



CONSERVATION RISKS OF MALE-SELECTIVE HARVEST FOR MAMMALS WITH
LOW REPRODUCTIVE POTENTIAL

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Abstract: We used harvested, stochastic population models for grizzly bears (*Ursus arctos*) and polar bears (*Ursus maritimus*) to illustrate the propensity for male-biased harvesting to reduce mean male age and numbers of sexually mature males for species with relatively low reproductive potential. We compared our results with those obtained from caribou (*Rangifer tarandus*), an annually reproducing species with relatively high reproductive potential. Differences in the rate at which mean ages and numbers of sexually mature males were reduced by harvesting was a function of differences in life history of species, but also the extent to which young animals were protected from hunting. Proportionately more young bears were protected from harvest than young caribou due to the multiannual, rather than annual, parental care afforded young bears (we assumed all females with accompanying offspring were invulnerable to harvest). This additional age-bias in the hunt served to direct offtake toward adult males; consequently, as male selectivity in the kill increased; mean ages of bears declined at rates that were higher than for caribou. For species with low reproductive potential, we believe there is a real possibility that persistence probabilities may be overestimated if, after prolonged sex-selective harvest, lack of sexually mature males in the population impairs fecundity. We encourage further development of population models that incorporate potentially negative, hunting-induced impacts on reproduction. In particular, we support the development of models that link the mean age of males or frequency of adult males in a population to the rate at which females are successfully mated.

Key words: caribou, fecundity, grizzly bear, hunting, polar bear, population viability analysis, reproduction, sex-selective harvest.

INTRODUCTION

A common application of wildlife management theory is to emphasize the harvesting of males to increase sustainable yield while conserving the reproductive potential of a population. The rationale for sex-selective harvesting is founded in a basic understanding that for polygynous species, as long as there are enough males to mate available females, it is the female component of the population that determines population growth rate (Caughley 1977:192). Application of male-biased harvesting is common in the management of ungulate game species, for which there exists several analyses of the risks and benefits of sex-selective harvesting (Ginsberg and Milner-Gulland 1994, Langvatn and Loison 1999, Jensen et al. 2000, Laurian et al. 2000, McCullough 2001, White et al. 2001, Sæther et al. 2003). Sex-selective harvesting is also common for large mammals with multiannual parental care (e.g., bears, elephants, marine mammals), particularly when females with accompanying offspring are protected from harvest and adult males are taken as trophies (LeFranc et al. 1987, Lee and Taylor 1994, Paulraj and Subramanian 2000, 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.

Most authors agree that there are limits to increases in sustained yield that can be realized from sex-selective hunting, since we must allow for at least some males to fertilize available females. Wildlife populations generally contain more males than are required to mate available females, but given that an individual male can copulate only so many times, there likely exists a minimum ratio of males to females that must be present to breed available females (Caughley 1977:192–196). Unfortunately, the limited number of attempts to identify minimum sex ratios has been equivocal (White et al. 2001). In practice, sex ratios required to maintain recruitment

may be quite low, particularly when mating is promiscuous or when a few, dominant males monopolize receptive females (e.g., 0.5–20% males in the population [Caughley 1977:193]). If the sex ratio is too low, however, demographic impacts may include breeding failures, or disruptions in timing of mating (Noyes et al. 1996, Sæther et al. 2003) that could be important if late parturition results in lower offspring survival or lack of synchrony in breeding increases exposure of newborns to predation (White et al. 2001).

