A bioeconomic model of trophy hunting

"Hunting is the noblest sport yet devised by the hand of man. There were 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 have traditionally been an activity for the *elite* in society. The hiring of professional white hunters to lead lengthy and luxurious shooting expeditions in East Africa for aristocrats, movie stars and business tycoons from the last part of the 19th century onwards is particularly renowned (Roosevelt 1910, Oldfield 2003). However, during the last few decades, this type of wildlife hunting has become increasingly accessible to many people throughout the world because of growing wealth and income, increasing leisure time and greater than ever mobility. For example, nonresident hunters in Alberta pay in excess of US$10,000 in permit and guiding fees to hunt male bighorn sheep, with even higher amounts paid for hunting trophy sheep in Asia (Jorgenson et al. 1998). Another example from Africa is that in the 2000 hunting season, 3,640 trophy hunters spent 15,450 hunter-days, taking 13,310 game animals in Namibia (Humavindu and Barnes 2003). Currently, trophy hunting takes place in 23 African countries (see Lindsey et al. 2006 for an overview). Therefore, as hunting tourism and the trade in wildlife products grow, the traditional meat versus trophy aspect of wildlife exploitation has become increasingly important to resource managers in both developing and industrialized countries (Oldfield 2003, The Economist November 2006).

Studies analyzing the biological effects of trophy hunting include goats in Alberta, Canada, where the trophy horns are the main object of hunters (Hamel et al. 2006). Similarly, Withman et al. (2007) consider the population viability effects of trophy hunting selection for lions in Tanzania. Parts of this biological literature have also given rise to some concerns about the potential negative ecological impacts of hunting. One important reason for this concern is that while meat and subsistence hunting typically takes a random sample of the hunted population, the trophy hunting of male ungulates has led to a skewed harvest scheme, whereby males are harvested more aggressively (Ginsberg and Milner-Gulland 1994). See also Milner-Gulland et al. (2004), Mysterud et al. (2002) and Langvatn and Loison (1999). Another concern, also studied in the applied ecological literature, is that because of the large amounts of money involved, criminal activity often accompanies trophy hunting (Milner-Gulland and Leader-Williams 1992).

Unfortunately, despite the rapid and sustained growth of hunting tourism, trophy hunting has received surprisingly little attention in the natural resource economic literature. The exception is the strand of literature following the work of Milner-Gulland and Leader-Williams (1992) that analyses poaching, often in an East African context (see, e.g., Johannesen and Skonhoft 2005 and the references therein). Without exception, this body of work has been concerned with biomass models (‘an elephant is an elephant’). However, to analyze the economics of trophy hunting properly, a cohort or age-structured model is required. In the natural resource economic literature, few such models exist. One example is Clark and Tait (1982), who analyzed sex-selective harvesting in a two-stage (male–female) model. Another example is the two-stage seal model in Conrad and Bjørndal (1991). See also the seminal work in Reed (1980) and a recent important contribution from the fishery economic literature in Tahvonen (2009). For a more general modeling overview from a biological perspective, see Getz and Haight (1989) and Caswell (2001).

In the following study, we formulate a four-stage (calves, yearlings, adult females and adult males) model for a population of moose and analyze the dynamics of trophy hunting. In this model, meat value is included for calves, yearlings and adult females, while the hunting of adult males is for trophy value. The trophy hunt is more valuable than hunting this stage only for meat because the meat is included in the trophy hunt as a byproduct. We carry out the analysis within a Scandinavian ecological and institutional context where the landowner (or landowner association) manages the population in a given specific area and receives the hunting value. In the present exposition, we omit any other cost and benefit components of landowners, such as forestry browsing damage. We also do not take into account other possible values relevant to the moose population, e.g., the costs associated with traffic accidents caused by moose.

In this analysis, we consider the exploitation of moose where the present value of landowner profit is maximized under two different assumptions concerning the trophy hunting market- namely, a price taking (PT) scenario and a monopolistic behavior (MB) scenario. The MB scenario is considered as the baseline scenario (section 3). Under both scenarios, the price of meat is assumed fixed. In the biological model, females, as well as the abundance of males, regulate fertility. However, in an extended model, we incorporate feedbacks where animals respond to hunting pressure by adapting their behavior to reduce harvest exposure. This is in line with recent ecological theory where animals respond cognitively to threats in their environment, and where this interaction often is described in terms of competition for scarce resources (such as food and mating opportunities, see Naevdal 2008 for a survey and a discussion of resource economic implications). There is a small economic literature on how animal behavior adapts to human activity and how this affects management, see, e.g., Pethig and Tschirhart (2001) and Finnoff and Tschirhart (2003a; 2003b), who examine animals as maximizers of net energy intake. Guttormsen et al. (2008) also analyzes adaptation through genetic selection mechanisms. In our extended model, we highlight a particular adaptation, whereby female moose adapt to hunting pressure by increasing vigilance, thereby lowering the risk of predation (Bowyer et al. 1999, White and Feller 2001). However, increased vigilance does come at the cost of reduced foraging effort, and this harms fecundity.

The overall aim of our paper is to address how different market behavior and biological conditions may lead to different optimal substitution patterns between trophy and meat harvesting, and thereby between different stages of the moose population. The focus is on the harvest composition, and the sex ratio of adult females to males. Moreover, we show how the population dynamics may be affected. The paper is organized as follows. In Section 2, we present the four-stage moose population model. Section 3 demonstrates the analytical solution of the model under the two optimization schemes while Section 4 provides a numerical solution. In Section 5, we develop the extended model where hunting impacts upon fertility. While we do discuss the changing analytical structure compared with the basic biological model, because of its complexity, our main consideration is numerical, especially the changing dynamic properties, and how the adult sex ratio is affected. Section 6 summarizes our findings.

2. Population model

As discussed, we analyze trophy hunting 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 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 in Scandinavia, with about 35,000 and 100,000 animals shot every year in Norway and Sweden alone, respectively. The value of this harvest is substantial, and the meat counts for more than 2% of yearly meat consumption in these countries (Statistics Norway 2004, Svenska Jägerförbundet 2006). The natural mortality rates are generally low because of a lack of predators, and there is no evidence of density-dependent mortality. That said, fecundity has proven to be affected by the female density while the number of males appears to be of negligible importance for a small and modestly skewed sex composition, i.e., when the male and female density do not differ too much. However, it may play a role with a small male population accompanied by a skewed sex composition (e.g., Nilsen et al. 2005 and Mysterud et al. 2002).

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 ($yr \geq 2$) $X_{m,t}$, such that the total population (measured in the spring before calving) is $X_t = X_{c,t} + X_{y,t} + X_{f,t} + X_{m,t}$. We assume all stages can be harvested, and hunting takes place in September–October. Natural mortality is assumed to take place during the winter, after the hunting season, as the natural mortality throughout the summer and fall is negligible. We impose the same natural mortality rate for both males and females, and an equal sex ratio assumed for yearlings when they enter the adult stages.

Neglecting any stochastic variations in biology and environment, and any possible dispersal into and out of the area considered, 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 (the number of calves per female). As discussed above, the fertility rate generally depends on both female and male density (the numbers of females and males). It decreases in female density $\partial r / \partial X_{f,t} = r'_f < 0$ and 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) $$X_{c,t} = r(X_{f,t}, X_{m,t})X_{f,t}.$$

The recruitment function starting from the origin may be a one-peaked value function in the female density, i.e., being of the Ricker type (see Section 4 below), though $\partial X_{c,t} / \partial X_{f,t} = (r + r'_f\ X_{f,t}) > 0$ should intuitively hold in an optimal harvesting program, at least when females represent only meat hunting value and hence no positive stock value (e.g., non-use value) is included. If not, less female hunting coincides with less recruitment, which can hardly represent an efficient harvest strategy. This is confirmed in the numerical illustrations in Section 4. As indicated, in Section 5 we extend the recruitment function to take into account the situation where hunting pressure may influence fecundity (and hence, the fertility rate).

Next, the number of yearlings is:

(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 respective abundance of (adult) females and (adult) males becomes:

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

and

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

where the same sex ratio (0.5) is assumed for yearlings when they enter the adult stages, s is the fixed natural survival rate (also identical for females and males), and s_y is the yearling survival rate. The variables $h_{y,t}$, $h_{f,t}$ and $h_{m,t}$ are the harvesting rates of yearlings, adult females and males, respectively.

The population model (1)–(4) has a recursive structure, such that 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) are a reduced-form model in three stages where all equations are first-order difference equations. We employ this form when studying exploitation below. Note that it is possible to hunt all adult females in a given year and still obtain the production of calves in the next year. This is because there is an inflow of females from the yearling class as it becomes reproductive. For the same reason, it is also possible to hunt all (adult) males. However, if this happens over a period of time, we find that the adults in the long term will be individuals of age two only, and this may lead to evolutionary drift causing, say, lower calf weight (e.g., Solberg et al. 2009). Therefore, we restrict the adult harvest rates to be below one. The calf and yearling harvest rates are also restricted to be less than one to omit stock depletion.

In biological equilibrium, it is a direct relationship between the harvesting rates and stock sizes. When combining equations (3) – (4) in biological equilibrium (or steady state), $X_{i,t+1} = X_{i,t} = X_i$ and $h_{i,t+1} = h_{i,t} = h_i$ $(i = f, m)$, we hence find the male – female sex ratio as $X_m / X_f = [1 - s(1 - h_f)] / [1 - s(1 - h_m)]$. Therefore, in steady state, sex – skewed adult harvesting rates translate directly into sex – skewed adult abundance.

