Abstract
During the last few decades wildlife trophy hunting has increasingly replaced traditional meat hunting. The economics of trophy hunting is analysed with the Scandinavian moose (Alces alces) serving as an example. A four-stage model (calf, yearlings, adult female and adult male) is formulated. The calves, yearlings and females are hunted for meat, while the males are hunted for trophies and where the demand for trophy hunting depends on price and quality. The dynamics of the exploitation turns out to be pulse harvesting of females and oscillation in the male trophy hunting while the harvest of calves and yearlings are zero all the time. The paper also demonstrates how the trophy price influences the amount of trophy harvesting, and how indirect effects, like the meat price of yearlings and females, may spill over to the trophy hunting marked. A novel finding is that trophy hunting may lead to a less sex-skewed harvest pattern than traditional meat hunting.

Key words: Trophy hunting, population model, pulse control
“Hunting is the noblest sport yet devised by the hand of man. There where mighty hunters in
the bible. And all the caves where the cave men lived are full of carvings of assorted game the
head of the house drug home. If you hunt to eat, or hunt for sport for something fine,
something that will make you proud, and make you remember every single detail of the day
you found him and shot him, that is good too” (The Old Man and the Boy, Robert Ruark
1954, p.167)

1. Introduction
Trophy and big game hunting has traditionally been an activity for the rich western elite. The
hunting of American and European aristocrats, movie stars and business tycoons in East
Africa from the last part of the 1900 century and onwards, hiring professional white hunters to
lead them on lengthy, luxurious shooting expeditions, has particularly been well-known
(Roosevelt 1910, Oldfield 2003). However, during the last few decades or so, wildlife is
increasingly entering the marketplace all over the world due to growing wealth and income,
more leisure time and an ever increasing degree of mobility. For example, non-resident
hunters in Alberta pay over $10,000 U.S. in permit and guiding fees to hunt bighorn sheep
males, and even higher amounts are paid for hunting trophy sheep in Asia (Jorgenson et al
1998). Another example from Africa is that 3,640 trophy hunters spent 15,450 hunter-days,
taking 13,310 game animals in Namibia for the hunting season 2000 (Humavindu and Barnes
2003). Therefore, as hunting tourism and trade in wildlife products grow, the traditional meat
versus trophy aspect of wildlife exploitation becomes increasingly important to resource
managers all over the world, in developing as well as industrialised countries (Oldfield 2003,
The Economist November 2006).

Although the income part of trophy hunting seems apparent, it has also given rise to some
concerns about potential ecological as well as social negative impacts. One important reason
for this concern is that while meat hunting and subsistence hunting may typically take a
random sample of the population, sport and trophy hunting of male ungulates has led to sex-
skewed harvest schemes (Ginsberg and Milner-Gulland 1994). See also Milner-Gulland et al.
(2004), Mysterud et al. (2002) and Langvatn and Loison (1999). Another concern is that due
to the big money involved, trophy hunting is often accompanied by criminal activities
(Milner-Gulland and Leader-Williams 1992). For example, the elephant population in the
South Luangwa Area Management Unit in Zambia decreased from 35,000 in 1973 to 15,000
in 1987 due to commercialization of illegal hunting (Jachmann 2003). The magnitude of illegal poaching may also be illustrated by the following example; when CITES began to close down illegal sources and unregulated sources of crocodilian skins, the number of skins in trade was reduced from an estimated peak high of 1.5 million per year to a low of about 500,000 per year (Hutton and Webb 2003).

Despite the growth of hunting tourism, trophy hunting has received a surprisingly little attention in the natural resource economic literature. The exception is the strand of literature that analyses commercialized poaching, often in an East-African context (see e.g., Johannesen and Skonhoft 2005 and the references therein). This literature has without exceptions been concerned with biomass models (‘an elephant is an elephant’). However, to analyse the economics of trophy hunting properly a cohort, or stage structured, model is needed. In the natural resource economic literature there exist some few such models. One example is Clark and Tait (1982) who analysed a sex-selective harvesting in a two stage (male-female) model. Another example is the two-stage seal model in Conrad and Bjørndal (1991). For a general modelling overview, basically from a biological side, see Getz and Haight (1989) and Caswell (2001) while Tahvonen (2008) is a recent contribution from the fishery economic literature.

