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RH: Cost and income in red deer management

Balancing cost and income in red deer management – a case study from Norway

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Abstract

This paper presents a bioeconomic analysis of a red deer population within a Norwegian institutional context. This population is managed by a well-defined manager, typically consisting of many landowners operating in a cooperative manner, with the goal of maximizing the present-value hunting related income while taking browsing and grazing damages into account. The red deer population is structured in five categories of animals (calves, female and male yearlings, adult females and adult males). It is shown that differences in the per animal values and survival rates ('biological discounted' values) are instrumental in determining the optimal harvest composition. Fertility plays no direct role. The numerical analysis, represented by a case study from an area in the Western part of Norway with high animal density, shows that the optimal harvest pattern stays quite stable under various parameter changes, but it is also revealed which parameters and harvest restrictions that is most important.

Key word:

Red deer, management, bioeconomic analysis, landowner, cost-benefit, hunting, meat value, crop damage.

Introduction

The management of deer have become in focus with recent large increases in population sizes in many areas of both Europe and North America (Gordon et al., 2004). Increased abundances increases potential yields. However, the increasing number of deer-vehicle collisions and their related costs (Langbein et al., 2010), deer damages to forestry and agriculture (Reimoser and Putman, 2010) and their general ecosystem impact (Mysterud, 2006; Reimoser and Putman, 2010) are also important concerns accompanying the population increase. Large herbivores are termed ecological keystone species because of their ability to affect vegetation community patterns and ecosystem functioning (Côté et al., 2004; Hobbs, 1996). Deer management decisions concerning population development are therefore important issues that generally influence both ecological and economic aspects.

A good example of this development is the Norwegian red deer (*Cervus elaphus*) population, which has increased and spread substantially during the last few decades (Milner et al., 2006). The red deer has become the most numerous wild ungulate in Norway both measured as the number of harvested individuals (Statistics Norway, 2010) as well as number of live animals in the population (Andersen et al., 2010). In 1970 the total number of harvested red deer was about 2,800, and animals were mainly found in scattered and low density populations along the south-western part of the country (Figure 1). In 2009 red deer are found in nearly all municipalities of southern Norway, and the total number of shot animals exceeded 39,000 animals. However, the main populations are still situated in the traditional core areas and more than 90 % of the red deer harvested are shot within five counties in the south-western part of Norway. The national population increase is therefore mainly due to increased densities in these traditional core areas (Milner et al., 2006).

Red deer are extensively utilized as a game species, and the management strategy in Norway has traditionally been oriented towards meat hunting rather than trophy hunting (Milner et al., 2006). Large deer populations both represent a potential source of income for the landowners possessing the hunting rights, as well as a potential cost related to damages from grazing and browsing. The harvest related incomes are typically associated with sale of meat and hunting rights, whereas additional services or products (cabin rental, guiding, etc.) generally represent a modest source of income (Olaussen and Mysterud, Unpublished). The main cost component is normally reduced production from agricultural crops (mostly grass production), both in terms of quality and quantity. In addition, browsing damage to economically important tree species may also be extensive. Costs related to deer-vehicle collisions are also significant (Mysterud, 2004). Such costs are both complex to quantify (Bissonette et al., 2008) and paid by the general public.

The present paper aims to analyze the cost and benefit of a red deer population from a landowner perspective. We use a five stage population model (calves, female and male yearlings, adult females and adult males) to simulate the population development and response to various harvesting scenarios. The main goal is to analyze the basic driving forces behind the optimal harvesting strategies given various constraints related to male-female composition, and current code of conduct among hunters regarding to avoid shooting the mother from calves. The meat value is assumed to be given by a fixed meat price, and the unit costs related to grazing damage are assumed to be constant, but stage specific. Since costs related to deer-vehicle collisions are external to landowners, they will not be taken into account here. The landowner, typically consisting of several landowners acting as a single agent through a landowner association (management unit), is assumed to be rational and well-informed aiming to maximize the profit from hunting when accounting for grazing costs. We also compare the results from our five stage model with the outcome of equivalent analyses using a uniform harvesting scheme. Finally we compare our results with the present harvesting pattern, which has been established through cohort analyses (Veiberg et al., 2010).

Methods and material

Management organization and red deer hunting practice

Decisions related to the management of red deer populations in Norway involve various levels of the management hierarchy. General hunting periods and regulations are decided by the Directorate for Nature Management. Within this framework, municipalities (local governments) are given authority to limit the hunting period and to regulate the 'minimum area required' (the basis for quotas) to local management aims, population situation and current challenges. Each municipality is responsible for developing a management plan which acts as a framework for private management. The municipality also has the responsibility for coordinating local management plans, deciding hunting quotas and license fees, and reporting harvest result to Statistics Norway (Andersen et al., 2010).

The hunting right belongs to the landowners. This means that landowners can benefit from hunting related activities and products that relates to their property. Larger management units are requested to present multi-annual management plans (3-5 years duration) containing concrete management aims and a detailed harvest plan. These plans need to be approved by the municipality, and harmonized with overall municipal management aims. This system represents a more flexible and locally adapted management alternative compared to the traditional alternative where the municipality enforce a more detailed and rigid practice (Andersen et al., 2010). However, there are still some landowners receiving a quota from the municipality. These quotas are related to the total area of suitable red deer habitat within an area. The quota is typically found by dividing the total area of suitable red deer habitat within an area by the minimum area required. The minimum area required does not differ between red deer sex and age classes, but it typically differs between, or within, municipalities due to differences in red deer population density and levels of deer related conflicts. Quotas are thus regulated indirectly by adjusting the minimum area required per license. Since most properties are rather small, association of two or more landowners into cooperative management units is very common. This triggers allocation of more licenses, simplifies the practical hunt and stimulates a more uniform management. For simplicity, we also refer to such cooperative management units as landowners.

The red deer hunting starts September 10th and ends November 15th (in some areas December 23rd). Hunting on agricultural pastures from stands or ground blinds, and drive hunts for a team of hunters, either with the aid from a dog on leach or a barking dog, are the most frequently used hunting practices. Some stalking also occurs in forested areas, especially during the rutting season when males are roaring (Meisingset, 2008).

Study area

Our study area is from the county of Sogn and Fjordane located on the western coast of Norway. The county consists of 26 municipalities, and has the overall highest red deer population in Norway. Flora and Gloppen (approx. 61.5°N and 5.5°E) are two neighboring municipalities with a common total area of 1721 km^2. Flora is a coastal municipality, whereas Gloppen is more of a fiord municipality located east of Flora (Figure 2). The topography along the coast is characterized by islands and fiords with rolling country that change over to narrow valleys with steep slopes leading to higher mountains and mountain range. Small scale agriculture is widespread in the flatter lowlands, and the arable land is mainly cultivated to pastures and meadows for grass production. The forest is dominated by either Scots pine (*Pinus sylvestris*), alder (*Alnus incana*) or birch (*Betula* sp.), while planted Norway spruce (*Picea abies*) dominate locally. Common undergrowth species are juniper (*Juniperus communis*), bilberry (*Vaccinium myrtillus*), heather (*Calluna vulgaris*) and grasses and herbs.

The climate in this region is characterized by the coastal location with annual precipitation between 1100-3500 mm, mean winter (December-February) temperatures between 0-3°C and mean summer (June-August) temperatures between 11-14°C (www.eklima.no). During winter number of days with snow cover normally increase and temperature decrease with altitude and distance from the coast (Langvatn et al., 1996; Mysterud et al., 2000).

Population model

In Norway mean dressed body weight (i.e., live weight minus skin, head, viscera, metapodials and bleedable blood) for males and females 2 years and older is usually between 60-125 kg and 50-70 kg, respectively (Solberg et al., 2010, see also Table 1). Due to lack of predators natural mortality rates are generally assumed to be low for all age and sex categories. The highest natural mortality rate is found for calves, followed by yearlings (Langvatn and Loison, 1999). As mortality throughout summer and fall is regarded to be small, all natural mortality is assumed to take place during the winter and after the hunting season. There has not been found evidence of density-dependent mortality for any age or sex categories in Norwegian red deer (Loison and Langvatn, 1998). On the other hand, fecundity is affected by female density (Langvatn et al., 2004), while the number of males seems to be of negligible importance for a small and moderately skewed sex composition (Mysterud et al., 2002). However, it may play a role when the male population becomes small accompanied by a highly skewed sex composition (Milner-Gulland et al., 2003). From the hunters' point of view, a reasonable proportion of adult males is clearly both attractive and wanted (see also Result section below). To comply with this wish and to avoid speculations regarding potential long-term consequences of strongly biased sex ratios, we specify a male harvesting constraint.

