1    Winter pastures and supplementary feeding in managing a reindeer-lichen system

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16   *Abstract*

17   In our study we use an age- and sex-structured reindeer-lichen model to examine the role of

18   different types of winter pastures, pasture rotation, and supplementary feeding on economically

19   optimal reindeer management. The model includes 17 age classes of females, 13 classes of males

20   and a detailed description of winter energy resource utilization by the reindeer population.

21   Reproduction is specified by a modified harmonic mean mating system. The diet choice made by

22   reindeer between ground and arboreal lichens and supplementary food follows the principles of the

23   optimal foraging theory. Energy intake during winter defines an individual's overwinter weight

24   decrease and its consequences on mortality, reproduction, and the birth weight of calves. If pasture

25   rotation is not in use, ground lichens are also consumed from spring to autumn in addition to winter.

26   Lichen growth depends on habitat type and lichen biomass after consumption. Arboreal lichen

27   consumption is affected by the availability of old forests and arboreal lichen biomass. The decision

28   variables are the animals chosen for slaughter from the age and sex classes and the amount of

29   supplementary food given. Results show that the availability of arboreal lichens, growth rate of

30   ground lichens, and pasture rotation all affect the optimal steady-state population level.

31   Supplementary feeding is used during the recovery process from very low lichen densities in the

32   case of zero interest rate but not in the optimal long-run steady state. With higher (3–5%) interest

33   rates intensive supplementary feeding may become optimal also in the long-term steady state, which

34   leads to the depletion of lichens. Government subsidies paid for breeding animals may promote

35   reindeer herders to base management on supplementary feeding and lower pasture conditions.

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37   Keywords: Herbivore-plant interactions, Reindeer husbandry, Structured model, Optimal

38   harvesting, Overgrazing, Supplementary feeding

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1. Introduction

Reindeer (*Rangifer tarandus*) is one of the key species in northern Fennoscandia. One fourth of the Earth's land surface is used by reindeer or caribou (Sandström et al., 2003) and nearly 40% of the land area in Fennoscandia is used as reindeer pasture (Jernsletten and Klokov 2002; Moen 2008; Pape and Löffler, 2012). The sociocultural and economic impacts of reindeer husbandry are also highly important in northern Fennoscandia, especially for the indigenous Sami people (Jernsletten and Klokov, 2002; Sandström et al., 2003; Pape and Löffler 2012). The various ecological, economic, and social aspects as well as the complexity of the grazing system should thus be taken into account when studying the reindeer herding system as a whole (Pape and Löffler, 2012).

Fennoscandian reindeer husbandry has experienced major changes since the nineteenth century (Pape and Löffler, 2012). Two major transitions have occurred in northern Finland: the traditional intensive herding has shifted towards a free-ranging system and supplementary feeding has become a regular practice in almost every herding district (Helle and Jaakkola, 2008). These changes together with an increase in reindeer numbers and various invasive land-use practices have led to the alarming deterioration of important winter pastures (Kumpula et al., 2014). According to Kumpula et al. (2014), several other factors besides reindeer numbers explain the reduction in ground lichens in the winter reindeer pasture areas. Changes in the grazing system have led to a situation where reindeer are allowed to freely graze on pastures, and only a few northern herding districts separate summer and winter grazing areas using pasture rotation fences (Helle and Jaakkola, 2008; Kumpula et al., 2014). Without seasonal pasture rotation lichen pastures are exposed to grazing and trampling throughout the year (Kumpula et al., 2011). A decrease in old coniferous forest area has also directly and indirectly influenced the reduction of ground lichens (Kumpula et al., 2014). Due to more favorable growth conditions both ground and arboreal lichens are more abundant in old coniferous forests compared to all younger coniferous forest classes.

65    Winter energy resources are important factors affecting the productivity of reindeer

66    management, and winter pastures are often described as a bottleneck for reindeer numbers

67    (Jernsletten and Klokov, 2002; Moen 2008). Lichens have been the most important winter reindeer

68    energy resource and when their amounts have reduced, supplementary food has been used to

69    compensate for the lack of natural fodder (Kumpula et al., 1998). Thus the changes in winter

70    pastures, supplementary feeding, and pasture rotation all affect the economics of reindeer herding

71    and optimal reindeer management. The importance of these changes is often pointed out (Kumpula

72    et al., 2002; Helle and Jaakkola, 2008; Pape and Löffler, 2012), but the impacts of these factors to

73    economics and the optimality of reindeer management have not been studied.

74    Kumpula et al. (2002) state that supplementary feeding has increased the productivity of

75    reindeer stocks in Finland, but the costs and other effects of feeding on reindeer management should

76    also be taken into account. Helle and Jaakkola (2008) interviewed 12 reindeer herders and found

77    that interviewees emphasized the importance of arboreal lichens. The interviewees also stated that

78    the lack of both arboreal lichens and old forests were the ultimate reason for the use of

79    supplementary food. They pointed out that the use of supplementary food was costly, but allowed

80    an increase in meat production. Kumpula et al. (2014) found that ground lichen biomass was clearly

81    lower in areas where pasture rotation was not used. A reduction in old forest area and arboreal

82    lichen pastures was also associated with lower ground lichen biomass.

83    The aim of our study is to examine the role of arboreal lichen pastures, pasture rotation, and

84    supplementary feeding on economically optimal reindeer herding. For this we use the dynamic age-

85    and sex-structured reindeer-lichen optimization model presented by Tahvonen et al. (2014). We

86    expand the model by including arboreal lichens and supplementary food as winter energy resources

87    for reindeer and by taking into account the reduction of lichen outside wintertime due to grazing

88    and trampling by reindeer. We additionally study the effects of ground lichen growth rate on

89    reindeer management. According to our knowledge optimization models with similar features do

90    not exist for reindeers or any similar herbivores.

91       Other earlier optimization models for reindeer include the two state-variable lichen-reindeer

92    models by Virtala (1992, 1996) and Moxnes et al. (2001). The control variable in these models is

93    harvesting, which is chosen for maximizing the harvesting income over a long time period, and

94    their results include optimal steady-state levels for lichen and reindeer densities. Both Moxnes et al.

95    (2001) and Tahvonen et al. (2014) also include other cratered food resources besides ground lichens

96    as winter fodder, but none of the previous studies consider the effects of arboreal lichens or

97    supplementary feeding. All previous studies also assume that pasture rotation is used and winter

98    pastures are consumed only during winter. Other age- and sex-structured reindeer models include

99    Petersson and Danell (1992), Danell and Petersson (1994) and Olofsson et al. (2011), but none

100    include supplementary feeding, arboreal lichen pastures, or optimized harvesting. Walters et al.

101    (1975) specify an age-structured model for Canadian caribou. They include arboreal lichens in their

102    model, but its use is combined with ground lichens and thus no compensatory use of arboreal

103    lichens to preserve ground lichen pastures is possible.

104       Our model includes 17 age classes of females and 13 classes of males and the sex structure

105    is specified by a modified harmonic mean mating system. Lichen resources develop over time but

106    arboreal lichen availability is constant. This is because most ground lichens are available to

107    reindeer, but over 95% of arboreal lichens grow on trees too high for reindeers to reach and every

108    winter a certain percentage of these arboreal lichens fall onto the snow and can be used by reindeer

109    (Esseen, 1985; Stevenson and Coxson, 2003). The energy available from arboreal lichens depends

110    on the area of arboreal lichen pastures as well as on the arboreal lichen biomass available to

111    reindeer (arboreal lichens both growing on trees at a height of under 2 m or falling from the upper

112    parts of trees down onto the snow). The amount of supplementary food offered to reindeer is

113    optimized. The wintertime diet choices of reindeer follow the principles of the optimal foraging
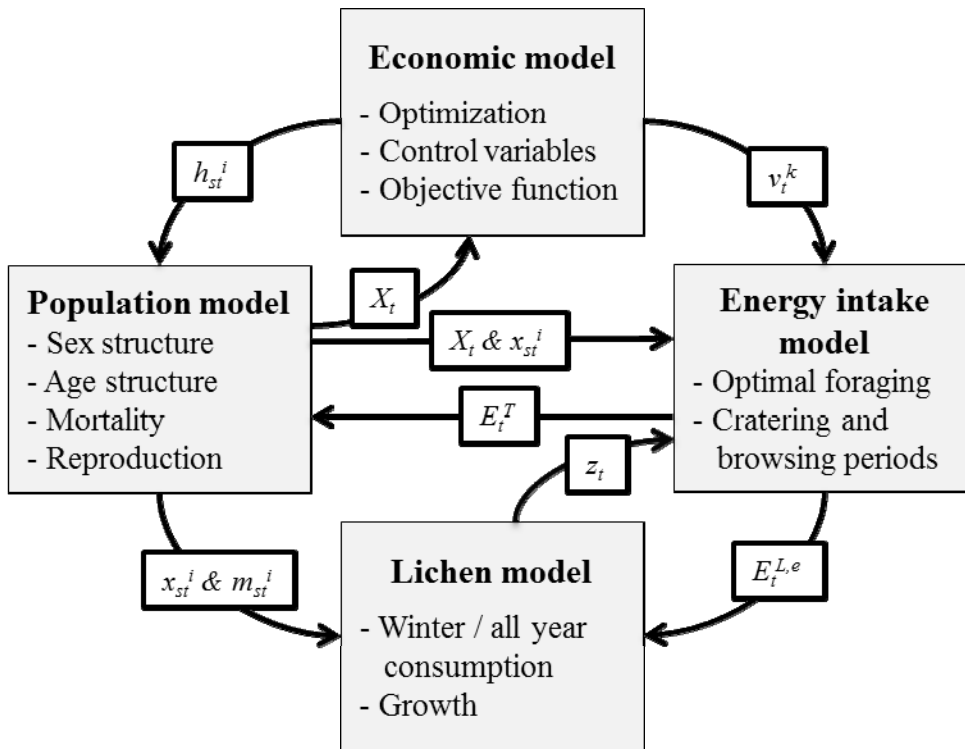
114    theory and the winter energy intake defines individuals' overwinter weight decrease and its

115    consequences on mortality, the number of calves per female, and the birth weight of calves. Lichen

116    is consumed in winter and, if pasture rotation is not in use, also in spring, summer, and autumn.

117    Lichen growth depends on lichen biomass after winter and spring consumption and also on the

118    habitat type of the lichen pastures. The decision variables are the animals chosen for slaughter from

119    the age and sex classes and the amount of supplementary food given. The results describe the

120    development of a reindeer-lichen system over time, optimal harvesting strategies, and whether or

121    not supplementary feeding is part of the economically optimal solution.

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123    2. The model and methods

124        In our study we further develop the reindeer-lichen optimization model presented in

125    Tahvonen et al. (2014). We expand the model with multiple winter energy resources, supplementary

126    feeding, over-year lichen consumption, and two different lichen growth rates. The optimization

127    model used in our study can be divided into four submodels shown in Fig. 1. These submodels

128    interact via variables shown in the figure. The population model includes the description of the state

129    and development of the age- and sex-structured reindeer population. It uses the energy intake of a

130    reindeer and the harvesting levels of each age and sex class to compute the mortality and

131    reproduction of the population. The energy intake model describes the diet choices and energy

132    intake of an individual reindeer. It uses population size and structure as well as lichen and

133    supplementary food biomasses to compute the total energy intake and the energy intake from

134    lichen. The lichen model describes the growth and consumption of lichen throughout the year.

135    Finally the economic model includes an objective function and an optimization algorithm for

136    computing the optimal harvesting and supplementary feeding levels needed to gain the highest

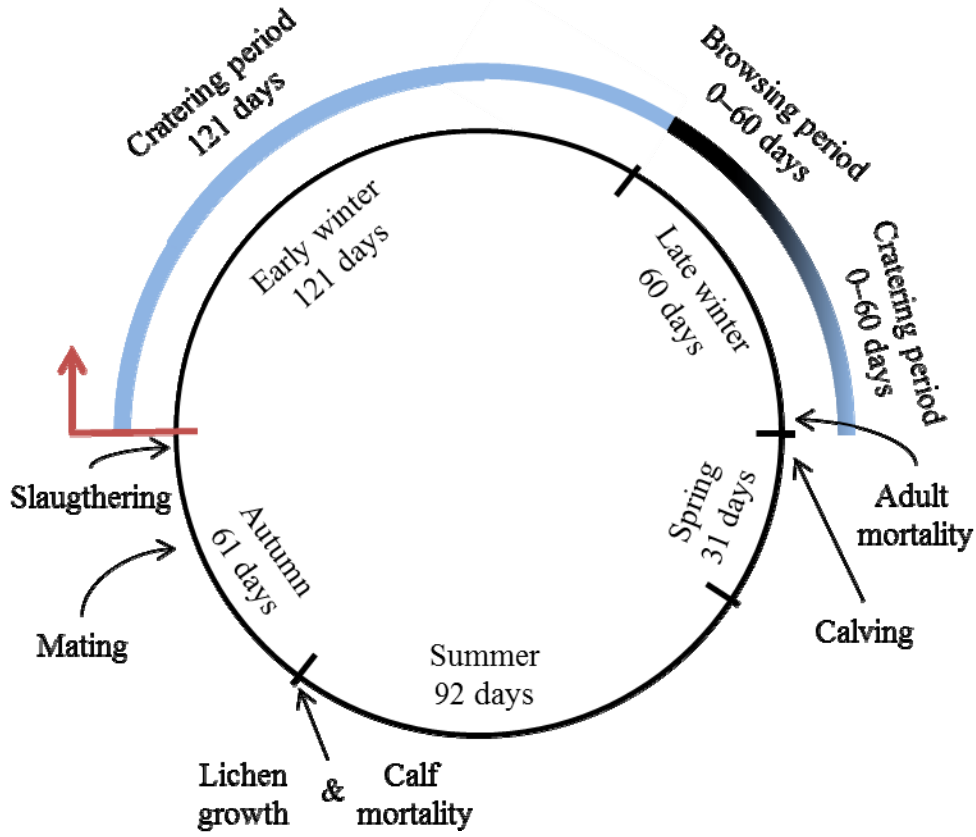137    present value of the net revenues over an infinite time horizon.