In the following study, a four-stage (calves, yearlings, adult females and adult males) population model is formulated for a moose population and the dynamics of trophy hunting is analysed. Meat value is included for calves, yearlings and adult females while adult males are hunted for the trophy value only. The analysis is carried out within a Scandinavian ecological and institutional context where the landowner, or a landowner association, manages the population in a given specific area and receive the hunting value. In the present exposition, other cost and benefits components of the landowners, such as forestry browsing damage, are neglected. Other possible values related to the moose population, e.g., costs associated with traffic accidents, are neither taken into account. The moose exploitation is studied when the present-value landowner profit is maximised under two different assumptions of the trophy hunting market; price-taking (PT-scenario) and monopolistic behaviour (MB-scenario). The meat price is assumed fixed under both scenarios. The overall aim of the paper is to address how different market behaviour may lead to different optimal substitution patterns between trophy and meat harvesting, and thereby between different stages of the moose population. Moreover, the ways different economic and ecological forces affect the dynamics of a demographic harvesting model are highlighted.
The paper is organized as follows. In the next section, the four-stage moose population model is presented. Section three demonstrates the analytical solution of the model under the two optimization schemes while section four provides a numerical solution of the model and presents the results, and where especially the dynamic properties of the model are studied. Section five summarizes our findings.

2. Population model
As mentioned, trophy hunting is analyzed for a moose (*Alces alces*) population in 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. The mean slaughter body weight (about 55% of live weight) for adult moose in Scandinavia is about 170 kg for males and 150 kg for females. It is by far the most important game species here, 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 % of the yearly meat consumption in these countries (Statistics Norway 2004, Svenska Jägerförbundet 2006). 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 for a small and modest skew sex composition. However, it may play a role when the male population becomes small accompanied by a skew sex composition (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 $X_{c,t}$, yearlings $X_{y,t}$, adult females $X_{f,t}$, and adult males $X_{m,t}$, so that the total population is $X_{c,t} + X_{y,t} + X_{f,t} + X_{m,t}$. The population is measured in spring before calving. All stages may be 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 adult stages.
Neglecting any stochastic variations in biology and environment, and any possible 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). As mentioned, the fertility rate generally depends on both female density (number of females) and male density. It decreases in the female density $\frac{\partial r}{\partial X_{f,t}} = r'_f < 0$, and it may also be reduced when the number of males becomes 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:

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

The recruitment function may be a one-peaked value function in the female density, i.e., it is of the Ricker type (see section four below), but intuitively $\frac{\partial r}{\partial X_{f,t}} = (r + r'_f X_{f,t}) > 0$ 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 hardly can represent an efficient harvest strategy. This is confirmed by the numerical simulations (section four).

The number of yearlings follows next as:

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

where $s_c$ is the fixed calf natural survival rate (fraction) and $h_{c,t}$ is the calf harvesting rate.

Finally, the abundance of (adult) females and (adult) males become:

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

and

$$
(4) \quad X_{m,t+1} = 0.5 s_y (1 - h_{y,t}) X_{y,t} + s(1 - h_{m,t}) X_{m,t}.
$$
respectively, and where the same sex ratio is assumed for the yearlings when they enter the adult 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:

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

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 exploitation below. Note that it is possible to hunt all adult females in a given year and still get production of calves in the next year. This is because there is an inflow of females from the yearling class which becomes reproductive. For the same reason, it is also possible to hunt all (adult) males.

