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Sex-Biased Harvesting and Population Dynamics in Ungulates: Implications for Conservation and Sustainable Use

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Abstract: *The consumptive use of wildlife, in particular trophy hunting and game ranching of ungulates, has been advocated as a tool for conservation in Africa. We show that these methods of harvesting differ significantly from natural predation, with trophy hunting showing extreme selection for adult males and game ranching leading to disproportionate harvests of young males. Little information, either theoretical or empirical, exists concerning the effect of these harvesting regimes on the long-term population dynamics of ungulate populations. Despite that, the potential effects of sex-skewed harvests are numerous. In this paper, we investigate one potentially deleterious effect of sex-skewed harvests. Both theory and experimental data suggest that male ungulates are limited in their absolute ability to inseminate females. Using a Leslie-Matrix model and published data on impala, we show that the interaction between sperm limitation and harvests with highly male-biased sex ratios can lead to greatly reduced female fecundity (defined as the number of young born) and population collapse. These results are robust and suggest that present methods of harvesting may not be optimal, or viable, in the long term.*

Cosecha sexualmente sesgada y dinámica poblacional en ungulados: Implicaciones para la conservación y el uso sostenido

Resumen: *El uso consumitivo de vida silvestre, en particular caza por trofeos y ganadería de ungulados para caza, han sido invocados como herramientas para la conservación en Africa. Mostramos que estos métodos de cosecha difieren significativamente de la predación natural, con la caza por trofeos mostrando una selección extrema por machos adultos y la ganadería para caza conduciendo a cosechas desproporcionadas de machos adultos. Existe poca información tanto teórica como empírica sobre el efecto de estos regímenes de cosecha en la dinámica poblacional a largo plazo de poblaciones de ungulados. A pesar de ello los efectos potenciales de cosechas sesgadas sexualmente son numerosos. En este trabajo, investigamos un efecto potencialmente deletéreo de las cosechas sesgadas sexualmente. Datos tanto teóricos como experimentales sugieren que los ungulados machos están limitados en su habilidad absoluta para inseminar hembras. Nosotros demostramos, usando un modelo de Matrices de Leslie y datos publicados sobre el impala, que la interacción entre la limitación de esperma y las cosechas con proporciones sexuales sesgadas hacia los machos puede llevar a una fecundidad (definida como el número de recién nacidos) altamente reducida en las hembras y a un colapso de la población. Estos resultados son robustos y sugieren que los métodos actuales de cosecha no serían óptimos, o viables, en el largo plazo.*

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Introduction

The consumptive use of wildlife has recently been advocated as a tool for the conservation of wildlife and sustainable development of protein resources in much of eastern and southern Africa (International Union for Conservation of Nature/United Nations . . . /World Wildlife Fund 1980; Kyle 1987; Hudson et al. 1989; Bothma 1989a). Consumptive use may include game ranching and sport hunting (papers in Hudson et al. 1989; Bothma 1989a) or small-scale hunting for subsistence (Marks 1973, 1989).

Animals are not usually chosen for slaughter randomly: the composition by sex and age-class of a cull results from the priorities of the cropping scheme employed. Sex ratios are intentionally skewed towards females and age distributions towards younger animals in order to increase the rate of reproduction (see Catto 1976; Fairall 1985). There is often selection for trophy males exhibiting the most developed secondary sexual characteristics such as horns or tusks (Johnstone 1974; Cummings 1989). Different methods of harvesting may have different effects on the patterns of growth of an ungulate population. Little research has been done to elucidate the potential effects of cropping on animal social and reproductive behavior and on animal production and demography (but see Catto 1976; Fairall 1985; Joubert 1989).

Cropping may have several effects, both deleterious and advantageous. In this paper a model is developed to demonstrate the possible effects of selective cropping and their interaction with assumptions concerning a male's ability to fertilize a large number of females in a short breeding season. This could also be expressed as the ease with which females can locate males during a breeding cycle. A single species, the impala (*Aepyceros melampus*), is used as an example, although the results are much more widely applicable. The impala is distributed across eastern and southern Africa (Kingdon 1972; Smithers 1983; East 1988, 1989), it occurs at high densities and has a high rate of increase (Dasmann & Mossman 1962; Jarman & Jarman 1973; Murray 1982), and it is suited to manipulation and harvesting by humans (Fairall 1985).

