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Optimal management of two ecologically interacting deer species—reality matters, beliefs don't

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Abstract

The aim of this paper is to analyze the optimal management of two ecologically interdependent, competing species, roe deer (*Capreolus capreolus*) and fallow deer (*Dama dama*). To this end, we develop a numerical stage-structured model, accounting for species-specific life history characteristics, gender, and stage-specific hunting values. Two contrasting management regimes are considered: optimal joint management of the two species and management where the decision maker is ignorant about interspecific competition. Results from our case study show that the presence of interspecific competition reduces roe deer population size and harvest by 30% and 47%, respectively, and reduces the net present value by 9%. High interspecific competition could lead to the exclusion of the roe deer from the area. In contrast, ignorance about the level and consequences of interspecific competition has no impact on harvest decisions and revenues. The explanation is the higher hunting benefits for fallow deer.

Summary for Managers

- Wildlife managers need bioeconomic models for decisions on ecologically interdependent species.
- This study investigates optimal joint management of roe and fallow deer when the fallow deer exerts a negative impact on roe deer due to interspecific competition.

- Results show that interspecific competition reduces the net present value of hunting at the study site by 9%.
- Regulations will not increase the net present value of hunting in a situation where the manager is ignorant of interspecific competition.

KEYWORDS

bioeconomic modeling, fallow deer, hunting, interspecific competition, roe deer, stage-structured model

1 | INTRODUCTION

Game species, especially large grazers, provide society a wide range of benefits such as meat, recreational hunting, aesthetic values, and maintenance of ecosystem balance (Chardonnet et al., 2002). The provision of benefits can be affected by the fact that large herbivores compete for resources such as food and space (Birch, 1957; Caughley & Sinclair, 1994). When species are interdependent, human activities that affect one species will also have an impact on the other species. If the management of a single species ignores indirect effects on other species, this can give rise to economic losses due to the reductions in the values generated by other wildlife. Hence, there is a need for management strategies that account for the synergies and trade-offs between different benefits and costs generated by the species. In addition, the value of many large game species, in terms of meat and trophies, is strongly dependent on the age and the sex of the individual animal, implying that consideration of the age and sex composition of the populations and harvest matters for the value generated.

There is limited knowledge about implications of interspecific interactions for the economically optimal management of wildlife. In our context, there are two strands of pertinent economic literature: studies on the management of large herbivores and studies on the management of interacting, competing species.

Economic studies on the management of large herbivores are usually applied to a single species, and use age- or stage-structured models (Collier & Krementz, 2007; Olaussen & Mysterud, 2012; Olaussen & Skonhoft, 2011; Skonhoft et al., 2013; Xu & Boyce, 2010). In addition to those, there are a couple of studies investigating interdependences between a large semidomesticated grazer, the reindeer, and its main winter food resource, lichen. Among those, Virtala (1992, 1996) and Moxnes, Danell, Gaare, and Kumpula (2001) are based on biomass models, whereas Tahvonen, Kumpula, and Pekkarinen (2014) apply age-structured modeling. The outcome differs considerably depending on the use of biomass or age-structured models (Tahvonen et al., 2014) and an obvious advantage of age-structured models is that they account for species life history.

Studies accounting for species competition are mostly found in fishery economics (Chaudhuri, 1986, 1987; Conrad & Adu-Asamoah, 1986; Finnoff & Tschirhart, 2003; Flaaten, 1988, 1991; Hannesson, 1983). These studies typically use a biomass approach, hence abstracting from the role of species' life history. Exceptions include Hamre (2003) and Nieminen, Lindroos, and Heikinheimo (2012, 2016), which consider multilateral interactions between one predator and two prey fish species within an age-structured modeling framework.

The aim of this paper is to evaluate the benefits and costs to hunters from two competing species, the roe deer (*Capreolus capreolus*) and the fallow deer (*Dama dama*). The roe deer is the second most valuable hunted deer species in Sweden (Mattsson, Boman, & Ericsson, 2008), while the fallow deer in recent years has been suggested to be introduced in additional locations, motivated, for example, by its hunting value as well as the grazing pattern, which helps maintaining an open landscape. The ecological literature suggest that the presence of fallow deer exerts negative effects on the foraging behavior of roe deer, but not *vice versa* (Focardi, Aragno, Montanaro, & Riga, 2006), implying that there is a unilateral, negative impact of the fallow deer on the roe deer in terms of the competition for food (Nichols, Åkesson, & Kjellander, 2016). This can have different economic implications, depending on the management regime. Two different regimes are therefore considered in the paper, one where the species are optimally and jointly managed, and one where the decision maker is ignorant about interspecific competition. We further explore the possibilities to introduce an efficient economic incentive, in terms of a tax on fallow deer populations, to ensure that the socially optimal outcome is achieved when decisions on the two species are taken by a manager who is ignorant about the negative impact of fallow deer on roe deer. As mentioned previously, age and gender of game is of major importance for the hunting value, which is also true for large grazers (Naevdal, Olaussen, & Skonhoft, 2012), motivating the use of a stage-structured model.

Our study contributes to the literature through the use of a stage-structured numerical model of interspecific competition. We have only found a few earlier studies using this approach, Hamre (2003) and Nieminen et al. (2012, 2016), applied to fishery. Further, we add to the literature on economically optimal management of competing species through the investigation of the potential of using efficient economic instruments when managers are unaware of species interdependences.

Our findings suggest that the magnitude of interspecific competition has modest effects on the economic returns to hunters, but significant importance for roe deer populations. In contrast, managers' knowledge about interspecific competition has minor effects on hunting revenues generated by the species. The marginal damage of fallow deer on roe deer is 177 SEK per unit of fallow deer,[1] but introduction of a tax on fallow deer would not improve on hunting revenues in a situation where the manager is ignorant about the impact of fallow deer on roe deer.

The paper is organized as follows. In Section 2, the interactions between roe and fallow deer are described. Section 3 presents the joint population model and Section 4 describes the bioeconomic model. A description of the data used in the simulations is available in Section 5 and results are presented in Section 6. Section 7 includes a discussion and conclusions.

2 | ROE DEER AND FALLOW DEER

Fallow deer is an exotic species in Sweden: it was introduced in the 1570s as a new game species (Carlström & Nyman, 2005). Since the late 1900s, the fallow deer population has increased substantially and it is currently present in several locations in the country even though the dispersal is slow. The fallow deer is a relatively large grazer, an adult weighs 45 to 120 kg. It is usually described as a gregarious species and it has a high tolerance for high animal densities (Carlström & Nyman, 2005). In contrast, roe deer is native to Sweden and found throughout most parts of the country (Cederlund & Liberg, 1995). It is a relatively small and solitary species: adult individuals weigh 20 to 30 kg, and population densities are generally lower than for fallow deer.

In areas of Sweden where the fallow deer currently exists in higher densities, people have expressed concerns about decreasing roe deer populations. Evidence from the literature suggests that the fallow deer often displaces the roe deer from feeding sites and from areas with high fallow population density (Ferretti, Bertoldi, Sforzi and Fattorini, 2011; Ferretti, Sforzi, & Lovari, 2008). Using a field experiment, Ferretti et al. (2008) show that encounters between fallow deer and roe deer led to the displacement of roe deer in 83% of the studied cases. As much as 94% of the displacement events occurred

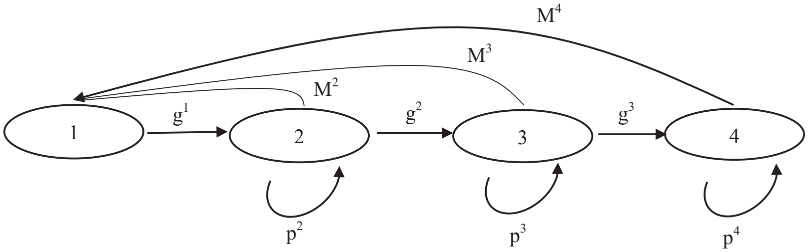

FIGURE 1 Stage-structured life cycle graph for roe and fallow deer

while the roe deer was feeding, implying that roe deer are interrupted and regularly abandon feeding site when living in sympatry with fallow deer. Even when fallow deer showed no sign of aggression, roe deer moves away in 72% of the encounters. This suggests that a high fallow deer density leads to reduced food access in roe deer, due to feeding displacement (Ferretti et al., 2008).

Roe deer as a selective feeder, prefers high quality forage such as easily digestible herbs and leaves, in contrast to fallow deer as a more grazing generalist herbivore (Hofmann 1989) adapted to a mixed diet, hence accommodated to a broad spectrum of plants, including grass, leaves, and bark (Alm, Birgersson, & Leimar, 2001; Ferretti et al., 2008; Nichols et al., 2016). In a joint habitat, fallow deer also eats the high quality plants preferred by roe deer, thereby reducing the habitat's carrying capacity for roe deer. Together, the empirical evidence thus suggests that there is a negative and largely unidirectional effect of the fallow deer on the roe deer.

