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Sex-selective harvesting of polar bears *Ursus maritimus*

Mitchell K. Taylor, Philip D. McLoughlin & François Messier

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We explored limits and consequences of male-biased harvesting of polar bears *Ursus maritimus* using a simulated population based on empirically-derived estimates of age-specific rates of survival and reproduction. The maximum sustainable yield (MSY) was identified as the total kill in which the number of females that could be taken resulted in $\leq$ 5% change in females older than 50 years. MSY depended on the proportion of males in the harvest, although the effect of male selection on the post-harvest population was to reduce the mean age and number of males. A practical limit to the increase in MSY possible from male-selective harvesting was identified at the 3 : 1 (M/F) sex ratio. At 3 : 1 (M/F), all males were eventually harvested as 2-year olds, and males were reduced to 25% of pre-harvest levels. A more conservative harvest strategy of 2 : 1 (M/F) resulted in a 30% reduction of males and a reduction of the mean age of males from 10.0 to 7.7 years post-harvest. We thus recommend that sex-selective harvesting of polar bears do not exceed 67% males (i.e. a harvest ratio of 2 : 1), a demonstrably safe and sustainable harvest strategy, to avoid depletion of males and possibly reduce recruitment by having too few sexually mature males in the population. When females are harvested below MSY, then harvest strategies that select for males at rates > 2 : 1 (M/F) can be conservative because the increase in females also increases the reproductive performance of the population. In the absence of information on density effects, managers should be conservative in their expectations of increases in the female population.

Key words: polar bear, population modelling, sex-selective harvesting, Ursus maritimus

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Male-biased harvesting is common in the management of annually reproducing game species, for which several analyses of the risks and benefits of sex-selective hunting exist (e.g. Langvatn & Loison 1999, McCullough 2001, White et al. 2001, Sæther et al. 2003). Sex-selective hunting is also common for large mammals with multiannual parental care (e.g. bears Ursidae, elephants Elephantinae and marine mammals), since females with accompanying offspring are often protected from harvest, adult males are taken as trophies, or males are predisposed to conflicts with humans (Lee & Taylor 1994, Paulraj & Subramanian 2000, Harris & Metzgar 1987, Harwood et al. 2002). Male-biased hunting of species with multiannual reproduction has not, however, been analyzed to the same extent as that of annually-reproducing species, upon which most theory is based.

The harvest of polar bears *Ursus maritimus* in Canada is presently controlled by an annual, sex-selective quota system. The polar bear quota is based on current population estimates, estimated population growth rates, and the planned sex ratio of the kill. The equation used to determine sustainable yields is based on simulation modelling (Taylor et al. 1987a, Miller 1990):

$$\text{SUSTAINABLE YIELD} = \frac{N \times 0.015}{P_F} \qquad (1),$$

where N = total population number, 0.015 is an empirical constant derived from a metaanalysis to estimate survival and recruitment rates for Canadian polar bears, and P_F = proportion of the harvest that is female. The rationale of this approach is that if a polygamous species, such as the polar bear (Amstrup 2003), is managed such that the reproductive potential (abundance of females) is not diminished, the harvest will be sustainable. Equation is logical only within limits. For example, if no females were taken, the predicted sustainable harvest would be infinite.

Here we investigate the limits of Equation and the long-term impacts of male-biased harvesting on the population composition of polar bears. We emphasize the population consequences of sex-selective harvesting, rather than methodology to estimate population trend or numbers based on observed changes in harvest sex ratio (e.g. Fraser et al. 1982, Harris 1984, Harris & Metzgar 1987). We also investigate an alternative to harvesting at maximum sustained yield (MSY) that results in increasing polar bear abundance over time with no reduction in the annual number taken.