3. Exploitation

As already indicated, the moose populations in Scandinavia is managed by the landowners, or landowner cooperative associations. The traditional landowner management goal of the Scandinavian moose hunting has, just as harvesting of ungulates many other places, been directed by maximising the meat value. Typically, the hunters have been the local people; the landowners and their families and friends, and the hunting has had some flavour of subsistence hunting. During the last two decades or so, however, a more commercialized hunting and wildlife industry has emerged, and Scandinavian moose hunting is gradually shifting to a game hunting market where trophy hunting of adult males plays an important role (Norges Skogeierforbund 2005). Moose trophy hunting typically means that the hunters not only hunt for the antlers, but also for the weight because this is also an important trophy attribute. Indeed, these two factors are often strongly correlated (Clutton-Brock et al. 1980). Coexisting with the game hunting, meat hunting of the local people still prevails. Therefore, trophy hunting is modelled by assuming that meat-value hunting of the other stages also takes place.
Because natural mortality basically takes place after the hunting season (section two 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 unit meat hunting price is assumed to be independent of the amount harvested and the stock sizes, and is assumed to be fixed over time as well. When further assuming that the cost of the landowners of organizing this hunting is stock independent, the ‘net’ harvest price (in NOK per kilogram) is fixed as $p$. The current meat value is accordingly $p(w_c h_{c,t} X_{c,t} + w_y h_{y,t} X_{y,t} + w_f h_{f,t} X_{f,t})$ and where $w_c < w_y < w_f$ are the (average) body slaughter weights (kilograms per animal) of the calf, yearling and female stages, respectively.

The market demand for male trophy hunting is assumed to be decreasing in the offtake in the standard manner. In addition to price, the demand may also be contingent upon ‘quality’, expressed by the abundance of males in the population$^1$. Typically, both the weight of the animal and the size of the antlers are the main targets of trophy hunters. As for many other terrestrial species, these attributes are mainly associated with males in the moose population. Hence, in general terms, the quality of trophy hunting is dependent on the abundance of males in the population. 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 as $q_t = Q(h_{m,t}X_{m,t}, X_{m,t})$ and where the licence price $q_t$ (NOK per animal) decreases with a higher harvest, $Q'_m = \partial Q / \partial (h_mX_m) < 0$ and increases with more animals available, $Q''_m > 0$, due to the quality effect$^2$.

Supplying trophy-hunting licences is also costly and depends on the number of licenses sold $C_t = C(h_{m,t}X_{m,t})$ 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 no fixed cost, which is assumed in the numerical illustration below, the cost structure is just as under the meat hunting scheme. Therefore, the yearly profit of the landowner is:

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$^1$ See Mattson (1994). In the recreational fishing literature the demand quality effect is explored in many papers (e.g., Anderson 1983).

$^2$ 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. In some areas there are typically many landowners (or landowner cooperative associations) and this pulls in the direction of price taking behaviour, but other places the trophy market may be in the possession of substantial monopoly power. Both these extremes are examined, and the trophy-hunting licences supply is analyzed under monopolistic behaviour (MB-scenario) as well as under price-taking (PT-scenario). We first study the MB-scenario. When the present-value profit is to be maximised, the landowner problem is then hence to find harvest rates that maximises \[ \sum_{t=0}^{\infty} \rho^t \pi_t \] subject to the biological constraints (3) – (5) and taking the downward falling demand schedule into account. \[ \rho = 1/(1 + \delta) \] is the discount factor with \( \delta \geq 0 \) as the (yearly) discount rate, assumed to be fixed. When the calf population is replaced (section two), the current-value Hamiltonian of this problem is:

\[
\psi = p[w_c h_{c,t} X_{c,t} + w_y h_{y,t} X_{y,t} + w_f h_{f,t} X_{f,t}] + Q(h_{m,t} X_{m,t}, X_{m,t}) h_{m,t} X_{m,t} - C(h_{m,t} X_{m,t}) \\
+ \rho \eta_{s,1} [s_c (1 - h_{c,t}) r(X_{f,t}, X_{m,t}) X_{f,t} - X_{y,t}] + \rho \lambda_{s,1} [0.5 s_y (1 - h_{y,t}) X_{y,t} + s(1 - h_{f,t}) X_{f,t} - X_{f,t}] \\
+ \rho \mu_{s,1} [0.5 s_y (1 - h_{y,t}) X_{y,t} + s(1 - h_{m,t}) X_{m,t} - X_{m,t}]
\]

where \( \eta_{s,1} \geq 0 \), \( \lambda_{s,1} \geq 0 \) and \( \mu_{s,1} \geq 0 \) are the shadow prices of the yearlings, female and male populations, respectively. No constraints are explicitly formulated for the harvesting fractions (but see below). The first order conditions of this maximization problem (when \( X_{y,t} > 0 \), \( X_{f,t} > 0 \) and \( X_{m,t} > 0 \)) are:

\[
\frac{\partial \psi}{\partial h_{c,t}} = pw_c - \rho \eta_{s,1} s_c \leq 0 \quad ; \quad 0 \leq h_{c,t} < 1,
\]

\[
\frac{\partial \psi}{\partial h_{y,t}} = pw_y - \rho \lambda_{s,1} 0.5 s_y - \rho \mu_{s,1} 0.5 s_y \leq 0 \quad ; \quad 0 \leq h_{y,t} < 1,
\]
(10) \[ \frac{\partial \psi}{\partial h_{f,j}} = pw_j - \rho \lambda_{v+1}s \leq 0 ; 0 \leq h_{f,j} < 1 , \]

(11) \[ \frac{\partial \psi}{\partial h_{m,t}} = Q''_{m} X_{m,t} h_{m,t} + q_{t} - C' - \rho \mu_{v+1}s = 0 ; 0 < h_{m,t} < 1 , \]

(12) \[-\frac{\partial \psi}{\partial X_{y,t}} = -pw_{y,t}h_{y,t} + \rho \eta_{v+1} - \rho \lambda_{v+1}0.5s_{y}(1-h_{y,t}) - \rho \mu_{v+1}0.5s_{y}(1-h_{y,t}) = \rho \eta_{v+1} - \eta_{t}, \]

(13) \[-\frac{\partial \psi}{\partial X_{f,t}} = -pw_{f, t}h_{f,t}(r + r'_{f} X_{f,t}) - pw_{f, t}h_{f,t} - \rho \eta_{v+1}s_{t}(1-h_{c,t})(r + r'_{f} X_{f,t}) + \rho \lambda_{v+1} - \rho \lambda_{v+1}s(1-h_{f,t}) = \rho \lambda_{v+1} - \lambda_{t} \]

and

(14) \[-\frac{\partial \Psi}{\partial X_{m,t}} = -pw_{c,t}h_{c,t}r'_{m} X_{f,t} - Q''_{m}h_{m,t}2X_{m,t} - q_{t}h_{m,t} + C' h_{m,t} - Q'_{m} h_{m,t}X_{m,t} - \rho \eta_{v+1}s_{t}(1-h_{c,t})r'_{m} X_{f,t} - \rho \mu_{v+1}s(1-h_{m,t}) + \rho \mu_{v+1} = \rho \mu_{v+1} - \mu_{t}. \]

Conditions (8)–(11) are the control conditions with the actual complementary slackness conditions stated and where the possibility for keeping each of the stages, except the male population, unexploited is considered. Condition (8) says that calf harvest should take up to the point where marginal harvest income is equal to, or below, the cost in terms of reduced yearling growth evaluated at its shadow price. Condition (9) indicates that harvesting of the yearlings should take place up to the point where the marginal meat income is equal to, or below, the cost in terms of reduced population of males and females, evaluated at their respective shadow prices. When it holds as an inequality, the marginal benefit is below its marginal cost and harvesting is thus not profitable, \( h_{f,t} = 0 \). The female condition (10) is simpler as reduced stock growth works only through its own stage. The male condition (11) is analogous to the female harvesting condition, but the marginal benefit is no longer meat income, but trophy hunting profit supplied under monopolistic condition\(^3\). Equations (12)-(14) are the portfolio conditions and steer the shadow price values. These conditions essentially

\(^3\) 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 \((Q''_{m} X_{m,t} h_{m,t} + q_{t} - C') > pw_{m}\) where \( w_{m} \) is the per animal adult male weight.
state that the number of the different categories of animals should be maintained so that natural growth is equal to the shadow price growth, adjusted for the discount factor.