In addition to producing female bias in the sex ratio, sex-selective hunting is also likely to affect population age structure. As male-biased hunting favors the sex ratio toward females, the mean age of males in the standing population is expected to decrease (Caughley 1977:196). The rate at which the average age of males is reduced may differ for species in response to different age-specific schedules of survival, but the rate may also differ if age-bias in the hunt varies. For example, if young males are protected from harvest by being associated with their mother, increased periods of parental care may result in proportionately more hunting effort being directed at adult age categories. Reproduction of females may be impaired if the mean age of males decreases too far below the age of sexual maturity. Females may avoid mating with young males (Clutton-Brock et al. 1992, Noyes et al. 1996, Komers et al. 1999), or physiological barriers may prevent immature males from successfully fertilizing females (e.g., fully-formed spermatozoa do not appear to be present in seminiferous tubules of polar and grizzly bears until ages 5–7; Stirling 1988, White et al. 1998, Rosing-Asvid et al. 2002).

We contend managers of species with low reproductive potential (e.g., bears, elephants, marine mammals) have yet to fully appreciate potential impacts of sex-selective hunting on population age and sex composition. For example, although stochasticity in sex ratio was identified as having potential importance to outcomes of population viability analysis (Brook et

al. 2000), it is only recently that implications of hunting-induced changes to the age and sex structure of populations have been considered in the light of population viability (e.g., Wielgus et al. 2001). We use harvested, stochastic population models for grizzly bears and polar bears to illustrate the propensity for male-biased harvesting to reduce the mean age and numbers of sexually mature males. We compare our results with those obtained from caribou, an annually-reproducing species with relatively high reproductive potential. We hypothesize that a harvest focused on independent males will reduce the mean age of males, and thus reduce numbers of sexually mature males, at a rate that is greater for species with multiannual vs. annual reproductive cycles. We believe the causal mechanism for this hypothesis is based in species differences in age and sex schedules of survival and reproduction and in differences regarding the extent to which male-biased hunting of multiannual species is targeted toward older males when family groups are protected from harvest. We discuss consequences of altered sex and age composition on mating rates for species with low reproduction, and we discuss the potential for population models to overestimate likelihood of persistence if numbers of sexually mature males are reduced through harvest such that the frequency at which females are successfully mated is compromised.

METHODS

Population Model

We used a life-table based, stochastic population model named Riskman (e.g., Taylor et al. 2001, 2002; McLoughlin et al. 2003a, McLoughlin and Messier 2004) to examine changes in the structure of simulated populations in response to male-biased hunting. Riskman differs from other models by providing an option to specifically simulate the population dynamics of species with multiyear reproductive schedules, such as bears, cetaceans, elephants, pinnipeds, and

primates (Taylor et al. 1987); however, the model can also accommodate annual reproduction. Effects of human-caused mortality (e.g., hunting) on populations can be incorporated into the model in a variety of ways, ranging from detailed simulations that include probabilistic age-specific vulnerability and selectivity of the kill to simple apportionment of the kill according to the abundance of sex and age types in the population. Effects of harvest are applied after reproduction and are additive to natural mortality. Riskman can model 3 types of stochasticity, including sampling, environmental, and demographic stochasticity (White 2000). The model uses Monte Carlo techniques (Manly 1997) to generate a distribution of results, and it then uses this distribution to estimate the variance of summary parameters, such as population size at a future time, final age and sex structure, population growth rate, and proportion of runs that result in a population decline set at a predetermined level by the user. We adopted the latter (i.e., persistence probability) to quantify the relative sustainability of a given harvest rate. We can provide Riskman freely upon request; the program is also available at <http://www.nrdpfc.ca/riskman/riskman.htm> (accessed 2005 Apr 26).

Simulations

We examined effects of long-term, male-biased hunting on the structure of simulated populations of grizzly bears, polar bears, and caribou. Age- and sex-specific natural survival and reproduction for all populations were derived empirically. For grizzly bears (Table 1), we used mean natural survival and recruitment rates and their associated standard errors for the population inhabiting mainland Nunavut and the Northwest Territories, Canada, 1988–1999 (McLoughlin et al. 2003*a,b*). Bears in this region (barren-ground grizzly bears) were adapted to poor and variable habitat, and they exhibited life history traits resulting in low productivity relative to other grizzly bear populations in North America (Ferguson and McLoughlin 2000,