3 | JOINT DEER POPULATION MODEL

To account for the interdependences between the two species, we develop a stage-structured population model, where a single decision maker seeks to maximize the net present benefits from the management of the two species on a given plot of land. We classify the life cycle of both species into four main stages: fawn, juvenile, adult, and senescent, based on species specific life history. Classification into life stages (age classes) allows us to account for nonlinear variations in reproduction, survival, and hunting value over age. Thus, in our stage classification, the roe population is structured as follows for both sexes: fawn (year < 1), juvenile ($1 \leq$ years < 3), adult ($3 \leq$ years < 8), and senescence ($8 \leq$ years < 12). The male fallow deer population is structured as fawn (year < 1), juvenile ($1 \leq$ years < 3), adult ($3 \leq$ years < 5), and senescence ($5 \leq$ years < 13), whereas the female fallow deer population is structured as fawn (year < 1), juvenile ($1 \leq$ years < 3), adult ($3 \leq$ years < 12), and senescence ($12 \leq$ years < 21). Notice that the stage duration differs due to species- and sex-specific differences in life span, physiological growth rate, reproductive maturation, and trophy size.

Using a four-stage structured projection matrix, see Figure 1, we show the population transition across stages with individuals in Stages 2 to 4 contributing to recruitment in Stage 1 via reproduction (M^i). Since the duration of Stages 2 to 4 does not vary directly with time moving from year t to $t + 1$, some of the surviving individuals, the younger ones, remain in the same stage while the oldest surviving individuals move on to the next stage. To model this nonlinear transition, let g^i and p^i represent, respectively, the probability of surviving and moving from stage i to $i + 1$, and the probability of surviving and remaining in stage i. Thus, g^i and p^i represent transition probabilities in our stage-structured life cycle model.

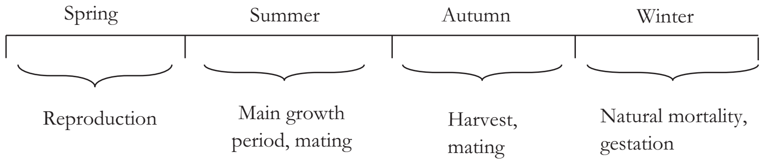

FIGURE 2 Within-year population cycle

3.1 | Population equations

In our two species population model, we define R and F as the number of roe and fallow deer, respectively, in the habitat. The species are grouped into four stages, denoted i, with $i = 1, 2, 3, 4$, where 1 denotes fawns, 2 denotes juveniles, 3 denotes adults, and 4 denotes senescence, as defined as above. Each species is further classified into different types: fawns (recruits), c; females, x; and males, y. This classification is denoted by an index j, with $j = c, x, y$. For ease of computation and analytical tractability, fawns are assumed to be gender neutral (Naevdal et al., 2012; Skonhoft et. al, 2013). This implies that for both species, the category $i = 1$ is identical with the category $j = c$, whereas Stages 2 to 4 are divided into males and females. The number of roe and fallow deer of type j in stage i at time t are then specified as $R^i_{j,t}$ and $F^i_{j,t}$,respectively.

We model the decisions and population development on an annual scale. However, within-year development of populations is assumed to be the following. First, population size is assumed to be measured in spring just before birth, which occurs in May to June. Mating is assumed to take place in the summer and early autumn (July to August). The hunting season, that is, the harvest, takes place in autumn (September to November), while natural mortality mainly occurs during the winter (cf., e.g., Naevdal et al., 2012; Olaussen & Skonhoft, 2011; Skonhoft et. al, 2013). The assumed timing over the year is thus as illustrated in Figure 2.

The harvests of the roe and fallow deer at time t is given as $HR^i_{j,t}$ and $HF^i_{j,t}$, respectively. It is assumed that $0 \le HR^i_{j,t} \le R^i_{j,t}$ and $0 \le HF^i_{j,t} \le F^i_{j,t}$.

We assume that the effect of competition on species populations is channeled through recruitment. This is motivated by competition affecting the nutritional status of the roe deer (Nichols et al., 2016), which in turn affects its fecundity, and hence the number of offspring (Gaillard, Festa-Bianchet, Yoccoz, Loison, & Toigo, 2000; Hewison, 1996). We model recruitment of both species within the framework of a modified Ricker (1954) recruitment function. The original version of this recruitment function takes into account the impact of population density on the number of births for the same species. We extend this function to allow also for the impact of fallow deer density on roe deer reproduction. Recruitment of roe deer at a given time t, is then expressed as:

$$R^1_{c,t} = \sum_{i>1} R^i_{x,t} \kappa^i_r \exp\left[-\sum_{ij}\left(\beta_r R^i_{j,t-1} + \mu F^i_{j,t-1}\right)\right], \tag{1}$$

where $R^1_{c,t}$ is the number of recruits and $R^i_{x,t}$ is the number of females in stage i at time t. The parameter κ^i_r denotes the fecundity, that is, the number of offspring for female roe deer in stage i in absence of inter- and intraspecific competition, and the subscript r indicates the species in question, that is, roe deer. The parameters β_r and μ, which are both assumed to be positive, can be interpreted as measures of the degree of intra- and interspecific competition, respectively. As roe dear and fallow deer have only partially overlapping diets, it can be expected that $\beta_r > \mu$, cf., for example, Pianka (1974). Equation (1) implies that fecundity of roe deer decreases with population density of both species. A consequence of this assumption is that the effect of competition is delayed. Food scarcity in year t would, in particular, imply a low nutritional status of roe deer in gestation over the winter period, when food availability is already limited. This would imply a lower reproduction in the following year $t + 1$, motivating the use of the lag-effect terms, $R^i_{j,t-1}$and$F^i_{j,t-1}$. As a consequence, a larger harvest of fallow deer implies increased access to food in winter and spring for roe deer, where females will be in better health status implying increased reproduction the following spring.[2]

The juvenile population at time $t + 1$ is given by the number of fawns that survive after harvest until the next period plus the number of juveniles that survive and remain in the stage:

$$R^2_{j,t+1} = 0.5g^1_{c,r}\left(R^1_{c,t} - HR^1_{c,t}\right) + p^2_{j,r}\left(R^2_{j,t} - HR^2_{j,t}\right), \quad \forall j = x, y, \tag{2}$$

where the same sex ratio, 0.5, is assumed for fawns when they enter into the juvenile stages, and with $g^1_{c,r}$denoting the probability of roe fawns surviving and growing into the juvenile stage. Further, the adult population equation is expressed as

$$R^3_{j,t+1} = g^2_{j,r}\left(R^2_{j,t} - HR^2_{x,t}\right) + p^3_{j,r}\left(R^3_{j,t} - HR^3_{j,t}\right), \quad \forall j = x, y, \tag{3}$$

where $g^2_{j,r}$and $p^3_{j,r}$ are the probabilities of a roe deer belonging to category j in Stage 2 surviving and moving to the next stage, and the probability of the roe deer population belonging to category j in Stage 3 surviving and remaining in the same stage, respectively.

Finally, senescent roe deer population is determined by the number of individuals surviving and moving from Stage 3 to 4 and the number surviving and remaining in Stage 4, as shown in Equation (4).

$$R^4_{j,t+1} = g^3_{j,r}\left(R^3_{j,t} - HR^3_{j,t}\right) + p^4_{j,r}\left(R^4_{j,t} - HR^4_{j,t}\right), \quad \forall j = x, y. \tag{4}$$

Fallow deer is assumed to be affected only by intraspecific competition, measured by the parameter β_f, where the subscript f indicates the fallow deer species. Thus, the recruitment function for fallow deer is expressed as:

$$F^1_{c,t} = \sum_{i>1} F^i_{x,t}\kappa^i_f \exp\left(-\sum_{ij}\beta_f F^i_{j,t-1}\right), \tag{5}$$

where $\kappa^i_f$is the fecundity rate, that is, the number of offspring, for female fallow deer in stage i. The remaining fallow deer stock equations, corresponding to Equations (2) to (4), are represented by Equations (6) to (8), where $g^i_{j,f}$ and $p^i_{j,f}$ are the corresponding transition probabilities.

$$F^2_{j,t+1} = 0.5g^1_{c,f}\left(F^1_{c,t} - HF^i_{c,t}\right) + p^2_{j,f}\left(F^2_{j,t} - HF^2_{j,t}\right), \quad \forall j = x, y, \tag{6}$$

$$F^3_{j,t+1} = g^2_{j,f}\left(F^2_{j,t} - HF^2_{j,t}\right) + p^3_{j,f}\left(F^3_{j,t} - HF^3_{j,t}\right), \quad \forall j = x, y, \tag{7}$$

$$F^4_{j,t+1} = g^3_{j,f}\left(F^3_{j,t} - HF^3_{j,t}\right) + p^4_{j,f}\left(F^4_{j,t} - HF^4_{j,t}\right), \quad \forall j = x, y. \tag{8}$$

4 | BIOECONOMIC MODEL

We assume that a single decision maker, managing the total hunting ground, aims at maximizing the joint net present value of the two species. This assumption is motivated by the right to manage and hunt in Sweden being tied to land ownership rights: any landowner has the exclusive right to hunt nonprotected species on his or her own land (Sandström, Wennberg-Di Gasper, & Öhman, 2013). Three types of hunting benefits are considered: meat, recreation, and trophies. We also take into account costs for supplemental winter feeding. In this section, we first present the economic model, followed by the associated first-order conditions (FOCs).