In addition, as indicated, the exploitation is also studied when price taking prevails in the trophy hunting market (PT-scenario). This solution is interesting for various reasons, not at least because it gives a comparison as to whether the MB-scenario may give rise to a too sex skewed distribution of harvest. It is easily recognized that the first order conditions of this problem will be just as above except that the first order condition for male harvest reduces to:

\[(11') \quad q_t - C' - \rho \mu_{t,s} s = 0 \quad ; \quad 0 < h_m < 1.\]

In a time discrete system like this, with three state variables (and four controls) it is difficult, if not impossible, to say very much analytically about the dynamics of the optimal solution. Therefore, we have to rely on numerical solutions. However, some few points can be made. First of all, we may suspect that the trophy hunting demand quality effect, *ceteris paribus*, may lead to a higher male population and hence work in the direction of a higher male-female sex ratio than without this effect. We may also suspect that the MB-scenario yields a higher male-female ratio than the PT-scenario because taking the downward sloping demand schedule into account typically work in the direction of less aggressive male harvesting. More important, we may also infer that hunting of the calf and yearling stages will not take place. This can be demonstrated as follows. Suppose that \( h_{x,t} > 0 \) and \( h_{f,t} = 0 \) while male harvest always takes place, \( h_{m,t} > 0 \). Combination of equations (9) – (11) then yields

\[ pw_x > 0.5(s_x / s)(pw_f + Q_{it} X_{m,t} h_{m,t} + q_t - C'). \]

As trophy hunting is assumed to be more profitable than male meat hunting (cf. footnote 3), this inequality may also be written as \( w_x > 0.5(s_x / s)(w_f + w_m) \). Because adult and yearling survival rates \( s \) and \( s_y \) are more or less identical (numerical section) and the yearling weight is below that of the females, which again is below that of the males, \( w_x < w_f < w_m \) (again, see numerical section), we find that the above inequality represents a contradiction. Yearling harvest together with zero female harvest (and positive male harvest) is thus not possible following the logic of the optimization. In a similar manner, it can also be shown that zero male and positive female harvest together with positive yearling harvest will contradict the optimality conditions. As \( w_x < w_f \) and the calf survival rate
is lower than that of the other stages, we will also find that calf harvest is not profitable. Therefore, adult harvest only takes place when the landowner aims to maximise the combined meat value and trophy hunting profit under monopolistic behaviour. This will also be so within the PT-scenario.

4. Numerical results

*Data and specific functional forms*

The exploitation 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. The function reads:

\[
(15) \quad r_i = r(X_{f,i}, X_{m,i}) = \frac{\tilde{r}}{1 + (X_{f,i} / K)^b}(1 - e^{-aX_{m,i}})
\]

with \(\tilde{r} > 0\) as the intrinsic growth rate (maximum number of calves per female). The fecundity rate 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. This parameter scales the population sizes, and its value is contingent upon factors like the size of the area, the biological productivity of the grazing and browsing resources, etc. The compensation parameter \(b > 0\) indicates to what extent density-independent effects compensate for changes in the stock size. Equation (15) implies a recruitment function

\[
X_{c,i} = r(X_{f,i}, X_{m,i})X_{f,i} = \tilde{r}(1 - e^{-aX_{m,i}})X_{f,i}/[1 + (X_{f,i} / K)^b]
\]

and is of the so-called Shepherd type. With \(b > 1\), which is assumed, we have the Ricker version meaning that \(\partial X_{c,i} / \partial X_{f,i} < 0\) for a high female density. However, as already indicated (section two), \(\partial X_{c,i} / \partial X_{f,i} > 0\) will hold in the optimal harvest programme and the recruitment function is concave\(^4\). It should be noted that this specification implies that there are rapidly decreasing returns to scale on males in reproductive production. Relatively few males are needed for the production of calves.

\(^4\) Differentiation yields \(\partial X_{c,i} / \partial X_{f,i} = [K^b + (1 - b)X_{f,i}^b](1 - e^{-aX_{m,i}})/(K^b + X_{f,i}^b)^2\). Moreover, we find \(\partial^2 X_{c,i} / \partial X_{f,i}^2 = -v[(b + 1)K^b + (1 - b)X_{f,i}^b]\) where the coefficient \(v\) collects terms and is positive. It is easily recognized that \(\partial X_{c,i} / \partial X_{f,i} > 0\) implies \(\partial^2 X_{c,i} / \partial X_{f,i}^2 < 0\) and hence a strictly concave recruitment function.
The trophy inverse 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:

\begin{equation}
q_i = \alpha e^{x_{n,i}} - \beta h_{m,i} X_{m,i}.
\end{equation}

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:

\begin{equation}
C_i = \bar{c} + c h_{m,i} X_{m,i}
\end{equation}

so that $\bar{c} \geq 0$ is the fixed cost, assumed to be zero, and $c > 0$ is the constant marginal cost. The cost structure is therefore assumed to be identical in trophy and meat hunting as the meat hunting price $p$, as mentioned, is considered as a ‘net’ price. Table 1 gives the baseline parameter values.