McLoughlin et al. 2003*b*). For polar bears, we used natural vital rates and their variances obtained from the population occupying Baffin Bay, Nunavut, 1974–1997 (Table 1), as originally presented in Taylor et al. (2005). For caribou, we used natural survival and reproduction data presented in Fancy et al. (1994) for the Porcupine caribou herd, northeast Alaska and northwest Canada, 1982–1992 (Table 1). Unharvested population growth rates for these populations largely reflected local conditions at the time of study, rather than species-specific intrinsic (Malthusian) growth rates. Underlying unharvested finite rates of increase were relatively low for the caribou and grizzly bear populations compared to the polar bear population (Table 1). We purposely modeled populations using presented growth rates to demonstrate that responses among species to sex-selective harvesting were inherent to life history strategy and not simply population rate of increase.

We modeled initial conditions as 500 males and 500 females at stable age distribution based on population-specific survival and recruitment parameters (Table 1). We assumed that population inventories capable of detecting major shifts in population structure would be conducted at 30-year intervals, or less, for large mammals like bears and caribou; therefore, we modeled populations over 30 years. We assumed no error in initial population size and a 50:50 sex ratio at birth. Although there are provisions within Riskman to include density-dependent effects on survival and reproduction, we modeled growth rates exponentially to avoid bias associated with unknown curves describing density-dependence or generic curves that may not be applicable to all species (e.g., effects may be observed for caribou at densities that are 1–2 times the order of magnitude of bear densities [Taylor et al. 1994; Messier et al. 1988]). Thus, all likelihoods of population persistence should be interpreted in the relative, rather than absolute, sense.

By increments of 1%, we simulated an annual, total harvest of 2–6% for each model population, and we applied harvest equally across age and sex categories excepting mothers and their accompanying offspring, which were protected from hunting. For bears this included females with cubs and yearlings; for caribou this included females with calves. For each level of annual harvest, we then varied, also by increments of 1%, the average percentage of males in the hunt (50–75%). Our applied harvest rates were realistic for modeled species. For example, polar bears in Baffin Bay were recently estimated to have been harvested annually at 5.8% with a 66% male sex ratio (Taylor et al. 2005). The hunt for Porcupine caribou was 68% male, at 2–4%/year for adults (Fancy et al. 1994). Known kill of grizzly bears in Nunavut and the Northwest Territories averaged approximately 2%/year and was 70% male (McLoughlin et al. 2003*a,b*).

For each simulation, we ran 1,000 stochastic population projections to provide the following estimates and their standard errors (after 30 years): (1) mean ratio of adult males to adult females, (2) mean ages of males and females, and (3) the proportion of outcomes falling below a set level of persistence. For the latter, we defined a successful outcome as a population decline <10% over 30 years. A 10% decline over 3 generation lengths (i.e., the average age of parents of a newborn cohort; roughly 8–10 years for the species we modeled) is a criterion used by the World Conservation Union (IUCN) to classify small (i.e., $N < 10,000$), discrete demographic units as vulnerable to endangerment (IUCN 2001:22–23).

Analysis

For the range of harvest percentages typically applied to caribou and bears in North America (i.e., 50–75% male harvest and 2–6% total annual harvest), we were also interested in determining the relative importance of harvest sex ratio vs. harvest rate to further changes in population composition. Both have the potential to alter the sex and age structure of populations.

We performed a series of 2-way, random-effects analyses of variance (Model II ANOVA [Sokal and Rohlf 1995]) that partitioned the variance of model outcomes (i.e., a variance components analysis) by percentage male harvest (Factor 1) and severity of the annual harvest (Factor 2). For each simulated population, we resampled 25 randomly chosen levels of male selectivity in harvest (50–75%) and 6 randomly chosen levels of annual harvest (2–6%), and generated an array of results (i.e., ratios of adult males to adult females, mean ages of males and females, and persistence probabilities). We then ascribed observations of simulation outcomes to cells in each ANOVA design. We transformed all observations (\log_{10}) prior to analysis to meet model assumptions. We estimated components of variance (absolute values) using the type III expected mean squares method (Sokal and Rohlf 1995), from which we calculated percentage variances in model outcomes explained by the factors of interest. We carried out statistical analyses with Statistica, Release 5.1 (Statsoft 1997).