In the present analysis the population at time (year) t is structured in five stages; calves $X_{c,t}$ ($yr<1$), female yearlings $X_{yf,t}$ ($1 \le yr < 2$), male yearlings $X_{ym,t}$, adult females $X_{f,t}$ ($yr \ge 2$) and adult males $X_{m,t}$. The total population reads $X_t = X_{c,t} + X_{yf,t} + X_{ym,t} + X_{f,t} + X_{m,t}$. The population is measured in spring before calving. All stages may be harvested. Neglecting any stochastic variations in biology and environment, and any net dispersal in or out of the considered area, the number of calves (recruitment) is first governed by $X_{c,t+1} = r_{yf,t} X_{yf,t} + r_{f,t} X_{f,t}$, so that $r_{yf,t}$ is the fertility rate of yearlings and $r_{f,t}$ the fertility rate of adults. Unless the number of males becomes extremely low, the male abundance and sex composition has probably negligible influence on female fertility rates. As already indicated, we therefore assume that only the total number of females, yearlings and adults, affect female fertility rates. Moreover, as female yearlings and adult females compete over the same resources, we assume that the fertility rates for both categories are affected only by the total number of females present. We then have $r_{yf,t} = r_{yf}(X_{yf,t} + X_{f,t})$, with $r_{yf}(0) > 0$ and $\partial r_{yf} / \partial (X_{yf,t} + X_{f,t}) = r'_{yf} < 0$ for yearlings, and $r_{f,t} = r_f(X_{yf,t} + X_{f,t})$, with $r_f(0) > 0$ and $r'_f < 0$, for adults. The density dependent recruitment function then yields:

$$X_{c,t+1} = r_{yf}(X_{yf,t} + X_{f,t}) X_{yf,t} + r_f(X_{f,t} + X_{yf,t}) X_{f,t} . \qquad (1)$$

The number of female and male yearlings follows next as:

$$X_{yf,t+1} = \psi s_c (1 - h_{c,t}) X_{c,t} \tag{2}$$

and

$$X_{ym,t+1} = (1 - \psi) s_c (1 - h_{c,t}) X_{c,t} \tag{3}$$

where s_c is the fixed calf natural survival rate (fraction) and ψ is the proportion of female calves. The proportion of female and male calves born is assumed to be equal, i.e., $\psi \approx 0.5$ (Table 1, numerical section). $0 \le h_{c,t} \le 1$ is the calf harvesting rate. Finally, the abundance of adult females and males become:

$$X_{f,t+1} = s_{yf} (1 - h_{yf,t}) X_{yf,t} + s_f (1 - h_{f,t}) X_{f,t} \tag{4}$$

and

$$X_{m,t+1} = s_{ym} (1 - h_{ym,t}) X_{ym,t} + s_m (1 - h_{m,t}) X_{m,t} , \tag{5}$$

respectively. s_f and s_m are the fixed natural survival rate of adult females and males, and where $s_f \ge s_m$. s_{yf} and s_{ym} are the yearling survival rates, also with $s_{yf} \ge s_{ym}$ (Table 1). $0 \le h_{yf,t} \le 1$ and $0 \le h_{ym,t} \le 1$ are the harvesting rates of female and male yearlings, respectively, while $0 \le h_{f,t} \le 1$ and $0 \le h_{m,t} \le 1$ are the harvesting rates of the two adult stages. Note that it is possible to hunt all adult females in a given year and still get production of calves in the next year. The reason for this is that the yearlings also reproduce.

Equation (2) and (3) together yield:

$$X_{ym,t} = [(1 - \psi) / \psi] X_{yf,t} . \tag{6}$$

Using this expression to eliminate $X_{ym,t}$ from equation (5), we find the abundance of adult males as:

$$X_{m,t+1} = s_{ym} (1 - h_{ym,t}) [(1 - \psi) / \psi] X_{yf,t} + s_m (1 - h_{m,t}) X_{m,t} \tag{7}$$

Equations (1), (2), (4) and (7) now constitute a reduced form model in four stages and five harvesting rates, and where all equations are first order difference equations. We employ this system of equations when studying exploitation below. The optimal number of animals and harvest ratios will result from the optimization procedure, except for the number of male yearlings which can be identified uniquely from the number of female yearlings using equation (6). With $\psi = 0.5$, the number of female and male yearlings will be identical at every point in time.

In biological equilibrium it is possible to say something about the adult sex ratio in our population model. Combing (4) and (7) when $X_{i,t+1} = X_{i,t} = X_i \ \ (i = c, yf, ym, f, m)$ for fixed harvesting rates, gives this sex ratio as $X_m / X_f = [(1 - \psi) / \psi][(1 - s_f (1 - h_f)) s_{ym} (1 - h_{ym})] / [(1 - s_m (1 - h_m)) s_{yf} (1 - h_{yf})]$ after some straightforward manipulations. Therefore, harvest of both the yearling and adult categories influence the adult equilibrium sex ratio. However, the calf harvest plays no role because there is no distinction between female and male calves in the model. With unprofitable yearling harvest so that $h_{ym} = h_{yf} = 0$, the adult sex ratio becomes $X_m / X_f = [(1 - \psi) / \psi](1 - s_f (1 - h_f)) s_{ym} / (1 - s_m (1 - h_m)) s_{yf}$. For identical female and male yearling survival rates together with similar proportion of female and male calves entering the yearling stages, $\psi = 0.5$, the ratio reduces further to $X_m / X_f = [(1 - s_f (1 - h_f)] / [(1 - s_m (1 - h_m)]$. Under these assumptions, sex-skewed adult harvesting rates directly translate into sex-skewed adult abundance. This last relationship may also be written as $h_f = (1/s)(1-s)(X_m / X_f - 1) + (X_m / X_f)h_m$ when $s_m = s_f = s$ (see Table 1). Therefore, in biological equilibrium, or steady state, we find that a skewed sex ratio like $X_m / X_f = 0.5$, can be met with hunting rates in the ranges $(1-s)/s \le h_m < 1$ together with $0 \le h_f < (s-0.5)/s$.

Landowner cost and benefits

The traditional landowner management goal has been directed towards maximizing the population productivity in order to produce meat, but also with a strong recreational component (Andersen et al., 2010; Milner et al., 2006). Typically, hunters have been local people, the landowners and their families and friends, and the hunting has had some flavor of subsistence hunting (Andersen et al., 2011; Olaussen and Mysterud, Unpublished). It has been a gradual shift towards more commercialization of the hunting during the last two decades or so. This is due both to higher red deer populations and to increased awareness of the economic potentials of red deer hunting and related products and activities (e.g., cabin renting and guiding; see e.g. Natur og Fritid, 2005), but also due to easier access to the various hunting areas and increased income among people. This has caused increased introduction of non-local hunters and a higher willingness to pay among all hunters regardless of local belonging. Still, the most important motivation for hunting among the local people is the prospect for meat and recreation (Olaussen and Mysterud, Unpublished), and only these kinds of hunting related income are considered here (but see Naevdal et al., Submitted, who analyzes moose trophy hunting). Therefore, we are thinking of the hunter as the local people, the landowners and their friends, enjoying the meat value and the recreational value of the hunt.

The number of animals removed through hunting in year t is defined as $H_{i,t} = h_{i,t} X_{i,t}$ ($i = c, yf, ym, f, m$). The value (price) per kg harvested meat $\hat{p}$ is assumed to be independent of number of animals hunted, population density and animal category, as well as assumed to be fixed over time. The current gross meat value is accordingly $\hat{p}(w_c h_{c,t} X_{c,t} + w_{yf} h_{yf,t} X_{yf,t} + w_{ym} h_{ym,t} X_{ym,t} + w_f h_{f,t} X_{f,t} + w_m h_{m,t} X_{m,t})$ and where $w_c < w_{yf} \le w_{ym} < w_f < w_m$ are the (average) dressed weights (kg per animal) of the different categories of animals (Table 1). For every animal shot the landowner pays a fixed fee q_i (NOK per animal) to the municipality. This fee is typically differentiated between calves and older animals (Table 2). For landowners the yearly net benefit from hunting measured as meat value is then defined as:

$$V_t = p_c h_{c,t} X_{c,t} + p_{yf} h_{yf,t} X_{yf,t} + p_{ym} h_{ym,t} X_{ym,t} + p_f h_{f,t} X_{,t} + p_m h_{m,t} X_{m,t}\,, \tag{8}$$

and where $p_i = (\hat{p} w_i - q_i)$ ($i = c, yf, ym, f, m$) is the net per animal meat value (NOK per animal).

In addition to the meat value, the hunters also obtain a recreational value related to the hunting. Studies from elk hunting in US (Aiken and Pullis La Rouche, 2001) report net consumer surplus for resident elk hunters (total willingness to pay minus actual fees and costs) of about \$60 per day in Wyoming. Empirical studies from Sweden (Boman et al., 2011) also indicates that time spent on hunting is valuable. In what follows, only the hunting time is considered as an indicator for recreational value and hence all other valuable aspects of the hunting, except of the meat value, are lumped into this indicator. When using a production function approach and where the production (harvesting) function is assumed to be of the standard Schaefer type with perfect selectivity (e.g., Clark, 1990), the number of hunted animals of category i becomes $H_{i,t} = \theta_i N_{i,t} X_{i,t}$ ($i = c, yf, ym, f, m$). $N_{i,t}$ indicates the hunting effort, measured in number of hunting days, and θ_i is the catchability (productivity) coefficient (1/hunting days). The catchability coefficient yields the hunting efficiency, and a higher value hence indicates a more efficient hunt. The value will typically differ somewhat between the various categories of animals, but probably not too much. In what follows, it is assumed to be identical for all categories. Therefore, with z as the recreational value (NOK per hunting day), the recreation value writes $B_t = z(N_{c,t} + N_{yf,t} + N_{ym,t} + N_{f,t} + N_{m,t})$, or

$$B_t = (z/\theta)(h_{c,t} + h_{yf,t} + h_{ym,t} + h_{f,t} + h_{m,t}) \qquad (9)$$

when substituting for the harvesting functions[1]. The total yearly hunting benefit is hence described as $(V_t + B_t)$.

