

The economics of a stage-structured wildlife population model

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Abstract

A simple three-stage model of the Scandinavian moose (*Alces alces*) (young, adult female and adult male) is formulated. Fecundity is density dependent while mortality is density independent. Two different harvesting regimes are explored; hunting for meat and trophy hunting. The paper gives an economic explanation of the biological notion of females as 'valuable' and males as 'non-valuable'. The paper also demonstrates how this notion may change under shifting economic and ecological conditions.

1. Introduction

The aim of this paper is two-fold; firstly, to demonstrate the economic content of a structured wildlife population model, and secondly, to show how this economic content may change under different management scenarios. Analysing structured wildlife harvesting models, i.e., models where the species is grouped in different classes according to age and sex, has a long tradition within biology and Caswell (2001) gives a recent in-depth overview. No economic considerations are, however, present here. This is also so in e.g., Milner-Gulland et al. (2004). Economic analysis is introduced in Cooper (1993) who formulates a simulation model that finds the economically optimal level of deer tags for hunting zones and where the deer population is structured in bucks and does. Skonhøft et al. (2002) analyses various management strategies for a mountain ungulate living in a protected area and a hunting area. Four stages are included here; females and males within and outside the protected area. Due to the complexity of these models, however, it is difficult to understand the various economic mechanisms influencing harvesting and abundance. The present paper analyses such economic mechanism more explicitly where a simple three stages model, including young, adult female and adult male, is formulated. The present analysis is most similar to that of Clark and Tait (1982) who studied the optimal harvest value in a sex-selective harvesting model and where the population hence was grouped in two stages. As in Clark and Tait, we are analysing biological equilibrium where natural growth is balanced by harvesting. However, in contrast

to Clark and Tait, trophy hunting, in addition to meat value maximisation, is analysed. We also calculate the shadow values of the adult males and females. We are thus giving an economic explanation of the biological notion of females as ‘valuable’ and males as ‘non-valuable’.

The model is applied for a moose population (*Alces alces*), and is studied within a Scandinavian ecological and institutional context. Moose is by far the most important game species in Scandinavia, and in Norway and Sweden about 40,000 and 100,000 animals, respectively, are shot every year. Moose hunting has traditionally been a local activity, and the landowners receive the hunting value. The hunters have basically been the local people; the landowners and their families and friends, and where the management goal has been to maximise the meat value for stable populations (more details are provided in Skonhøft and Olausen 2005). During the last years, however, a more commercialised hunting and wildlife industry has emerged, and the Scandinavian moose hunting is gradually shifting from a ‘family and friend’ activity to a game hunting market. The trophy value of old males plays an important role here. Both the traditional exploitation scheme and the new commercialised scheme are studied, and the consequences for harvesting and the population composition are analysed.

The paper is organised as follows. In the next section, the three stage moose population model is formulated. Section three demonstrates what happens when the hunting is steered by the traditional landowner goal of maximising meat value. Next, in section four we study the sex and age composition under the new exploitation regime of trophy hunting. A downward sloping inverse demand curve for hunting old males is introduced. In addition, it is also assumed that the demand may shift due to a ‘quality’ effect captured by the density of old males. Section five illustrates the models by some numerical simulations, while section six summarises the findings.

2. The population model

The *Alces alces* is a large ungulate with mean slaughter body weight (about 55% of live weight) for adult moose in Scandinavia of about 170 kg for males and 150 kg for females. The non-harvest mortality rates are generally low due to lack of predators, and there is no evidence of density dependent survival. On the other hand, fecundity has proven to be

affected by the female density while the number of males, within the range of moose densities in Scandinavia, seems to be of negligible importance (see, e.g., Nilsen et al. 2005 for more details).

