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Balancing income and cost in red deer management

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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 meat values and survival rates ('biological discounted' values) are instrumental in determining the optimal harvest composition. Fertility plays no direct role. It is argued that this is a general result working in stage-structured models with harvest values. In the numerical illustration it is shown that the optimal harvest pattern stays quite stable under various parameter changes. It is revealed which parameters and harvest restrictions that is most important. We also show that the current harvest pattern involves too much yearling harvest compared with the economically efficient level.

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1. 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 abundance 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 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 2800, and animals were mainly found in scattered and low-density populations along the south-western part of the country (Fig. 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.

Red deer are extensively utilized as a game species, and the management strategy in Norway has traditionally been oriented toward 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 benefits 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

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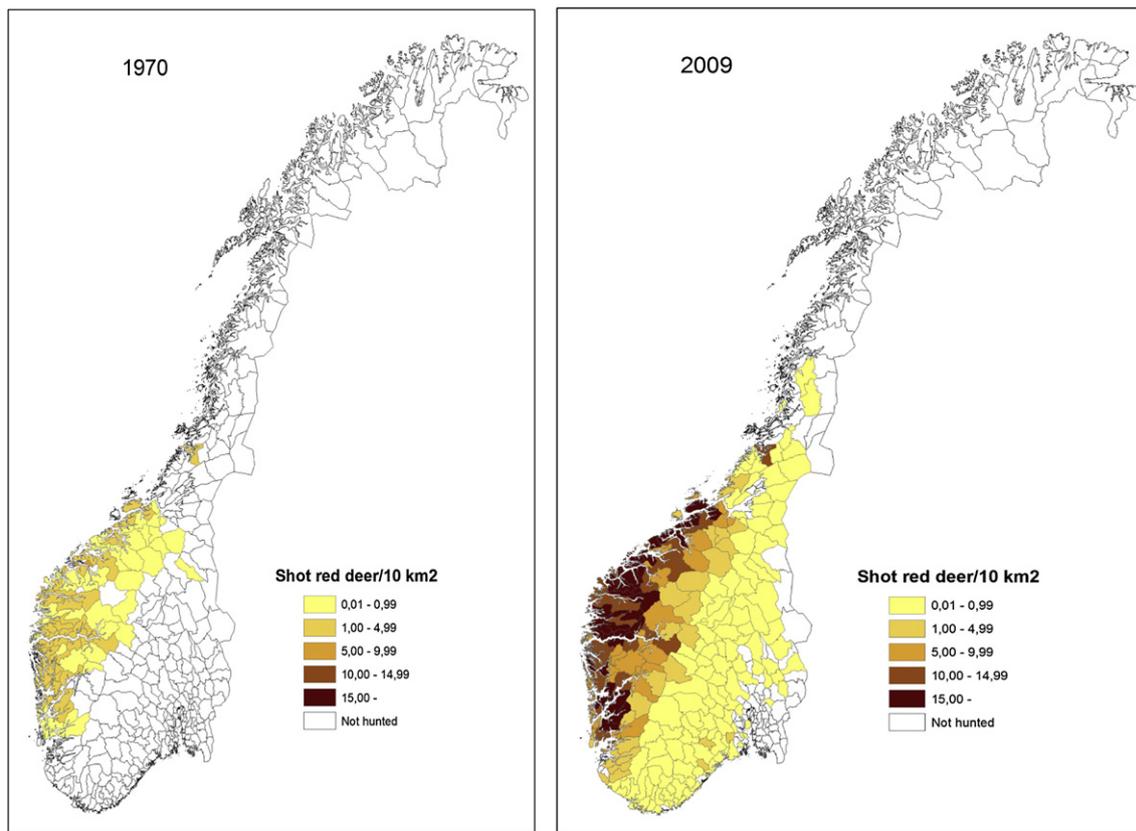


Fig. 1. Number of harvested red deer per 10 km² in Norwegian municipalities in 1970 (left) and 2009 (right). The figure illustrates both the change in population density and geographical distribution. Source: Statistics Norway.

income (Olaussen and Mysterud, 2012). 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 important in some areas. There are also significant costs related to deer–vehicle collisions (Mysterud, 2004). Such costs are both complex to quantify (Bissonette et al., 2008) and paid by the general public.

