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THE ECONOMICS OF A STAGE-STRUCTURED WILDLIFE POPULATION MODEL

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Abstract

A four-stage model (calves, yearlings, adult female and adult male) of the Scandinavian moose (*Alces alces*) is formulated. Fecundity is density dependent while mortality is density independent. The paper aims to demonstrate the economic content of such a wildlife model and how this content may change under shifting economic and ecological conditions. Two different harvesting regimes are explored: hunting for meat, and trophy hunting. It is shown how different ways to compose the harvest influences the profitability while, at the same time, the population levels of the different stages may only change modestly. It is also shown why different market situations require different compositions of the harvest, knowledge that is disregarded in the traditional bioeconomic modelling approach.

Key words: wildlife, meat hunting, trophy hunting

1. Introduction

The aim of this paper is twofold: first, to demonstrate the economic content of a structured wildlife population model; and second, to show how this economic content may change under different management scenarios. Analysing structured wildlife harvesting models, i.e., models where the species are grouped in different classes according to age and sex, has a long tradition within biology. Caswell (2001) gives an in-depth overview; see also Getz and Haigh (1989). However, economic analysis plays only a minor role in these works. Economic reasoning is taken into account in Skonhoft et al. (2002) who analyses various management strategies for a mountain ungulate living in a protected area and a hunting area. Four stages are included: females and males within and outside the protected area. Because of the complexity of this model due to the dispersal mechanism, however, it is difficult to understand the various economic mechanisms influencing harvesting and abundance. The present paper analyses such economic mechanisms more explicitly where a four-stage model (calves, yearlings, adult females and adult males) is formulated. Our analysis has some similarities to that of Clark and Tait (1982), who studied the optimal harvest value in a sex-selective harvesting model where the population was grouped into two stages. See also the two-stage seal model in Conrad and Bjørndal (1991). As in Clark and Tait, we basically analyse the steady state where natural growth is balanced by harvesting. However, in contrast to Clark and Tait, trophy hunting, in addition to meat-value maximization, is studied. We also calculate the shadow values of the different population groups, and it is shown how these values are different from what are found in the market.

The model is formulated for a moose population (*Alces alces*) and is studied within a Scandinavian ecological and institutional context. The moose is the world’s largest member of the deer family and is found in the northern forests of North America, Europe and Russia. It 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. The value of this harvest is substantial, and the meat counts for more than 2 per cent of the yearly meat consumption in these countries. Moose hunting has traditionally been a local activity, and landowners receive the hunting value. The hunters have been the local people; the landowners and their families and friends, and the management goal has been to maximize the meat value, possibly corrected for forest browsing damage, for stable populations (more details are provided in Skonhoft and Olaussen 2005 and the references therein). During the last few years, however, a more commercialized hunting and wildlife industry has emerged, and 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 commercialized scheme are studied, and the consequences for harvesting and the population composition are analysed. All the time the management problem is studied from the landowner’s perspective, meaning that other values related to the moose population, like recreation value and intrinsic value, are neglected. Possible damage costs through forest browsing are neither taken into account. The meat value harvesting scheme is analysed given a fixed meat price while the landowner is assumed to exercise market power under the trophy hunting scheme. A ‘quality’ effect, expressed by the male density, is also assumed to influence the trophy hunting demand.

The paper is organized as follows. In the next section, the moose population model is formulated. Section three demonstrates what happens when the hunting is steered by the traditional landowner goal of maximizing meat value. In section four we study the sex and age composition under the new exploitation regime of trophy hunting. Section five illustrates the models by some numerical simulations, while section six summarizes our findings.

2. 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 mortality. On the other hand, fecundity has proven to be affected by the female density while the number of males seems to be of negligible importance within the range of moose densities in Scandinavia. However, it may play a role if the sex composition is very skew (see, e.g., Nilsen et al. 2005 and the references therein for more details).

The population at time (year) t is structured in four stages (Lande et al. 2003): calves $X_{c,t}$ ($yr < 1$), yearlings $X_{y,t}$ ($1 \leq yr < 2$), adult females ($yr \geq 2$) $X_{f,t}$ and adult males ($yr \geq 2$) $X_{m,t}$ so that the total population is $X_t = X_{c,t} + X_{y,t} + X_{f,t} + X_{m,t}$. The population is measured in spring before calving. All stages are generally harvested, and the hunting occurs in September–October. 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, and the same sex ratio is assumed for the yearlings when they enter the old stages.

Neglecting any stochastic variations in biology and environment, and any dispersal in and out of the considered area, the number of calves (recruitment) is first governed by $X_{c,t} = r_t X_{f,t}$ with $r_t = r(X_{f,t}, X_{m,t})$ as the fertility rate (number of calves per female). The fertility rate generally depends on both female density (number of females) and male density. It decreases in the female density $\partial r / \partial X_{f,t} = r'_f < 0$, and may also be reduced when the number of males become low, $r'_m \geq 0$. In addition, we have $r(0, X_{m,t}) > 0$ when $X_{m,t} > 0$ and $r(X_{f,t}, 0) = 0$. Therefore, the recruitment function yields:

(1) $$X_{c,t} = r(X_{f,t}, X_{m,t})X_{f,t}.$$

The recruitment function may be a one-peaked value function in the female density, but intuitively $\partial X_{c,t} / \partial X_{f,t} = (r + r'_f X_{f,t}) > 0$ should hold in an optimal harvesting programme, at least when females represent meat hunting value only (as here). If not, less female hunting coincides with less recruitment which barely can represent an efficient harvest strategy. This is confirmed by the numerical simulations (section five)[1].