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Fig. 1. Interactions between the four submodels.

*2.1. Winter period lengths*

Fig. 2. shows the yearly cycle of reindeer husbandry as it is described in the model. The yearly cycle begins after autumn slaughtering. The winter is divided into a cratering period denoted by *a* and a browsing period denoted by *b*. Cratering is easier in early winter (here 121 days) and reindeer use cratered food and, if available, supplementary food as an energy resource. In late winter (60 days) when snow is hard, cratering is more time- and energy-consuming, and where arboreal lichen pastures are present reindeers turn to a mixed diet and the browsing period begins. The cratering period continues after the arboreal lichen pastures have been consumed if not enough arboreal lichen pastures exist to last for the entire 60 late-winter days.

152

153    Fig. 2. The yearly reindeer husbandry cycle as described in the model.

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155         A single reindeer can be estimated to browse 0.03 ha of arboreal lichen pastures in one hour

156    (Kumpula, unpubl; Rytkönen et al., 2013). The sufficiency of the arboreal lichens thus depends on

157    the area (in ha) of arboreal lichen pastures $A_Q$, the number of reindeer $X_t$, and on the length (in

158    hours) of the daily foraging time $F_t^b$ during the winter period $b$. The length (in days) of the winter

159    period $b$ is denoted by $d_t^b$ and depends on the sufficiency of arboreal lichens but cannot exceed 60

160    days (for the specification in the optimization model see Appendix 1):

161    $$d_t^b = \min\left[60, \frac{A_Q}{0.03 X_t F_t^b}\right] \quad t = 0,1,\dots .$$    (1)

162    Length of the winter period $a$ is given as:

163    $$d_t^a = d^W - d_t^b, \quad t = 0,1,\dots,$$    (2)

164    where $d^W$ is the number of winter days and $d_t^a$ the length of the cratering period.

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166    *2.2. Population model*

167    Let $s = 0,...,n_f$ denote the female age classes, $x_{0,t}^f$ the number of female calves born during

168    the spring of year $t$, and $x_{s,t}^f, s = 1,...,n_f$, $t = -1,0,1,...$ the number of females in each age class at the

169    beginning of each yearly cycle. Variables $x_{s,t}^m, s = 0,...n_m, t = -1,0,1,...$ describe the number of males

170    respectively and $X_t$ denotes the total number of reindeer at the beginning of the yearly cycle, i.e.

171    $X_t = \sum_{i=f}^{m} \sum_{s=1}^{n_i} x_{s,t}^i$. The number of calves born (Eq.(T1)) and the mating function (Eq.(T2)) are

172    presented in Table 1.

173    The numbers of individuals in different age and sex classes evolve according to

174
$$x_{1,t+1}^i = \left(1-m_0^i\right)u_i x_{0,t} - h_{0,t}^i, \; i = f,m, \; t = 0,1,..., \tag{3}$$
$$x_{s+1,t+1}^i = \left[1-m_s^i\left(wd_t\right)\right]x_{s,t}^i - h_{s,t}^i, \; i = f,m, \; s = 1,...,n_i - 1, \; t = 0,1,..., \tag{4}$$

175    where $h_{s,t}^i$, $s = 0,...,n_i -1$, $i = f,m$, $t = 0,1,...$, denotes the number of harvested reindeer, $u_i, i = f,m$

176    the share of calves belonging to sex class $i$, and $m_0^i$ the summer mortality of calves. The winter

177    mortalities of adult reindeer are denoted by $m_s^i\left(wd_t\right)$, $i = f,m$, $s = 1,...,n_i$ and $wd_t$ denotes the

178    proportion of overwinter weight decrease from autumnal weight. Functions for the number of calves

179    per mated female (Eq.(T5)) and the winter mortalities (Eq.(T6) and Eq.(T7)) are presented in Table

180    1. They depend on the overwinter weight decrease, which is a function of the average energy intake

181    in winter $E_t^T$ and is given as (Fig. 3a):

182
$$wd_t = 0.5\exp\left(-\exp\left(\frac{E_t^T - 0.72}{0.22}\right)\right), \; t = 0,1,.... \tag{5}$$
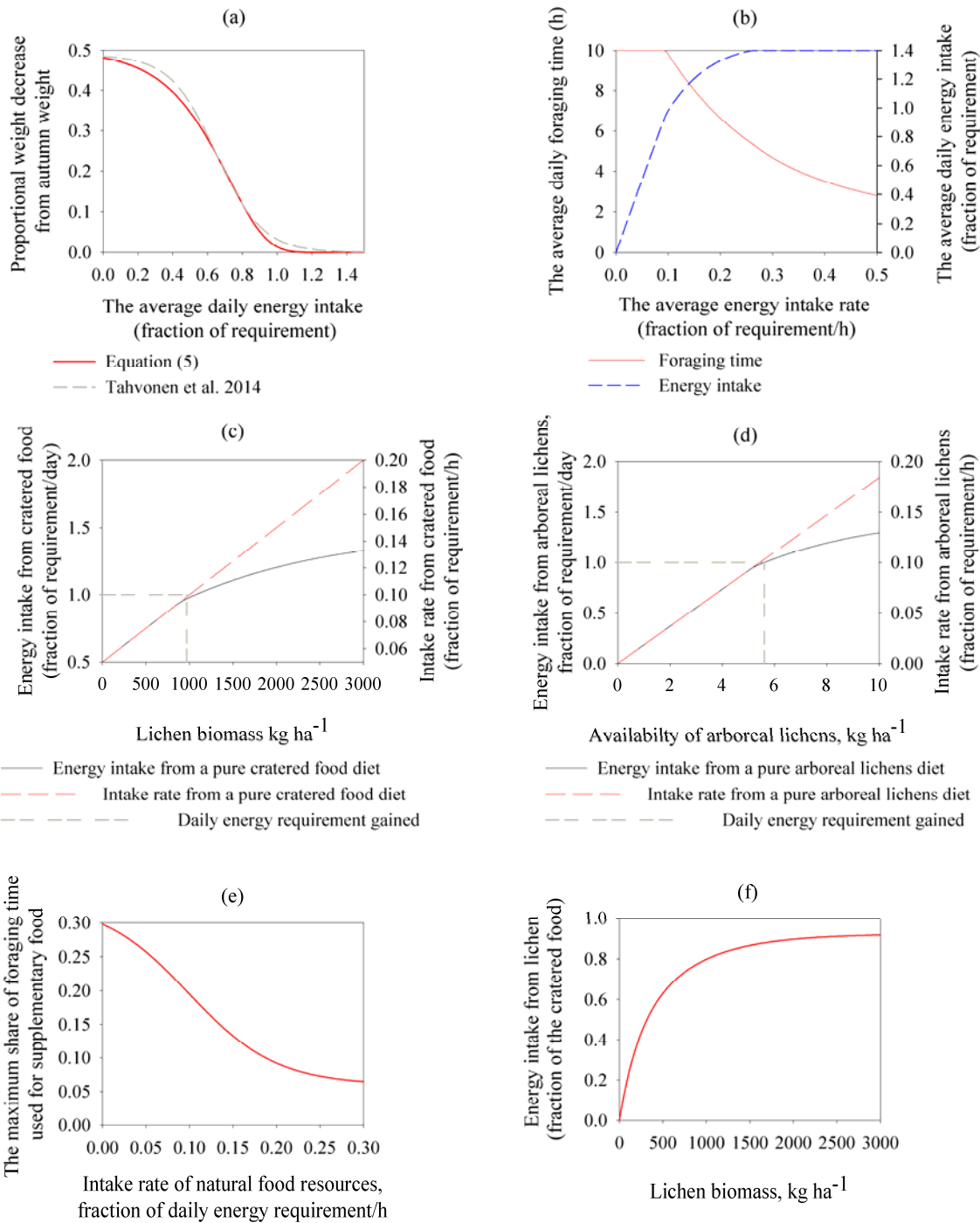
183    The decrease in an animal's body condition should be minimal when its energy requirement is

184    fulfilled. Equation (5) thus differs from Tahvonen et al. (2014) by giving a slightly smaller weight

185    decrease when the daily energy intake is close to the requirement.

186     Table 1. Equations (T1)–(T9) (Tahvonen et al. 2014).

| Variable | Units | Equation | Equation no. |
|---|---|---|---|
| The number of calves born during the spring | | $x_{0,t} = \sum_{s=1}^{n_f} \beta_{t-1} f_s (wd_t) \left[ 1 - m_s^f (wd_t) \right] x_{s,t}^f, \ t = 0,1,...$ | (T1) |
| Modified harmonic mean mating function (Bessa-Comes et al. 2010) | | $\beta_t = min \left\{ 1, \dfrac{2X_t^{em}}{X_t^{ef} + X_t^{em}} \right\}, \ t = -1,0,1,...$ | (T2) |
| Total number of potentially bred females | | $X_t^{ef} = \sum_{s=1}^{n_f} \left[ 1 - m_s^f (wd_t) \right] x_{s,t}^f$ | (T3) |
| The effective number of males | | $X_t^{em} = \sum_{s=1}^{n_m} fm_s \left[ 1 - m_s^m (wd_t) \right] x_{s,t}^m$ | (T4) |
| Average number of calves per female | | $f_s (wd_t) = \hat{f}_s \left\{ 1 - \left[ 1 + \exp\left( \dfrac{0.2715 - wd_t}{0.0239} \right) \right]^{-0.1488} \right\} 1.2272$ | (T5) |
| Overwinter mortality | | $mo_t^i(wd_t) = \left[ 1 + \exp\left( \dfrac{0.36 - \sigma_i wd_t}{0.011} \right) \right]^{-0.25}, \ \sigma_f = 1, \ \sigma_m = 1.1$ | (T6) |
| Total mortality | | $m_{st}^i = min \left\{ 1, mo_t^i + ma_s^i \right\}, \ s = 1,...,n_i, \ i = f,m, \ t = 0,1....$ | (T7) |
| The birth weight of calves | kg | $wc_{st}^i = \alpha^i w_s^c 1.0275 \left[ 1 + \exp\left( \dfrac{wd_t - 0.3146}{0.0876} \right) \right]^{-1},$ <br> $i = f,m, \ s = 1,...,n_f$ | (T8) |
| Average slaughtering weight of male and female calves | kg | $\overline{w}_0^i \left( z_t, wd_t, \mathbf{x}_t^f \right) = \dfrac{8 \sum_{s=1}^{n_f} \left[ 1 - m_{st}^f (wd_t) \right] \beta_{t-1} f_s (wd_t) x_{st}^f wc_{st}^i}{x_{0t}}$ <br> $i = f,m, \ s = 1,...,n_f$ | (T9) |

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Fig. 3. (a–f) Some main properties of the model.