Natural and Human Predation

Data for predation by lion (*Panthera leo*, Schaller 1972), spotted hyaena (*Crocutta crocutta*, Kruuk 1972), cheetah (*Acinonyx jubatus*, FitzGibbon & Fanshawe 1989), and African wild dog (*Lycaon pictus*, Ginsberg, Hwange National Park, unpublished data; Estes & Goddard 1967; FitzGibbon & Fanshawe 1989, personal communication) are presented in Figs. 1 and 2. Data are also presented for trophy hunting by humans

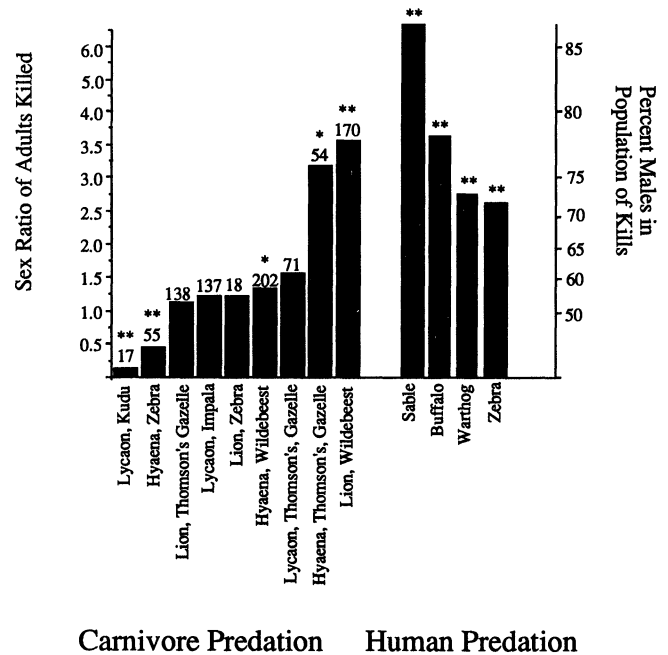


Figure 1. Selection of adult prey, by sex, for different predators and prey species. In four out of nine cases, predators appear to take their prey, by sex, in proportion to its representation in the population. By contrast, human trophy hunters show a disproportionate selection for males. Samples sizes and significance levels (shown by asterisks) are given above the bars. See text for data sources.

(Matetsi Safari Area, Zimbabwe, Fergusson 1990) and game ranching (Fairall 1985; Bothma 1989b). The data are tested for the significance of the difference between the population structure of the kill and that of the living population, using chi-square with small-sample correction. Data on the sex and age structure of living populations are taken from a number of sources: impala (Dasmann & Mossman 1962; Jarman & Jarman 1973); wildebeest (*Connochaetes taurinus*) (Estes 1966, 1976); sable (*Hippotragus niger*) (Estes & Estes 1969; Grobler 1974; Wilson & Hirst 1977; Fergusson 1990; Ginsberg unpublished data); Thomson's gazelle (*Gazella thomsoni*) (FitzGibbon & Fanshawe 1989); zebra (*Equus burchelli*) (Schaller 1972); kudu (*Tragelaphus strepsiceros*) (Ginsberg unpublished data). Where possible, data used were taken from the same population and the same time period in which data on hunting was collected. Where these data did not exist, species-specific data on ungulate population structure were collected from other populations in similar ecological zones.

Wild carnivores may show disproportionate selection for either males or females (males: hyaena hunting wildebeest or Thomson's gazelle [$p < 0.05$]; females: African Wild Dog hunting kudu [$p < 0.01$], hyaena hunt-