The number of yearlings follows next as:

(2) $$X_{y,t+1} = s_c(1 - h_{c,t})X_{c,t}$$

where s_c is the fixed calf natural survival rate (fraction) and $h_{c,t}$ is the calf harvesting rate. Finally, the abundance of (old) females and (old) males become:

(3) $$X_{f,t+1} = 0.5 s_y (1 - h_{y,t}) X_{y,t} + s(1 - h_{f,t}) X_{f,t}$$

---

[1] In the numerical section the recruitment function is specified and parameterized so that $\partial X_{c,t} / \partial X_{f,t} < 0$ when $X_{f,t}$ becomes large. However, as indicated, the peak value is not reached in the optimal harvesting programmes. At the same time, this means that the recruitment function is strictly concave in the actual region of optimization (section five).

and

(4) $$X_{m,t+1} = 0.5s_y(1-h_{y,t})X_{y,t} + s(1-h_{m,t})X_{m,t}\,,$$

respectively, and where the same sex ratio is assumed for the yearlings when they enter the old stages. s is the fixed natural survival rate, identical for females and males while s_y is the yearling survival rate. $h_{y,t}$, $h_{f,t}$ and $h_{m,t}$ are the harvesting rates of yearlings, females and males, respectively.

The population model (1) - (4) has a recursive structure, and when combining (1) and (2) we find:

(5) $$X_{y,t+1} = s_c(1-h_{c,t})r(X_{f,t}, X_{m,t})X_{f,t}$$

Therefore, equations (3) – (5) is a reduced form model in three stages and where all equations are first order difference equations. This form is used when studying the different exploitation schemes below. The system may, however, be reduced further when omitting the yearling population. When combining equations (5) and (3), the female population growth hence reads $X_{f,t+1} = 0.5s_y(1-h_{y,t})s_c(1-h_{c,t-1})r(X_{f,t-1}, X_{m,t-1})X_{f,t-1} + s(1-h_{f,t})X_{f,t}$ while combining equations (5) and (4) yields the male population growth as $X_{m,t+1} = 0.5s_y(1-h_{y,t})s_c(1-h_{c,t-1})r(X_{f,t-1}, X_{m,t-1})X_{f,t-1} + s(1-h_{m,t})X_{m,t}$. These two equations represent a system of two interconnected second order non-linear difference equations, and numerical analyses demonstrate that the equilibrium is unique and stable for fixed harvesting rates (see e.g., Gandolfo 2001 for a theoretical exposition).

Omitting the time subscript, the female equilibrium (when $X_f > 0$ and $X_m > 0$) reads:

(6) $$1 = 0.5s_y(1-h_y)s_c(1-h_c)r(X_f, X_m) + s(1-h_f)$$

while

(7) $$X_m = 0.5s_y(1-h_y)s_c(1-h_c)r(X_f, X_m)X_f + s(1-h_m)X_m$$

represents the male population equilibrium. The female equilibrium condition (6) slopes upward in the $X_m - X_f$ plane for 'small' values of X_m, but becomes flat when the number of males has a negligible fertility effect. Higher harvesting rates h_c, h_y and h_f shift it down. The male equilibrium equation (7) slopes upward as well for 'small' values of X_f, but will bend backwards if $(r + r'_f X_f)$ becomes negative (cf. footnote 1)[2]. As indicated, it will be an unique biological equilibrium for fixed harvesting rates (see Figure 1). Higher harvesting rates h_c, h_y and h_m shift the male equilibrium condition inwards. Therefore, not surprisingly, more intensive harvesting of all stages reduces the female as well the male density. On the other hand, the yearlings abundance $X_y = s_c(1-h_c)r(X_f, X_m)X_f$ increases under higher harvesting pressure if the harvesting activity initially is modest and the intersection of the male and female equilibrium conditions takes place on the backward bending part of the male equilibrium schedule. The same will be so for the equilibrium calf population, $X_c = r(X_f, X_m)X_f$. On the other hand, if the intersection between the male and female equilibrium schedules takes place on the upward sloping part of the male schedule, increased harvesting activity reduces all stages of the population.

Figure 1 about here

When combing the above equilibrium equations (6) and (7), the male–female proportion may be written as $X_m / X_f = [1 - s(1-h_f)]/[1 - s(1-h_m)]$. Therefore, the yearling harvest (as well as the calf harvest) does not influence the adult population proportion because the natural mortality of males and females is equal, and the same fraction of yearlings enters the female and male populations. It is also seen that sex-skewed harvesting rates translate directly into sex-skewed adult abundance. In an unexploited system, we have $X_m / X_f = 1$ together with equation (6) as $r(X_f, X_m) = (1-s)/0.5s_y s_c$.

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[2] The slope of the female population equilibrium (6) is given by $dX_f / dX_m = -r'_m / r'_f$ while $dX_f / dX_m = [1 - s(1-h_m) - 0.5s_y(1-h_y)s_c(1-h_c)X_f r'_m]/[0.5s_y(1-h_y)s_c(1-h_c)(r + r'_f X_f)]$ is for the male population equilibrium (7).

3. The traditional regime: hunting for meat

We first study the situation where the landowner maximises the meat value. Because natural mortality is assumed to take place after the hunting season (see above), the number of animals removed in year t is $H_{c,t} = h_{c,t}X_{c,t}$, $H_{y,t} = h_{y,t}X_{y,t}$, $H_{f,t} = h_{f,t}X_{f,t}$ and $H_{m,t} = h_{m,t}X_{m,t}$. The current meat value is accordingly $\pi_t = p(w_c h_{c,t}X_{c,t} + w_y h_{y,t}X_{y,t} + w_f h_{f,t}X_{f,t} + w_m h_{m,t}X_{m,t})$ where $w_c < w_y < w_f < w_m$ are the (average) body slaughter weights (kilogram per animal) of the four stages and p (NOK per kilogram) the meat price. As mentioned, the meat hunters have traditionally been the landowners and their friends, indicating that a market for meat hunting barely exists. Therefore, the unit meat hunting price is assumed to be independent of the amount harvested and the stock sizes. When further assuming that the cost of the landowner of organizing this hunting is stock independent, the 'net' harvest price p is fixed. The meat price will for obvious reasons not affect the optimization except for scaling the shadow price values (see below).