(a) Weight decrease as a function of energy intake. (b) The daily foraging time and energy intake as functions of the intake rate. (c and d) Energy intakes and intake rates of a pure cratered food diet ($\mu$ = 3 m$^2$/h) and a pure arboreal lic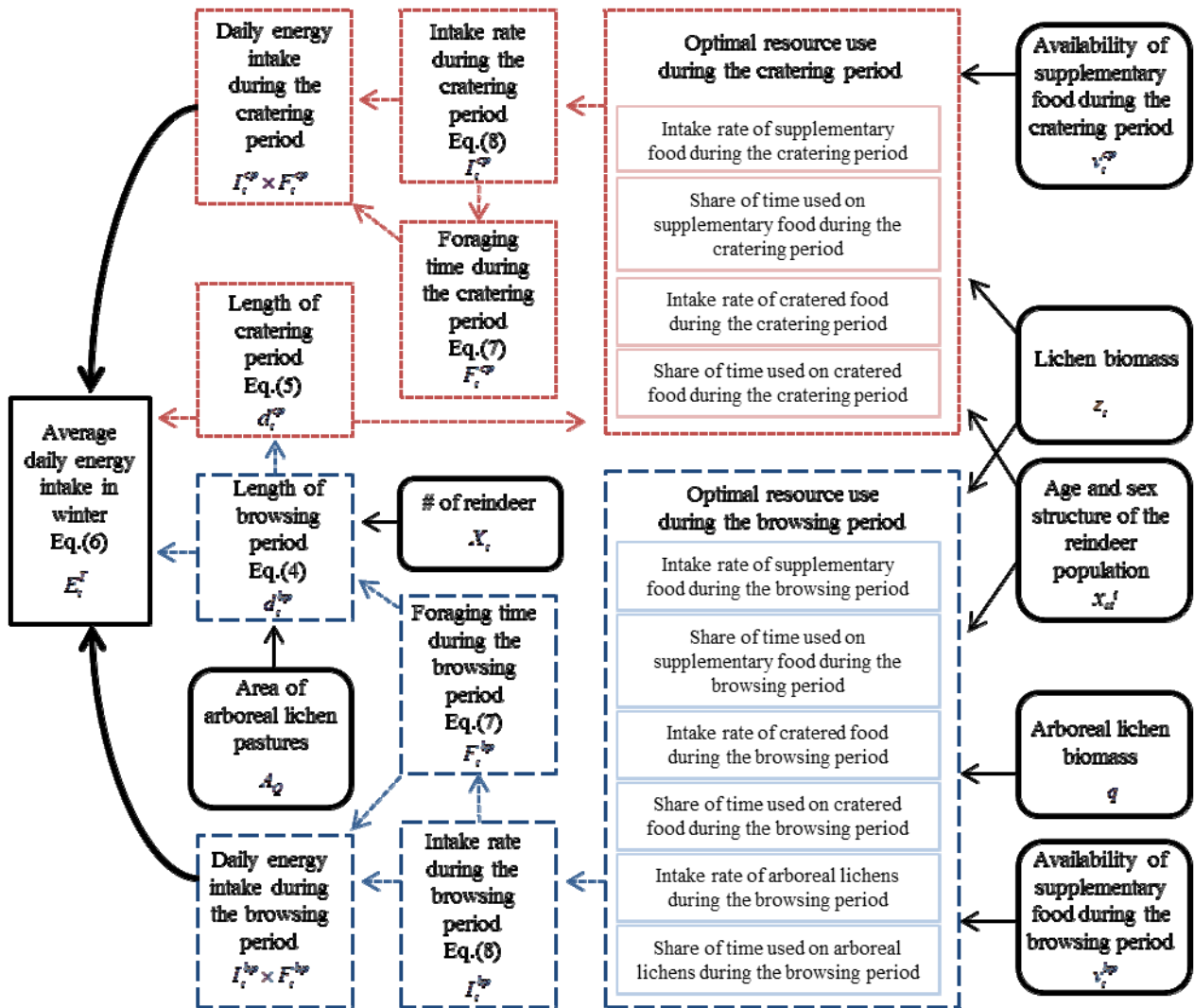hen diet as functions of their availabilities. (e) The maximum share of time used for supplementary food as a function of the intake rate of natural resources. (f) Winter energy intake from lichen as a fraction of the energy intake from cratered food.

*2.3. Energy intake model*

197  Fig. 4. shows the structure and internal interactions of the energy intake model. It uses the

198 size and structure of the reindeer population from the population model, lichen biomass from the

199 lichen model, and the availability of supplementary food from the optimization to compute the

200 average daily energy intake of reindeer, used in the population model. It is also used for computing

201 the variables necessary for the calculation of lichen consumption in winter (see Eq.(26)). It

202 additionally uses arboreal lichen pasture area and biomass for the length and energy intake during

203 the browsing period, respectively.

204



205

206 Fig. 4. Winter energy intake of reindeer as described in the model.

207

208   The average daily energy intake $E_t^T$ during winter relative to the energy requirement is a

209 weighted mean of the average intake rates $I_t^k$ times the daily foraging times $F_t^k$ of the winter

210 periods:

211 $$E_t^T = \sum_{k=a}^{b} \frac{d_t^k I_t^k F_t^k}{d^W}, \qquad k=a,b,\ t=0,1,....$$     (6)

212 The daily time used for foraging $F_t^k$ (h/day) depends on the speed of energy intake, i.e. the intake

213 rate (fraction of the daily energy requirement/foraging hour). A reindeer uses the maximum

214 foraging time (here 10 h) if the intake rate is lower (here <0.1) than what is needed to fulfill the

215 daily energy requirement in maximum time. If the intake rate exceeds 0.1, the daily foraging time is

216 less than 10 hours. Observations show that given no shortage of ground and arboreal lichens, lichen

217 consumption will exceed the energy requirement (Nieminen et al., 1987). The maximum average

218 daily intake is therefore set to 1.4 times the energy requirement, from which follows that the daily

219 foraging time cannot exceed $1.4 / I_t^k$. The realized average daily foraging time as a function of

220 intake rate is given as (for the specification in the optimization model see Appendix 1):

221 $$F_t^k = min\left\{ \frac{1.4}{I_t^k}, \left\{ 1.8508 + 8.1492 \left[ 1+\exp\left( \frac{I_t^k - 0.0953}{0.0013} \right) \right]^{-0.0066} \right\} \right\}, t=0,1,....,\ k=a,b.$$  (7)

222 Figure 3b shows that when the intake rate is below 0.1 the daily foraging time is close to the

223 maximum of 10 hours, but as the intake rate increases the daily foraging time shortens. At first the

224 decrease in foraging time is less than the corresponding rise in intake rate. The energy intake thus

225 rises nearly linearly until the level of daily energy requirement is met, but after that it rises slowly

226 until reaching the maximum daily energy intake (Fig. 3b dashed line).

227   The average intake rate during winter period $k$ depends on the intake rates $I_{j,t}^k$ of different

228 resources and on the share of foraging times $T_{j,t}^k$ spent on each of the resources:

229 $\quad I_t^k = \sum_{j=Z}^{V} T_{j,t}^k I_{j,t}^k,$ $\qquad k = a, b, \ j = Z, Q, V, \ t = 0, 1, ...,$ (8)

230 where $T_{j,t}^k$ is the share of foraging time used for resource $j$ during winter period $k$ of year $t$ and $Z, Q$

231 and $V$ denote cratered food, arboreal lichens, and supplementary food.

232 $\qquad$ The mean daily winter cratering area of a female reindeer can be determined at 30 m$^2$

233 (Kumpula, 2001; Kumpula et al., 2004). The energy content for lichens is 10.8 MJ/kg and 6.0

234 MJ/kg for dwarf shrubs and graminoids (Isotalo, 1974; Salo et al., 1982). A female reindeer

235 receives 0.054 kg of dwarf shrubs and graminoids from 1 m$^2$ of cratered area, when lichen biomass

236 is zero, fulfilling 55% of the daily energy requirement with a cratering area of 30 m$^2$. When lichen

237 biomass approximately equals 1000 kg/ha (here 970 kg/ha), a reindeer receives its daily energy

238 requirement with a purely cratered food diet from a 30 m$^2$ cratering area (Fig. 3c)(Kumpula, 2001).

239 Assuming that the intake rate from cratered food increases linearly as lichen biomass increases, the

240 intake rate for cratered food during the winter period $a$ can be given as:

241 $\quad I_{Z,t}^a = \dfrac{\mu_t^a}{3} \left( 0.055 + 5 \times 10^{-5} z_t \right), \ t = 0, 1, ... ,$ (9)

242 where $z_t$ is the dry weight of lichen (kg) per hectare at the beginning of the annual cycle. With a

243 foraging time of 10 h/day the cratering speed is 3 m$^2$/h, but snow conditions also affect the speed of

244 cratering. We thus use an average cratering area of 3.3 m$^2$/h for early winter and 2.4 m$^2$/h for late

245 winter. Let $\mu_t^a$ denote the mean cratering speed (m$^2$/h) during period $a$, which depends on the

246 length of period $b$ and is given as:

247 $\quad \mu_t^a = \dfrac{3.3 \times 121 + 2.4 \left( d_t^a - 121 \right)}{d_t^a}, \ t = 0, 1, ....$ (10)
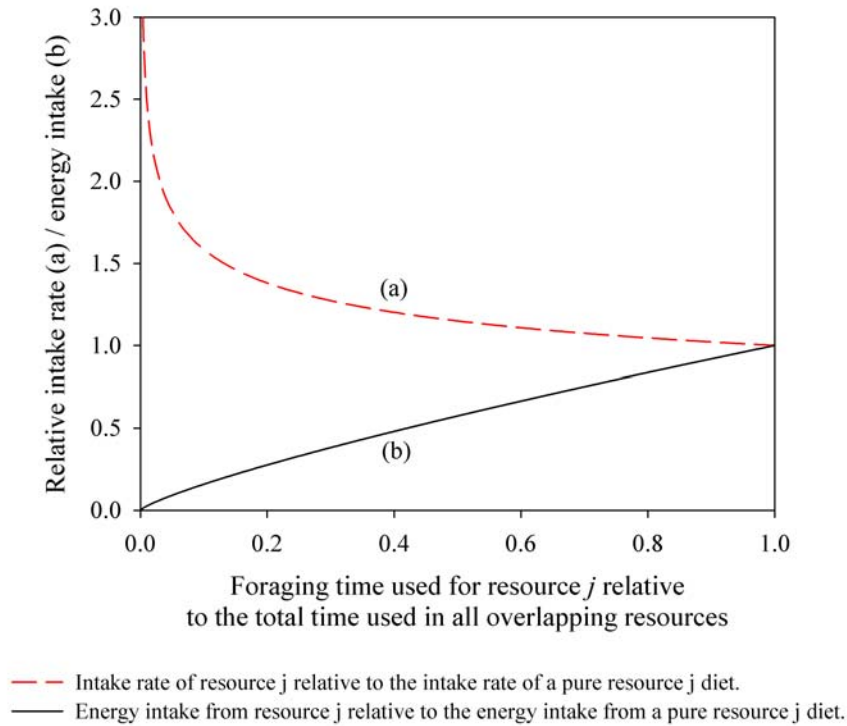
248 $\qquad$ During winter period $b$ reindeer forage in pastures, where they can combine cratered food

249 and arboreal lichens in their diet. While a reindeer uses time for searching and handling one food

250 resource (e.g. cratered food) it can also, to some extent, simultaneously search and handle the other

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251    resource (here arboreal lichens). Thus, when using a mixed cratered food / arboreal lichens –diet the

252    intake rates of both resources are higher than what they would be when using a single-resource diet.

253    We take this into account by raising the time used for one resource (in relation to the total time used

254    for both resources) to the power of -0.2, resulting in the intake rates of both resources being

255    approximately 15% higher than with a single-resource diet when the time is evenly allocated

256    between the two resources (Fig. 5). Taking into account the combined use of cratered food and

257    arboreal lichens, the intake rate of cratered food during winter period $b$ is given as:

258    $$I_{Z,t}^b = \frac{\mu^b}{3}\left(0.05 + 5\times10^{-5} z_t\right)\left(\frac{T_{Z,t}^b}{T_{Z,t}^b + T_{Q,t}^b}\right)^{-0.2} \quad t = 0,1,\dots,$$  (11)

259    where $\mu^b$ is the mean cratering speed (m$^2$/h) during period $b$, which is a constant 2.4 m$^2$/h.

260



Fig. 5. The intake rate of resource $j$ increases as the time used for resource $j$ relative to the total time used for all overlapping resources decreases.

261

262    Fig. 5. The intake rate of resource $j$ increases as the time used for resource $j$ relative to the total time

263    used for all overlapping resources decreases.

264

265       The intake rate for arboreal lichens depends on the arboreal lichen biomass (kg/ha) available

266    to reindeer denoted by $q$. As mentioned above reindeer can use 0.03 ha of arboreal lichen pastures

267    in one hour and the energy content for arboreal lichens is 10.8 MJ/kg. Thus, when arboreal lichen

268    availability is approximately 5.6 kg/ha, a reindeer receives its daily energy requirement when

269    foraging an area of 0.3 ha (Fig. 3d). We assume that the intake rate of pure arboreal lichens is a

270    linear function of arboreal lichen availability. Taking into account the simultaneous search and

271    handling times for a mixed diet the intake rate for arboreal lichens in winter period $b$ is given as:

272    $$I_{Q,t}^{b} = \frac{0.03 \times 10.8 q}{17.6} \left( \frac{T_{Q,t}^{b}}{T_{Z,t}^{b} + T_{Q,t}^{b}} \right)^{-0.2} \qquad t = 0,1,..., \qquad (12)$$

273    and the average intake rate from all natural energy resources in winter is:

274    $$I_{Z+Q,t}^{k} = \frac{I_{Z,t}^{k} T_{Z,t}^{k} + I_{Q,t}^{k} T_{Q,t}^{k}}{T_{Z,t}^{k} + T_{Q,t}^{k}} \qquad t = 0,1,... ,k = a,b. \qquad (13)$$

275       The supplementary food is assumed to be brought daily to a small area. The intake rate of

276    supplementary food is therefore not limited by searching time but only by handling time. We

277    assume that handling time is not effected by the availability of supplementary food, and the intake

278    rate is therefore a constant. Reindeer can consume one kilogram of supplementary food in one hour

279    and the energy content of commercial supplementary food is 10 MJ/kg (Maijala 1998). The intake

280    rate of supplementary food for an average-sized female reindeer is thus $I_V = 10 \times 17.6^{-1}$.