Methods

Polar bear life history

Polar bears are a long-lived, late-maturing species with a low rate of annual recruitment (DeMaster & Stirling 1981, Stirling 1988, Derocher & Stirling 1994, Amstrup 2003). Polar bears exhibit 'birth pulse' reproduction (Caughley 1977). Typically, a small fraction of females produce cubs for the first time at age 5 (initial age = 0). Adult recruitment rates are observed from five to six years. During the first two years following birth, cubs remain with the female, and she is unavailable for mating; however, some females with cubs lose their litters and become available for mating at the next season. Females with 2-year-old cubs are ready for mating because virtually all cubs are weaned at the age of 2.5 years (Stirling et al. 1975, DeMaster & Stirling 1981, Stirling 1988, Derocher & Stirling 1994). In any given year, however, as evidenced by the proportion of females available to mate, but that do not have cubs the following spring, 10-40% of the available adult females may not breed or are not impregnated (Lentfer et al. 1980, Amstrup & DeMaster 1988).

The mating season for polar bears is from early spring to early summer. Cubs are born in late December or January (Lønø 1970, Lentfer 1976). Data from captive polar bears suggest that, typically, two young are born (Kostyan 1954). However, because of intrauterine and post-partum mortality occurring before den emergence, the average litter size of adult females ranges within 1.58-2.00 (Lønø 1970, Stirling et al. 1975, Lentfer 1976, Lentfer et al. 1980, Ramsay & Stirling 1988). The sex ratio of cubs is 1 : 1 (DeMaster & Stirling 1981). The long period of female parental care results in high first-year survival rates of cubs (0.70-0.85; DeMaster & Stirling 1983). Annual survival rates range within 0.76-0.96 for subadults and adults (Stirling et al. 1975, Lentfer et al. 1980, Amstrup 2003).

Model description

Taylor et al. (1987c) documented systematic errors that can occur when multiannual reproductive cycles are summarized with mean annual rates. To avoid this type of error, our simulation model was constructed to mimic, not summarize, the

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reproductive biology of polar bears. Our simulation model was an algebraic description of the actual 3-year reproductive cycle (Taylor et al. 1987a, b). The census period occurs after adult females emerge from their dens in spring. Our age-specific recruitment rate had three components: proportion of females available to mate and produce offspring (A) the following year, litter production rate of reproducing females (B), and litter size of recruits (L) at time of census.

We used a life table, rather than a Leslie matrix, approach because we prefer the life-table recruitment term 'm_x' to the Leslie matrix fecundity term 'F_x' (Taylor & Carley 1988). Our definition of age-specific recruitment rate was:

$$m_x = \frac{N_{x\text{-}1,t\text{-}1} \cdot A_{x\text{-}1} \cdot B_{x\text{-}1} \cdot p_{x\text{-}1} \cdot L_x}{N_{x,t}} = A_{x\text{-}1} \cdot B_{x\text{-}1} \cdot L_x \quad (2),$$

and the total number of cubs (both male and female) produced was:

$$= \sum_{X=1}^{w} m_x \cdot N_x \quad (3),$$

where: 0 = initial age class (cubs), w = final age class (25 years), x = discrete age class, t = discrete time interval (1 year), $N_{x,t}$ = number of females of age x at time t, $p_{x\text{-}1}$ = fraction of $N_{x\text{-}1,t\text{-}1}$ 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 number of $N_{0,t}/N_{x,t}$ at the time of census), $A_{x\text{-}1}$ = proportion of $N_{x\text{-}1,t\text{-}1}$ available for mating, $B_{x\text{-}1}$ = proportion of $A_{x\text{-}1,t\text{-}1}$ available for reproduction at time t-1 that would produce recruits at time t if all $N_{x\text{-}1,t\text{-}1}$ 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.

Our model was deterministic with time units of one year. We assumed that there were no density-dependent effects and no directional change in the ecosystem. The population was structured into 25 age classes with the following sex/family status categories: males, females with no offspring, females with one cub, females with two cubs, females with one yearling, females with two yearlings, and females with 2-year-old subadults.