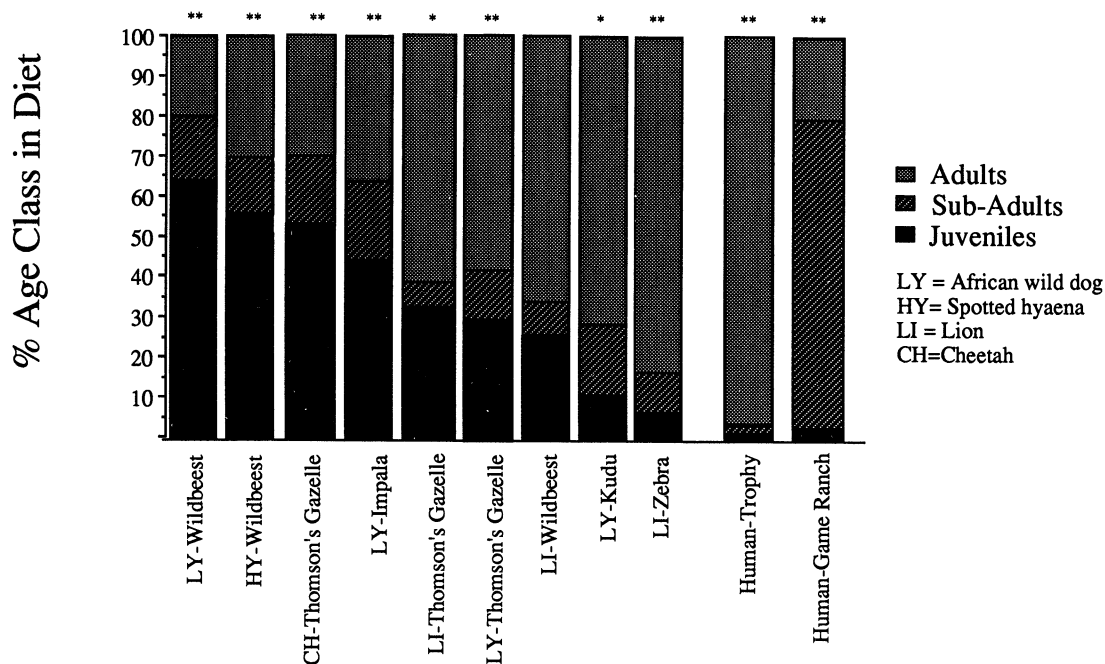


Figure 2. Selection of prey, by age class, for different predators and prey species. Most species preferentially kill juveniles, but there is no exclusive predation of a single age class for any prey species. By contrast, humans show strong preference for either adults (trophy hunting) or yearlings (game ranching). Significance levels (shown by asterisks) are given above the bars. See text for data sources.

ing zebra [$p < 0.01$]). In four out of nine cases studied, predators appear to take their prey, by sex, in proportion to its representation in the population (Fig. 1). In contrast, human trophy hunters show a disproportionate selection for males. This is true whether the species is highly dimorphic (African buffalo, *Syncerus caffer*), moderately dimorphic (sable, warthog, *Phacochoerus aethiopicus*), or essentially monomorphic (zebra). In over half the cases studied, wild predators take juveniles in greater numbers than would be expected from random hunting. In contrast, humans show strong preference for either adults (trophy hunting, $p < 0.001$) or yearlings ($p < 0.001$) (Fig. 2; Johnstone 1974; Fairall 1985; Cummings 1989).

Potential Male Fertility

Hunting methods and species-specific ecological and behavioral factors will determine how cropping affects population dynamics (Ginsberg 1991). Advantageous effects of highly female-biased sex ratios include reduced aggression and mortality among males and reduced harassment of females by bachelor males. Potential deleterious effects include disruption of territorial structure, increased mortality of calves born out of season, artificial selection for inferior males, or an inadequate number of males to inseminate all females. Deleterious effects of highly selective hunting are particu-

larly likely to affect species with synchronized breeding seasons in which a short disruption may reduce rates of conception and population growth for a year (impala, Dasmann & Mossman 1962; sable, Estes & Estes 1969; Grobler 1974; wildebeest, Estes 1966; saiga [*Saiga tatarica*], Bannikov et al. 1961).

