



SEX-SELECTIVE HARVESTING OF POLAR BEARS

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Abstract: We explored limits and consequences of male-biased harvesting of polar bears (*Ursus maritimus*) using a population simulation model. Our model was based on a life table analysis of polar bears inhabiting Nunavut, Canada, using empirically-derived estimates of age-specific rates of survival and reproduction. The maximum sustainable harvest of females was identified as the number that could be taken with $\leq 5\%$ decline over 50 years. The maximum sustainable harvest of both males and females 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 maximum sustained yield that was 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 not exceed 67% males (i.e., 2:1 harvest ratio)—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 at levels less than the maximum sustainable level, harvest strategies that select for males at rates greater than 2:1 (M/F) can be conservative because the increase in females also increases the reproductive performance of the population. For example, when the harvest rate is determined as the maximum sustainable yield at 2:1 (M/F), increasing the proportion of males is conservative so long as the number taken does not increase. Increases in population numbers resulting from harvests at less than maximal rates will eventually be regulated by density effects. In the absence of information on density effects, managers should be conservative in their expectations of increases in the female population.

Introduction

The harvest of polar bears in Nunavut, Canada is presently controlled by an annual 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, Bunnell, DeMaster & Schweinsburg 1987, Miller 1990):

$$SUSTAINABLE\ YIELD = \frac{N \times 0.0156}{P_F}$$

Eqn. 1

where N = total population number, 0.0156 is an empirical constant derived from a meta-analysis 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, like polar bears, is managed such that the reproductive potential (abundance of females) is not diminished, the harvest will be sustainable. Of course, Equation 1 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 1 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, Gardner, Kolenosky & Strathearn 1982, Harris 1984, Harris & Metzgar 1987). We also investigate an alternative to harvesting at maximum sustained yield 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). 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 age 6. During the first 2 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 2.5 years (Stirling, Andriashak, Latour & Calvert 1975, DeMaster & Stirling 1981, Stirling 1988, Derocher & Stirling 1994). In any given year, however, 30–60% of the available adult females do not breed or are not impregnated (Lentfer, Hensel, Gilbert & Sorenson 1980, Amstrup & DeMaster 1988; M.K. Taylor, unpubl. data).

The mating season for polar bears is from early spring to early summer. Cubs are born in late December or January (Lónó 1970, Lentfer 1976). Data from captive polar bears suggest that, typically, two young are born (Kostyan 1954). However, because of intrauterine and den mortality, the average litter size of adult females ranges from 1.58 to 2.00 (Lónó 1970, Stirling et al. 1975, Lentfer 1976, Lentfer et al. 1980, Ramsay & Stirling 1988, PBTC 2003). 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 from 0.76 to 0.96 for subadults and adults (Stirling et al. 1975, Lentfer et al. 1980, PBTC 2003).

Model Description

Taylor, Carley & Bunnell (1987) 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 reproductive biology of polar bears. Our simulation model was an algebraic description of the actual 3-year reproductive cycle (Taylor et al. 1987a, Taylor, Bunnell, DeMaster, Schweinsburg, & Smith 1987). The census period occurs after adult females emerge from their dens in spring. Our age specific recruitment rate had three components: availability to mate and produce offspring the following year (A), 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 lifetable recruitment term " m_x " to the Leslie matrix fecundity term " F_x " (Taylor & Carley 1988). Our definition of age-specific recruitment rate was:

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

Eqn. 2

The number of cubs at time t , produced by x -year-old females, is $m_x \cdot N_x$. The total number of cubs produced is:

$$= \sum_{x=1}^w m_x \cdot N_x$$

Eqn. 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-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 number of $N_{0,t}/N_{x,t}$ at the time of census);
- A_{x-1} = proportion of $N_{x-1,t-1}$ available for mating;
- 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.

Our model was deterministic with time units of 1 year. We assumed that there were no density-dependent effects. The population was structured into 25 age classes with the following sex/family status categories: males, females with no offspring, females with 1 cub, females with 2 cubs, females with 1 yearling, females with 2 yearlings, and females with 2-year-olds.