3. Exploitation

As already discussed, landowners or landowner cooperative associations manage the moose population in Scandinavia. The traditional landowner management goal of Scandinavian moose hunting—just as with the harvesting of ungulates in many other places—has been to select a harvesting composition aimed at maximizing the meat value. Typically, hunters have been the local people (landowners and their families and friends) and so moose hunting in Scandinavia has traditionally been executed for personal consumption of meat. However, during the last two decades or so, a more market oriented hunting and wildlife industry has emerged, and Scandinavian moose hunting has gradually shifted to a game hunting market where the trophy hunting of adult males plays a more important role (Norges Skogeierforbund 2005). Moose trophy hunting typically means that the hunters not only hunt for antlers, but also for weight, because this is also an important trophy attribute. Indeed, these two factors are often strongly correlated (Clutton-Brock et al. 1980). Coexisting with game hunting, the meat hunting of the local people still continues. Therefore, we model trophy hunting by assuming that meat-value hunting in the other stages also takes place.

Because natural mortality basically takes place after the hunting season (see Section 2), 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

$H_{m,t} = h_{m,t} X_{m,t}$. We assume the unit meat-hunting price is independent of the amount harvested and the stock size, and fixed over time. When further assuming that the cost for the landowners organizing the hunting is stock independent, the 'net' harvest price (in NOK per kilogram) is fixed as p.[1] Accordingly, the current meat value is $p(w_c h_{c,t} X_{c,t} + w_y h_{y,t} X_{y,t} + w_f h_{f,t} X_{f,t})$, where $w_c < w_y < w_f$ are the (average) body slaughter weights (kilograms per animal) in the calf, yearling and female stages, respectively (see also Table 1).

In the more commercialized marked for male trophy hunting, we assume the market demand to be decreasing in the offtake (see also Johansson et al. 1988). In addition to price, demand may also be contingent upon 'quality', as expressed by the abundance of males in the population. A high density of males may be attractive for several reasons. First, it gives hunters the option to choose between different males based on their differencing characteristics (including antler size, skin, and weight). Second, and related to the first reason, the male density increases the number of shooting possibilities ("action") during a given hunting day. Finally, it also reduces the time (hunting days) required to shoot a trophy male.[2] Following Scandinavian practice, where one license allows the buyer to kill one animal (paid only if the animal is killed, cf. Footnote 1), the inverse market demand for male hunting licenses is written as $q_t = Q(h_{m,t} X_{m,t}, X_{m,t})$, where the license price q_t (NOK per animal) decreases with a higher harvest, $Q'_H = \partial Q / \partial (h_m X_m) < 0$, and increases with the availability of male animals, $Q'_X > 0$, because of the quality effect.[3] Therefore, the quality effect works partially in the direction that the landowner will find it beneficial to keep more male animals.

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[1] Following Scandinavian practice, the hunters participating in the traditional hunting for meat activity first buy a licence from the landowner. One licence allows the hunter to shoot one animal (e.g., one yearling), but is paid only if the animal is killed. The final payment is a payment per kilo of the moose actually shot. Hussain and Tschirhart (2010) describe a far more complicated licence-price system for elk hunting in the US.

[2] Mattson (1990) recognized this demand quality effect in moose hunting in Sweden. In the recreational fishing literature, many studies explore the demand quality effect (see, e.g., Anderson 1983), where it is modeled as a stock externality through the average size of fish caught. McConnell and Sutinen (1979) develop another biomass model including the same quality attribute, but where an age-structured model explicitly accounts for the quality aspect. However, these models consider the demand for fishing trips, not the harvest. On the other hand, in seminal work by Bishop and Samples (1980), the focus is on harvests, not fishing trips, where the net benefit per pound of recreational catch increases with the stock size. The male stock density effect modeled here works in an analogous way by increasing the hunting quality, *ceteris paribus*.

[3] It may appear unrealistic that the quality demand effect draws on the *current* period male density, not on, say, the density in the previous year. However, this assumption is justified by the fact that the monitoring of the moose stock is usually during the spring and summer, before hunting starts.

Supplying trophy hunting licenses 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 the various transportation services. With $C'' = 0$ and no fixed cost, which is assumed in the numerical illustration given below, the cost structure is as for the meat hunting scheme. Therefore, the yearly profit of the landowner is:

(6) $$\pi_t = p(w_c h_{c,t} X_{c,t} + w_y h_{y,t} X_{y,t} + w_f h_{f,t} X_{,t}) + Q(h_{m,t}X_{m,t}, X_{m,t})h_{m,t}X_{m,t} - C(h_{m,t}X_{m,t})\,.$$

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 behavior, but in other places the trophy market may be in possession of substantial monopoly power. We consider both of these extremes by analyzing trophy-hunting license supply under both monopolistic behavior (the MB scenario) and price-taking behavior (the PT scenario). Because Scandinavian moose trophy hunting still is in its infancy (Norges Skogeierforbund 2005), the MB scenario is considered as the baseline scenario.

We first examine the MB scenario. When the present value of profit is to be maximized, the landowner problem is then to find harvest rates that maximize $\sum_0^\infty \rho^t \pi_t$ subject to the biological constraints (3)–(5) while taking the downward sloping demand schedule into account. Here, $\rho = 1/(1+\delta)$ is the discount factor with $\delta \geq 0$ as the (yearly) discount rate, assumed fixed. When the calf population is replaced (see Section 2), the current value Hamiltonian of this problem is written as:

(7)
$$\begin{aligned}\psi &= p[w_c h_{c,t} r(X_{f,t}, X_{m,t})X_{f,t} + w_y h_{y,t} X_{y,t} + w_f h_{f,t} X_{f,t}] + Q(h_{m,t}X_{m,t}, X_{m,t})h_{m,t}X_{m,t} - C(h_{m,t}X_{m,t}) \\ &+ \rho\eta_{t+1}\left[s_c(1-h_{c,t})r(X_{f,t}, X_{m,t})X_{f,t} - X_{y,t}\right] + \rho\lambda_{t+1}\left[0.5s_y(1-h_{y,t})X_{y,t} + s(1-h_{f,t})X_{f,t} - X_{f,t}\right] \\ &+ \rho\mu_{t+1}[0.5s_y(1-h_{y,t})X_{y,t} + s(1-h_{m,t})X_{m,t} - X_{m,t}]\end{aligned},$$

where $\eta_t > 0$, $\lambda_t > 0$ and $\mu_t > 0$ are the shadow prices of the yearling, female and male populations, respectively. We formulate no explicit constraints for the harvesting fractions (but see below). The first-order necessary conditions of this maximization problem (when $X_{y,t} > 0$, $X_{f,t} > 0$ and $X_{m,t} > 0$) are then:

$$\partial\psi / \partial h_{c,t} = rX_{f,t}(pw_c - \rho\eta_{t+1}s_c) \leq 0\,;\;\; 0 \leq h_{c,t} < 1\,, \tag{8}$$

$$\partial\psi / \partial h_{y,t} = X_{y,t}(pw_y - \rho\lambda_{t+1}0.5s_y - \rho\mu_{t+1}0.5s_y) \leq 0\;;\;\; 0 \leq h_{y,t} < 1\,, \tag{9}$$

$$\partial\psi / \partial h_{f,t} = X_{f,t}(pw_f - \rho\lambda_{t+1}s) \leq 0\;\;;\; 0 \leq h_{f,t} < 1\,, \tag{10}$$

$$\partial\psi / \partial h_{m,t} = X_{m,t}(Q'_H X_{m,t}h_{m,t} + q_t - C' - \rho\mu_{t+1}s) \leq 0\;\;;\; 0 \leq h_{m,t} < 1\,, \tag{11}$$

$$-\partial\psi / \partial X_{y,t} = -pw_y h_{y,t} + \rho\eta_{t+1} - \rho\lambda_{t+1}0.5s_y(1 - h_{y,t}) - \rho\mu_{t+1}0.5s_y(1 - h_{y,t}) = \rho\eta_{t+1} - \eta_t\,, \tag{12}$$

$$\begin{aligned} -\partial\psi / \partial X_{f,t} = {} & -pw_c h_{c,t}(r + r'_f X_{f,t}) - pw_f h_{f,t} - \rho\eta_{t+1}s_c(1 - h_{c,t})(r + r'_f X_{f,t}) \\ & + \rho\lambda_{t+1} - \rho\lambda_{t+1}s(1 - h_{f,t}) = \rho\lambda_{t+1} - \lambda_t\,, \end{aligned} \tag{13}$$

and

$$\begin{aligned} -\partial\Psi / \partial X_{m,t} = {} & -pw_c h_{c,t} r'_m X_{f,t} - Q'_H h_{m,t}^2 X_{m,t} - q_t h_{m,t} - Q'_X h_{m,t} X_{m,t} + C' h_{m,t} \\ & - \rho\eta_{t+1}s_c(1 - h_{c,t}) r'_m X_{f,t} - \rho\mu_{t+1}s(1 - h_{m,t}) + \rho\mu_{t+1} = \rho\mu_{t+1} - \mu_t\,. \end{aligned} \tag{14}$$

Conditions (8)–(11) are the control conditions with the actual complementary slackness (Kuhn–Tucker) conditions stated and where the possibility for keeping each of the stages unexploited is considered while harvesting down whole subpopulations is not assumed a possible option (Section 2). Condition (8) states that the calf harvest should take place up to the point where the marginal harvest income is equal or below the cost, in terms of the reduced yearling growth evaluated at its shadow price. When this holds as an inequality, the marginal benefit is below the marginal cost and harvesting is thus not profitable, $h_{c,t} = 0$. Condition (9) indicates that the harvesting of yearlings should take place up to the point where the marginal meat income is equal or below the cost, in terms of the reduced population of males and females evaluated at their respective shadow prices. When this holds as an inequality, we also find a zero harvest, $h_{y,t} = 0$. The female condition (10) is simpler as the reduced stock growth works only through the female stage. Hence, females should be harvested up to the point where the marginal meat income is equal, or below, the cost in terms of reduced stock growth evaluated at the female shadow price. The male condition (11) is analogous to the female harvesting condition. However, the marginal benefit is no longer meat income, rather trophy hunting profit supplied under monopolistic conditions. With no harvest, equations (10) and (11) also hold as inequalities. Equations (12)–(14) are the stock portfolio conditions. The yearling stock condition (12) may also be written as

$\eta_t = pw_y h_{y,t} + \rho\lambda_{t+1} 0.5 s_y (1-h_{y,t}) + \rho\mu_{t+1} 0.5 s_y (1-h_{y,t})$. This condition states that the number of yearlings should be maintained such that the shadow price of yearlings equalizes the meat value of an additional animal at the margin, and its growth contribution to the adult stages, again evaluated at their shadow prices, where discounting is also taken into account. The remaining stock portfolio conditions (13)–(14) can be given similar interpretations.

