MODELING THE SUSTAINABLE HARVEST OF FEMALE POLAR BEARS

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Abstract: We explored the boundaries of sustainable harvest of polar bears (*Ursus maritimus*) by considering a range of values for population parameters in a discrete, age specific model structured to mimic polar bear life history. Survival rate of adult females is the predominant factor affecting population growth rate and sustainable harvest of polar bears although other factors may also be significant; e.g., cub survival, litter size, and age of 1st reproduction. The parameter of least importance is litter production rate. Deferred reproduction has a small effect on population growth rate. These findings are consistent with theoretical predictions for populations experiencing density independent mortality mainly restricted to juveniles. The critical issue, when considering the long-term effect of any harvest, is the effect on numbers of breeding females. Under optimal conditions the sustainable yield of adult female polar bears is typically <1.6% of the total population.

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We use a model to explore the constraints that polar bear life history structure places on sustainable rates of harvest. We develop a mathematical description of polar bear life history, including harvest as a separate source of mortality. By simulating several harvest types, the model yields information on the effects of harvest types and on the sensitivity of the harvest to changes in vital rates (parameter values). Additionally, a "best case" scenario can be developed using maximum values for survival and reproduction.

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The life history pattern of polar bears is typical of species in which environmental fluctuations strongly affect recruitment rate and survival of the young (Hairston et al. 1970; Schaffer 1974*a*,*b*; Stearns 1977; Horn 1978; Goodman 1979, 1981). Polar bears are a long-lived, late maturing species with a low rate of annual recruitment (DeMaster and Stirling 1981).

Polar bears exhibit "birth pulse" (Caughley 1977) reproduction. Typically, a small fraction of polar bear females breed for the 1st time at age 3, and slightly more begin breeding at age 4. Generally all females breed at adult rates from age 5 onwards (initial age = 0). However, age specific litter production rates vary according to environmental conditions (Stirling et al. 1975, 1977, 1978).

During the 1st 2 years following birth, cubs remain with the female and she is unavailable for breeding. Some females with cubs lose their litters and become available for breeding at the next season. Females with 2-year-old cubs are ready for breeding because virtually all cubs are weaned at 2.5 years (Stirling et al. 1975, DeMaster and Stirling 1981). In any given year, however, 30–60% of the available adult females do not breed or are not impregnated (Lentfer et al. 1980; I. Stirling, pers. commun.)

The breeding season for polar bears is from early spring to early summer. Cubs are born in late December or January (Lønø 1970, Lentfer 1976) and are called cubs-of-the-year or COY's to distinguish them from older cubs. Data from captive polar bears suggest that, typically, 2 young are born (Kostyan 1954). However, because of intrauterine and den mortality, the average litter size of adult females ranges from 1.58 to 1.87 (Lønø 1970; Stirling et al. 1975, 1977, pers. commun.; Lentfer 1976; Lentfer et al. 1980). The sex ratio of cubs is 1:1 (DeMaster and Stirling 1981). The long period of female parental care results in high 1st year survival rates of cubs (0.70–0.85) (DeMaster and Stirling 1983). Annual survival rate estimates range from 0.76 to 0.95 for subadults and adults (Stirling et al. 1975, DeMaster et al. 1980, Lentfer et al. 1980).

DESCRIPTION OF MODEL

The use of reproduction terminology is not consistent in the literature. Fecundity, natality, birth, reproduction, and recruitment rates are all used to refer to the female offspring in the initial age class at the time of census. The traditional census period for polar bears occurs just after adult females emerge from their dens in spring. In the context of life-table projections, we feel that recruitment rate is the most appropriate and descriptive term.