The kill of male bears by hunters depends on the relative abundance and vulnerability of the various age/sex strata and family groups, and 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 compensate 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. For the remainder of the unprotected categories, the harvest was unselective with respect to age. Females accompanying cubs and yearlings were also protected. To make the simulation as realistic as possible, females with 2-year olds were considered to be 75% as vulnerable as females with no cubs because many Inuit hunters avoid taking family groups of any type (M.K. Taylor, unpubl. data).

Initial conditions were 500 males and 500 females at stable age distribution based on the following natural (i.e., unharvested) survival and recruitment parameters: 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, age of first (subadult) litter production = 5, age of female reproductive maturity = 6, and litter size of cubs = 1.8. These parameters are realistic for polar bears and results in a stable age population growth rate (λ) of 1.039 with no harvest mortality (Taylor et al. 1987a).

Three sets of simulations were run. Each simulation was run for 50 years with the mean age of harvested bears and number of males and females recorded each year. The first set of simulations examined effects of sex-selective harvesting at maximum sustainable levels for selectivities ranging between 50% and 28% females. The maximum sustainable harvest was identified by iteration, and was defined as a value that did not result in more than a 5% change in the number of females over the 50 year period. This simulation is essentially the current harvest policy for polar bears in Nunavut, Canada. The second set of simulations examined the consequences of leaving the quota at 47 bears per year (i.e., the maximum sustained yield at 33%

female harvest for our example population of 1000) for selectivities ranging between 40% and 10% female. These 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). In our third set of simulations, we examined the outcome of a harvest scenario aimed at increasing population size by harvesting females below sustained yield. All simulations were repeated with the age of first reproduction increased from 5 to 6 to examine sensitivity of the results to delayed maturation and consequently lower population growth rate.

Results

With an unselective (i.e., 50% female) maximum sustainable kill, the mean age of harvested males 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 possessed 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 re-defined 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.

Selecting for males in the harvest reduced the fraction of the population that was male (Figs. 2 and 3) and reduced the mean age of males (Figs. 1 and 4). As per our harvest sustainability criteria, the abundance and mean age of females remained invariant with respect to changes in selectivity for males (Figs. 1 and 2). Sustainable harvest sex ratios at maximum sustained yield ranged from 50% female to 28% female for the example population of 1000 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 (Fig. 3). The sustainable harvest (males and females) at 33% females was 47.2. 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).

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 potential (i.e., abundance of females) of the population increased (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 (Fig. 6). However, where increased selectivity for males allowed females to increase (Fig. 5B), the initial decline in mean age of males recovered as the total population increased (Fig. 6A). The eventual mean age of both males in the population and harvested males depended on the stable age distribution realized when the population had increased such that per capita rates of harvest mortality (constant numbers taken) were no longer significant relative to per capita rates of natural mortality.

When the age of first reproduction was increased from 5 to 6 (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 6 to 7, 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 sustainable yield at a given harvest sex ratio was reduced.

For our example population, the maximum yield given a harvest of 25% females was 62.3 according to Equation 1. 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 female harvest below maximum sustainable yield, 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.

Discussion

The hunting of polar bears is an Inuit right guaranteed in Nunavut under land claim agreements between the federal and territorial governments. Traditionally, population dynamics of polar bears were viewed by Inuit as a force of nature, neither predictable nor controllable by man. Contemporary Inuit hold views ranging from the traditional perspective to acceptance of modern demography principles. The diversity of views and high demand for hunting opportunities can

make it difficult to gain support for reducing quotas as a management action. Increasing selectivity for males to increase the total harvest has been viewed as an acceptable management practice by Inuit; however, some concerns over long-term effects on males have been voiced. Since the inception of hunting quotas for polar bears in Canada in 1968, quotas increased from about 300 to a maximum of 610. Currently there are approximately 500 polar bears killed each year in Canada and about 630 killed from all jurisdictions that have or share populations in Canada (PBTC 2003).