The underlying causes explaining the occurrence and extent of deer damages are complex and not fully understood, but crop type and population density are assumed to be the most relevant factors (Reimoser and Putman, 2010). In a descriptive study from a neighboring municipality of our study are, Thorvaldsen et al. (2010) found that crop damages on agricultural land was more important than damages to commercial tree species. Based on knowledge about the primary production in our study area, we therefore make the assumption that only agricultural damages is of significant importance to the general landowner.

As crop damage on agricultural land takes place during the spring, summer and early fall, it is the pre-harvest population size that is relevant. Separate damage function for each animal category is specified. These cost functions may be written as $D_i(X_{i,t})$ ($i = c, yf, ym, f, m$), and where no animals means zero damage and more animals means more damage; that is, $D_i(0) = 0$ and $D_i^{'} > 0$. Except for these two properties, we do not know very much about these damage cost functions (but see Wam and Hofstad, 2007 for an assessment of forest damage costs). They may be concave or convex, or partly concave and convex. For simplicity we use linear functions, i.e., $D_i(X_{i,t}) = d_i X_{i,t}$, and where d_i is the fixed per animal damage cost. The per animal damage varies for different categories of animals, and we assume $d_c < d_{yf} \le d_{ym} < d_f < d_m$ (Table 2).The agricultural damage costs are thus:

$$D_t = d_c X_{c,t} + d_{yf} X_{yf,t} + d_{ym} X_{ym,t} + d_f X_{f,t} + d_m X_{m,t}. \qquad (10)$$

Therefore, the landowner yearly net benefit is described by:

$$R_t = V_t + B_t - D_t \qquad (11)$$

Optimal management

Outcome based on hunting meat value benefit only

We first study the situation where the landowner maximizes the hunting benefit meat value only. This means that the recreation aspects of the hunting, as well as the damage costs, are not taken into account when optimizing the harvesting strategy. The goal is thus to find harvest rates, and hence hunting quotas, that maximizes the present-value

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[1] The recreation value z is here assumed fixed. In reality it is likely to decrease with effort use, at least above a certain level, making B_t a concave function of the number of hunting days. However, to say more about this, the number of hunters has to be included in the analysis which is beyond the scope of our study.

$\max_{h_{c,t}, h_{yf,t}, h_{ym,t}, h_{f,t}, h_{m,t}} \sum_{t=0}^{t=\infty} \rho^t V_t$ subject to the biological growth equations (1), (2), (4) and (7). $\rho = 1/(1+\delta)$ is the discount factor with $\delta \geq 0$ as the (yearly) fixed discount rate.

Due to the common code of conduct among hunters to avoid shooting the mother from calves, a female – calf harvest restriction is included (Olaussen and Skonhoft, 2011). This restriction is included simply as:

$$h_{f,t} X_{f,t} \leq h_{c,t} X_{c,t} . \qquad (12)$$

In addition, a restriction on the number of harvested adult males is incorporated to avoid a too skewed sex ratio. One way to include this restriction is simply to impose an upper limit on the adult male harvesting fraction. Such male harvesting restriction may be strengthened if we additionally also impose a similar restriction on the male yearling hunting. This is what is actually done and we hence include:

$$h_{m,t} \leq \bar{h}_m \text{ and } h_{ym,t} \leq \bar{h}_m . \qquad (13)$$

In the Supplement section the first order necessary control conditions are stated and it is shown that it is possible to say something about the basic driving forces steering the harvest composition. We now discuss these driving forces, first by disregarding the code of conduct constraints (12) and (13).

For both sexes, we find that simultaneous harvest of both yearlings and adults does not satisfy the optimality criteria. Next, it can be shown that positive female yearling harvest together with zero adult female harvest implies $p_{yf} / s_{yf} > p_f / s_f$; that is, the ‘biological discounted’ female yearling hunting value (in NOK per animal) exceeds the ‘biological discounted’ adult female hunting value. Because the adult category is more valuable than the yearling category, $p_f > p_{yf}$, and the survival rates s_{yf} and s_y do not differ too much (Tables 1 and 2, numerical section), this inequality represents a contradiction. In the same manner, we also find that positive male yearling harvest together with zero adult male harvest implies $p_{ym} / s_{ym} > p_m / s_m$ which also represent a contradiction within the range of actual parameter values. Therefore, positive female yearling harvest and zero female adult harvesting and positive male yearling harvest and zero adult male harvesting are not possible options when the code of conduct constraints (12) and (13) are not binding and when the harvest recreation value is small and hence neglected.

These results show that the marginal hunting benefit (in NOK per animal) and the survival rates are instrumental in determining the optimal harvest composition (see also Olaussen and Skonhoft, 2011; Reed, 1980). Since, the ‘biological discounted’ value for the calf category is lower than for the yearlings, $p_c / s_c < p_i / s_i$ $(i = yf, ym)$ (see Table 1 and 2), we may also suspect that calf harvest together with zero adult harvest will not represent an optimal harvesting policy when the code of conduct constraint (12) is not binding. It is not possible to prove this by only using the first order necessary control conditions, but numerical solutions demonstrate that this will be the case for realistic parameter values.

On the other hand, when the female – calf constraint (12) and the male harvesting constraint (13) still do not bind, 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 is simply that the per animal values are higher for the adults than for yearlings while the survival rates do not differ too much. However, based on the optimality conditions it is difficult to say something definite about the harvest composition among the adults. There are two effects involved here. First, a direct economic effect working through the relative hunting value of females and males, and where males are more valuable due to a higher net per animal hunting value. Second, only the females contribute to reproduction (under our assumption of a not too skewed sex ratio). This last effect may also indirectly (because fertility is not included in the control conditions; see Supplement section) pull in the direction of a higher harvesting pressure on males than females.

However, if both adult females and males are harvested in the unbinding case, this result may change when the restrictions (12) and (13) are included. First suppose that restriction (12) is included, while we still neglect restriction (13) and the harvest recreation value. If females are harvested, the code of conduct restriction (12) indicates that at least the same number of calves must be harvested. Since the restriction is unbinding if more calves than females are harvested, we already know from the unbinding case that no calves should be harvested. Therefore, harvesting more calves than females represents a contradiction both in the unbinding as well as the binding case. Hence, the restriction must bind with the same positive number of calves and females harvested, or zero harvest of both. When constraint (12) binds, it will certainly also influence the various possibilities of yearling harvest together with adult female and male harvest. We may hence find that yearling harvest together with male harvest occurs in the optimal solution. When condition (13) binds and $h_{m,t} = h_{ym,t} = \overline{h}_m$, this will generally also influence the various optimal harvest options. Both yearling female, calf and adult female harvest may be affected due to less yearling and adult male harvest. The intuition is straightforward as e.g., calf harvest is an indirect way of controlling the yearling category when the yearling male harvest is restricted. Hence, even if calf harvest is not an optimal option in the unrestricted case, it may very well be optimal in the restricted case.

Summing up, we have demonstrated that differences in the ‘biological discounted’ value of various animal categories are the basic driving forces behind the optimal harvest composition. Fertility plays no direct role. However, certain modifying and complicating factors related to the common code of conduct constraint (12) and male harvest constraint (13) are present. These constraints also complicates our understanding of how the harvest composition and the populations may evolve over time; that is, the dynamic properties of the model. However, because of the strong degree of linearity in the model together with density dependent regulation through the recruitment function, we may suspect that oscillations will not be present and that the harvesting composition will approach a stable equilibrium.

Crop damage taken into account

We then look at the problem when also the damage costs are taken into account, but the recreational hunting value is still not included. This damage cost component is often inadequately compensated in real life management situations. One important reason for this is that animal migration pattern often generates mismatch between landowner hunting benefits and damage costs (Skonhoft and Olaussen, 2005). Therefore, the problem now is to find the harvesting strategy that $\max\limits_{h_{c,t}, h_{yf,t}, h_{ym,t}, h_{f,t}, h_{m,t}} \sum_{t=0}^{t=\infty} \rho^t (V_t - D_t)$, again subject to the biological growth equations (1), (2), (4) and (7) and the code of conduct constraints (12) and (13).

Because the damage in year t takes place *before* the harvest (see Eq. 10), the first order necessary control conditions will be identical to the above problem of maximizing the hunting benefit only (see Supplement section). Therefore, the equations determining the structure of the harvesting composition remain unchanged. On the other hand, we find that a new term reflecting the fixed marginal damage costs will be included in all the first order necessary portfolio conditions. The harvest of the different stages and the harvest composition will thus generally change. One reason for this is that the shadow prices of the various restrictions, including the female–calf harvest constraint, change. Just as in biomass models (e.g., Clark, 1990), we may also suspect that the harvesting pressure will be higher and the number of animals lower when damage costs are included (see e.g., Skonhoft and Olaussen, 2005). This is confirmed by the numerical results.