Our definition of age specific recruitment rate m_x, is:

$$m_x = \frac{N_{x-1,t-1} \cdot A_{x-1} \cdot B_{x-1} \cdot p_{x-1} \cdot L_x}{N_{x,t}}$$

$$= A_{x-1} \cdot B_{x-1} \cdot L_x.$$

The number of COY's at time t, produced by x-year-old females is then:

$$= m_x \cdot N_{x,t}$$

and the total number of COY's produced is:

$$= \sum_{x=1}^{w} m_x \cdot N_{x,t}$$

where

- 0 = initial age class,
- w = final age class = 23,
- x = discrete age class,
- t = discrete time interval (i.e., 1 year),
- $N_{x,t}$ = number of females of age x at time t,
- p_{x-1} = fraction of $N_{x-1,t-1}$ that survive to be $N_{x,t}$ (i.e., annual survival rate),
- m_x = age specific recruitment rate of $N_{x,t}$ (i.e., the no. of $N_{0,t}/N_{x,t}$ at the time of census),
- A_{x-1} = proportion of $N_{x-1,t-1}$ available for breeding,
- B_{x-1} = proportion of $A_{x-1,t-1}$ available for reproduction at time $t-1$ that would produce recruits at time t if all $N_{x-1,t-1}$ survived to be $N_{x,t}$ (i.e., litter production rates), and
- L_x = litter size of female recruits produced by those $N_{x,t}$ that produce recruits.

Taylor et al. (1987*a*) document systematic errors that can occur when multi-year reproduction cycles are summarized with mean annual rates. To avoid this type of error our parameters were chosen to mimic, not summarize, the reproduction cycle of arctic polar bears. Our age specific recruitment rate comprises 3 components: availability to reproduce (A), litter production rate of reproducing females (B), and litter size of recruits (L) at time of census.

Table 1. Sustainable harvest (as % of the total pop) for a nonselective harvest of adult female polar bears for a range of adult survival rates and other parameters. (These pop parameter values are representative of high arctic pops not experiencing density effects during favorable environmental conditions. The projected sustainable harvests may be interpreted as maximal rates.)

Parameter set	Ad F survival rate										
	0.90	0.91	0.92	0.93	0.94	0.95	0.96	0.97	0.98	0.99	1.00
A[a]	0.0	0.0	0.0	0.20	0.58	0.91	1.23	1.50	1.75	1.94	2.11
B[b]	0.0	0.26	0.65	0.99	1.30	1.59	1.83	2.05	2.22	2.36	2.48

[a] Individual cub-of-year (COY) survival rate = 0.85, individual yrl survival rate = 0.85, COY whole litter survival rate = 0.90, yrl whole litter survival rate = 0.90, adult litter production rate = 0.70, age 3 litter production rate = 0.15, age 4 litter production rate = 0.30, litter size of COY's = 1.80, and age of adult reproduction = 5+.

[b] Individual cub-of-year (COY) survival rate = 0.95, individual yrl survival rate = 0.95, COY whole litter survival rate = 0.90, yrl whole litter survival rate = 0.95, adult litter production rate = 0.70, age 3 litter production rate = 0.15, age 4 litter production rate = 0.30, litter size of COY's = 1.80, and age of adult reproduction = 5+.

Survival Rates

Cub survival rates, adult female survival rates, litter size, and litter production rates determine the fraction of females available for breeding, and thereby recruitment. As cub and litter survival rates increase, the average breeding interval increases and the number of females available for breeding in any year decreases.

Failure to become inseminated, failure to be fertilized, resorption of the fetus, intrauterine mortality, and cub mortality inside the den all reduce the estimate of litter production rate. For each age class the fraction of breeding, nursing, and surviving females was monitored. The harvest was subtracted from the appropriate sex and age strata of the population vectors.

Cub survival rate was divided into 3 types:

1. survival rate of mother (death of F results in loss of COY or yrl litters),
2. loss of whole litters as units given that the mother survived (litter survival rate or [p_{litter}]), and
3. survival rate of individual cubs given that the mother survived and the litter was not lost as a unit ($p_{\text{individual}}$).

Abandonment of single cub litters (Tait 1980) has not been observed in polar bears and was not included in the model.