The kill of male bears by hunters depends on the relative abundance and vulnerability of the various age/sex strata and family groups, and the hunter selectivity. We developed the harvest component of our model to consider both the total number killed and the sex ratio and family status of the kill. We recognized that a selective harvest will change relative abundances over time; hence, our model stipulated that hunter selectivity compensates in a dynamic fashion to keep the sex ratio of the kill constant. Our harvest algorithm allowed the number of individuals of each sex taken to be specified. The harvest of both sexes was apportioned according to relative abundance except for cubs (age 0) and yearlings (age 1), which were protected from harvest. Females accompanying cubs and yearlings were also protected during our simulations. Despite lack of any official protection in most jurisdictions where polar bears are harvested, females accompanied by 2-year-old subadults are not generally hunted at the same rates as unaccompanied females, and so for our simulations we reduced their likelihood of being harvested at rates of lone females by 75% (e.g. in Baffin Bay, Nunavut, a female accompanied by two, 2-year-old subadults was 78% less likely to be shot compared to a female with no accompanying offspring (based on ratios of the estimated standing age distribution to harvest distribution; M.K. Taylor, Government of Nunavut). For the remainder of the unprotected categories, the harvest was unselective with respect to age.

Initial conditions were 500 males and 500 females at stable age distribution based on the following natural (i.e. unharvested) survival and recruitment parameters, accounting for whole litter loss: cub survival = 0.72, yearling (age 1) survival = 0.77, subadult (ages 2-5) survival = 0.95, adult survival (ages 6-25) = 0.96, litter production rate of females available to mate = 0.70 (i.e. proportion of cubs available to mate that produce a litter the following year), age of first (subadult) litter production = 5, age of female reproductive maturity = 6, and litter size of cubs = 1.8. These example parameters are realistic for polar bears (IUCN 2006) and result in a stable age population growth rate (λ) of 1.039 with no harvest mortality (Taylor et al. 1987a). We ran every simulation for 50 years with the mean age of harvested bears and number of males and females recorded each year.

Simulations

Simulations were run to explore behaviour of the example population under different situations: unselective harvests, selective harvests, harvests at or below maximum sustainable yield (MSY), harvesting with a constant total take, or through changes in the age at maturity of females. Here, MSY was

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identified by iteration, and was defined as the total harvest that resulted in no more than a 5% change in the number of females in the population over a 50-year period. Initial conditions (described above) were the same for all simulations. Simulations that varied sex-selectivity in the harvest did so at MSY for selectivities ranging within 50-28% females, and at 47 bears per year (i.e. the MSY at 33% female harvest for our example population of 1,000) for selectivities ranging within 40-10% female. The latter simulations explored a scenario whereby quotas were held constant, but harvest sex ratio could be altered by regulations or conservation education (i.e. simulations were not limited to only sustainable levels of harvest). We also examined the outcome of a harvest scenario aimed at increasing population size by harvesting females below sustained yield. Finally, to examine sensitivity of the results to delayed maturation and consequently lower population growth rate, we present results for the above simulations with the age of first reproduction increased from five to six years.

Results

Unselective harvest at MSY

With an unselective (i.e. 50% female) harvest at MSY, the mean age of harvested males at the end of simulation was 10.0 years whereas the mean age of harvested females was 7.8 years (Fig. 1). The mean age of harvested females was lower in the unselective harvest simulation because many older females had cubs and were invulnerable to harvest; thus, a larger fraction of the female harvest was relatively young (i.e. pre-reproductive). The number of males in the unselective harvest example (520) was slightly higher than the number of females (504) after 50 years (Fig. 2) because age distributions had not completely converged on the stable age distribution. The stable age distributions for both males and females were redefined by the addition of harvest mortality; however, the dynamics of convergence to the new stable age distribution were different for females compared to males because age specific harvest mortality rates were different for each sex.

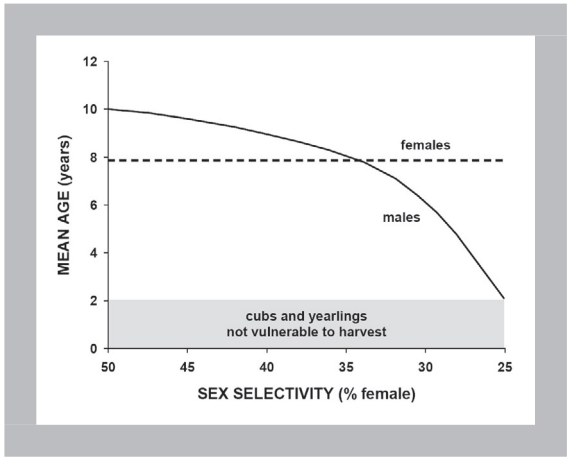


Figure 1. Effect of increasing selectivity for male polar bears on the mean age of harvested male and female polar bears after harvesting for 50 years at MSY (i.e. the rate at which the total number of females remains constant, i.e. changes by $\leq$ 5%).