Our results support the validity of this management practice; however, we also point out limits to increases in harvest that can be sustained by increasing selectivity for males. Since males are renewed at the same rate as females, the effect of a male-selective harvest at maximum sustained yield 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 (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 put forward. Equation 1 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 1), 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.

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 for males is decreased, and the total kill is kept constant, the population declines due to over-harvest 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 the number of males taken annually does not deplete the males, the increased rate at which males are recruited eventually compensates for the initial over-harvest of this sex (Fig. 7). These results assume 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 increased from 28% to 25% female, and 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, Stirling & Lentfer 1986, Lentfer et al. 1980), Hudson Bay (Derocher 1991, Derocher,

Stirling & Calvert 1997), and Viscount-Melville Sound (Taylor, Laake, Cluff, Ramsay & Messier 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 over-hunting over a period of 30 years while subject to a harvest that was sustainable and selective for males (Derocher 1991, Derocher et al. 1997). 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 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, 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.

Additional Considerations

Our definition of maximum sustained yield in this paper is the maximum number of bears that can be taken that does not allow for a decrease in abundance of females (i.e., reproductive potential) and retains males older than 2 years of age. More typically, the maximum sustained yield is used to describe the density at which the yield curve is maximized (e.g., $\frac{1}{2}$ 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 maximum sustained yield, 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 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 over-harvest 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 conservative in

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

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Figure Legends

Figure 1. Effect of increasing selectivity for males on the mean age of harvested male and female polar bears after harvesting for 50 years at the maximum sustainable rate.

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

Figure 3. Changes in male abundance over time at various levels of female selectivity under sustainable rates of harvest.

Figure 4. Changes in mean age of male polar bears over time at various levels of female selectivity under sustainable rates of harvest.

Figure 5. 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 maximum sustainable yield at 33% females for this example.

Figure 6. 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 maximum sustainable yield at 33% females for this example.

Figure 7. Changes in male (**A**) and female (**B**) polar bear abundance over time for an initial population of 1000 individuals and an average annual harvest of 62.3 bears at 15% females in the harvest.