Adult survival was assumed to be constant from age 2 to 23. Cub survival rate and litter survival rate were age specific for both COY's and yearlings. Litter production rate and litter size were constant from sexual maturity to age 23. The sex ratio of cubs was 1:1 in all cases.

Model Parameterization

The sustainable harvest can be determined for any configuration of parameters that gives a population growth rate >1.0. We selected a set of representative parameter values (Taylor et al. 1987*b*), then explored the sensitivity of sustainable harvest to variation in each parameter. The effect of variation of a particular parameter depends on the values of the other vital parameters. Our results are particular to the parameter values specified as representative. However, our results are conservative because most vital rates chosen as representative were near their maximum observed values. Substantial reduction of the life history parameter values used in this paper would result in a declining population, even with no harvest.

The population parameters shown in Table 1 were used as representative of polar bear populations not experiencing density effects in favorable environments (Stirling et al. 1978, Lentfer et al. 1980, Taylor 1982, DeMaster and Stirling 1983, Taylor et al. 1987*b*). The reproductive parameter values and the model structure are inappropriate for Hudson Bay polar bears, which typically wean cubs as yearlings and have 3-cub litters approximately 10% of the time (Ramsay and Stirling 1983).

Projections of a Sustainable Harvest

There can be no sustainable harvest if population growth rate is ≤ 1.0. The relationship between population size (N), population growth (λ), annual recruitment [$(\lambda - 1)\cdot N$], and sustainable yield (Y) is:

$$Y = ([\lambda - 1]\cdot N)\cdot X,$$

where X is a variable adjusting for the sex, age, and social composition of the harvest. Leslie (1945) showed that if all sex and age classes are taken in the same frequency as they exist in the population, X would equal unity. Sex and social strata, identified for each age class, were categorized as males, females without cubs, females with COY's, females with yearlings, and females with 2-year-olds. A category of bears without

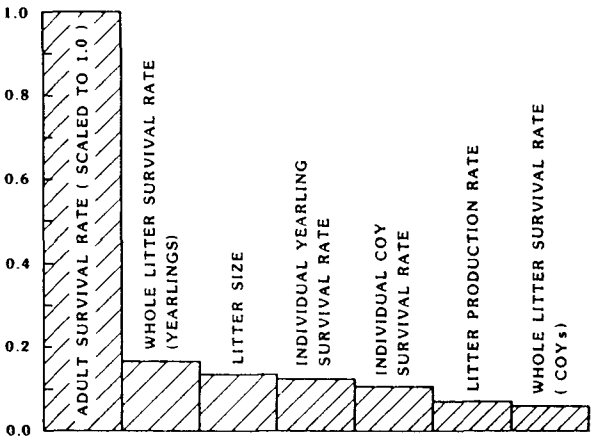

Fig. 1. The mean effects of unit change in polar bear population parameters on sustainable harvest rate are shown relative to adult survival rate (i.e., λ effect from unit change in ad survival rate scaled to 1.0). Calculation procedures are given in the text and the numerical values for the bars shown are given in Table 1.

cubs (i.e., M and F) was also identified. Harvested animals of each category were taken according to the abundance of each adult (3+ years) age class. If harvested females were accompanied by COY's or yearlings, those cubs were also counted as harvested, since they could not survive on their own. Harvested animals were subtracted from the population vector. The categories of harvest were: (1) bears without cubs (includes M and F without cubs); (2) females with COY's; (3) females with yearlings; (4) females with 2-year olds; and (5) females without cubs.

Sustainable yield was expressed as percent of total population taken as adult (age 3+) females of the type specified. Starting conditions for the simulations were determined by the stable age distribution specified by the parameter values. A convergence algorithm was employed to find the sustainable harvest of a particular type. Only the parameter being examined was varied from the default values during a simulation. The range of responses gave the sensitivity of each harvest type to the population parameters. In addition, the relative impact of each harvest type was observed.