4.1 | The model

We account for three different kinds of hunting benefits: meat, recreation, and trophy values. First, let $\hat{q}_r$ and $\hat{q}_f$ denote meat price per kg for roe and fallow deer, while w^i_j and ψ^i_j denote gender- and stage-specific slaughter weight of roe and fallow deer, respectively. These parameters are assumed to be fixed over time and independent of harvest level. This is a simplification as population densities and hence food scarcity, could affect body mass (Hamre, 2003; Tahvonen et al., 2014). However, the simplifying assumption of constant weight is frequently applied in the fishery (Skonhoft, Vestergaard, & Quaas, 2012; Tahvonen, Quaas, Schmidt, & Voss, 2013) and wildlife (Naevdal et al., 2012; Skonhoft et al., 2013) literature. Adding to the meat value, is a recreational value per animal shot, *m,* assumed. We assume this value to be equal for the two species and across different stages and gender. Finally, trophy hunting benefits can be considerable (Naevdal et al., 2012). Let $z^i_{r,j}$and $z^i_{f,j}$ denote the trophy prices for roe and fallow deer, respectively. We assume that prices are constant, implying that the manager of the hunting ground is a price taker. This is a reasonable assumption for commercial hunting, where European sellers of hunting experiences advertise their prices on the Internet, and buyers travel abroad to purchase hunting experiences. Also, the model applies on smaller spatial scale, and we assume that the manager does not possess market power. The total benefits associated with harvesting of the two species can then be expressed as:

$$B_t = \sum_{i,j} q^i_{r,j} HR^i_{j,t} + \sum_{i,j} q^i_{f,j} HF^i_{j,t}, \tag{9}$$

where $q^i_{r,j} = (\hat{q}_r w^i_j + m + z^i_{r,j})$ and $q^i_{f,j} = (\hat{q}_f \psi^i_j + m + z^i_{f,j})$ are the benefits per harvested individual of roe and fallow deer, respectively, in stage *i*.

The manager further incurs costs for supplemental, artificial, feeding during the winter season, when natural food resources are scarce. Artificial feeding is here defined as food, such as grass silage or oats, which is provided at regular intervals at artificially created feeding sites. Here, the fallow deer is assumed to be the only species that is artificially fed during the winter. This is motivated as follows: in southwest Sweden, where these results are applied, fallow deer typically needs artificial feeding to survive the winter. During harsh winters, fallow deer spend almost all their time in big groups around the feeding stations, while the considerably smaller and solitary roe deer have very little access to the food, cf., for example, Ferretti et al. (2008). Moreover, grass silage, which is the most common winter feeding, is not preferred by roe deer because it has generally too low quality in relation to its digestive system (Alm et al., 2001; Chapman & Chapman, 1975; Ferretti et al., 2008). The cost of winter feeding is specified as:

$$C_t = \sum_{ij} d^i_j \left(F^i_{j,t} - HF^i_{j,t} \right), \tag{10}$$

where d_j^i is the constant marginal cost of feed per fallow deer of type j in stage i. The assumption of a constant marginal cost of feed is motivated by the manager being a price taker on the market for silage and oats, where silage and oats are used not only for wildlife but also for domestic livestock. The constant marginal cost is also related to the assumption of a constant weight per fallow deer of type j in stage i: if the weight per fallow deer had been assumed variable over time, it might be necessary to adjust the cost function in Equation (10).

The manager's decision problem then is to maximize the discounted present value of the future stream of net benefits, Total Net Present Value (*TNPV*):

$$\underset{HR^i_{j,t}, HF^i_{j,t}}{Max} \; TNPV = \sum_{t=1}^{T} \rho^t \left(B_t - C_t \right), \tag{11}$$

subject to the population Equations (1) to (8) and harvest restrictions. In Equation (11), $\rho = 1/(1+\delta)$ refers to the discount factor, which measures the rate of time preference, with $\delta \geq 0$ as the annual discount rate.

4.2 | Optimality conditions

The manager of the two-species ecosystem is assumed to choose levels of harvest of roe and fallow deer that maximizes Equation (11) subject to Equations (1) to (8) and the lower and upper bounds on the harvest constraints. Let $\lambda^i_{j,t}$ and $\gamma^i_{j,t}$ denote the Lagrange multipliers for constraints (1) to (4) and (5) to (8), respectively. Also, let $\varpi^i_{j,t}$ and $\theta^i_{j,t}$ denote the shadow values associated with the upper bounds on the harvest variable for roe and fallow deer, respectively. The Lagrangian of the above problem can then be formulated as:

$$L = \sum_{t=1} \rho^t \left\{ \begin{aligned} & \left[\sum_{i,j} q^i_{r,j} HR^i_{j,t} + \sum_{i,j} q^i_{f,j} HF^i_{j,t} - \sum_{i,j} d^i_j \left(F^i_{j,t} - HF^i_{j,t} \right) \right] \\ & + \lambda^1_{c,t} \left[\sum_{i>1} R^i_{x,t} \kappa^i_r \exp \left(- \sum_{ij} \left(\beta_r R^i_{j,t-1} + \mu F^i_{j,t-1} \right) \right) - R^1_{c,t} \right] \\ & + \rho \sum_j \lambda^2_{j,t+1} \left[0.5 g^1_{c,r} \left(R^1_{c,t} - HR^1_{c,t} \right) - R^2_{j,t+1} \right] \\ & + \rho \sum_{i>2,j} \lambda^i_{j,t+1} \left[g^{i-1}_{j,r} \left(R^{i-1}_{j,t} - HR^{i-1}_{j,t} \right) + p^i_{j,r} \left(R^i_{j,t} - HR^i_{j,t} \right) - R^i_{j,t+1} \right] \\ & + \gamma^1_{c,t} \left[\sum_{i>1} F^i_{x,t} \kappa^i_f \exp \left(- \sum_{ij} \left(\beta_f F^i_{j,t-1} \right) \right) - F^1_{c,t} \right] \\ & + \rho \sum_j \gamma^2_{j,t+1} \left[0.5 g^1_{c,f} \left(F^1_{c,t} - HF^1_{c,t} \right) - F^2_{j,t+1} \right] \\ & + \rho \sum_{i>2,j} \gamma^i_{j,t+1} \left[g^{i-1}_{j,f} \left(F^{i-1}_{j,t} - HF^{i-1}_{j,t} \right) + p^i_{j,f} \left(F^i_{j,t} - HF^i_{j,t} \right) - F^i_{j,t+1} \right] \\ & + \omega^i_{j,t} \left(R^i_{j,t} - HR^i_{j,t} \right) + \theta^i_{j,t} \left(F^i_{j,t} - HF^i_{j,t} \right) \end{aligned} \right\}. \tag{12}$$

Following the Kuhn–Tucker theorem, we proceed to present the FOCs, which are associated with the above maximization problem. For brevity, we present only the optimality conditions for the adult cohorts, see Equations (13) to (17). Also, the FOCs for the different stages are qualitatively similar and hence carry similar interpretations. The remaining FOCs can be found in Appendix A. Equations (13) and (14) represent the optimal harvest conditions for adult male and female roe and fallow deer, respectively:

$$\rho^{-t} L'_{HR^3_{j,t}} = q^3_{r,j} - \rho\lambda^3_{j,t+1} p^3_{j,r} - \rho\lambda^4_{j,t+1} g^3_{j,r} - \varpi^3_{j,t} \le 0; 0 \le HR^3_{j,t}, \tag{13}$$

$$\rho^{-t} L'_{HF^3_{j,t}} = q^3_{f,j} + d^3_j - \rho\gamma^3_{j,t+1} p^3_{j,f} - \rho\gamma^4_{j,t+1} g^3_{j,f} - \theta^3_{j,t} \le 0; 0 \le HF^3_{j,t}. \tag{14}$$

Equation (13) states that an adult roe deer can be harvested up to the point where the marginal harvest benefit, q^3_r, is, at most, equal to the marginal user cost, $\rho(\lambda^3_{j,t+1} p^3_{j,r} + \lambda^4_{j,t+1} g^3_{j,r})$, where the latter is determined by the discounted value of the expected reduction of adult and senescence populations in the following time period. When this condition holds with equality, the harvest is positive. If it holds with inequality, the harvest is zero since the marginal benefit of harvesting will be less than the associated marginal user cost. If $\varpi^3_{j,t} > 0$, the expression holds with equality and $\varpi^3_{j,t}$ expresses the shadow cost of the upper bound on the harvest. The optimal harvesting condition for adult fallow deer, Equation (14), is analogous to Equation (13) and hence carries a similar interpretation, except for the inclusion of the marginal cost of winter feeding, d^3_j. Here, an adult fallow deer is optimally harvested up to the point where the incremental benefit from one more unit of harvest is, at most, equal to the marginal user cost, which equals $\rho\gamma^3_{j,t+1} p^3_{j,f} + \rho\gamma^4_{j,t+1} g^3_{j,f} - d^3_j$. Thus, the inclusion of feeding costs implies that the marginal user cost is lower, reflecting the fact that fallow deer that remain unharvested in the autumn must be fed at a cost over the following winter.