Table 1 about here

Results

The results are first shown for the two scenarios under the baseline parameter values. Next, some comparative dynamics are shown where the values of some of the crucial model parameters are changed. The model is solved for a long time horizon, but in most cases only the results for the first 40 years are reported.

We first present the results for the optimal harvest rates (fractions). One important aspect of the solution is that the optimal harvest rates for calves and yearlings are zero all the time. As explained above (section three), the reason for this is that the weights of these stages are

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5 The optimization was performed with the Premium Solver, an extended version of the Solver tool bundled with Microsoft Excel.

6 The model is solved for 70 years. The long horizon ensures that the reported solutions will be numerically indistinguishable from the infinite horizon solution over the reported period of 40 years. See Naevdal (2003) for an elaboration on this approach.
below that of the adult while the meat price (NOK per kilogram) is the same; that is, the adult stages have a higher per animal value. Figure 1 demonstrates what happens to the adults. The harvest rates for males and females are strikingly different. Perhaps surprisingly, the harvest rate of females exhibit pulse harvesting both under the MB- and PT-scenario while the male harvest exhibits oscillations. The possibility of pulse harvesting is an intrinsic feature of resource management models with an age-structured formulation (see, e.g., Clark 1990, Ch. 9) and the solution has therefore similarities with the optimal management of trees, cf. the Faustmann harvesting rule. The harvest rate of males exhibit oscillations because the reproductive productivity of males is affected by the stock of females. If the stock of females is low, the reduction in reproduction can partly be compensated by allowing a greater stock of males. This explains why the harvest rate of males decreases during and/or just after a pulse of intense harvesting of females. This also explains why the male harvest rate peaks between the pulses. As the number of females is high, few male moose are needed to ensure high rates of reproduction whereas during harvest of females, more efficient reproduction is ensured by allowing a higher stock of males.

Note that Clark (1990, p.298-301) primary argues that pulse harvesting relies upon imperfect harvest selectivity across cohorts, which is certainly not the situation in our model. Tahvonen (2008) also finds pulse harvesting under imperfect selectivity. Clark (p. 294) also notes that zero harvest costs (or more generally zero marginal harvest costs) combined with stock independent recruitment can contribute to pulse behaviour. In our model, pulse harvesting is caused by the dynamic interaction between a downward sloping demand curve for male adult moose and the dominant role of females in producing yearlings. The fact that there is a downward sloping demand curve for hunting males implies that, except for very low stock levels, there will always be a positive marginal profit from harvesting adult males. These low levels will not be manifest along an optimal path except initially when starting from very low levels. Females will however be more valuable when producing calves than when hunted for meat. However, when the stock of calves and yearlings reach above a certain threshold, there is a sufficient number of female yearlings to maintain the male stock and supply new adult females for a few years. To see this it is important to note that the stock and harvest rates of adult males are barely affected by the pulse harvesting of adult females. The mathematical explanation is that the Hamiltonian is strictly concave in \( h_{m,t} \) and one would therefore often expect to see an interior solution. However, the Hamiltonian is linear in \( h_{f,t} \) which gives rise to a bang-bang control.
When comparing the two management scenarios, it is evident that the male hunting is much less aggressive under the MB-scenario than the PT-scenario. This is in line with what one often finds in natural resource models when the market power of the supplier(s) is exploited. Perhaps surprising, however, we find that the hunting of females is less aggressive under the PT- than under MB-scenario. This may again be explained by their contribution to reproduction. When males are hunted aggressively under the PT-scenario, the landowner compensates by hunting fewer females in order to ensure the desired levels of reproduction.