The effect of a unit change in each parameter on sustainable harvest was indexed as the absolute value of the slope of the line between the maximum harvest point (parameter value = 1.0) and the minimum harvest point (pop growth rate = 1.0). The slopes recorded for each parameter were scaled by dividing each by the maximum slope recorded for any parameter, e.g., ad survival rate. The scaled index was thus relative to the adult survival rate slope, defined as 1.0. The index neglected nonlinearity in the sensitivity curve and could not treat age of 1st reproduction (range = 4–8) in a manner consistent with the other parameters, which ranged between 0.0 and 1.0. Because litters have either 1 or 2 cubs, litter size could be represented as the probability of 2-COY rather than 1-COY litters.

RESULTS

Sustainable harvest was most affected by changes in adult female survival rate (Fig. 1). Litter survival rate of yearlings, litter size, individual yearling survival rate, and individual COY survival rate were between 10 and 16.5% as influential as adult survival rate (Fig. 1). Changes in litter production rate and whole litter survival rate of COY's had only 6–7% the effect of changes in the adult survival rate (Fig. 1). Age of 1st reproduction was comparable in percent effect on sustainable harvest to litter survival rate of yearlings, individual survival rate of yearlings, individual COY survival rate, and litter size (Fig. 1). Harvest type had a minimal effect on the sensitivity of harvest rate to population parameters (Table 2). The sensitivity curves (vs. parameter values) were nonlinear for each harvest type (Fig. 2). The relative effects of harvest types converged at the point where