We apply a five-stage population model (calves, female and male yearlings, adult females, and adult males). The main goal is to analyze the basic economic and biologic driving forces behind 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 theoretical results are illustrated numerically. 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, but also taking the recreational aspect of the hunting into account. We also compare the results with the present harvesting pattern, which has been established through cohort analyses (Veiberg et al., 2010). Our analysis may be related to the small, but growing literature, on economic analysis of stage structured fishery and animal models, exemplified by Tahvonen (2009) and Olaussen and Skonhoft (2011). Like these studies a dynamic optimization framework is used, but different from these studies more value components are included in the management problem.

2. Methods and material

2.1. 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. As mortality throughout summer and fall is regarded to be small, all natural mortality is supposed to take place during the winter and after the hunting season and are assumed density-independent (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).

In the present analysis the population at time (year) t is structured in five stages: calves $X_{c,t}$ ($yr < 1$), female yearlings $X_{yf,t}$ ($1 \leq yr < 2$), male yearlings $X_{ym,t}$, adult females $X_{f,t}$ ($yr \geq 2$) and adult males $X_{m,t}$. The population is measured in spring before calving. All stages may be harvested, and where the hunting starts early September and ends mid-November. Neglecting any 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 negligible influence on female fertility rates (Mysterud et al., 2002). We therefore assume that only the total number of females, yearlings and adults, affect female fertility rates.

Table 1
Baseline biological parameter values.

Parameters	Description	Value	Reference/source
\bar{r}_{yf}	Maximum specific growth rate yearlings	0.6	Langvatn et al. (2004)
\bar{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	

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:

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

The number of female and male yearlings follows next as:

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

and

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

where s_c is the fixed calf natural survival rate (fraction) and ψ is the proportion of female calves. $0 \leq h_{c,t} \leq 1$ is the calf harvesting rate. Finally, the abundance of adult females and males become:

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

and

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

respectively. s_f and s_m are the fixed natural survival rate of adult females and males, and where $s_f \geq s_m$. s_{yf} and s_{ym} are the yearling survival rates, also with $s_{yf} \geq s_{ym}$ (Table 1). $0 \leq h_{yf,t} \leq 1$ and $0 \leq h_{ym,t} \leq 1$ are the harvesting rates of female and male yearlings, respectively, while $0 \leq h_{f,t} \leq 1$ and $0 \leq h_{m,t} \leq 1$ are the harvesting rates of the two adult stages.

Eqs. (2) and (3) together yield:

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

Therefore, with $\psi \approx 0.5$ the number of female and male yearlings will be similar at every point in time. Using Eq. (6) to eliminate $X_{ym,t}$ from Eq. (5), we find the abundance of adult males as:

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

Eqs. (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.

2.2. Landowner benefits and costs

As indicated, management units regularly consist of several landowners. Each landowner contributes to the total area (the counting area) with the part of their property that satisfies given criteria defined in regulations. On the basis of the total counting area, the municipality then allows harvest of a given number of deer. Within the management unit, decisions related to e.g. distribution of hunting licenses, costs and income are made by majority of votes. In the voting process all landowners either represent equal votes or their influence is differentiated through weighted voting on the basis of their contribution to the common counting area. The traditional landowner management goal has been directed toward maximizing the population productivity in order to produce meat, but also with a strong recreational component (Andersen et al., 2010; Milner et al., 2006). The hunters have typically 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, 2012). In what follows, we think of the hunters as the local people enjoying the meat value and the recreational value of the hunting. The utility derived from the meat value is assumed to be linear in the hunt, while the recreational value is linear in the hunting rates. As will be seen, this difference has a substantial impact on the solution of the model.

We start to look at the hunting where 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 $w_c < w_{yf} \leq w_{ym} < w_f < w_m$ 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:

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

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. Studies from elk hunting in US (Aiken and Pullis La Rouché, 2001) and from Sweden (Boman et al., 2011) indicate 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 $H_{i,t} = \theta_i N_{i,t} X_{i,t}$ ($i = c, yf, ym, f, m$). $N_{i,t}$ hence indicates the hunting effort, measured in number of hunting days, and θ_i is the catchability (productivity) coefficient (1/hunting days). The value will typically differ somewhat between the various categories of animals, but probably not too much. In what follows, it

Table 2
Baseline economic parameter values.