When the present-value meat value is to be maximised, and the calf population is replaced (see above), the problem is hence to

(7)

$$\max_{X_{y,t},X_{f,t},X_{m,t},h_{c,t},h_{y,t},h_{f,t},h_{m,t}} \sum_{t=0}^{t=\infty}\rho^t\pi_t = \sum_{t=0}^{\infty}\rho^t p\left(w_c h_{c,t} r(X_{f,t},X_{m,t})X_{f,t} + w_y h_{y,t}X_{y,t} + w_f h_{f,t}X_{f,t} + w_m h_{m,t}X_{m,t}\right)$$

subject to the biological constraints (3) - (5). $\rho = 1/(1+\delta)$ is the discount factor with $\delta \geq 0$ as the (yearly) discount rent. The Lagrangian of this problem may be written as (see, e.g., Conrad and Clark 1987)

$$\begin{aligned} L = \sum_{t=0}^{\infty}\rho^t \Big\{ & \left[p\left(w_c h_{c,t} r(X_{f,t},X_{m,t})X_{f,t} + w_y h_{y,t}X_{y,t} + w_f h_{f,t}X_{f,t} + w_m h_{m,t}X_{m,t}\right)\right] \\ & - \rho\eta_{t+1}\left[X_{y,t+1} - s_c(1-h_{c,t})r(X_{f,t},X_{m,t})X_{f,t}\right] \\ & - \rho\lambda_{t+1}\left[X_{f,t+1} - 0.5s_y(1-h_{y,t})X_{y,t} - s(1-h_{f,t})X_{f,t}\right] \\ & - \rho\mu_{t+1}\left[X_{m,t+1} - 0.5s_y(1-h_{y,t})X_{y,t} - s(1-h_{m,t})X_{m,t}\right]\Big\} \end{aligned}$$

and where $\eta_t \geq 0$, $\lambda_t \geq 0$ and $\mu_t \geq 0$ are the shadow prices of the yearling, female and male populations, respectively. No constraints are explicitly formulated for the harvest fractions (but see below). The first-order conditions of this maximizing problem (when $X_{y,t} > 0$, $X_{f,t} > 0$ and $X_{m,t} > 0$) are:

(8) $$\frac{\partial L}{\partial X_{y,t}} = pw_y h_{y,t} - \eta_t + \rho\lambda_{t+1} 0.5 s_y (1 - h_{y,t}) + \rho\mu_{t+1} 0.5 s_y (1 - h_{y,t}) = 0,$$

(9)
$$\frac{\partial L}{\partial X_{f,t}} = pw_c h_{c,t}(r + r'_f X_{f,t}) + pw_f h_{f,t} + \rho\eta_{t+1} s_c (1 - h_{c,t})(r + r'_f X_{f,t}) - \lambda_t + \rho\lambda_{t+1} s (1 - h_{f,t})$$
$$= 0,$$

(10) $$\frac{\partial L}{\partial X_{m,t}} = pw_c h_{c,t} r'_m X_{f,t} + pw_m h_{m,t} + \rho\eta_{t+1} s_c (1 - h_{c,t}) r'_m X_{f,t} - \mu_t + \rho\mu_{t+1} s (1 - h_{m,t}) = 0,$$

(11) $$\frac{\partial L}{\partial h_{c,t}} = pw_c - \rho\eta_{t+1} s_c \le 0 \;;\; 0 \le h_c < 1,$$

(12) $$\frac{\partial L}{\partial h_{y,t}} = pw_y - \rho\lambda_{t+1} 0.5 s_y - \rho\mu_{t+1} 0.5 s_y \le 0 \;;\; 0 \le h_y < 1,$$

(13) $$\frac{\partial L}{\partial h_{f,t}} = pw_f - \rho\lambda_{t+1} s \le 0 \;;\; 0 \le h_f < 1$$

and

(14) $$\frac{\partial L}{\partial h_{m,t}} = pw_m - \rho\mu_{t+1} s \le 0 \;;\; 0 \le h_m < 1.$$

The second-order conditions are fulfilled due to the concavity of the recruitment function. This also secures a unique steady state which is confirmed by the numerical simulations. The portfolio equations (8) - (10) steer the shadow price values while conditions (11)–(14) are the control conditions where the possibility for keeping each of the stages unexploited at the steady state are considered. In this time discrete system with three state variables (and four controls) it is difficult to find the dynamics when originally being outside steady-state. The Lagrangian is linear in the four controls, but the so-called Most Rapid Approach Path (*MRAP*) does not generally apply to a system with more than one state variable[3].

As mentioned, the traditional exploitation of the Scandinavian moose has been directed by maximizing the meat value for stable populations (again, see Skonhoft and Olaussen 2005). It is well known that such an exploitation scheme coincides with the steady-state of the above dynamic problem for a zero discount rent, $\rho = 1$ (see e.g., Clark 1990, Ch. 2). The first order conditions of the traditional hunting regime may then be written as:

(8’) $$\eta = pw_y h_y + (\lambda + \mu)0.5 s_y (1 - h_y),$$

(9’) $$\lambda = pw_f h_f + [pw_c h_c + \eta s_c (1 - h_c)](r + r'_f X_f) + \lambda s(1 - h_f),$$

(10’) $$\mu = pw_m h_m + pw_c h_c r'_m X_f + \eta s_c (1 - h) r'_m X_f + \mu s(1 - h_m),$$

(11’) $$pw_c - \eta s_c \leq 0;\ 0 \leq h_c < 1,$$

(12’) $$pw_y - (\lambda + \mu)0.5 s_y \leq 0;\ 0 \leq h_y < 1,$$

(13’) $$pw_f - \lambda s \leq 0;\ 0 \leq h_f < 1$$

and

(14’) $$pw_m - \mu s \leq 0;\ 0 \leq h_m < 1.$$

The shadow price equations (8’) - (10’) indicate that the different stages are valued higher than their marginal harvest value in the market (see also below). Condition (11’) says that the steady state harvest of calves should take place up to the point where the marginal harvest benefit is equal to, or below, the cost in terms of reduced yearling population growth

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[3] Clark 1990, Ch. 10.3 discusses this problem in a two state variables *continuous* time system. He argues that the transitional dynamics generally will not be of the *MRAP*-strategy, but this strategy will be the ‘practice acceptable approach’ in this model.