In addition, and as indicated, we also study exploitation when price taking prevails in the trophy hunting market (the PT scenario). This solution is interesting for a number of reasons, not least because it provides a comparison as to whether the MB scenario potentially gives rise to an excessively high ratio of adult males to females. We can easily recognize that the first-order conditions of this problem are as above, with the exception that the first-order condition for male harvest reduces to:

(11’) $$X_{m,t}(q_t - C' - \rho\mu_{t+1}s) \le 0 \;\; ; \;\; 0 \le h_m < 1,$$

while the male portfolio condition (14) reads:

(14’) $$\begin{aligned} -\partial\Psi / \partial X_{m,t} &= -pw_c h_{c,t} r'_m X_{f,t} - q_t h_{m,t} + C' h_{m,t} \\ &\quad - \rho\eta_{t+1} s_c (1-h_{c,t}) r'_m X_{f,t} - \rho\mu_{t+1} s(1-h_{m,t}) + \rho\mu_{t+1} = \rho\mu_{t+1} - \mu_t . \end{aligned}$$

These first-order conditions, together with the biological constraints, comprise a complex dynamic system with ten unknowns and ten equations in both scenarios. Therefore, it is difficult, if not impossible, to assess the dynamics analytically, and we must rely on numerical solutions. However, it is possible to say something about the harvesting composition in the optimal solution. To see this, we first ask whether it is more likely to harvest calves, yearlings or both stages. These stages may essentially be considered as substitutes because both activities reduce the female and male stock, and we find under which conditions a positive calf harvest cannot be optimal suggested that there is no yearling harvest. It turns out that this will be the case as long as $w_c / s_c > w_y \rho$ does not hold.[4] When $w_c = w_y$, this inequality is satisfied. Furthermore, if $w_c < w_y$ and additionally s_c and $\rho = 1/(1+\delta)$ are sufficiently low,

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[4] The inequality is derived as follows: With zero yearling harvest, $h_{y,t} = 0$, the yearling portfolio condition (12) writes $\eta_t = \rho\lambda_{t+1} 0.5 s_y + \rho\mu_{t+1} 0.5 s_y$, while the yearling control condition (9) holds as an inequality, $pw_y < \rho\lambda_{t+1} 0.5 s_y + \rho\mu_{t+1} 0.5 s_y$. These two conditions yields $\eta_t > pw_y$. When using the calf control condition (8) under the assumption of a positive harvest together with the above inequality, we next find $(1/\rho s_c) w_c > w_y$, or $w_c / s_c > w_y \rho$. That is, a higher ‘biological discounted’ value of the calf age class than the economic discounted value of the yearlings.

this inequality may still hold. However, this outcome is not likely because of the substantial higher weight and more valuable yearling harvest than calf harvest, and the high survival rate of the calves (see Table 1 numerical section). In fact, it only holds under unrealistically high discount rate values.[5] We can then conclude that the above inequality implies a contradiction under realistic parameter values. Therefore, suggested that there is no yearling harvest, it can not be beneficial to harvest the calf population.

Next, we explore under which conditions it is uneconomical to harvest yearlings. This occurs when the adult and yearling survival rates s and s_y ('biological discount rates') are not to different and the yearling weight is below that of females, which again is below that of males, $w_y < w_f < w_m$ (Table 1). To see this, suppose first that yearling, but also female and male harvest, take place; that is, $h_{y,t} > 0$, $h_{f,t} > 0$ and $h_{m,t} > 0$. All the control conditions (9)–(11) in the MB scenario then hold as equations. Combining these equations (with positive stock sizes) yields $pw_y = 0.5(s_y / s)(pw_f + Q_H' X_{m,t} h_{m,t} + q_t - C')$. As the trophy hunting price is higher than the male meat value, $(Q_H' X_{m,t} h_{m,t} + q_t - C') > pw_m$, the above equality implies $w_y > 0.5(s_y / s)(w_f + w_m)$. Note first that if we assume $w_y = w_f = w_m$, the inequality holds, suggested that $s_y < s$. Furthermore, if $w_y < w_f < w_m$, and additionally if s_y is sufficiently lower than s, the inequality still holds. However, in the specific case of moose hunting in Scandinavia considered here, this outcome seems very unlikely. We hence find that under realistic parameter values the above inequality represents a contradiction.

In a similar manner, we find that a positive yearling harvest together with zero male and positive female harvest yields $pw_y > 0.5(s_y / s)(pw_f + Q_H' X_{m,t} h_{m,t} + q_t - C')$, which again contradicts the optimality conditions for realistic parameter values. The assumption of a positive yearling harvest together with a positive male and zero female harvest also yields the same inequality and again contradicts the optimality conditions for realistic parameter values. This will also be the case for a positive yearling harvest together with a zero female and zero male harvest. We can hence conclude that a positive yearling harvest does not make economic sense under the assumption of a more profitable trophy hunting than (male) meat hunting. Therefore, under the given structure of the parameter values harvesting of calves and

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[5] For the parameter values in Table 1 (numerical section), it holds if $\delta > 0.87$ (or 87%).

yearlings together with zero adult harvesting is uneconomical under the MB scenario. Note that this is not merely a steady-state property, it holds for all t. We also find the same in the PT scenario, given the assumption that trophy hunting is more profitable than meat hunting $(q_t - C') > pw_m$.

On the other hand, we find that zero yearling harvest together with positive harvest of one, or both, of the adult categories do not contradict the optimality conditions. The reason for this outcome, in line with the above reasoning, is simply that the per animal values are higher for the adults than the yearling category while the survival rates do not differ too much.[6] However, based on the above optimality conditions it is difficult to say something definitely about the harvest composition among the adults. There are two obvious tradeoffs involved here. First, a direct economic effect works through the relative valuation of females and males, and where trophy hunting is more profitable than meat hunting (if not, there would clearly be meat hunting only). Secondly, both stages contribute to reproduction, but males are superfluous unless they become very few (see Section 2 above). The direct economic effect of trophy hunting on the harvest rate of males is clearly ambiguous. A high per animal value gives incentives to aggressive male harvest while the quality effect working through the male stock size gives incentives to boost the male stock. Therefore, if the quality effect in the trophy demand function is weak and of minor importance, both the economic value and the fertility difference between males and females typically pulls in the direction of more aggressive male than female harvesting. On the other hand, if the quality effect in trophy demand is strong and dominates, the economic effect pulls in the direction of less aggressive adult male harvest compared to females and hence a possible high male – female sex ratio.

4. Numerical results

Data and specific functional forms

We now illustrate this process of exploitation numerically. We specify the fecundity rate, decreasing in the number of females, as a sigmoidal function with an increasing degree of density dependence at high densities. In addition, it shifts outwards with more males. The function reads:

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[6] The similarity with the findings in the seminal Reed (1980) paper is apparent. Reed studies a simpler, static model where only age classes are included. He finds that the differences in the weight – survival ratio (or ‘biological discounted’ biomass content) of the various harvestable age classes determines the maximum sustainable yield fishing composition.

(15) $$r_t = r(X_{f,t}, X_{m,t}) = \frac{\tilde{r}(1-e^{-aX_{m,t}})}{1+(X_{f,t}/K)^b},$$

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 the density-dependent fertility is equal to the 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 such as the size of the area, and the biological productivity of the grazing and browsing resources. The compensation parameter $b > 0$ indicates to what extent the density-independent effects compensate for changes in the stock size. Equation (15) implies a recruitment function $X_{c,t} = r(X_{f,t}, X_{m,t})X_{f,t} = \tilde{r}(1-e^{-aX_{m,t}})X_{f,t}/[1+(X_{f,t}/K)^b]$ and is of the so-called Shepherd type. With $b > 1$, as assumed, we have the Ricker version, meaning that $\partial X_{c,t}/\partial X_{f,t} < 0$ for a high female density. However, as already argued (Section 2), $\partial X_{c,t}/\partial X_{f,t} > 0$ should hold in an optimal harvest program and the recruitment function is then strictly concave in the number of females.[7] Note also that this specification for realistic values of a implies that there are rapidly decreasing returns to scale for males in terms of reproductive production. That is, few males are needed for the production of calves. For the baseline parameter values (Table 1), we find that only about 250 males are sufficient to secure full reproduction; that is, more males have no longer any effect on the fertility rate.

This formulation (15) is a compromise with Nilsen et al. (2005), where the total density of animals regulates the fertility rate for the youngest mature females, while the sex ratio between all mature males and females also plays a role for the fertility rate of older females. This compromise is due to the fact that we do not separate between different age classes of adult females. Altogether, Nilsen et al. (2005) consider sixteen age classes for each sex. See

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[7] Differentiation yields $\partial X_{c,t}/\partial X_{f,t} = [K^b + (1-b)X_{f,t}{}^b](1-e^{-aX_{m,t}})/(K^b + X_{f,t}{}^b]^2$. Moreover, we find $\partial^2 X_{c,t}/\partial X_{f,t}{}^2 = -v[(b+1)K^b + (1-b)X_{f,t}{}^b]$, where the coefficient v collects terms and is positive. It is easily recognized that $\partial X_{c,t}/\partial X_{f,t} > 0$ implies $\partial^2 X_{c,t}/\partial X_{f,t}{}^2 < 0$. The recruitment function is also strictly concave in the number of males.

also Saether et al. (2001) and Mysterud et al. (2002) for a review of the role of males in ungulate reproduction.[8]

We specify a linear trophy inverse demand function. In addition, we assume that the quality effect, as given by the number of males through the parameter $\gamma \geq 0$, shifts the demand function uniformly upwards:

(16) $$q_t = \alpha e^{\gamma X_{m,t}} - \beta h_{m,t} X_{m,t} .$$

Accordingly, the choke price $\alpha > 0$ provides 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 also given linear:

(17) $$C_t = \bar{c} + c h_{m,t} X_{m,t} ,$$

such that $\bar{c} \geq 0$ is the fixed cost, assumed zero, and $c > 0$ is the constant marginal cost. Therefore, the cost structure is identical in trophy and meat hunting as the meat-hunting price p, as discussed, is a 'net' price. Table 1 shows the baseline parameter values. Some of these values, including the trophy hunting demand parameters, are calibrated and based on qualified guesswork. With a zero quality effect, the choke price is assumed to be 30,000 (NOK/animal). For the baseline quality demand effect of $\gamma = 0.0001$, this means that a male animal number of, say, 3,000, indicates a quality-adjusted choke price of about 40,500 (NOK/animal). The biological parameters are generally based on solid evidence. Note again that the parameter K in the fecundity function scales the population size.

