Dissertationes Forestales 249

Ecology and economics of reindeer herding systems

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Academic dissertation

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The reindeer (*Rangifer tarandus* L.) is a key species in Fennoscandia, where nearly 40% of the land area is used as reindeer pasture. Reindeer herding is an important source of income for local people and an intrinsic part of the Sami culture In this thesis, the reindeer herding system is studied using a detailed interdisciplinary dynamic model. An age- and sex-structured reindeer-lichen model is developed using findings from previous research and novel data. The model also takes other winter resources, including supplementary food, into account in addition to ground lichens. This ecological model is combined with economic optimization and a description of the herding system with empirically estimated prices, costs, and governmental subsidies. The model is validated and calibrated to describe the reindeer herding system in the northern part of Finnish Lapland.

The results for population dynamics without harvesting show that the reindeer-lichen system described by the model is unstable in the absence of predators. However, high availability of arboreal lichens stabilizes the system. In economically optimal solutions increasing the interest rate increases the steady-state reindeer population level, opposite to classical understanding in resource economics. Natural mortality is close to zero in optimal steady-state solutions and harvesting is concentrated on calves. The number of adult males is kept as low as possible without decreasing the reproduction rate of the population. This leads to much higher shadow values for males compared to females.

The results show that in order to study sustainable and economically viable reindeer management, both ecological and economic factors must be taken into account, as they strongly affect the solutions and management recommendations. One of the main findings is that the economically optimal steady-state lichen biomass can be surprisingly low. High interest rate, lack of pasture rotation, low growth rate of ground lichen, high availability of arboreal lichens, and government subsidies all decrease the steady-state lichen biomass. Using intensive supplementary feeding to support larger reindeer herds, which leads to the depletation of lichens, can additionally become optimal in certain cases. When recovering from overgrazed lichen pastures, use of supplementary feeding and the amount of arboreal lichens have an important role in the optimal adaptation process.

The wintertime wastages estimated in this study are close to earlier suggestions, but summertime wastage is higher than expected. Seasonal pasture rotation could thus considerably help reduce the summertime trampling of winter pastures. The model validation solutions show that the model is able to describe changes in lichen biomass with good accuracy. Using the validated model and calibrated wastage values we found that reindeer numbers in northernmost Finland in the present situation are in most cases higher than in the management solutions given by the model.

Keywords: optimal harvesting, herbivore-plant interactions, herbivore management, overgrazing, supplementary feeding, trampling

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Helsinki February 2018

LIST OF ORIGINAL ARTICLES

This thesis consists of an introductory review followed by three research articles. These papers are reproduced with permission from the publishers.

I Tahvonen O., Kumpula J., Pekkarinen A.-J. (2014). Optimal harvesting of an age-structured, two-sex herbivore–plant system. Ecological Modelling 272: 348-361. https://doi.org/10.1016/j.ecolmodel.2013.09.029

II Pekkarinen A.-J., Kumpula J., Tahvonen O. (2015). Reindeer management and winter pastures in the presence of supplementary feeding and government subsidies. Ecological Modelling 312: 256-271. https://doi.org/10.1016/j.ecolmodel.2015.05.030

III Pekkarinen A.-J., Kumpula J., Tahvonen O. (2017). Parameterization and validation of an ungulate-pasture model. Ecology and evolution 7(20): 8282-8302. https://doi.org/10.1002/ece3.3358

AUTHOR'S CONTRIBUTION

Author Antti-Juhani Pekkarinen was solely responsible for the summary. The author, together with Olli Tahvonen and Jouko Kumpula, constructed and analyzed the model in paper **I** and commented on the manuscript. The author was mainly responsible for papers **II** and **III**, and conducted the mathematical formulation, analyses, and computations for these papers. The author was also mainly responsible for writing papers **II** and **III**.

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1 INTRODUCTION

The reindeer/caribou (*Rangifer tarandus* L.) is a medium-sized ungulate with circumpolar distribution (Burch Jr. 1972). It is a key species in its rangelands and has a large impact on socio-cultural conditions in northern boreal regions, especially with indigenous people (Forbes et al. 2006). Nearly 40% of the Fennoscandian land area is used as reindeer pasture (Pape and Löffler 2012). Reindeer herding is an important source of income for local people and an intrinsic part of Sami culture.

However, the increasing number of reindeer together with the effects of forestry and other land uses in the reindeer herding area has led to a situation where the important winter lichen pastures are highly grazed (Väre et al. 1996, Kumpula et al. 2009). In some areas, the lichen biomass has decreased to such low levels that reindeer are no longer able to maintain their body condition well enough throughout the winter without supplementary feeding (Kumpula et al. 1998). This growing concern for the high numbers of reindeer diminishing their pastures and reducing biodiversity has continued for over two decades (Torp 1999, Kitti et al. 2006), and recently this debate has become heated in Finland (Järvinen 2016). Reindeer herding is argued to be ecologically unsustainable and reindeer numbers are said to be much too high compared to the ecological carrying capacity of the pastures. Herders themselves also recognize the problem of pasture degradation, but in their opinion the biological assessments provide a one-sided picture of the pasture state (Kitti et al. 2006). Indeed, numerous factors affect reindeer herding and the condition of lichen pastures (Forbes et al. 2006, Kumpula et al. 2014).

The scientific study on reindeer and reindeer herding is wide, and varies from ecology and genetics to anthropology and resource economics. However, there are still only a few interdisciplinary studies that combine the knowledge from previous research and study the reindeer management system in a wider context. Pape and Löfler (2012) emphasize the importance of interdisciplinary research in their meta-analysis. They concluded that reindeer research has mainly focused on biological and ecological aspects of reindeer and that only 5% of current studies assess the reindeer herding system as a whole. The need for interdisciplinary system analysis is not only limited to the reindeer herding system. Gordon et al. (2004) state that future management of wild large herbivores in general will require ecologists to co-operate with sociologists, economists, politicians, and the public. One way to approach this goal is to use mathematical system models as a method to describe complex systems and analyze system dynamics. Indeed, Schmolke et al. (2010) concluded that ecological models are an apt method for supporting and informing policy- and decision-makers, and they should be used more widely in the future.

In this thesis, the reindeer herding system is studied using a detailed ecological-economic dynamic model. Findings from previous research and novel data are used in developing an age- and sex-structured reindeer-lichen model that also takes into account other winter resources in addition to lichens. This ecological model is combined with detailed economic optimization and a description of the herding system with empirically estimated prices, costs, and government subsidies. Various management practices are also taken into account. The model describes the northern part of Finnish Lapland, for which it is also calibrated and validated in studies presented in this thesis.

1.1 Reindeer herding system

The reindeer is a semi-domesticated ungulate that mainly feeds on natural pastures. In Finland reindeer are herded and allowed to graze freely within the herding district area during most of the year (Helle and Jaakkola 2008). Thus, the reindeer herding system differs clearly from other meat or livestock industries, where animal movement and feeding are highly regulated. Although reindeer graze freely, their population dynamics also differ from wild populations. Human impact is much stronger on reindeer than on wild deer species. As reindeer are gathered in autumn, the slaughtering can be targeted based on age, sex, and condition. Selective breeding, medication, and supplementary feeding are also common practices in reindeer management (Helle and Jaakkola 2008).

Winter pastures are the generic scarcity factor for reindeer numbers and reindeer population productivity in many areas (Pape and Löffler 2011). Lichens especially are an important energy resource for reindeer during winter. However, reindeer numbers are high in many districts, which may lead to overgrazing of lichen pastures (Mysterud 2006) and decreases in bird species richness and biodiversity (Ims and Henden 2012). Large herd sizes are the main reason for the reduction in lichen biomass, but forestry, mining, and other land uses also affect the situation (Kumpula et al. 2014). Other land uses also prevent reindeer herders from expanding to new areas, as the available pasture area has reduced during previous decades. Even though reindeer were still allowed to use an area, the quality of pastures is often low because of forestry or other factors (Kumpula et al. 2007). Reindeer management is based on natural pastures, but supplementary winter feeding forms a permanent practice in the present herding systems in Finland (Kumpula et al. 2002). Winter feeding is also intensified especially during harsh winters.