Parameters	Description	Value	Reference/source
\hat{p}	Meat price	75 (NOK/kg)	Olaussen and Mysterud (2012)
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 (2012)
d_{yf}	Crop damage cost yearling female	295 (NOK/animal)	Olaussen and Mysterud (2012)
d_{ym}	Crop damage cost yearling male	338 (NOK/animal)	Olaussen and Mysterud (2012)
d_f	Crop damage cost adult female	393 (NOK/animal)	Olaussen and Mysterud (2012)
d_m	Crop damage cost adult male	532 (NOK/animal)	Olaussen and Mysterud (2012)
z	Recreational value	50 (NOK/day)	Thorvaldsen et al. (2010)
$\hat{\delta}$	Discount rate	0	

is assumed to be identical. 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

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

when substituting for the harvest functions. 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 one of the core hunting areas in Norway Thorvaldsen et al. (2010) found that crop damages on agricultural land was more important than damages to commercial tree species. Only crop damage is considered here, and as it takes place during the spring, summer and early fall, it is the pre-harvest population size that is relevant. When assuming that the agriculture damage cost functions are linear, with unit values as $d_c < d_{yf} \leq d_{ym} < d_f < d_m$ (Table 2), these costs may thus be written as:

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

Therefore, the landowner yearly net benefit is described by:

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

2.3. Optimal management

2.3.1. Hunting meat value benefit only

We first study the situation where the landowner maximizes the hunting benefit meat value only. With $\rho = 1/(1 + \delta)$ as the discount factor with $\delta \geq 0$ as the (yearly) fixed discount rate, the goal is thus to find harvest rates that maximizes the present-value $\max_{h_{c,t}, h_{yf,t}, h_{ym,t}, h_{f,t}, h_{m,t}} \sum_{t=0}^{\infty} \rho^t V_t$ subject to the biological growth Eqs. (1), (2), (4) and (7). In addition, a female–calf harvest restriction is included (Olaussen and Skonhøft, 2011) due to the common code of conduct among hunters to avoid shooting the mother from calves:

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

A restriction on the number of harvested males is also incorporated to avoid a too skewed sex ratio:

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

In a Supplement section the optimal control conditions are stated and the basic driving forces steering the harvest composition

are revealed. 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. When the adult category is more valuable than the yearling category, $p_f > p_{yf}$, and as long as 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 realistic 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.

Since, the 'biological discounted' value of the calf category is lower than for the yearlings, $p_c/s_c < p_i/s_i$ ($i = yf, ym$) (see Tables 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. 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.

Based on the optimality conditions it is difficult to say something definite about the harvest composition among the adults. 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). 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 restriction (13) is included and binds, $h_{m,t} = h_{ym,t} = \bar{h}_m$, 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.

2.3.2. 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. Therefore, the problem now is to find the harvesting strategy that $\max_{h_{c,t}, h_{yf,t}, h_{ym,t}, h_{f,t}, h_{m,t}} \sum_{t=0}^{\infty} \rho^t (V_t - D_t)$, again subject to the biological growth Eqs. (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 (Supplement section). However, we may suspect that the harvesting pressure will be higher when damage costs are included (see e.g., Skonhoft and Olausen, 2005).

2.3.3. Recreational value included

When taking the recreational value of hunting into account, the current net benefit is defined by Eq. (11), and the problem is hence to $\max_{h_{c,t}, h_{yf,t}, h_{ym,t}, h_{f,t}, h_{m,t}} \sum_{t=0}^{\infty} \rho^t (V_t + B_t - D_t)$, subject to the same constraints as above. The solution to this problem gives the 'overall' optimal solution for the landowners. In this case, not only differences in per animal values and survival rates ('biological discounted' values) are instrumental in determining the harvest composition, but also the demographic composition of the population (see Supplement section). 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.

3. Results

3.1. Data and specific functional forms

The model is now illustrated numerically for an area located in the county Sogn and Fjordane on the south-western coast of Norway. This county is the core area for red deer hunting in Norway. 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:

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

with $\hat{r}_i > 0$ as the intrinsic growth rate (maximum number of calves per female), $K > 0$ as the female 'carrying capacity' and $b_i > 0$ as a compensation parameter. Eq. (14) then implies the recruitment function (1) of the 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 and is 4000 (animals). See Table 1.

