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Harvesting and sex differences in demography

Jan Lindström

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In studies of population dynamics and harvesting, differences in the demographic parameters of males and females are rarely dealt with explicitly. However, polygyny and sexual dimorphism, commonly observed in game animals, often result in sex differences in demographic parameters. A structurally simple deterministic two-sex model was used to study the equilibrium population size and adult sex-ratio under constant-quota harvesting. The model allowed varying harem and brood size, condition dependent sex allocation and sex differences in recruitment probability and adult survival. The results show that demographic sex differences may lead to a recommendation for female biased culling. Adult sex-ratio optimal for population growth is not evolutionarily stable. However, constant-quota harvesting can lead to the optimal adult sex-ratio for population growth in situations in which the mating system and female reproductive strategies would result in a radically different adult sex-ratio if the population were left unharvested.

Key words: demography, game management, harvesting, sex allocation, Trivers-Willard hypothesis, two-sex model

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The usual practice in both harvesting theory and population ecology in general has been to describe population growth either by not distinguishing the sexes explicitly or by excluding males (e.g. May 1976, Getz & Haight 1989). Excluding males, population growth can be described with the number of offspring produced by an adult individual, or the number of female offspring produced per adult female. This is justified if life cycles of both sexes are identical or the population dynamics are governed by one sex, independently of the relative abundance of the other (Caswell 1989). In reality, these assumptions are often violated in game animals. For instance, the mortality rates of the sexes commonly differ for at least some life stage in birds (Lindén 1981, Angelstam 1984, Whitehead, Freeland & Tschirner 1990), ungulates (Clutton-Brock, Major & Guinness 1985b, Takatsuki, Miura, Suzuki & Ito-Sakamoto 1991, Owen-Smith 1993) and other mammals (Norbury, Coulson & Walters 1988, Desportes, Andersen & Bloch 1994). This pattern is more typical in dimorphic and polygynous species than in species with more equal sized sexes, where sex differences in mortality are small or absent (Clutton-Brock, Albon & Guinness 1985a, Berger & Cunningham 1995, Cooch, Lank & Cooke 1996). Although male-biased mortality is most common, in some cases female mortality rates exceed those of males or there is intra-

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specific variation in the direction of mortality differences (Clutton-Brock 1991 and references therein).

Large size-dimorphism is generally related to intrasex mating competition and consequently, in both dimorphic birds and mammals, males are likely to be larger than females. In size-dimorphic species, small males may have more difficulties acquiring mates, and thus transfer fewer genes to the next generation. In contrast, small or otherwise poor-quality females do not have difficulties finding mates. This difference commonly leads to greater variation in male than female reproductive success and led Trivers & Willard to formulate their hypothesis concerning the sex-ratio of offspring in relation to maternal condition (Trivers & Willard 1973). Some of the most unambiguous evidence for the Trivers-Willard hypothesis has been found in game mammals. Red deer *Cervus elaphus* (Clutton-Brock, Albon & Guinness 1984, 1986), American bison *Bison bison* (Rutberg 1986), reindeer *Rangifer t. tarandus* (Skogland 1986, Kojola & Eloranta 1989, see however, Kojola & Helle 1994), southern elephant seals *Mirounga leonina* (Arnbom, Fedak & Rothery 1994), bighorn sheep *Ovis canadensis* (Wauters, de Crombrugghe, Nour & Matthysen 1995) and roe deer *Capreolus capreolus* (Bérubé, Festa-Bianchet & Jorgenson 1996) have been shown to alter the sex-ratio of their offspring according to body condition and/or size of female.

Strong sexual dimorphism in body size has important implications for juvenile growth rates as male offspring have more stringent growth requirements than females (Clutton-Brock, Guinness & Albon 1982, Lindén, Milonoff & Wikman 1984). The consequences of size dimorphism can also be seen in sex differences in adult mortality (Clutton-Brock & Albon 1985 and references therein) or in first winter calf mortality (Coulson, Albon, Guinness, Pemberton & Clutton-Brock 1997).