The herding system has developed in somewhat different directions in the northern and southern parts of the Finnish reindeer management area (Helle and Kojola 2006). A distinct seasonal pasture rotation system was used in traditional herding in northernmost Fennoscandia. Reindeer habited winter pastures in lichen-rich forests during winter, but migrated as far as the Arctic Ocean coast for summertime (Müller-Wille et al. 2006). However, this practice ended in Finland because the migration routes over the borders between Finland and its neighboring countries were closed at the end of the 19th century (Müller-Wille et al. 2006). Many northern co-operatives still use the seasonal pasture rotation system, but only within the boundaries of each district. In these cases, winter pastures are separated from summer pastures by fences.

In the southern part of the Finnish reindeer herding area a clear seasonal pasture rotation system has never been a regular practice and herd sizes have been smaller (Helle and Kojola 2006). However, even without a seasonal pasture rotation system the reindeer move from one pasture type to another according to the seasons, and can remain feeding for long periods in the same areas if pastures are in good condition. Thus, a natural rotation has occurred between various pasture types. However, disturbances and pasture fragmentation caused by intensive forestry and other land uses, can disrupt this traditional pasture use, and increase the movement of reindeer between feeding habitats, increasing the grazing and trampling pressure on the lichen pastures (Kumpula et al. 2014).

1.2 Reindeer management models

Predator-prey systems (including plant-herbivore systems) have been widely studied using mathematical system models based on coupled difference or differential equations (Begon et al. 2005). These models describe how predators affect prey populations (i.e. functional response) and how prey density affects the predator population (i.e. numerical response). This approach is fit for studying reindeer-lichen systems, as the main factor affecting the productivity and growth of the reindeer population is its winter food, mainly ground lichens (Kumpula 2001), and the main factor affecting lichen biomass (in northern Finland) is the reindeer population (Kumpula et al. 2014). Thus, using a similar structure as in predator-prey models, the dynamic description of the reindeer herding system can be built on a reindeer-lichen population model. This approach has also been adopted in some previous models for reindeer management (e.g. Virtala 1992, Moxnes et al. 2001). When using such a model, the density-dependence effect for a reindeer population is endogenously created through the dynamics with lichen. This allows the bioeconomic reindeer-lichen models to be used for studying the optimal lichen biomasses in addition to reindeer population management.

Bioeconomics is the study of economically optimal utilization (also including other values besides monetary income) of biological resources. Since the seminal book by Colin Clark (1976), titled Mathematical Bioeconomics: The Optimal Management of Renewable Resources, bioeconomic models solved by dynamic optimization have been at the center of bioeconomic research. Many, and sometimes very detailed, bioeconomic models have been developed and published for fisheries and forest resources, but only seldom for wild or semi-domesticated mammalian populations (Getz and Haight 1989). The first bioeconomic model published for Scandinavian reindeer lichen systems was a model by Virtala (1992, 1996). He developed a simple two-state variable reindeer-lichen model for analyzing optimal harvest policy. The reproduction rate of a reindeer population in the model depends only on lichen biomass, and thus Virtala (1996) finds that optimal harvesting can be expressed as a function of lichen biomass alone. Moxnes et al. (2001) adapted a similar two-state variable approach in their much more complex bioeconomic reindeer-lichen model. They included a detailed description of energy intake from various energy resources, took into account lichen wastage, and also included summer pastures. Skonhoft et al. (2017) specified a reindeer population model to study the effects of predation on a ‘tragedy of the commons’ situation. They found that predation may improve the economic lot of reindeer herders in unmanaged setting. The model includes three age/sex classes, but no mating function, resource dynamics or optimization.

Gaare and Skogland (1979) developed a reindeer-lichen population model that took into account lichen wastage caused by trampling, but their study did not include economic optimization or age structure. Olofsson et al. (2011) included age and sex structure along with a detailed description of energy intake from pastures. The model is complex, but does not include economic optimization and the sex structure of the population does not affect reproduction. Danell and Petersson (1994) constructed a very detailed model of the reindeer herding system and divided the year into 11 time steps. However, they did not include pasture dynamics, and no simulation or optimization results for the model were presented.

Age- and sex-structured models have also been specified for other similar herbivores. But as for reindeer models, they typically do not include food resources or optimization, nor are they usually validated. Xie et al. (1999) specified an age- and sex-structured model for white-tailed deer management. The model was parameterized and validated with data, but does not include optimization, food resources, or a mating function. They found that both the quantity and quality goals were best achieved by a moderate harvest of bucks and does without sex bias. Xu and Boyce (2010) present a stage- and sex-structured model for moose populations. They found that intense calf harvesting is important when maximizing the sustainable yield. De Roos et al. (2009) analyze an age-, size-, and sex-structured model for the Konik horse population. The model is detailed, including a mechanistic description of individual energetics and life history along with food resources. They found that the oscillations in population abundance rise from interaction with the food resource and from different survival rates between age classes. However, as often with ecological models, the number of males does not affect the reproduction, as it is assumed high enough for natural populations. Also, no optimization of harvest levels is applied.

Milner-Gulland (1997) specifies a dynamic programing model for the optimal management of the saiga antelope, and found that the inclusion of breeding sex ratio is a key assumption. Altough the model takes breeding into account, it has no age structure or food dynamics. Walters et al. (1975) include food resources and specify an age-structured model for Canadian caribou. They found that the population was overexploided at the time of the study and that hunting was the critical factor limiting the population size instead of food supply. Sleep and Loehle (2010) evaluated the performance and validity of a demographic model for woodland caribou. They found that the simple model was unable to predict the population growth rate and additional variables might improve the performance of the model.

1.3 Shortcomings of current reindeer management models

Models have been used for studying a reindeer-lichen system, but only a few have taken both ecological and economic aspects of reindeer herding into account. These few models have been used for studying reindeer-lichen dynamics and the economically optimal management of reindeer populations. However, current bioeconomic models have not taken into account the internal structure of the reindeer population, various management practices (pasture rotation, feeding, detailed harvesting strategy), or different winter energy resources (lichens, arboreal lichens, dwarf shrubs, mosses, graminoids, supplementary food). Ecological models (Danell and Petersson 1994, Olofsson et al. 2011) include some elements mentioned above, but these models have not been used for analyzing management practices or optimal harvesting and feeding strategies.

Gordon et al. (2004) conclude that the management of large ungulates should be tailored to the age and sex structure of the population, but all previous bioeconomic optimization models for a reindeer herding system describe the reindeer population only using a single state variable. The few age-structured reindeer models published have not been used for studying management of the reindeer population. Gerber and White (2014) studied population models used in species conservation and conclude that two-sex matrix models should be used especially with polygamous species and that the importance of including details of male vital rates has been underestimated in population models. None of the previous reindeer models include a description of the polygamous mating system of reindeer. Models for other mammalian herbivores also often disregard the effects of the number of males on the reproduction rate of the population. It is additionally rare to have an interdisclipinary approach, where a detailed ecological model would be combined with economic optimization.

Models used for quantitative descriptions and predictions should be based on empirical data and research as much as possible. The research and data concerning reindeer grazing, food selection, energy intake, metabolism, and pasture use are vast and can be incorporated into a pasture use / energy intake model for reindeer. However, indirect effects of herbivory, such as trampling, can be as important as the direct effects (Hobbs 1996). Lichen wastage by grazing reindeer is mainly due to trampling and has been taken into account in the current models. However, the wastage level has not been quantified by empirical data and the parameter values have been based on preliminary or unpublished research or on estimates made by experts. As the estimated wastage levels used in previous studies vary from 0.5 to 10 times the intake rate (Moxnes et al. 2001, Gaare and Skogland 1979), wastage should clearly be estimated using data. As it has not, wastage can be seen as a weak link in current reindeer-lichen models.