Table 1 about here

Results

We first provide the results for the two scenarios under the baseline parameter values. We then present the comparative dynamics where the values of some of the crucial model parameters are changed. While we solve the model over a long time horizon, we only report the results for the first 40 years.[9,10]

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[8] Mysterud et al. (2002, p. 907) states: 'In general, even in harvested populations with highly skewed sex ratios, males are usually able to fertilize all females, though detailed studies document a lower proportion of younger females breeding when sex ratios are heavily female biased.'

[9] The optimization was performed with the fmincon solver, supplied in the Optimization Toolbox for recent versions of Matlab.

The results for the optimal harvest rates (fractions) are presented first. One important aspect of the solution is that the optimal harvest rates for calves and yearlings are zero all of the time. As explained in Section 3, the basic rationale is that the per animal values are higher for the adults than calf and yearlings while the survival rates do not differ too much. Figure 1 demonstrates what happens to the adults. As shown, the dynamics have similarities with saddle paths, but with some small initial oscillations for the male harvest rate. Importantly, the steady state harvest rates for males and females are different with higher rates of females than males. Moreover, while the steady states for females are more or less equal under the MB and PT scenarios, the harvesting of males, perhaps not surprisingly, is significantly less aggressive under the MB scenario than the PT scenario. These results indicate a skewed sex ratio with a high ratio of males, and this will particularly be so under the MB scenario (more details below).

Figure 1 about here

Table 2 reports the number of males and females under both scenarios, and where the resulting adult sex ratios more directly can be observed. A no-hunting scenario is also included in Table 2. Given the yearlings enter the (adult) male and female stages at the same sex ratio (Section 2), the number of males and females are the same without hunting. First, without hunting, the male and female populations converge smoothly towards the steady state. Second, with hunting, the populations also converge smoothly towards the steady state, but the numbers of males and particularly females are substantially lower than without hunting. However, this does not necessarily apply for the calf and yearling populations because of 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 (the recruitment function peaks at $X_{f,t} = K = 2{,}000$, see Footnote 7, and Table 1). Under the MB scenario, we find a steady state male – female sex ratio of $X_m / X_f = 4{,}420/1{,}727 = 2.56$ while it becomes 1.41 under the PT scenario.[11] As explained above (Section 2), it is direct relationship between sex skewed harvesting rates and sex skewed stock composition in steady state. Hence, under the

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[10] We solve the model over 70 years. This long horizon ensures that the reported solutions will be numerically indistinguishable from the infinite horizon solution over the reported period of 40 years. The results over 70 years are available from the authors upon request.

[11] Notice that the steady state is still not reached for the male stock size after 40 years in the MB as well as in the PT scenario. This is also so for the male harvesting rate, cf. Figure 1.

MB scenario we have
$X_m / X_f = [1 - s(1 - h_f)] / [1 - s(1 - h_m)] = [1 - 0.95(1 - 0.24)] / [1 - 0.95(1 - 0.06)] = 2.56$.

Table 2 about here

As already indicated, few males are required to secure full reproduction. Therefore, the skewed sex-ratio can not be explained by the specification of the recruitment function.[12] The high male – female sex ratio hinges critically on the fact that a high male stock boosts profitability for the landowners, both under the PT scenario, but particularly under the MB scenario. It simply pays to keep a large male population to be rewarded with a high trophy hunting price. Under the MB scenario, we find a steady state trophy hunting price of *q*= 29,800 (NOK/animal) while it becomes *q*=15,440 under the PT scenario. Both these values are within the range of actual trophy hunting prices in Scandinavia (Skogeierforbundet 2005 and Sylvén 1995). Note also that these values are substantially higher than the male meat value since we have $pw_m =$ 50x170= 8,500 (NOK/animal) (Table 1).

We examine the robustness of the results by changing some of the key parameters values. The effect of omitting the trophy hunting demand quality effect is first considered; that is, the parameter value γ equals zero while all the other parameters are kept at their baseline values. Figure 2 demonstrates what happens under the MB scenario. As explained above (section 3), $\gamma = 0$ leads to a more aggressive male harvesting. The male – female steady state sex ratio hence reduces dramatically from its previous value of $X_m / X_f = 2.56$ to $X_m / X_f = 611/1622 = 0.38$, comprising $h_m = 0.30$ and $h_f = 0.08$. Somewhat surprisingly, we find that the number of males hunted is lower without than with the quality effect; that is, 611*0.30=183 when $\gamma = 0$ compared to 4420*0.06= 265 when the quality effect is included. On the other hand, the steady state trophy hunting license price becomes substantial lower when $\gamma = 0$ as the movement along the demand function is dominated by the quality demand shift effect. The price reduces from $q =$29,800 to 20,890 (NOK/animal). As also explained

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[12] We have also tested how sensitive our results are to the formulation of the recruitment function. If we instead use the sex ratio term for older females and the parameter values from Nilsen et al. (2005) (and Saether et al. 2001); that is, the term $(1 - e^{-aX_{m,t}})$ in our recruitment function (15) is replaced by $(1 - e^{-aX_{m,t}/X_{f,t}})$, we find the same sex-ratio pattern. With the *a* value from Saether et al. (2001) and Nilsen et al. (2005) of 6.9 and 10.0, respectively, and using our baseline parameter values, the male – female sex ratio becomes 2.38 in both cases (1.36 in the PT scenario).

above, changes in the reproductive pattern plays a minor role as the decreasing number of males has only a negligible effect on the average and marginal female reproduction. Notice also that the number of females reduces only modestly without the quality effect in the MB scenario; from its previous steady state value of 1,727 to 1,622 animals without the quality effect. Hence, when including the demand quality effect, we find no support for the concern in the biological literature that trophy hunting may lead to a sex-skewed harvesting pattern where males are harvested aggressively (cf. the introductory section). This general picture also holds under the alternate PT scenario. Indeed, our results point in the direct opposite direction with high male – female ratios, accompanied by high, but realistic, trophy hunting prices.

Figure 2 about here

Next, we observe what happens to the adult harvest rates when the meat price p shifts under both scenarios. A higher price of meat hunting spills over to trophy hunting through the relatively lower profitability of the latter form. However, we find the effects of a 50% price hike to be almost negligible, although the harvest of males is now somewhat less aggressive under the MB scenario as well as the PT scenario. Therefore, the adult sex ratio is only modestly affected under both scenarios. We also considered the effects of changes in the discount rate δ, but these effects are also negligible within a reasonable range of values. The same happens, not surprisingly, for the parameter a governing the male fertility density effect.

On the other hand, the effects of changing adult mortality rates were more notable. Decreasing the male survival rate from 0.95 to 0.90 while keeping female survival rate at 0.95 has a considerable effect on male harvest rates, increasing the steady state harvest rate from 0.06 to about 0.28. Further, it became optimal to harvest yearlings at the significant rate of $h_y = 0.46$. This is in line with standard resource economic theory where reduced growth rate of a resource is accompanied by more aggressive harvesting. What is surprising is the magnitude of the effect where increased male mortality appears to completely crowd out the quality effect of a large moose stock. However, it is optimal to compensate with a lower harvesting rate of females, which ensures that calf production remains high. Indeed, the increased male mortality implies a reduced steady state female harvest rate from $h_f = 0.25$ to

0.11. This compensation ensures that calf production remains almost unchanged with a reduction of the steady state calf stock slightly less than 2%.

Decreasing the female survival rate from 0.95 to 0.9 does interestingly not affect the optimal harvest of males in any numerically significant way. As long as the male mortality rate is sufficiently low, it pays to maintain a high stock to keep the trophy price high. Interestingly, the increased mortality of females does not lead to more aggressive female harvesting, but instead to a slightly lowered harvest rate. In this case, the meat value of females and the decrease in survival rate induces the manager to compensate by reducing female harvest rates so that a profitable stock of males can be maintained. This also implies that it is still optimal not harvest calves and yearlings. These and the other sensitivity results are available in more detail from the authors upon request.

5. Incorporating the ecological theory of animal adaptation into harvesting

In the population model in Section 2, fertility is only governed by female and male abundance. Here we explore the implications of ecological results where animals respond behaviorally to predation risk. This literature is huge, but Ericsson and Wallin (1997), White and Feller (2001), White and Berger (2001), Ripple and Beschta (2006) are studies of general ungulate responses to predator risk. Bowyer et al. (1999) and Laurian et al. (2000) examine responses to human hunting efforts. All these papers indicate that increased presence of predators, including human hunting pressure, induces animals to exhibit more vigilance and mobility. Both of these activities affect reproductive productivity, particularly for females. Vigilance and mobility are both costly in terms of ecological reproductive fitness in that they both reduce the time spent on foraging. If females forage less they are less able to produce and support healthy off-spring. Mobility is also costly, and possibly reduces mating opportunities for the animal involved. This obviously has implications for management, as the effect of harvesting in one year is to reduce the productivity of females the next year.