There is little data on potential male fertility in wild or farmed wild animals. Breeding sex ratios in the wild have been observed (kudu 1:12, Owen-Smith 1984; red deer [*Cervus elaphus*] 1:4, Clutton-Brock et al. 1979; impala 1:3, Jarman 1979; Murray 1982; bighorn sheep [*Ovis canadensis*] 1:3, Geist 1971; Soay sheep [*Ovis arvensis*] 1:1.5 to 1:5, Clutton-Brock et al. 1991; fallow deer 1:4 to 1:20, Langbein & Thirgood 1989). The effect of variation in breeding sex ratio on female fecundity has received little attention. Bergerud (1974) suggests that at sex ratios of greater than 1:12, caribou (*Rangifer tarandus*) suffer a decline in female fecundity. In moose (*Alces alces*), Bannikov (1970) noted a decline in female fecundity when the sex ratio exceeded 1.2; Rausch (in Markgren 1974) suggested that no decline in fecundity was observed at sex ratios of 1:10. In a growing kudu population in Kruger National Park, a shortage of adult males may have led to a reduction in female fecundity, but no sex ratios have been published (Bothma 1989b). Over-harvesting of adult Dall sheep (*Ovis dalli*) rams may (Heimer 1980) or may not (Murphy et al. 1990) have an effect on lamb production.

Experience with game ranching of cervids, in particular red deer and fallow deer (*Dama dama*), is greater than that with all other wild ungulates combined (see papers in Fennessy & Drew 1985; Hudson et al. 1989). Yet even in these species, experiments have not been conducted to assess the effects on female fecundity of increasing skews in sex ratio (Fennessy, personal communication). A single male fallow deer was capable of inseminating 9–10 hormonally synchronized females within a single cycle (Jabbour et al. 1991); in other studies, a single male was able to inseminate up to 20 synchronously cycling females in a single cycle (Jabbour, personal communication).

Fairall (1985) argues that, in impala, highly male-biased hunting is unlikely to limit female fecundity (defined as the number of young born) because there are excess males in “bachelor herds characteristic of such populations.” Detailed behavioral data on known individuals (Jarman 1979) suggest that an excess of males in impala cannot be assumed from the observation of bachelor groups because (1) bachelor herds include many young males not yet biologically reproductive but necessary to ensure future breeding males; (2) breeding is highly synchronized (Jarman 1979; Murray 1982) and, in a single breeding season, a territory may be held by several males. Hence, “excess” males may actually be breeding males who have lost or not yet gained a territory.

Fairall (1985) states that “a male to female ratio of 1:10 should be quite adequate to ensure breeding with no decrease in fecundity as much higher ratios are attained in domestic stock.” Other authors have assumed that, as in domestic animals, a male impala’s physiological capacity to inseminate females will not be a limiting factor (see Catto 1976; papers in Bothma 1989a). Daily sperm production, sperm density, and absolute numbers of sperm per ejaculate are all directly related to testes size (Moller 1989). Domestic animals have undergone centuries of artificial selection resulting in larger testes size than in wild ungulates. Furthermore, in ungulates and elephants, dominant males frequently cover more females than do subordinates (see Bergerud 1974; Lott 1974 [all on ungulates]; Jarman 1979; Clutton-Brock et al. 1983; Clutton-Brock 1989; Ginsberg 1989; Poole 1987 [on elephants]). While adult impala males have relatively large testes for their body weight, the size of their testes is significantly smaller than that of domestic animals and cervids of similar size (Fig. 3; data from Neely et al. 1980, 1982; Clutton-Brock et al. 1983; Knight 1984; Ginsberg & Rubenstein). Therefore, sperm may be limited (Birkhead 1991; Birkhead & Fletcher 1992).

Social disruption can be caused by hunting biased toward either males or females. Reducing the proportion of adult females in the population might lead to increased competition for females among the remaining

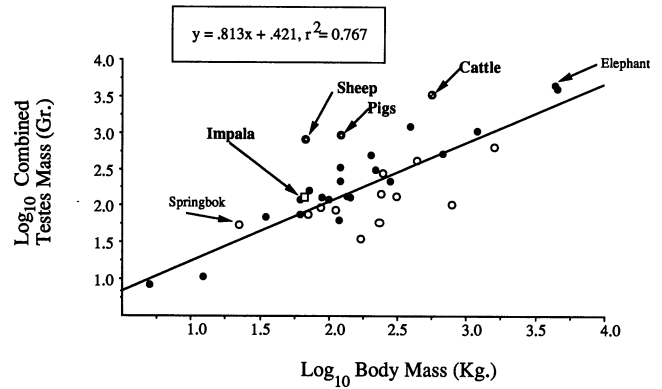


Figure 3. The relationship between body weight and testis size for 35 species of wild ungulates and three species of domestic ungulates. Domestic ungulates have large testes for their body weight, reflecting selection for increased sperm production and fertility. Species in which females are mated by more than one male are denoted by hollow circles, monogamous females by black circles. Impala are indicated by the hollow square. See text for sources of data and statistics (after Ginsberg and Rubenstein 1990).

males. Selecting for the largest adult males might result in an inadequate number of dominant males available to fertilize receptive females, or in breeding by partially incompetent yearlings (Prothero et al. 1980). Social disruption caused by the removal of both matriarchs and trophy males has been documented in the elephant, where it is particularly acute due to the highly structured nature of elephant social life (Poole 1989).