evaluated at its shadow price. When (11’) holds as an inequality, the marginal harvest benefit is below its marginal cost and harvesting is thus not profitable, $h_c = 0$. The interpretation of the yearling harvest condition (12’) is similar, but here the costs come through two stages; reduced female as well as male growth. When it holds as an inequality, harvesting is again not profitable and $h_y = 0$. The interpretation of the female harvest condition (13’) is simpler. Because of the fecundity density effect, meaning that one more female on the margin yields a smaller recruitment when the female population is ‘high’ than when ‘low’, $h_f = 0$ seems less likely. The male control condition (14’) is analogous to the female harvest condition. Keeping this population unexploited is also considered as a possibility, but is not likely. There are two reasons for this; the marginal harvest value is above that of the other stages, and the fecundity effect is small and negligible when the population density is high. Therefore, the marginal cost for the males will not be above its marginal benefit. On the other hand, the fecundity effect is the only reason why it is not beneficial to harvest down the whole male population. With $r'_m = 0$ and combining conditions (10’) and (14’), it is hence easily revealed that we find $s = 1$, or zero natural mortality. Conditions (10’) and (14’) are therefore consistent only with $r'_m > 0$. As r'_m may be small even for a modest male population, the optimal harvest rate h_m is suspected to be quite high (see also numerical section).

From condition (14’), when $0 < h_m < 1$, it is seen (as already indicated) that the optimal male shadow value exceeds it’s marginal harvest value, $\mu = pw_m / s$ (NOK per animal). The female shadow value exceeds its marginal harvest value as well (conditions 9’ and 13’). Suggested that females are hunted (which holds for all realistic parameter values, cf. numerical section), condition (13’) yields $\lambda = pw_f / s$. The female shadow price is hence lower than the male shadow price and the difference is directly reflected by the difference in slaughter weight. From (11’) it is seen that keeping the calves unexploited demands $\eta > pw_c$ while keeping yearlings unexploited demands $(\lambda + \mu)0.5s_y > pw_y$ (condition 12’). Therefore, the condition for not harvesting the yearlings is directly related to the marginal harvest values of both females and males. The shadow price is then $\eta = (\lambda + \mu)0.5s_y$ (equation 8’).

4. Present time: trophy hunting

The moose-harvesting regime in Scandinavia (like wildlife hunting elsewhere, see e.g., Anderson and Hill 1995) is gradually changing, and a hunting and wildlife industry is emerging. 'Present time' is modelled by introducing a market for trophy hunting of males while still having meat-value hunting of the other stages. In a standard manner, the market demand is assumed to slope downwards for a higher offtake. In addition to price, the demand for trophy-hunting licences may also be contingent upon 'quality', expressed by the abundance of males[4]. When the practice in Scandinavia is followed where one licence allows the buyer to kill one animal, which is paid only if the animal is killed, the inverse market demand for male hunting licences is written:

(15) $$q_t = q(h_{m,t}X_{m,t}, X_{m,t})$$

and where the licence price q_t (NOK per animal) decreases with a higher harvest, $q'_H = \partial q / \partial(h_{m,t}X_{m,t}) < 0$ and increases with more animals available, $q'_X > 0$, due to the quality effect[5].

Supplying trophy-hunting licences is also costly and depends on the number of licenses sold:

(16) $$C_t = C(h_{m,t}X_{m,t})$$

with fixed cost $C(0) \geq 0$, 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 organizing the permit sale, the costs of guiding and various transportation services. With $C'' = 0$ and fixed marginal cost, which is assumed in the numerical illustration below, the cost structure is just as under the above meat hunting scheme.

The current meat value and trophy hunting profit is now $\pi_t = p[w_c h_{c,t} r(X_{f,t}, X_{m,t})X_{f,t} + w_y h_{y,t} X_{y,t} + w_f h_{f,t} X_{f,t}] + q(h_{m,t}X_{m,t}, X_{m,t})h_{m,t}X_{m,t} - C(h_{m,t}X_{m,t})$.

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[4] See Mattson (1994). In the recreational fishing literature the demand quality effect is explored in many papers (see, e.g., Anderson 1983).

[5] It may seem unrealistic that the quality demand effect is based on current period male density and not on, say, previous year(s) density. However, this assumption is justified by the fact that the stock usually is monitored during the spring and summer, before the hunting starts.

The market for trophy hunting is probably something between a competitive market and a monopoly. One of these extremes is chosen, and we assume that trophy-hunting licences are supplied under monopolistic conditions (the opposite will not change the results qualitatively). When the present-value again is to be maximised, the landowner problem is to

(17)

$$\begin{aligned}\max_{X_{y,t},X_{f,t},X_{m,t},h_{c,t},h_{y,t},h_{f,t},h_{m,t}} \sum_{t=0}^{t=\infty}\rho^t\pi_t = \sum_{t=0}^{t=\infty}\rho^t\Big[p(w_c h_{c,t} r(X_{f,t},X_{m,t})X_{f,t} + w_y h_{y,t} X_{y,t} + w_f h_{f,t} X_{f,t}) \\ + q(h_{m,t}X_{m,t},X_{m,t})h_{m,t}X_{m,t} - C(h_{m,t}X_{m,t})\Big]\end{aligned}$$

under the biological constraints (3) – (5). The first-order conditions of this problem are (8), (9), (11), (12) and (13) together with:

(18)

$$\begin{aligned}\frac{\partial L}{\partial X_{m,t}} = p w_c h_{c,t} r'_m X_{f,t} + q'_H (h_{m,t})^2 X_{m,t} + q_t h_{m,t} - C' h_{m,t} + q'_x h_{m,t} X_{m,t} + \rho\eta_{t+1} s_c (1-h_{c,t}) r'_m X_{f,t} \\ -\mu_t + \rho\mu_{t+1} s(1-h_{m,t}) = 0\end{aligned}$$

and

(19) $$\frac{\partial L}{\partial h_{m,t}} = q'_H X_{m,t} h_{m,t} + q_t - C' - \rho\mu_{t+1} s = 0 \ ; \ 0 < h_m < 1$$

when we assume that male hunting always takes place at the steady state [6].