In what follows, we consider this in a simplified manner where we assume that the total harvest pressure experienced in the *previous* year negatively affects the fecundity rate; that is, $r_t = r(X_{f,t}, X_{m,t}, h_{t-1})$ with $r'_h < 0$ and where h_{t-1} indicates the hunting pressure in the previous year. The reason for lagging the harvest pressure effect is obvious, as the previous year's mating governs the current year's fertility. This is because, as outlined in Section 2, calves are newborn in early spring while hunting takes place in the fall. When expressing the hunting pressure simply by the sum of the harvest rates for all stages, the fecundity rate (15) is now:

$$(15') \qquad r_t = r(X_{f,t}, X_{m,t}, h_{t-1}) = \frac{\tilde{r}\left(1-e^{-aX_{m,t}}\right)}{1+\left(\frac{X_{f,t}}{K}e^{\theta(h_{c,t-1}+h_{y,t-1}+h_{f,t-1}+h_{m,t-1})}\right)^{b}},$$

where $\theta > 0$ is a parameter indicating how the hunting pressure translates into reduced fertility, and where a higher value indicates a larger reduction.[13] This is a key parameter and as will be seen, the feedback effect from hunting working through θ may cause oscillations.[14]

When applying this extended fecundity rate, the analytical results discussed in Section 3 change. First, we find that the previous control conditions (8) - (11) now are replaced by conditions where the stock variables are included such that the number of animals directly influences which of the different categories of animals it is beneficial to harvest. [15] Therefore, not only differences in the per animal values and the survival rates (‘biological discounted’ values) determine the harvest composition in the extended model. Moreover, stock and control variables, as well as the shadow prices, are included at different points of time. The portfolio conditions (12) - (14) also become progressively more complicated than in the previous model. For all these reasons, we cannot exclude the possibility that the yearling and calf harvest can be an optimal option. Because of, among other things, the lag structure in the new control conditions working through θ, we may also as indicated find that the dynamics no longer converge smoothly towards a steady state. These new control and portfolio conditions are available from the authors upon request.

Generally, we find the numerical results to be strikingly different from those previously reported in Section 4, especially as oscillating harvest rates (OHRs) now emerge. Figure 3 indicates this under the MB scenario showing the female harvesting rates, where OHRs become evident when the described fertility effect becomes ‘strong’, i.e., for $\theta = 0.25$.

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[13] A micro-based model analyzing this fertility effect is available from the authors on request.

[14] However, the introduction of this harvesting pressure effect has, within our chosen parameter range values, modest effect on the fertility rate. At the steady state under the MB-scenario, without the harvesting pressure effect (Table 2 and Figure 1), the fecundity rate becomes $r = 0.66$ .With animal adoption to harvesting and $\theta = 0.25$ (see main text below), the fecundity rate reduces to $r = 0.61$, given the same stock sizes and harvest rates.

[15] The male stock was also included in the previous control condition (11). However, it could be omitted because trophy hunting is more profitable than male meat hunting.

However, for the baseline parameter values, Figure 4 indicates that there is no evidence of oscillating harvesting of males and there are almost negligible changes of the harvesting rate compared to the previous situation. While, as mentioned, the possibility of calf harvest cannot be excluded, we still find that there is no harvest of this category.

Figure 3 about here

Figure 4 about here

The possibility of an OHR is an intrinsic feature of resource management models with an age-structured formulation (see, e.g., Clark 1990, Ch. 9) and demonstrated empirically in Diekert et al. (2010).[16] In general, our situation differs but still relates to Clark's (1990) discussion of nonselective gear. In our specific extended case, the spillover from harvest is stronger as it affects the next year's female fecundity rate directly. Therefore, OHRs are a way of managing the productivity of females. Harvesting affects fertility, but is reversible. If the harvesting effect is strong, it then pays to divide the possible harvest into periods without harvesting and those with aggressive harvesting. By not harvesting, females are lulled into the belief they are safe and fecundity increases. It results that if this effect is sufficiently strong, it is profitable to harvest females in cycles, and this can cause cycles in yearlings as well (see below). Of course, this may appear as a trivial result directly related to the functional form imposed. However, note that the total harvest pressure affects female fecundity, and hence, the cyclical harvesting of one of the other stages instead of females would *a priori* be just as likely. The intuition why this takes places for females is as follows. The male trophy effect provides an incentive to boost the male stock as before through the stock quality effect. In turn, we can achieve a high male stock through both a zero yearling harvest and a low female harvest. By not harvesting any females in a given year, the male stock subsequently builds up. At the same time, the female stock also builds up and requires a higher harvest rate the following year to keep the female stock below the peak of the recruitment function. Hence, to avoid this; that is, to keep the total harvest pressure low on average, it is optimal to harvest the yearling stock aggressively in the same year. Hence, there are two goals of harvesting: one is to keep the fecundity effect as small as possible to keep average harvest pressure low, and the other is

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[16] In the literature, OHRs are sometimes referred to as 'pulse harvesting'. Indeed, Clark (1990) treats the terms synonymously in the sense that harvesting is heavy at regular intervals, separated by periods of no or little harvesting.

to keep the male stock high. When harvesting females, we then need to keep the yearling harvest at a minimum to ensure recruitment to the next year's male stock.

Formally, our results are similar to those derived theoretically in Wirl (1992). The modification of (15) into (15') introduces quite a few interaction terms between the control variables and state variables such that cross-derivatives have considerable numerical magnitude (see also above). Wirl (1992) shows that under these conditions, cyclical movements in state-variables become more likely exacerbated by bounds on the control variables. However, the results in Wirl (1992) only apply to problems with two-state variables and one control variable. The derivation of the exact analytical results for when oscillating harvesting or cycles appear in problems with additional state variables is beyond the scope of this paper.

One would expect that the females' behavioral adaptation to hunting pressure would affect the relative values of males and females and therefore affect the sex ratio. As higher θ implies less fecund females, the marginal value of the female stock is reduced and harvesting of females should therefore decrease. However, the OHR for $\theta = 0.25$ implies that the male to female sex ratio should also oscillate. Figure 5 confirms this. In the present model the effect of θ on the sex-ratio is modest. Increasing it from 0 to 0.1 has only negligible effect. Increasing it further to 0.25 does imply that the sex ratio fluctuates, but in this case the ratio fluctuates in a stable manner around the underlying trend.

Figure 5 about here

6. Concluding remarks

We have in this paper analyzed 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 landowner association) where 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 behavior (the MB scenario) and price taking (the PT scenario), and where the MB-scenario is considered as the baseline scenario because trophy hunting is still in its infancy. The meat hunting price is assumed to be independent of the amount harvested in any of these stages. Under both scenarios, the present value profit is maximized. The different ways to compose the harvest (e.g., in terms of males or females) are highlighted. Such knowledge is disregarded in the traditional bioeconomic modeling approach.

In line with the theoretical analysis of the baseline model where fertility is only governed by female and male abundance, the numerical results show that a zero calf and yearling harvest are accompanied by male and female harvest. Trophy hunting boosts the male population, particularly under the MB scenario, and we find a high male – female steady state sex ratio. Therefore, concerns expressed in the biological literature that trophy hunting leads to a high male harvest and a sex-skewed harvest may be misleading. The main reason is that we are considering a management scheme with well defined property rights and not of the 'open-access' type, and where the key mechanism in our model is that trophy hunting is connected to a quality, or density-dependent, demand effect. When present, this demand force gives the resource manager an incentive to boost the male stock (trophy stock) at the sacrifice of total meat production. The robustness of these numerical results is examined by changing some of the key parameter values. A changing meat hunting price, rate of discount, and the parameter governing the male fertility effect yield small, if not almost negligible, effects. In contrast, when the trophy hunting demand quality effect is disregarded, we find a substantially more aggressive harvesting pattern for male moose and the male – female sex ratio reduces drastically.

In an extended model where the total hunting pressure is assumed to influence the biology negatively through a lagged effect on recruitment, the numerical dynamic results turn out to be strikingly different as the dynamics now are characterized by oscillating harvest rates (OHR) of females. We still find a high male female sex ratio when the trophy demand quality effect is included. Our mechanisms for cyclical harvesting have similarities with the results derived theoretically in Wirl (1992), but unlike what is found in most of the existing literature. See, e.g., Wirl 1995, Liski et al. 2001, and Tahvonen 2009 who demonstrates pulse harvesting under imperfect selectivity, and Aadland (2003) who find cycles in an age structured cattle model with price expectations.

References

Anderson, L., 1983. The demand curve for recreational fishing with an application to stock enhancement activities. Land Economics 59, 279-287.

Anderson, T. L., Hill, P.J., 1995. Wildlife in the marketplace. Rowman and Littlefield, Lanham.

Bishop, R.C., Samples, K., 1980. Sport and commercial fishing conflicts: A theoretical analysis. Journal of Environmental Economics and Management 7, 220-233.

Bowyer, R., van Ballenberghe, V., Kie, J. G., Maier, J.A., 1999. Birth-site selection by Alaskan moose: Maternal strategies for coping with a risky environment, Journal of Mammalogy 80, 1070–1083.

Caswell, H., 2001. Matrix Population Models. Sinauer, Boston

Clark, C., 1990. Mathematical Bioeconomics. Optimal Management of Renewable Resources, Wiley, New York, 2nd ed.

Clark, C., Tait, D., 1982. Sex-selective harvesting of wildlife populations. Ecological Modelling 14, 251-260.

Clutton-Brock, T.H., Albon, S., Harvey, P., 1980. Antlers, body size and breeding group size in Cervidae. Nature 285, 565-567.

Conrad, J., Bjørndal, T., 1991. A bioeconomic model of the harp seal in the Northwest Atlantic. Land Economics 67, 158-171.

Diekert, D., Hjermann, O., Naevdal, E., Stenseth, N.C., 2010. Spare the young fish: Optimal harvesting policies for north-East arctic cod. Environmental and Resource Economics 47, 455-474.

Ericsson G., Wallin, K., 1997. The Impact of Hunting on Moose Movements. Alces 32, 31-40.