In ungulate species that are seasonal breeders, hunting or cropping during the breeding season is common in Europe and Africa (reindeer [*Rangifer tarandus*], Skjenneberg 1989; saiga, Bannikov et al. 1961; red deer, Gill 1990; S. D. Albon, personal communication; African antelope, Cummings 1989; Smithers 1983; Fergusson 1990). This may lead to disruption of territorial structure, increased male-male conflict, and, as a result, reduced rates of conception. Females not inseminated on their first cycle may either not conceive in that year or continue cycling, which could lead to a decrease in synchrony of birth. In saiga, continued hunting during the mating season led to a drop in conception rates, from 85% in one year olds and 96% in adults to 55% and 86% respectively (Bannikov et al. 1961). Using a simulation model, Gruver et al. (1984) demonstrated that, for white-tailed deer (*Odocoileus virginianus*), a delay in the hunting season for bucks results in increased fecundity and in an increased proportion of does fertilized on their first estrous cycle.

If births either are timed to ecological factors (rainfall and food abundance) or are effective in predator swamping, a reduction in calving synchrony may lead to increased mortality of juveniles and a decline in the

population size (Kiltie 1988). Such a scenario has been invoked as a cause of the decline in fecundity of sable in Matetsi, Zimbabwe (Fergusson 1990). Wildebeest calves born away from the peak of parturition appear to suffer greater mortality, apparently due to predation (Estes 1976; Estes & Estes 1979). Environmental variation alone, however, can account for increase mortality in late-born young (American bison [*Bison bison*], Rutberg 1984). In red deer, late calving has two negative effects: calf mortality increases by 1% for each day the calf is born following the median calving date (Clutton-Brock et al. 1987), and in the following breeding season females suffer a reduction in fertility of 1% for every day past the date of median conception in the previous year (Clutton-Brock et al. 1983). Delay in breeding for a single cycle (18 days) can result in a 36% decline in a female's reproductive success.

A Model of Impala Population Dynamics

A deterministic age-structured Leslie matrix was used to characterize impala population dynamics. In a Leslie matrix model, the number of animals in each age-class in a year is calculated as the number in the previous age-class in the previous year, minus those that died as a result of natural mortality or hunting. The number of animals in the first age-class is calculated from the number of calves that the female population would have given birth to in the previous year. The model was constructed using age-dependent survivorship and female fecundity rates derived from published data on impala (Dasmann & Mossman 1962; Jarman & Jarman 1973; see Table 1). These data suggest that male mortality from age four to seven is at or near zero; while this is unlikely, our model is conservative because increased male mortality in these age classes would only amplify any effects of sex-ratios bias. Female fecundity is assumed to be 70% in the first year of breeding and 90% in successive years.

Table 1. Age structure of impala used in model.

Age	% Males Surviving	% Male Mortality	% Females Surviving	% Female Mortality
Juvenile	100	40	100	40
Yearling	60	20	60	10
3	48	5	54	5
4	46	0	51	3
5	46	0	50	3
6	46	0	48	5
7	46	0	46	5
8	46	25	44	5
9	34	66	41	30
10	12	100	29	20
11	0	0	50	
12	0	0	100	
13	0	0		

See text for data sources.

Hunting is assumed to take place directly preceding a temporally peaked mating season and to be additive to natural mortality. Half the natural mortality occurs before hunting and half after mating. The model assumes simple logistic density dependence, acting on infant survival. In a Leslie matrix model with hunting mortality as a constant proportion of the population, the population structure and population growth rate reach an equilibrium, depending on the hunting rate and selectivity (Getz & Haight 1989). The population is allowed to reach this equilibrium for each hunting strategy before output is produced. This allows the long-term effects of a hunting strategy to be assessed independently of the values assumed for the starting population.