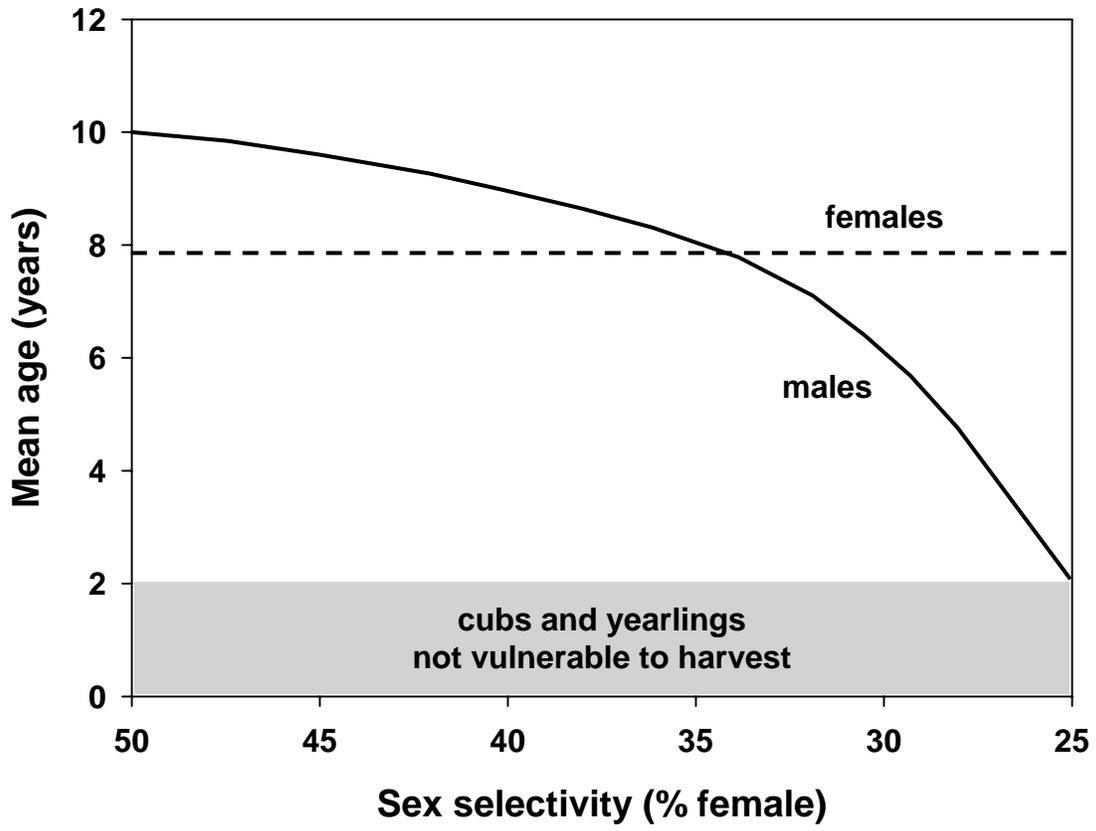


Figure 1

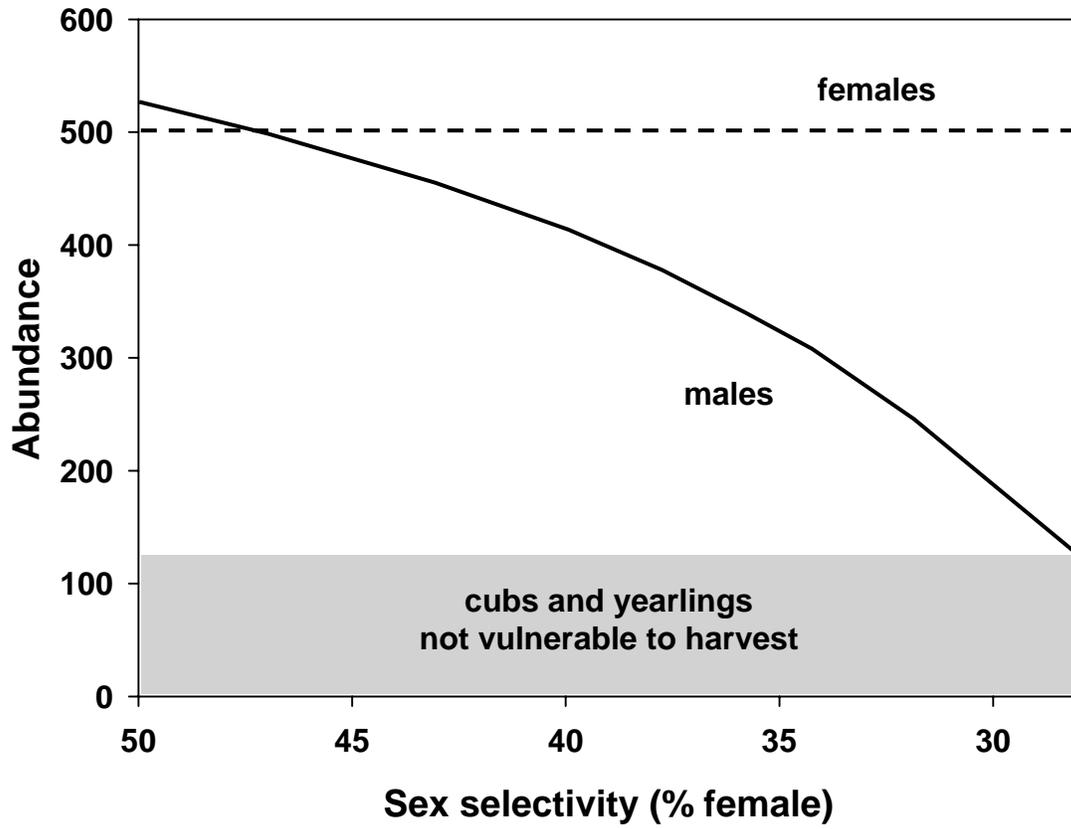


