rate at which female recruits are produced is the product of litter recruitment rate, litter size, and proportion of cubs that are female ($0.269 \times 1.689 \times 0.50 = 0.227$). This value is termed the "unweighted mean recruitment rate" (Caughley 1977).

The estimated mean mating interval (1.999 years, Table 1) suggests that about 50% of the total adult females were available for mating each year, but only about 30% of all adult females were producing litters. The substantial fraction of females that reach maturity but never breed (0.102, Table 1) or produce only 1 litter (0.201, Table 1), resulted from the long period of maternal care and the numerical effect of fractional mortality on younger (more abundant) age classes.

A mean annual survival rate of 0.95 with the standard error equal to 0.011 (Taylor, unpubl. data) was used to calculate recruitment and mating intervals.

DISCUSSION

The census period for polar bears captured in arctic latitudes typically begins after most females emerge from the den and extends through most of the mating season. Active ice areas where polar bears concentrate for hunting are most intensively searched. In areas where the offshore sea ice is extensive, females with cubs often remain on the shore-fast ice to feed. However, in island archipelago areas, the active ice areas are not so large and not as distant from the shore-fast ice. Depending on the area searched and the effort made to collect a representative sample, the possibility of bias in availability of some family group types may exist. The existence and extent of this bias can be examined by learning more about the relationship between the maternal status of polar bears and their geographical distribution.

Because the census period extends through the mating season, some females may have already separated from their 2-year-old offspring. Males seeking mating opportunities sometimes force 2-year-olds away and 2-year-olds may leave the female to hunt for themselves. Trends in litter size of 2-year-olds during the spring tagging season can verify this type of bias and provide a method to extrapolate the "before-weaning" spring litter size.

Table 1. Age specific observations of family status of female polar bears between 1970 and 1984 were pooled for the Canadian High Arctic. These data (Appendix A) were used to provide estimates of individual and litter survival rate as described in the text.

Parameter	Mean	Standard error
Individual cub survival rate	0.880	0.051
Individual yearling survival rate	0.796	0.096
Cub litter survival rate	0.770	0.120
Yearling litter survival rate	0.769	0.147
Combined cub survival rate	0.678	—
Combined yearling survival rate	0.612	—
Litter size cubs	1.689	0.032
Litter size yearlings	1.560	0.050
Litter size 2-year-olds	1.398	0.066
Adult litter recruitment rate	0.589	0.279
Average age of 1st recruitment	5.789	1.294
Litter recruitment interval	3.720	0.1222
Mating interval	1.999	0.0730
Litter recruitment rate	0.269	0.0085
Mating rate	0.501	0.0192
Fraction of females with only 1 litter	0.201	0.0206
Fraction of females that mature, but mate unsuccessfully	0.102	0.0124

Appendix A. Pooled mark-recapture data for female polar bears in arctic Canada between 1970 and 1984.

Age	Females with						
	No cubs	1 cub	2 cubs	1 1-yr-old	2 1-yr-old	1 2-yr-old	2 2-yr-old
0	126	0	0	0	0	0	0
1	88	0	0	0	0	0	0
2	76	0	0	0	0	0	0
3	85	0	0	0	0	0	0
4	83	0	1	0	0	0	0
5	101	14	42	3	2	0	0
6	88	13	18	10	7	6	1
7	61	6	16	0	6	4	5
8	73	4	22	6	3	6	4
9	49	7	3	9	6	7	1
10	30	1	9	2	6	3	2
11	30	1	7	2	6	2	1
12	29	3	4	2	5	1	3
13	26	1	6	3	4	1	4
14	18	0	4	3	3	2	0
15	13	1	2	0	3	0	0
16	14	2	1	1	1	1	4
17	12	0	3	2	3	1	0
18	9	1	1	1	2	0	0
19	11	0	3	1	1	2	1
20	3	0	0	1	0	0	0
21	7	0	0	2	1	1	0
22	4	0	0	0	1	1	0
23	3	1	1	0	0	1	0
24+	18	0	1	1	0	1	0

Bias in litter size will affect estimates of individual young survival rate. Bias in abundance of family groups will affect the estimate of young litter survival rate. Hansson and Thomassen (1983) found no differences in litter size between family groups leaving the den early or late in Svalbard. Even if the number of females with cubs was underestimated, the estimate of litter size and independent cub survival would not be affected.

DeMaster and Stirling (1983) state that the mean litter size of cubs must be larger than the mean litter size of yearlings. This is only true if individual cubs in 2-cub litters survive at a rate < that of individual cubs in 1-cub litters. DeMaster and Stirling (1983) cited Lentfer et al. (1980) as recording a higher mean litter size for yearlings than cubs in Alaska, and attributed the discrepancy to a sampling bias against 2-cub litters. However, Lentfer et al. (1980) noted that the difference between cub and yearling litter size was not significant. Subsequent data and all data pooled for Alaska give a mean litter size of cubs larger than the mean litter size of yearlings (Taylor 1982, S. Amstrup, pers. commun.).

Tait (1980) showed that it can be advantageous for female grizzly bears to abandon single cub litters. Although an increase in the lifetime mean litter size can result from abandonment of single cub litters, the small maximum litter size (2.0), late age of reproductive maturity, and low litter production rate for breeding females (DeMaster and Stirling 1981) make abandonment by polar bears an unlikely reproductive strategy.

The likelihood that a female will be observed with a litter of cubs or yearlings, lose the litter, and produce a litter the following year is very small. Only 1 example of this type has been observed in arctic latitudes (Ramsay and Stirling 1986). The ANURSUS procedure for determining adult litter recruitment rate does not count those females with cubs or yearlings as available for mating. Thus, the number of available females may be slightly underestimated and the adult litter recruitment rates may be slightly overestimated. Because the actual number of litters counted at census is the age specific product of litter recruitment rate and the number of available females, this error does not affect population projections.

A measure analagous to *LRAF* termed "litter production rate" was defined by Stirling et al. (1980) as:

$$\frac{\text{No. females aged x+1 with cubs + No. females aged x+2 with yrl}}{\text{No. females aged x+1 + No. females aged x+2}}.$$

The Stirling et al. (1980) estimate assumed no mortality of cubs or adults, although they estimated adult mortality at 13% and noted a decline in number of litters and litter size from cubs to yearlings to 2-year-olds. Furnell and Schweinsburg (1984) also defined an analogous "probability of parturition" that considered adult mortality but not cub mortality.

Estimates of population parameters may be combined to provide summary statistics. Examples defined in the text include average age of 1st reproduction, mean litter recruitment rate, and mean mating rate. Population parameters may also be combined to provide accurate estimates of sustainable harvest and descriptions of population dynamics (Taylor et. al, in press).

ANURSUS provides estimates of population parameters and summary statistics that are internally consistent and match the life history of polar bears. The data for these estimates are readily collected in the field. The ANURSUS approach does not require assumptions regarding the stability of age distribution or population growth rate. Nonparametric estimates of the mean and standard errors allow statistical comparisons and Monte Carlo population projections. The ANURSUS approach can be modified for brown (*U. arctos*) and black bears (*U. americanus*), or any animal with a multi-year reproduction cycle.

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