The baseline economic parameter values are given in Table 2. The value of the catchability coefficient $\theta = 0.0001$ (1/hunting days) is calibrated based on reported hunting productivity. The per day recreational hunting value $z = 50$ (NOK/day) is taken from a study from the actual area (Thorvaldsen et al., 2010). The crop damage cost parameters are based on Olausen and Mysterud (2012) while the meat value \hat{p} is assumed similar among all categories of animals. We assume a zero discount rate in the baseline scenario. As 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.

3.2. Results when recreation value is not included

We first present the basic dynamic harvesting results.¹ 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. Because the profit function is linear in harvest, economic theory for one-stage models (or biomass models) suggest that harvest should be adjusted such as to lead the populations to their optimal steady states as rapid as possible – if no constraints are binding (for proof of the Most Rapid Approach Path theorem, see Spence and Starrett, 1975). Fig. 2 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 also in our linear multi-stage model. 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 harvest until the optimal population size is reached would lead to overshooting. We also studied the effect of changing the discount rate on the time path and steady state in this Case 1. We find, not surprisingly, that increasing the discount rate results in progressively smaller populations 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. 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 rates and population sizes for all

¹ The dynamic optimization was performed with the KNITRO for MATLAB solver from Ziena Optimization, with MATLAB release 2011b.

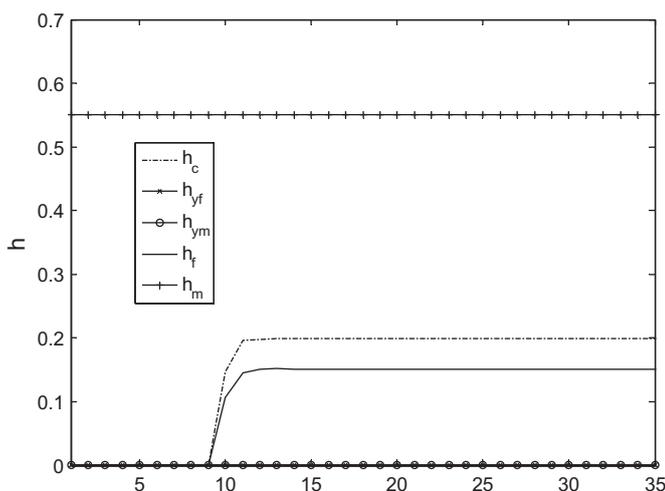


Fig. 2. Dynamic harvest pattern Case 1. Harvesting rates h and time (years). Harvest rates of both male and female yearlings are zero all the time.

stages. Table 4 presents the economic results. From Table 3 we see that 20% of the calves are harvested in Case 1, 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 $h_m = 0.55$. It is not beneficial with harvest of yearlings because the ‘biologically discounted’ values are lower for yearlings than for adults. The adult male/female sex ratio becomes $740/2158 \approx 0.34$. In this case, as well as in the other cases, we find identical numbers of yearling males and yearling females because of equal sex ratio in the recruitment, $\psi = 0.5$ (see Methods and material section and Table 1). From Table 4, we find the total yearly meat value to be 4071 (1000 NOK), with grazing damage costs being 1843. Net average yearly income per hunted animal is 2.102 (1000 NOK).

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

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	1060	1088	1096	951	732
X_c	1651	1717	1799	1632	1165
X_{yf}	494	520	555	612	360
X_{ym}	494	520	555	612	360
X_f	2158	2449	3042	2097	1165
X_m	740	778	830	916	1102
X	5532	5984	6780	5869	4151

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: As Case 1, but meat price increased by 50%.

Case 3: As Case 1, but maximizing meat value only.

Case 4: As Case 1, but excluding the female-calf constraint (12).

Case 5: Uniform harvest pattern. Maximizing meat value minus grazing damage.

Table 4

Steady-state landowner yearly cost and benefit (in 1000 NOK).

	Case 1	Case 2	Case 3	Case 4	Case 5
Meat value (V)	4071	6477	4303	4521	2620
Crop damage (D)	1843	2006	2303	1984	1476
Net benefit ($R = V - D$)	2228	4472	2000	2537	1144
Net benefit per total hunted animal (R/H)	2.102	4.108	1.825	2.667	1.563
Net benefit per total 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: As Case 1, but meat price increased by 50%.