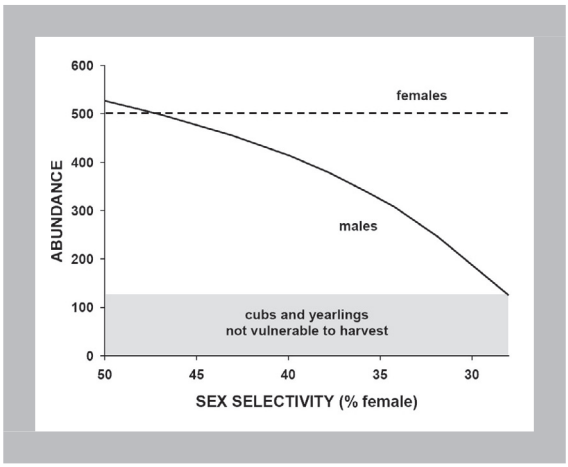


Figure 2. Increased selectivity for male polar bears reduces the number of males that remain in the population after 50 years of harvesting at MSY.

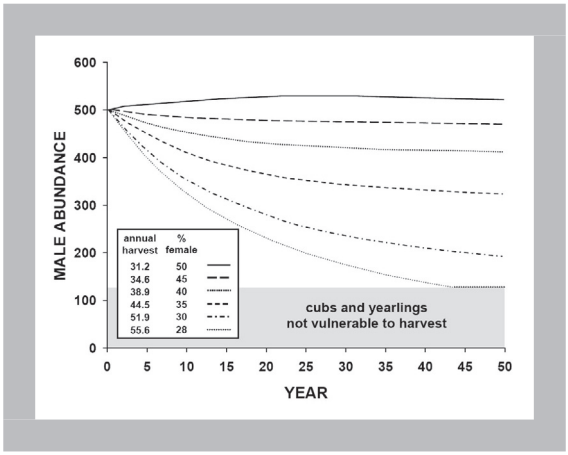


Figure 3. Simulated changes in abundance of male polar bears over time at various levels of female selectivity under MSY.

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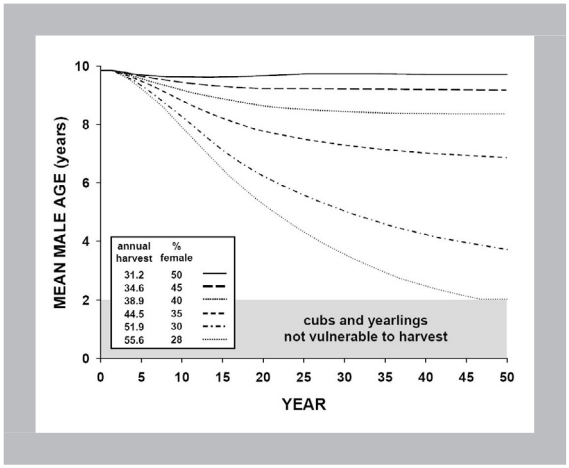


Figure 4. Simulated changes in mean age of male polar bears over time at various levels of female selectivity under MSY.

Selective harvest at MSY

Selecting for males in the harvest reduced the fraction of the population that was male (see Figs. 2 and 3) and reduced the mean age of males (see Figs. 1 and 4). As per MSY criteria, the abundance and mean age of females remained invariant with respect to changes in selectivity for males (see Figs. 1 and 2). Sustainable harvest sex ratios at MSY ranged within 50-28% female for the example population of 1,000 bears; however, at 28% females in the hunt, all males were eventually harvested as 2-year-olds, and males were reduced to 25% of pre-harvest levels (see Fig. 3). MSY at 33% females was 47.2 (males and females). At 33% females, the harvest resulted in a 30% reduction in males (i.e. 500 to 352), and a 23% reduction of mean age in harvested males (from 10.0 to 7.7 years).