The simulations are performed for a harvest of either both sexes or of males only. Selectivity is varied by age and by sex. Three particular scenarios are modelled: selective hunting of old males, of young males, and hunting according to the availability of each sex and age class. These selectivities simulate trophy hunting, ranching, and nonselective hunting, respectively. The model assumes that there is no female choice of males, nor is there differential mortality between pregnant and non-pregnant females. The model further assumes that females not conceiving on their first cycle will cycle a second time, as is seen in nature (Fairall 1982). However, juveniles born out of synchrony with their cohort suffer a 30% increase in mortality.

The model is used to investigate the ramifications of the assumption that the number of females that a male can fertilize varies with the age of the male, and that there is a maximum and finite number of females that a male can cover. Males are assumed to begin breeding at age five and finish at age nine (Jarman & Jarman 1973; Jarman 1979). The number of females that males of different ages can fertilize is given in Table 2. In the wild, breeding sex ratios are approximately 1:3, but breeding is not evenly distributed among territorial males (Jarman 1979; Murray 1982). In the model, which reflects breeding behavior in wild populations, breeding is highly skewed towards dominant males, with age differentials between males of up to 12:1. Sensitivity analyses show the effect of relaxing this assumption.

Table 2. Females inseminated by each breeding male as a function of age, including a "soft" and a "hard" option.

Male Age	Soft Option Females/Male	Hard Option Females/Male
5	3	1
6	4	2
7	6	3
8	12	12
9	6	2

The maximum differential between the number of females inseminated by males of different ages is 4:1 in the soft option and 12:1 in the hard option.

Results

The Effects of Different Cropping Regimes

That all males are equally capable of fertilizing females and each male has an essentially infinite capacity to inseminate females is the assumption made by Fairall (1985), Catto (1976), and others (Fig. 4a). In this case, for any given proportion of males in the hunt, hunting mortality has a nearly linear effect on population size. Furthermore, because males are never the limiting sex, maximum population levels are obtained by a policy of limiting the hunt predominantly to males (>90%). Even at high levels of hunting (16% of the population), if the assumptions are valid the population size will not be affected if males greatly predominate in the offtake.

Figure 4(b & c) shows the effect of differential male fertility on population size when hunting is nonselective with respect to age; Fig. 4b shows the results under "soft" differential fertility assumptions and 4c under "hard" assumptions (Table 2). In both cases, at relatively low levels of hunting mortality (<6% of the population), the proportion of males taken in the hunt has little effect on population size. As hunting mortality increases past 8% of population, equilibrium population size becomes extremely sensitive to the proportion of males taken in the hunt. The effect is nonlinear and leads

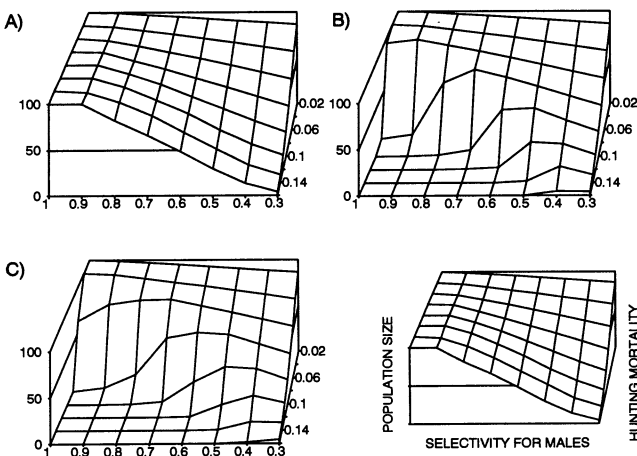


Figure 4. The effect of hunting mortality and selectivity for males on population size. Population size is expressed as a percentage of carrying capacity, hunting mortality as the percentage of the population killed each year, and selectivity for males as the proportion of the kill that is male. Males are hunted randomly with respect to age. (a) The number of males in the population has no effect on female fecundity. This is the usual assumption of game managers. (b) and (c) Males have a limited, age-related ability to fertilize females. (b) shows the soft option in Table 2; (c) shows the hard option.

to rapid population collapse if a highly male-biased harvest is taken.