Theoretical and empirical studies of harvesting (Fowler 1981, Basson, Beddington & May 1991, Smith 1992, Wickens, Shelton, David, Field, Oosthuizen, Roux & Starfield 1992, Clutton-Brock & Lonergan 1994, Ginsberg & Milner-Gulland 1994, Milner-Gulland 1994, van Rooyen 1994, Cruywagen 1996) or fisheries (Tyutyunov, Arditi, Büttiker, Dombrovsky & Staub 1993) have seldom taken sex into account. To my knowledge, no study has examined separately the effect of sex differences in demographic parameters (e.g. recruitment and adult mortality) on the outcome of harvesting. In this paper, I study the effect and relative importance of sex differences in recruitment, adult mortality, unequal offspring sex-ratio and polygyny on sustainable harvesting. As polygyny is common in game animals, the optimal sex-ratio for population growth may lie far away from the one which would evolve in the population without culling. This discrepancy between the evolutionarily stable sex-ratio (Fisher 1958) and the optimal sex-ratio for population growth (Caswell 1989) is of importance, for instance, in trophy hunting. Here the numerical solution is found for a structurally simple two-sex model under varying assumptions, and the relative importance of demographic sex differences on harvesting outcome is evaluated. In order to concentrate on the effects of sex differences on sustainable harvesting, I consider a highly simplified age-structure only.

Model description

In a discrete two-sex matrix model the transition matrix **A** can be written as:

$$\mathbf{A} = \begin{bmatrix} 0 & F_m & F_f \\ J_m & S_m & 0 \\ J_f & 0 & S_f \end{bmatrix}, \qquad (1a)$$

where F_m and F_f are the fecundity values of males and females, J_m and J_f give the probability of male and female newborn to recruit into the adult population, and S_m and S_f denote the survival of adult males and females (Caswell 1989). Then the population size, $N(t) = N_{juv}(t) + N_m(t) + N_f(t)$, grows according to

$$\mathbf{N}(t+1) = \mathbf{A}\mathbf{N}(t). \qquad (1b)$$

This matrix can be modified to let sex-specific juvenile recruitment, adult survival and probability of giving birth to a male change as functions of population density. First, writing the recruitment probabilities of male and female calves, J_m and J_f, as

$$\begin{aligned} J_m(t) &= p_m\,(t-1)\,j_m(t) \\ J_f\,(t) &= (1 - p_m(t-1))\,j_f(t) \end{aligned}, \qquad (2)$$

where the coefficient p_m(t-1) expresses the probability that the juvenile recruiting to adult population at time t, was born as a male (1 - p then gives probability of a female). Hence, the sex determination depends on the population density before juvenile recruitment. The juvenile survival probabilities j_m and

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j_f, for males and females, respectively, were also set to depend linearly on population size, and they become

$$\begin{aligned} j_m(t) &= j_{m0} - a_m N(t) \\ j_f(t) &= j_{f0} - a_f N(t) \end{aligned} \quad . \qquad (3)$$

Here j_{m0} and j_{f0} represent the male and juvenile survival in zero population density (i.e. the model intercept), a_m and a_f give the slope for density dependence for males and females. Negative values are interpreted as zeros. Survival parameters for adult males and females, S_m and S_f, were modified to describe sex differences in a similar manner:

$$\begin{aligned} S_m(t) &= S_{m0} - bmN(t) \\ S_f(t) &= S_{f0} - bf\,N(t) \end{aligned} \quad . \qquad (4)$$

S_{m0} and S_{f0} denote the survival of adult males and females, respectively, in zero population density and negative values are set to zero as in Equation 3. The slopes for dependency on density are given by b_m for males and b_f for females.

Also, in a two-sex model, one has to decide the form of the fecundity function, which relates the number of births to the number of males and females. As the harmonic mean birth function is considered the least flawed one (Caswell 1989), it is used here with a modification allowing for polygyny (Rosen 1983, Caswell & Weeks 1986). Then, the fecundities F_m and F_f become:

$$\begin{aligned} F_m(t) &= \frac{kN_f(t)}{N_m(t) + N_f(t)h^{-1}} \\ F_f(t) &= \frac{kN_m(t)}{N_m(t) + N_f(t)h^{-1}} \end{aligned} \quad , \qquad (5)$$

where k is the average number of female offspring a female produces and h represents the harem size.