Usually, the moose population is structured in four stages; calves, yearlings, adult males and adult females. In what follows, however, to obtain a traceable analytical model, while still catching the main ecological content, just three stages are considered as yearlings are left out. The population at time (year) t is hence structured as calves X_t^0 , adult females (≥ 1 yr) X_t^f , and adult males (≥ 1 yr) X_t^m , so that the total population is $X_t = X_t^0 + X_t^f + X_t^m$. Yearlings are therefore included among the adult male and female. These three stages are henceforth called young, female and male. The population is measured in spring after calving. All stages are generally harvested, and the hunting takes place in September-October. All natural mortality is assumed to take place during the winter, after the hunting season as the natural mortality throughout summer and fall is small and negligible. The same natural mortality rate is imposed for males and females. As indicated, natural mortality is fixed and density independent, while reproduction is density dependent. It is further assumed the same sex ratio for the young when they enter the old stages (again, see Nilsen et al. 2005).

Neglecting any stochastic variations in biology and environment, and neglecting any dispersal in and out of the considered area, the number of young at time $(t+1)$ is first governed by:

$$(1) \quad X_{t+1}^0 = r_t X_t^f$$

with $r_t > 0$ as the fertility rate (number of young per female). The fertility rate is density dependent in the number of females:

$$(2) \quad r_t = r(X_t^f)$$

with $dr/dX^f = r' < 0$ (when omitting the time subscript) and where $r(0) > 0$ is fixed.

Combing (1) and (2) gives the recruitment function $X^0 = r(X^f)X^f$ and differentiating yields $dX^0/dX^f = (r'X^f + r)$. The recruitment function is assumed to be concave. For obvious reasons $dX^0/dX^f \geq 0$ should hold in an optimal harvesting programme.

The abundance of (old) female follows next as:

$$(3) \quad X^f_{t+1} = 0.5(1-m^0)(1-h^0_t)X^0_t + (1-m)(1-h^f_t)X^f_t$$

where $m^0 > 0$ and $m > 0$ are the density independent mortality fractions of young and female (and male), respectively, while h^0_t and h^f_t are the harvesting fractions. Half of the young population enters the female, after harvesting and natural mortality. The number of (old) males is finally given by:

$$(4) \quad X^m_{t+1} = 0.5(1-m^0)(1-h^0_t)X^0_t + (1-m)(1-h^m_t)X^m_t$$

where h^m_t is the male harvesting fraction.

When combining equations (1) - (3), the female population dynamic reads

$X^f_{t+1} = 0.5(1-m^0)(1-h^0_t)r(X^f_t)X^f_{t-1} + (1-m)(1-h^f_t)X^f_t$. This is a second order non-linear difference equation, and numerical analyses demonstrate that the equilibrium is stable for fixed harvesting fractions (see, e.g., Gandolfo 2001 for a theoretical exposition). Omitting the time subscript, the equilibrium reads:

$$(5) \quad X^f = 0.5(1-m^0)(1-h^0)r(X^f)X^f + (1-m)(1-h^f)X^f.$$

There are two equilibria; the trivial one of $X^f = 0$ and $X^f > 0$ given

by $1 = 0.5(1-m^0)(1-h^0)r(X^f) + (1-m)(1-h^f)$. Because $r' < 0$, the non-trivial equilibrium will be unique and may be written as:

$$(5') \quad X^f = F(h^0, h^f)$$

where $F(\dots)$ represents a functional form. We find $\partial F / \partial h^0 = F_0 < 0$ and $F_f < 0$. The iso-population female lines slope therefore downwards in the (h^0, h^f) plane, and where lines closer to the origin yield a higher stock.

By combining equations (1), (2) and (4), the male population growth reads

$X^m_{t+1} = 0.5(1-m^0)(1-h^0_t)r(X^f_t)X^f_{t-1} + (1-m)(1-h^m_t)X^m_t$. The dynamic of the males is therefore contingent upon the female growth (but not the vice versa as only female abundance regulates fertility), and again numerical analyses demonstrate that the equilibrium is stable. The equilibrium is:

$$(6) \quad X^m = 0.5(1-m^0)(1-h^0)r(X^f)X^f + (1-m)(1-h^m)X^m.$$

There are two equilibria for the male population as well; the trivial one when $X^f = 0$, and $X^m > 0$ when $X^f > 0$. Equation (6) may also be written as:

$$(6') \quad X^m = G(h^0, h^m)r(X^f)X^f$$

where $G(h^0, h^m) = 0.5(1-m^0)(1-h^0)/[1-(1-m)(1-h^m)]$. Again, it may be confirmed that higher harvesting rates mean fewer animals, $G_0 < 0$ and $G_m < 0$. The male iso-population lines hence slope downwards in the (h^0, h^m) plane, and lines closer to the origin yield a higher stock. On the other hand, a higher female sub-population shifts these iso-population lines away from the origin (suggested that the slope of the recruitment function is positive, see above) meaning that there is room for more male harvesting for a given young sub-population harvesting, and the vice versa.