Case 3: As Case 1, but maximizing meat value only.

Case 4: As Case 1, but excluding the female-calf constraint (12).

Case 5: Uniform harvest pattern. Maximizing meat value minus grazing damage.

standing populations (Table 3). This result contrasts standard biomass harvesting theory (e.g., Clark, 1990). 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 harvest activity, a price increase leads to an equal increase in income. When costs are unchanged, the increase in net benefit will, however, 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 Eq. (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, is reduced. This leads to a change in harvest pattern and population size that works in the same direction as the price increase. 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).

The female-calf constraint (12) is excluded in Case 4. As expected, there is no harvest of calves. 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 2228 (1000 NOK) to 2537, 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.

The contours in Fig. 3 indicate the steady state net economic benefit ($V - D$) for different combinations of h_f and h_m , and demonstrate 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. The left panel is for the baseline Case 1, while the right panel is for Case 4 (i.e., 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 the left panel 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 2000 (1000 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 the right, panel, where the code of

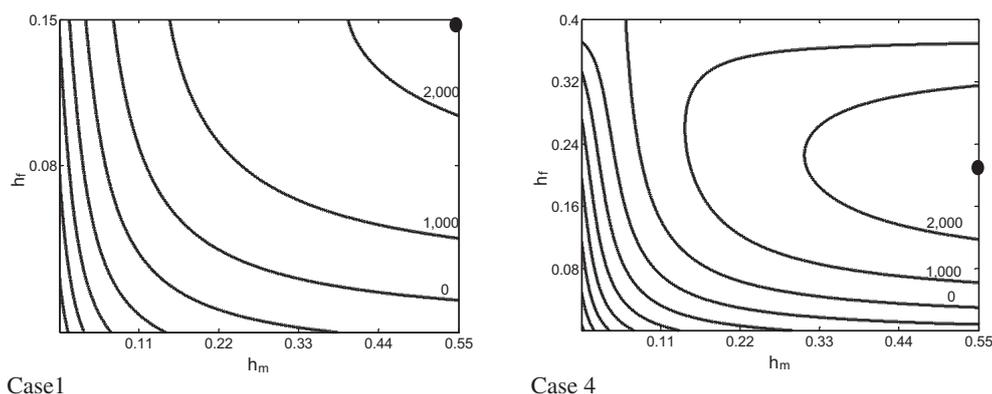


Fig. 3. Contour plots showing how different levels of landowner net benefit, meat-hunting value minus grazing damage ($V-D$) (1000 NOK) relates to variation in harvest rates of adult males (h_m) and adult females (h_f). The left and right panel illustrates the conditions described in Case 1 and Case 4, respectively. The optimal steady state is identified with dots in both panels. The numbers along the level curves indicate net economic benefit (in 1000 NOK), and the distance between two adjacent curves is 1 mill. NOK. Note the different scaling of the two panels.

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 profit is to a large extent due to grazing damage being linearly related to population size, an assumption that may be unrealistic for large populations.

3.3. 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 Tables 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.

3.4. 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. Fig. 4 shows that, under the same assumptions as in Case 1, 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, 0.30 and 1, respectively.

The pulse cycle lengths seem to be quite similar for the different stages. However, the periods of hunting are not synchronized and where the top of the cycles occurs earlier for the adult than the yearlings and the calves. As indicated above (Optimal management section), more complex dynamics 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. All these factors may also influence the synchronizing of the pulse hunting. For baseline parameter values, pulse harvesting occurs only if the recreational parameter z value exceeds a certain critical value ($z = 25$).

4. Discussion and conclusion

In this paper we have analyzed the cost and benefit of a red deer population within a five-stage model with density-dependent