RESULTS

At the minimum harvest percentages considered (i.e., equal sex ratio and 2% annual offtake), the adult sex ratio (males:females) at the end of 30 years of simulation remained close to unity for all populations (Fig. 1). The ratio of adult males to females in the population decreased as the percentage of males in the harvest and total harvest increased. This change was greatest for the grizzly bear population, followed by the polar bear and caribou populations. At 75% male and 6% total annual harvest and with the maximum rates considered, mean ratios of adult sexes were reduced to 6.8, 13.0, and 43.2 males per 100 females for grizzly bears (Fig. 1A), polar bears (Fig. 1B), and caribou (Fig. 1C), respectively. Standard errors of all estimates were <0.1 .

As harvest rate and selectivity for males increased, the mean age of males for all simulated populations decreased (Fig. 2). In contrast, average female age was static in response to harvest manipulation. For grizzly bears, the mean age of males decreased from 9.1 years of age with a 50:50 harvest sex ratio and 2% annual offtake, to only 1.6 years with 75% male selectivity and 6% annual harvest (Fig. 2A). Mean female age remained unchanged at 9.2 years. A similar reduction in the mean age of males was encountered for polar bears: at 75% male selectivity and 6% annual harvest, the mean age of males was 2.1 years, down from 6.5 years at minimum harvest percentages (Fig. 2B). Mean female age of polar bears was static at 7.5 years. Although the mean age of males was also reduced in the caribou population, the overall change was much less than that experienced by the bear populations. The mean age of male caribou was reduced from 4.1 years at minimum harvest levels to 2.5 years at maximum levels (Fig. 2C); however, mean female age remained at 4.2 years. Standard errors of all the above parameters were <0.1 .

In all cases, the mean age of males at the end of simulation could be increased by lifting protection afforded to offspring by association with their mothers. For example, at 6% annual harvest and 75% male selectivity, removing yearling grizzly bears from harvest protection (i.e., only cubs remained protected), mean male age at the end of simulation was raised to 2.6 years, and the adult sex ratio was raised to 15.5 males per 100 females (compared to 1.6 years and 6.8 adult males per 100 adult females when both cubs and yearlings were protected [above]). Removing harvest protection from all offspring served to increase mean male age of grizzly bears to 4.1 years, and it increased the adult sex ratio to 27.6 males per 100 females. By comparison, removing protection from caribou calves increased mean male age at the end of

simulation from 2.5 to 3.0 years, and it increased the adult sex ratio from 43.2 to 51.6 males per 100 females.

Likelihoods of persistence reflected underlying population growth rates (Fig. 3, Table 1). For any given level of annual harvest, progressively biasing the harvest sex ratio toward males increased the total number of females—and males (albeit at reduced ages)—remaining in the population at the end of simulation, and hence likelihood of population persistence also increased (Fig. 3). Thus, without taking into consideration final sex ratio or age effects, the apparent sustainability of a given annual harvest rate always increased in response to biasing the sex ratio toward males.

Sex ratio of the harvest and harvest rate generally contributed equally to reducing the ratio of adult males to females and mean age of males; however, the primary factor varied slightly among species (Table 2). Annual harvest rate was the primary contributor to changes in probability of population persistence, excepting the polar bear population for which most observations were fixed at 1.0 (Fig. 3B, Table 2).