In addition to being based on empirical research, models should be validated for the purpose they are intended for (Mayer and Butler 1992). This is especially important if the model is used for providing quantitative predictions and solutions for management and policy purposes. None of the current reindeer population models has been validated for any purpose. This is also very common in models for other natural resources, as it is very difficult, costly, and time-consuming to acquire new data needed for model validation (Brown and Kulasiri 1996). In addition, overly simplistic models are often unable to predict the data, while overly complex models are difficult to calibrate, which makes the task even more demanding.

Thus, none of the current models describe the reindeer population with required detail or take into account the relevant ecological, economic, and management aspects needed to describe the reindeer herding system as a whole. In addition, wastage due to e.g. trampling in the current models is not based on data and has not been validated. We attempt to answer these shortcomings in the studies presented in this thesis, and to advance the research of reindeer management regarding these issues.

1.4 Objectives

The overall objective of this thesis is to construct, parameterize, and validate an age- and sex-structured reindeer-lichen model and use the model to study the reindeer-lichen system and management of a reindeer population. All parameters and functions used in the model are based on existing literature and data collected by the Natural Resources Institute Finland and the Finnish Reindeer Herders' Association. In study **I**, the economically optimal (slaughtering) solutions for an age- and sex-structured reindeer-lichen model are computed. In study **II**, the model and its analysis are extended by including supplementary feeding, pasture rotation, arboreal lichen pastures, and government subsidies. In study **III**, the model is validated and the level of lichen wastage and its effects on optimal solutions are studied. More detailed research questions for each of the sub-studies (referred to by their Roman numbers **I**–**III**) are:

I) What is the size and structure of a reindeer population along with the lichen biomass in pastures in economically optimal solutions? What is the optimal steady-state slaughtering strategy? What are the dynamic properties of a reindeer-lichen system with and without optimal slaughtering? What are the shadow values for a marginal lichen pasture hectare and female and male reindeer in different age classes?

II) What are the effects of various winter pasture types and management practices on sustainable and adaptable reindeer management? How much and when supplementary food should be offered to reindeer in different situations? What are the effects of government subsidies on the reindeer management system?

III) What is the level of lichen wastage during different seasons in northernmost Finland? How accurately can the model describe and predict the actual changes in lichen biomass in the reindeer herding co-operatives in Finland? How do actual reindeer numbers and lichen biomasses in 20 northernmost herding districts in Finland fit together with the optimal management solutions given by the model?

To achieve these goals an age- and sex-structured reindeer-lichen model was developed, parameterized, and validated in the three sub-studies. The main tasks for developing, parameterizing, and validating the reindeer-lichen model in each substudy were:

I) To develop an age- and sex-structured reindeer model with an endogenous mating function and a detailed description of reindeer population structure. To include a dynamic description of the growth and consumption of ground lichens along with the costs and prices related to reindeer herding.

II) To include late-winter energy intake from arboreal lichens and various growth functions for ground lichen pastures. To include a description of supplementary food and seasonal pasture rotation usage along with a description of the choice between various energy resources based on the optimal foraging theory.

III) To include the effects of infrastructure-associated disturbance and heavy metal accumulation on the growth and consumption of ground lichens. To estimate the function and parameters for ground lichen wastage. To validate the model's ability to describe and predict changes in lichen biomass.

2 MODEL AND METHODS

This chapter describes the model and methods used in the study. The bioeconomic model can be divided into four submodels. The **population model** describes the development of the age- and sex-structured reindeer population. The **energy intake model** computes the daily energy intake of reindeer from various energy resources. The **lichen model** describes the growth, consumption, and wastage of ground lichen. The **economic model** includes prices, costs, and subsidies for a reindeer management system. It also describes the objective function and optimization method. The arrows in Figure 1 show the main interactions between these submodels. For example, the population model describes the size and structure of the reindeer population. This together with the daily lichen energy intake determines the consumption of lichen per reindeer. Similarly, the available biomass of lichen, computed in the lichen model, influences the optimal foraging decisions of reindeer, computed in the energy intake model A more detailed description with complete mathematical notation can be found in studies **I** and **II**.

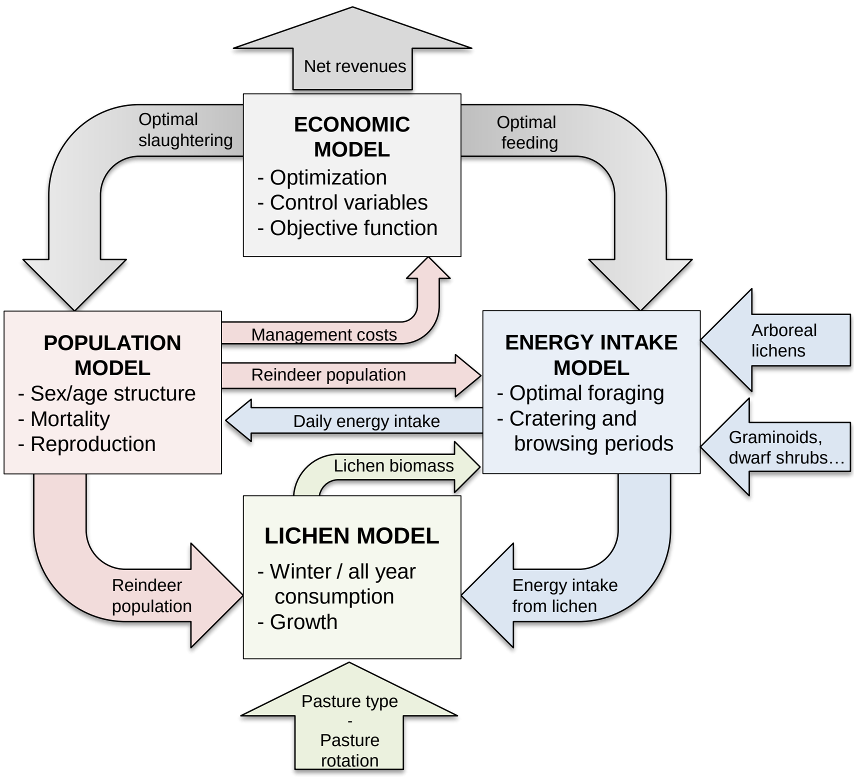

Figure 1. Interactions between the four submodels.

2.1 Age- and sex-structured population model

The population model describes the development of the age- and sex-structured reindeer population. The core of the model is based on classic coupled predator-prey equations, but includes much more complexity and endogenous interactions. The main difference to these classic models is the age and sex structure that can be described with Leslie matrixes for both sexes. The population model also includes descriptions for growth, mortality, and reproduction.

The variables $x_{s,t}^{i}, s = 1, \dots, n_i, i = f, m, t = -1,0,1 \dots$ denote the number of reindeer in age class *s*, in sex class *i*, at the beginning of period *t*. The period length is one year and the start of the period is right after autumn slaughterings. The numbers of individuals in various age and sex classes evolve according to:

$$x_{1,t+1}^{i} = \left(1 - m_0^i\right) u_i x_{0,t} - h_{0,t}^{i}, i = f, m, t = 0,1, \dots, \qquad (1)$$

$$x_{s+1,t+1}^{i} = [1 - m_s^i(wd_t)] x_{s,t}^{i} - h_{s,t}^{i}, i = f, m, s = 1, \dots, n_i - 1, t = 0,1, \dots, \qquad (2)$$

where $h_{s,t}^{i}, s = 0, \dots, n_i - 1, i = f, m, t = 0,1, \dots$ denotes the number of harvested reindeer (at the end of each period), m_0^i the summer mortality of calves, and $u_i, i = f, m$ the share of calves belonging to sex class i. The winter mortalities of adult reindeer are denoted by $m_s^i(wd_t), i = f, m, s = 1, \dots, n_i$ and wd_t denotes the proportion of overwinter weight decrease from autumnal weight. The total number of calves born in spring is given by:

$$x_{0,t} = \sum_{s=1}^{n_f} \beta_{t-1} f_s(wd_t) \left[1 - m_s^f(wd_t)\right] x_{s,t}^{f}, t = 0,1, \dots, \qquad (3)$$

where β_{t-1} is the fraction of females mated at the end of period $t - 1$, which is described by the modified harmonic mean mating function suggested by Bessa-Gomes et al. (2010) for polygynous species with distinct breeding seasons. Variables $f_s(wd_t), s = 1, \dots, n_f$ specify the number of calves per mated females in different age classes as a function of overwinter weight loss wd_t. Overwinter weight loss is a function of the average energy intake in winter E_t^T, which is computed by the energy intake submodel.