Constant total take

When the number of polar bears taken was held constant, the effect of varying the sex ratio in the kill depended on whether the female component increased or declined (Figs. 5 and 6). When increasing selectivity for males allowed numbers of females to increase, the number of males first declined because of increased *per capita* harvest mortality, but eventually recovered and increased as the reproductive

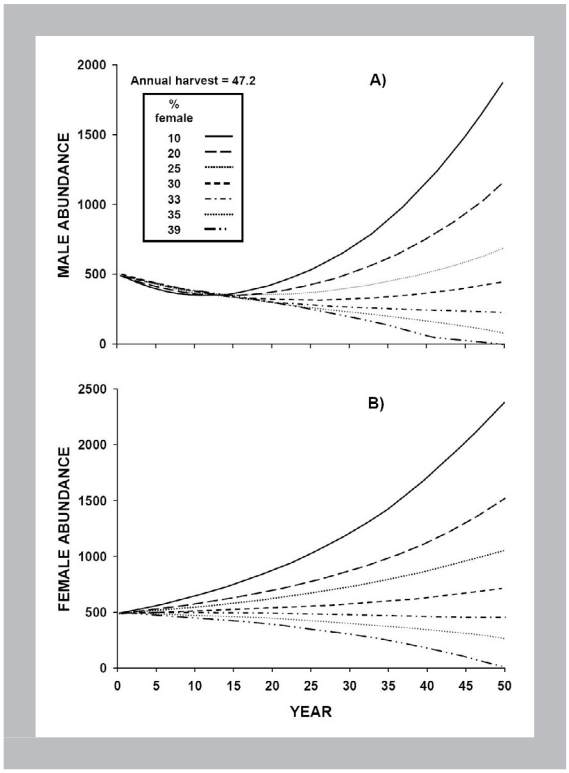


Figure 5. Simulated changes in male (A) and female (B) polar bear abundance over time at various levels of male selectivity and a fixed average annual harvest of 47.2 bears per year. This harvest rate was the MSY at 33% females in the harvest.

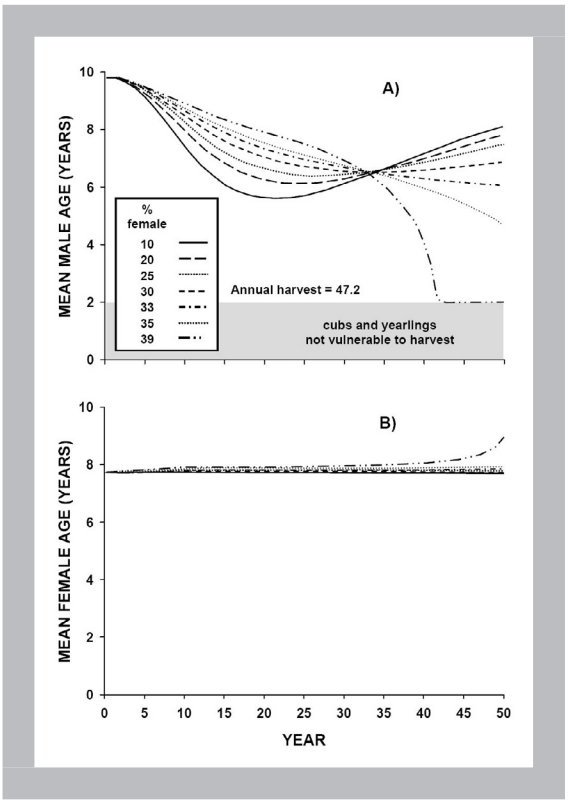


Figure 6. Simulated changes in mean age of male (A) and female (B) polar bears over time at various levels of male selectivity and a fixed average annual harvest of 47.2 bears per year. This harvest rate was the MSY at 33% females in the harvest.