281       Reindeer weight (and size) varies between the age and sex classes, resulting in differences in

282    the energy requirements and in resource-gathering efficiencies. Larger animals are more efficient in

283    gathering resources but they also have higher daily energy requirements. We assume that these

284    contrasting effects eliminate each other and therefore use the same intake rates for all age and sex

285    classes, even though they are primarily calculated for average-sized adult females with energy

286    requirements of 17.6 MJ/d. Energy intake speed relative to energy requirements is thus the same

287    between different age and sex classes, but absolute energy intake (MJ/day) and resource

288    consumption (kg/day) depend on individual weight.

289

290    *2.4. Optimal time allocation between energy resources*

291       For the diet choices and time allocation between different winter energy resources we follow

292    the principles of the optimal foraging theory (e.g. Stephens, 1986), first presented by Emlen (1966)

293    and MacArthur and Pianka (1966). They propose that foraging decisions are based on an animal's

294    tendency to maximize its net energy gained per unit of time (i.e. energy intake rate), and that this

295    tendency is driven by natural selection. We thus assume that during winter a reindeer seeks to

296    maximize its average energy intake rate by optimally choosing the share of foraging time spent on

297    each available energy resource.

298       The intake rate of supplementary food (0.568 MJ/h) is always higher than the highest

299    possible average intake rate of natural food resources (Equations (9) and (13)) when $z_t < 8881$ kg/ha

300    and $q < 27$ kg/ha. An intake rate-maximizing animal should thus allocate all foraging time to

301    supplementary food if its availability is not limiting. However, reindeer living in natural pastures

302    have a high preference for ground and arboreal lichens (Danell et al., 1994) and they also prefer

303    natural food to supplementary food when natural food availability is high. We take this into account

304    in the allocation of foraging time. If natural pastures offer no resources, a reindeer uses

305    supplementary food until its daily energy requirement is exceeded. But if natural pastures are in

306    good condition then the time used for consuming supplementary food is shorter (Fig. 3e). The share

307    of foraging time used for supplementary food as a function of the natural food resource intake rate

308    and supplementary food availability is given as (for the optimization formulation, see Appendix 1):

309
$$T_{V,t}^{k} = \min\left\{ \left\{ 0.3\left[ 0.2 + \frac{0.9}{1+\exp\left(\frac{I_{Z+Q,t}^{k}-1}{0.5}\right)} \right] \right\}, \left( \frac{0.1 \times 17.6 v_t^k}{\sum_{i=f}^{m}\sum_{s=1}^{n_i} x_{s,t}^i Ed_s^i} \right) \right\} \quad t=0,1,\dots, \; k=a,b, \qquad (14)$$

17

310 where $v_t^k$ is the weight (in kg/day) of supplementary food brought to the reindeer population during

311 winter period $k$. The first upper limit results from the preference for natural food resources and the

312 second from the availability of supplementary food. Based on empirical observations an average

313 female (energy requirement 17.6 MJ/d) consumes one kilogram of commercial supplementary food

314 in one hour and the total hourly consumption of a reindeer population depends on the total energy

315 requirement of that population.

316     During winter period $a$, the remaining foraging time $(1-T_{V,t}^a)$ is used for cratered food:

317 $\quad T_{Z,t}^a = 1 - T_{V,t}^a,\ t = 0,1,\dots,$                 (15)

318 but during winter period $b$ the remaining time $(1-T_{V,t}^b)$ is allocated between cratered food and

319 arboreal lichens in a way that maximizes the intake rate. Equation (11) gives the intake rate for

320 cratered food during the browsing period and Equation (12) the intake rate for arboreal lichens. The

321 optimal share of the total foraging time used for cratered food during the browsing period that

322 maximizes the intake rate of a mixed diet is thus (for details see Appendix 2):

323 $\quad T_{Z,t}^b = \dfrac{\left(1-T_{V,t}^b\right)\left(\dfrac{\mu_t^b}{3}\left(0.05+5\times10^{-5}z_t\right)\right)^5}{\left(\dfrac{\mu_t^b}{3}\left(0.05+5\times10^{-5}z_t\right)\right)^5+\left(\dfrac{0.03\times10.8q}{17.6}\right)^5},\ t = 0,1,\dots,$     (16)

324 and for arboreal lichens:

325 $\quad T_{Q,t}^b = 1 - T_{V,t}^b - T_{Z,t}^b,\ t = 0,1,\dots.$             (17)

326

327 *2.5. Lichen model*

328     Let $z_t$ denote the dry weight of lichen (kg) per hectare at the beginning of the annual cycle

329 and $z_t^e$ the lichen biomass (kg/ha) at the beginning of season $e$. The lichen biomasses at the

330 beginning of different seasons and at the beginning of year $t+1$ are:

$$z_t^{wi} = z_t, \ t = 0,1,..., \tag{18}$$

$$z_t^{sp} = z_t^{wi} - l_t^{wi}, \ t = 0,1,..., \tag{19}$$

331 $\quad z_t^{su} = z_t^{sp} - l_t^{sp}, \ t = 0,1,..., \tag{20}$

$$z_t^{au} = z_t^{su} - l_t^{su} + G\left(z_t^{su}\right), \ t = 0,1,..., \tag{21}$$

$$z_{t+1} = z_t^{au} - l_t^{au}, \ t = 0,1,.... \tag{22}$$

332 where $G\left(z_t^{su}\right)$ is the lichen growth during summer, $l_t^e, \ t = 0,1,...,e = wi,sp,su,au$ is the

333 consumption of lichen per hectare in dry weight (kg) during season $e$, and $wi,sp,su,au$ denote the

334 winter, spring, summer, and autumn seasons respectively.

335 Lichen growth depends on lichen biomass after winter and spring consumption and also on

336 the average vegetation type of the lichen pastures. Lichen growth is given as:

337 $\quad G\left(z_t^{su}\right) = g \left[ -0.7008\left(z_t^{su}\right) + \left(z_t^{su}\right)\left(1 + \dfrac{z_t^{su}}{100.5832}\right)^{-0.0853} \right], \tag{23}$

338 where parameter $g$ depends on the pasture vegetation type and scales the growth rate compared to

339 the growth rate in mature and old pine forests. The growth function for mature and old pine forests

340 ($g$=1) is based on Kumpula et al. (2000) and on new data collected in a long-term monitoring study

341 at Kaamanen field station (Kumpula et al., unpublished, see more details from Tahvonen et al.,

342 2014). However, results in Kumpula et al. (2014) indicate that lichen production in young pine

343 forests, logging areas, and mountain birch forests is approximately 60% and approximately 40% in

344 mountain heaths of the production in old or mature pine forest. In our study we thus compute the

345 results also by using a lower growth rate, which describes a situation where the vegetation type of

346 lichen pastures is mixed. Assuming that lichen pastures are evenly distributed between vegetation

347 types corresponding to different levels of lichen production, the parameter value $g$ for the lower

348 growth rate can be given as: $g=[\ 1(1/3)+0.6(1/3)+0.4(1/3)]$.

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

350 $\quad l_{s,t}^{i,e} = w^e \dfrac{Ed_{s,t}^{i,e}E_t^{L,e}}{10.8} d^e, \ t = 0,1,... , i = f,m, \ s = 1,...,n_i, e = wi,sp,su,au, \tag{24}$

351 where $Ed_{s,t}^{i,e}$ is the energy requirement, $E_t^{L,e}$ the average daily energy intake from lichen in winter,

352 $d^e$ the length (in days) of season $e$, and $w^e$ denotes the fact that reindeer grazing causes loss of

353 lichen additional to that consumed for energy (Moxnes et al. 2001). Consumption depends on an

354 animal's energy requirement $Ed_{s,t}^{i,e}$. Calves consume lichen only during the autumn season, and

355 their consumption is calculated as:

356
$$l_{0,t}^{i,au} = w^{au} \frac{Ed_{0,t}^{i,au} E_t^{L,au}}{10.8} d^{au}, t = 0,1,\dots, i = f, m. \tag{25}$$

357 The average daily energy intake from lichen during winter relative to the energy

358 requirement is the average energy intake from cratered food times the fraction gained from lichen:

359
$$E_t^{L,wi} = L(z_t) \frac{\sum_{k=a}^{b} d_t^k F_t^k T_{Z,t}^k I_{Z,t}^k}{d^W}, \qquad t = 0,1,\dots, \ k = a,b. \tag{26}$$

360 The fraction of cratered food energy that is received from lichen is an increasing function of the

361 lichen biomass (Fig. 3f):

362
$$L_t = 0.3621\left(1 - e^{-0.0048985 z_t}\right) + 0.5603\left(1 - e^{-0.0015299 z_t}\right), t = 0,1,\dots. \tag{27}$$

363 For calculating energy intake from lichen during other seasons we adapt the energy intake

364 function from Tahvonen et al. (2014):

365
$$E_t^{L,e} = \tau^e \left(1.3242 - 4.0292\left[1 + \exp\left(\frac{z_t^e + 1000}{495.3806}\right)\right]^{-0.522}\right), t = 0,1,\dots, e = sp, su, au, \tag{28}$$

366 but the function is multiplied with a constant $\tau^e$ that indicates the importance of lichen as an energy

367 source during season $e$ relative to its importance during winter. The energy requirements of reindeer

368 during different seasons are given as:

369
$$Ed_{s,t}^{i,wi} = 0.683\left(w_{s-1}^i\right)^{0.75}, t = 0,1,\dots, i = f, m, \ s = 1,\dots, n_i, \tag{29}$$
$$Ed_{s,t}^{i,e} = 0.683\left(w_s^i\right)^{0.75}, t = 0,1,\dots, i = f, m, \ s = 0,\dots, n_i, \ e = sp, su, au, \tag{30}$$

370 and their total consumptions of lichen during different seasons are:

$$l_t^{wi} = \left[ \sum_{s=1}^{n_f} l_s^{wi,f}(E_t^{L,wi}) x_{st}^f + \sum_{s=1}^{n_m} l_s^{wi,m}(E_t^{L,wi}) x_{s,t}^m \right] / A, \, t = 0,1,..., \tag{31}$$

$$l_t^{sp} = \left[ \sum_{s=1}^{n_f} l_s^{sp,f}(E_t^{L,sp}) \left[1 - m_s^f(wd_t)\right] x_{s,t}^f + \sum_{s=1}^{n_m} l_s^{sp,m}(E_t^{L,sp}) \left[1 - m_s^m(wd_t)\right] x_{s,t}^m \right] / A, t = 0,1,..., \tag{32}$$

$$l_t^{su} = \left[ \sum_{s=1}^{n_f} l_s^{su,f}(E_t^{L,su}) \left[1 - m_s^f(wd_t)\right] x_{s,t}^f + \sum_{s=1}^{n_m} l_s^{su,m}(E_t^{L,su}) \left[1 - m_s^m(wd_t)\right] x_{s,t}^m \right] / A, t = 0,1,..., \tag{33}$$

$$l_t^{au} = \left[ \sum_{i=f}^{m} x_{0,t}^i \left(1 - m_0^i\right) l_0^{au,i}(E_t^{L,au}) + \sum_{i=f}^{m} \sum_{s=1}^{n_i} l_s^{au,i}(E_t^{L,au}) \left[1 - m_s^i(wd_t)\right] x_{s,t}^i \right] / A, \, t = 0,1,.... \tag{34}$$

*2.6. Economic model*

The objective function is given as:

$$\max_{\left\{ h_{s,t}^i, v_t^k, t=0,1,...,i=f,m, s=0,...,n_i, k=a,b \right\}} J = \sum_{t=0}^{\infty} (R_t - C_t)^\alpha \left( \frac{1}{1+r} \right)^t, \tag{35}$$

where $r$ is the annual interest 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. The annual revenues from slaughtering equal:

$$R_t = p\gamma \left[ \bar{w}_0^f \left(z_t, wd_t, \mathbf{x}_t^f\right) h_{0,t}^f + \bar{w}_0^m \left(z_t, wd_t, \mathbf{x}_t^f\right) h_{0,t}^m + \sum_{i=f}^{m} \sum_{s=1}^{n_i} w_s^i h_{s,t}^i \right], \, t = 0,1,... , \tag{36}$$

where parameter $\gamma$ is the fraction of carcass weight and $p$ the meat price. $\bar{w}_0^i \left(wd_t, \mathbf{x}_t^i\right)$ are the average autumn weights of calves (Eq.(T9) in Table 1) and $\mathbf{x}_t^f = \left[ x_{1,t}^f,..., x_{n_f,t}^f \right]$. Costs depend on the number of individuals slaughtered, the total number of individuals, the total land area used by a reindeer herding cooperative, and the total weight of the supplementary food given during winter:

$$C_t = C_s \sum_{i=f}^{m} \sum_{s=0}^{n_i} h_{s,t}^i + C_x X_t + C_L \left( A + K \right) + C_V \sum_{k=a}^{b} v_t^k, \, t = 0,1,... , \tag{37}$$

where $A+K$ equals the total land area and $C_{co}$, $co = s, x, L, V$ denote the associated unit costs.