Equation (15) shows the optimal stock condition for adult female roe deer:

$$\begin{aligned}\rho^{-t} L'_{R^3_{x,t}} = {} & \lambda^1_{c,t} \kappa^3_r \exp\left[-\sum_{ij}\left(\beta_r R^i_{j,t-1} + \mu F^i_{j,t-1}\right)\right] - \rho\lambda^1_{c,t+1}\beta_r \sum_{i>1} R^i_{x,t+1}\kappa^i_r \\ & \times \exp\left[-\sum_{ij}\left(\beta_r R^i_{j,t-1} + \mu F^i_{j,t-1}\right)\right] + \rho\lambda^3_{x,t+1} p^3_{x,r} + \rho\lambda^4_{x,t+1} g^3_{x,r} - \lambda^3_{x,t} + \varpi^3_{j,t} \le 0; R^3_{x,t} \ge 0.\end{aligned} \tag{15}$$

The first term on the right-hand side of the equation is the marginal increase in roe deer recruitment resulting from holding an additional unit of female adult roe deer. It measures the direct positive value of holding one more adult female roe deer on the roe deer recruitment. Meanwhile, the second term on the right-hand side captures the indirect, negative value of holding an additional adult female roe deer, due to the impact on roe deer recruitment via increased intraspecific competition. The third and fourth terms capture, respectively, the value of the expected contributions of an additional female adult roe deer to female roe deer populations in Stages 3 and 4. The fifth term is the shadow value of holding an additional female adult roe deer in time t until the following year $t + 1$. Finally, the additional term $\varpi^3_{j,t}$, if positive, expresses the value of relaxing the upper bound on the harvest at time t when the restriction is binding. Rewriting Equation (15) assuming an interior solution, we obtain Equation (16), which states that the number of female adult roe deer should be maintained such that their shadow price is equal to the sum of its discounted net contribution to roe deer recruitment, evaluated at the shadow price of fawns, and its discounted contribution to the expected growth of the adult and senescent female stages, evaluated at their respective discounted shadow prices:

$$\begin{aligned}\lambda^3_{x,t} = {} & \lambda^1_{c,t}\kappa^3_r \exp\left(-\sum_{ij}\left(\beta_r R^i_{j,t-1} + \mu F^i_{j,t-1}\right)\right) - \rho\lambda^1_{c,t+1}\beta_r \sum_{i>1} R^i_{x,t+1}\kappa^i_r \\ & \times \exp\left(-\sum_{ij}\left(\beta_r R^i_{j,t-1} + \mu F^i_{j,t-1}\right)\right) + \rho\lambda^3_{x,t+1}p^3_{x,r} + \rho\lambda^4_{x,t+1}g^3_{x,r}.\end{aligned} \tag{16}$$

Examining Equation (16) reveals that it is only worthwhile to keep the one more roe deer if the net value of its contributions to recruitment and population in different stages is positive. A higher intraspecific competition among roe deer will reduce the net contribution to recruitment, hence reducing the overall marginal benefit of holding an additional unit of the stock until the following year, and vice versa. In a similar manner, a higher interspecific competition from fallow deer will reduce the roe deer recruitment, and hence reduce the marginal benefit of holding an additional adult female roe deer.

Compared to Equation (16), the corresponding condition for fallow deer, Equation (17), shows how the presence of interspecific competition affects the optimal stock of adult female fallow deer:

$$\begin{aligned}\gamma^3_{x,t} = {} & \gamma^1_{c,t}\kappa^3_f \exp\left(-\sum_{ij}\beta_f F^i_{j,t-1}\right) - \rho\gamma^1_{c,t+1}\beta_f \sum_{i>1} F^i_{x,t+1}\kappa^i_f \exp\left(-\sum_{ij}\beta_f F^i_{j,t-1}\right) \\ & + \rho\gamma^3_{x,t+1}p^3_{x,f} + \rho\gamma^4_{x,t+1}g^3_{x,f} - \rho\lambda^1_{c,t+1}\mu \sum_{i>1} R^i_{x,t+1}\kappa^i_r \exp\left(-\sum_{ij}\left(\beta_r R^i_{j,t-1} + \mu F^i_{j,t-1}\right)\right) - d^3_x.\end{aligned} \tag{17}$$

The stock condition in (17) states that the number of adult female fallow deer should be maintained such that their shadow value, $\gamma^3_{x,t}$, is equal to the sum of the value of its net contribution to fallow deer recruitment, captured by the two first terms on the right-hand side, and the value of its contribution to the growth of the adult and senescent stage, captured by the third and fourth terms on the right-hand side, less the value of its indirect effect on roe deer recruitment due to interspecific competition, $\rho\lambda^1_{c,t+1}\mu\sum_{i>1}R^i_{x,t+1}\kappa^i_r \exp[-\sum_{ij}(\beta_r R^i_{j,t} + \mu F^i_{j,t})] = \rho\lambda^1_{c,t+1}\mu R^1_{c,t}$, and the cost of winter feeding, d^3_x. Thus, an increase in interspecific competition, μ, reduces the marginal benefit of keeping an additional adult female fallow deer.

4.3 | The marginal damage of fallow deer on roe deer

The term $\rho\lambda^1_{c,t+1}\mu R^1_{c,t}$ appears in a similar manner in all stocks conditions for fallow deer, see the Appendix, and reflects the marginal damage of fallow deer on roe deer reproduction, with consequential effects on roe deer populations and harvests. If the manager of the habitat is ignorant about interspecific competition, that is, believes that $\mu = 0$, and takes his harvesting decisions accordingly, a unit tax on fallow deer at time t, set equal to $\rho\lambda^1_{c,t+1}\mu R^1_{c,t}$ for all stages, would lead him to internalize the effects of interspecific competition (cf., e.g., Baumol & Oates, 1988), implying that his decisions would be equal to the one that would be taken if the two-species system was optimally managed.

5 | CASE STUDY AND DATA

The model is illustrated numerically using empirical data, mainly obtained from the Koberg estate in southwest Sweden. The Koberg estate is a private property, covering approximately 90 km^2, and providing opportunities for commercial hunting of wildlife. Several wildlife species are actively comanaged at the estate and in their natural habitat. The totally dominating wildlife species in the habitat is fallow deer followed by wild boar (*Sus scrofa*), but smaller populations of roe deer and moose (*Alces alces*) also occur, together with even smaller numbers of red deer (*Cervus elaphus*) and mufflon sheep (*Ovis aries*). The landowner sells hunting permits both for certain occasions, implying hunting over one or a few days, and for longer periods to individuals and groups. The hunters are then allowed to hunt in restricted areas of the estate during the hunting season. The choice of the Koberg estate as a study area is motivated by the availability of high quality data on harvests, populations, and life history data, which can be used to calibrate our model to an empirically relevant baseline. Similar data, in particular for populations, are rarely available for large herbivores.

5.1 | Data

Fallow deer fecundity and survival data were obtained from a field study carried out at the Koberg estate during 2006 to 2014 (Kjellander, 2014). Roe deer fecundity and survival were based on estimates from the Bogesund research area in east-central Sweden (Kjellander, 2000). Following Crouse, Crowder, and Caswell (1987) and Chaloupka (2002), we estimate transition probabilities based on the stage-specific survival rates and stage duration, assuming constant survival and growth rates within each stage. Stage-specific slaughter weights are a close proxy of the edible meat weight from the two species. The slaughter weight is assumed to be 70% of dressed weight, based on the examination of 1,183 and 2,712 harvested roe and fallow deer, respectively (Andersson, Glöersen, Brittas, & Huldt, 1996; Cederlund, Stålfelt, & Kjellander, 1991).

We assume constant inter- and intraspecific competition across stages and time, but differing between species. By using reproduction and survival data from the Bogesund research area, where roe deer has an unharvested carrying capacity of 35 animals/km^2, we calibrate the roe deer intraspecific competition to be consistent with this carrying capacity in the steady state when there is zero harvests, and only roe deer is present in the habitat. For fallow deer, we use population and harvest data from the Koberg area, where fallow deer is harvested and yet dominating, and population density is estimated to 45 fallow deer/km^2. We calibrate the fallow deer intraspecific competition such that it is consistent (in steady state) with the population density in the Koberg area, while assuming that the fallow deer is optimally harvested and that it is the single species in the habitat. Having obtained calibrated intraspecific competition parameters, we proceed to calibrate the interspecies competition parameter using the two species population model described in Section 3. To this end, we used empirical data on populations and harvest of roe and fallow deer from the Koberg estate over 6 years, in combination with the estimated intraspecific competition parameters, to calibrate the interspecies competition parameter to be consistent with these observations.[3] These exercises give an intraspecific competition for roe and fallow deer, respectively, equal to 0.000421 and 0.000217. The higher intraspecific competition for roe deer is a consequence of its lower carrying capacity, explained by the more selective feeding habits discussed in Section 2. Further, calibration resulted in an interspecific competition parameter equal to 0.000114. The lower interspecific competition, compared to intraspecific competition, was expected given the partially overlapping diets and habitats. Having calibrated the inter- and intraspecific competition parameters, initial total roe and fallow deer populations were set equal to the steady-state levels in the socially optimal two-species bioeconomic equilibrium.