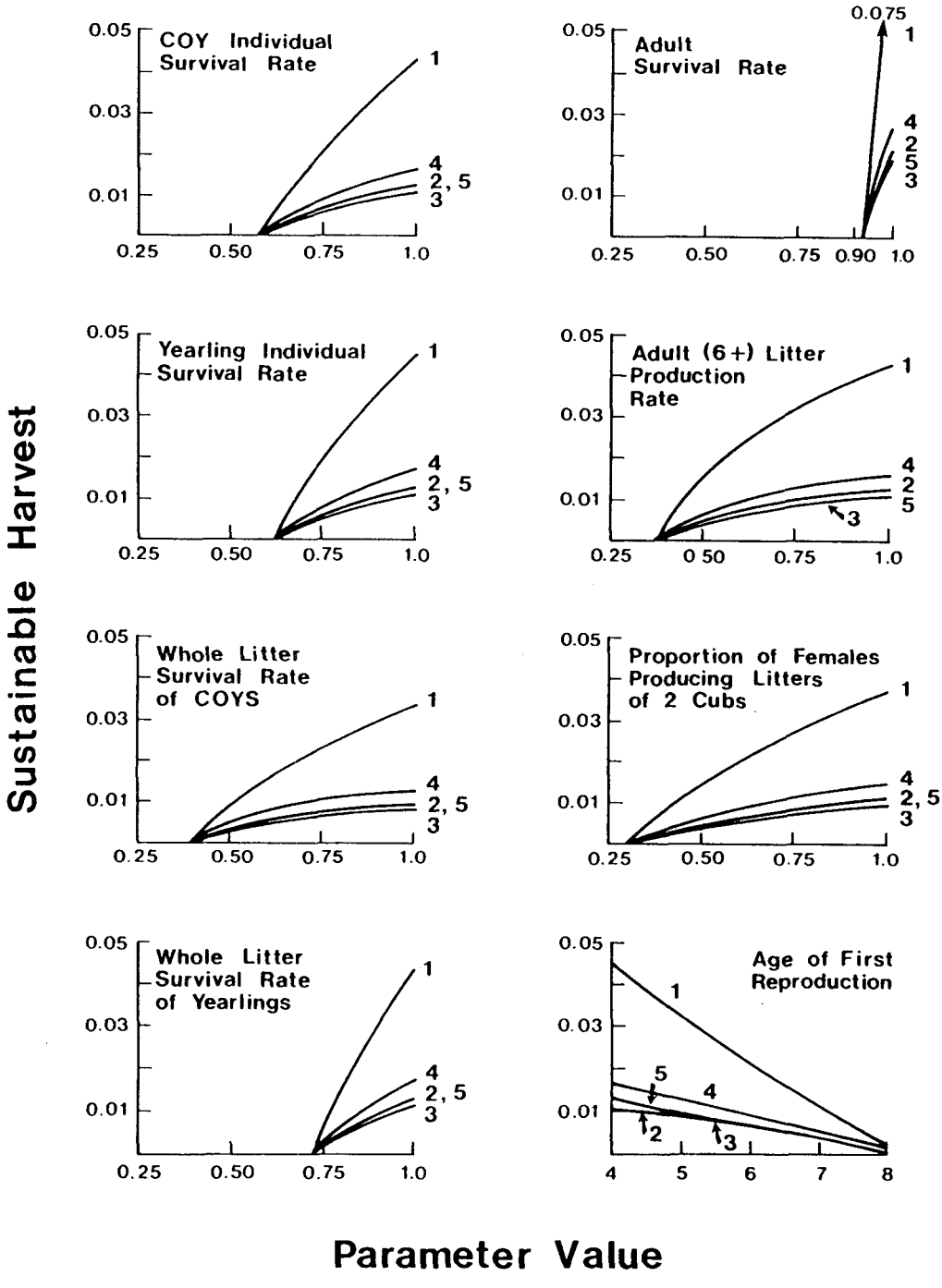

Fig. 2. Sustainable harvest (as % of the total pop) for 5 harvest types are given as functions of 8 polar bear population parameters. The 5 types of harvest were: (1) bears without cubs (M + F without cubs), (2) female with COY's, (3) female with yearlings, (4) female with 2-year olds, and (5) female without cubs. The parameters and their values were Parameter Set A in Table 1. (These pop parameter values are representative of arctic pops not experiencing density effects during favorable environmental conditions. The projected sustainable harvests may be interpreted as max. rates.)

Table 2. The relative effects of polar bear population parameters (ad survival rate effects scaled to 1.0) are given for 5 harvest types. Calculation procedures for the relative effect of population parameters are given in the text. Column 6 contains the mean and column 7 the standard error of the parameter effect given by pooling all 5 harvest types.

Parameter	Harvest type[a]						
	1	2	3	4	5	$\bar{x}$	Pooled SE
Ad F survival rate	1.00	1.00	1.00	1.00	1.00	1.00	0.00
Whole litter survival (yrl)	0.1539	0.1620	0.1598	0.1761	0.1753	0.1654	0.0098
COY litter size	0.1232	0.1319	0.1268	0.1423	0.1421	0.1332	0.0087
Yrl survival rate	0.1176	0.1206	0.1162	0.1305	0.1327	0.1235	0.0076
COY survival rate	0.0996	0.1033	0.0997	0.1096	0.1116	0.1048	0.0056
Litter production rate	0.0666	0.0707	0.0679	0.0724	0.0701	0.0695	0.0023
Whole litter survival (COY's)	0.0555	0.0573	0.0558	0.0610	0.0611	0.0581	0.0027

[a] 1 = bears without cubs (M and F without cubs), 2 = F with cubs-of-the-year (COY), 3 = F with yrl, 4 = F with 2-year-olds, and 5 = F with no cubs

population growth rate (λ) equalled 1.0 and no harvest of females could be sustained.

The absolute differences in sustainable harvest among the various female family group strata were small (Table 2). Harvests of females with 2-year olds could be higher because we assumed the cubs were not killed and could live on their own. Harvesting females with COY's and females with no cubs was nearly equivalent. Females with yearlings were able to sustain the lowest rate of harvest. The bears without cubs category sustained high levels of harvest because most of the animals taken were males. Although the effects of harvest type were particular to each combination of population parameters, the effect of the harvest type appeared robust (Table 2, Fig. 2).