Table 2 shows adult autumn weights and the parameter values for additional wastage of lichen mainly caused by trampling. These value estimates are based on the observed differences of lichen biomass between different seasonal reindeer grazing areas (Kumpula et al., 2011, 2014) and lichen vulnerability to trampling due to the common weather conditions and their moisture content

390    during each season. The parameter values for the importance of lichen as an energy resource outside

391    the winter period are also presented in Table 2 and are based on the general food selection by

392    reindeer during each season (Nieminen and Heiskari, 1989; Danell et al., 1994; Ophof et al., 2013;

393    Bezard et al., unpubl). Table 2 additionally shows unit costs and producer meat prices for the 20

394    northernmost herding districts (years 2010–2011), which are based on data from the Reindeer

395    Herder's Association.

396        The optimization problem is to choose $h_{s,t}^{i}$, $i = f, m$, $s = 0,...,n_i$, $t = 0,1,...$ and

397    $v_{t}^{k}$, $k = a, b$, $t = 0,1,...$ in order to maximize $J$ subject to constraints (1)–(37) and (T1)–(T9),

398    including the non-negativity constraints

$$x_{s,t}^{i} \geq 0, \; i = f, m, \; s = 1,...,n_i, \; t = 0,1,..., \tag{38}$$

399    $$h_{s,t}^{i} \geq 0, \; i = f, m, \; s = 0,...,n_i, \; t = 0,1,..., \tag{39}$$

$$z_t \geq 0, \; t = 0,1,..., \tag{40}$$

$$v_{t}^{k} \geq 0, \; k = a, b, t = 0,1,..., \tag{41}$$

400    and the initial levels for the state variables

$$x_{s,0}^{i}, \; i = f, m, \; s = 1,...,n_i \; given, \tag{42}$$

401    $$x_{s,-1}^{i}(1 - m_{s,-1}^{i}), \; i = f, m, \; s = 1,...,n_i \; given, \tag{43}$$

$$z_0 \; given. \tag{44}$$

402

403    *2.7. Optimization procedure*

404        The model presented in this chapter (Equations (1)–(44) and (T1)–(T9)) forms a discrete-

405    time optimal control problem. Optimization algorithms built on the Karush-Kuhn-Tucker theorem

406    of non-linear programming require that all functions are smooth and differentiable with respect to

407    the optimized variables. Equations (4), (7), and (13) are thus used in the form presented in

408    Appendix 1 when using the model in an optimization context. Our study applies Knitro

409    optimization software (version 7.0.0) that includes state-of-the-art interior point algorithms (Byrd et

410  al., 2006). The dynamic solutions are computed using time horizons from 100 to 200 periods. These

411  horizons are long enough to produce a close approximation toward the optimal steady states.
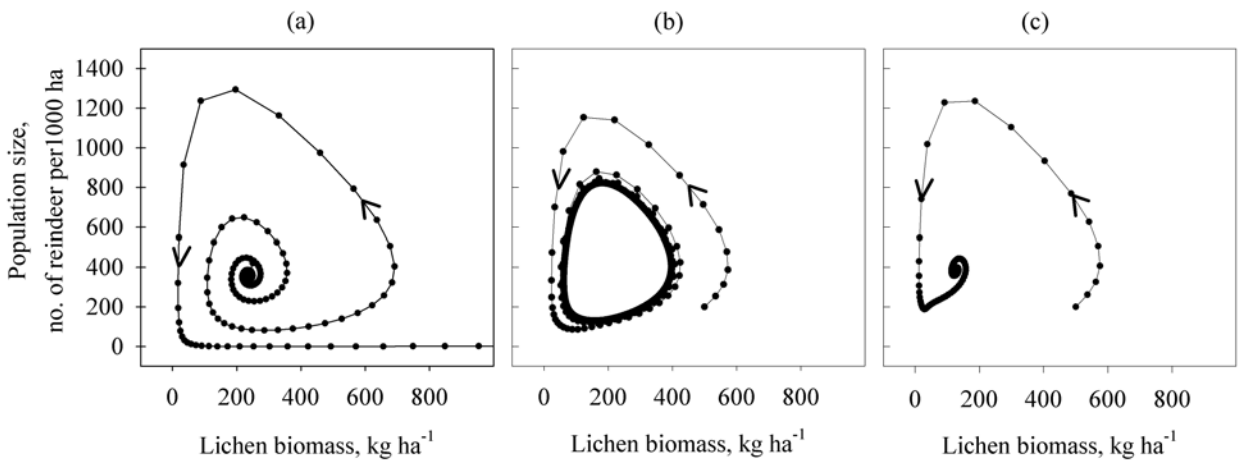
412

413  Table 2. Parameter values.
414

| Parameter | Unit | Value |
|---|---|---|
| $n_f, n_m,$ | - | 16, 12 |
| $w_s^f, s = 0,..16$ | kg | 46,63,70,76,78,80,82,82,82,82,80,80,80,78,75,72,70 |
| $w_s^m, s = 0,1,...,12$ | kg | 50,74,91,108,115,120,122,122,120,118,115,110,105 |
| $\hat{f}_s, s = 1,...,16$ | calves/female | 0,.6,.85,.9,.92,.92,.92,.93,.93,.85,.75,.6,.4,.2,.05,0 |
| $u_f, u_m$ | - | 0.48, 0.52 |
| $fm_s, s = 1,...,12$ | females/male | 1,7,15,20,22,20,18,15,10,7,3,1 |
| A, K | ha | 1000, 2000 |
| $A_Q$ | ha | 0–1500 |
| $\alpha^f, \alpha^m$ | - | 1, 1.08 |
| $w_s^c, s = 1,...,16$ | kg | 4.7, 4.7,5,5.4,6,6.2,6.2,6.2,6.2,6,5.8,5.6,5.4,5,4.7,4.7 |
| $\gamma$ | - | 0.48 |
| $C_s, C_x$ | €/animal | 13.35, 39.54 |
| $C_L$ | €/ha | 1.14 |
| $C_V$ | €/kg | 0.1–1 |
| r | p.a. | 0-0.07 |
| p | €/kg | 8 |
| $mo_0^i, i = f, m$ | - | 0.02 |
| $ma_s^m, s = 1,...,n_m$ | - | 0,0,0,0,0,0,0,0,.2,.5,.8,1 |
| $ma_s^f, s = 1,...,n_f$ | - | 0,0,0,0,0,0,0,0,0,0,0,0,.1,.2,.5,.8,1 |
| $d^W$ | days | 181 |
| $\mu_t^a, \mu_t^b$ | m²/h | 3–3.3, 2.4 |
| q | kg/ha | 0–15 |
| g | - | 1, 2/3 |
| $w^e, e = wi, sp, su, au$ | - | 1.3, 1.6, 3, 1.6 |
| $d^e, e = wi, sp, su, au$ | days | 181, 31, 92, 61 |
| $\tau^k, e = sp, su, au$ | - | 0.8, 0.3, 0.6 |

415

416 3. Results

417 *3.1. Population development with no harvest*

418       The steady-state solution for the model, assuming no harvest

419 ( $h_s^i = 0$, $s = 0,...,n_i - 1$, $i = f,m$ ) or supplementary feeding ( $v^k = 0$, $k = a,b$ ), depends on the growth

420 rate of lichen, arboreal lichen availability, and whether or not pasture rotation is in use. With a high

421 ground lichen growth rate and without arboreal lichens or pasture rotation the lichen biomass in

422 steady state is 237 kg/ha and the reindeer population size 356 individuals per 1000 hectares of

423 lichen pasture. Without arboreal lichens the solutions are unstable. If the initial state is even slightly

424 outside the steady state, the system approaches one of the other two nonnegative steady states,

425 where the reindeer population is zero and the lichen biomass is either zero or within the carrying

426 capacity (Fig. 6a). Increasing arboreal lichen availability decreases the steady-state lichen biomass

427 and stabilizes the system. A small amount of arboreal lichen pastures and their lichens yield a cycle

428 around the steady state (Fig. 6b). Increasing arboreal lichen availability to a high level makes the

429 steady state stable (Fig. 6c) and with extremely high availability the steady state is stable, but

430 ground lichen biomass is zero.



431

432 Fig. 6. (a–c) Development of the reindeer-lichen system without predators, harvesting or

433 supplementary feeding. Solutions represent a system with closed pasture rotation, and all lichen

434 pastures are located in old or mature pine forests (high lichen growth rate), and with different

435     arboreal lichen availabilities: (a) no arboreal lichens, (b) lower availability, $q = 5$ kg ha$^{-1}$, $A_Q$ =

436     1000 ha, (c) high availability, $q = 10$kg ha$^{-1}$, $A_Q = 1000$ ha.
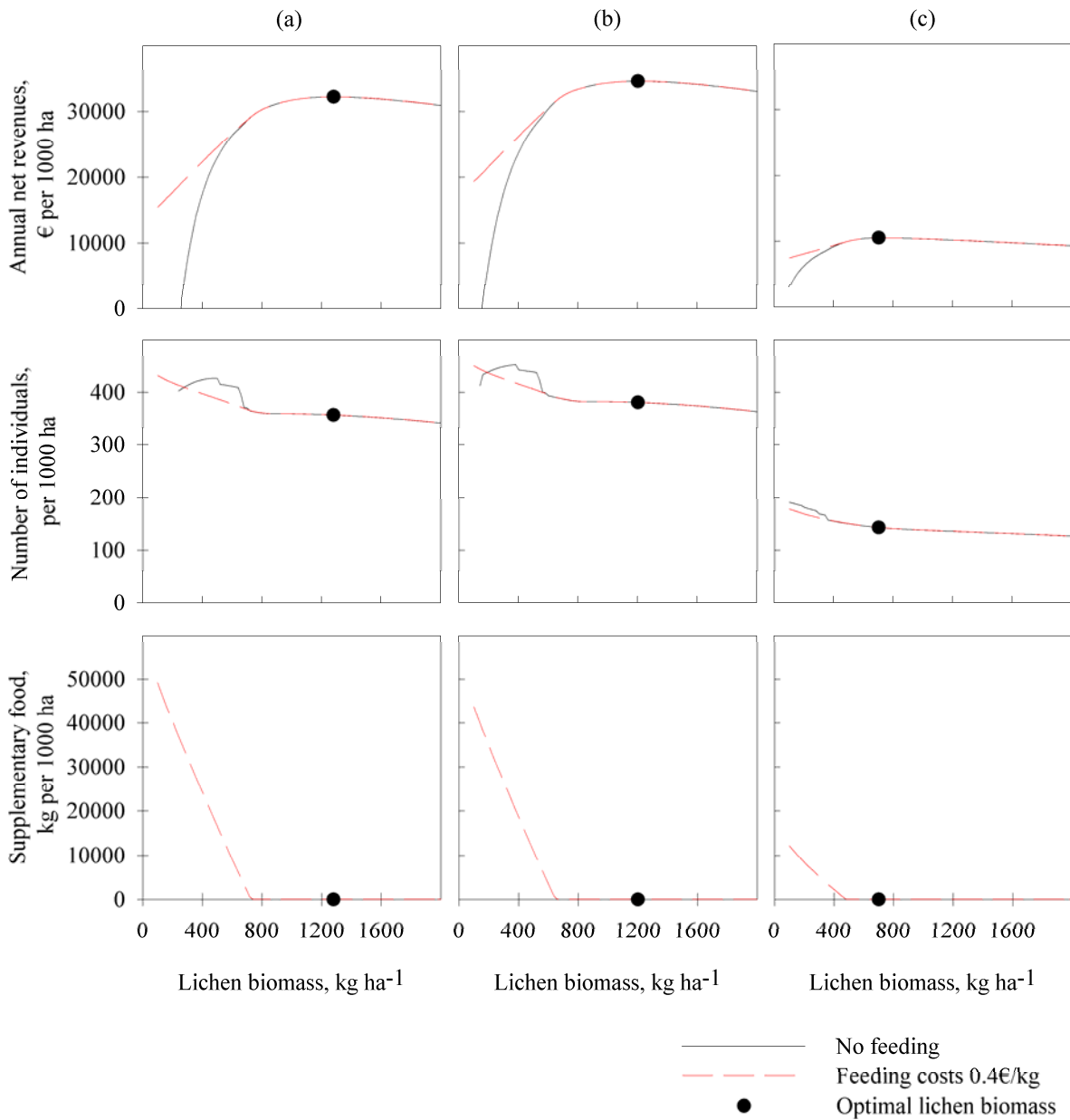
437