Finnoff, D., Tschirhart, J., 2003a. Harvesting in an eight-species ecosystem. Journal of Environmental Economics and Management 45, 589–611.

Finnoff, D., Tschirhart, J., 2003b. Protecting an endangered species while harvesting its prey in a general equilibrium ecosystem model. Land Economics 79, 160–180.

Getz, A., Haigh, R.G., 1989. Population Harvesting. Princeton University Press, Princeton.

Ginsberg, J. R., Milner-Gulland, E. J., 1994. Sex-biased harvesting and population dynamics in ungulates: Implications for conservation and sustainable use. Conservation Biology 8, 157-166.

Guttormsen, A., Kristofersson, D., Naevdal, E., 2008. Optimal management of renewable resources with Darwinian selection induced by harvesting. Journal of Environmental Economics and Management 56, 167–179.

Hamel, S., Côtè, S., Smith, K., Festa-Bianchet, M., 2006. Population Dynamics and Harvest Potential of Mountain Goat Herds in Alberta. Journal of Wildlife Management 70, 1044-1053.

Humavindu, M. N., Barnes, J., 2003. Trophy hunting in the Namibian economy: an assessment. South African Journal of Wildlife Research 33, 65-70.

Hussain, A., Tschirhart, T., 2010. Optimal harvest licensing when harvest success is uncertain. American Journal of Agricultural Economics 92, 125-140.

Johannesen, A. B., Skonhoft, A., 2005. Tourism, poaching and wildlife conservation: What can integrated conservation and development projects accomplish? Resource and Energy Economics 27, 208-226.

Johansson, P. O., Kriström, B., Mattsson, L., 1988. How is the willingness to pay for moose hunting affected by the stock of moose? An Empirical study of moose hunting in the County of Västerbotten. Journal of Environmental Management 26. 163-171.

Jorgenson, J., Festa-Bianchet. M., Wishart, W., 1998. Effects of population density on horne development in Bighorne Rams. Journal of Wildlife Management 62, 1011-1020.

Lande, R., Engen, S., Saether, B. E., 2003. Stochastic population dynamics in ecology and conservation. Oxford University Press, Oxford.

Langvatn, R., Loison, A., 1999. Consequences of harvesting on age-structure, sex ratio and population dynamics of red deer Cervus elaphus in central Norway. Wildlife Biology 5, 213-223.

Laurian , C., Ouellet, J. P., Courtois, R., Breton, L., St-Onge, S., 2000. Effects of Intensive Harvesting on Moose Reproduction. Journal of Applied Ecology, 37, 515–531.

Lindsey, P. A., Frank, L.G., Alexander, R., Mathiesen. A., Romañach, S. S., 2006. Trophy hunting and conservation in Africa: Problems and one potential solution. Conservation Biology 21, 880-883.

Liski, H., Kort. P., Novak, A., 2001. Increasing returns and cycles in fishing. Resource and Energy Economics 23, 241-258.

Mattsson, L., 1990. Moose management and the economic value of hunting: Towards bioeconomic analysis. Scandinavian Journal of Forest Research 5, 575-581.

McConnell, K. E., Sutinen, J., 1979. Bioeconomic models of marine recreational fishing. Journal of Environmental Economics and Management 6, 127-139.

Milner-Gulland, E. J., Leader-Williams, N., 1992. A model of incentives for the illegal exploitation of Black Rhinos and Elephants: poaching pays in Luangwa Valley, Zambia. Journal of Applied Ecology 29, 338-401.

Milner-Gulland, E. J., Coulson, T., Clutton-Brock, T., 2004. Sex differences and data quality as determinants of income from hunting red deer Cervus elaphus. Wildlife Biology 10, 167-180.

Mysterud, A., Coulson, T., Stenseth, N. C., 2002. The role of males in the dynamics of ungulate populations. Journal of Animal Ecology 71, 907-915.

Nilsen, E., Pettersen, T., Gundersen, H., Mysterud, A., Milner, J., Solberg, E., Andreassen, H., Stenseth, N.C., 2005. Moose harvesting strategies in the presence of wolves. Spatially structured populations. Journal of Applied Ecology 42, 389-399.

Norges Skogeierforbund, 2005. Markedet for jaktopplevelser. Oslo

Naevdal, E., 2008. Animal rationality and implications for resource management: the case of biological reserves for moose and pine, Journal of Bioeconomics, 10, 145-163.

Oldfield, S. (ed.), 2003. The Trade in Wildlife. Regulation for Conservation. Earthscan Publications Ltd, London.

Pethig, R., Tschirhart, J., 2001. Microfoundations of population dynamics. Journal of Bioeconomics, 3, 27-49.

Reed, W., 1980. Optimal age-specific harvesting in a nonlinear population model. Biometrics 36, 579-593.

Roosevelt, T., 1910. African Game Trails: an account of the African wanderings of an American hunter-naturalist. St Martins Press.

Ripple, W., Beschta, R., 2006. Linking wolves to willows via risk-sensitive foraging by ungulates in the northern Yellowstone ecosystem, Forest Ecology and Management 230, 96-106.

Saether, B. E., Engen, S., Solberg, E., 2001. Optimal Harvest of age-structured populations of moose *Alces alces* in a fluctuating environment. Wildlife Biology 7, 171-179.

Solberg, E., Røed, K., Flagstad, Ø., Saether, B. E., Heim, M., Andersen, R., Rolandsen, C., 2009. The genetic structure of moose in Norway. NINA Report 467, Trondheim

SSB Statistics Norway, 2004 Hunting Statistics, Oslo.

Svenska Jägerförbundet 2006. Artspresentasjon Älg.

http://www.jagareforbundet.se/viltvetande/artpresentation/alg.asp

Sylvèn, S., 1995. Moose harvest strategy to maximize yield value for multiple goal management. A simulation study. Agricultural Systems 49, 277-298

Tahvonen, O., 2009. Economics of harvesting age-structured fish populations. Journal of Environmental Economics and Management 58, 281-299.

The Economist, 2006. A palpable hit. November 18th 2006, page 41.

Wirl, F., 1992. Cyclical strategies in two-dimensional optimal control models: necessary conditions and existence. Annals of Operations Research 37, 345-356.

Wirl, F., 1995. The cyclical exploitation of renewable resource stocks may be optimal. Journal of Environmental Economics and Management 29, 252-261.

White, K. S., Berger, J., 2001. Antipredator Strategies of Alaskan Moose: are Maternal Trade-offs Influenced by Offspring Activity? Canadian Journal of Zoology 79, 2055-2062.

White, C. A., Feller, M., 2001. Predation risk and elk-aspen foraging patterns. USDA Forest Service Proceedings, RMRS-P-18. 2001.

Withman, K., Starfield, A., Quadling, H., Packer, C., 2007. Modeling the effects of trophy selection and environmental disturbances on a simulated population of African lions. Conservation Biology 21, 591-601.

Aadland, D., 2003. Cattle cycles, hetrogeneous expectations and the age distribution of capital. Journal of Economic Dynamics and Control 2004, 1977 – 2002.

Table 1: Biological and economic baseline 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	2,000 animals	Scales the population sizes
b	density compensation parameter	2	Nilsen et al. (2005)
a	male population density effect	0.007	Calibrated from Nilsen et al. (2005)
w_c	average weight calf	65 kg	SSB (2004)
w_y	average weight yearling	135 kg	SSB (2004)
w_f	average weight female	150 kg	SSB (2004)
w_m	average weight male	170 kg	SSB (2004)
s_c	natural survival calf	0.90	Nilsen et al. (2005)
s_y	natural survival yearling	0.95	Nilsen et al. (2005)
s	natural survival female and male	0.95	Nilsen et al. (2005)
p	meat price	50 NOK/kg	Nilsen et al. (2005)
α	choke price	30,000 NOK/animal	Calibrated from Sylvén (1995)
γ	quality parameter demand	0.0001	Calibrated from Sylvén (1995)
β	slope parameter demand	60 NOK/animal^2	Calibrated

c	marginal harvest cost	2,000 NOK/animal	Calibrated
δ	Discount rate	0.05	

Table note. Exchange rate: 1 EUR = 7.80 NOK (Aug. 2011)

Table 2: Number of females and males under different scenarios. Baseline parameter values

	No hunting		*MB-Scenario*		*PT-scenario*	
Time	Females	Males	Females	Males	Females	Males
1	600	600	600	600	600	600
2	950	950	950	777	950	675
3	1169	1169	1169	828	1169	628
4	1491	1491	1490	989	1488	691
5	1845	1845	1688	1186	1728	789
6	2224	2224	1691	1414	1730	921
7	2603	2603	1694	1640	1732	1058
8	2961	2961	1697	1850	1734	1184
9	3288	3288	1699	2046	1735	1301
10	3580	3580	1702	2227	1737	1407
11	3838	3838	1704	2396	1738	1505
12	4064	4064	1706	2553	1739	1594
13	4264	4264	1708	2698	1740	1676
14	4440	4440	1710	2834	1741	1751
15	4596	4596	1712	2959	1742	1820
16	4735	4735	1714	3075	1743	1882
17	4858	4858	1715	3183	1743	1939
18	4967	4967	1716	3283	1744	1992
19	5065	5065	1718	3376	1745	2040
20	5152	5152	1719	3462	1745	2083
21	5231	5231	1720	3541	1746	2123
22	5301	5301	1721	3615	1746	2160
23	5364	5364	1722	3683	1747	2193
24	5420	5420	1722	3746	1747	2223
25	5471	5471	1723	3804	1747	2251
26	5517	5517	1724	3858	1748	2276
27	5558	5558	1724	3908	1748	2299
28	5595	5595	1725	3954	1748	2320

29	5629	5629	1725	3997	1748	2339
30	5659	5659	1726	4036	1748	2356
31	5686	5686	1726	4072	1749	2372
32	5711	5711	1727	4106	1749	2386
33	5733	5733	1727	4137	1749	2399
34	5753	5753	1727	4165	1749	2411
35	5771	5771	1727	4191	1749	2421
36	5788	5788	1727	4215	1749	2431
37	5803	5803	1727	4237	1749	2439
38	5816	5816	1727	4257	1749	2447
39	5828	5828	1727	4276	1749	2453
40	5839	5839	1726	4292	1748	2459