Meat and trophy price data as well as data on recreational value were obtained from the Koberg area. Meat prices are prices paid when hunters choose to buy the meat after participating in a hunt. The recreational value of hunting is calculated as the average net revenue per animal shot during arranged hunts.[4] Trophy values are determined by their size and quality, graded in three classes (bronze, silver, and gold medal). We use the weighted average of trophy prizes as trophy values in the model. We assign trophy values to only the adult roe deer males and senescent fallow deer males, since these trophies are the most valuable to hunters due to their large size and high quality. The supplemental winter feeding costs was estimated for each fallow deer stage, using the total feeding cost and adjusting for metabolic body weight in each stage using the approach of Putman (1980). It should be noted that the fact that all economic data have been obtained from the Koberg area implies that hunting values are high compared to those for the typical Swedish hunter as the commercial hunting sector is a subsector in the higher end of the market. The reference scenario assumes a 3% discount rate as recommended in cost–benefit analysis of public projects, see Boardman, Greenberg, Vining, and Weimer (2011). All parameter values are shown in Table 1.

6 | RESULTS

Results are computed with a numerical programming model using the CONOPT3 solver and the GAMS software (Brooke, Kendrick, & Meeraus, 1988). For the empirical analysis, we make use of three different scenarios, chosen to illustrate the role of interspecific competition. The first scenario, OPTIMAL, assumes that the manager is aware of interspecific competition effects. Decisions are thus identical with the problem described in Section 3. The second scenario, NOCOMP, illustrates the outcome that would result if there was no interspecific competition, $\mu = 0$. This implies that the carrying capacity of the habitat would be larger, as more deer would be sustained in the biological equilibrium. We also include a third scenario, IGNOR, where we assume that the manager is not aware of interspecific competition. In this case, we simulate the system forward in time. As the manager incorrectly anticipates the future at time t, he has to adapt his harvesting strategy every time step to the new conditions, that is, the stock sizes in $t + 1$, which are different than anticipated due to the species interactions. To determine the time path of harvests and stocks over 70 years, the optimization is done 70 times in a rolling horizon fashion: For every next time step, a new initial state is computed (using the correct population model) from the previous period's initial state, and the harvest rates are determined by the imperfectly planning manager. For all scenarios the dynamic model solves the problem over a 120-year period. A relatively long time period is necessary to avoid end-of-time effects, for example, in the IGNOR scenario 50 future time periods remain at $t = 70$.

All scenarios are computed for two data sets, which differ with respect to the harvesting benefits included. The first data set includes all harvesting benefits: meat, trophy, and recreation values. The second data set includes only recreation values. The motivation for using only recreation values in some of the calculations is the following: fallow deer has multiple advantages for the manager: high population densities are possible, each individual provides more meat than roe deer of the same age and sex, and trophy values are higher. This suggests that the manager may prioritize fallow deer before roe deer under the reference set of parameters. The use of recreation benefits, equal for both species and all stages, illustrates how interspecific competition affects optimal joint management under less extreme conditions. Inclusion of these calculations increases the possibilities to draw more general conclusions from the results.

We use our scenarios to investigate, first, the implications of interspecific competition for the economically optimal harvesting of the two species, and the consequential effects for deer populations. This is followed by an investigation of the value of the marginal damage of fallow deer, in terms of its impact on roe deer reproduction and hence populations and harvests. Finally, a sensitivity analysis is conducted to assess effects of assumptions about the discount rate.

TABLE 1 Parameter values. Methods are described in the text

		Stage			
	Parameter	**1**	**2**	**3**	**4**
κ_r^i	Fecundity rate for female roe deer[a]	0	1.23	1.83	1.58
κ_f^i	Fecundity rate for female fallow deer[a]	0	0.89	0.96	0.76
$g_{x,r}^i$	Probability of female roe surviving and moving from stage i to $i+1$[b]	0.72	0.391	0.170	0.111
$g_{y,r}^i$	Probability of a male roe surviving and moving from stage i to $i+1$[b]	0.85	0.301	0.160	0.103
$g_{x,f}^i$	Probability of a female fallow surviving and moving from stage i to $i+1$[b]	0.857	0.472	0.092	0.092
$g_{y,f}^i$	Probability of a male fallow surviving and moving from stage i to $i+1$[b]	0.759	0.50	0.305	0.023
$p_{x,r}^i$	Probability of a female roe surviving and staying in stage i[b]	0	0.459	0.775	0.629
$p_{y,r}^i$	Probability of a male roe surviving and staying in stage i[b]	0	0.419	0.770	0.617
$p_{x,f}^i$	Probability of a female fallow surviving and staying in stage i[b]	0	0.491	0.871	0.871
$p_{y,f}^i$	Probability of a male fallow surviving and staying in stage i[b]	0	0.50	0.421	0.703
w_x^i	Meat weight of female roe deer, kg/animal [a]	7.6	7.6	12.1	12.1
w_y^i	Meat weight of male roe deer, kg/animal [a]	7.6	7.6	12.1	12.1
ψ_x^i	Meat weight of female fallow deer, kg/animal [a]	13.2	21.6	26	26
ψ_y^i	Meat weight of male fallow deer, kg/animal [a]	13.2	28.5	49.7	49.7
$R_{x,0}^i$	Initial roe female population at $t=0$[c]	397	264	458	78
$R_{y,0}^i$	Initial roe male population at $t=0$[c]		331	100	0
$F_{x,0}^i$	Initial fallow female population at $t=0$[c]	1108	950	448	0
$F_{y,0}^i$	Initial fallow male population at $t=0$[c]		841	726	222
β_r	Intraspecific competition, roe deer[d]	0.000421			
β_f	Intraspecific competition, fallow deer[d]	0.000217			
μ	Interspecific competition[d]	0.000114			
d_x^i	Winter feeding cost female fallow deer, SEK[e]	49.4	71.6	82.3	82.3
d_y^i	Winter feeding cost male fallow deer, SEK[e]	51.6	88.2	134.7	134.7
$z_{r,y}^i$	Trophy price for roe deer, SEK[e]	NA	NA	6,000	NA
$z_{f,y}^i$	Trophy price for fallow deer, SEK[e]	NA	NA	NA	18,580
q_r^i	Meat price roe deer, SEK/kg[e]	65			
q_r^i	Meat price fallow deer, SEK/kg[e]	65			
M	Recreational value, SEK/animal[e]	3,167			
δ	Discount rate, %[f]	3			

[a] Kjellander (2000).

[b] Authors' calculation, based on Kjellander (2000, 2014).

[c] Set to steady-state level. For fawns, the figure refers to the total number for both sexes.

[d] Calibrated.

[e] Study area. Exchange rate: 1 EUR = 9.47 SEK (average for 2016).

[f] Boardman et al. (2011).

6.1 | Optimal harvesting strategies

The OPTIMAL scenario generates a uniform[5] harvesting regime for fallow and roe deer with the reference set of parameters (Table 1). Pulse harvesting is found in several cases when the interspecific competition parameter or the discount rate is altered (Table B1). In scenarios where pulse harvests occur, they disappear if the effect of inter- and intraspecific competition is, instead, assumed to occur without a time lag. This confirms the observation in Naevdal et al. (2012) that pulse harvest tends to occur when there is a time lagged effect on recruitment. The likely reason for the occurrence of pulse harvesting is the beneficial effect on recruitment in the following year.

In Table 2, we present the harvesting strategies in terms of the average annual outcomes. When all harvesting benefits are included, the OPTIMAL and IGNOR scenarios yield identical outcomes for all variables. This shows that knowledge about the interspecific competition does not imply that the manager reduces the fallow deer population in order to benefit the roe deer population and harvest. The reason is that the cost for reducing the fallow deer population, in terms of fallow deer harvests foregone, exceeds the benefits in terms of a higher roe deer population and hence higher roe deer harvest. The NOCOMP scenario yields the same fallow deer management as the two other scenarios, further confirming that fallow deer harvesting is unaffected by the presence of interspecific competition. Roe deer population density and harvest are, respectively, 42% and 87% higher under NOCOMP compared to the other scenarios, and the net present value is 10% higher.

When all harvesting benefits are included, female fallow deer are harvested in Stage 3, while female roe deer are harvested in Stage 4, which might be explained by the larger fall in reproduction between Stages 3 and 4 for fallow deer. Male fallow and roe deer are harvested in Stages 4 and 3, respectively, when the trophy value is the highest.

In contrast, simulations with only recreation benefits lead to a solution where the fallow deer population is adjusted when the manager is aware of interspecific competition. Here, the OPTIMAL scenario implies a reduction of fallow deer population density and harvest by 7% and 2%, respectively, compared to the NOCOMP scenario, that is, fallow deer populations are adjusted downward in the presence of interspecific competition. Under the IGNOR scenario, the fallow deer population is equally high as under NOCOMP, hence ignoring the adverse impact on roe deer. This has consequences for roe deer, implying a 9% larger population size but 3% lower harvest compared to the OPTIMAL scenario. Consequently, fallow deer revenues increase, and roe deer revenues decrease compared to the OPTIMAL scenario. In spite of the strategy under the IGNOR scenario being suboptimal, the average annual net revenues in steady state (in current value) are equal to those under the OPTIMAL strategy. However, the net present value in the OPTIMAL scenario exceeds the one in the IGNOR scenario by 0.4%. This is explained by the OPTIMAL scenario generating pulse harvests, whereas only minor traces of pulse harvests are found under the IGNOR scenario. The pulses under OPTIMAL are associated with variations in net revenues, where periods with high net revenues are skewed toward the early time periods.