Table 2 and Figure 2 reports the number of males and females under both scenarios. As a benchmark, a no-hunting scenario is included in Table 2 as well. Since the yearlings enter the (adult) male and female stages at the same sex ratio (section two), the number of males and females are the same without hunting. It is first noticed that without hunting male and female populations converge smoothly towards a steady state whereas hunting implies oscillating stocks. Second, it is seen that the number of males and females with few exceptions is substantially lower with hunting than without hunting. This is necessarily not so for the calf and the yearling population due to the fact that the no-hunting scenario implies a female population located to the right hand side of the peak value of the recruitment function (for the baseline parameter values, see Table 1 and footnote 4, the recruitment function peaks at $X_f = 2,000$).

Figure 3 shows more clearly the adult sex ratio. The sex ratio fluctuates under both scenarios. However, under the MB-scenario there are episodes with a low male to female ratio whereas the ratio is consistently above one under the PT-scenario. We may therefore conclude that by including simple economic forces into the biological picture, the concern with trophy hunting leading to high male harvest and a sex-skewed harvest may be misleading. The key mechanism is that trophy hunting is connected to a quality, or density dependent, demand effect. If present, this demand force gives the resource manager an incentive to increase the
male stock (trophy stock) at the sacrifice of the total meat production. Hence, relative harvest rates in trophy hunting may be more in accordance with natural selection than traditional meat hunting if the manager takes this demand force into account (see also below)\textsuperscript{7}.

Figure 3 about here

An important finding is that pulse harvesting and the oscillating sex ratios are caused by the trophy hunting. To see this, we have also included a case with meat hunting for males as well under the MB-scenario. Figure 4 indicates then a Most Rapid Approach Path (MRAP), but with some degree of undershooting, for adult males and a saddle-point path for the female stock. Therefore, females are initially hunted at a low rate until a desired steady state stock is reached while males initially are hunted aggressively. It is therefore important to note that even if it is the age structured population model that facilitates cyclic harvesting patterns, this is not a sufficient condition for this to occur. Rather, it is the combination of an age structured model and trophy hunting with a downward sloping demand curve that generates this result through the trophy-induced concavity of the Hamiltonian in male harvest.

Figure 4 about here

The robustness of the results is examined by changing some of the key parameter values. Figure 5 first demonstrates what happens to the adult harvest rates when the meat price shifts under the MB-scenario. A higher meat hunting price spills over to trophy hunting through a relatively lower profitability of this hunting. As seen, the effects of a 50% price hike are almost negligible, but males are harvested somewhat less aggressively. However, the difference is so small that it may be explained by the inherent uncertainties in numerical optimization methods. The basic pulse pattern of the female harvest rate persists all the time and is somewhat strengthened under the price hike.

Figure 5 about here

Next, it is examined what happens when the trophy hunting demand quality effect is neglected; that is, the parameter value $\gamma$ equals zero. As expected, this lead to more aggressive

\textsuperscript{7} Natural selection refers here to a random mortality rate with respect to gender.
harvest patterns for male moose. This is confirmed by Figure 6 where it is seen that the male stock size is significantly lowered without the quality effect in the MB-scenario.

The male demand quality effect has, however, in principle an ambiguous effect on the female stock. On the one hand, the higher male stock in the presence of a quality effect implies that average female reproductive productivity decreases. On the other hand, marginal reproductive productivity may increase and imply a less aggressive hunting strategy for females. As it turns out, it is this last effect that dominates, and the absence of the quality effect leads to a slightly smaller female stock as well. However, overall, the difference seems to be of negligible magnitude in this case. See Figure 7.