438     *3.2 Optimal steady states with zero interest rate*

439        For computing the candidates for optimal solutions the minimum biomass of lichen is

440     restricted to 100 kg/ha. This is because numerical computation becomes overly tedious with such

441     exceptionally low lichen biomasses. With closed pasture rotation ( $d^{wi} = 181$, $d^e = 0, e = sp, su, au$ )

442     and a high lichen growth rate (all lichen pastures in old or mature pine forest), the highest annual

443     steady-state net revenues (€ 32200 1000 ha$^{-1}$) are obtained when lichen biomass is 1278 kg per

444     hectare of lichen pasture and the reindeer winter population size is 357 individuals per 1000

445     hectares. Fig. 7 shows that reindeer population size and the annual net revenues are clearly lower

446     without pasture rotation and with a lower lichen growth rate (see also Table 3). Increasing the

447     availability and the area of arboreal lichen pastures decreases the optimal steady-state lichen

448     biomass but increases the reindeer population size and annual net income (Fig. 7 and Table 3). With

449     a low ground lichen growth rate and without pasture rotation the optimal lichen biomass is

450     especially low: 709 kg/ha with high availability of arboreal lichens and 320 kg/ha with extremely

451     high availability ($q = 15$, $A_Q = 1500$). The slaughter targets calves, nine-year old females and five-

452     year old males at all the steady states with optimal lichen levels. But if lichen biomass is far below

453     optimal and supplementary feeding is not used, the slaughter of males concentrates on the one-year

454     olds rather of the calves and five-year olds. This can be seen in Fig. 7 as a sudden increase in the

455     winter population size of reindeer.

456        When the total feeding costs equal 0.4 €/kg, supplementary feeding is not used in the

457     optimal steady state with zero interest rate (Fig. 7 and Table 3). However, supplementary feeding is

458     used in the steady states corresponding to low lichen biomasses. In these cases the annual net

459     revenues are higher than without feeding and slaughtering concentrates on calves, nine-year old
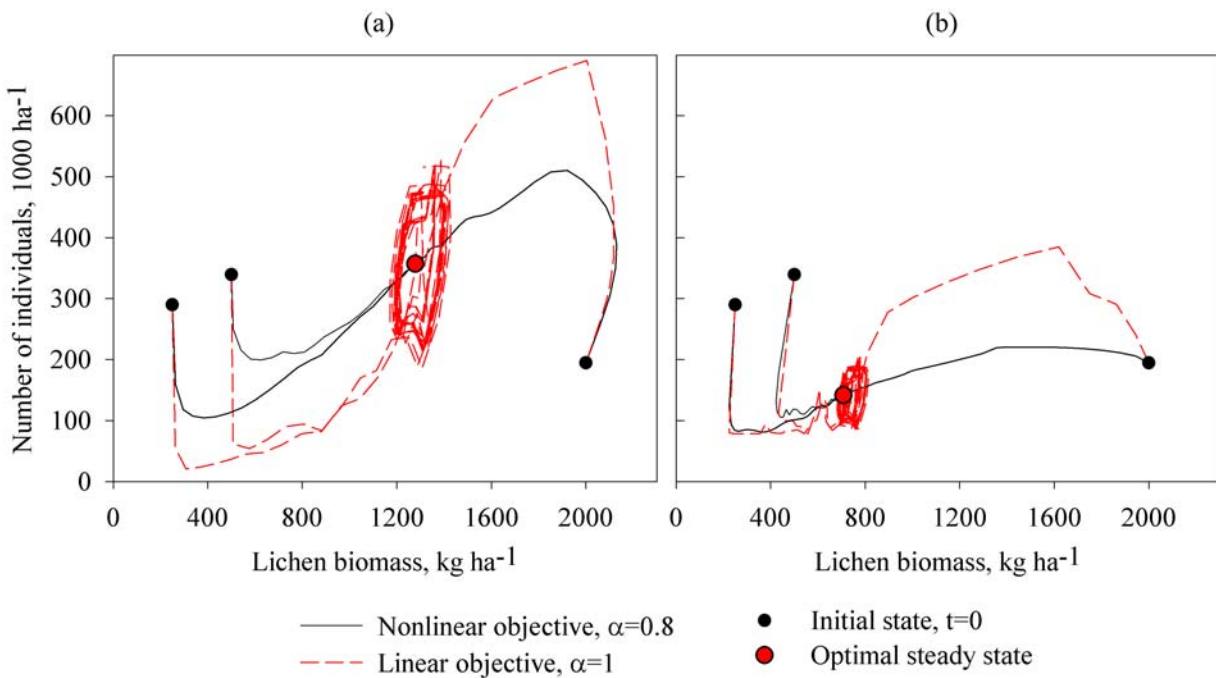
females and five-year old males. Increasing arboreal lichen availability decreases the need for
supplementary feeding in low lichen biomasses.



Fig. 7. Optimal steady states corresponding to different lichen biomasses with zero interest rate. Solid lines represent solutions without the possibility of supplementary feeding and dashed lines with supplementary feeding costs of 0.4€/kg. (a) Closed pasture rotation and high lichen growth rate. (b) Closed pasture rotation, high ground lichen growth rate, and high arboreal lichen availability. (c) No pasture rotation, low ground lichen growth rate, and high arboreal lichen availability.

*3.3 Dynamic solutions with zero interest rate*

470      Fig. 8 shows the optimal development of the reindeer-lichen system starting from three

471   different initial states outside the optimal steady state. The development leads to the optimal steady

472   state if the objective function is nonlinear (α < 1) and to a cycle around the steady state if the

473   objective is linear (α = 1). When feeding costs equal or top 0.4 €/kg, the use of supplementary food

474   is not optimal in the long-term steady state with zero interest rate. However, feeding is optimal in

475   the transition periods when lichen biomass is low in the initial state (Fig. 9). The use of

476   supplementary food during the transition periods keeps system productivity at a higher level by

477   preventing the collapse of the number and weight of the calves in the first years of the transition

478   phase. This allows for a higher number of slaughtered calves and reindeer. Increasing arboreal

479   lichen availability decreases the number of years when supplementary feeding is used in the

480   transition period.



481

482   Fig. 8. Optimal solutions over time (zero interest rate) from different starting points with linear (α =

483   1) and nonlinear (α = 0.8) objectives. (a) Closed pasture rotation and high lichen growth rate. (b)

484   No pasture rotation, lower lichen growth rate, and high arboreal lichen availability.

485

Fig. 9. Recovery from overgrazing with zero interest rate and nonlinear objective (α = 0.8). Solid lines: no possibility of offering supplementary food. Dashed lines: feeding costs of 0.4 €/kg. (a) Closed pasture rotation and high lichen growth rate. (b) Closed pasture rotation, high lichen growth rate, and high arboreal lichen availability. (c) No pasture rotation, low lichen growth rate, and high arboreal lichen availability.

491

492     *3.4 Effects of interest rate*

493          Table 3. shows the optimal steady-state solutions for different interests rates, arboreal lichen

494     availabilities, pasture rotations, and ground lichen growth rates. Increasing the availability of

495     arboreal lichens increases the annual net revenues and reindeer population size but decreases the

496     steady-state lichen biomass. Pasture rotation and a higher lichen growth rate both significantly

497     increase the annual net income. They also increase the steady-state lichen biomass and reindeer

498     population size. With a higher interest rate the steady-state reindeer population size is higher and

499     lichen biomass is lower. The costs of supplementary feeding are 0.4 € $kg^{-1}$ in all of solutions.

500     Feeding is not optimal with a low interest rate, but intensive supplementary feeding may become a

501     part of the optimal solution with a higher interest rate. With a lower lichen growth rate, feeding

502     becomes optimal in the steady state if the interest rate is 5%. Additionally if pasture rotation is not

503     used, feeding is also optimal with a 3% interest rate (Table 3).

504          In the solutions presented in Table 3, the lichen biomass is 100 kg/ha when intensive

505     feeding is optimal. This is due to the restriction for the minimum lichen biomass. In these solutions

506     it is optimal to offer as much supplementary food as allowed by the other restrictions of the model.

507     The density dependence for the reindeer population in the model is only through energy intake in

508     winter. Without the minimum lichen biomass restriction, the size of the supplementary- fed reindeer

509     population could thus increase indefinitely, because the survival of the population would not be

510     bounded by natural food resource availability. In reality, other density dependence or social factors

511     would begin limiting the growth of the population at some point even in the case of unbounded

512     access to winter energy. However, intensive supplementary feeding would lead to the overgrazing

513     of natural pastures, if the other density-dependence factors would limit the growth of the population

514     only at very high reindeer densities.

515

Table 3. Optimal steady states with different interest rates.

| Pasture rotation | Interest rate (p.a.) | No arboreal lichen pastures | | | | High availability of arboreal lichens, $q=10$, $A_Q=1000$ | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | z | X | Y | v | z | X | Y | v |
| High lichen growth rate (all lichen pastures in old or mature pine forests) | yes | | | | | | | | |
| | | 1278 | 357 | 32200 | 0 | 1209 | 381 | 34600 | 0 |
| | | 1064 | 359 | 31900 | 0 | 983 | 382 | 34200 | 0 |
| | | 850 | 360 | 30800 | 0 | 759 | 383 | 32900 | 0 |
| | | 758 | 374 | 29900 | 0 | 706 | 386 | 32400 | 0 |
| | no | | | | | | | | |
| | | 1103 | 186 | 15000 | 0 | 870 | 202 | 16470 | 0 |
| | | 926 | 189 | 14900 | 0 | 729 | 205 | 16400 | 0 |
| | | 802 | 192 | 14500 | 0 | 650 | 209 | 16100 | 0 |
| | | 738 | 200 | 14000 | 0 | 603 | 211 | 15800 | 0 |
| Low lichen growth rate (mixed-type lichen pastures ) | yes | | | | | | | | |
| | | 1215 | 241 | 20500 | 0 | 1108 | 265 | 23000 | 0 |
| | | 960 | 244 | 20300 | 0 | 820 | 268 | 22600 | 0 |
| | | 772 | 247 | 19400 | 0 | 665 | 273 | 21900 | 0 |
| | | 100* | 306 | 10000 | 113 | 100* | 324 | 13900 | 90 |
| | no | | | | | | | | |
| | | 1075 | 125 | 8900 | 0 | 709 | 142 | 10500 | 0 |
| | | 858 | 128 | 8800 | 0 | 613 | 145 | 10300 | 0 |
| | | 100* | 168 | 3900 | 112 | 100* | 178 | 7500 | 69 |
| | | 100* | 168 | 3900 | 112 | 100* | 178 | 7500 | 69 |

Interest rate values per row group: 0, 1, 3, 5.

z = steady-state lichen biomass, kg ha$^{-1}$
X = steady-state population size, reindeer per 1000 ha

Y = Annual net revenues, € per 1000 ha
v = total annual supplementary feeding, kg per reindeer

$q$ = biomass of the available arboreal lichens, kg ha$^{-1}$

$A_Q$ = area of arboreal lichen pastures, ha

* minimum biomass of lichen restricted to 100 kg ha$^{-1}$

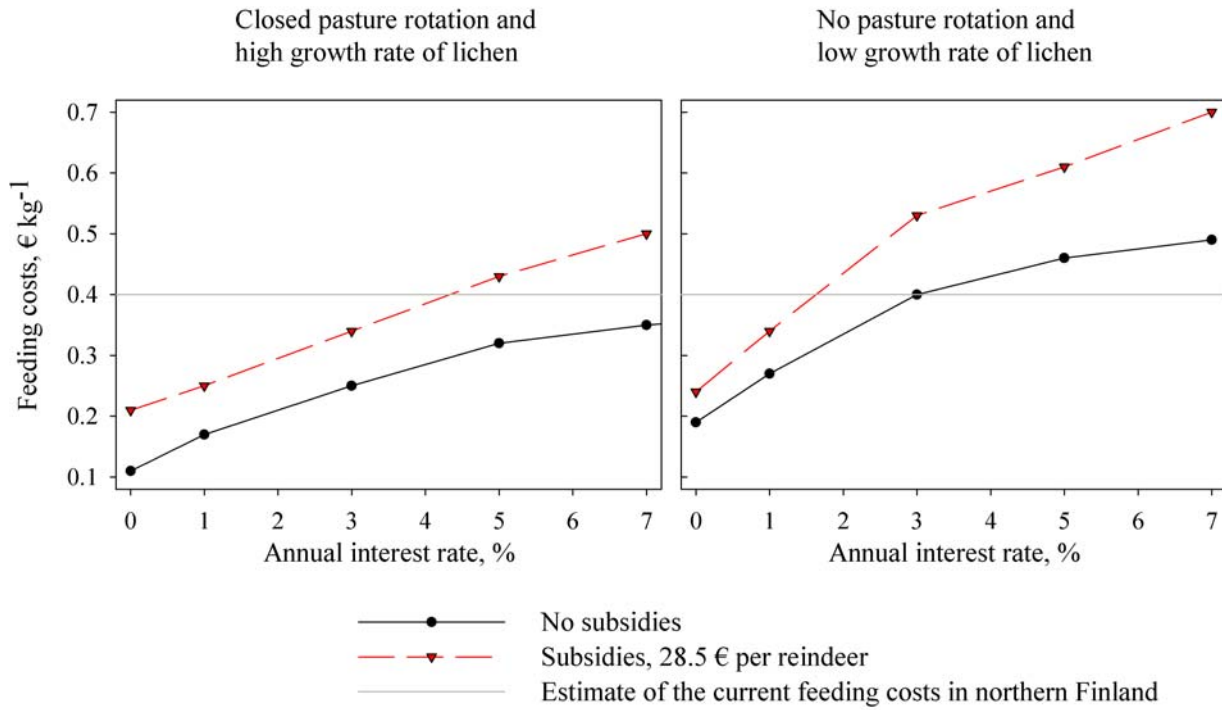*3.5 Effects of feeding costs and subsidies*