Figure 2

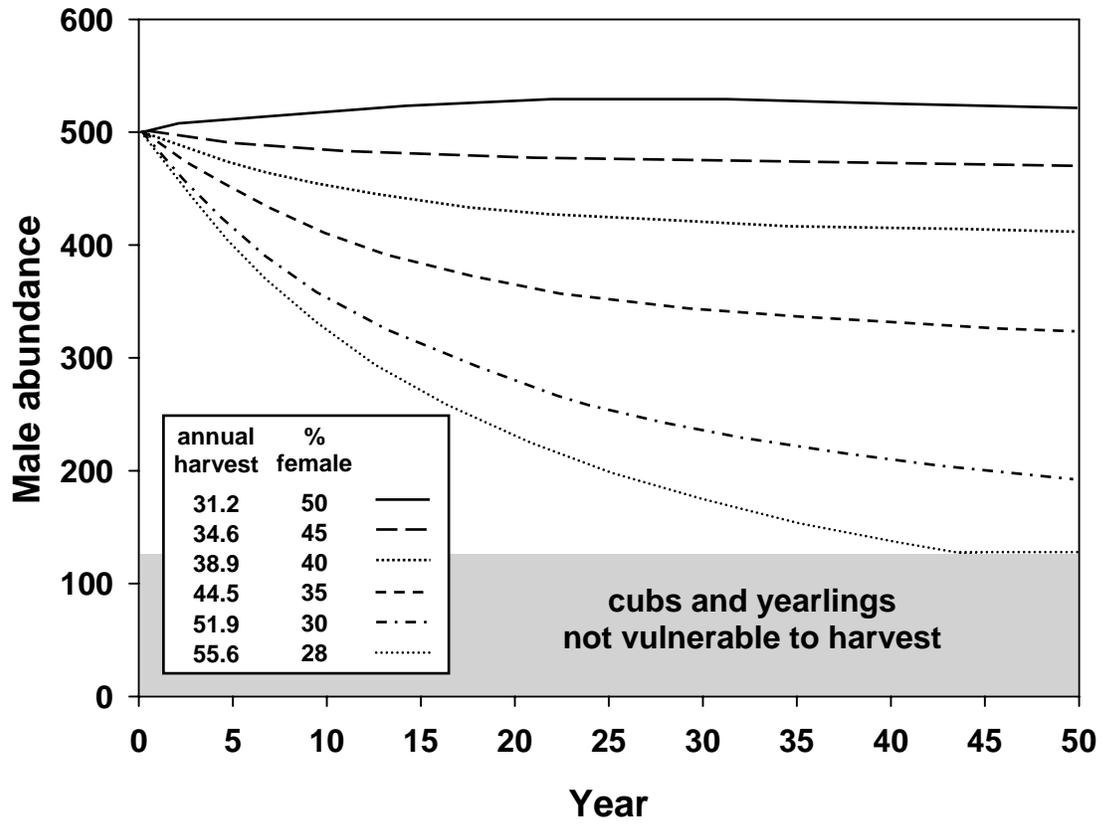


Figure 3