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potential (i.e. abundance of females) of the population increased (see Fig. 5). Similarly, the mean age of males and females in the harvest declined when reduced selectivity for males caused the number of females (and subsequently the sustainable yield) to decline (see Fig. 6). However, where increased selectivity for males allowed females to increase (see Fig. 5B), the initial decline in mean age of males recovered as the total population increased (see Fig. 6A).

Harvesting below MSY

For our example population, the MSY given a harvest of 25% females was 62.3 according to Equation . However, as Figures 2 and 3 indicate, that harvest was not sustainable because of depletion of males. By reducing the proportion of the harvest that was female to 15%, the harvest of 62.3 was sustained, and the population increased over time (Fig. 7). This result was brought about by the reduction of the kill of females below what we had used to define MSY (i.e. $\leq$ 5% change in abundance of females over 50 years), which resulted in increasing female abundance and increasing production of both males and females. The initial decline in males was thus reversed by the increasing production of males from the increasing number of females.

Effect of age at maturity

When the age of first reproduction was increased from five to six years (i.e. 15% of available females producing cubs) and the age of reproductive maturity (i.e. 70% of available females producing cubs) was increased to from the age of six to seven years, the stable age population growth rate without harvest was reduced to 1.029. The results of simulations at the reduced population growth rate were qualitatively the same. The main difference was that diminished reproductive potential allowed sustainable harvests at selectivities up to 25% females, although the MSY at a given harvest sex ratio was reduced.

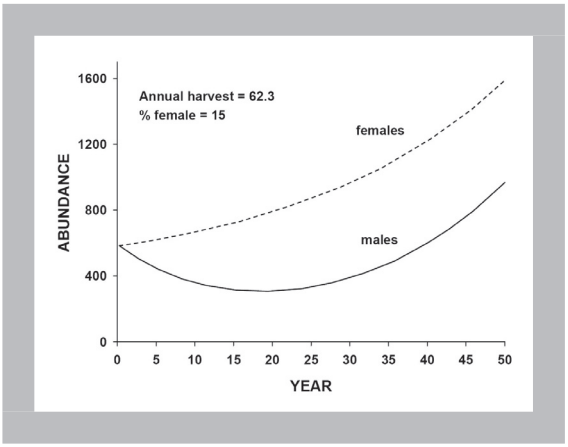


Figure 7. Simulated changes in male and female polar bear abundance over time for an initial population of 1,000 individuals and an average annual harvest of 62.3 bears at 15% females in the harvest.

Discussion

Our results support the validity of sex-selective harvesting as a strategy for increasing the sustainable hunt for polar bears, compared to that available from a non-selective harvest. However, we also point out limits to increases in harvest that can be sustained by increasing selectivity for males. As males are renewed at the same rate as females, the effect of a male-selective harvest at maximum sustained yield (MSY) is to cause a decline in the number of males and a decline in the mean age of males. In our example population, a harvest of 28% females was sustainable only when males were harvested as 2-year-old, sexually immature cubs (see Figs. 1 and 3). Thus, a 3 : 1 (M : F) selectivity of harvest may be numerically sustainable, but would not be biologically realistic. That said, a 2 : 1 (M : F) harvest would not likely reduce the abundance or mean age of male bears to the point of reducing mating success/annual production. Effects of sex-selective harvest on population composition must therefore be considered when management recommendations are made. Equation only applies within the range of selectivity that is normally sustainable (i.e. harvest composition of 28-50% females for the same population parameters used to produce Equation), and does not describe the reduction in mean age of males and number of males that occurs. When the effects of sex-selective harvesting on the mean age and number of males in the population is considered, a harvest ratio of 2 : 1 (M : F) appears to be the maximum selectivity possible within conservation limits. This sex ratio provides for the possibility of higher harvests but with an acceptable impact (reduced numbers of males and reduced mean age) on the population.

The effect of varying selectivity for males suggests useful management options that do not cause long-term reductions in male abundance or mean age of males, and do not result in major reductions in the number of bears taken. When the selectivity

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for males is decreased, and the total kill is kept constant, the population declines due to overharvest of females. However, when the selectivity for males is increased and the total kill is kept constant, the female segment (and recruitment of both males and females) increases over time. Provided that the number of males taken annually does not deplete the males, the increased rate at which males are recruited eventually compensates for the initial overharvest of this sex (see Fig. 7). These results assume that there are no density effects or reductions in recruitment caused by the initial decline in males. Density effects would eventually limit the rate of increase and the number of females. These constraints suggest caution when applying this harvest strategy with an expectation of increased population numbers.