Sustainable levels of a nonselective harvest of adult females were determined for a range of adult survival rates using the default values for the other population parameters (Fig. 3). The nonselective harvest was similar in effect to the harvest of females with COY's (Type 2) and females with no cubs (Type 5).

The mean reproduction interval (Taylor 1987*b*) (years between litters produced) and mean breeding interval (Taylor 1987*b*) (years between availability for mating) were calculated for a range of survival values using the default parameters (Fig. 4). The reciprocal of mean reproduction interval is sometimes used as a nonweighted estimate (for age) of reproduction rate (Caughley 1977). A nonweighted estimate of annual recruitment rate can be calculated by multiplying the reproduction rate times the mean number of females/litter. Similarly, a nonweighted breeding rate may be calculated.

Estimates of mean annual recruitment rates ranged from 0.226 (Lentfer et al. 1980) to 0.274 (DeMaster and Stirling 1981). Estimates of reproduction interval have varied from 3.5 to 3.8 years (Lentfer 1976, Lentfer et al. 1980). DeMaster and Stirling (1981) give an estimate of reproduction interval of 3.1 years; however, in our terminology this is called breeding rather than reproduction interval (Taylor et al. 1987*b*). The minimum possible reproduction interval for arctic polar bears is 3.0 and the maximum possible recruitment rate is 0.333 (DeMaster and Stirling 1981). The range of reproduction intervals calculated, using the default parameter estimates, ranged from 3.47 (ad survival = 1.0) to 3.32 (ad survival = 0.81). Unweighted annual recruitment rates ranged between 0.288 (ad survival = 1.0) and 0.301 (ad survival = 0.81).

DISCUSSION

The life history strategy of polar bears is consistent with that predicted for animals that experience fluctuations in recruitment due to an unpredictable environment (Stearns 1977). The arctic environment undergoes large-scale fluctuations between and within years (Vibe 1967). Polar bears are well adapted to and are in delicate ecological balance with their environment. This balance was particularly apparent during years of locally abundant ice, such as 1974 and 1975 (Stirling et al. 1975, 1977; Uspenskii 1977; Smith 1980) and years of locally sparse ice, such as 1979 (S. M. Uspenskii, pers. commun.). During those years, litter production rate and subadult (age 3–5) survival rates were reduced. For species exploiting a niche requiring a large body and behavioral plasticity, the evolutionary response to an unpredictable environment can include delayed maturity, reduced reproductive effort, and fewer young (Stearns 1977). Polar

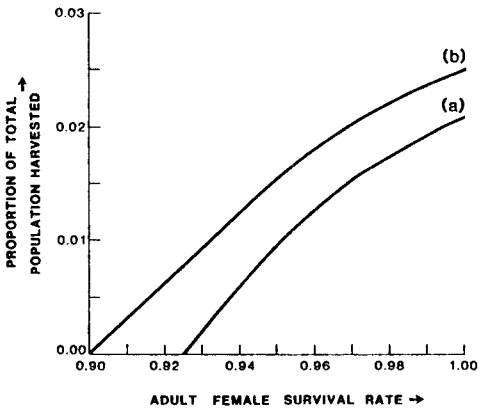

Fig. 3 "Sustainable harvest" refers to the percent of the total polar bear population (young and males included) that is harvested as adult females. "Harvested" also includes problem bears and illegally taken bears. In this example adult females were harvested without regard to maternal status; i.e., the harvest was nonselective. The percent of sustainable adult (age 3+) female harvest is given for 2 population parameter sets, A and B, set to maximum observed for all populations studied where females are taken according to abundance; i.e., no family status selectivity.