The Lagrangian is no longer linear in all four controls. Therefore, the dynamics will be different from the previous regime of meat harvesting only and may possible be more close to the saddle-point type characterized by gradually adjustment of the harvesting until harvesting equalizes natural growth of all categories of animals (the dynamics is explored in an accompanying paper). At the steady state, conditions (18) and (19) may be written as:

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[6] It is here tacitly assumed that male trophy hunting is more profitable than male meat hunting. The condition for trophy hunting only may easily be found through the complementary slack conditions when considering male meat hunting and trophy hunting as two male hunting alternatives. Not surprisingly, we then find $(q'_H X_{m,t} h_{m,t} + q_t - C') > p w_m$.

(18’)

$$\mu = pw_c h_c r'_m X_f + q'_H (h_m)^2 X_m + qh_m - C' h_m + q'_X h_m X_m + \rho\eta s_c (1-h_c) r'_m X_f + \rho\mu s (1-h_m)$$

and

(19’) $q'_H X_m h_m + q - C' - \rho\mu s = 0$; $0 < h_m < 1$,

respectively. The interpretations of these conditions are straightforward (see also above). The male harvest benefit is now expressed by a marginal profit term plus a marginal stock effect through the demand quality effect. Combining these conditions yield $(1-\rho s)(q'_H X_m h_m + q - C') - \rho s q'_X h_m X_m - \rho s p w_c h_c r'_m X_f - \rho\eta s_c (1-h_c) r'_m X_f = 0$ after some small rearrangements. The marginal harvest profit is hence above zero at the optimal steady-state, $(q'_H X_m h_m + q - C') > 0$. Not surprisingly, from condition (18’) (as well as from 19’), this implies a strictly positive male shadow price. Notice that this holds when zero discounting ($\rho = 1$) as well. On the other hand, with hypothetically no male fertility effect ($r'_m = 0$) and no demand quality effect ($q'_X = 0$), the male shadow price equals zero.

While the first-order conditions for harvesting calves, yearlings and female are the same as in the traditional harvest regime, the new conditions for male harvesting will obviously spill over to these stages and the number of hunted animals will generally change for all stages. In line with standard harvesting theory (i.e., Clark 1990), we may also find that the male harvest increases as the males under trophy hunting are valued higher in the market than in the meat hunting regime (cf. footnote 6). However, both the exercise of monopoly power and the quality effect will typically work in an opposite manner. Particularly if the quality demand effect is strong, the male harvest will decrease and the male population will increase compared to the meat hunting regime. As a consequence, the steady-state male–female proportion X_m / X_f is suspected to increase compared with the traditional regime. How the meat hunting is affected is, however, far from clear as either more males may be sustained by more yearlings or, at an earlier stage, more females. Moreover, while the meat price p had no effect on the optimal harvest policy in the traditional regime, it will now influence the optimal harvesting policy of all four stages. Again in line with standard harvesting theory, one may suspect that a larger harvest and fewer animals will be accompanied by a higher price. However, the picture is far from clear as there are many conflicting forces at work, not at least because of the demand quality effect. The shadow prices will also change between the regimes, except that the female value will be the same when female harvest takes place. The male shadow price is suspected to increase as the price per animal in the market will increase compared to the traditional regime. However, also this intuition may be questioned as the market power term in equation (19`), *ceteris paribus*, reduces the shadow price.

5. Numerical illustration

Data and specific functional forms

The steady state of the exploitation schemes will now be illustrated numerically. The fecundity 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). In addition, it shifts out with more males. When the time subscript is omitted the function reads:

$$r = r(X_f, X_m) = \frac{\tilde{r}}{1 + (X_f / K)^b}(1 - e^{-aX_m}) \tag{20}$$

with $\tilde{r} > 0$ as the intrinsic growth rate (maximum number of calves per female). The maximum number of calves per female shifts down with a smaller male population and where $a > 0$ yields the male density effect. $K > 0$ is the female stock level for which density-dependent fertility is equal to 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. Equation (20) implies a recruitment function $X_c = r(X_f, X_m)X_f = \tilde{r}X_f / [1 + (X_f / K)^b](1 - e^{-aX_m})$ and is of the so-called Shepherd type. With $b > 1$, which is assumed, we have the Ricker version meaning that $\partial X_c / \partial X_f < 0$ for a large female density. However, as already indicated (footnote 1), $\partial X_c / \partial X_f > 0$ will hold in the optimal programmes and the recruitment function is concave[7].

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[7] Differentiation yields $\partial X_c / \partial X_f = [K^b + (1-b)X^b]/(K^b + X^b]^2$. Moreover, we find $\partial^2 X_c / \partial X_f{}^2 = -q[(b+1)K^b + (1-b)X^b]$ where $q > 0$ is a positive term. It is easily recognized that $\partial X_c / \partial X_f > 0$ implies $\partial^2 X_c / \partial X_f{}^2 < 0$.

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:

(21) $q = \alpha e^{\gamma X_m} - \beta h_m X_m$.

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 linearly as well:

(22) $C = \overline{c} + c h_m X_m$

so that $\overline{c} \geq 0$ is the fixed cost and $c > 0$ is the constant marginal cost. Table A1 gives the baseline parameter values.

Results

To make a meaningful comparison between the two management schemes, a zero discount rent is assumed in all regimes. Table 1 reports the results for the baseline parameter values. As a benchmark, a no-hunting scenario is included (first row). Since the yearlings enter the (adult) male and female stages at the same sex ratio, the number of males and females are the same here. In the traditional regime with meat-value maximization, the female and male harvest rates become 0.23 and 0.68, respectively, while there are no harvest of yearlings and calves. Therefore, the marginal harvest benefits of these stages are below that of their marginal costs in term of losses from reduced harvest of males and females. The number of calves and yearlings are higher in the traditional regime than in the unexploited system. As explained above (section two) the reason is that the number of females is above the value representing the peak value of the recruitment function $dX_c / dX_f = (r' X_f + r) < 0$. The male shadow value is somewhat higher than that of the female shadow value, and as demonstrated in section three, this is due to the meat weight difference only. The yearling shadow value is slightly above that of the female value, and follows simply as $\eta = (\lambda + \mu)0.5 s_y$ when $h_y = 0$ (see also section three).