Equation (6') also indicates that the equilibrium male-female proportion decreases with more females. This holds, but the male-female proportion may more easily be recognized when combining (5) and (6) which yields $X^m / X^f = [1-(1-m)(1-h^f)]/[1-(1-m)(1-h^m)]$. We therefore simply have $X^m / X^f = 1$ if $h^m = h^f$, as the mortality of the male and female are equal, and the same fraction of young enters the female and male sub-populations.

3. Exploitation. The traditional regime; hunting for meat

As indicated, the traditional exploitation of the Scandinavian moose has been directed by maximising the meat value in ecological equilibrium. Because natural mortality takes place

after the hunting season, the equilibrium numbers of animals removed are simply

$$H^0 = h^0 r X^f, \quad H^f = h^f X^f \quad \text{and} \quad H^m = h^m X^m \quad \text{so that the total harvest equals}$$

$H = H^0 + H^f + H^m$. The management goal of the landowner(s) in the given area is accordingly:

$$(7) \quad \max_{X^f, X^m, h^0, h^f, h^m} U = p(w^0 H^0 + w^f H^f + w^m H^m) = p[w^0 h^0 r(X^f) X^f + w^f h^f X^f + w^m h^m X^m]$$

subject to the ecological constraints (5') and (6'). $w^0 < w^f < w^m$ are the (average) body slaughter weights (kg per animal) of the three stages while p is the meat price (NOK per kg). However, for obvious reasons, the meat price will not affect the optimization except for scaling the shadow price values (see below).

The Lagrangian of this problem writes

$$L = p[w^0 h^0 r(X^f) X^f + w^f h^f X^f + w^m h^m X^m] - \lambda[X^f - F(h^0, h^f)] - \mu[X^m - G(h^0, h^m)r(X^f) X^f]$$

with $\lambda > 0$ and $\mu > 0$ as the shadow prices of the female and male population, respectively¹.

The first order conditions of this maximising problem are (the second order conditions are fulfilled due to the concavity of the recruitment function):

$$(8) \quad \partial L / \partial X^f = p[w^0 h^0 (r' X^f + r) + w^f h^f] - \lambda + \mu G(r' X^f + r) = 0,$$

$$(9) \quad \partial L / \partial X^m = p w^m h^m - \mu = 0,$$

$$(10) \quad \partial L / \partial h^0 = p w^0 r X^f + \lambda F_0 + \mu G_0 r X^f \leq 0; \quad 0 \leq h^0 < 1,$$

$$(11) \quad \partial L / \partial h^f = p w^f X^f + \lambda F_f \leq 0; \quad 0 \leq h^f < 1$$

and

¹ The interpretation of λ and μ as shadow prices are not obvious as the population sizes are determined within the model. However, when adding \bar{X}^f , interpreted as an exogenous number of introduced females, to the stock constraint (5') it can be shown that $\partial U^* / \partial \bar{X}^f = \lambda$, and where U^* denotes the maximum value of U . In the same manner, adding \bar{X}^m as an exogenous number of introduced males to (6'), gives $\partial U^* / \partial \bar{X}^m = \mu$.

$$(12) \quad \partial L / \partial h^m = p w^m X^m + \mu G_m r X^f \geq 0; \quad 0 < h^m \leq 1.$$

Conditions (8) and (9) steer the shadow price values, and (9) says that the male shadow price should just be equal its marginal harvesting value. Equation (8) is somewhat more complex, but says basically that the female shadow price should be equal the sum of the marginal harvesting value of the female and the young sub-populations, plus the indirect male marginal harvesting value, evaluated at its shadow price. Rewriting equation (8) when using condition (9) yields $\lambda = p(w^0 h^0 + w^m h^m G)(r' X^f + r) + p w^f h^f$. As the slope of the recruitment function is non-negative, $(r' X^f + r) \geq 0$ (see above), $\lambda \geq p w^f h^f$ holds. While the shadow value of the male population is exactly equal its marginal harvesting value, we therefore find that the shadow value of the female population is above its marginal harvesting value. In this sense, females may be considered as more ‘valuable’ than males and is line with the biological notion of females as valuable and male as non-valuable.