Fig. 10 shows that when pasture rotation is used, lichen growth rate is high, and interest rate is zero, feeding becomes optimal in the steady state if the total cost of supplementary feeding is equal or below 0.11 € kg$^{-1}$. If pasture rotation is not used and ground lichen growth rate is low, the highest cost when optimal feeding is still optimal is 0.19 € kg$^{-1}$. If the interest rate is higher, feeding becomes an optimal solution also with higher feeding costs. Supplementary feeding is not optimal in the steady state with the estimated current feeding costs (0.4 €/kg) in northern Finland, even with a 7% interest rate if the growth rate of lichen is high and pasture rotation is used. However, if subsidies are paid (28.5 € per reindeer in the winter population) feeding becomes a part of the

528  optimal solution with 5% and higher interest rates. Arboreal lichen availability has only minor a

529  effect on these solutions.

530



Fig. 10. Effect of interest rate on the optimality of supplementary feeding in the optimal steady states. Curves represent the feeding costs for which it is optimal to offer supplementary food as a main winter energy resource for reindeer, resulting in very low lichen densities.

531

532  Fig. 10. Effect of interest rate on the optimality of supplementary feeding in the optimal steady

533  states. Curves represent the feeding costs for which it is optimal to offer supplementary food as a

534  main winter energy resource for reindeer, resulting in very low lichen densities.

535

536

537   4. Discussion

538       Arboreal lichens play an important role in our study concerning the stability of the reindeer-

539  lichen system in the absence of harvesting or supplementary feeding. Tahvonen et al. (2014) shows

540  that if the winter energy intake of reindeer comes solely from cratered food, it leads to a crash of the

541  unharvested reindeer population. In our extended model the population can remain at a stable level

542  or in a stable cycle even without harvesting and predators if arboreal lichen pastures are present.

543  This is in line with results from more general predator-prey models, where alternate food resources

544 for predators may promote the persistence of a predator population (van Baalen et al., 2001). In our

545 model the system stabilizes because, unlike ground lichens, most of the arboreal lichens are not

546 available for grazing. Similarly Riseth et al. (2002) found that in their two-pasture – herbivore

547 model reindeer-pasture dynamics stabilize if the reindeer population is limited by winter pastures

548 and part of the winter pastures is kept ungrazed. Earlier studies (Kumpula and Nieminen, 1992;

549 Helle & Kojola, 1993; Kumpula et al., 1998) have also observed the availability increase of arboreal

550 lichen pastures to balance out and increase the productivity of a reindeer herd.

551 The optimal lichen levels with zero interest rate were 33% and 50% lower in Moxnes et al.

552 (2001) and Tahvonen et al. (2014) respectively than the lichen density that maximized lichen

553 growth (MSY). Optimal lichen density with zero interest rate is usually 50–70% less than MSY in

554 our study, depending on arboreal lichen availability, ground lichen growth rate, and whether or not

555 pasture rotation is in use. Optimal lichen level can be as low as 15% of the MSY lichen level with

556 extremely high arboreal lichen availability combined with a low lichen growth rate and lack of

557 pasture rotation. Economically optimal reindeer management could thus lead to very low lichen

558 densities in some special cases even with a zero interest rate. However, this would not adversely

559 affect the body condition or weights of the reindeer because energy from arboreal lichen would

560 compensate the lower energy intake from cratered food.

561 With current feeding costs (0.4 €/kg) it is not optimal to use supplementary food in the

562 optimal steady state if the interest rate is zero. However, if lichen biomass is 50% or less of the

563 optimal, then the maximized steady-state yearly net income would be significantly higher with

564 supplementary feeding than without it (Fig. 7). This is because supplementary feeding decreases the

565 mortality and increases the body condition and calf production of a reindeer herd in poor winter

566 pasture conditions (Helle and Kojola, 1993; Kumpula et al., 1998; Ballesteros et al., 2013). By

567 using supplementary feeding the slaughtering strategy also remains similar compared to the steady

568 state with optimal lichen biomass, but if feeding is not used and lichen biomass is low the

569    slaughtering of males is targeted to one-year old reindeer. The same difference is seen in the

570    slaughtering strategies used in Finland and Finnmark, Norway. Supplementary feeding is common

571    in Finland and slaughtering targets calves, but in Finnmark, where feeding is not used and reindeer

572    usually have lower body condition and small calves, the main portion of slaughtered animals are

573    formed by males at one and a half years of age (Holand et al., 2010).

574          Virtala (1996) and Moxnes et al. (2001) found a variant of the constant escape solution to be

575    optimal in their non-structured model. Tahvonen et al. (2014) obtained a solution that the constant

576    escapement policy is not optimal in their age- and sex-structured reindeer-lichen model and that the

577    optimal recovery from overgrazed pastures may be longer than with constant escapement. Our

578    results show that even with zero interest rate supplementary feeding is optimal during the first years

579    of recovery from highly overgrazed pastures. The use of supplementary feeding does not affect the

580    length of optimal recovery, but allows smoother adjustment of the age structure. In line with

581    empirical results of Bårdsen et al. (2009), in our model the improved energy intake during winter

582    increases the adult body mass in spring but not in the following autumn. Thus, feeding keeps

583    reindeer in better body condition and also increases the birth and slaughtering weight of calves,

584    which has great importance on the quality of the slaughtered animals and produced reindeer meat.

585    Without feeding it would not be optimal to continue calf slaughtering during the first years of

586    recovery. If arboreal lichen pastures are present, the use of supplementary feeding during the

587    recovery period is not as intense as without them, as the reindeer also gain energy from arboreal

588    lichens and not only from overgrazed ground lichen pastures.

589          Moxnes et al. (2001) concluded that economically rational management based on a high

590    interest rate cannot be the cause of overgrazing. More recently Tahvonen et al. (2014) found that

591    increasing the discount rate up to 6–7% causes an approximately 50% decrease in the steady-state

592    lichen level. However, neither of the previous studies considered the impact of supplementary

593    feeding. According to our results economically optimal reindeer management can lead to very low

594 lichen biomass even with a moderate (2–5%) discount rate and with the current price of

595 supplementary food. Whether or not intensive supplementary feeding, leading to low lichen levels,

596 becomes an optimal solution, depends on ecological and economic parameters, especially on the

597 interest rate, subsidies, and lichen growth rate.

598 Moxnes et al. (2001) varied the height of the lichen growth curve and found that it only

599 produces a simple scaling effect. In our model, changing the lichen growth rate (height of the

600 growth curve) can cause significant differences in the optimal solutions. The optimal steady-state

601 lichen biomass is lower with a lower growth rate, especially if arboreal lichen availability is very

602 high. Additionally, with a 5% interest rate the change from a high growth rate to a lower growth

603 rate makes supplementary feeding optimal with current supplementary food prices. Without pasture

604 rotation the same effect is also found with a 3% interest rate. Arboreal lichen pastures have only a

605 minor effect on the optimality of supplementary feeding in the optimal steady state in our model.

606 However, arboreal lichen availability considerably affects the optimal use of supplementary food

607 with low lichen biomasses and the optimal recovery process from overgrazed pastures. In Finland

608 subsidies are paid for the breeding animals of a reindeer population in winter. According to our

609 results, these types of subsidies can favor intensive supplementary feeding as part of the optimal

610 solution. Another possibility of subsidizing reindeer husbandry is subsidizing the investments that

611 enable more effective lichen pasture rotation. Such a policy would increase lichen biomass and the

612 net income of reindeer husbandry if most lichen pastures could be used only during winter.

613

614 Conclusions

615 Our study presents the description and solutions for the dynamic reindeer-lichen model with

616 extensions that recognize the impact of arboreal lichen pastures, pasture rotation, different growth

617 rates for ground lichen and supplementary feeding. Reindeer herding and the herding environment

618 in Finland has gone through major changes during the last decades and our results clearly indicate

619   that such changes have a strong effect on the optimal management of a reindeer population.

620   Understanding the driving mechanisms of these solutions can also help to explain the overgrazing

621   of winter lichen pastures.

622       Traditional intensive herding has changed to a free-ranging system and pasture rotation is

623   not in use in most of the herding districts. Forestry and other land use forms have caused pasture

624   fragmentation and changes in forest structure, which have made it difficult to preserve or develop

625   workable pasture rotation systems. According to our results the lichen level becomes lower without

626   pasture rotation and in some cases supplementary feeding is part of the optimal solution in a long-

627   term steady state only if pasture rotation is not used. Our results also suggest that the net income

628   would be clearly higher if it was possible to utilize most of the lichen pastures only in winter,

629   following clear annual pasture rotation, compared to a situation without pasture rotation.

630       Another major change in reindeer herding has been the use supplementary feeding. Reindeer

631   herders interviewed by Helle and Jaakkola (2008) expressed that the lack of both arboreal lichens

632   and old forests were the ultimate reason for the use of supplementary food. Our results show that in

633   some cases lichen pasture quality (which is connected to the growth rate of lichens) affects the

634   optimality of supplementary feeding. With moderate or high interest rates a quality reduction of

635   lichen pastures, e.g. due to forest harvesting, can make supplementary food utilization an optimal

636   solution in reindeer management. The lack of arboreal lichen pastures also increases the need for

637   supplementary feeding in the optimal recovery from low ground lichen densities. According to

638   Helle and Jaakkola (2008) subsidies paid to farmers for leaving their fields uncultivated (haymaking

639   for reindeer was allowed) was one reason behind the rapid expansion of supplementary feeding in

640   Finland. According to our solutions the subsidies paid for breeding animals in a reindeer herd can

641   promote reindeer management where supplementary feeding is intensively utilized. Economically

642   rational reindeer management will lead to very low levels of lichen biomass if long-term intense

643 supplementary feeding becomes optimal. Whether or not this happens is affected by the several

644 economic and ecological factors presented in our study.

645

650

651 References

652 Ballesteros, M., Bårdsen, B.-J., Fauchald, P., Langeland K., Stien A., Tveraa, T., 2013. Combined

653     effects of long term feeding, population density and vegetation green-up on reindeer

654     demography. Ecosphere 4(4), 1-13.

655 Bessa-Comes, C., Legendre, S., Clobert, J., 2010. Discrete two-sex models of population dynamics:

656     on modelling the mating function. Oecologica 36, 439-445.

657 Bezard, P., Brilland, S., Kumpula, J.. Composition of late summer diet by semi-domesticated

658     reindeer in different grazing areas in northernmost Finland. (Manuscript submitted to

659     Rangifer)

660 Byrd, R.H., Nocedal, J., Waltz, R.A., 2006. KNITRO: An integrated package for nonlinear

661     optimization. In: di Pillo G, Roma M. (Eds.), Large -Scale Nonlinear Optimization. Springer,

662     New York, pp. 35-59.

663 Bårdsen, B.-J., Fauchald, P., Tveraa, T., Langeland, K., Nieminen, M., 2009. Experimental

664     evidence of cost of lactation in a low risk environment for a long-lived mammal. Oikos 118,

665     837 -852.

666 Danell, Ö., Petersson, J. C., 1994.  A comprehensive transition matrix model for projecting

667     production and resource consumption in reindeer herds. Rangifer 14, 99 -112.

668    Danell, K., Utsi, P.M., Palo, R.T., Eriksson, O. 1994: Food plant selection by reindeer during winter

669          in relation to plant quality. Ecography 17(2), 153-158.