2.2 Energy intake model

The energy intake submodel computes the average energy intake in winter E_t^T following the principles of optimal foraging theory. The submodel computes the intake rates for various food sources available to reindeer, and selects the combination that gives the highest average energy intake rate. Our model takes into account the energy from ground lichens, other cratered food resources (dwarf shrubs, mosses, and graminoids), arboreal lichens, and supplementary food. Lichen biomass develops according to the lichen submodel, but the availabilities of the other cratered food resources and arboreal lichens are exogenous and constant for each simulation and optimization. The availability of supplementary food is determined by economic optimization, except in the model validation and calibration, which are described in study III. The energy intake model also computes the energy intake rate from lichen that is needed in the lichen model to compute the consumption of lichen during winter.

2.3 Lichen model

The lichen submodel describes the growth and consumption of the lichen biomass during various seasons. Lichen biomass in year *t* is denoted by z_t and develops according to:

$$z_{t+1} = z_t - l_t^{wi} - l_t^{sp} - l_t^{su} + G(z_t^{su}) - l_t^{au}, t = 0,1, \dots. \tag{4}$$

where $G(z_t^{su})$ is the lichen growth during summer (snow free season), $l_t^e, t = 0,1, \dots, e = wi, sp, su, au$ is the consumption of lichen per hectare in dry weight (kg) during season *e*, and *wi*, *sp*, *su*, *au* denote the winter, spring, summer, and autumn seasons respectively. Lichen growth is a function of lichen biomass in summer (z_t^{su}) after winter and spring consumption.

The lichen consumption of adult males and females during season *e* is given as:

$$l_{s,t}^{i,e} = w^e \frac{Ed_{s,t}^{i,e} E_t^{L,e}}{10.8} d^e, t = 0,1, \dots, i = f, m, s = 1, \dots, n_i, e = wi, sp, su, au \tag{5}$$

where $Ed_{s,t}^{i,e}$ is the energy requirement for reindeer in different age and sex classes in various seasons, $E_t^{L,e}$ the average daily energy intake from lichen in winter, d^e the length (in days) of season *e*, and w^e the wastage that denotes the fact that reindeer grazing causes loss of lichen additional to that consumed for energy (Moxnes et al. 2001). The value for wastage in studies **I** and **II** is based on an estimation by experts in this field. The wastage function and parameters in study **III** are estimated using data and the model.

2.4 Economic model and optimization

For economic optimization the reindeer herding district is assumed to maximize

$$J = \sum_{t=0}^{\infty} (R_t - C_t)^{\alpha} \left(\frac{1}{1+r}\right)^t, \qquad (6)$$

by choosing to slaughter reindeer in different age and sex classes $\left(h_{s,t}^i, s = 0, \ldots, n_i - 1, i = f, m, t = 0,1, \ldots\right)$ and by choosing the amount of supplementary food offered to reindeer during winter $(v_t, t = 0,1, \ldots)$. In (6) r is the annual interest (discount) rate, $\alpha=1$ refers to the aim of maximizing the present value of net revenues and $0<\alpha<1$ to the preferences for a smooth annual net income level. Variable R_t is the annual revenues from slaughtering and C_t the total annual costs. The price for reindeer meat (8 €/kg) is based on the estimation of the market price in year 2010. The total costs include the constant annual management cost (1.14 €/ha), the variable management cost (39.54 €/reindeer), and the slaughtering costs (13.35 €/reindeer), which are all estimated in study I from the data describing the 20 northernmost herding districts of Finland for years 2010–2011. The data for the 20 northernmost districts are used, as the model is designed to describe the reindeer herding system in that area.

In study II, the effects of Finnish and Swedish government subsidy systems are analyzed. In Finland, reindeer owners with large enough herds are subsidized by 28.5€ per reindeer belonging to the winter population. The consequences of this subsidy system can be studied by decreasing the management costs in the model by 28.5€ per reindeer. In Sweden a meat production subsidy is used (2€ per kg of produced meat), and this can be taken into account by increasing the meat price with 2€ per kg.

The objective functional (6) is maximized subject to the submodels presented, and the initial state of the system is given. All the optimizations are carried out using the AMPL programing language and Knitro (version 7.0.0) optimization software (Byrd et al. 2006). The optimization codes are available on the journal's webpages as supplementary data for the original articles (studies **I** and **II**).

2.5 Model validation methods

In study **III** the parameters for the wastage function are estimated using both data and a model. Lichen biomasses for year 1995 (Kumpula et al. 2009) and the sizes and structures for the reindeer populations in the 20 northernmost herding districts for years 1995–2007 (data from the Reindeer Herders' Association presented in the Appendix of study **III**) are used as input for the model. Then the model and input data are used for calculating the lichen biomasses in 2008, which are compared with the measured biomasses in year 2008.

By choosing the wastage parameters that minimize the difference between simulated and measured lichen biomass we can estimate the wastage level. As comparisons between the model predictions and data are performed with a numerical method (rather than by visual comparison), an optimization algorithm can be used for solving the wastage parameters that give the best fit between the model and data.

Modeling efficiency is used as a statistical method for comparison between model predictions and data. It is suggested by Mayer and Butler (1993) as the best overall measurement between model and data. Modeling efficiency directly relates the prediction to the measured data and is given by (in the context of this study):

$$EF = 1 - \frac{\sum_{HD=1}^{n} \left(z_{d,HD} - z_{m,HD}\right)^2}{\sum_{HD=1}^{n} \left(z_{d,HD} - z_{d,a}\right)^2}, HD = 1, \ldots, 20, \qquad (7)$$

where $z_{d,HD}$ denotes the measured lichen biomass for year 2008 in a herding district *HD* and $z_{m,HD}$ denotes the model prediction for lichen biomass in herding district *HD* for year 2008. *HD* is the number of herding district and $z_{d,a}$ is the average biomass in 2008 for all herding districts used in the calculation of modeling efficiency.

The aim of study **III** is also to validate the model with respect to its ability to describe and predict the measured changes in lichen biomass. The comparison between model predictions and the measured data is performed with visual and statistical methods. As a visual comparison we use observed vs. predicted plots, and modeling efficiency is used as a statistical method (Eq. 7). As we only have 20 data points we use the cross-validation method (also known as jackknife sampling) (Fielding and Bell 1997; Hawkins et al. 2003). Using cross-validation we can use the same data for parameter estimation and model validation. Data for each herding district are left out in turn and the parameter estimation is performed using the remaining 19 herding districts. We then used the model and estimated a wastage-parameter to predict the change in lichen biomass in the herding district that was left out from the parameter estimation. This is repeated for all 20 districts. Thus, the wastage parameter for each herding district used in the model validation is estimated without using data from that particular district.

3 RESULTS AND DISCUSSION

Studies **I** and **II** provide solutions for the population dynamics and management of a reindeer-lichen system as described by the model. The parameter values for the wastage function are estimated in study **III** and the model's ability to predict the measured changes in lichen biomass is validated. The main findings of the studies are presented below and a more detailed description of the results can be found from the original research articles.

3.1 Population dynamics without harvesting or supplementary feeding

Without harvesting, supplementary feeding, or arboreal lichens the reindeer-lichen system in our model has only one nontrivial steady state (papers **I** and **II**). However, this is an unstable steady state and the system development is characterized as an unstable cycle (Figure 2 a). Eventually the reindeer population will grow to very high levels and deplete the lichen resource. Without lichens, the reindeer population dies out and eventually the lichen biomass will grow back to its own carrying capacity level. Similar development has been observed on isolated islands where reindeer have been introduced (Klein 1968). Reindeer numbers have increased to high levels on these islands and have depleted the lichen resources, which has led to a crash in reindeer numbers. However, probably due to changes in local climatic conditions, lichen has not fully recovered on these sites (Klein 1987).