DISCUSSION

Differences in the rate at which mean ages and numbers of sexually mature males were reduced by sex-selective harvesting was likely a function of differences in life history of species; however, differences also appeared dependent on the extent to which young animals were protected from hunting. Of particular interest, the length of each species' reproductive cycle appeared to determine the degree to which sex-biased harvesting was also age-biased. Proportionately more young bears were protected from harvest than young caribou due to the multiannual, rather than annual, parental care afforded young bears (all females with accompanying offspring were invulnerable to harvest). This additional age-bias in the hunt

served to direct offtake toward adult males; consequently, as male selectivity in the kill increased, mean ages of bears declined at rates that were higher than for caribou. When we reduced the amount of protection afforded to offspring accompanying their mothers, the total harvest was spread more evenly across male age categories, and mean ages of males increased. Differences in sex and age specific schedules of survival and fecundity also appeared to influence results. We modeled grizzly bears and polar bears with the same reproductive cycle, but they demonstrated different sensitivity to male-biased harvesting.

Our results also suggest that changes in population composition may be brought about by either increasing male-bias in the hunt or overall harvest rate: final ratios of adult males to females and mean ages of males were equally well-explained by variation in either of these factors. Effects of harvest rate and percentage male-bias in the kill appeared to be additive, which prompts us to make the following predictions: 1) high harvests may not affect population composition if the sex ratio of the harvest is close to unity; 2) sex ratio of the harvest may be strongly biased and have little impact on age and sex structure if we harvest at low annual rates; and 3) the largest impacts on population composition will be experienced at high levels of both harvest rate and male-bias in the hunt.

Total annual harvest rate was the primary determinant of population likelihood of persistence, which was not surprising considering that an increase in total annual harvest always increased the total number of females removed from the population (for a given percentage of males in the harvest). However, increasing male-bias in the hunt always improved persistence probabilities, supporting the notion of emphasizing the hunting of males to increase sustainable yield while conserving the reproductive potential of the population. We believe, however, that for modeled species most vulnerable to hunting-induced changes in population composition (i.e.,

bears), our simulations underestimated negative effects of increasing harvest and overestimated positive effects of increasing hunter selectivity on likelihoods of persistence. This is because our models failed to consider potentially negative impacts on female reproduction due to substantial changes in numbers of adult males and mean ages of males.

For example, persistence in the polar bear model was assured at 6% total harvest when hunter selectivity was 75% male (Fig. 3B). However, after 30 years, this harvest strategy would also result in a mean of 13 adult (i.e., ≥ 5 years old) males per 100 adult females and an average male age of only 2.1 years (Figs. 1B and 2B, respectively). For polar and grizzly bears, sexual maturation of males is not reached until 5–7 years of age, and breeding generally does not occur until 8–10 years of age (Stirling 1988; White et al. 1998; Rosing-Asvid et al. 2002). It is possible that impaired reproduction resulting from relatively few numbers of sexually mature males would lower the true likelihood of persistence and compromise sustainability of the hunt; however, we did not model this explicitly.

If sex-selective harvesting affects reproduction by reducing availability of males for mating, we could expect this to principally manifest itself in the pregnancy or parturition rates of unencumbered females (i.e., females that are free to mate in a given year). Empirical observations of pregnancy rates within the bear populations we modeled support this hypothesis. Of the populations considered, the grizzly bear population in McLoughlin et al. (2003*a,b*) was historically exposed to the strongest male-biased hunt (70% male). Bears in McLoughlin et al. (2003*a,b*) also expressed the lowest rates of parturition: on average, only 60% of females ≥ 8 years of age that were available to mate in a given year produced litters the following year (McLoughlin et al. 2003*a*). In contrast, polar bears inhabiting Baffin Bay, which are harvested at annual rates $\leq 66\%$ male, show an average parturition rate close to 100% for receptive females

(Taylor et al. 2005). Close observation of parturition rates is often used to assess potential negative effects of sex-selective hunting on ungulate species (review in White et al. 2001). We recommend a similar approach for managers of harvested mammals with multiannual reproductive cycles.