Recreational value included

When taking the damage costs into account, the current net benefit is defined by equation (11), and the problem is hence to $\max_{h_{c,t},h_{yf,t},h_{ym,t},h_{f,t},h_{m,t}} \sum_{t=0}^{t=\infty} \rho^t (V_t + B_t - D_t)$, subject to the same constraints as above. The solution to this problem gives the 'overall' optimal solution for the landowners. In this case, however, we find it difficult to draw any analytical conclusions about the harvest composition because the population sizes $X_{i,t}$ $(i = c, yf, ym, f, m)$ now are included in the control conditions such that the number of animals directly influence which of the different categories of animals it is beneficial to harvest (see Supplement section).

Therefore, not only differences in per animal values and survival rates ('biological discounted' values) are instrumental in determining the harvest composition when the recreational aspect of the hunting is included, but also the demographic composition of the population. This effect may of course be of particular importance if the recreation value is significant; that is, the value per hunting day z is 'high'. We may also suspect that the harvesting composition is more prone to changes over time because the strong degree of linearity in the model is no longer present. Generally, we find the dynamics now to be strikingly different. See Results section.

Results

Data and specific functional forms

The fertility rate (see Methods and material section) is expressed as a sigmoid function predicting increased degree of density dependence with higher population densities (Langvatn et al., 2004). The function reads:

$$r_{i,t} = r_i\left(X_{yf,t} + X_{f,t}\right) = \frac{\tilde{r}_i}{1 + \left[\left(X_{yf,t} + X_{f,t}\right)/K\right]^{b_i}}\ ;\ (i = yf, f) \tag{14}$$

with $\hat{r}_i > 0$ as the intrinsic growth rate (maximum number of calves per female) and $K > 0$ as the female population level for which density-dependent fertility is equal to density-independent fertility (female 'carrying capacity'). Thus, for a population 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, the biological productivity of the grazing and browsing resources, and so forth. The compensation parameter $b_i > 0$ indicates to what extent density-independent effects compensate for changes in the population size. Equation (14) implies a recruitment function (1) as

$X_{c,t+1} = \tilde{r}_{yf} X_{yf,t} \Big/ \left\{1 + \left[\left(X_{yf,t} + X_{f,t}\right)/K\right]^{b_{yf}}\right\} + \tilde{r}_{f} X_{f,t} \Big/ \left\{1 + \left[\left(X_{yf,t} + X_{f,t}\right)/K\right]^{b_{f}}\right\}$ and is of the so-called Shepherd type.

Table 1 gives the baseline parameter values for this function as well as the other biological parameter values. The parameter K is scaled for our study area (Methods and material section) and set to 4,000. The survival rates are from a population in the northern margin of the red deer range (Langvatn and Loison, 1999), and might underestimate survival further south. The fertility rates are based on ovulation rates (Langvatn et al., 2004), and may thus overestimate recruitment. However, for our purpose, these potential biases are likely to be unimportant.

The baseline economic parameter values are given in Table 2. The value of the catchability coefficient θ is calibrated based on the assumption that three hunting days are needed to shoot one animal when the population size is about 3,000 animals; that is catch per unit effort (*CPUE*) is 0.33 (animal/day). With $H_{i,t} = \theta N_{i,t} X_{i,t}$ (Methods and material section), or *CPUE* as $H_{i,t} / N_{i,t} = \theta X_{i,t} = 0.33$ and $X_{i,t} = 3{,}000$, we then have $\theta \approx 0.0001$ (1/hunting day). The per day recreational hunting value $z = 50$ (NOK/day) is based on studies from the actual area (Thorvaldsen et al., 2010). The crop damage cost parameters are taken from Olaussen and Mysterud (unpublished), and range from 175 (NOK/calf) to 532 (NOK/adult male). The meat value $\hat{p}$ is assumed similar among all categories of animals, and is set to 75 (NOK/kg) (see also Methods and material section).The per animal hunting fee is 210 (NOK/calf) and 350 (NOK/yearling and adult). We assume a zero discount rate in the baseline scenario. As is well known (e.g., Clark, 1990), this means that the (possible) steady state of the dynamic optimization problem coincides with the solution to the problem of maximizing current net benefit in biological equilibrium. The numerical results are first presented when only meat value and damage costs are included. Then we present results when also the recreation value of the hunting is taken into account.

Results when recreation value is not included

We first present the basic dynamic harvesting results[2]. As already indicated, because of the strong degree of linearity in the model together with density dependent regulation through the recruitment function, the model solution approaches a stable equilibrium. As the profit function is linear in harvest, economic theory suggests that harvest should be adjusted such as to lead the populations to their optimal steady states as rapidly as possible – if no constraints are binding (for proof of the Most Rapid Approach Path theorem, see Spence and Starrett, 1975). Hence, populations that are below their optimal steady state will not be harvested until they have reached their optimal size, and populations above their steady states will be harvested down to the optimal level within the first year.

Figure 3 demonstrates the optimal harvest rate dynamics with the baseline parameter values, and when both meat value and grazing damage are included (Case 1 in Table 3 below). The results here seem to partly confirm the most rapid approach principle. Starting with populations equal to 300 for all categories, calves and adult females are not harvested until they have grown to their optimal population sizes. Adult males, on the other hand, are harvested at the maximum rate even though the population is below its optimal steady state. This occurs because constraint (13) binds for adult males in the steady state, so postponing

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[2] The dynamic optimization was performed with the KNITRO for MATLAB solver form Ziena Optimization, with MATLAB release 2011b.

harvest until the optimal population size is reached would lead to overshooting. The reason why we find that calves are harvested in the steady state, despite the fact calves have a lower 'biologically discounted' value than the other age classes, is that constraint (12) binds in the steady state, meaning that some calves must be harvested to allow any harvest of adult females.

Figure 4 demonstrates the effect of changing the discount rate on the time path and steady state of the total population size (with all categories taken together), and where the baseline scenario (Case 1) is included with zero discount rate (upper curve). We find, not surprisingly, that increasing the discount rate results in progressively smaller populations, with correspondingly higher harvest rates, while the dynamics do not change qualitatively. The effects of other initial population values were examined as well without changing the qualitative structure of the dynamics; that is, the transitional dynamics were following the most rapid approach principle. Neither was other steady state values found ('ergodic' dynamics).

Tables 3 and 4 report the detailed steady state results for different configurations of parameter values and constraints. Table 3 shows the optimal harvest ratios and population sizes for all stages, along with total harvest and number of animals. Table 4 indicates the economic results.

Again, Case 1 describes the outcome under the baseline parameter values, and with all constraints included. From Table 3 we see that 20 % of the calves are harvested, because the female-calf harvesting constraint (12) is binding, and the harvest rate of adult females is 0.15. The adult male harvest constraint (13) also binds with $h_m = 0.55$. In addition, in Case 1 as in all cases in Table 3 except from Case 5, we find that yearlings of both sexes are not harvested. This is because the 'biologically discounted' values are lower for yearlings than for adults. From Table 4, we find the total yearly meat value to be 4,071 (1,000 NOK), with grazing damage costs being 1,843. Net average yearly income per hunted animal is 2.102 (1,000 NOK), while net income per living animal is 403 (NOK).

The recruitment function (1) assumes that males (adults as well as yearlings) represent no constraint in relation to female reproduction rates. Still, a harvest restriction on both yearlings and adult males is imposed to avoid a too skewed sex ratio. In the baseline Case 1, we find the adult male/female sex ratio to be $740/2{,}158 \approx 0.34$ (Table 3). In this case, as well as in the other cases, we find identical numbers of yearling males and yearling females in the pre-harvest population. This is simply a consequence of equal sex ratio in the recruitment, $\psi = 0.5$, equal harvesting rates for male and female calves, and identical survival rates for both sexes through their first winter (see Methods and material section and Table 1).

Case 2 describes what happens when the meat value is increased with 50 % while all other parameter values are kept constant. This leads to a slight adjustment in the harvest ratios for calves and adult females, but probably more important, to higher standing populations (Table 3). This is not generally obvious as standard biomass harvesting theory (e.g., Clark, 1990) predicts that populations should be kept at a level where the animal biomass growth rate equals the discount rate when meat income only matters and there are no population dependent costs; a criterion that is independent of the harvesting value. When a population effect, such as the grazing damage, is included in the benefit function, however, the meat price will influence the optimal population sizes. Obviously, the net economic value per animal both when hunted and when alive (as 'capital') increases when the meat value shifts up. For a given production level, or harvest activity in our case, a price increase leads to an equal percentage increase in income. When costs are unchanged, the percentage increase in profits – income minus costs - will always be higher. In addition, the harvest activity will be adjusted to take further advantage of the price change. Following the 50 % price increase, we hence find a doubling of total net benefit (Table 4).

In Case 3 the grazing damage D_t in equation (10) is ignored; that is, the landowners optimize without taking the grazing damage into account. Optimal population sizes are affected as the cost of keeping the population, as viewed by the landowner, reduces. This leads to a change in harvest pattern and population size that works in the same direction as the price increase, and in both cases the net value per living animal (as 'capital') goes up. The overall population size now increases with more than 20 % compared to Case 1. The population increase is particularly strong for adult females, and harvest ratios are correspondingly lower. The implied economic effect, on the other hand, goes in the opposite direction as the *actual* grazing damage will be larger, and amounts to a 10 % decrease in total net benefit (Table 4). In Cases 2 and 3, populations are increased through lowering the harvest ratios of calves and adult females, which implies a decrease in the adult male/female sex ratios to $778/2,449 \approx 0.32$ and $830/3,042 \approx 0.27$, respectively.