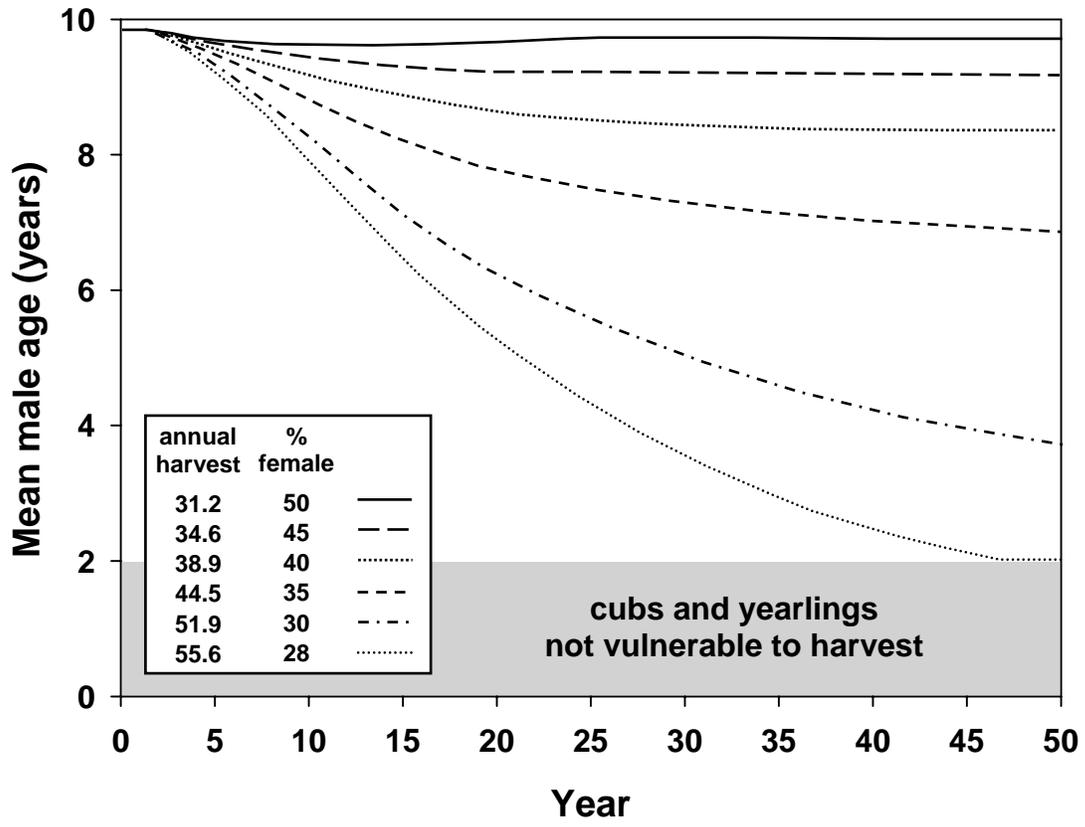
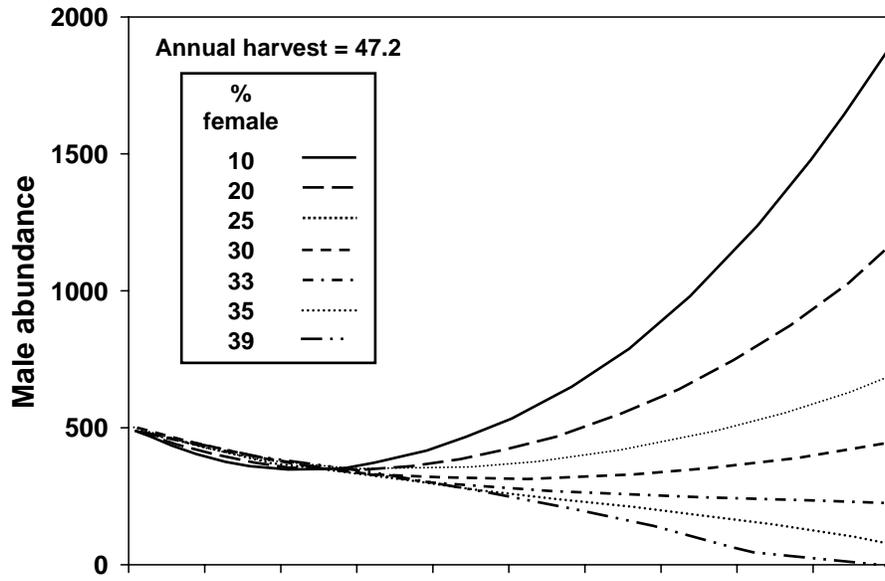


Figure 4

A.



B.