Table 1 about here

The trophy hunting scheme is first studied when the quality effect is disregarded and the inverse demand function (21) reads $q = \alpha - \beta h_m X_m$. The male harvest fraction shifts substantially down and becomes $h_m = 0.31$. Somewhat surprisingly, the female harvest fraction decreases as well. On the other hand, the yearling harvest becomes significant, $h_y = 0.5$, while it is still beneficial to keep the calf population unexploited. The demand mechanism is of crucial importance to explain this. In order to take advantage of the downward sloping demand schedule, the male harvest fraction is reduced to secure a high harvest price of males. However, since a reduced harvest rate of males increases the male population, *ceteris paribus*, and thereby reduces the harvest price of males through total male harvesting, a change in the composition of female and yearling harvest is required. By harvesting more of the yearlings, less male moose are produced compared to a situation with a low male harvest rate and no yearling harvest. The reduced female harvest translates into yearling harvest in such an amount that the female population is more or less unchanged (Eq. 3). Hence, by altering the composition of the harvest, the profit increases even if the population size at each stage is left almost unchanged. Because of the modest adult population changes, the calf population is also more or less the same (Eq. 1). The male and yearling shadow values decrease compared to the meat hunting regime and the shadow value of both stages are now below their market value. The reduced male shadow value may seem surprising since the market price of males have increased, but as discussed above this is readily explained by the market power term in Eq. (19`). The yearling shadow value is reduced as well because of the lower male shadow value (Eq. 8`). Finally, the trophy hunting profit exceeds the traditional regime of meat hunting (which happens per definition, cf. footnote 6).

The male harvest rate is further reduced when the quality effect is included. The female harvest rate, on the other hand, increases and becomes (by accident) just as in the meat hunting regime. Because the yearling harvest again is zero the female population size changes just slightly while the male population is substantially higher than without the quality effect. With such a high male stock, the demand (through the slope term) is very sensitive to the male harvest rate which is just 0.06 in this case. The reason why the yearling harvest rate again is zero is also strictly due to the quality term because by altering the harvest composition from young to female a high male population is secured. Thus, this is exact the same driving force as described above when altering the female-yearling harvest rate from meat hunting to trophy hunting, only now a high male population is desired due to the quality effect. The difference between the male and female harvest rate becomes smaller than without the quality effect, and the male shadow value is higher than the female shadow value. The yearling shadow value increases as well and is now above its value in the market: that is, letting this stage grow into adults is more valuable than harvesting just as in the traditional meat hunting regime. Table 1 also demonstrates that the trophy hunting price and profit further increase when the demand quality effect is added.

Shifting up the meat price p scales up the shadow price values in the traditional regime but has no allocation effect. In the trophy hunting regime, the shadow prices increase as well except for the male population when the quality effect is present (Table A2, Appendix). The reason for this can be found in the quite dramatic harvest rate difference for males and the male population falls from about 4,700 to below 900 individuals. The reason is simply that for such a price hike, the relative profitability between the male and the other stages are changed. Trophy hunting is still profitable and the quality effect still influences the harvest, but not to the extreme extent as under the baseline meat price value. In line with intuition, a further increase in the meat price will eventually lead to unprofitable trophy hunting and hence meat hunting only. The decrease in the male shadow price under the demand quality effect is therefore simply explained by the relative profitability increase of meat hunting compared to trophy hunting.

The prediction from the standard harvesting model (e.g., Clark 1990) is that more profitable harvest leads to a higher exploitation pressure and more harvest. As Table 2 shows, however, this result does not unconditionally hold in a stage structured model. More total biomass is harvested in the meat hunting regime than in either of the trophy hunting regimes. This is readily explained by the market power mechanism already discussed. More interesting, however, is the fact that there is more meat hunting (the biomass sum of calves, yearlings and females) under trophy hunting than under the meat hunting only scheme. Moreover, the result of an increased meat price under trophy hunting in absence of the quality effect is that the total biomass harvested decreases (even if slightly). The reason is that reduced male harvest dominates increased meat hunting of yearlings and females.

Table 2 about here

Sensitivity analyses also demonstrate that the demand parameter α, which yields the maximum willingness to pay with a zero quality effect, generally has large allocation effects, and a relatively small change means that the male harvest fraction increases both with and without the demand quality effect included (Table A3 Appendix). Obviously, this also pulls in the direction of more profitable trophy hunting. The effects of a changed demand quality effect γ are also studied (not reported). Not surprisingly, we find that when the quality effect is strengthened, it becomes more profitable to keep more male animals.

Finally, we show to what extent the profit is sensitive to changes in the harvest rates. By studying how profitability changes when some of the harvest rates are taken as given, the importance of making the correct harvest rate choice is highlighted. This new constrained optimisation problem is demonstrated for the traditional meat harvest regime with the female harvest rate level as exogenously given. The problem now is hence to maximise profit (7) subject to the ecological constraint (3) – (5), in addition to $h_{f,t} = \bar{h}_f$. As above, we just consider steady state with zero discounting and under the baseline parameter values. Figure 2 illustrates how the profit changes for different values of $\bar{h}_f$. As indicated by the figure, it turns out that there is a relatively flat area around the (unconstrained) optimal female harvest level ($h_f = 0.23$, see Table 1). Even when imposing a zero female harvest level, the profit does not change dramatically; from 7,154 (Table 1) to about 6,100. The reason is that reduced female harvest is compensated by more harvest of yearlings and males. For example, at a zero female harvest, the (constrained) optimal yearling harvest rate becomes $h_y = 0.81$ while the male harvest rate is $h_m = 0.09$. The high yearling harvest rate secures that the recruitment stays high while the low male harvest rate is simply a consequence of the massive yearling harvest. Hence, there is more to gain by securing high recruitment than by harvesting a higher fraction of the male stock.