If males are selected by age, the results are similar, with a rapid population collapse at high hunting mortalities and proportions of males in the hunt (Fig. 5). Selecting for young males leads to higher population sizes at low proportions of males, but the point of population collapse is earlier for this strategy than if older males are selected.

A high proportion of females in the hunt reduces the population growth because fewer females are left in the breeding population. Thus, at low proportions of males, population size increases as the proportion of males in the hunt increases. When only a small proportion of the kill is males, selecting for the younger, less fertile, or behaviorally excluded males leads to relatively higher population fecundity, and so to higher population sizes than does selecting for the older, prime males. At high selectivities for males, however, population collapse occurs earlier for ranching than for trophy hunting. This is because when old males are killed, a high proportion of them would have died anyway through natural mortality, and this reduces the effective hunting mortality. At lower proportions of males in the hunt, the effect of improved fertility when young males are taken first obscures this factor.

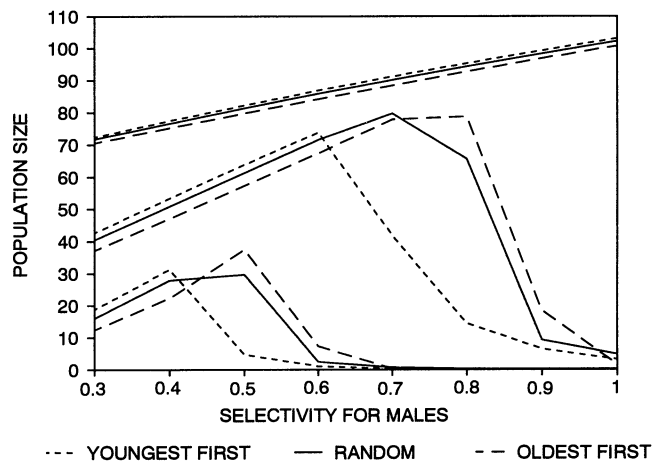


Figure 5. The effects of hunting that selects by both age and sex on the population size. Population size is expressed as a percentage of carrying capacity, selectivity for males by the proportion of the kill that is male. Hunting in proportion to the availability of an age-class ("random") is compared to trophy hunting ("old first") and game ranching ("young first"). The results are shown for three hunting mortality levels, 4%, 8%, and 12%. Although at low selectivities for males and low hunting mortalities, game ranching produces higher population sizes than trophy hunting, the population collapses earlier as the selectivity for males increases. Random hunting by age is intermediate in effect.

Sensitivity Analyses

Two of the assumptions used in this analysis were investigated, under the assumption of nonselective hunting because of its intermediate effect. First, the male reproductive dominance schedule was more highly skewed so that the largest differential in the number of females mated between age classes was 12:1 ("hard" option, Table 2). This assumption makes little difference in the general results, as can be seen in a comparison of Figs. 4b (soft option) and 4c (hard option). For any given hunting mortality, population collapse occurs at a rather lower proportion of males killed (Fig. 6).

In the second sensitivity analysis and in using the hard option, females are assumed to cycle only once, with no potential for remating if they are not inseminated. This is a stricter assumption than that made in the earlier analyses and allows us to examine the importance of the second breeding cycle for population fecundity. Eliminating the second breeding cycle has little effect on the overall shape of the graph but leads to a large decrease in equilibrium population size at higher hunting mortalities and proportions of males in the hunt (Fig. 6).

Discussion

The analysis presented here suggests that, under certain circumstances, strongly sex- and age-biased cropping, as