Here, using numerical examples I show the effect of different plausible density-dependent parts of the model on the harvesting outcome in four categories of examples: 1) Males and females alike ($j_{m0} = j_{f0}$, $a_m = a_f$, $S_{m0} = S_{f0}$ and $b_m = b_f$), 2) Sex-dependent recruit survival ($j_{m0} = j_{f0}$, $a_m \neq a_f$), 3) Sex-dependent adult survival ($S_{m0} = S_{f0}$, $b_m \neq b_f$) and 4) Density-dependent probability of giving birth to a male, where the probability of giving birth to a male, p_m, decreases with population size according to

$$p_m(t) = P_{m0} - cN(t). \qquad (6)$$

p_{m0} sets the level for the proportion of males born in zero population density and c shows the slope of density dependence in this probability, and again, as in Equations 3 and 4 negative values are interpreted as zeros.

All the numerical solutions were searched using a constant harvesting strategy, because usually there is a desire to maximise the actual number of harvested animals rather than the proportion of the population which can be harvested. Also, while the sustainable quota has been found by modelling, it can later be approached as a corresponding proportional strategy for any given number of males and females, as the population will stabilise at the same level as in the constant quota strategy, but with safer properties, i.e. counterbalancing downward fluctuations. So, even though the constant quota harvesting is unlikely to be the best strategy adopted in practice (e.g. Engen, Lande & Sæther 1997), it relates here to the expected population response to a desired yield, and also defines an absolute upper limit for the population culling without pushing it into extinction.

The equilibrium population size was obtained numerically for the equation

$$N(t+1) = \mathbf{A}(t)\mathbf{N}(t) - \begin{bmatrix} 0 \\ v_m(t) \\ v_f(t) \end{bmatrix}, \qquad (7)$$

where v_m and v_f give the number of males and females killed. The resulting equilibrium population sizes were represented as proportions of the original population equilibrium size obeying Equation 1b.

Optimal sex-ratio for population growth

The definition of h requires some explanation. It is a parameter that relates sex ratios to the number of births in the population, and the value $h = 1$ has been equalled to monogamy as it puts equal emphasis on the role of males and females in reproduction (Caswell 1989). However, monogamy with more efficient mate search may be better represented by $h > 1$ (Lindström & Kokko 1998). Therefore, the strict interpretation of h as a harem size in the sense of number of females that are fertilised by one male may be misleading. A pragmatic interpretation is that with an increasing h, a smaller sex ratio (proportion of males in the population) suffices to yield a given per capita fecundity of females, and h is thus highest

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in polygynous species. The ratio of adult females to males $N_f : N_m = \sqrt{h}$ leads to maximum population growth rate (Caswell & Weeks 1986). Thus, the calculation of the optimal sex ratio for population growth rate only calls for the number of males and females and harem size. It is therefore insensitive to the form of density dependence and sex differences in demography. It is important to notice that the optimal sex ratio for population growth is evolutionarily unstable (Fisher 1958), but management usually attempts to maximise population growth rate (Clark 1990). Therefore, the question of whether the optimal sex ratio for population growth is attainable using a certain management strategy is important, since the optimal sex-ratio for management does not match the evolutionarily optimal sex-ratio individual females should produce in polygyny.

Model elasticity

To test the robustness of the model and its implications for real situations, such as sustainable harvesting, an elasticity analysis must be performed (e.g. Horvitz, Schemske & Caswell 1997). Here population growth rate was altered by increasing the values of harem size, h, number of female offspring, k, and decreasing the values of a_m (Equation 3) and b_m (Equation 4) by one percent. Thus, the magnitude of change caused by a given parameter alteration in the outcome can be compared with the corresponding changes in the other parameters.