Figure 2 about here

Such compensating mechanism is not to the same extent present when imposing too high female harvest. The consequences are more severe for two reasons. First, the optimal yearling harvest rate is zero above $h_f = 0.18$. This means that the possibility of compensating for a higher female harvest rate by reducing the yearling harvest rate is absent when the imposed female harvest fraction is above its (unconstrained) optimal level. Second, due to the shape of the recruitment function, decreased recruitment of a further reduction in the female stock are now intensified. This is illustrated by the steep fall in the profit function above $h_f = 0.30$.

Making similar “mistakes” by optimising given fixed levels of some of the other harvest rates, yield the same type of mechanisms. As long as recruitment can be kept up by changing the harvest at other stages, the economic consequences are less severe than in the opposite case. Furthermore, the same pattern is found in the trophy hunting regimes when imposing similar types of restrictions on the optimization problem.

6. Concluding remarks

The paper has analysed a four-stage model of the Scandinavian moose population with density-dependent fertility. Two steady state exploitation schemes have been studied and it is demonstrated how the changing harvest of different stages is accompanied by significant profit changes while, in most cases, leaving the population densities of the different classes more or less unchanged. The different ways to compose the harvest, e.g. in yearlings or females, and why different market situations require different composition of the harvest, are highlighted. Such knowledge is disregarded in the traditional bioeconomic modelling approach. Moreover, we have demonstrated that shadow prices may change counter intuitively, and why this may happen.

The numerical section illustrates the predictions from the theoretical model. In the traditional meat hunting only harvest scheme, we find that zero calf and yearling harvest and modest female harvest are accompanied by a high male harvest rate. 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 may be higher than that of the females. The male stage is more intensively harvested since its influence on recruitment is small, even for small and modest stock levels. The emerging exploitation scheme with a market for trophy hunting changes the optimal harvest decision of males, and hunting down a large fraction of the male population will no longer represent and optimal policy. In addition, the trophy-hunting market allocation spills over to the conditions for meat-value maximization of young and females. The male–female population ratio increases and contingent upon the trophy hunting market, both more and less female harvest may take place.

The present model encompasses some general results that will survive in more complex stage-structured models. Most importantly, we have highlighted the economic forces influencing harvest in four different stages that, in various degrees, are present in many structured population models. Our model has four stages that recruit in different ways. The calf represents a value through recruitment to the yearling stage in the same way as the yearling represents a value through recruitment to the (adult) male and female stages. As long as density-dependent growth factors are weak, or non-existent (as here), harvesting calves, or yearlings, does not pay off in a meat maximising harvest regime. The fact that the optimal harvest policy under trophy hunting may involve harvest of the yearling stage is surprising and reflects an important insight: The composition of the harvest in the meat harvesting stages may involve seemingly sub-optimal strategies because they are driven by the male trophy hunting activity. 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 (adult) male stage is considered as the biological ‘end’ product as its influence on recruitment is substantial only for small densities. However, irrespective of this; our model demonstrates that the male optimal harvest policy depends critically on economic conditions.

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Appendix

Table A1 here

Table A2 here

Table A3 here

Figures and tables

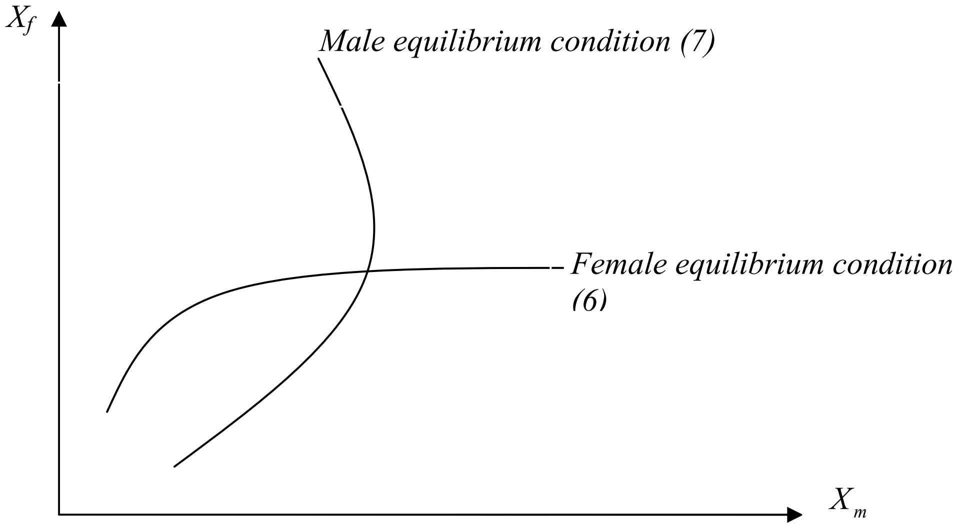

Figure 1: *Biological equilibrium male and female population stages. Fixed harvest rates.*

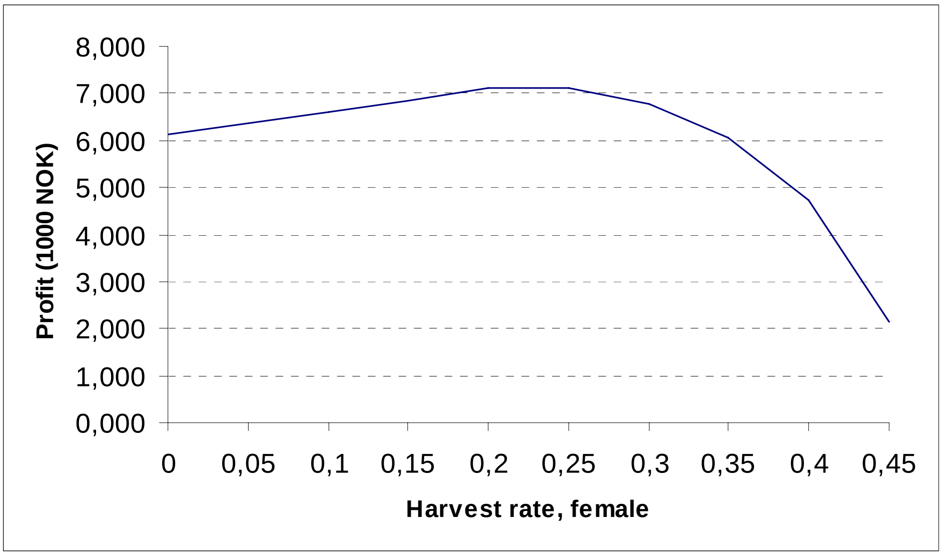

Figure 2: *Profit meat hunting regime when estriction female harvest rate.* Baseline parameter values.