Simulations with only recreation benefits imply that younger individuals of both species are harvested in the OPTIMAL scenario, as there is no reason to postpone harvesting in order to obtain higher meat and trophy values. This does not apply to the IGNOR scenario, where the manager fails to account for beneficial effects of fawn harvesting on roe deer reproduction, leading to declining reproduction, and a large share of mature female roe deer, and a smaller share of fawns, compared to the OPTIMAL scenario.

The lack of adjustment of fallow deer harvesting in the presence of interspecific competition discussed above raises the question of how the magnitude of interspecific competition affects the existence of a bioeconomic equilibrium, where both species are present in positive numbers. Figure 3 shows the development of fallow and roe populations under different assumptions about the size of μ. The simulations show that if μ is increased by a factor 3 or more, compared to our calibrated data, an equilibrium with both species present does not exist in our model.

TABLE 2 Average steady-state population harvest and net present value (TNPV) under different scenarios

	Meat, Trophy, and Recreation Benefits			**Only Recreation Benefits**				
	Fallow Deer	**Roe Deer**		**Fallow Deer**		**Roe Deer**		
	OPTIMAL/ NOCOMP/ IGNOR	**OPTIMAL/ IGNOR**	**NOCOMP**	**OPTIMAL**	**NOCOMP/ IGNOR**	**OPTIMAL**	**NOCOMP**	**IGNOR**
Population								
Fawns	1,047	413	663	1489	1537	482	729	492
Females Stage 2	897	275	375	1204	1317	293	344	328
Females Stage 3	424	478	649	567	622	509	599	569
Females Stage 4	0	81	110	0	0	87	102	97
Males Stage 2	795	345	470	534	583	187	223	209
Males Stage 3	686	104	141	0	0	0	0	0
Males Stage 4	209	0	0	0	0	0	0	0
Total pop	4,058	1,696	2,408	3,794	4,058	1,558	1,996	1,695
Harvest								
Fawns	0	0	98	80	0	41	211	0
Females Stage 2	0	0	0	0	0	0	0	0
Females Stage 3	424	0	0	567	622	0	0	0
Females Stage 4	0	81	110	0	0	87	102	97
Males Stage 2	0	0	0	534	583	187	220	209
Males Stage 3	0	104	141	0	0	0	0	0
Males Stage 4	209	0	0	0	0	0	0	0
Total harvest	633	185	349	1,182	1,205	315	533	306
TNPV incl. both species, kSEK [b]		224,194	246,599			134,123	153,521	133,552

[a] Average over year 1–70. Exchange rate: 1 EUR = 9.47 SEK (average for 2016).

[b] Over 70 years.

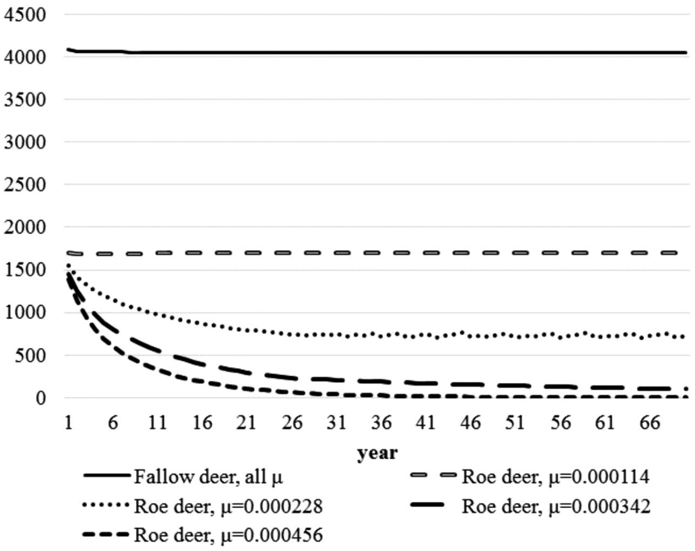

FIGURE 3 Development of deer population sizes for different assumptions about interspecific competition in the OPTIMAL scenario with all harvesting benefits included. "Fallow deer, all μ" indicate the fallow deer population size under $\mu = 0.000114$, 0.000228, 0.000342, and 0.000456

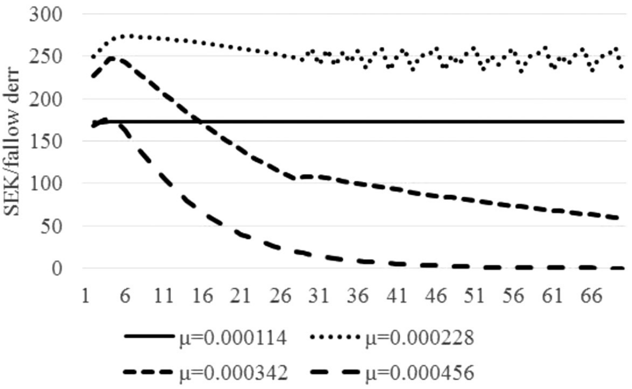

FIGURE 4 Marginal damage of fallow deer on roe deer calculated from the OPTIMAL scenario with all harvesting benefits included. Exchange rate: 1 EUR = 9.47 SEK (average for 2016)

6.2 | The marginal damage of fallow deer on roe deer

The marginal damage of fallow deer on roe deer is calculated according to the definition in Section 4.3. Figure 4 shows the development of the marginal damage for different assumptions about interspecific competition when all harvesting benefits are included in the calculations. Using the reference set of data the marginal damage equals 177 SEK per fallow deer, and is constant over time, given the steady state with uniform harvests. A doubling of μ leads to a higher marginal damage for all time periods. If μ is increased by a factor 3, the marginal damage is first higher, but over time roe deer population size and reproduction falls, implying a decreasing marginal damage. When μ is increased by a factor 4, roe deer reproduction immediately falls, the marginal damage then declines toward zero as the roe deer get extinct. Qualitatively similar results are obtained when only recreation benefits are included, although the marginal damage level is lower due to the smaller harvesting benefits of roe deer.

TABLE 3 Steady-state marginal damage of fallow deer, populations, harvests, and annual revenues under different discount rates. Results from OPTIMAL scenario with all harvest benefits included

Discount Rate (%)	Marginal Damage of Fallow Deer on Roe Deer (SEK)[a]	Population		Harvest	
		Roe	Fallow	Roe	Fallow
0	216	1,697	4,058	185	633
3	177	1,697	4,058	185	633
6	151	1,697	4,058	185	633
9	139	1,458	4,058	193	633
12	127	1,212	4,058	189	840
15	118	1,034	3,809	185	1,182

[a] Exchange rate: 1 EUR = 9.47 SEK (average for 2016).

6.3 | Implications of the choice of discount rate

A high discount rate implies that current consumption is valued relatively higher than future consumption. This reflects a high degree of impatience, and tends to imply larger harvest in early time periods, but can also imply a smaller population size and harvest in the long run (Tahvonen et al., 2014).

The calculations shows that steady states with positive population sizes for both deer species are obtained for all discount rates between 0 and 15 (Table 3). Results are not affected by a change in the discount rate for discount rates between 0 and 6, except the marginal damage of fallow deer, which falls with increases in the discount rate due to the lower value associated with the impact on future outcomes. When the discount rate is further increased, the harvest composition changes toward the less valuable gender and younger life stages, and harvested numbers tend to increase. Roe deer populations decline for discount rates 9% and higher, and fallow deer populations when then discount rate is increased to 15%. The low impact of the discount rate on the steady-state outcome is consistent with observations in Tahvonen et al. (2013) and Naevdal et al. (2012).

7 | DISCUSSION AND CONCLUSIONS

The main goal of this paper is to analyze, and demonstrate empirically, the role of competition between two sympatric deer species for the optimal management and to identify whether efficient policy instruments could be applied when such competition is unknown to hunting managers. To this end, we develop a stage-structured numerical bioeconomic model of roe and fallow deer in the presence of interspecific competition.

The theoretical analysis shows that if fallow deer exerts a negative, unilateral impact on roe deer, this implies a lower value of holding additional fallow deer, which can be a motive for reducing the population density of fallow deer. The marginal damage of fallow deer, in terms of the impact on the roe deer population size and harvest at equilibrium, depends on the magnitude of interspecific competition between species and the size of the two populations.

The model is simulated using empirical data on species' life history characteristics, three types of hunting benefits, and costs for winter feeding of fallow deer. Results suggest that ignorance of interspecific competition does not affect fallow deer holdings compared to a situation where the manager is aware of such competition. This contrasts with expectations, but is explained by the economic advantages of fallow deer to the manager, compared to roe deer. If, instead, economic benefits of harvesting are assumed equal for the two species, the model shows the intuitively expected outcome where the optimal solution implies that the fallow deer population is adjusted downward in order to reduce the negative impact on the roe deer.

The above suggests that the existence of interspecific competition can be a problem with respect to the possibilities to sustain viable roe deer populations, independently of whether the manager is aware of interspecific competition or not. Our estimate of the magnitude of interspecific competition is based on scarce data, and if the parameter level is increased by a factor 3 or more, the optimal solution does not include roe deer in the bioeconomic equilibrium. This suggest that further research on the magnitude of interspecific competition is valuable if, for example, roe deer generate significant ecosystem services.