Results

Initially, the model was run with the same male and female parameters. The situation presented in Figure 1 represents a monogamous system ($h = 1$) and the females have, on average, 0.7 female offspring in each time step. In such a situation the maximum yield per any given end population size is obtained by culling both males and females equally (see Fig. 1A), a method, which also results in a sex-ratio of 0.5 (see Fig. 1B). Understandably, increasing the relative amount of females in the bag makes the sex-ratio male-biased (see Fig. 1B).

In polygyny the outcome changes. The most remarkable change compared with monogamy is that the maximum yield per given resulting population size is not necessarily obtained with equal hunting effort devoted to males and females. At the most extreme cases a certain amount of male culling,

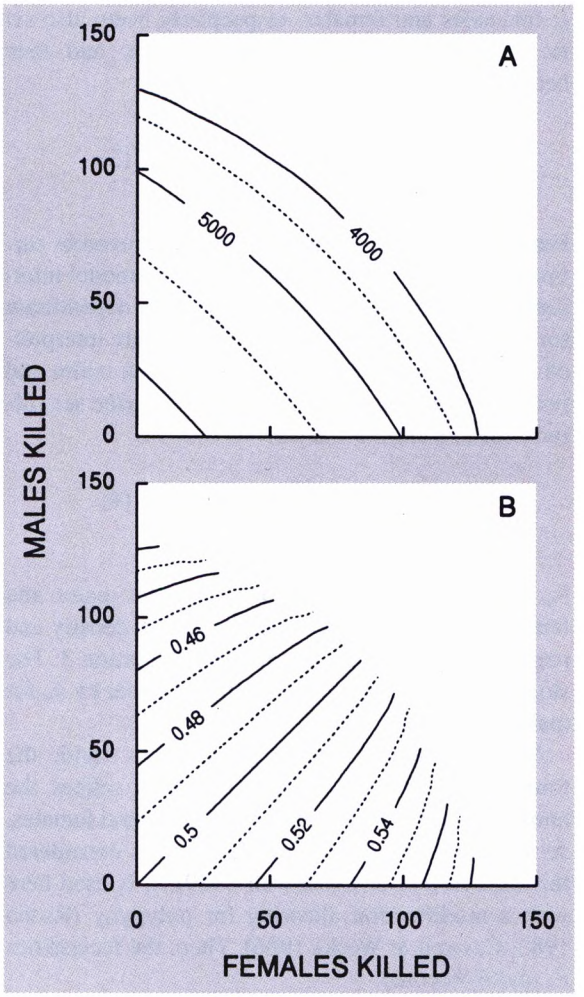


Figure 1. Effects of hunting on the equilibrium population size (A) and sex-ratio (B). The parameters used are $h = 1$, $k = 0.7$, $j_{m0} = j_{f0} = 0.95$, $a_m = a_f = 0.00004$ (Equation 3), $S_{m0} = S_{f0} = 0.8$ and $b_m = b_f = 0.00001$ (Equation 4) and thus the parameters for density-dependent recruitment from juvenile to adult stage and adult mortalities are equal for males and females. Without hunting the population size would stabilise at 6250 and the sex-ratio would be 0.5. Here the contours depict the population size and sex-ratio obtained under sex-specific constant-effort harvesting.

while simultaneously keeping the population at a certain size, is only possible by also increasing the number of females taken. This can be seen in Figure 2F. The highest sustainable harvesting quotas lead to an equilibrium population size of 60% of the population size attained with the same parameter values without harvesting (depicted by the 0.6 contour in Figure 2F). For instance, taking a number of males corresponding to 7% of the non-harvested equilibrium population size is sustainable if 4% of females are also killed, but not if the female harvesting pressure is 3%