The female-calf constraint (12) is excluded in Case 4. As expected, there is no harvesting of calves in this scenario. The male harvesting constraint still binds with $h_m = 0.55$, and the adult female harvest rate increases to $h_f = 0.21$. Population sizes increase moderately, except for adult females. Total net benefit increases with about 14 %, from 2,228 (1,000 NOK) to 2,537, and there is a significant increase in the net benefit per hunted animal as the average weight of a hunted animal is higher. Therefore, the cost of the code of conduct constraint (12) is quite significant. As only the stock of adult females reduces, we also find an increase in the adult male/female sex ratio to $916/2,097 \approx 0.44$.

The contours in Figure 5 indicate the steady state net economic benefit $(V - D)$ for different combinations of h_f and h_m, and demonstrates the sensitivity of the net economic benefit to changes in the adult harvesting rates, when all the other harvesting rates are kept constant at their optimal levels. Panel a) is for the baseline Case 1, while panel b) is for Case 4 (without the cow-calf constraint). When the female-calf harvesting constraint is included as in Case 1, the maximum possible harvest ratio of adult females is around 0.15, as a higher harvest ratio implies a violation of constraint (12) when the harvest rate of calves is kept constant. In Case 4 however, the maximum sustainable harvest rate of adult females is around 0.4, which is equal to the recruitment rate of adult females when no calves or female yearlings are harvested.

From panel a) it is seen that combinations of the male harvesting rates within the range 0.40 – 0.55 and female rates within the range 0.15 – 0.10 yields a net benefit of about 2,000 (1,000 NOK) which implies an approximate 10 % reduction in net benefit compared to the optimal steady state (see also Table 4). This indicates that the profit loss is modest within a quite wide range of harvesting combinations. In panel b), where the code of conduct constraint (12) is omitted, net benefit is even less sensitive to adjustments in the adult harvest ratios. The inclusion of the zero profit contour line indicates when profit turns negative because of high grazing damage, and occurs when harvest rates become low and populations become large. In Case 4, net benefits decrease to around -7 mill. NOK for zero harvest of adults (while still keeping other harvest rates constant at their optimal levels). This dramatic impact on profits is to a large extent due to grazing damage being linearly related to population size, an assumption that is possibly unrealistic for large populations.

Uniform harvesting pattern

One interesting aspect of stage structured harvesting is to what extent the complexity involved in this kind of management practice pays its way through a significantly higher economic benefit yield than a *uniform* harvest rate across all stages. Such uniform hunting pattern implies an exploitation scheme where the present value benefit is maximized under the same biological constraints as above (but not constraints 12 and 13), but with the additional constraint of equal harvest rates across *all* age classes imposed. Results from this uniform harvesting scheme are reported as Case 5 in Table 3 and 4. As indicated here, uniform harvest implies a highly inefficient exploitation pattern, where the net benefit is reduced with about 50 % compared to the baseline Case 1. Population sizes are significantly reduced, except for adult males, due to excess harvesting of younger age classes. The positive effect on grazing damage of smaller populations is also somewhat counteracted by the fact that the younger stages are the ones that impose the least grazing damage. The implied inefficient composition of age categories results in substantially reduced net benefit both per hunted animal and per living animal. The male–female ratio also changes significantly, and is in this Case 5 equal to 1,102/1,165= 0.95. The reason why we do not find the exact same number of adult females and males is because of the survival rates among female and male yearlings are different (Table 1).

Also including the recreational aspect

So far, the hunting recreational value has not been included in the numerical analysis. As mentioned above (Optimal management section) this adjustment complicates the solution considerably. The long term optimal solution may no longer be a steady state, but perpetual oscillations between more profitable, but unsustainable, outcomes. Figure 6 shows that, under the same assumptions as the Case 1 scenario and with a recreational value of $z = 50$ (NOK/day) included, oscillating harvest rates for the calves and the female categories emerge. The harvest rates of both adult and yearling males become constant and equal to their upper constraint levels, whereas the harvest rates of calves, yearling and adult females oscillates between zero and 0.45, 0.3 and 1, respectively. As indicated above (Optimal management section), cycles may evolve when the strong degree of linearity, or concavity, in the model is no longer present. Once the non-concavity is introduced by the recreational value, the possibility for oscillations depends on combinations of all parameters in the model. Generally, it seems that this non-concavity effect is stronger for smaller populations, so that everything that leads to reduced populations will increase the possibility of oscillations, once the recreational value is incorporated into the analysis. This includes higher discount rates, higher grazing damage, lower meat price and also the magnitude of the recreational value itself. For baseline parameter values, pulse harvesting occurs only if the recreational parameter z value exceeds a certain critical value ($z = 25$).

Concluding Remarks

In this paper we have analyzed the cost and benefit of a red deer population within a five stage model with density-dependent fertility and density independent mortality, and where the cost and benefit functions are approximated by linear functions. This population is managed by a well-defined manager, typically consisting of many landowners operating in a cooperative manner, with the goal of maximizing the present-value hunting related income while taking grazing damages into account. The different ways to compose the harvest across age and sex categories and the implied economic benefits are highlighted. Without any restrictions on the harvest, and ignoring the recreation aspect of the hunting, we find the optimal harvest composition to be determined basically by the same factors as in Reed (1980) - such that differences in the 'biological discounted' values are instrumental in determining the optimal harvesting composition. The meat value – survival ratio comprises the 'biological discounted' values. Therefore, it may be seen as a marginal gain – cost ratio, where the marginal gain is given by the by the meat value increase from a younger to an older animal category while the marginal cost as reduced survival.

The Results section illustrates the predictions from the theoretical model. In the baseline case (Case 1) where the meat value and the grazing damage, but not the recreational value, are included, we find that all stages except yearlings are harvested. The females and calves are harvested only moderately, and calves are harvested due to the imposed code of conduct restriction (12). We also find that the same pattern persists when the meat price goes up (Case 2) and when grazing damage costs are ignored (Case 3), but the total population becomes substantially higher in both cases. However, the implied economic effect differs between the two cases, and yields a 100 % increase and 10 % decrease in total net benefit respectively. When the code of conduct constraint (12) was excluded (Case 4), we found that no calves where harvested, and the harvest of adult females increased to 21 %. Net benefit increased by 14 %.

The landowner net benefit was also calculated when the optimal selective harvesting patterns were replaced by 'optimal' uniform harvest rates (Case 5) as considered in the traditional bioeconomic models ('an animal is an animal'). We found that such a uniform harvesting pattern typically reduced the economic benefit by about 50 % compared to the optimal selective scheme. This clearly underlines the importance of using stage dependent models when populations can be structured into sex and age categories that significantly differentiate either in reproductive value or in economic return, and when perfect selectivity in harvest is possible.

When the recreational hunting value was included in the objective function, we found that the optimal harvesting scheme involved oscillating harvest rates. This result is not a new one within the resource management literature; it has been shown to exist in various models (Wirl, 1995), and in particular when there is imperfect selectivity in the harvest (Tahvonen, 2009). In our case however, there are reasons to be cautious when interpreting this result, as the formulation of the assumption of constant recreational value per hunting day may be questionable. In any case, it is doubtful whether a landowner would consider a pulse harvesting regime to be 'optimal' in a context such as this, not the least because of the difficulties involved with implementing such a management programme in practice.

Our results may be compared to the current red deer harvesting practices. The present harvesting regimes of red deer in Norway varies a great deal as a consequence of variation in local population density, demography and red deer related conflicts. On the other hand, a general pattern is that calves and yearlings are rather extensively harvested, and this is also so in our study area. As the traditional management practice in general has been oriented towards stimulating population increase, males have also been subject to a more extensive harvest compared to females. This male-biased harvest has resulted in female-biased populations with a high growth potential. Based on extensive data series from culled animals, population size and demographic composition have been reconstructed through cohort analyses for three regions in Norway (Veiberg et al., 2010). The adult sex ratio varied between 3-3.7 females per male. The harvest rates for adult females were rather moderate and stable through all of their lifespan (0.13-0.16). In contrast, the harvest rates of adult males were significantly higher (0.40-0.49) and varied considerably with age. The empiric harvest rates for adult females are quite in line with the steady state alternatives described for Case 1-3. These three cases also represent the most realistic harvest scenarios given the present code of conduct and the Norwegian hunting tradition. The experienced adult sex ratio was also quite equal to the steady state sex ratios in Case 1-3. A striking difference between the current hunting practice and all the steady state alternatives, apart from Case 5, is that yearling harvest represents a significant proportion of the total red deer harvest. On the national level yearlings in general represent 30 % of the total red deer harvest (Statistics Norway, 2010), and the sex specific harvest rates were found to vary between 0.16-0.26 for yearling females and 0.40-0.49 for yearling males (Veiberg et al., 2010). This indicates that there is scope for improving the economics of the present hunting practice by lowering the yearling harvest.

Defined management aims and basic knowledge about the productivity and the demographic structure of the local population is important to accomplish a given management practice. Still, considerations regarding practical feasibility and necessary harmonization with common codes of conduct represent important limitations. In addition, landowners and hunters share a common interest of securing predictable future population development. Management practices that involve regular alterations of the harvest pattern (see Figure 6) are therefore as indicated less likely to be implemented than more static practices. Apart from this, all the presented case studies represent highly feasible management practices.