Results indicate that the introduction of a tax on fallow deer, set equal to the marginal damage on roe deer, would not improve on the outcome in a situation where the manager is ignorant about interspecific competition because of the larger hunting benefits from fallow deer. If, instead, harvesting benefits were equal for the two species, the introduction of a tax would increase roe deer harvests, but the net effect on the manager's revenues would still be insignificant. Also, absence of a tax has no obvious negative effects on roe deer population numbers, and the share of mature females increases, which is typically seen as positive for the viability.

Pulse harvesting is common in age- and stage-structured models (Clark, 1990; Clark, Edwards, & Friedlaender, 1973; Hannesson, 1975; Tahvonen et al., 2013; Walters, 1969). Earlier studies have shown that pulse harvests can be generated by the choice of discount rate (Clark et al., 1973; Tahvonen et al., 2013), imperfect selectivity (Tahvonen, 2009), the shape of the objective function (Tahvonen et al., 2013), and the size of the hunting recreation value (Skonhoft et al., 2013). Our results indicate the level of interspecific competition, and the existence of the time-lag on inter- and intraspecific competition, are additional factors that can explain the occurrence of pulse harvests.

A restraint of this study is that neither aesthetic nor existence values of the species are accounted for. The same holds for the costs of browsing damages on agricultural crops and on trees in commercial forest stands. Moreover, interspecific competition could have an effect through alternative channels, such as reproduction, survival, and individual growth (Elofsson & Gren, 2015; Hamre, 2003), and our choice of modeling these effects is a simplification. These limitations should be borne in mind when interpreting the results.

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ENDNOTE

[1] Exchange rate: 1 EUR = 9.47 SEK (average for 2016).

[2] Harvest continues throughout the winter implying that in practice, the population equals the number in population count in the spring in year t in the beginning of the hunting season in year t and approaches the population count in year $t+1$ in the end of the same season. Therefore, reproduction functions with and without a time lag could both be plausible. Our choice to use a time lag is determined by the data: the population data from the study site indicate that a high fallow deer population density in the spring in a given year is negatively correlated with roe deer population density in the following year. The relationship between species densities in the same year is more ambiguous.

[3] This is done by minimizing the square of the difference between a slack variable and the interspecific competition parameter.

[4] Hunting fees are paid in advance, as a lump sum, hence it is not possible to calculate different recreational values for the species.

[5] Also referred to as continuous, smooth, or stationary harvesting.

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REFERENCES

Alm, U., Birgersson, B., & Leimar, O. (2001). The effect of food quality and relative abundance on diet choice in fallow deer. *Animal Behaviour*, *64*, 439–445.

Andersson, Å., Glöersen, G., Brittas, R., & Huldt, H. (1996). *Ung eller gammal. Konsten att bestämma åldern på vilda djur och fåglar* (pp. 48) [Young or old. The art of determining the age of wildlife and birds]. Uppsala: Almqvist och Wiksell.

Baumol, W. J., & Oates, W. E. (1988). *The theory of environmental policy*(2nd ed.). Cambridge: Cambridge University Press.

Birch, L. C. (1957). The meanings of competition. *The American Naturalist*, *91*(856), 5–18.

Boardman, A., Greenberg, D., Vining, A., & Weimer, D. (2011). *Cost-benefit analysis: Concepts and practice*(4th ed.). Boston: Pearson Education.

Brooke, A., Kendrick, D., & Meeraus, A. (1988). *GAMS: A user's guide*. San Francisco: The Scientific Press.

Caughley, G., & Sinclair, A. R. E. (1994). *Wildlife ecology and management*. Boston: Blackwell.

Carlström, L., & Nyman, M. (2005). *Dovhjort* [Fallow deer]. Kristianstad: Jägareförlaget, Svenska Jägareförbundet.

Cederlund, G., & Liberg, O. (1995). *Rådjuret: Viltet, ekologin och jakten*. [The roe deer: the wildlife, the ecology and the hunting]. Uppsala: Almqvist & Wiksell.

Cederlund, G., Stålfelt, F., & Kjellander, P. (1991). Age determination of roe deer by tooth wear and cementum layers: Test with known age material. *Transactions of the 20th IUGB Congress Gödöllö*, 540–545.

Chapman, D., & Chapman, N. (1975). *Fallow deer: Their history, distribution and biology*. Lavenham: Terence Dalton.

Chardonnet, P. H., des Clers, B., Fischer, J., Gerhold, R., Jori, F., & Lamarque, F. (2002). The value of wildlife. *Revue Scientifique et Technique*, *21*(1), 15–51.

Chaudhuri, K. S. (1986). A bioeconomic model of harvesting a multispecies fishery. *Ecological Modelling*, *32*, 267–279.

Chaudhuri, K. S. (1987). Dynamic optimization of combined harvesting of a two-species fishery. *Ecological Modelling*, *41*, 17–25.

Chaloupka, M. (2002). Stochastic simulation modelling of southern Great Barrier Reef green turtle population dynamics. *Ecological Modelling*, *148*, 79–109.

Clark, C. (1990). *Mathematical bioeconomics, optimal management of renewable resources*(2nd ed.). New York: Wiley.

Clark, C., Edwards, G., & Friedlaender, M. (1973). The Beverton-Holt model of commercial fisheries: Optimal dynamics. *Journal of the Fisheries Research Board of Canada*, *30*, 1629–1640.

Conrad, J. M., & Adu-Asamoah, R. (1986). Single and multispecies systems: The program of tuna in the eastern tropical Atlantic. *Journal of Environmental and Economic Management*, *13*, 50–68.

Crouse, D. T., Crowder, L. B., & Caswell, H. (1987). A stage-based population model for Loggerhead Sea Turtles and implications for conservation. *Ecology*, *68*(5), 1412–1423.

Collier, B. A., & Krementz, D. G. (2007). Uncertainty in age-specific harvest estimates and consequences for white-tailed deer management. *Ecological Modelling*, *201*, 194–204.

Elofsson, K., & Gren, I-M. (2015). Regulating invasive species with different life history. *Journal of Bioeconomics*, *17*(2), 113–136.

Ferretti, F., Bertoldi, G., Sforzi, A., & Fattorini, L. (2011). Roe and fallow deer: Are they compatible neighbours?. *European Journal of Wildlife Research*, *57*, 775–783.

Ferretti, F., Sforzi, A., & Lovari, S. (2008). Intolerance amongst deer species at feeding: Roe deer are uneasy banqueters. *Behavioural Processes*, *78*(3), 487–491.

Flaaten, O. (1988). *The economics of multispecies harvesting: Theory and application to the Barents Sea Fisheries*. Berlin: Springer-Verlag.

Flaaten, O. (1991). Bioeconomics of sustainable harvest of competing species. *Journal of Environmental and Economic Management*, *20*, 163–180.

Finnoff, D., & Tschirhart, J. (2003). Harvesting in an eight-species ecosystem. *Journal of Environmental Economics and Management*, *45*, 589–611.

Focardi, S., Aragno, P., Montanaro, P., & Riga, F. (2006). Inter-specific competition from fallow deer *Dama dama* reduces habitat quality for the Italian roe deer *Capreolus capreolus italicus*. *Ecography*, *29*, 407–417.

Gaillard, J-M., Festa-Bianchet, M., Yoccoz, N. G., Loison, A., & Toigo, C. (2000). Temporal variation in fitness components and population dynamics of large herbivores. *Annual Review of Ecology and Systematics*, *31*, 367–393.

Hamre, J. (2003). Capelin and herring as key species for the yield of north-east Arctic cod: Results from multispecies model runs. *Scientia Marina*, *67*, 315–323.

Hannesson, R. (1975). Fishery dynamics: A North Atlantic cod fishery. *The Canadian Journal of Economics*, *8*(2), 151–173.

Hannesson, R. (1983). Optimal harvesting of ecologically interdependent fish species. *Journal of Environmental Economics and Management*, *10*(4), 329–345.

Hewison, A. J. M. (1996). Variation in the fecundity of roe deer in Britain: Effects of age and body weight. *Acta Theriologica*, *41*(2), 187–198.

Hofmann, R.R. (1989). Evolutionary steps of ecophysiological adaptation and diversification in ruminants: a comparative view of their digestive system. *Oecologia 78*, 443–457.

Kjellander, P. (2000). *Density dependence in roe deer population dynamics*. PhD Thesis. Silvestria 154, Department of Wildlife Ecology, Swedish University of Agricultural Sciences.

Kjellander, P. (2014). Annual project status report. Unpublished document.

Mattsson, L., Boman, M. & Ericsson, G. (2008). *Jakten i Sverige: Ekonomiska värden och attityder jaktåret 2005/2006* [The hunting in Sweden: Economic values and attitudes in the hunting year 2005/2006]. Report 1, Adaptiv Förvaltning av Vilt och Fisk [Adaptive Management of Wildlife and Fish], Umeå.

Moxnes, E., Danell, Ö., Gaare, E., & Kumpula, J. (2001). Optimal strategies for the use of reindeer rangelands. *Ecological Modelling*, *145*, 225–241.