670    Emlen, J. M., 1966. The role of time and energy in food preference. American Naturalist, 611-617.

671    Esseen, P.-A., 1985. Litter fall of epiphytic macrolichens in two old Picea abies forests in Sweden.

672          Canadian Journal of Botany, 63(5), 980-987.

673    Helle, T., Kojola, I., 1993. Reproduction and mortality of Finnish semi-domesticated reindeer in

674          relation to density and management strategies. Arctic 46(1), 72-77.

675    Helle, T., Jaakkola, L., 2008. Transitions in herd management of semi-domesticated reindeer in

676          northern Finland.  Annales Zoologici Fennici  45(2), 81-101. Holand, Ø., Ims, A. Aa.,

677          Weladji, R. B., 2010. Scale dependent effects of summer density on autumn weight mass in

678          reindeer. Rangifer 30(1), 15-29.

679    Isotalo, A., 1974. Porojen luonnonvaraisten rehujen ravintoarvoista (In Finnish). In: Lapin

680          tutkimusseuran vuosikirja XII,  28-45.

681    Jernsletten, J.-L., Klokov, K., 2002. Sustainable reindeer husbandry. Arctic council 2000-2002,

682          Universty of Tromsø, Centre for Sami Studies, 157 p.

683    Kumpula, J., 2001. Productivity of the semi-domesticated reindeer (Rangifer t. tarandus L.) stock

684          and carrying capacity of pastures in Finland during 1960-90's (Ph.D-thesis). –Acta

685          Universitatis Ouluensis, A Scientiae Rerum Naturalium 375. Oulun yliopisto, Oulu.

686    Kumpula, J., Nieminen, M., 1992. Pastures, calf production and carcass weights of reindeer calves

687          in the Oraniemi co-operative, Finnish Lapland. Rangifer 12 (2), 93-104.

688    Kumpula, J., Colpaert, A., Nieminen, M., 1998. Reproduction and productivity of semidomesticated

689          reindeer in northern Finland. Canadian Journal of Zoology 76, 269-277.

690    Kumpula, J., Colpaert, A., Nieminen, M., 2000. Condition, potential recovery rate, and productivity

691          of lichen (Cladonia spp.) ranges in the Finnish reindeer management area. Arctic 53, 152-160.

692  Kumpula, J., Colpaert, A., Nieminen, M., 2002. Productivity factors of the Finnish semi-

693       domesticated reindeer (Rangifer t. tarandus) stock during the 1990s. Rangifer 22(1), 3-12.

694  Kumpula, J., Lefrère, S., Nieminen, M., 2004. The use of woodland lichen pasture by reindeer in

695       winter with easy snow conditions. Arctic 57(3), 273-278.

696  Kumpula, J., Stark, S., Holand, Ø., 2011. Seasonal grazing effects by semi-domesticated reindeer

697       on subarctic mountain birch forests. Polar Biology 34, 441-453.

698  Kumpula, J., Kurkilahti, M., Helle, T., Colpaert, A., 2014. Both reindeer management and several

699       other land use factors explain the reduction in groung lichens (*Cladonia* spp.) in pastures

700       grazed by semi-domesticated reindeer in Finland. Regional Environmental Change 14, 541-

701       559.

702  MacArthur, R. H., Pianka, E. R., 1966. On optimal use of a patchy environment. American

703       Naturalist, 606-609.

704  Maijala, V., 1998. Rehuntarve ja ruokinnan toteuttaminen (in Finnish). In: Poron ruokinta (Eds.

705       Nieminen, M. Maijala, V., Soveri T.), published by Finnish Game and Fisheries Research

706       Institute 1998, pp. 110-125.

707  Moen, J., 2008. Climate Change: Effects on the Ecological Basis for Reindeer Husbandry in

708       Sweden. Ambio: A Journal of the Human Environment  37, 304-311.

709  Moxnes, E., Danel, Ö., Gaare, E., Kumpula, J., 2001. Optimal strategies for the use of reindeer

710       rangelands. Ecological Modelling 145, 225-241.

711  Nieminen, M., Heiskari, U., 1989. Diets of freely grazing and captive reindeer during summer and

712       winter. Rangifer 9(1), 17-34.

713  Nieminen, M., Pokka, A.-S., Heiskari, U., 1987.  Artificial feeding and nutritional status of semi-

714       domesticated reindeer during winter. Rangifer 7(2): 51-58.

715  Olofsson, A., Danell, Ö., Forslund, P., Åhman, B., 2011. A model of herbivore-pasture dynamics

716       for range management in reindeer husbandry. Manuscript in Olofsson A. Towards adaptive

717        management of reindeer grazing resources. Doctoral Thesis, Swedish University of

718        Agricultural Sciences, Uppsala.

719    Ophof, A.A., Oldeboer, K.W., Kumpula, J., 2013. Intake and chemical composition of winter and

720        spring forage plants consumed by semi-domesticated reindeer (Rangifer tarandus tarandus) in

721        Northern Finland. Animal Feed Science and Technology 185, 190-195.

722    Pape, R., Löffler, J., 2012. Climate Change, Land Use Conflicts, Predation and Ecological

723        Degradation as Challenges for Reindeer Husbandry in Northern Europe: What do We Really

724        Know After Half a Century of Research? Ambio 41, 421-434.

725    Petersson, C. J., Danell, Ö., 1992. Simulated production losses in reindeer herds caused by

726        accidental death of animals. Rangifer 12, 143-150.

727    Riseth, J. Å., Johansen, B., Vatn, A., 2004. Aspects of a two-pasture – herbivore model. Rangifer

728        Special Issue No. 15, 65-81.

729    Rytkönen, A.-M., Sarikoski, H., Kumpula, J., Hyppönen, M., Hallikainen, V., 2013. Metsätalouden

730        ja porotalouden väliset suhteet Ylä-Lapissa (In Finnish with English abstract: Interactions

731        between forestry and reindeer husbandry in Upper Lapland -syntesis of research data). Riista-

732        ja kalatalous, Tutkimuksia ja selvityksiä 6/2013, 39 p. (http://www.rktl.fi/julkaisut/j/660.html)

733    Salo, M.-L., Tuori, M., Kiiskinen, T., 1982. Rehutaulukot ja ruokintanormit, märehtijär-siat-

734        siipikarja-turkiseläimet (In Finnish, Feed tables and feeding norms, ruminants-swine-poultry-

735        fur animals).  Helsingin yliopiston monistepalvelu, Helsinki, 70 p.

736    Sandström, P., Granqvist Pahlén, T., Edenius, L., Tømmervik, H., Hagner, O., Hemberg, L.,

737        Olsson, H., Baer, K., Stenlund, T., Brandt, L., Egberth, M., 2003. Conflict Resolution by

738        Participatory Management: Remote Sensing and GIS as Tools for Communicating Land-use

739        Needs for Reindeer Herding in Northern Sweden. Ambio 32(8), 557-567.

740    Stephens, D. W., 1986. Foraging Theory. Princeton University Press.

741    Stevenson, S.K., Coxson, D.S., 2003. Litterfall, growth, and turnover of arboreal lichens after

742        partial cutting in an Engelmann spruce – subalpine fir forest in north-central British

743        Columbia. Canadian Journal of Forest Research 33(12), 2306-2320.

744    Tahvonen, O., Kumpula, J., Pekkarinen, A.-J., 2014. Optimal harvesting of an age-structured two-

745        sex herbivore-plant system. Ecological Modelling 272, 348–361.

746    Tømmervik, H., Johansen, B., Riseth, J. Å., Karlsen, S. R., Solberg, B., Høgda, K. A., 2009. Above

747        ground biomass changes in the mountain birch forests and mountain heaths of

748        Finnmarksvidda, northern Norway, in the period 1957–2006. Forest Ecology and

749        Management 257, 244–257.

750    Walters, C. J., Hilborn, R., Peterman, R., 1975. Computer simulation of barren-ground caribou

751        dynamics. Ecological Modelling 1, 303-315.

752    van Baalen, M., Křivan, V., van Rijn, P. C., Sabelis, M. W., 2001. Alternative food, switching

753        predators, and the presistance of predator-prey systems. The American Naturalist 175(5),

754        512–524

755    Virtala, M.,1992. Optimal management of a plant - herbivore system – Lichen and reideer in

756        Northern Finland. Ecological Modelling 3-4, 233-255.

757    Virtala, M., 1996. Harvesting a lichen – reindeer system is an uncertain environment. Ecological

758        Modelling 89, 209-224.

759

760    Appendix 1: Equations (1), (7) and (14) in the optimization context.

761    Equation (1) in the optimization context:

762    $d_t^b \leq \dfrac{A_Q}{0.03 X_t F_t^b\left(I_t^b\right)}, \; t = 0,1,... \;$ and $\; d_t^b \leq 60, \; t = 0,1,... \;.$

763    In our model cratered food is a dynamically developing resource but arboreal lichens are not. Thus

764    it is never optimal to reduce arboreal lichen utilization if it increases the consumption of cratered

765    food and the above notation corresponds with Equation (1) in the optimization framework.

766

767    Equation (7) in the optimization context:

768    $F_t^k = 1.8508 + \dfrac{8.1492}{\left[1 + \exp\left(\dfrac{I_t^k - 0.0953}{0.0013}\right)\right]^{0.0066}}, \; t = 0,1,....,\; k = a,b,$

769    The maximum boundary of $1.4 / IR_t^k$ is not used in optimization because energy intake is lower than

770    1.4 in all economically optimal solutions.

771

772    Equation (14) in the optimization context:

773    $T_{V,t}^k \leq 0.3 \left[0.2 + \dfrac{0.9}{1 + \exp\left(\dfrac{I_{Z+Q,t}^k - 1}{0.5}\right)}\right] \;$ and $\; T_{V,t}^k = \dfrac{0.1 \times 17.6 v_t^k}{\sum_{i=f}^{m} \sum_{s=1}^{n_i} x_{s,t}^i Ed_s^i}, \; t = 0,1,... \,,\; k = a,b$

774    The preference for natural food resources in the optimization context is expressed as a restriction to

775    the amount of supplementary food that can be given daily. This notation can be used, as with a

776    positive food price it is never optimal to offer more supplementary food than what the reindeer

777    would use.

778

779

780    Appendix 2: Finding the optimal share of the foraging time for cratered food during winter period $b$.

781

782    Equation (11) gives the intake rate for cratered food and Equation (12) for arboreal lichens. Both

783    functions satisfy the following:

784    $$I_{j,t}^b = f_j(av_{j,t}^b)\left(\frac{T_{j,t}^b}{T_{Z,t}^b + T_{Q,t}^b}\right)^{-0.2}, \qquad t = 0,1,\dots, \ j = Z,Q,$$

785    where $av_{j,t}^k$ is the availability of resource $j$. If we mark the time share used for cratered food relative

786    to the total time used for natural food resources by:

787    $$TS_{Z,t}^b = \left(\frac{T_{Z,t}^b}{T_{Z,t}^b + T_{Q,t}^b}\right) \quad t = 0,1,\dots,$$

788    it follows that the average intake rate for natural food is

789    $$I_{Z+Q,t}^b = TS_{Z,t}^b f_Z(z_t)\left(TS_{Z,t}^b\right)^{-0.2} + \left(1 - TS_{Z,t}^b\right) f_Q(q)\left(1 - TS_{Z,t}^b\right)^{-0.2} \quad t = 0,1,\dots.$$

790    If $f_Z(z_t)$ and $f_Q(q)$ are positive the second derivate of function $I_{Z+Q,t}^b$ with respect to $TS_{Z,t}^b$ is

791    always negative, i.e. the function is concave. Therefore by taking the first derivate of equation

792    $IR_{Z+Q,t}^b$ with respect to $TS_{Z,t}^b$ and solving the zero point for it, it follows that the share of remaining

793    foraging time used for cratered food that maximizes the intake rate satisfices the equation:

794    $$TS_{Z,t}^b = \frac{T_{Z,t}^b}{T_{Z,t}^b + T_{Q,t}^b} = \frac{\left(f_Z(av_{Z,t}^b)\right)^5}{\left(f_Z(av_{Z,t}^b)\right)^5 + \left(f_Q(av_{Q,t}^b)\right)^5} = \frac{\left(\frac{\mu^b}{3}\left(0.05 + 5\times10^{-5}z_t\right)\right)^5}{\left(\frac{\mu^b}{3}\left(0.05 + 5\times10^{-5}z_t\right)\right)^5 + \left(\frac{0.03\times10.8q}{17.6}\right)^5},$$

795    following that the optimal share of the total foraging time used for cratered food is (Equation (16)):

796    $$T_{Z,t}^b = \frac{\left(1 - T_{V,t}^b\right)\left(\frac{\mu_t^b}{3}\left(0.05 + 5\times10^{-5}z_t\right)\right)^5}{\left(\frac{\mu_t^b}{3}\left(0.05 + 5\times10^{-5}z_t\right)\right)^5 + \left(\frac{0.03\times10.8q}{17.6}\right)^5}, \quad t = 0,1,\dots.$$