MANAGEMENT IMPLICATIONS

Our results suggest that for species with low reproductive potential, there is a real possibility that persistence probabilities may be overestimated if changes in population composition after prolonged, sex-selective harvesting are not evaluated in light of the potential for reduced numbers of mature males to successfully mate available females. To monitor for potential impacts of excessive male-biased harvesting, we suggest managers be vigilant of trends in the proportion of females that are available to mate in a given year that indeed produce offspring the following year (e.g., through telemetry-based surveys). We encourage further development of population models that incorporate potentially negative, hunting-induced impacts on reproduction (e.g., Wielgus et al. 2001). In particular, we support the development of models that link the mean age of males or frequency of adult males in a population to the rate at which females are successfully mated (e.g., White et al. 2001).

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Table 1. Demographic parameters and unharvested finite rates of increase (λ) for modeled populations of grizzly bears (1995–1999)^a, polar bears (1974–1997)^b, and caribou (1983–1992)^c. Survival rates are natural rates upon which harvests were added. Parameters are means and standard errors (SE), and include survival of female and male newborns (S_{nf} and S_{nm}), female and male yearlings (S_{yf} and S_{ym}), subadult females (S_{sf}), subadult males (S_{sm}), adult females (S_{af}), adult males (S_{am}), litter size (L), age at first reproduction (R_F), age at senescence (R_L), and maximum age of survival (w). For grizzly and polar bears, subadults were 2–4-years-old and adults ≥ 5 -years-old; for caribou, subadults were 2-years-old only and adults ≥ 3 -years-old.

	Grizzly bear ($\lambda = 1.03$) ^a		Polar bear ($\lambda = 1.05$) ^b		Caribou ($\lambda = 1.02$) ^c	
	Mean	SE	Mean	SE	Mean ^d	SE ^e
S_{nf}	0.737	0.060	0.620	0.095	0.510	0.038
S_{nm}	0.737	0.060	0.570	0.094	0.510	0.038
S_{yf}	0.683	0.074	0.938	0.042	0.959	0.036
S_{ym}	0.683	0.074	0.938	0.045	0.877	0.075
S_{sf}	0.831	0.148	0.938	0.042	0.989	0.028
S_{sm}	0.833	0.150	0.938	0.045	1.000	0.000
S_{af}	0.979	0.012	0.953 ^f	0.020 ^f	0.860	0.020
S_{am}	0.983	0.017	0.947 ^g	0.022 ^g	0.865	0.038
L	2.23	0.13	1.59	0.07	1.0	0.00
R_F	8 ^h		5 ^h		3 ^h	
R_L	30		30		15	
w	30		30		15	

^a McLoughlin et al. (2003a,b).

^b Taylor et al. (2005).

^c Fancy et al. (1994).

^d Natural rates obtained by removing annual harvest (1.8% and 3.9% for cows and bulls ≥ 2 years old, respectively).

^e Standard errors obtained from 95% confidence limits.

^f Estimates for ages 5–20 only. For ages ≥ 21 , $S_{af} = 0.919$, $SE = 0.046$.

^g Estimates for ages 5–20 only. For ages ≥ 21 , $S_{am} = 0.887$, $SE = 0.060$.

^h Twenty percent of female grizzly bears allowed to reproduce for ages 5–7; 9.6% of female polar bears allowed to reproduce at age 4; 3.8% of female caribou allowed to reproduce at age 2.

Table 2. Absolute values and percentage of components of variances (in parentheses) accounted for by percentage male harvest and percentage total annual harvest in ratios of adult males (AdM) to adult females (AdF), mean ages of males, and population likelihood of persistence after 30 years of simulation. Results are for Model II ANOVA; all main effects are significant at $P < 0.0001$.