Predators, diseases, or fluctuating winter survival due to stochastic weather and snow conditions might affect the dynamics of the system, but these were not studied in this thesis. However, in paper **II** we found that arboreal lichens stabilize the system (Figure 2). Large numbers of arboreal lichens grow at high heights in trees and beyond reach. However, some part of this biomass drops onto the snow due to hard winds and storms in winter (Esseen, 1985). This implies that arboreal lichens can provide an additional winter resource for reindeer in the pasture areas with plenty of old-growth coniferous trees, especially because a fraction of arboreal lichen always remains unconsumed. With high enough availability of arboreal lichens, the system goes into a steady state even if the initial state is far outside the steady state (Figure 2c). Similarly when analyzing more general predator-prey models, alternative food resources have been found to potentially stabilize the dynamics of predator population (van Baalen et al. 2001).

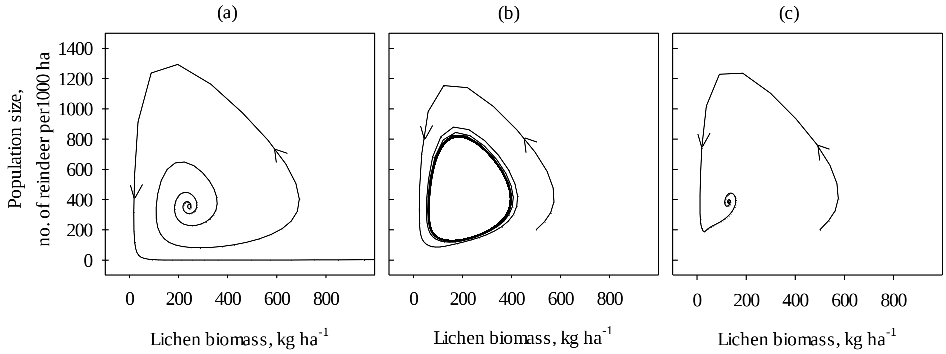

Figure 2. Development of the reindeer-lichen system without predators, harvesting, or supplementary feeding. Solutions represent a system with closed pasture rotation and high lichen growth rate (all lichen pastures located in old or mature pine forests). The stability of the system is affected by arboreal lichen availability: (a) no arboreal lichens, (b) lower availability, (c) high availability.

3.2 Management of a reindeer-lichen system

This thesis shows that the solutions for economically viable management of a reindeer-lichen system are strongly affected by both ecological and economic properties of the system. In optimization solutions, the system converges towards an optimal steady state (Figure 3. solid lines) or approaches a limit cycle around the steady state (Figure 3. dashed lines).

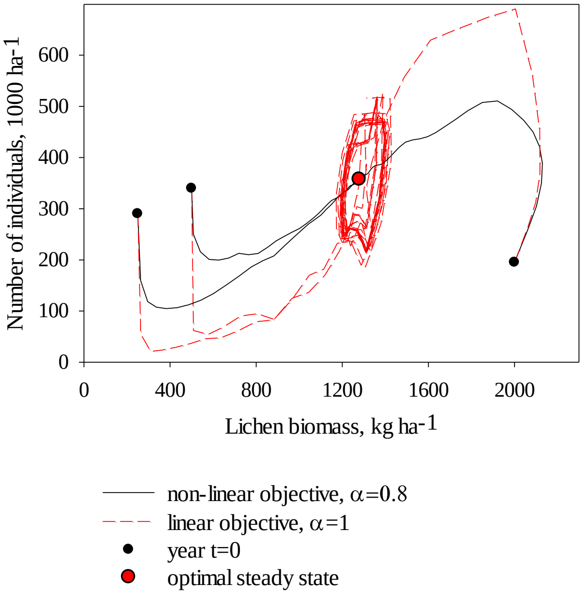

Figure 3. Examples of the optimization solutions over time from different initial states with zero interest rate using linear (dashed lines) and non-linear (solid lines) objectives. Solutions describe a theoretical herding district using the seasonal pasture rotation system, with all ground lichen pastures located in old or mature pine forests, and without available arboreal lichen pastures.

3.2.1 Steady states with zero interest rate

Studies **I** and **II** show that a 0% interest rate results in an optimal steady-state lichen biomass, reindeer population structure, and slaughtering strategy, which give the highest yearly net income for the system. Increasing or decreasing lichen biomass from this steady state decreases the steady-state income. The optimal lichen and reindeer population size depends on economic and ecological factors, and whether or not seasonal pasture rotation is used. In the absence of seasonal pasture rotation, the steady-state lichen biomass and reindeer population size are lower. Also, steady-state lichen biomass and reindeer numbers are lower if the availability of old and mature pine forests is decreased, implying a lower growth rate for ground lichens. High availability of arboreal lichens increases the steady-state net income and reindeer population size but decreases the optimal ground lichen biomass. According to the solutions in study **II**, it is not optimal to use supplementary feeding in the steady state with zero interest rate with the estimated costs for supplementary feeding (0.4–0.5 €/kg). Instead, the lichen resource should be kept in good condition so that the management system and the winter energy intake by reindeer are based on natural pastures.

Moxnes et al. (2001) found the optimal steady-state lichen biomass with 0% interest rate in their reindeer management model to be approximately 70% of the maximum sustainable yield (MSY) level for lichens and that this was mainly due to the wastage function used in their model. In our results the optimal lichen biomass varies between 30% and 50% of the MSY level despite the wastage relative to intake rate not depending on lichen biomass in studies **I** and **II**. In our model the optimal lichen biomass is lower than the MSY level because a lower lichen biomass level implies a larger reindeer population. Pastures with lower lichen biomass can still support the energy requirement of a large reindeer population, because reindeer shift their diet towards other food items when lichen biomass decreases. This mixed diet provides enough energy for reindeer throughout the winter, and thus the body condition of reindeer remains at a sufficient level even if the energy intake from lichens decreases. However, at very low lichen biomasses the energy intake from cratered food items (lichens and dwarf shrubs) is not enough without arboreal lichens or supplementary food. In this case the number and birth weight of calves initially begins decreasing, and finally also the winter mortality of adults increases if additional winter resources are unavailable.

3.2.2 Steady states with positive interest rate

With a positive interest rate, marginal capital productivity of the system is required to be positive. This implies that part of the capital could be invested into alternative investment possibilities, if a fraction of the capital tied up in the reindeer herding system is less productive than the required marginal productivity. In Finland, the expected return from investment to reindeer herding is 5% according to Rantamäki-Lahtinen (2008). In such complex herding systems, it is not a priori clear what the effects of a positive interest rate are.

Studies **I** and **II** show that the steady-state reindeer population size is higher with higher interest rate, but lichen biomass decreases. This result seems contradictory with the classical understanding in natural resource economics, which is that a higher interest rate implies a lower population level of the harvested resource (Clark 1990). However, our result can be understood if the lichen biomass is seen as the scarce renewable capital. The other energy resouces for reindeer further complicate the issue. With the combined effects of a high interest rate, low growth rate of ground lichens, and lack of seasonal pasture rotation, the lichen biomass in the optimal steady state is very low (ca. 600 kg/ha) even without the use of supplementary feeding. Also, if the availability of arboreal lichens is high, the steady-state lichen biomass can be kept at a lower level, as reindeer gain energy from arboreal lichens in addition to cratered food resources.