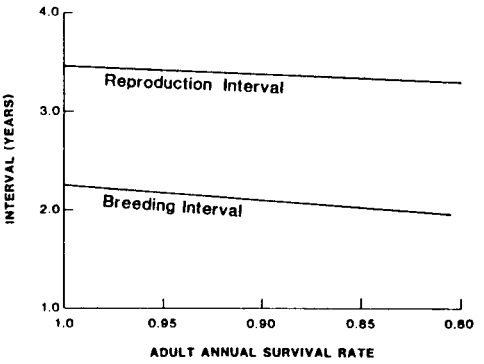

Fig. 4. The mean interval between reproduction (producing a litter) and breeding (being available to breed) is a function of adult survival, cub survival (litter loss rates), and litter production rate (fraction of those available that actually produce a litter). The reproduction and breeding intervals produced by the default parameter values (Set A in Table 1) are given for a range of survival rates.

bear life history strategy is typified by high adult survival rates and minimal effects on mean population growth rate due to fluctuations in recruitment.

Polar bear recruitment depends on the age specific past history of each female age class. Environmental instability affects the number of females available for breeding, and the number that actually produce offspring, by affecting survival rates of cubs and the nutritional status of breeding females (Stirling et al. 1975, Lentfer et al. 1980, Larsen 1985). Sustainable harvest is sensitive to litter size, but relatively insensitive to the proportion of females, available for breeding in a given year, that breed successfully. This result is important because: (1) it identifies deferred reproduction as the least costly method of avoiding the nutritional drain of maternity and the subsequent 2.5 years of rearing cubs; and (2) it raises the question of why female polar bears in most populations have only 2 cubs. Although almost 10% of the subarctic Cape Churchill population have 3-cub litters (Ramsay and Stirling 1983), 3-cub litters are rare in the high arctic areas of Siberia, Greenland, Svalbard, Alaska, and Canada.

Polar bears evolved from brown bears (*Ursus arctos*) (Kurten 1964), which often have 3 or more cubs/litter, but Bunnell and Tait (1981) suggested that nutritional stress in winter was responsible for the 2-cub maximum litter size in arctic areas. In Hudson Bay polar bears are forced on shore near Cape Churchill from ice-out in mid-summer until ice-up in mid-November. Ramsay and Stirling (1983) speculated that seals might be exceptionally abundant or available in this area to allow rearing 3-cub litters and weaning cubs as yearlings. Estimates of the trade-offs between adult survival rate and breeding success have not been made. If we accept that such energetic trade-offs do exist (Bunnell and Tait 1981), then we can understand the relatively long period of maturation as a similar trade-off. Immediate reproductive output with low probability of success is exchanged for increased likelihood of survival. Bunnell and Tait (1981) note a strong correlation between litter size and weight in brown and black (*Ursus americanus*) bears.

The effects of environmental stress on survival rates apparently occur most strongly in subadults having no mother to intercede, no breeding success to "barter," and a smaller store of fat reserves (Stirling et al. 1975, Uspenskii 1977, Smith 1980). Observations of density dependent and density independent effects on populations of other marine mammals indicate that these effects are typically 1st manifest as reductions in annual breeding success and reduced subadult survival rates (Eberhardt 1977, Eberhardt and Siniff 1977). Reduced survival rates of subadult polar bears have a greater impact on pop-

ulation growth rate and sustainable harvest than reduced litter production rates. Subadult survival rates may be important in density independent fluctuations of polar bear populations.

Our model did not discriminate between subadult (ages 3–4) and adult survival rates. Although subadult age classes are relatively abundant, they do not produce many recruits. Reduction of subadult survival rates is roughly equivalent to a fractional reduction in adult survival rates. The fraction would be the ratio of subadults : adults. Subadults are more vulnerable than adults to environmental effects and are the age strata that most often become "problem bears" (Stenhouse 1983). As problem bears, they have reduced expectations of survival. Problem bear mortality may be of increasing significance as northern development proceeds.