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Table 1. Baseline biological parameter values.

Parameters	Description	Value	Reference/source
$\tilde{r}_{yf}$	maximum specific growth rate yearlings	0.6	Langvatn et al. (2004)
$\tilde{r}_{f}$	maximum specific growth rate adults	0.96	Langvatn et al. (2004)
K	carrying capacity females	4000 (animals)	Calibrated
b_{yf}	density compensation parameter yearlings	2	Nilsen et al. (2005)
b_{f}	density compensation parameter adults	2	Nilsen et al. (2005)
w_{c}	mean weight calves	25.5 (kg)	Solberg et al. (2010)
w_{yf}	mean weight female yearlings	43.1 (kg)	Solberg et al. (2010)
w_{ym}	mean weight male yearlings	49.4 (kg)	Solberg et al. (2010)
w_{f}	mean weight females	57.3 (kg)	Solberg et al. (2010)
w_{m}	mean weight male	77.6 (kg)	Solberg et al. (2010)
s_{c}	survival rate calves	0.75	Langvatn and Loison (1999)
s_{yf}	survival rate female yearlings	0.92	Langvatn and Loison (1999)
s_{ym}	survival rate male yearlings	0.87	Langvatn and Loison (1999)
s_{f}	survival rate adult females	0.93	Langvatn and Loison (1999)
s_{m}	survival rate adult males	0.93	Langvatn and Loison (1999)
Ψ	calf sex ratio	0.5	

Table 2. Baseline economic parameter values.

Parameters	Description	Value	Reference/source
$\hat{p}$	meat price	75 (NOK/kg)	Olaussen and Mysterud (Unpublished)
q_c	hunting fee calf	210 (NOK/animal)	Directorate for Nature Management
q_{yf}	hunting fee yearling female	350 (NOK/animal)	Directorate for Nature Management
q_{ym}	hunting fee yearling male	350 (NOK/animal)	Directorate for Nature Management
q_f	hunting fee female	350 (NOK/animal)	Directorate for Nature Management
q_m	hunting fee male	350 (NOK/animal)	Directorate for Nature Management
θ	catchability coefficient	0.0001 (1/hunting day)	Calibrated
d_c	crop damage cost calves	175 (NOK/animal)	Olaussen and Mysterud (Unpublished)
d_{yf}	crop damage cost yearling female	295 (NOK/animal)	Olaussen and Mysterud (Unpublished)
d_{ym}	crop damage cost yearling male	338 (NOK/animal)	Olaussen and Mysterud (Unpublished)
d_f	crop damage cost adult female	393 (NOK/animal)	Olaussen and Mysterud (Unpublished)
d_m	crop damage cost adult male	532 (NOK/animal)	Olaussen and Mysterud (Unpublished)
z	recreational value	50 (NOK/day)	Thorvaldsen et al. (2010)
δ	discount rate	0	

Table 3. Steady state harvest rates and populations. Recreational value not included. h_c , h_{yf} , h_{ym} , h_f , and h_m are harvest rates for calves, female yearlings, male yearlings, adult females and adult males, respectively. H is total harvest (in number of animals) and X_c , X_{yf} , X_{ym} , X_f , and X_m are population sizes (in number of animals) of calves, female yearlings, male yearlings, adult females and adult males, respectively. X is total population size.

	Case 1	Case 2	Case 3	Case 4	Case 5
h_c	0.20	0.19	0.18	0	0.18
h_{yf}	0	0	0	0	0.18
h_{ym}	0	0	0	0	0.18
h_f	0.15	0.13	0.11	0.21	0.18
h_m	0.55	0.55	0.55	0.55	0.18
H	1,060	1,088	1,096	951	732
X_c	1,651	1,717	1,799	1,632	1,165
X_{yf}	494	520	555	612	360
X_{ym}	494	520	555	612	360
X_f	2,158	2,449	3,042	2,097	1,165
X_m	740	778	830	916	1,102
X	5,532	5,984	6,780	5,869	4,151

Case 1: Baseline parameter values. Maximizing meat value minus grazing damage. Both constraints (12) and (13) included, and (13) with $\overline{h}_{ym} = \overline{h}_m = 0.55$.

Case 2: Meat price increased by 50 %

Case 3: Maximizing meat value only

Case 4: Excluding constraint (12)

Case 5: Uniform harvest pattern

Table 4. *Steady state landowner yearly cost and benefit (in 1,000 NOK).*

	Case 1	Case 2	Case 3	Case 4	Case 5
Meat value *(V)*	4,071	6,477	4,303	4,521	2,620
Crop damage *(D)*	1,843	2,006	2,303	1,984	1,476
Net benefit *(R=V-D)*	2,228	4,472	2,000	2,537	1,144
Net benefit per hunted animal *(R/H)*	2.102	4.108	1.825	2.667	1.563
Net benefit per living animal *(R/X)*	0.403	0.747	0.295	0.432	0.276

Case 1: Baseline parameter values. Maximizing meat value minus grazing damage. Both constraints (12) and (13) included, and (13) with $\bar{h}_{ym} = \bar{h}_m = 0.55$.

Case 2: Meat price increased by 50 %

Case 3: Maximizing meat value only

Case 4: Excluding constraint (12)

Case 5: Uniform harvest pattern

Figure 1. Number of harvested red deer per 10 km^2 in Norwegian municipalities in 1970 (left) and 2009 (right). The figure illustrates both the change in population density and geographical distribution. Source: Statistics Norway.

Figure 2. The study area consisted of two municipalities, Flora (A) and Gloppen (B), situated on the west coast of Norway.

Figure 3. Dynamic harvest pattern Case 1. Harvesting rates h and time (years). Harvest rates of both male and female yearlings are zero all the time.

Figure 4. Dynamic harvest pattern and discount rate. Case 1 is for zero discount rate. Total population size X and time (years).

Figure 5. Contour plots showing how different levels of landowner net benefit, meat hunting value minus grazing damage $(V-D)$ (1,000NOK) relates to variation in harvest rates of adult males (h_m) and adult females (h_f). The left and right panel illustrates the conditions described in Case 1 and Case 4 respectively.The optimal steady state is identified with dots in both panels. The numbers along the level curves indicate net economic benefit (in 1,000 NOK), and the distance between two adjacent curves is 1 mill. NOK. Note the different scaling of the two panels.

Figure 6. Dynamic harvest pattern when recreational value is included. $z=50$ (NOK/hunting day). Other parameter values and constraints as in Case 1. Harvesting rates and time (years). Harvest rates of both adult males and yearlings are kept constant at 0.55.

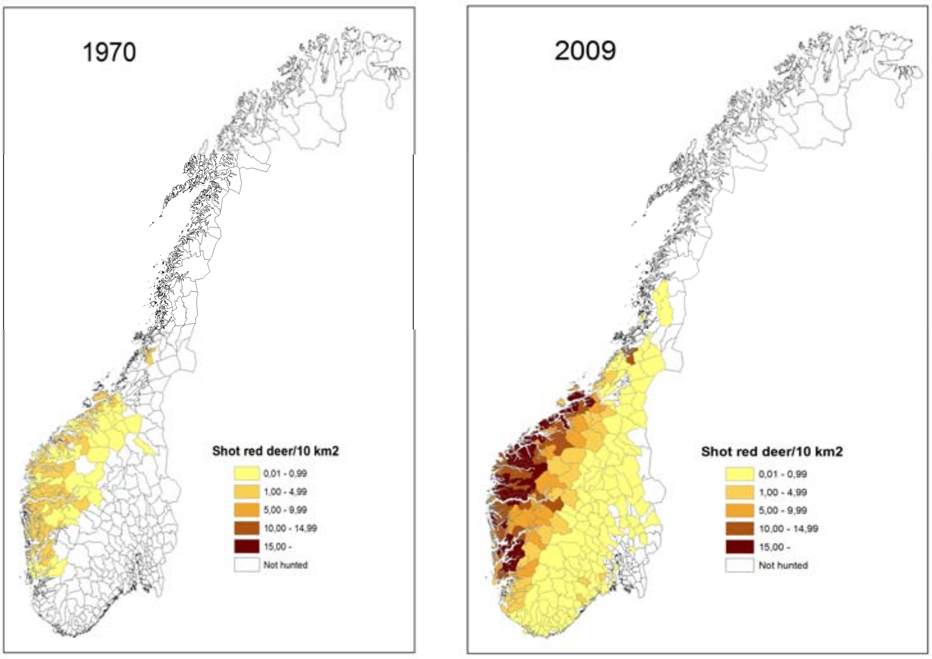

1970
Shot red deer/10 km2
0,01 - 0,99
1,00 - 4,99
5,00 - 9,99
10,00 - 14,99
15,00 -
Not hunted
2009
Shot red deer/10 km2
0,01 - 0,99
1,00 - 4,99
5,00 - 9,99
10,00 - 14,99
15,00 -
Not hunted