Study **II** shows that in certain cases it becomes optimal to change from a reindeer herding system relying on natural pastures to a reindeer management system based on intensive supplementary feeding. This switch can happen if interest rate is high, the price of supplementary food is low, and the productivity of lichens on natural pastures is low. When the use of supplementary food as a primary energy resource for reindeer during winter becomes optimal, the number of reindeer increases, because the density-dependence effect of scarce lichen pastures is no longer binding. In real situations the maximum reindeer numbers would then be regulated by other factors for example diseases, parasites, or the sufficiency of summer pastures, which are not included in our model. In our solutions the large reindeer population consumes the lichen biomass to a very low level (for optimization solutions the minimum lichen biomass is constrained to 100 kg/ha). However, in our model reindeer still gain some part of energy from natural resources (grasses, dwarf shrubs, and arboreal lichen if available) during winter. Eventually these other energy resources along with summer pastures would also diminish if reindeer numbers were to remain very high for an extended time.

Moxnes et al. (2001) found that interest rate has only a minor effect on the optimal steady state. In our solutions we found that increasing the interest rate changes the steady-state reindeer population size, lichen biomass, and yearly net revenues. Increasing the interest rate can have extreme effects if the reindeer management shifts from being based on natural pastures to being based on supplementary feeding. In this case the reindeer population size increases to a very high level since the growth rate of lichen no longer binds the growth rate of the reindeer population. Again, this solution appears opposite to classical bioeconomic understanding (Clark 1990), where the level of a harvested population can go to zero with a high interest rate. In our case the population increases to a very high (theoretically to infinite) level, as lichen growth rate no longer binds the growth rate of the reindeer population. However, the lichen biomass decreases to an extremely low level. It is possible that the response of reindeer husbandry to a high discount rate combined with a reduction in winter pastures and the low price of supplementary food could have promoted the process during last decades in Finland, where reindeer numbers have increased to a higher level than the available lichen pasture resources allowed and lichen biomass has decreased. However, many other factors, such as forestry, other land use forms and the associated pasture fragmentation and increased disturbances have also affected the reindeer-lichen system and lichen biomass (Kumpula et al. 2014).

3.2.3 Age structure and harvesting strategy

In all optimal steady-state solutions introduced in this thesis, the age and sex structure and the harvesting strategy of the reindeer population is as shown in Figure 4. According to the model solutions, it is optimal to slaughter ca. 94% of male calves and 67% of female calves during their first autumn. Adult mortality is very low in the optimal steady state. Thus, the winter population has almost an equal share of females in all age classes from 1 to 9 and males from 1 to 5. The adult females are slaughtered at the age of 9 ½ years and the males are kept alive until the age of 5 ½ years. This is the first time that the economically optimal age and sex structure as well as harvesting strategy have been studied and solved for reindeer. A similar slaughtering strategy is adopted and has been used for a long time in Finnish reindeer management systems. Slaughtering in the co-operatives mainly target the calves and the main part of the winter population consists of adult females (Kojola and Helle 1993).

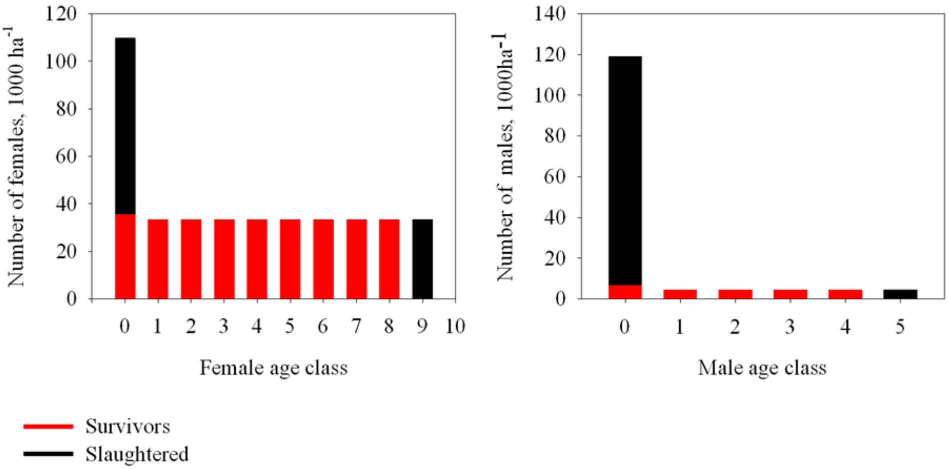

Figure 4. Optimal structure and harvesting strategy of a reindeer population in the steady state.

The shadow values for females and males in the steady state are also computed in paper **I**. As the number of males is kept as low as possible in the optimal steady state, losing one male means that the number of calves born in the following year is lower than if one female were killed. This is the case even with the modified harmonic mean mating function used in our model, where other males compensate some of the loss in reproductive output. Thus, in a steady state the value of one adult male is much higher than that of one female. In many Finnish reindeer herding districts the actual number of males is close to these optimal model solutions. Thus, in these empirical situations the value of males could be close to the computed shadow values and higher than the value of one female. However, in practice the reproductive output of a male reindeer benefits the entire co-operative, and not only its owner. Thus, an individual herder might consider the value of a single male as much lower than what our study shows, and a free-riding problem might exist concerning the ownership of males.

3.2.4 Dynamic solutions and recovery from overgrazed pastures

Optimal transition solutions to steady states from various initial points were computed when solving the optimal steady-state solutions. By using a nonlinear objective function ($\alpha<1$), the system goes into an optimal steady state after the transition (Figure 3, Figure 5). However, with a linear objective the system goes into a cycle around the steady state (Figure 3). The difference in the objective value between the cyclic solution and steady state is very small (<1%). Figure 3 shows three examples of optimal development from different initial lichen biomasses and reindeer population sizes. The transition to the steady state (marked with a red dot) takes more than ten years. In the two example solutions, where lichen biomass in the initial state is lower than in the optimal steady state, the reindeer population is first heavily reduced by slaughtering. This occurs despite initial reindeer numbers being lower than the optimal steady state population size in both cases. If the objective is nonlinear, i.e. reindeer herders prefer a steady income flow, the reduction in reindeer numbers is smaller during the first years. However, even in these solutions the reindeer population size is reduced to approximately half of its initial size to increase the lichen biomass.

In paper **I** we showed that the yearly net revenues first decrease when the interest rate is increased, and begin increasing only after a few years, until they finally decrease to a steady-state level. This delay in the rise of net revenues as a response to increasing the interest rate is untypical. The reason for the delay is that lichen is a scarce resource limiting the productivity of the system. Thus, first the slaughtering intensity must be lowered to increase the size of the reindeer population, leading to a lower net income for a few years. After this the larger population can be harvested more heavily, and the net income increases before stabilizing to a new steady-state level.

Virtala (1996) and Moxnes et al. (2001) suggested that a constant escape type solution should be used for transitioning to the steady state. In a constant escape solution the transition would be as fast as possible. However, in paper **I** we found that in an age- and sex-structured model this would lead to a loss of income. Instead, a smoother transition is used, especially with a nonlinear objective. This takes a longer time, but allows optimal adjustment of the slaughtering strategy and age structure.

In paper **II** we found that if the lichen biomass is very low in the initial situation (overgrazed lichen pastures), it is optimal to use supplementary feeding in the first years of the recovery process (Figure 5). Without using supplementary feeding the number and weight of the calves would be lower during the first years. If arboreal lichen availability is high, the need for supplementary food is clearly lower. The solution for economically optimal recovery leads to a clear reduction in net income for decades, and only after the transition does the system converge to a steady state, where the yearly net income is higher than it would be in the steady state corresponding to the initial low lichen biomass level.

3.2.5 Effects of government subsidies

The effects of government subsidies on optimal steady-state solutions were analyzed in study **II**. The solutions show that both studied subsidy systems, i.e. the reindeer number subsidy (28.5€ per reindeer in the winter population) and the meat production subsidy (2€ per kg of produced meat), favor the use of supplementary feeding in the optimal steady state. This occurs in each of these cases because the subsidies increase the benefits of having a larger herd. However, without supplementary feeding it would be difficult or impossible to increase the herd size by relying only on natural pastures. Despite the larger reindeer population gaining extra energy from supplementary food, they still keep eating natural food resources. Lichens especially are preferred by reindeer even when supplementary food is available. Therefore, when using supplementary feeding to increase the herd size becomes optimal, a situation arises where lichen biomass is depleted to very low levels. Large herds additionally increase the reduction rate of lichen biomass by trampling.