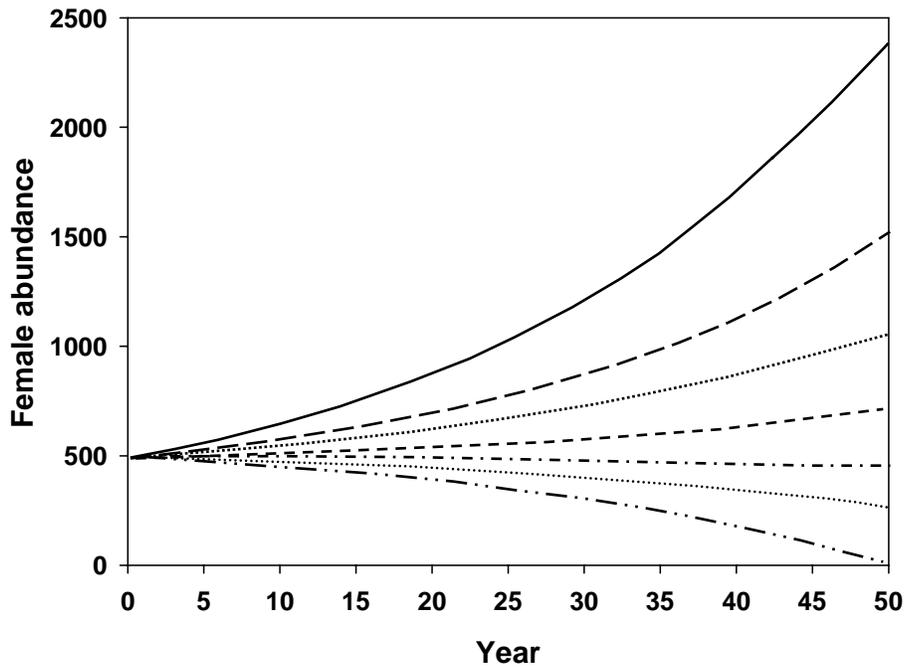
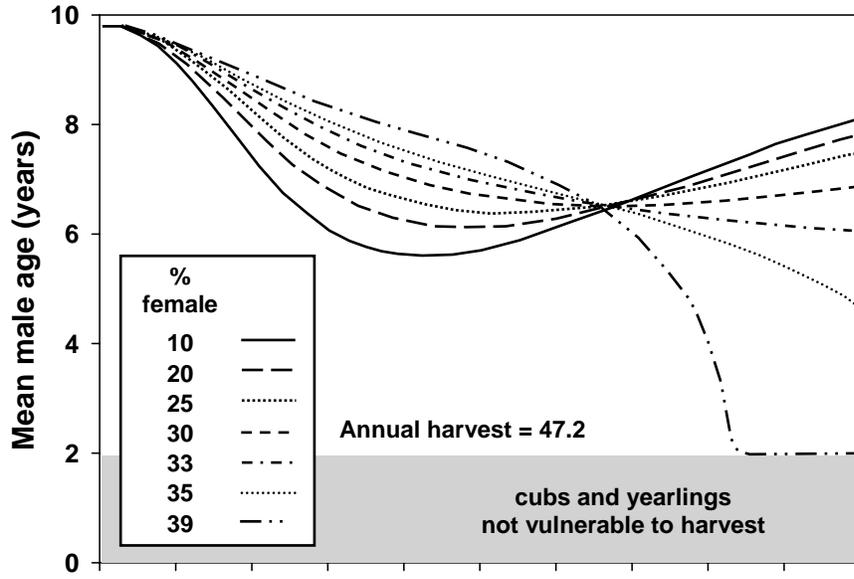


Figure 5

A.



B.