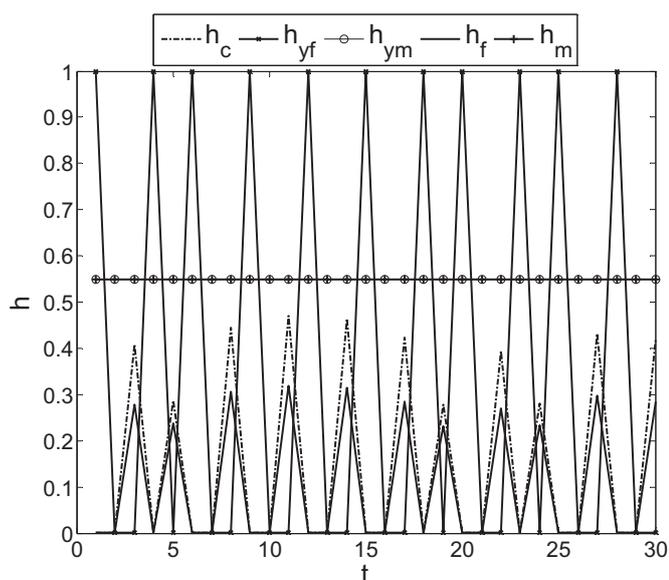


Fig. 4. Dynamic harvest pattern when recreational value is included. $z = 50$ (NOK/hunting day). Other parameter values and constraints are as in Case 1. Harvesting rates and time (years). Harvest rates of both adult males and yearlings are kept constant at 0.55.

fertility and density-independent mortality. This population is managed by a well-defined manager 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 that the 'biological discounted' values for the various categories of animals are instrumental in determining the optimal harvesting composition. The difference in the 'biological discounted' value between two animal categories is made up of the net per animal meat value difference as the marginal gain while the difference in natural mortality rate represents the marginal loss. The importance of these factors seems to be a general result in stage structured models where harvest value is maximized. See e.g., the moose harvest model in Olausen and Skonhoft (2011), the fishery analysis in Skonhoft et al. (2012) and the classical Reed (1980) fishery article.

The Results section illustrates numerically 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. When the code of conduct constraint (12) is excluded (Case 4), we find that no calves are harvested, and the harvest of adult females increased to 21%. Net benefit increased by 14%. The landowner net benefit is also calculated when the optimal selective harvesting patterns were replaced by 'optimal' uniform harvest rates (Case 5).

When the recreational hunting value is included in the objective function, we find 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 (e.g., Wirl, 1995), and in particular when there is imperfect selectivity in the harvest (Tahvonen, 2009).

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. This is also so for calves in our numerical illustration. As the traditional management practice in general has been oriented toward 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 and 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 empirical 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 a clear scope for improving the economics of the present hunting practice by lowering the yearling harvest. The current harvesting strategy is consolidated through a mixture of economic, ecological and evolutionary factors in addition to cultural history and former management aims lingering after the aim has been achieved (Milner et al., 2011). The current practice with a relatively large proportion of both yearlings and calves in the harvest in both Sweden and Norway for both red deer and moose was introduced many decades ago when population growth was a main management goal. There is, however, an increasing awareness of red deer as an economic resource (Olausen and Mysterud, 2012) which may stimulate a future approach to a more economically optimized harvesting strategy as presented here.

Appendix A. Supplement section

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

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

$\gamma_t > 0$, $\eta_t > 0$, $\lambda_t > 0$, $\mu_t > 0$ 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:

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

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

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

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

and

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

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, conditions (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 interpretation, 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:

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

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

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

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

and

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

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, $D_t = d_c X_{c,t} + d_{fy} X_{fy,t} + d_{my} X_{my,t} + d_f X_{f,t} + d_m X_{m,t}$, but still not including the recreational hunting value, the landowner problem is to $\max_{h_{c,t}, h_{yf,t}, h_{ym,t}, h_{f,t}, h_{m,t}} \sum_{t=0}^{\infty} \rho^t (V_t - D_t)$,

again subject to the biological growth Eqs. (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 included 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 $\sum_{t=0}^{\infty} \rho^t (V_t - D_t + B_t) = \sum_{t=0}^{\infty} \rho^t \{p_c h_{c,t} X_{c,t} + [p_{yf} h_{yf,t} + p_{ym} h_{ym,t} (1 - \psi) / \psi] X_{yf,t} + p_f h_{f,t} X_{f,t} + p_m h_{m,t} X_{m,t} - (d_c X_{c,t} + d_{fy} X_{fy,t} + d_{my} X_{my,t} + d_f X_{f,t} + d_m X_{m,t}) + (z/\theta)(h_{c,t} + h_{yf,t} + h_{ym,t} + h_{f,t} + h_{m,t})\}$ 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:

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

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

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

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

and

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

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

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