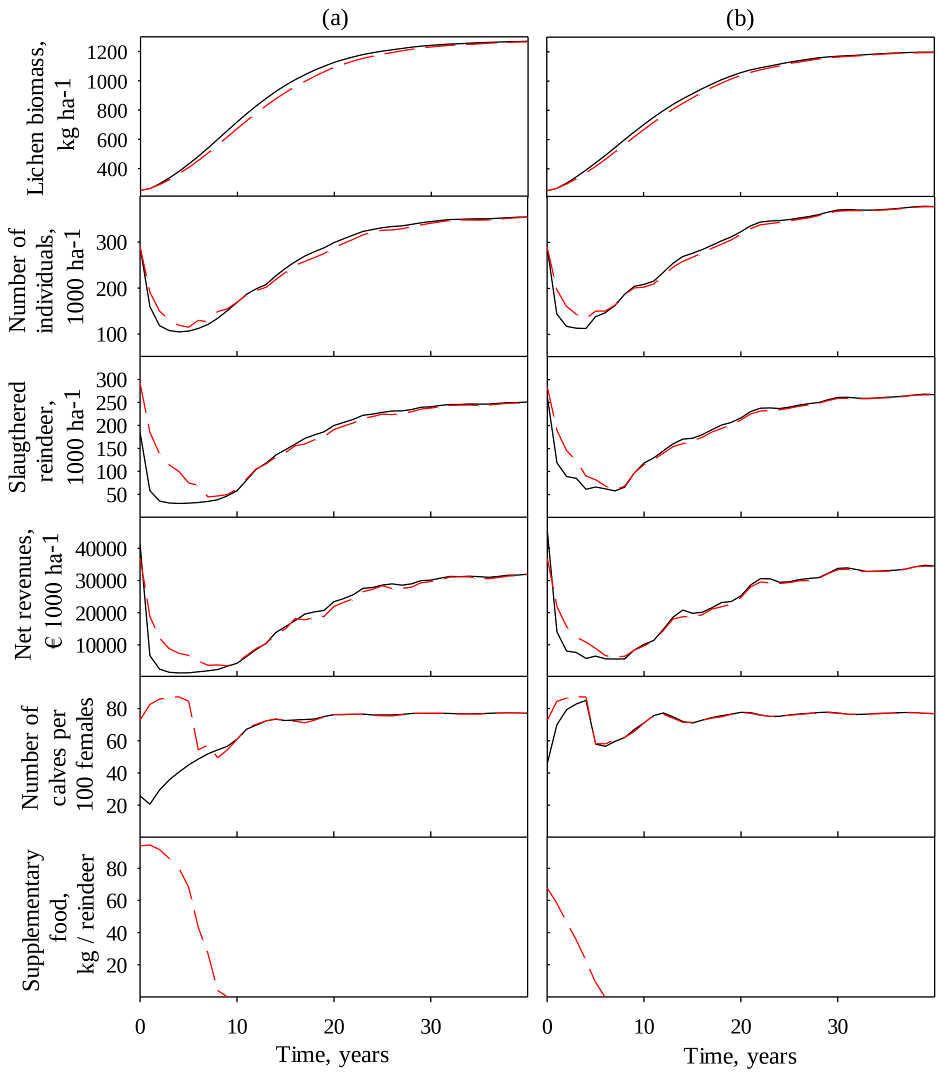

Figure 5. Recovery from overgrazing with zero interest rate and nonlinear objective ($\alpha = 0.8$). A herding district with closed pasture rotation and all lichen pastures in old or mature pine forests (high lichen growth rate). Solid lines: no possibility of offering supplementary food. Dashed lines: feeding costs of 0.4 €/kg. (a) No arboreal lichen pastures. (b) High arboreal lichen availability.

Reindeer herders interviewed by Helle and Jaakkola (2008) told that the subsidies paid to farmers for leaving their fields uncultivated was one reason why supplementary feeding became a regular practice in Finland. Using these subsidized uncultivated fields for haymaking was still allowed, and the grass from these fields was then used as supplementary food for reindeer. Thus, such a subsidy system decreases the costs of supplementary feeding when haymaking is still allowed on these subsidized uncultivated fields. According to the solutions presented in this thesis, the present reindeer subsidy system used in Finland also creates an incentive for supplementary feeding. Changing the subsidy system to the meat production subsidy used in Sweden would not change this incentive to increase the herd size.

3.3 Parameter estimation and model validation

Paper **III** estimated lichen wastage relative to intake rate using the model and detailed data from 20 northernmost herding districts in Finland. The best fit between the model and data was found to be obtained when wastage is described by an increasing (linear) function of the lichen biomass. In this case the average wastage value (relative to intake rate) is 5.7 for the summer season and 0 for winter at a 0 kg/ha lichen biomass level (Figure 6.). At a lichen biomass level of 1000 kg/ha, the wastages are 9.6 and 0.7 for summer and winter, respectively. If the wastage relative to intake rate is described only with a constant, the best fit between model and data is obtained when wastage is 8.5 for summer and 0.5 for winter. The values for wastage estimated in study **III** are relatively close to the ones used in studies **I** and **II** and by Moxnes et al. (2001) (Figure 6). However, wastage used in the study by Gaare and Skogland (1979) and later by Olofson et al. (2011) appears to be too high for winter wastage.

The estimated wastage values in study **III** are somewhat larger than the ones used in studies **I** and **II**. The higher wastage might be partly explained by the fact that other factors also affect the lichen biomass apart from the ones taken into account in our analyses. The results presented in studies **I** and **II** remain qualitatively the same, as the wastages used are within the range found in study **III**. However, the quantitative solutions depend on the values and function used for lichen wastage. More research with detailed data is needed to discover the exact values and functional forms for wastage in various habitats and during different seasons.

During model validation we found that the developed model was able to describe the data with good accuracy when the new estimated wastage functions were used. The modeling efficiency value was 0.75 with a linear wastage function and 0.52 with constant wastage. A visual comparison also showed that the model predictions were close to the data. Bioeconomic models for reindeer or any other similar herbivore have not been validated before, as far as I know. Sleep and Loehle (2010) studied the predictive ability of the caribou model by Sorensen et al. (2008), but found it to be low. They proposed that the model might have been too simple and that more elements should have been included. A similar effect was also found in study **III**, where excluding parts of the complex model and making it simpler reduced the model’s ability to predict the change in lichen biomass. Including a description of the pasture rotation system was particularly important.

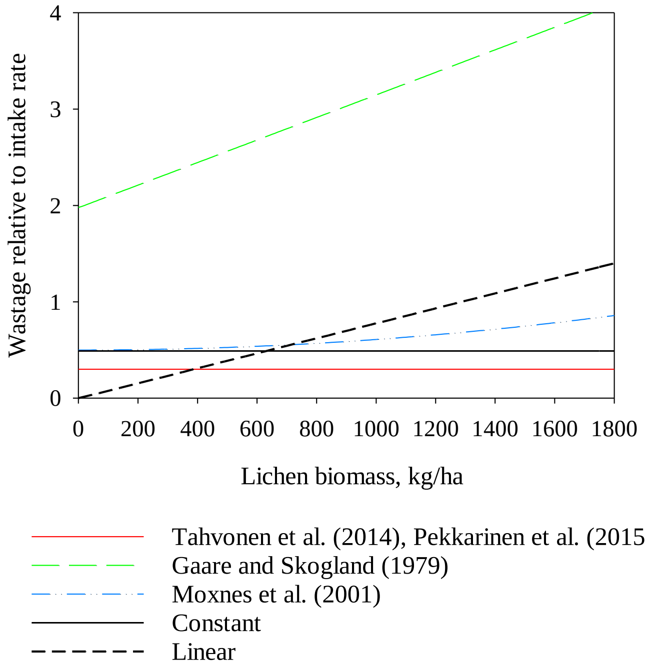

Figure 6. Lichen wastages relative to intake rate during winter. Wastages from previous research along with results for the constant and linear wastages found in our study are reported.