The effects of a changed discount rate $\delta$ were studied as well, but these effects are small and negligible within the reasonable range of values. The same happens for the parameter $a$ governing the male population fertility density effect. These results are not reported here, but are available from the authors on request. The results are finally analysed under three different sets of initial conditions $X_m = X_f = 200, 400$ and 600 under the MB-scenario and baseline parameter values, and where 600 coincides with the previous simulations. The results are shown in Figure 8. The figure clearly indicates that the male stock appears to exhibit oscillations and that the differences caused by different initial conditions to some extent are maintained. The female stock also appears to settle in a cyclic pattern in all cases. However again it is unclear whether the cycles will converge or not as discrepancies caused by different initial conditions are preserved. It is however clear that if there is convergence, this will happen beyond the planning horizon for both the male and female stock.\(^8\)

5. Concluding remarks

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\(^8\) No convergence is clearly discernible even if the time horizon is extended to the limit of the solvers capacity.
The paper has analysed a four-stage model of the Scandinavian moose population with density-dependent fertility and density independent mortality. The moose population is managed by a landowner (or a landowner association). Trophy hunting is the motive for the male harvest while calves, yearlings and females are harvested for their meat value. The exploitation is studied under two stylized extremes of the market for trophy hunting; monopoly behaviour (MB-scenario) and price-taking (PT-scenario). The meat hunting price is all the time assumed to be fixed and independent of the amount harvested of these stages. Under both scenarios the present-value profit is maximised. The different ways to compose the harvest, e.g. in yearlings or females, and why the different scenarios require different composition of the harvest, are highlighted. Such knowledge is disregarded in the traditional bioeconomic modelling approach.

The numerical results show that zero calf and yearling harvest are accompanied by male and female harvests that fluctuate widely over time under both scenarios. The female harvest exhibits pulse (or cyclic) harvesting while the male harvest exhibits oscillations. The reason for this is that the reproductive productivity of males is affected by the stock of females. If the stock of females is low, the reduction in reproduction can partly be compensated by allowing a greater stock of males. This explains why the harvest rate of males decreases during and/or just after a pulse of intense harvesting of females. The pulse harvesting and the oscillating male-female sex ratios are caused by trophy hunting with a downward sloping demand curve as meat hunting only of all stages yields a dynamics of the Most Rapid Approach Path (MRAP) for the male adults while it is of the saddle-path type for the female stock. This mechanism for pulse harvesting is different compared to what is found in the existing literature. For example, Wirl (1995) analysing a fishery biomass model with two types of capital (the fish fleet, in addition to fish), finds that a positive externality from the stock of fish may cause pulse harvesting while Liski et al. (2001), also using a biomass model, demonstrates pulse harvesting due to scale economics. Clark (1990) argues that pulse harvesting in cohort models relies upon imperfect harvest selectivity across cohorts, and Tahvonen (2008) also demonstrates pulse harvesting under imperfect selectivity. In contrast to this, we assume perfect selectivity. The robustness of our numerical results is examined by changing some of the key parameter values. A shifting meat hunting price, rate of discount and the parameter governing the male fertility effect yields small, if not negligible effects. On the other hand, when the trophy hunting demand quality effect is neglected we find a more
aggressive harvest pattern for male moose. However, all the time female harvest is governed by pulse harvesting.

We also find that the concern with trophy hunting leading to high male harvest and a sex-skewed harvest may be misleading. Thus, the traditional meat maximisation regimes advocated by biologists for a number of species during the past decades may under reasonable assumptions be far more sex-selective than a true trophy hunting regime. The key mechanism is that trophy hunting may be connected to a quality, or density dependent, demand effect. If present, this demand force gives the resource manager an incentive to increase the male stock (trophy stock) at the sacrifice of the total meat production. Hence, relative harvest rates in trophy hunting may be more in accordance with natural selection than traditional meat hunting if the manager takes this demand force into account.

References


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F. Wirl 1995. The cyclical exploitation of renewable resource stocks may be optimal. \textit{Journal of Environmental Economics and Management} 29, 252-261
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### Table 2: Number of females and males under different scenarios

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Figure 1: Harvest rates under MB- and PT-scenario
Figure 2: Number of female and male adults under MB- and PT-scenario
Figure 3: Male/female ratio under MB- and PT-scenario
Figure 4: Harvest rates when harvesting for meat value only
Figure 5: Harvest rates under different meat prices, MB-scenario
Figure 6: Number of adult males with and without preferences for quality, MB-scenario
Figure 7: Number of females with and without preferences for quality, MB-scenario
Figure 8: Number of male and female adults under varying initial conditions, MB-scenario