Conditions (10) – (12) are the control conditions with the actual complementary slackness conditions stated. From the male condition (12), harvesting down the whole population is hence considered as a possibility as this is the biological ‘end’ product. On the other hand, keeping the female and young sub-populations unexploited are options as these stages represent the reproductive and potentially reproductive biological capital. Condition (10) indicates that the harvesting of the young should take place up to the point where the harvesting benefit is equal, or below, the cost in terms of reduced population of males and females evaluated at their respective shadow prices. When (10) holds as an inequality, we have that the marginal harvesting benefit is below its marginal cost and harvesting is thus not profitable, $h^0 = 0$. The interpretation of the female harvesting condition (11) is somewhat simpler. Due to the fecundity density effect, meaning that one more female on the margin yields a smaller recruitment when the female population is ‘high’ than when being ‘low’, $h^f = 0$ seems less likely.

The male harvesting condition (12) is parallel to that of the female harvesting condition (11), but the cost-benefit ratio works generally in the opposite direction. It can be shown that this condition always will hold as an inequality. This is revealed when first combining conditions (9), (12) and (6') which yields $(G + h^m G_m) \geq 0$. When next inserting for G (and G_m) from equation (6) this condition reads

$\{0.5(1-m^0)(1-h^0)/[1-(1-m)(1-h^m)]\} \{1-(1-m)h^m/[1-(1-m)(1-h^m)]\} \geq 0$. After some small rearrangements, this condition boils down to $m \geq 0$. Accordingly, because $m > 0$, we find $h^m = 1$ and the whole male population should be harvested. Notice that this result holds irrespective of the values of males and females (as given by the body weights).

The reason for harvesting down the whole biological ‘end’ product as the best option is the lack of any trade-offs when the meat value is maximised; there is neither any biological feedback effects from the other stages nor any price demand response. The male-female proportion becomes accordingly $X^m / X^f = [1-(1-m)(1-h^f)]$ (section two above) in the optimal program while one more male (cf. also footnote 1) yields a benefit of $\mu = pw^m$ (NOK per animal). If the optimal policy at the same time yields $h^0 = 0$, the female shadow price reads $\lambda = pw^m G(r'X^f + r) + pw^f h^f$. As $G = 0.5(1-m^0)$ when $h^m = 1$ and $h^0 = 0$ (equation 6'), and $w^f < w^m$, the female shadow price may be lower than the male shadow price irrespective of the above notion of females as more ‘valuable’ than males. In addition, from condition (8), it may also be shown that if $1-G(r'X^f + r) > w^f h^f$ then $\mu > \lambda$. This shows more directly that a low female slaughter weight may pull in the same direction.

4. Exploitation. Modern times; trophy hunting

The moose harvesting regime in Scandinavia (like wildlife hunting other places) is gradually changing, and a hunting and wildlife industry is emerging (see e.g., Skogeierforbundet 2004). ‘Modern times’ is modelled by introducing a market for trophy hunting for males while still having meat value hunting of the other two stages. The market for trophy hunting is probably something between a competitive market and monopoly. One of these extremes is chosen, and we assume that trophy hunting licences are supplied under monopolistic conditions.

Following the practice in Norway, one licence allows the buyer to kill one animal, which is paid only if the animal is killed. In addition to price, the demand for trophy hunting licences may also be contingent upon ‘quality’, expressed by the abundance of males (Skonhøft and Olausen 2005). The inverse market demand for male hunting licences is hence given as:

$$(13) \quad q = q(h^m X^m, X^m).$$

The licence price q (NOK per animal) decreases with a higher offtake,

$q_H = \partial q / \partial (h^m X^m) < 0$, while it shifts up with more animals available, $q_X > 0$. Supplying trophy hunting licences is also costly and depends on the number of animals shot:

$$(14) \quad C = C(h^m X^m)$$

with fixed cost $C(0) > 0$, and variable cost $C' > 0$ and $C'' \geq 0$. The fixed component includes the cost of preparing and marketing the hunting, whereas the variable component includes the cost of organising the permit sale, the costs of guiding and various transportation services, and so forth.