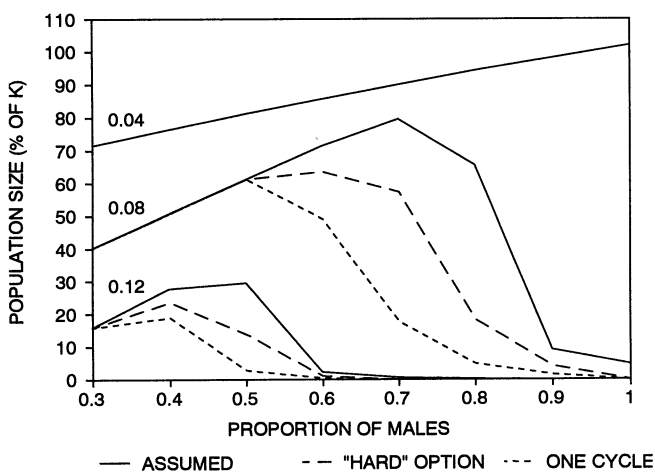


Figure 6. Sensitivity of the results to changes in assumptions, shown for three hunting mortalities, 4%, 8%, and 12%. Population size is expressed as a percentage of carrying capacity, selectivity for males by the proportion of the kill that is male. The results under the assumptions used ("assumed", soft option for age-related mating success, Table 2: any female who is unmated in the first mating cycles again and may be mated the second time) are compared to the results when there are large age-related differentials in male mating ability, (hard option) unmated females do not mate again that year, and the hard option is assumed (one cycle).

occurs with ranching and trophy hunting, may have catastrophic effects on populations. Overcropping, particularly when males constitute a high proportion of animals killed, can result in greatly reduced standing populations and, in the extreme, in the total collapse of a population.

Data presented on predation by three species of wild African carnivores hunting five species of ungulates show clearly that, in comparison with the extreme selectivity exhibited by humans practising game ranching and trophy shooting, hunting patterns of wild carnivores more closely reflect prey availability. While many carnivores show a preference, relative to availability, for hunting juveniles, in no case is the ratio of juveniles to adults in the diet greater than 3:1. Similarly, even in the most extreme example of sex-biased predation, adult males constitute only approximately 50% of the individuals taken. In sport hunting, males account for at least 70% of the kill.

Hunting has been implicated as a possible cause for the decline of two large mammal populations in Africa. Fergusson (1990) suggests that a decline in the sable population in the Matetsi Safari Area, a hunting precinct in northwest Zimbabwe, may be due to disproportionate hunting of males. Calving rates are exceedingly low in Matetsi (35%) compared to other areas in southern Africa: 100% in South Africa (Wilson & Hirst 1977); 60% in Matopos (Grobler 1974). Furthermore, while calving is usually very seasonal, in Matetsi calves are born over a 4–6-month period. Fergusson suggests that over-hunting of prime males, reduced survivorship of young due to the spreading of the parturition period, and disruption of territorial structure by hunting during the breeding season all contribute to a decline in population size.

Illegal hunting of African elephants (*Loxodonta africana*) offers another opportunity to examine how unusually skewed sex ratios can affect female fecundity. Older elephant bulls have larger tusks and hence are killed preferentially by poachers (Milner-Gulland & Mace 1991). These same males are responsible for the majority of mating in undisturbed populations (Poole 1987). In two areas in eastern Africa, Poole (1989) observed declining female fecundity that was correlated with heavy poaching leading to extremely skewed sex ratios and disruption of social structure.

Previous work has assumed some threshold proportion of males in the population below which fecundity will decrease as the proportion of unmated females in the population increases (Beddington 1974; Caughley 1977). Authors of these studies however, dismiss as unimportant the effects of age-limited male fecundity and social disruption caused by hunting on female fecundity. We have shown that both these factors do have important effects on female fecundity, and that these effects are exaggerated when hunting is targeted on a particular

age group. This occurs both in game ranching when younger individuals are targeted, and in trophy hunting when the older, dominant males are targeted.

The validity of the conclusions reached here depends on the likelihood of male fertility being a limiting factor in population growth when highly male-biased harvesting occurs. We have shown that there is a large amount of both quantitative and anecdotal evidence for this being the case. The model does not take into account other potentially deleterious effects of sex-biased cropping. Those concerned with wildlife management have in general assumed that ungulate population structures can be manipulated for maximum yields without cost. There is an urgent need for studies to elucidate the possible effects of manipulation of sex ratio and age structure if we are to maximize the inherent potential of wildlife as a source of protein and income for Africa. By coordinating present and future game harvesting programs with a carefully planned set of behavioral experiments, sufficient data could be gathered to test predictions made from theory. Such a program of research would benefit conservation biologists interested in the consumptive use of ungulates, as well as development planners. The model presented in this paper has shown that the manipulation of sex ratios occurring at present could lead to much reduced fecundity and possibly to population collapse.

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