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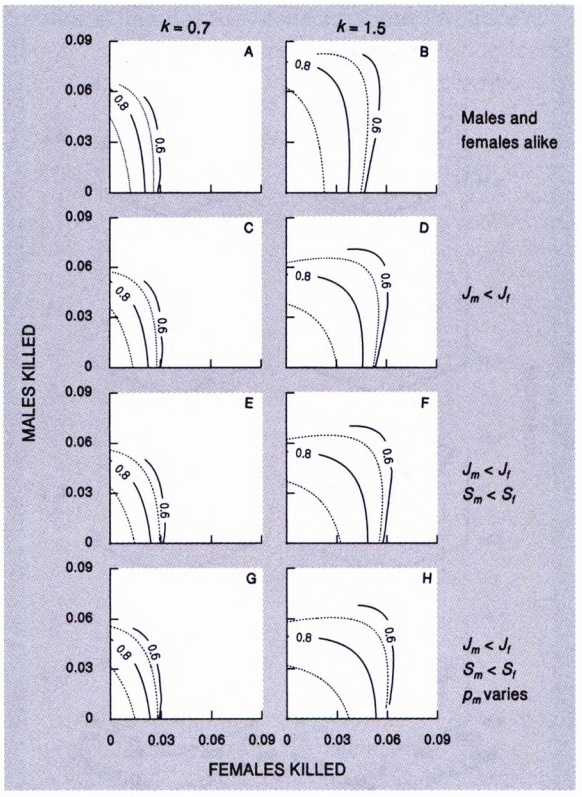


Figure 2. Equilibrium population sizes under different harvesting pressures with the number of female offspring per female, $k = 0.7$ and 1.5 and harem size, $h = 5$. To make the different parameter combinations more comparable, both population sizes after harvesting (contours) and percentages of males and females killed (x and y-axes) are reported as proportions of the equilibrium population size reached with the corresponding parameter values without harvesting (harvesting strategy is not proportional itself, see text). The highest yield is achieved where the sum of the number of males and females killed reaches its maximum, i.e., on the brink of extinction in the upper right corner in the contours. In panels A and B the demographic parameters for male and female are equal, $j_{m0} = j_{f0} = 0.95$, $a_m = a_f = 0.00004$ (Equation 3), $S_{m0} = S_{f0} = 0.8$ and $b_m = b_f = 0.00001$ (Equation 4). These parameter values are kept the same in the other panels unless otherwise stated. The effect of sex difference in recruitment is shown in panels C and D, where a_m is set to 0.00005 (Equation 3). The effect of sex-specific juvenile recruitment and adult survival ($a_m = 0.00005$ and $b_m = 0.000015$) is shown in panels E and F. In panels G and H the probability of giving birth to a male, p_m, is also allowed to vary according to Equation 6 and setting $p_{m0} = 0.55$ and c = 0.000006.

