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Optimal harvesting of an age-structured, two-sex herbivore–plant system

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ABSTRACT

This study presents an optimal harvesting model for the semi-domesticated reindeer (*Rangifer t. tarandus*) and its main winter energy source, ground lichens (*Cladonia* spp.). Females are divided into 17 age classes and males into 13. Reproduction is specified by a modified harmonic mean mating function and an age-specific reproduction success. Lichen availability determines individuals' overwinter weight decrease, natural mortality, the number of calves per females and calves' birth weight. The reindeer herding cooperative can choose the number of animals harvested from the 30 age/sex classes and is assumed to maximize the preset value of net income. The structured optimization model is solved as a fully dynamic system and for initial states that may not be close to the optimal steady state. This enables to study optimal recovery from overgrazed pastures and the optimality of the constant escapement policy. We show that given zero interest rate the optimal steady-state lichen density is less than 50% of the maximum sustainable yield level but nearly twice as high as empirically observed. Density dependence at optimal equilibrium is realized in calf weight and in the average number of calves per female. Optimal slaughtering is concentrated on six-month-old calves. Adult females are slaughtered at the age of 9.5 years and males at the age of 5.5 years. A moderate or high interest rate increases the steady state reindeer population but decreases pasture conditions. Dynamic solutions deviate from constant escapement, implying that the optimal recovery from initially overgrazed pastures is slower than suggested in existing studies and actual policy. The shadow value for males is three times higher than for females.

1. Introduction

Reindeer husbandry is an important livelihood and integral part of the sociocultural life in Northern Fennoscandia Norway, Sweden, Finland and Russia. One main threat of the livelihood in Finland and some other parts of Fennoscandia is the alarmingly deteriorating conditions of the important wintertime ground lichen (*Cladonia* spp.) pastures. This is caused by overgrazing and the reduction of pastures by forestry, mining and tourism (Väre et al., 1996; Berg et al., 2008; Vistnes and Nellemann, 2008; Kumpula et al., 2013). One possible solution is artificial complementary feeding. However, this may lead to an insidious cycle: high population levels are maintained, pasture conditions continue to decrease, complementary feeding is increased and finally the intensive feeding and its high expenses endanger sociocultural traditions and the future of the livelihood. High reindeer densities may additionally decrease bird species richness and biodiversity (Ims and Henden, 2012). In Finland reindeer husbandry is organized into 56 cooperatives formed by private reindeer owners. Reindeer herd sizes are controlled by the Ministry of Agriculture and Forestry, who sets the upper bounds for each cooperative. Until now however, research has only offered limited understanding on the nature of reindeer husbandry as a livelihood and a dynamic human-controlled herbivore–plant system.

In a recent survey Pape and Löffler (2012) conclude that "interdisciplinary approaches to assess the system 'reindeer husbandry' as a whole remain scarce". During the last decade, this topic is dealt with in approximately 5% of publications. Three interdisciplinary studies on reindeer husbandry as a system are Virtala (1992, 1996) and Moxnes et al. (2001). They developed a two state variable lichen-reindeer model, where harvesting is chosen for maximizing harvesting income over a long time period. Results include constant escapement as an optimal harvesting solution and optimal steady-state levels for lichen and reindeer densities. However, these studies do not include the population age/sex structure. These play essential roles in recruitment and harvesting, since a major part of slaughtering targets calves (Kojola and Helle, 1993; Kumpula et al., 1998). Population structure is

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also important in maintaining lichen pasture conditions. Gordon et al. (2004) reviewed the studies on wild large herbivores and emphasized "that management must be tailored to the age and sex structure of the population, rather than to simple population counts."

Petersson and Danell (1992) used a Leslie matrix-type of model to evaluate the production consequences of lost animals. According to their results the consequences of losing an adult female were 1.2–1.7 times higher than their carcass weight, while the loss of males equated to less than their carcass weight. Their model includes age and (fixed) sex structure but no pastures, energy budgets or optimization. In Danell and Petersson (1994) structured model the yearly cycle is divided up to 11 time steps. Pasture resources are included as an external factor. Adding density dependences and the possibility of finding parameter values to such a model were discussed. Olofsson et al. (2011) developed a model with interacting lichen, energy and herd modules. The lichen module describes lichen growth as a function of lichen height. The energy module describes energy intake and expenditure for each animal category and the herd module projects the change in the number of individuals in various age and sex classes. The model is very detailed but sex structure does not impact reproduction and harvesting is not optimized. According to the main findings limited pasture conditions are realized as lower fecundity and smaller body size.

The objective of our study is to develop, solve and analyze a two-sex, age-structured optimal harvesting model for a reindeer-lichen system. The main emphasis is specifying lichen–herbivore interaction, the effect of sex structure on recruitment and dynamically optimizing the harvest over the age and sex structure. According to our knowledge optimization models with similar features do not exist for reindeers or any similar herbivores.