	Effect		
	% Male harvest	% Annual harvest	Interaction
Grizzly bear			
AdM:AdF	0.036 (42.5%)	0.032 (37.6%)	0.017 (19.8%)
Mean age of males	0.015 (40.8%)	0.015 (40.6%)	0.007 (18.5%)
Likelihood of persistence	0.25 (3.5%)	6.54 (90.0%)	0.471 (6.5%)
Polar bear			
AdM:AdF	0.015 (38.8%)	0.018 (46.3%)	0.006 (14.9%)
Mean age of males	0.006 (39.3%)	0.007 (47.2%)	0.002 (13.5%)
Likelihood of persistence	0.004 (4.1%)	0.029 (33.1%)	0.055 (62.7%)
Caribou			
AdM:AdF	0.004 (54.6%)	0.002 (31.1%)	0.001 (14.3%)
Mean age of males	0.001 (42.2%)	0.001 (45.4%)	0.0004 (12.4%)
Likelihood of persistence	0.231 (3.4%)	6.08 (89.9%)	0.450 (6.7%)

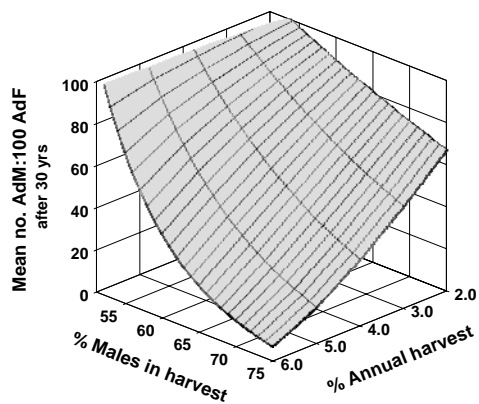
FIGURE CAPTIONS

Fig. 1. Changes in the mean number of adult males (AdM) per 100 adult females (AdF) after 30 years of simulation in response to harvest sex ratio and harvest severity for grizzly bears, polar bears, and caribou.

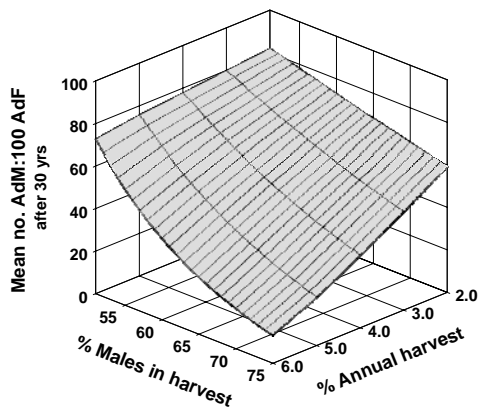
Fig. 2. Changes in the mean age of males (years) after 30 years of simulation in response to harvest sex ratio and harvest severity for grizzly bears, polar bears, and caribou.

Fig. 3. Changes in the likelihood of population persistence ($\leq 10\%$ decline from initial population size) after 30 years of simulation in response to harvest sex ratio and harvest severity for grizzly bears, polar bears, and caribou.

A. Grizzly Bear



B. Polar Bear



C. Caribou

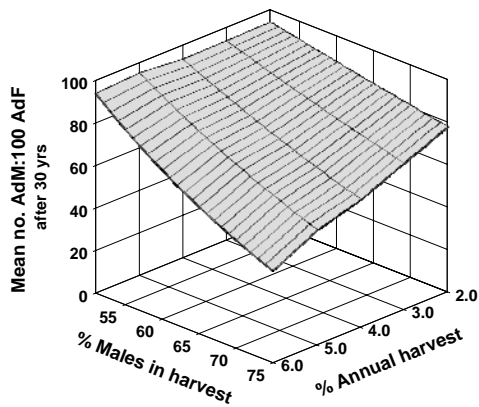
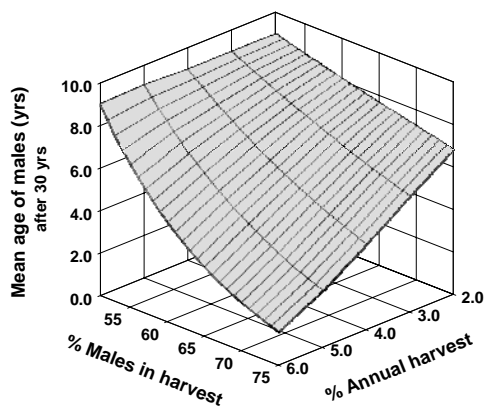
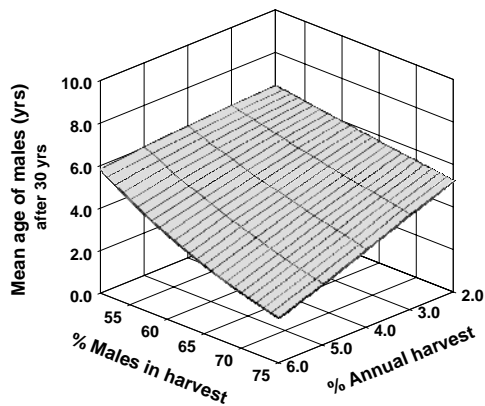