Figure 1

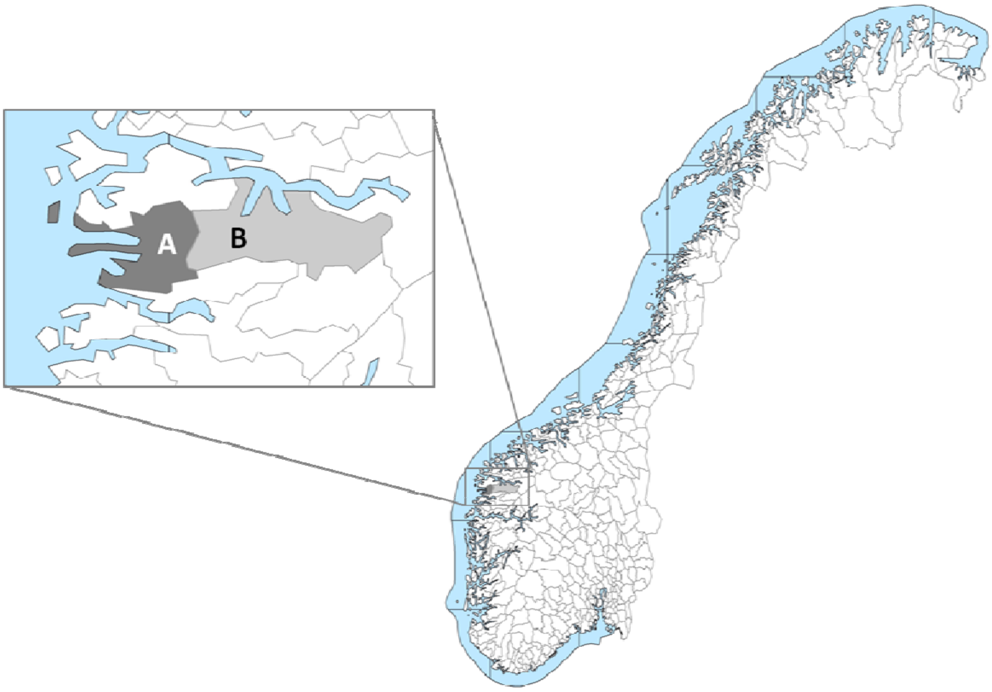


Figure 2

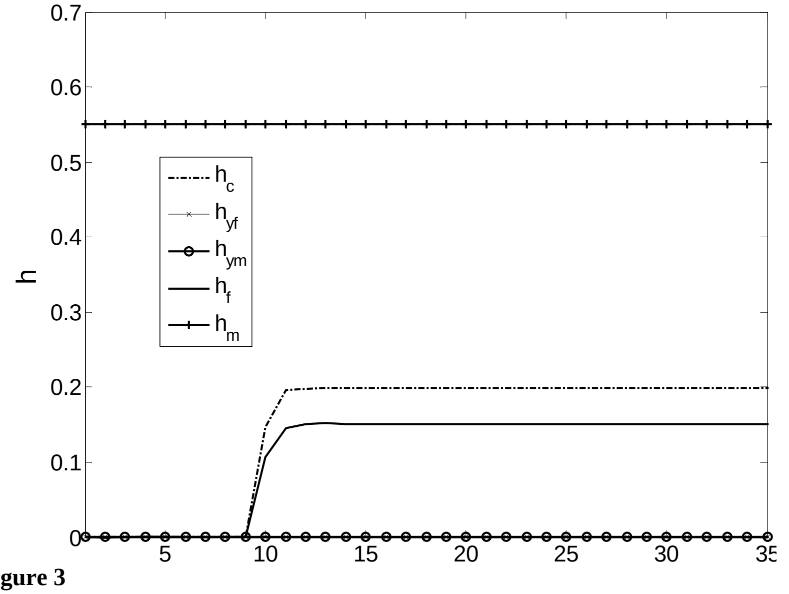


Figure 3

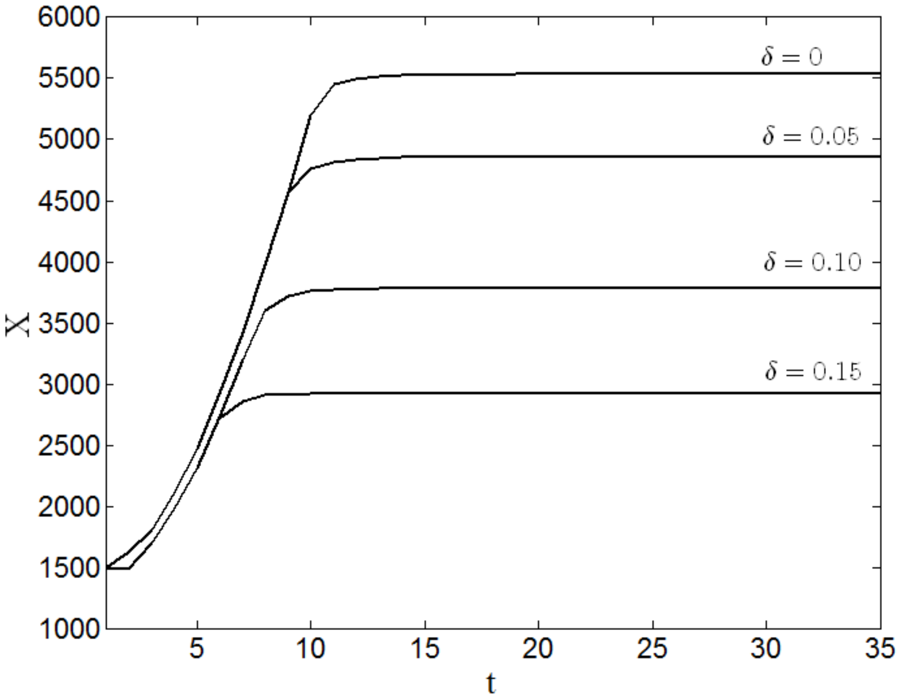
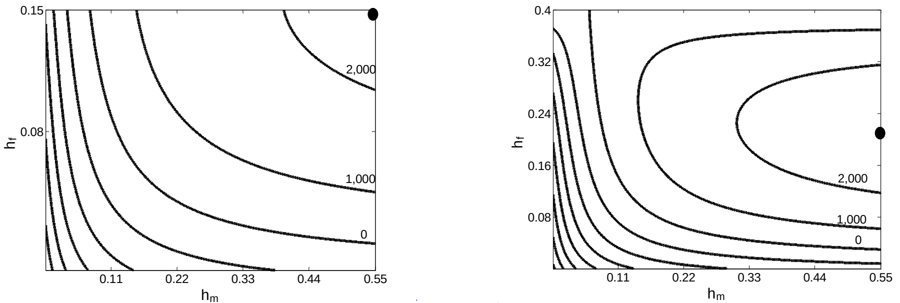


Figure 4



Case 1

Case 4

Figure 5

Formatert: Skrift: 12 pt, Understreking, Skriftfarge: Hyperkobling

Formatert: Skrift: 12 pt, Understreking, Skriftfarge: Hyperkobling

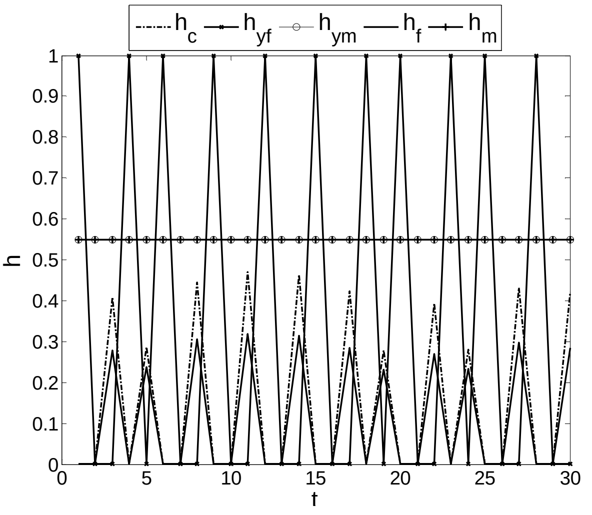


Figure 6

Supplement

The maximization problem

The Lagrangian of the problem of maximizing the present value benefit when only meat hunting value is included given the biological constraints plus constraints (12) and (13) may be written as

$$
\begin{aligned}
L = \sum_{t=0}^{\infty} \rho^t \Big\{ & \; p_c h_{c,t} X_{c,t} + \left[p_{yf} h_{yf,t} + p_{ym} h_{ym,t} (1-\psi)/\psi) \right] X_{yf,t} + p_f h_{f,t} X_{,t} + p_m h_{m,t} X_{m,t} \\
& - \rho\gamma_{t+1} \left[X_{c,t+1} - r_{yf} \left(X_{yf,t} + X_{f,t} \right) X_{yf,t} - r_f \left(X_{f,t} + X_{yf,t} \right) X_{f,t} \right] \\
& - \rho\eta_{t+1} \left[X_{yf,t+1} - \psi s_c \left(1 - h_{c,t} \right) X_{c,t} \right] \\
& - \rho\lambda_{t+1} \left[X_{f,t+1} - s_{yf} \left(1 - h_{yf,t} \right) X_{yf,t} - s_f \left(1 - h_{f,t} \right) X_{f,t} \right] \\
& - \rho\mu_{t+1} \left[X_{m,t+1} - [s_{ym} (1 - h_{ym,t})(1-\psi)/\psi] X_{yf,t} - s_m (1 - h_{m,t}) X_{m,t} \right] \\
& - \rho\omega_{t+1} \left(h_{f,t} X_{f,t} - h_{c,t} X_{c,t} \right) - \rho\zeta_{t+1} \left(h_{m,t} - \bar{h}_m \right) - \rho\chi_{t+1} \left(h_{ym,t} - \bar{h}_m \right) \Big\}
\end{aligned}
$$

$\gamma_t > 0$, $\eta_t > 0$, $\lambda_t > 0$, $\mu_t > 0$ are the shadow prices of the calf population constraint (1), female yearling constraint (2), adult female constraint (4) and adult male population constraint (7), respectively. $\omega_t \geq 0$ is the shadow price of the female – calf harvesting restriction (12), and $\zeta_t \geq 0$ and $\chi_t > 0$ are the shadow prices of the adult male and male yearlings harvesting restrictions (13). Notice that the population constraint shadow prices, in contrast to the two harvesting constraints (12) and (13), always will be strictly positive because these constraints always bind (Kuhn-Tucker theorem).