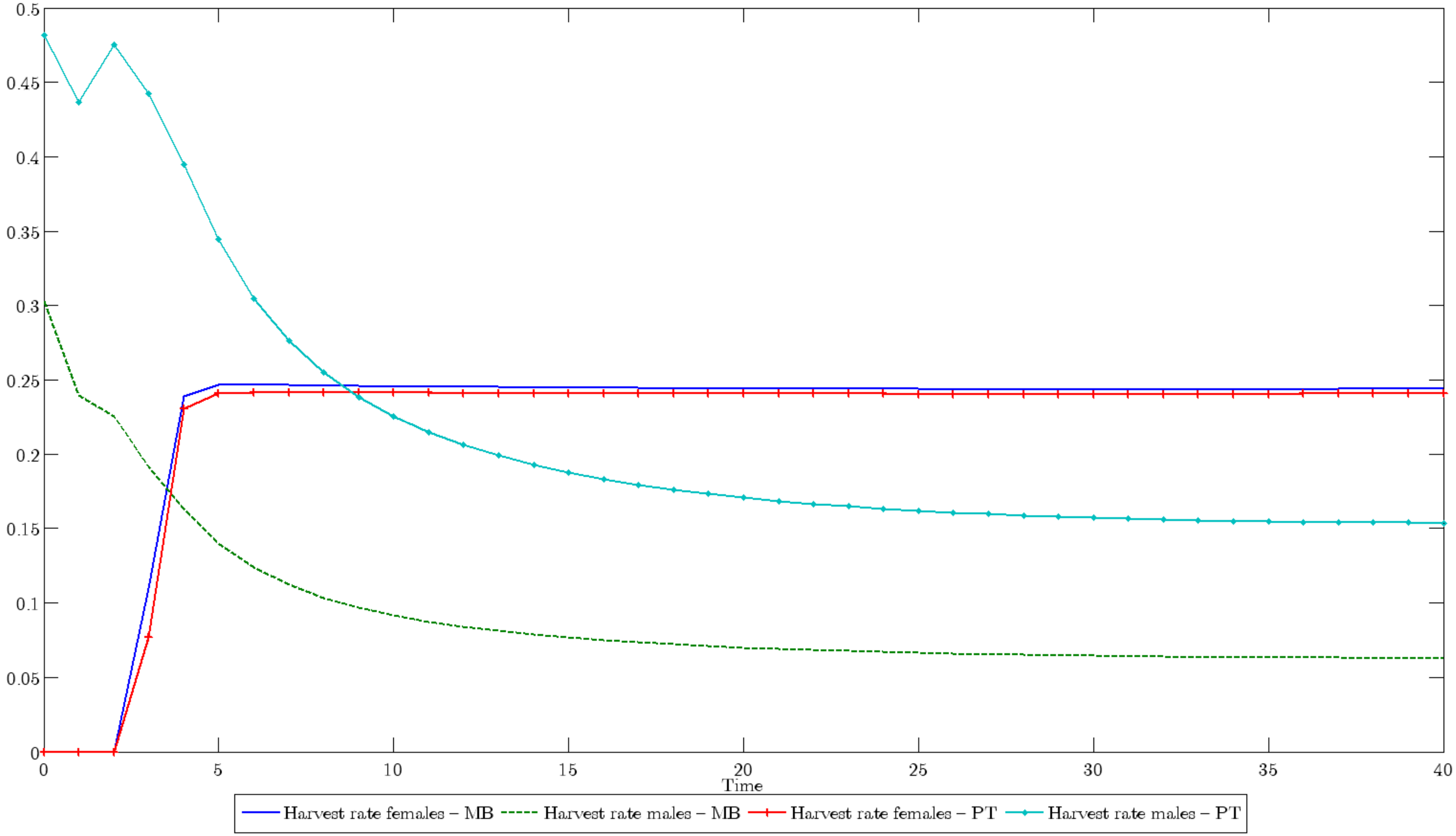

Figure 1: Harvest rates under MB- and PT-scenario. Baseline parameter values.

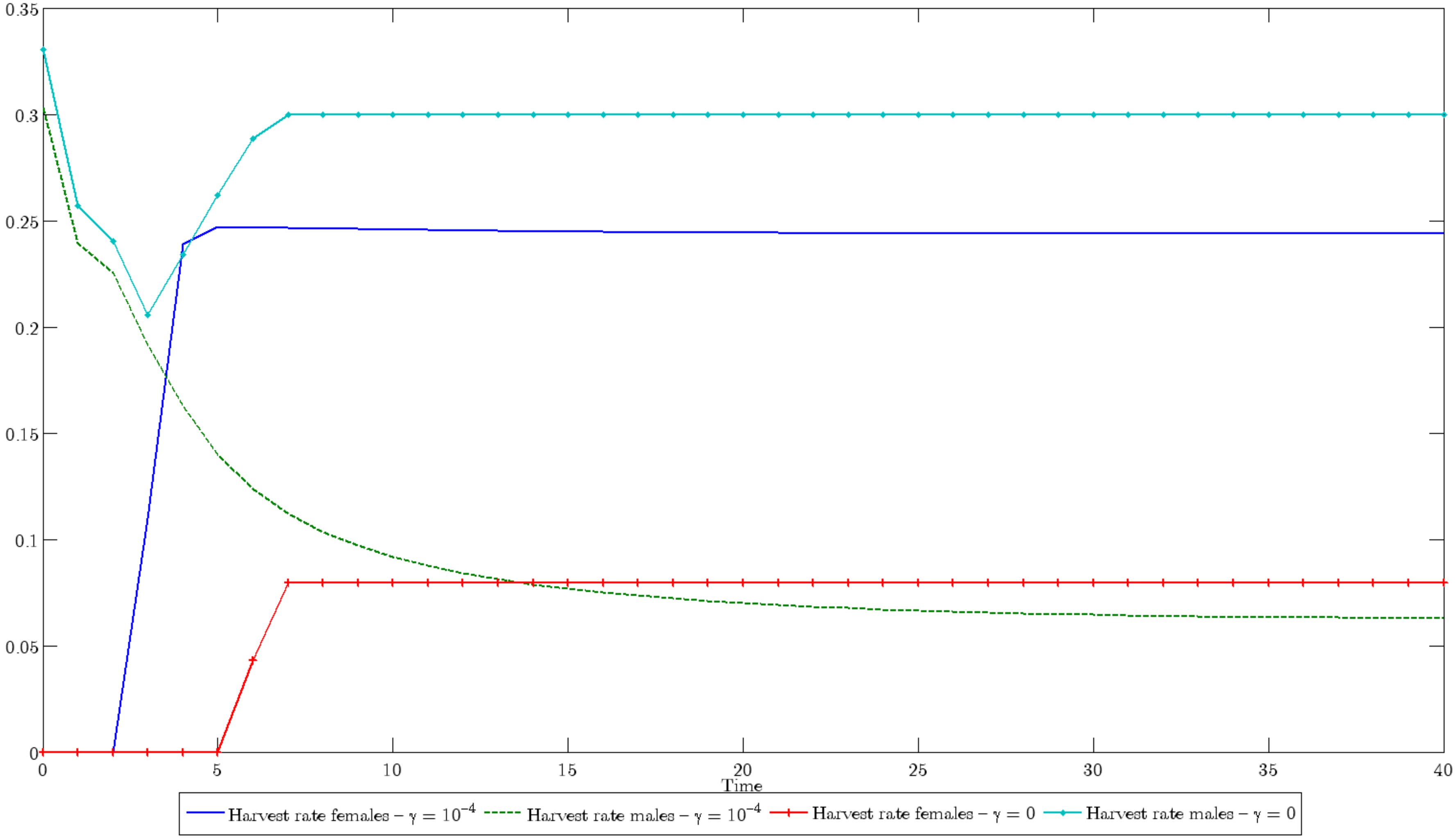

Figure 2: Female and male harvest rates with and without preferences for quality. MB-scenario