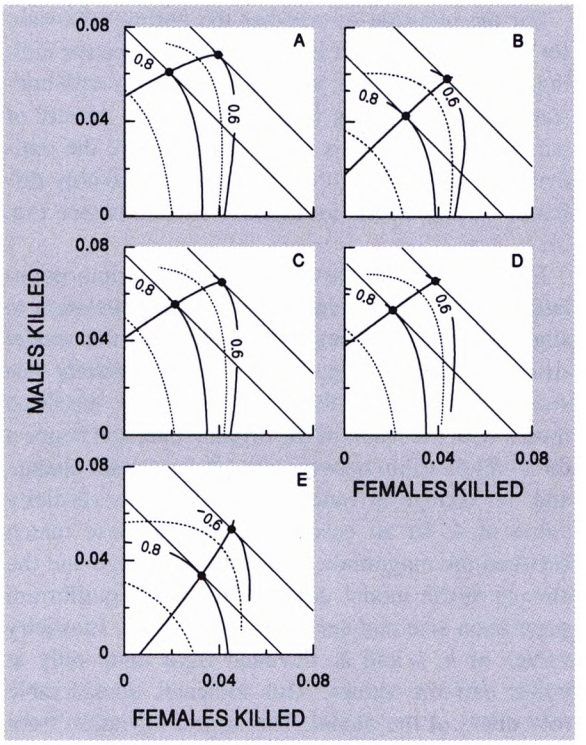


Figure 3. Optimal sex-ratio for population growth (see page 195) allows maximal hunting yield per given equilibrium population size. The contours depict the population size as a fraction of the equilibrium population size attainable without hunting. Likewise, the x and y-axes scales are set to correspond to the sex-specific harvesting quota as proportions of the non-hunted equilibrium population size attained with the corresponding parameter values. In this example, the number of female offspring per female, $k = 1.2$. The thick solid lines show the contour for optimal sex-ratio for population growth, which is here 0.33 for $h = 4$. Thin diagonal lines indicate the tangents for remaining population fractions 0.8 and 0.6 of the original population. In panel A, the demographic parameters for males and females are equal ($j_{m0} = j_{f0} = 0.95$, $a_m = a_f = 0.00004$ (Equation 3), $S_{m0} = S_{f0} = 0.8$ and $b_m = b_f = 0.00001$ (Equation 4)). In panel B only the male juvenile recruitment is decreased by setting $a_m = 0.00005$ and the other parameters are kept as in panel A. In panel C only adult male survival is diminished by setting $b_m = 0.000015$ while keeping the other parameters as in panel A. The probability of giving birth to a male, p_m, is allowed to vary as a function of population density (Equation 6) in panel D ($p_{m0} = 0.55$ and $c = 0.000006$). In panel E, all the sex differences presented above act simultaneously ($a_m = 0.00005$, $b_m = 0.000015$ and p_m is allowed to vary as in panel D; and the rest of the parameters are as in panel A).

(parameter space outside the contours indicate extinction). Generally, if a female produces a low number of offspring, and no demographic sex differences exist, male biased hunting gives the highest sustainable yield (see Fig. 2A). This result is less pronounced when the brood size is higher (see Fig. 2B). In more realistic cases where polygyny is related to sex-specific demographic values the result is more similar to the one obtained in monogamy (see Fig. 1) if the brood size is high enough (see Fig. 2D,F,H). On the contrary, with small brood sizes male biased culling is most profitable even with demographic sex differences (see Fig. 2C,E,F). With a high number of female offspring per female, the most profitable hunting practice shifts from male biased (see Fig. 2B) to more balanced culling (see Fig. 2H) if demographic sex differences exist.

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For the question of whether the optimal sex-ratio for population growth is attainable by selective culling, the answer is yes, at least partly, even with constant quota harvesting (Fig. 3). In a wide variety of parameter settings it is possible to achieve the optimal sex-ratio although this requires remarkably different culling efforts in different situations (see Fig. 3).

Exploring the sensitivity of the equilibrium population size and sex-ratio of a harvested population to slight parameter changes revealed that the model structure is robust (Fig. 4). The model elasticity was studied by dividing the outcome of the modified model with the result of the original one, and hence a direct relationship between the 1% parameter change and the change in outcome results in an elasticity value of 1. In all cases there was a close match between the magnitude of parameter change and the change in the model outcome for both equilibrium population size and sex-ratio (see Fig. 4). Elasticity values of h, k and b_m deviated from unity only at rather extreme values. This indicates considerable robustness of the model. The largest deviation from unity occurred in the form of density dependence when juvenile male survival, a_m (Equation 3), was varied. Increasing the juvenile male survival resulted in a change slightly greater than the original 1% alteration in the maximum number of males in a sustainable bag (see Fig. 4C). This was also seen in the higher than unity elasticity values of sex-ratio (see Fig. 4c).