Age- and sex-structured models have been specified for several other closely related herbivores, but typically without including food resources or detailed optimization. Walters and Bandy (1972) analyze an age-structured model for a hypothetical deer population, and demonstrate that the yield from non-selective hunting is maximized by applying periodic harvesting. Walters et al. (1975) specify an age-structured model for Canadian caribou, including food dynamics, and show that hunting appears to be the critical factor instead of food supply. Milner-Gulland (1994) specifies a stochastic age- and sex-structured model for saiga antelopes but without optimization. Milner-Gulland (1997) applies dynamic programming in a model for saiga antelope with state variables for total population size and shares of adult males and females. The decision variables are hunting mortality and the proportion of hunted males. The inclusion of the breeding sex ratio is found to be a key model feature. Xu and Boyce (2010) present a stage class model for moose population in Alberta. The population is divided into calves and adult females and males. Density dependence limits recruitment and calf survival. Food resources are excluded. It is found that (static) MSY requires intensive harvesting of calves and males but low harvesting for females.

Our model includes 16 age classes of adult females and 12 classes of adult males, in addition to the first-year calves. Sex structure is specified by a modified harmonic mean mating system which recognizes the polygynous nature of reindeer. Lichen resources develop over time and the intake per animal per winter day takes into account the individual's weight, lichen density and alternative energy sources. Density dependence is realized as the effects of energy availability on individuals' overwinter weight decrease and as its consequences on mortality, number of calves per female, and the birth weight of calves. These relationships are based on existing empirical studies and some original data. Describing reindeer husbandry as a dynamic optimization problem becomes plausible as herd owners decide the age- and sex-specific slaughtering levels during annual reindeer round-ups. These decisions determine annual meat production quantities and incomes, but also the development of the population and lichen pastures. It is assumed that the herders' cooperative aim is to reach the highest possible present value of net income stream over an infinite horizon. The decision variables are the animals chosen for slaughter from the age and sex classes. The optimization model is solved as a large-scale, non-linear programming problem. The results describe optimal steady states and how the reindeer–lichen system develops over time from its initial state (perhaps far) outside the long run equilibrium. Compared with earlier age-structured herbivore–plant studies that have solved only static equilibria, our dynamic results enable to analyze the crucial question of optimal recovery from overgrazed pastures.

2. The population model and optimization problem

Assume that the yearly cycle begins after autumn slaughtering. Let $s = 0, \ldots, n_f$ denote female age classes, x^f_{0t} the number of female calves born during the spring (May) of year t and x^f_{st}, $s = 1, \ldots, n_f$, $t = -1, 0, 1, \ldots$ the number of females in each age class at the beginning of each yearly cycle. Variables x^m_{st}, $s = 0, \ldots n_m$, $t = -1, 0, 1, \ldots$ describe the number of males respectively. The number of calves born during the spring is given as

$$x_{0t} = \sum_{s=1}^{n_f} \beta_{t-1}\hat{f}_s f(wd_t)[1 - m^f_s(wd_t)x^f_{st}], \quad t = 0, 1, \ldots \tag{1}$$

where β_{t-1} is the fraction of females mated at the end of year $t-1$, $\hat{f}_s$, $s = 1, \ldots, n_f$ are the benchmark number of calves per female in different age classes, $f(wd_t)$ is the proportional decrease in the number of calves per mated females, and $m^f_s(wd_t)$ the female winter mortality. Both are functions of overwinter weight loss wd_t. Reindeer is a polygynous species but reproduction will suffer if the fraction of males is too low. Let $fm_s(\geq 1)$, $s = 1, \ldots, n_m$ denote the potential number of bred females per males in different age classes, $m^m_s(wd_t)$ the male winter mortality and specify the "effective number of males" at the end of year t as

$$X^{em}_t = \sum_{s=1}^{n_m} fm_s[1 - m^m_s(wd_t)]x^m_{s,t}.$$

Thus the effective number of males describes the male reproductive success in the population. Accordingly, the total number of potentially bred females is

$$X^{ef}_t = \sum_{s=1}^{n_f}[1 - m^f_s(wd_t)]x^f_{s,t}.$$

Caswell (2001, p. 574) suggests a harmonic mean mating function

$$B_t = \frac{2X^{em}_t X^{ef}_t}{X^{em}_t + X^{ef}_t},$$

where B_t, $t = 0, 1, \ldots$ is the number of bred females. If the effective number of males is lower than females, the fraction of mated females becomes less than 1 but somewhat higher than the fraction of effective males per females. This reflects some plasticity in the efficient reproductive rates per males. All females mate if numbers are equal, and if the efficient number of males exceeds the number of females, females will give birth more than once during a year. However, reindeers only have one breeding event per year.