Table 1: *Steady state different management regimes (no discounting, $\rho = 1$).Baseline parameter values. $h_{c,}$ harvest fraction calf, h_y harvest fraction young, h_f harvest fraction female, h_m harvest fraction male, $X_{c,}$ number of calves (in 1,000 animals), X_y number of young (in 1,000 animals), X_f number of females (in 1,000 animals),X_m number of males (in 1,000 animals), η young shadow price (in NOK 1,000/animal), λ female shadow price (in NOK 1,000/animal), μ male shadow price (in NOK 1,000/animal), q trophy price male (in NOK 1,000/male), and π profit (in NOK 1,000).*

(--indicates not calculated)

Hunting regimes	h_c	h_y	h_f	h_m	X_c	X_y	X_f	X_m	η	λ	μ	q	π
No harvest	0	0	0	0	0.70	0.63	5.94	5.94	--	--	--	--	--
Traditional regime. Hunting for meat	0	0	0.23	0.68	1. 14	1.02	1.83	0.69	8.00	7.90	8.95	--	7,154
Trophy hunting. No quality effect	0	0.50	0.09	0.31	1.14	1.02	1.80	0.72	6.75	7.90	6.30	18.99	7,883
Trophy hunting. With quality effect	0	0	0.23	0.06	1.15	1.03	1.83	4.71	7.69	7.90	8.29	23.31	8,373

Table 2: *Steady state different management regimes (no discounting,* $\rho = 1$*). Baseline parameter values. H total harvest (in 1,000 animals), wH biomass harvested (in 1,000 kg). Different meat prices; p=50 (NOK/kg) and p=60 (NOK/Kg).*

		H	$H_c+H_y+H_f$	H_m	wH	$w_cHc + w_yHy + w_f H_f$	w_mH_m
Meat hunting		0.89	0.42	0.47	140,31	62,35	80,73
Trophy hunting. No quality effect	*p=50*	0.89	0.67	0.22	130,30	92,84	37,43
	p=60	0.89	0.68	0.21	129,70	94,39	35,35
Trophy hunting. With quality effect	*p=50*	0.69	0.42	0.27	108,60	62,96	45,68
	p=60	0.89	0.66	0.22	130,00	92,03	37,98

Table A1: *Baseline biological and economic parameter values*

Parameters	Description	Baseline value	Reference/source
$\tilde{r}$	max. specific growth rate	1.15	Nilsen et al. (2005)
K	female stock level where density dependent factors dominates density independent factors	2 000 animal	Nilsen et al. (2005)
a	male density recruitment factor	0.007	
b	density compensation parameter	2	Nilsen et al. (2005)
w_c	Average weight calve	65 kg	SSB (2004)
w_y	average weight young	135 kg	SSB (2004)
w_f	average weight females	150 kg	SSB (2004)
w_m	average weight male	170 kg	SSB (2004)
s_c	survival rate calves	0.90	Nilsen et al. (2005)
s_y	natural mortality young	0.95	Nilsen et al. (2005)
s	natural mortality female and male	0.95	Nilsen et al. (2005)
p	meat price	50 NOK/kg	Storaas et al. (2001)
α	choke price	30,000 NOK/kg	Calibrated
γ	quality parameter demand	0.000043	Calibrated
β	slope parameter demand	50 NOK/animal^2	Calibrated
$\overline{c}$	fixed harvest cost	500,000 NOK	Calibrated
c	marginal harvest cost	2,000 NOK/animal	Calibrated

Table A2: *Sensitivity, increased meat price, p=60. Steady state different management regimes (no discounting, $\rho = 1$). h_c, harvest fraction calf, h_y harvest fraction young, h_f harvest fraction female, h_m harvest fraction male, X_c, number of calves (in 1,000 animals), X_y number of young (in 1,000 animals), X_f number of females (in 1000 animals),X_m number of males (in 1,000 animals), η young shadow price (in NOK 1,000/animal), λ female shadow price (in NOK 1000/animal), μ male shadow price (in NOK 1000/animal), q trophy price male (in NOK 1,000/male), and π profit (in NOK 1,000).*

(--indicates not calculated)

Hunting regimes	h_c	h_y	h_f	h_m	X_c	X_y	X_f	X_m	η	λ	μ	q	π
Trophy hunting. No quality effect	0	0.52	0.08	0.29	1.14	1.02	1.80	0.72	8.10	9.47	7.59	19.60	8,824
Trophy hunting. With quality effect	0	0.48	0.09	0.26	1.15	1.03	1.89	0.86	7.99	9.47	7.15	19.96	9,035

Table A3: *Sensitivity, increased choke price, α=35,000. Steady state different management regimes (no discounting, $\rho = 1$). h_c, harvest fraction calf, h_y harvest fraction young, h_f harvest fraction female, h_m harvest fraction male, X_c, number of calves (in 1,000 animals), X_y number of young (in 1,000 animals), X_f number of females (in 1,000 animals), X_m number of males (in 1,000 animals), η young shadow price (in NOK 1,000/animal), λ female shadow price (in NOK 1,000/animal), μ male shadow price (in NOK 1,000/animal), q trophy price male (in NOK 1,000/male), and π profit (in NOK 1,000).*

(--indicates not calculated)

Hunting regimes	h_c	h_y	h_f	h_m	X_c	X_y	X_f	X_m	η	λ	μ	q	π
Trophy hunting. No quality effect	0	0.40	0.12	0.38	1.14	1.02	1.80	0.72	6.76	7.90	6.33	21.51	9,108
Trophy hunting. With quality effect	0	0	0.23	0.07	1.15	1.03	1.85	4.16	8.92	7.90	10.87	27.09	10,050