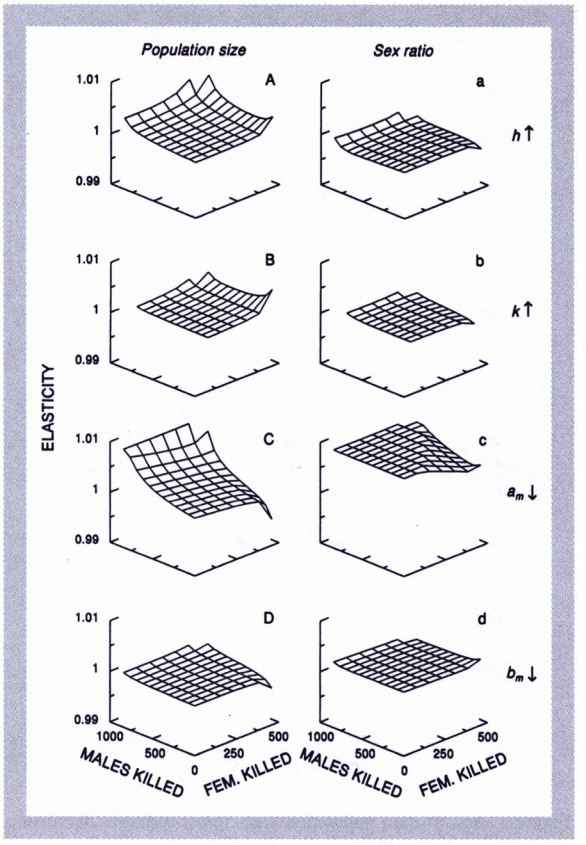


Figure 4. Sensitivity analysis of equilibrium population size and sex-ratio of harvested populations to parameter changes. Elasticity is expressed as the ratio of the outcome of the model modified by 1% parameter changes and the original one. Hence elasticity value 1 indicates an exact match between the magnitude of the change and its effect. In the original model $h = 10$, $k = 0.8$, $j_{m0} = j_{f0} = 0.95$, $a_f = 0.00004$, $a_m = 0.00005$, $S_{m0} = S_{f0} = 0.8$ and $b_f = 0.00001$, $b_m = 0.000015$. Note different scaling in x and y-axes.

Discussion

With the aid of a sex-structured population model, I have shown here that sex differences in demography may lead to radically different sustainable management strategies compared to those assuming no sex differences or considering females only. Sometimes the results are counterintuitive as is the case when increasing the number of females culled also increases the potential number of male offtake. This result bears a qualitative similarity to the results of Clutton-Brock & Lonergan (1994). They built a harvesting model based on observed sex differences in red deer reproduction and survival and concluded that increasing the number of mature females culled also increased the potential offtake of mature males.

Of all the sex differences I studied, the effect of the difference in juvenile recruitment appears to be the strongest, while harem size, brood size and differences in adult survival are less important in their relative effects on the hunting stamina of the population. This result of the elasticity analysis does not imply, however, that the importance of the other demographic parameters were negligible since they may vary much more in natural populations. For instance, brood size shows marked variation among game animals (e.g. Johnsgard 1983, Putman 1988, Riedman 1990). Larger brood sizes give higher population growth rates and thus increase sustainable harvesting quota. However, it also affects the most profitable hunting strategy, which is more male biased with low brood sizes and more equal with large brood size (see Fig. 2).

Considering practical management situations,

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where management decisions have to be made under uncertainty, one might argue that the delicate model structure presented here is not useful, and thus the elasticity analysis also has no practical applications. A detailed model containing complicated evolutionary structures is usually not the best one either for management planning or for forecasting population fluctuations (Hilborn & Mangel 1997). Yet, it may be beneficial to develop a detailed model to acquire a deeper understanding of the system under study. In management planning, a structurally simpler model may be used simultaneously with the more complicated one, particularly in the beginning (Daellenbach 1994, Starfield 1997). As knowledge of the system accumulates and is added into the detailed model, the results of the detailed and simple model ideally converge, although the simpler one may remain a more robust tool for some purposes despite this convergence. Some questions may never be solved without the more detailed model. In adaptive management strategies, harvesting itself is utilised in improving the estimates of uncertain population parameters (e.g. Walters 1986, Williams, Johnson & Wilkins 1996). Here the practical value of the elasticity analysis is seen as it shows the direction and magnitude of different changes and hence may show what is the likely source of mismatch between model and the actual estimates.

The results achieved here support the idea that sex differences in demography and condition-dependent sex allocation have important implications for planning harvesting. Furthermore, sex-specific behavioural traits may lower the sustainable bag as, for instance, the immigrant males in both lions *Panthera leo* and brown bears *Ursus arctos* tend to kill the young of a group or an area if the resident male is removed (Starfield, Furniss & Smuts 1981, Swenson, Sandegren, Söderberg, Bjärvall, Franzén & Wabakken 1997). In species where infanticide is common, killing of adult males may thus greatly decrease population growth rate. Hence, in game management, it is important to note that the optimum offspring sex-ratio for female, as well as other evolutionary stable behavioural strategies, may differ radically from the management optimum in terms of maximal population growth.

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