The landowner management goal is now accordingly to find a harvesting policy that maximises the sum of the meat value and trophy hunting profit, or

$$(15) \quad \max_{X^f, X^m, h^0, h^f, h^m} \pi = p[w^0 h^0 r(X^f) X^f + w^f h^f X^f] + [q(h^m X^m, X^m) h^m X^m - C(h^m X^m)],$$

again subject to the constraints (5') and (6'). The first order conditions of this problem are (where L again is referring to the Lagrange function):

$$(16) \quad \partial L / \partial X^m = q_H (h^m)^2 X^m + q h^m - C' h^m + q_X h^m X^m - \mu = 0$$

and

$$(17) \quad \partial L / \partial h^m = q_H (X^m)^2 h^m + q X^m - C' X^m + \mu G_m r X^f \geq 0; \quad 0 < h^m \leq 1,$$

in addition to conditions (8), (10) and (11).

The male harvesting benefit is now expressed by a marginal profit term plus a marginal stock effect through the demand quality effect and the interpretation of (16) and (17) is straightforward (see also above). Combing these conditions and (6') yields

$$(q_H X^m h^m + q - C')(G + h^m G_m) + q_X h^m X^m G_m \geq 0, \text{ and where the term } (G + h^m G_m) \text{ still is}$$

strictly positive because $m > 0$ (see section three above). When first disregarding the quality

effect, $q_x = 0$, we therefore find that $h^m < 1$ and hence not harvesting all males, will represent the optimal solution if the marginal harvesting profit equalises zero, $(q_H X^m h^m + q - C') = 0$. From condition (16) (as well as from equation 17), it is seen that this implies a zero value male shadow price. A zero value shadow value while not harvesting down the whole stage is a counterintuitive result, but hinges on the biological ‘end’ product nature of the adult males; the fertility is not contingent upon the number of males. The zero marginal harvesting profit condition may be met if the marginal cost is high and/or the inverse demand schedule is steep (or in-elastic). On the other hand, if the marginal revenue exceeds the marginal cost for $h^m = 1$, we obtain the same solution type as above and where μ is positive.

When taking the demand quality effect into account, $q_x > 0$, $h^m < 1$ may still hold as an optimal solution when the marginal revenue exceeds the marginal cost $(q_H X^m h^m + q - C') > 0$, as $G'_m < 0$ and $(G + h^m G'_m) > 0$ (see above). The economic reason for this result is simple as constraining the harvest and keeping a high stock size works in the direction of a higher trophy hunting licence price. From equation (16) it is seen that this situation implies $\mu > 0$. The corner solution of $h^m = 1$ is also now a possibility, but the marginal harvesting profit must then exceed a certain minimum, equal the shadow price.

While the first order conditions for harvesting female and young are the same as in the traditional harvesting regime, the new conditions for male harvesting will obviously spill over to these stages. With $h^m < 1$, we may typically find that the male-female proportion X^m / X^f increases compared to the traditional regime which may be reinforced if h^f shifts up at the same time. Moreover, while the meat price p had no effect on the optimal harvesting policy in the traditional regime, it may now influence the optimal harvesting policy of all three stages. This will generally occur when the quality effect is included and we have $\mu > 0$. In line with the standard harvesting theory, one may expect that more harvest and fewer animals of male and young then will go hand in hand with a higher price. On the other hand, with no quality effect and with a zero shadow price value of the males it will have no effect as the equations (5), (8), (10) and (11) then alone determine h^0 , h^f , X^f and λ .