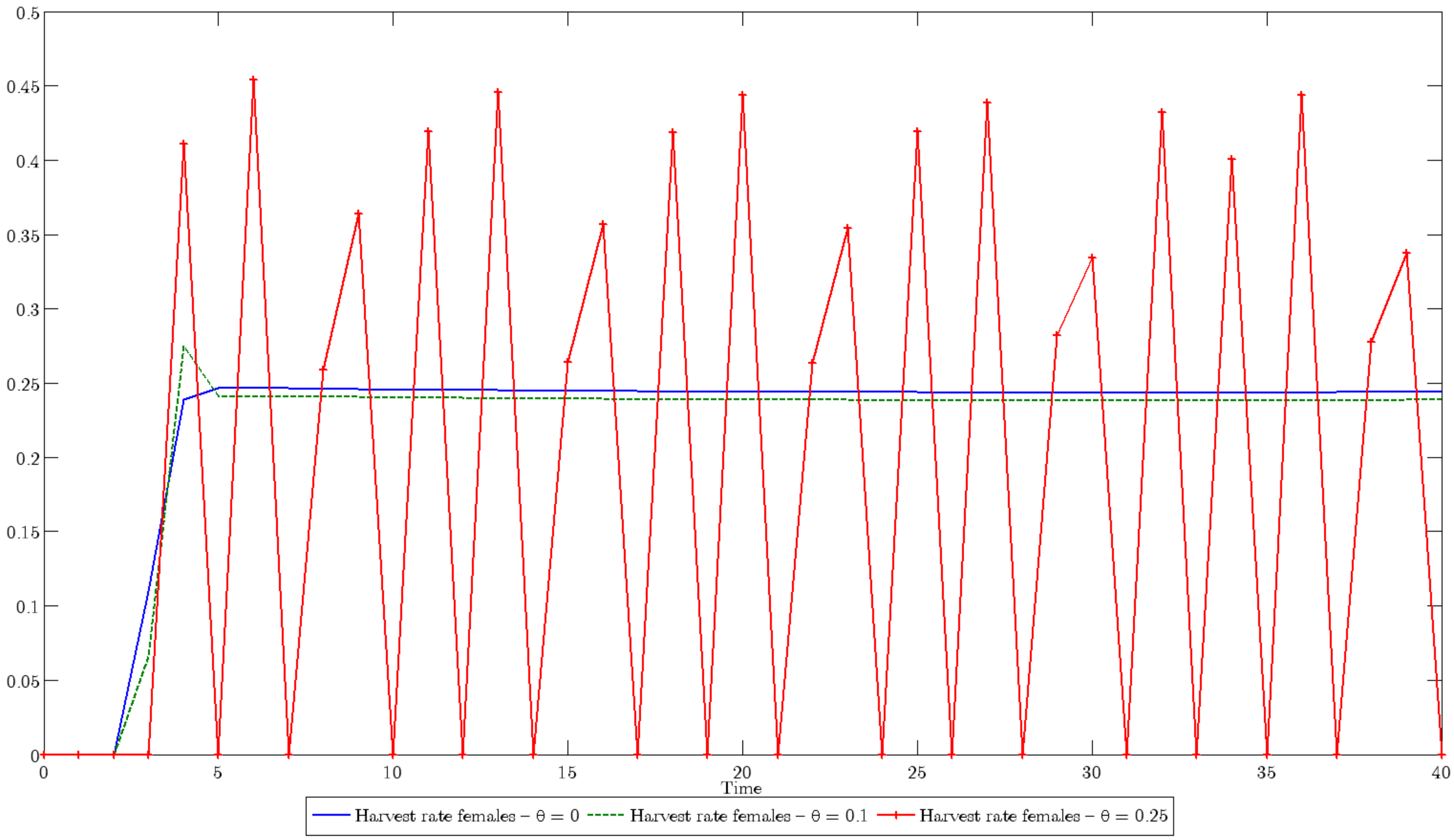

Figure 3: Female harvest rates with fertility effect hunting pressure. MB-scenario.

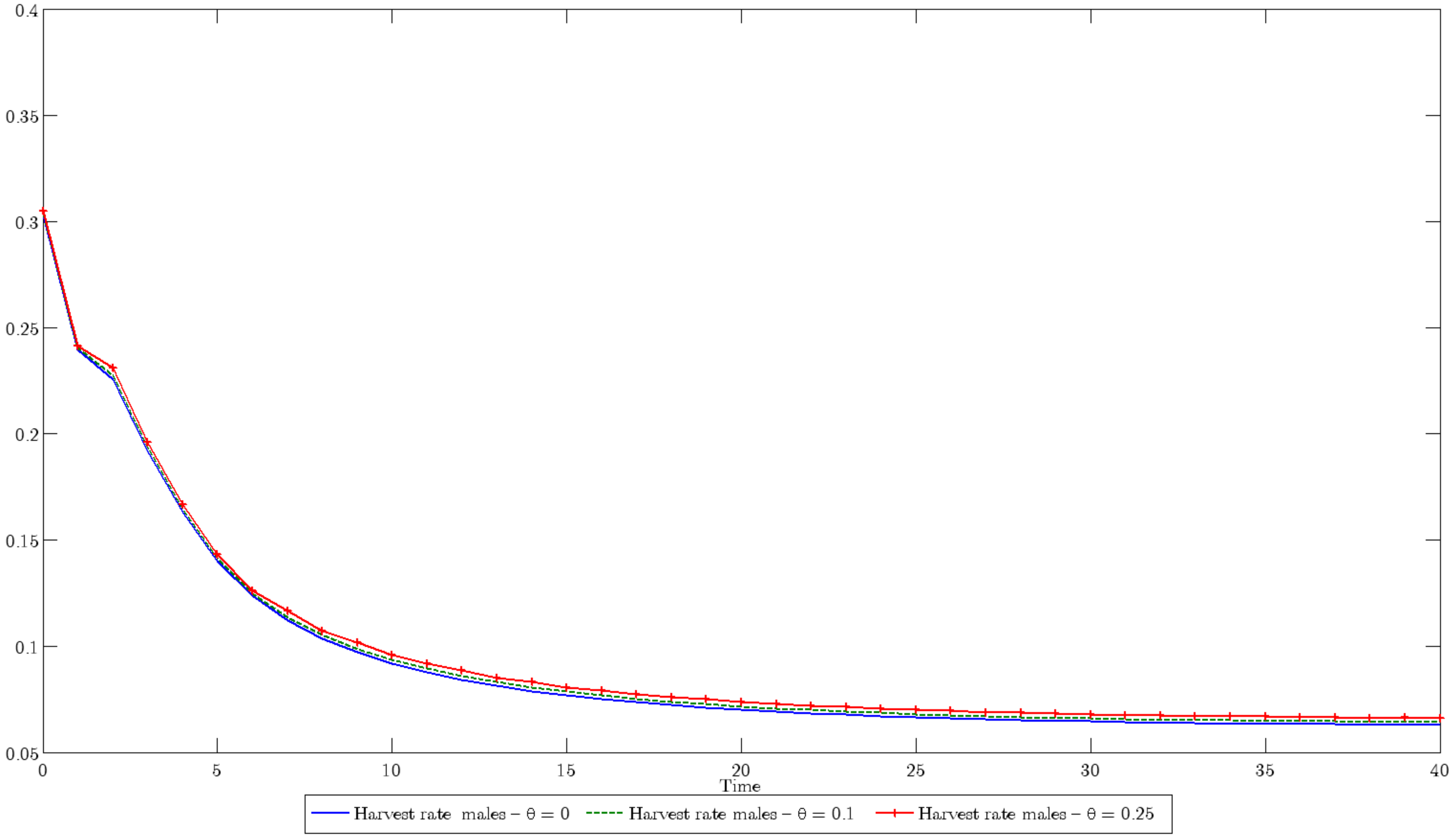

Figure 4: Male harvest rates with fertility effect hunting pressure. MB-scenario

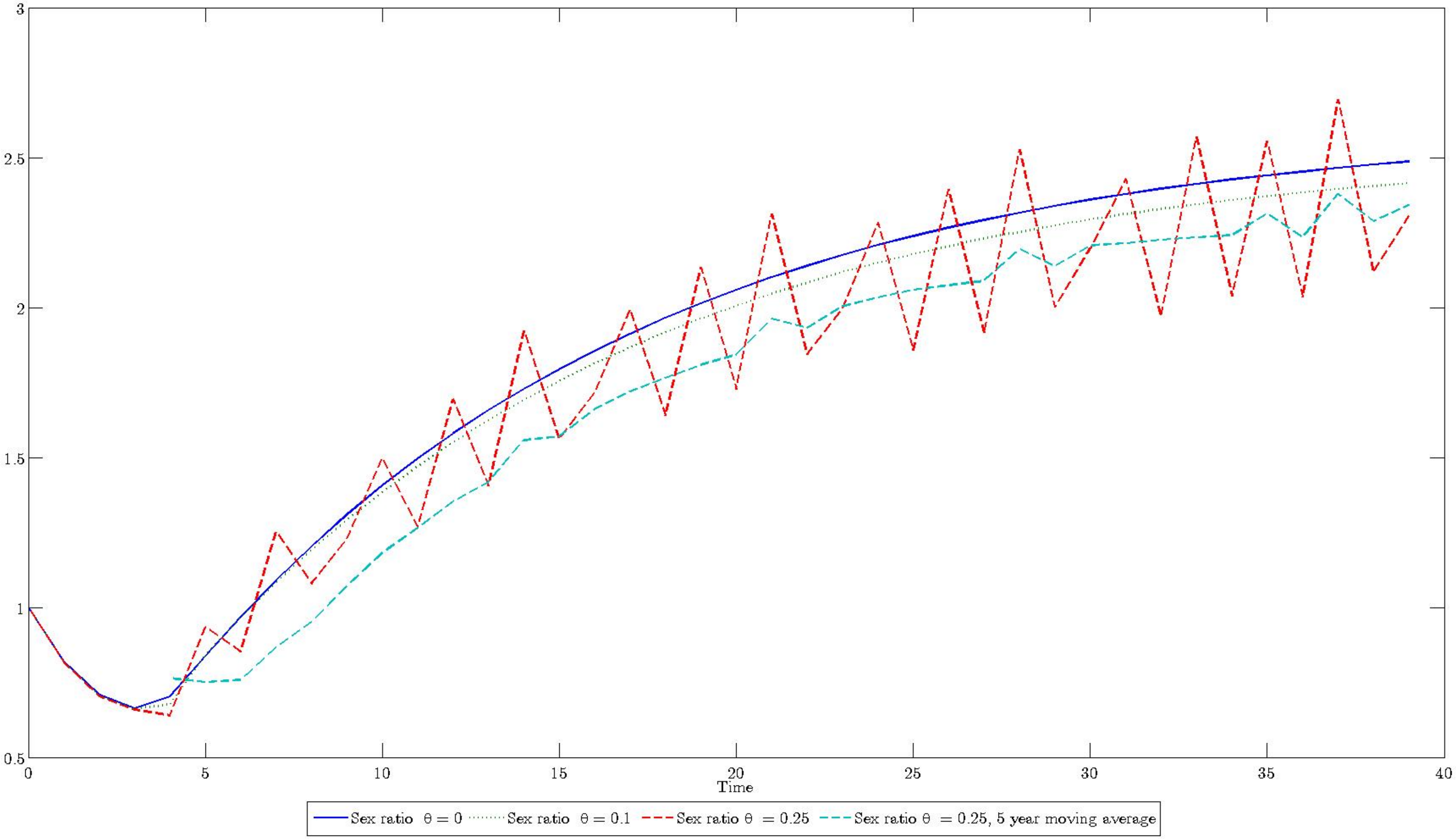

Figure 5, Ratio of males to females with fertility effect hunting pressure. MB-scenario.