The mechanism of density dependent regulation of polar bear populations is an open question. Any mathematical functions chosen to describe it are, at best, conjecture and, at worst, misleading. The allure of using compensatory models in harvest analysis is that a *maximum* sustainable yield can be calculated. Density dependent models can be inappropriate for populations in environments perceived as unpredictable, because such populations rarely are numerous enough to experience density effects (Andrewartha and Birch 1954, Wilbur et al. 1974). Additionally, Eberhardt and Siniff (1977) and Fowler (1981*a*,*b*) marshall both arguments, and evidence suggesting that the effect of increased number is minimal at low and intermediate densities for long-lived animals with delayed reproduction. The vital parameter values specified in model (Table 1) are representative of a population not experiencing density effects in a favorable environment. Thus, sustainable harvest projections represent a best case situation. Vital parameter rates were chosen as the maximum values from published (DeMaster and Stirling 1981, Taylor et al. 1987*b*) and unpublished analyses (I. Stirling, pers. commun.). The mean annual recruitment rates stemming from our default values (0.288–0.301) exceed those reported in the literature (0.226–0.274) (Lentfer et al. 1980, DeMaster and Stirling 1981). Assuming that adult survival rate equals 0.95, the stable-age, unharvested, population growth rate was 1.017 for Parameter Set A (Table 1) and 1.051 for Parameter Set B (Table 1).

There is some suggestion of sampling bias against family groups (I. Stirling, pers. commun.). This bias would cause litter production rates, and subsequently recruitment rates, to be underestimated. We elected to use published values because the existence or extent of this bias has not been quantified. It could be argued that our assumed rates of COY and yearling survival and litter production are not absolute maxima. However, because of the relative insensitivity of harvest rates to changes in either of these parameters (Figs. 1 and 2), we feel that our conclusions are reasonably robust.

Mating in polar bears is promiscuous, thus recruitment is primarily a function of the number of adult females. A male-only harvest would not affect annual recruitment until males were in short supply. However, some hunters may not distinguish males from females without cubs and other hunters take females on opportunity. Pregnant females are particularly vulnerable to shore-based hunters when they return to land for maternity denning. Adult females are especially important to population growth rate because reproductive maturity indicates survival through the vulnerable subadult period. Females have few litters because of sustained parental care given to their cubs and the possibility of deferring reproduction during bad years or between litters. Loss of a female with cubs is only slightly worse, in terms of loss of recruitment to the population, than loss of a female unencumbered with cubs (Table 2).

The breeding population is augmented by approximately 25% of the annual recruitment rate because only 50% of the cubs produced are female, and 4–6 years of annual mortality occur before the juvenile and vulnerable subadult classes reach maturity (Taylor 1982). If adult females were immortal, the breeding segment of the population would receive an annual increment of only 2.5% of the total population. Assuming a more realistic (i.e., 5.0%) natural mortality, the annual increment of adult females would be between 1.0 and 1.6% of the total population.This annual increment is the sustainable harvest of adult females.

Although the effect of population parameters on growth rate depends on the values of the other parameters, the ranking (Table 1) appears robust through the range of biologically plausible values. The dependence of polar bear life history strategy on constantly high adult survival rates causes polar bears to be particularly

vulnerable to overharvest. The nature or existence of compensatory mechanisms is not known for any polar bear population. Conservative management and comparisons with other long-lived species suggest that noncompensatory harvest models are most appropriate for polar bears.

The structure of polar bear life history biology reduces the question of sustainable harvest to essentially 3 factors: (1) population numbers; (2) adult female survival rates; and (3) number of harvested bears that are adult females. As Figure 2 and Table 2 indicate, the family status of a harvested female is relatively unimportant to the sustainable harvest level. Within the range of biologically reasonable survival and recruitment values, polar bear populations sustain <1.6% harvest of adult (3+ years) females. This value can only be increased by about 1% by assuming that adult females are immortal except for harvest.

The implications for existing harvests have already been addressed for 1 polar bear population in North America. The Inuit communities of Clyde River and Broughton Island, on northeast Baffin Island, have voluntarily reduced their harvest of polar bears to a sustainable level. Similar measures may also be required in other areas to avoid population depletion.

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