The generality of these results is apparent when we consider effects of increasing the age of first reproduction. The range of sustainable harvest selectivities was marginally changed from 28 to 25% female, and the results were qualitatively the same. As with the first scenario, the number of males were reduced with a sustainable sex-selective harvest because males were renewed at the same rate as females. Increased harvest mortality for males over females must result in fewer males in the population. Similarly, the mechanism by which male selective harvesting was sustained was that the harvest became concentrated on younger, more abundant, age classes. Increased harvest mortality reduced the number of males in older age classes, and subsequently increased the harvest pressure on younger age classes.

Sex-selective harvesting has altered the sex ratio of polar bear populations in Alaska (Amstrup et al. 1986, Lentfer et al. 1980), Hudson Bay (Derocher 1991, Derocher et al. 1997) and the Viscount-Melville Sound (Taylor et al. 2002). Harvest records and population composition for the Alaskan and western Hudson Bay regions were not recorded during initial phases of harvest; however, the western Hudson Bay population is thought to have recovered from overhunting over a period of 30 years while subject to a harvest that was sustainable and selective for males (Derocher 1991, Derocher et al. 1997), although recent declines are now apparent (IUCN 2006). The Viscount-Melville population differs from the western Hudson Bay population in that there was little harvesting in the area before harvest recording commenced. The Viscount-Melville population can be assumed to have been reasonably close to stable age distribution at the beginning of the harvest period. The sex ratio of the Viscount-Melville polar bear population was 43% males in a pooled sample taken in from 1973 to 1976, and 29% males in a pooled sample taken from 1989 to 1992 (Taylor et al. 2002). The harvest of the Viscount-Melville polar bear population was selective for males (63.4% males) during this period. Both the field data and our simulation results were consistent with more general treatments of the effects of sex-selective harvesting (e.g. Kelker 1943, Chapman 1955, Rupp 1966, Paloheimo & Fraser 1981, Clark & Tait 1982, Fraser et al. 1982).

Our definition of maximum sustained yield (MSY) in this paper is the maximum number of bears that can be taken without allowing for a decrease in abundance of females (i.e. reproductive potential). More typically, MSY is used to describe the density at which the yield curve is maximized (e.g. $\frac{1}{2}$ of the carrying capacity for the logistic model; Caughley & Sinclair 1994:289-290). Unfortunately, managers of polar bear populations do not know how yield curves change with density (Derocher & Taylor 1994); hence, the management objective for most harvested populations is to maximize yield without reducing current population numbers. This is the context of our use of MSY, and a limitation in current management practices for harvested bear populations. If population growth rates of polar bears have a non-linear response to increasing density similar to other species of long-lived mammals (Fowler 1987), then most contemporary populations of bears may have been reduced by man to densities at which density effects are negligible. Our simulations at MSY did not, by definition, change numbers of females, but reduced the number of males. We suggest that our simulations were more realistic because they did not contain density effects. Any inclusion of density-dependent effects on recruitment or survival would have been hypothetical. The exception was the increasing females scenario, which would eventually be regulated by density effects.

Harvest strategies that allow females to increase during a period of overharvest for males may be sustainable if males are not depleted to the point that mating success is reduced during the period when females are increasing. A harvest of this type could be conservative in that the limiting factor to population increase would be natural population regulation rather than harvest. However, in the absence of information on density effects, managers should be

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conservative in their expectations of increases in recruitment that will be realized from increasing the number of females in a given population.

Our results may also apply to sex-selective harvesting of grizzly bears *Ursus arctos* or other species that have similar life histories (e.g. marine mammals and elephants). Managers of populations that have low reproductive potential should consider changes in population composition that will occur and the limits to increases in sustainable harvests that can be realized from sex-selective harvest strategies.

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