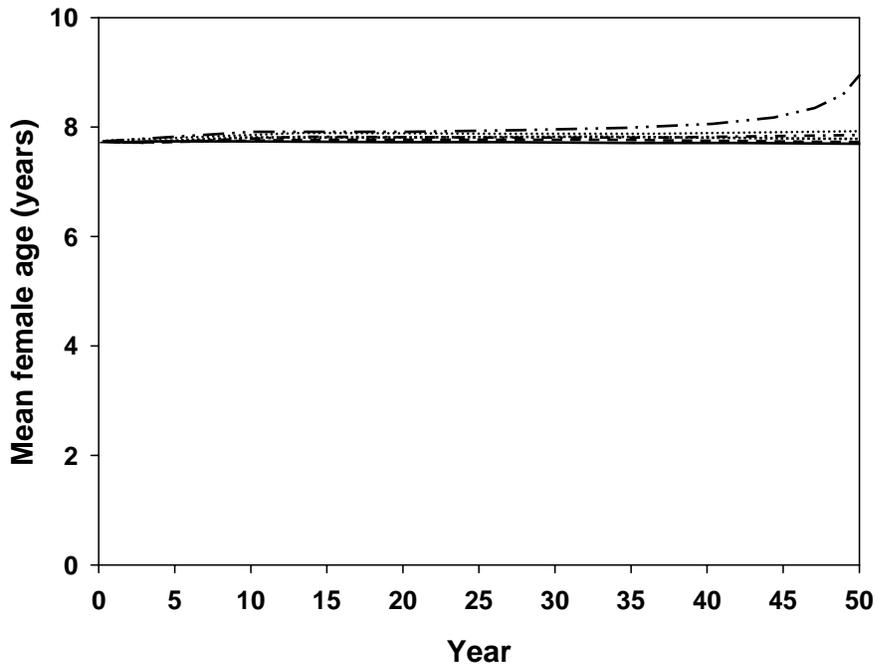


Figure 6

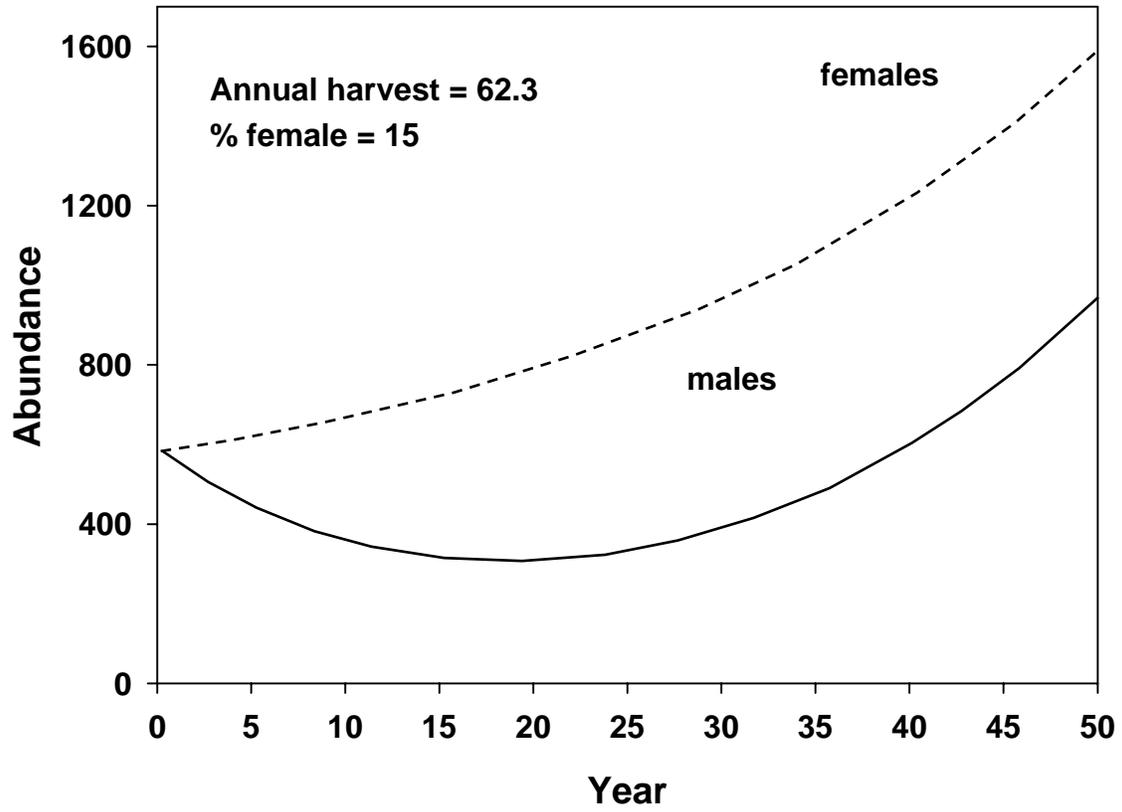


Figure 7