Fig. 1

A. Grizzly Bear



B. Polar Bear



C. Caribou

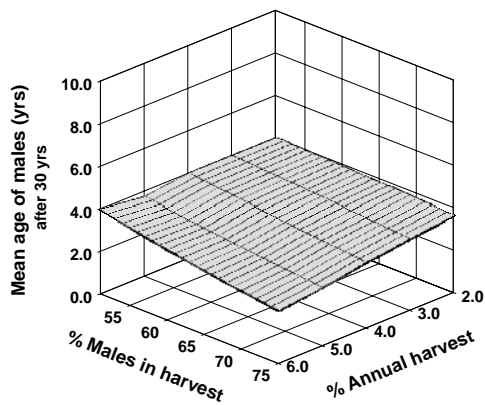
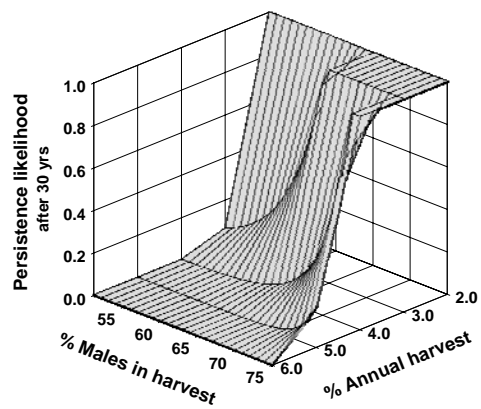
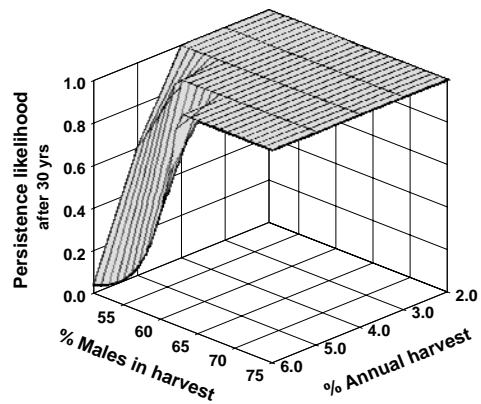


Fig. 2

A. Grizzly Bear



B. Polar Bear



C. Caribou

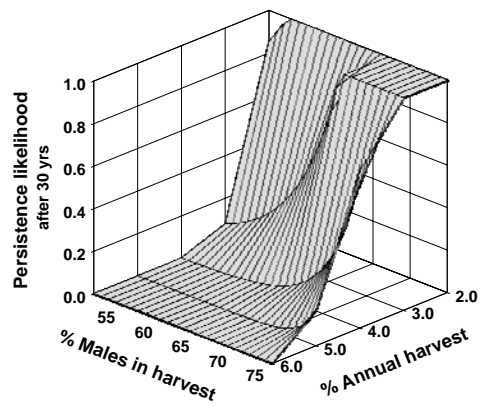


Fig. 3