5. Numerical illustrations

Data and specific functional forms

The two exploitation schemes will now be illustrated numerically. The reproduction rate, decreasing in the number of females, is specified as a sigmoidal function with an increasing degree of density dependence at high densities (Nilsen et al. 2005):

$$(2') \quad r = r(X^f) = \frac{\tilde{r}}{1 + (X^f / K)^b}$$

with $\tilde{r} > 0$ as the intrinsic growth rate (maximum number of young per female) and $K > 0$ as the female stock level for which density dependent fertility equalises density independent fertility. Thus, for a stock level above K , density dependent factors dominate. The compensation parameter $b > 0$ indicates to what extent density independent effects compensate for changes in the stock size. (2') implies a recruitment function $X^0 = r(X^f)X^f = \tilde{r}X^f / [1 + (X^f / K)^b]$ which is of the so-called Sheperd-type.

The trophy demand function is specified linear. In addition, it is assumed that the quality effect as given by the number of males, through the parameter $\gamma \geq 0$, shifts the demand uniformly up:

$$(13') \quad q = \alpha e^{\gamma X^m} - \beta h^m X^m.$$

Accordingly, the choke price $\alpha > 0$ gives the maximum willingness to pay with a zero quality effect, $\gamma = 0$, whereas $\beta > 0$ reflects the market price response in a standard manner. The trophy cost function is given linear as well:

$$(14') \quad C = \bar{c} + ch^m X^m$$

so that $\bar{c} \geq 0$ is the fixed cost and $c > 0$ is the constant marginal cost. Table 1 gives the baseline parameter values. For these demand and cost functions we find that the optimal number of hunted males will be $h^m X^m = (\alpha - c) / 2\beta$ without demand quality effect and when $\mu = 0$ at the same time (equation 16).

Table 1 about here

Results

Table 2 reports the results with baseline parameter values. As a benchmark, a no-hunting scenario is also included (first row). Since the young enters the (adult) male and female stages at the same sex ratio, the number of males and females are here the same. In the traditional regime with meat value maximisation, the female harvest rate becomes 0.26 while no harvest of young represents an optimal policy. The marginal harvesting benefit of young is hence below the marginal cost in term of losses from reduced harvesting of males and females. Notice that the number of young is lower in the no-hunting scenario than in the traditional regime. This is due to the fact that the number of females is above the value representing the peak value of the recruitment function and we have $dX^0 / dX^f = (r' X^f + r) < 0$ without harvesting. The male shadow value is about four times above that of the female shadow value. As demonstrated in section three, the male shadow value is exactly equal its marginal harvesting value $\mu = pw^h$ while the female shadow value should be above its marginal harvesting value. However, due to the low female harvesting fraction and an optimal harvesting policy close to the peak of the recruitment function; that is $(r' X^f + r)$ is small positive (see above), the female shadow value becomes low.

Table 2 about here

The modern times exploitation scheme is first studied when the quality effect is disregarded; that is $\gamma = 0$ and the inverse demand function (13') reads $q = \alpha - \beta h^m X^m$. Harvesting down all the males is no longer an optimal policy, and we now find a substantial lower harvesting fraction, $h^m = 0.24$. As expected, the male-female proportion increases, and at the same time the female harvesting fraction shifts somewhat up compared to the traditional regime. However, it is still beneficial to keep the young population unexploited.

When the quality effect is added, the male harvesting rate, as expected, is further reduced accompanied by a positive shadow value indicating that the marginal harvesting income exceeds the marginal cost in optimum. The difference between the male and female shadow values is now quite small. The female harvesting rate decreases somewhat as well. As a

consequence, the total stock size is higher when the quality effect is included and substantially higher than that of the traditional harvesting scheme of meat value maximisation. The table also demonstrates that the profit increases compared to the traditional regime, and it further increases when the demand quality effect is added. However, for obvious reasons, the specification of the demand function and parameterisation play a critical role here.

Shifting up the meat price p , just scales up the shadow price values in the traditional regime. In the trophy hunting regime with no quality effect and with a zero shadow price value of the males, the harvesting activity and stock sizes will be unaffected as well. As indicated, the logic behind this result is that the equations (5), (8), (10) and (11) alone determine h^0 , h^f , X^f and λ when $\mu = 0$. On the other hand, with the quality included and $\mu > 0$, the male harvesting activity interacts with the other stages and hence p has an allocation effect. However, sensitivity analyses show that the female harvest rate increase only modestly even for a quite dramatic price increase. The reason for this hinges on the fact that female stock is close to the peak of the recruitment function.