3.4 Comparing management results with data

A 2% interest rate and data from the herding districts were used for computing the optimal steady-state model results in the validated model of paper **III** for each of the 20 northernmost herding districts of Finland. The optimization results were compared with the data for lichen biomass and reindeer numbers for each herding district (Figure 7). Using a linear wastage function, the lichen biomass in the optimization solutions varied from 220 kg/ha to 640 kg/ha depending on the herding district. The range in the measured lichen biomasses was similar in the data, but the measured biomass was lower than in the model solution in more than half of the herding districts. In addition, in all but two herding districts the actual number of reindeer was higher than in the model solution.

These solutions suggest that reindeer numbers might be too high for current pasture conditions in many districts. This can lead to a further decrease in lichen resources and to a situation where lichen biomass is at a very low level. In this case supplementary feeding has to be increased to ensure population productivity. The situation would be undesirable from an ecological viewpoint, but it might be economically rational if the interest rate used by herders was high, feeding costs were low, and the productivity of natural pastures was low because of reasons unrelated to reindeer herding. Also, if other factors limit the option of enhancing the state of lichen pastures, supplementary feeding could be the only viable option. Cultural and other social factors additionally affect decisions concering herd sizes and management decisions (Heikkilä 2006).

Although our results suggest that the present number of reindeer is higher than in optimal case in certain districts, they also show that other factors besides the amount and availability of ground lichens highly affect how large a sustainable and productive reindeer population can be. If the amount of old and mature pine forests and arboreal lichen pastures were higher, larger reindeer populations could be upheld. In certain areas the use of seasonal pasture rotation could also help to keep the lichen pastures in good condition even without large changes in the reindeer population. Thus, when decisions concerning reindeer numbers are made, various reindeer management practices, different structures and charcteristics of herding environment and other land uses in the herding area must also be taken into account and considered.

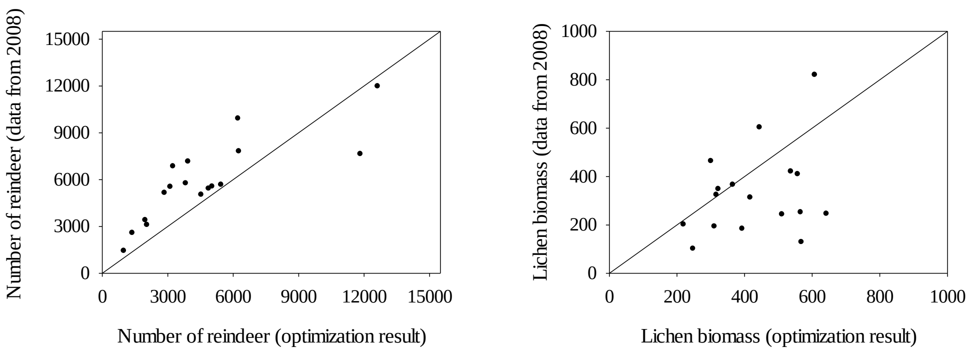

Figure 7. Actual reindeer numbers and lichen biomasses according to data from the herding districts in 2008 compared with the management solutions from the model. Management solutions are computed with a 2% interest rate and data from the herding districts. The line presents the perfect fit between model results and the data.

4 CONCLUSIONS

This thesis studies the reindeer herding system using a detailed ecological-economic dynamic model. I show that in order to study sustainable and economically viable reindeer management, both ecological and economic factors along with various management actions must be taken into account, as they strongly affect the optimal solutions and management recommendations. Strongly simplified settings cannot capture all relevant internal interactions of the reindeer herding system. Although the need for interdisciplinary research of this system has also been recognized in earlier studies (Pape and Löffler 2012) and by herders themselves (Kitti et al. 2006), this is the first study where a detailed description of the ecology of reindeer and herding practices is combined with a detailed economic optimization method. Detailed age- and sex-structured models are specified for other mammalian herbivores, but as far as I know none include both economic optimization and a dynamic description of the interaction with food resources. Mating functions and multiple energy resources (including supplementary feeding) are also rarely included in age-structured population models. In addition, this is also the first validated model for a reindeer herding system as far as I know.

In this thesis a detailed description of the reindeer population structure allowed the study of an optimal slaughtering strategy and taking the delays caused by reindeer living for several years into account. Including various winter energy resources significantly affected both ecological and economic solutions and increased the understanding of the system. Combining a detailed description of the ecology and economics of the management system has allowed studying various aspects of sustainable reindeer management. I found that alternative food resources play a significant role on the condition and productivity of the reindeer population, especially in situations with low ground lichen biomass in pastures. The solutions for reindeer populations living on natural pastures show that arboreal lichens can stabilize the fluctuations of a reindeer population. When concidering a managed population, arboreal lichens increase the profitability of reindeer herding. Arboreal lichens also reduce the need for supplementary feeding during the recovery process from overgrazing situations.

One of the main findings of this thesis is that the steady-state lichen biomass that gives the highest sustainable economic output depends on many factors in the system and can be surprisingly low. Earlier suggestions for optimal lichen biomass have varied from MSY lichen biomass level to 0.7 times the MSY level (Helle et al. 1990, Moxnes et al. 2001). In this thesis the solutions for optimal lichen biomass without supplementary feeding vary from 0.2 to 0.5 times MSY. However, the present lichen biomass is still lower than in these solutions in many of the herding districts in Finland. Present reindeer numbers in many districts are additionally somewhat higher than the sustainable management recommendations suggested by this study.

Earlier studies (e.g. Müller-Wille et al. 2006) have recognized wastage by trampling as an important factor in the deterioration of lichen pastures. However, this is the first time that the wastage level is estimated using published data. According to the results, wastage outside wintertime can be very high. Thus, the seasonal pasture rotation system could help slow down the degradation of lichen pastures and also increase the profitability of reindeer herding in many areas. This would be especially beneficial if large uniform areas of old or mature pine forests could be preserved and included as winter grazing areas. According to the results presented in this thesis, the current subsidy systems favors intensive supplementary feeding withlow lichen biomasses. Another option could be to subisidize investments that enable more effective seasonal pasture rotation. This could help reduce the trampling pressure on winter lichen pastures during the summer season. However, more research on the wastage and trampling of lichen is definitely needed to produce accurate estimations of the wastage level during different seasons and in various landscapes.

The optimization results in this thesis describe a situation where a reindeer herding co-opertative maximizes its long-term net income. However, many deviations from this assumption occur during real-life situations. Individual herders may have other preferences in addition to monetary income. Johannesen and Skonhoft (2011) indeed found that herders prefer larger herd sizes as an insurance against potential population crashes and as social status. This may be one of the reasons why actual herd sizes are larger than in optimal solutions. Herding districts are additionally composed of many reindeer owners, who all have their own, and sometimes contradictory, objectives. However, many of the current practises in Finnish reindeer herding are in line with the optimal solutions found in this thesis. A similar optimal slaughtering strategy as found in study **I** is used in almost all herding co-operatives. Also, the optimal solutions for reindeer population sizes found in study **III** are close to actual numbers, especially if interest rate is assumed to be moderate or high. However, actual reindeer numbers are somewhat higher, which can be partly explained by the findings in study **II**,which showed the current subsidy system to promote larger herds.

The studies presented in this thesis provide quidelines and preliminary management recommendations for developing the reindeer herding system in Finland. Although the model is more detailed than previous reindeer-lichen models, it still describes a theoretical simplified system. Thus, the interpretation of the results to practical management recommendations requires understanding of the real and far more complex and stochastic system. Therefore, more research on stochastic events and special situations is needed. Varying winter conditions, the amount and state of winter and summer pastures, predators, and the various aims of herders all affect the dynamics of the system and economically viable solutions along with management recommendations (Forbes et al. 2006). When applying these solutions to real management situations it is also important to incorporate them with the practical and traditional knowledge of the reindeer herders themselves (Heikkilä 2006).

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