The first-order necessary control conditions of this maximizing problem are stated with the actual complementary slackness conditions and where the possibility for keeping each of the stages unexploited is considered while harvesting whole subpopulations are not considered as a possible option. These control conditions with $X_{i,t} > 0$ ($i = c, yf, ym, f, m$) read then:

(A1) $$\frac{\partial L}{\partial h_{c,t}} = X_{c,t} \left(p_c - \rho\eta_{t+1}\psi s_c + \rho\omega_{t+1} \right) \leq 0 \;;\; 0 \leq h_{c,t} < 1,$$

(A2) $$\frac{\partial L}{\partial h_{yf,t}} = X_{yf,t} \left(p_{yf} - \rho\lambda_{t+1} s_{yf} \right) \leq 0 \;;\; 0 \leq h_{yf,t} < 1,$$

(A3) $$\frac{\partial L}{\partial h_{ym,t}} = X_{ym,t} \left(p_{ym} - \rho\mu_{t+1} s_{ym} \right) \leq 0 \;;\; 0 \leq h_{ym,t} < 1,$$

(A4) $$\frac{\partial L}{\partial h_{f,t}} = X_{f,t} \left(p_f - \rho\lambda_{t+1} s_f - \rho\omega_{t+1} \right) \leq 0;\; 0 \leq h_{f,t} < 1$$

and

(A5) $$\frac{\partial L}{\partial h_{m,t}} = X_{m,t} (p_m - \rho\mu_{t+1} s_m - \rho\xi_{t+1} / X_{m,t}) \leq 0 \;;\! 0 \leq h_{m,t} < 1.$$

The portfolio conditions $\partial L / \partial X_{i,t} = 0$ ($i = c, yf, f, m$) are rather messy and are not stated here.

Condition (A1) says that calf harvest should take up to the point where marginal harvest value is equal to, or below, the cost in term of reduced yearling growth of both categories evaluated at their shadow prices while also taking the discounting into account. The female - calf harvesting restriction shadow price is also included in this condition. When this condition holds as an inequality, the marginal benefit is below its marginal cost and harvesting of this stage is thus not profitable, $h_{c,t}=0$. In a similar manner, condition (A2) and (A3) indicate that harvesting of the yearling female (male) category should take place up to the point where the marginal benefit is equal to, or below, the cost in terms of reduced population of adult females (males). The female and male adult conditions (A4) and (A5), respectively, can be given a similar interpretations, but the shadow cost of the female - calf harvesting constraint is included in the female condition (A4) while the shadow cost of the male harvesting rate is included in condition (A5).

These first order control conditions together the portfolio conditions and the biological constraints comprise a complex dynamic system. It is therefore difficult, if not impossible, to assess the dynamics analytically. However, based on the control conditions, it is possible to draw some important conclusions about the harvesting composition. To see this, we look away from the constraints (12) and (13). The above conditions are then simplified to:

(A1’) $\frac{\partial L}{\partial h_{c,t}}=X_{c,t}(p_c-\rho\eta_{t+1}\psi s_c)\le 0\ ;\ 0\le h_{c,t}<1,$

(A2’) $\frac{\partial L}{\partial h_{yf,t}}=X_{yf,t}(p_{yf}-\rho\lambda_{t+1}s_{yf})\le 0\ ;\ 0\le h_{yf,t}<1,$

(A3’) $\frac{\partial L}{\partial h_{ym,t}}=X_{yf,t}(p_{ym}-\rho\mu_{t+1}s_{ym})\le 0\ ;\ 0\le h_{ym,t}<1,$

(A4’) $\frac{\partial L}{\partial h_{f,t}}=X_{f,t}(p_f-\rho\lambda_{t+1}s_f)\le 0;\ 0\le h_{f,t}<1$

and

(A5’) $\frac{\partial L}{\partial h_{m,t}}=X_{m,t}(p_m-\rho\mu_{t+1}s_m)\le 0\ ;0\le h_{m,t}<1.$

From these conditions it is straightforward to find that harvesting female yearlings and females at the same time cannot represent a possible optimal policy. To see this, assume first that female yearling harvest is optimal. (A2’) (with $X_{yf,t}>0$) holds then as $p_{yf}=\rho\lambda_{t+1}s_{yf}$. In a similar manner, assume next that female harvest is optimal. With $X_{f,t}>0$, (A4’) then reads $p_f=\rho\lambda_{t+1}s_f$. Combining these two equation yields then $p_{yf}/s_{yf}=p_f/s_f$. As only parameters are included here, this equation holds only by accident, Therefore, harvesting both these two stages at the same time cannot represent an optimal solution when the constraints (12) and (13) are not binding and when the harvest recreation value is not included. When combining (A3’) and (A5’) we can draw a similar type of conclusion; that is, harvesting male yearlings and males at the same time is not in accordance with the optimality conditions. In the main text (section 5.1) more discussions based on (A1’) – (A5’) are found. For example, harvesting female yearlings together with zero adult female harvesting yields $p_{yf}/s_{yf}>p_f/s_f$, which represents a contradiction due to the structure of the parameter values.

When including grazing damage, $D_t=d_cX_{c,t}+d_{fy}X_{fy,t}+d_{my}X_{my,t}+d_fX_{f,t}+d_mX_{m,t}$, but still not including the recreational hunting value, the landowner problem is to

$\max\limits_{h_{c,t}, h_{fy,t}, h_{my,t}, h_{f,t}, h_{m,t}} \sum_{t=0}^{t=\infty} \rho^t (V_t - D_t)$, again subject to the biological growth equations (1), (2), (4) and (7) together with constraints (12) and (13). It is easily recognized that the control conditions of this problem will be similar to that of (A1) – (A5) because the harvest rates are not includet in the D_t expression; that is, the damage occurs before the hunting.

When the recreational value also is included, the problem is to maximize

$$\sum_{t=0}^{\infty} \rho^t (V_t - D_t + B_t) = \sum_{t=0}^{\infty} \rho^t \Big\{ \; p_c h_{c,t} X_{c,t} + \left[p_{yf} h_{yf,t} + p_{ym} h_{ym,t} (1-\psi)/\psi) \right] X_{yf,t} + p_f h_{f,t} X_{,t} + p_m h_{m,t} X_{m,t}$$
$$- (d_c X_{c,t} + d_{fy} X_{fy,t} + d_{my} X_{my,t} + d_f X_{f,t} + d_m X_{m,t}) + (z/\theta)\left(h_{c,t} + h_{yf,t} + h_{ym,t} + h_{f,t} + h_{m,t} \right) \}$$

to the same constraints as above.

The first-order necessary control conditions with $X_{i,t} > 0 \, (i = c, yf, ym, f, m)$ read now:

(A1’’) $\dfrac{\partial L}{\partial h_{c,t}} = X_{c,t}\left(p_c + z/\theta X_{c,t} - \rho \eta_{t+1} \psi s_c + \rho \omega_{t+1} \right) \leq 0 \;\; ; \; 0 \leq h_{c,t} < 1,$

(A2’’) $\dfrac{\partial L}{\partial h_{yf,t}} = X_{yf,t}\left(p_{yf} + z/\theta X_{yf,t} - \rho \lambda_{t+1} s_{yf} \right) \leq 0 \; ; \; 0 \leq h_{yf,t} < 1,$

(A3’’) $\dfrac{\partial L}{\partial h_{ym,t}} = X_{ym,t}\left(p_{ym} + z\psi/(1-\psi)\theta X_{yf,t} - \rho \mu_{t+1} s_{ym} \right) \leq 0 \; ; \; 0 \leq h_{ym,t} < 1,$

(A4’’) $\dfrac{\partial L}{\partial h_{f,t}} = X_{f,t}\left(p_f + z/\theta X_{f,t} - \rho \lambda_{t+1} s_f - \rho \omega_{t+1} \right) \leq 0; 0 \leq h_{f,t} < 1$

and

(A5’’) $\dfrac{\partial L}{\partial h_{m,t}} = X_{m,t}(p_m + z/\theta X_{m,t} - \rho \mu_{t+1} s_m - \rho \xi_{t+1} / X_{m,t}) \leq 0 \;\; ; 0 \leq h_{m,t} < 1.$

The important difference is now that the population sizes are included in these control conditions.