6. Concluding remarks

The paper has analysed a three stages model of the Scandinavian moose with fertility as the only density dependent factor. Two exploitation schemes have been studied and it is demonstrated that harvesting down the whole biological ‘end’ product, i.e., the (adult) male population in this model, always represents the best option when meat value maximisation is the goal. In the numerical examples, this option is accompanied by zero harvesting of the young and modest female harvesting. Within this regime the biological notion of females as ‘valuable’ and males as ‘non-valuable’ is easily recognized even if the shadow value of the males might be higher than that of the females. The modern times exploitation scheme with a market for trophy hunting, changes the optimal harvesting condition of the males. Hunting down the whole population will no longer be the best option suggested that a well developed market for trophy hunting is present. In addition, the allocation in the trophy hunting market also spills over to the conditions of meat value maximisation of young and females. The male-female population ratio will increase, and the numerical examples show that more female harvesting may take place.

Although the model is simple and therefore somewhat unrealistic, it encompasses some general results that will survive in more complex stage-structured models. Most important, we have highlighted the economic forces influencing harvest in three different stages that, in various degrees, are present in many structured population models. In our model there are two recruiting stages which recruit in different ways. The young represents a value through recruitment to the (old) male and female stages. As long as density dependent growth factors are weak, or non-existing (as here), harvesting young does not pay off. For the females, on the other hand, a traditional trade-off between recruitment and harvest is present through the density dependent fertility mechanism. This mechanism will also be present in more complex models. Finally, the (old) male stage is considered as the biological 'end' product, and thus influences not the recruitment. It is therefore tacitly assumed that there are always enough males for reproduction. However, irrespective of this, our model demonstrates that the male optimal harvest policy depends critically on economic circumstances.

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Table 1: Biological and economic parameter values

Parameters	Description	Baseline value	Reference/source
\tilde{r}	max. specific growth rate	1.15	Nielsen et al (2005)
K	female stock level where density dependent factors dominates density independent factors	1,000	Nielsen et al (2005)
b	density compensation parameter	2	Nielsen et al (2005)
w^0	average weight young	60 Kg	SSB 2004
w^f	average weight females	150 Kg	SSB 2004
w^m	average weight male	170 Kg	SSB 2004
m^0	natural mortality young	0.05	Nielsen et al (2005)
m	natural mortality female and male	0.05	Nielsen et al (2005)
p	meat price	50 NOK	Storaas og Henriksen (2002)
α	choke price	30,000 NOK	Calibrated
γ	quality parameter demand	0.0001	Calibrated
β	slope parameter demand	60 NOK	Calibrated
\bar{c}	fixed harvest cost	500,000 NOK	Calibrated
c	marginal harvest cost	2,000 NOK	Calibrated

Table 2: Ecological and economic equilibrium, different management regimes. h^0 harvest fraction young, h^f harvest fraction female, h^m harvest fraction male, h total harvest fraction, X^0 number of young (in 1000 animals), X^f number of females (in 1000 animals), X^m number of males (in 1000 animals), X total stock (in 1,000 animals), λ female shadow price (in 1,000 NOK per animal), μ male shadow price (in 1,000 NOK per animal) and, π profit (in 1,000 NOK)

<i>Hunting regimes</i>	h^0	h^f	h^m	h	X^0	X^f	X^m	X	λ	μ	π
No harvest	0	0	0	0	0.33	3.15	3.15	6.63	--	--	--
Traditional regime, hunting for meat	0	0.26	1	0.29	0.57	0.92	0.27	1.76	2.2	8.5	4,099
Modern times; trophy hunting. No quality effect	0	0.28	0.24	0.20	0.57	0.85	0.97	2.39	2.1	0	4,599
Modern times; trophy hunting. With quality effect	0	0.25	0.09	0.12	0.57	0.95	2.01	3.53	2.0	1.85	5,594

(-- indicates value not calculated)