Naevdal, E., Olaussen, J. O., & Skonhoft, A. (2012). A bioeconomic model of trophy hunting. *Ecological Economics*, *73*, 194–205.

Nichols, R. V., Åkesson, M., & Kjellander, P. (2016). Diet assessment based on rumen contents: A comparison between DNA metabarcoding and macroscopy. *PLoS ONE*, *11*(6), e0157977. https://doi.org/10.1371/journal.pone.0157977.

Nieminen, E., Lindroos, M., & Heikinheimo, O. (2012). Optimal bioeconomic multispecies fisheries management: A Baltic Sea case study. *Marine Resource Economics*, *27*, 115−136.

Nieminen, E., Kronbak, L. G., & Lindroos, M. (2016). International agreements in the multispecies Baltic Sea fisheries. *Environmental and Resource Economics*, *65*(1), 109–134.

Olaussen, J. O., & Mysterud, A. (2012). Red deer hunting: Commercialising versus availability. *European Journal of Wildlife Research*, *58*, 597−607.

Olaussen, J. O., & Skonhoft, A. (2011). A cost-benefit analysis of moose harvest in Scandinavia. A stage structured approach. *Resource and Energy Economics*, *33*, 589−611.

Pianka, E. R. (1974). Niche overlap and diffuse competition. *Proceedings of the National Academy of Sciences of the United States of America*, *71*, 2141−2145.

Putman, R. J. (1980). Consumption, protein and energy intake of fallow deer fawns on diet of differing nutritional quality. *Acta Theriologica*, *25*, 403−413.

Ricker, W. E. (1954). Stock and recruitment. *Journal of the Fisheries Research Board of Canada*, *11*, 559–623.

Sandström, C., Wennberg-Di Gasper, S., & Öhman, K. (2013). Conflict resolution through ecosystem-based management: The case of Swedish Moose Management. *International Journal of the Commons*, *7*, 549−570.

Skonhoft, A., Veiberg, V., Gauteplass, A., Olaussen, J. O., Meisingset, E. I., & Mysterud, A. (2013). Balancing income and cost in red deer management. *Journal of Environmental Management*, *115*, 179−188.

Skonhoft, A., Vestergaard, N., & Quaas, M. (2012). Optimal harvest in an age structured model with different fishing selectivity. *Environmental and Resource Economics*, *51*(4), 525−544.

Tahvonen, O. (2009). Economics of harvesting age-structured fish populations. *Journal of Environmental Economics and Management*, *58*, 281–299.

Tahvonen, O., Quaas, M. F., Schmidt, J. O., & Voss, R. (2013). Optimal harvesting of an age-structured schooling fishery. *Environmental and Resource Economics*, *54*(1), 21–39.

Tahvonen, O., Kumpula, J., & Pekkarinen, A-J. (2014). Optimal harvesting of an age-structured, two-sex herbivore–plant system. *Ecological Modelling*, *272*, 348–361.

Virtala, M. (1992). Optimal management of a plant–herbivore system: Lichen and reindeer in Northern Finland. *Ecological Modeling*, *3–4*, 233–255.

Virtala, M. (1996). Harvesting a lichen–reindeer system in an uncertain environment. *Ecological Modeling*, *89*, 209–224.

Walters, C. J. (1969). A generalized computer simulation model for fish population studies. *Transactions of the American Fisheries Society*, *98*, 505–512.

Xu, C., & Boyce, M. S. (2010). Optimal harvesting of moose in Alberta. *Alces*, *46*, 15–35.

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APPENDIX A

Optimality conditions

The Kuhn–Tucker FOCs for the above optimization problem, including the slack conditions are:

$$\rho^{-t}L'_{HR^1_{c,t}} = q^1_{r,j} - 0.5\rho\left(\sum_{j=x}\lambda^2_{j,t+1}\right)g^1_{c,r} - \varpi^1_{j,t} \leq 0; 0 \leq HR^1_{c,t}; t = 0, 1, \ldots, T, \tag{A1}$$

$$\begin{aligned}\rho^{-t}L'_{HR^2_{j,t}} &= q^2_{r,j} - \rho\lambda^3_{j,t+1}g^2_{j,r} - \varpi^2_{j,t} \leq 0; 0 \leq HR^2_{j,t};\\ t &= 0, 1, \ldots, T; j = x, y;\end{aligned} \tag{A2}$$

$$\begin{aligned}\rho^{-t}L'_{HR^3_{j,t}} &= q^3_{r,j} - \rho\lambda^3_{j,t+1}p^3_{j,r} - \rho\lambda^4_{j,t+1}g^3_{j,r} - \varpi^3_{j,t} \leq 0; 0 \leq HR^3_{j,t};\\ t &= 0, 1, \ldots, T; j = x, y;\end{aligned} \tag{A3}$$

$$\begin{aligned}\rho^{-t}L'_{HR^4_{j,t}} &= q^4_{r,j} - \rho\lambda^4_{j,t+1}p^4_{j,r} - \varpi^4_{j,t} \leq 0; 0 \leq HR^4_{j,t};\\ t &= 0, 1, \ldots, T; j = x, y;\end{aligned} \tag{A4}$$

$$\begin{aligned}\rho^{-t} L'_{HF^1_{c,t}} &= q^1_{f,j} + d^1_j - 0.5\rho\left(\sum_{j=1} \gamma^2_{j,t+1}\right) g^1_{c,f} - \theta^1_{j,t} \le 0; 0 \le HF^1_{c,t}\\ &\quad t = 0, 1, \ldots, T;\end{aligned} \tag{A5}$$

$$\begin{aligned}\rho^{-t} L'_{HF^2_{j,t}} &= q^2_{f,j} + d^2_j - \rho\gamma^3_{j,t+1} g^2_{j,f} - \varpi^2_{j,t} \le 0; 0 \le HF^2_{j,t};\\ &\quad t = 0, 1, \ldots, T; j = x, y;\end{aligned} \tag{A6}$$

$$\begin{aligned}\rho^{-t} L'_{HF^3_{j,t}} &= q^3_{f,j} + d^2_j - \rho\gamma^3_{j,t+1} p^3_{j,f} - \rho\gamma^4_{j,t+1} g^3_{j,f} - \theta^3_{j,t} \le 0; 0 \le HF^3_{j,t}\\ &\quad t = 0, 1, \ldots, T; j = x, y;\end{aligned} \tag{A7}$$

$$\begin{aligned}\rho^{-t} L'_{HF^4_{j,t}} &= q^4_{f,j} + d^4_j - \rho\gamma^4_{j,t+1} p^4_{j,f} - \theta^4_{j,t} \le 0; 0 \le HF^4_{j,t};\\ &\quad t = 0, 1, \ldots, T; j = x, y;\end{aligned} \tag{A8}$$

$$\begin{aligned}\rho^{-t} L'_{R^1_{c,t}} &= -\rho\lambda^1_{c,t+1}\beta \sum_{i>1} R^i_{x,t+1}\kappa^i_r \exp\left(-\sum_{ij}\left(\beta_r R^i_{j,t} + \mu F^i_{j,t}\right)\right) - \lambda^1_{c,t}\\ &\quad + 0.5\rho\left(\sum_j \lambda^2_{j,t+1}\right) g^1_{c,r} + \varpi^1_{c,t} \le 0; R^1_{j,t} \ge 0; t = 0, 1, \ldots, T; j = c, x, y,\end{aligned} \tag{A9}$$

$$\begin{aligned}\rho^{-t} L'_{R^2_{x,t}} &= \lambda^1_{c,t}\kappa^2_r \exp\left(-\sum_{ij}\left(\beta_r R^i_{j,t-1} + \mu F^i_{j,t-1}\right)\right)\\ &\quad - \rho\lambda^1_{c,t+1}\beta \sum_{i>1} R^i_{x,t+1}\kappa^i_r \exp\left(-\sum_{ij}\left(\beta_r R^i_{j,t} + \mu F^i_{j,t}\right)\right)\\ &\quad - \lambda^2_{x,t} + \rho\lambda^3_{x,t+1} g^2_{x,r} + \varpi^2_{x,t} \le 0; R^2_{1,t} \ge 0; t = 0, 1, \ldots, T; j = c, x, y,\end{aligned} \tag{A10}$$

$$\begin{aligned}\rho^{-t} L'_{R^2_{y,t}} &= -\rho\lambda^1_{c,t+1}\beta_r \sum_{i>1} R^i_{x,t+1}\kappa^i_r \exp\left(-\sum_{ij}\left(\beta_r R^i_{j,t} + \mu F^i_{j,t}\right)\right)\\ &\quad - \lambda^2_{y,t} + \rho\lambda^3_{y,t+1} g^2_{y,r} + \varpi^2_{y,t} \le 0; R^2_{y,t} \ge 0; t = 0, 1, \ldots, T; j = c, x, y,\end{aligned} \tag{A11}$$

$$\begin{aligned}\rho^{-t} L'_{R^3_{x,t}} &= \lambda^1_{c,t}\kappa^3_r \exp\left(-\sum_{ij}\left(\beta_r R^i_{j,t-1} + \mu F^i_{j,t-1}\right)\right)\\ &\quad - \rho\lambda^1_{c,t+1}\beta_r \sum_{i>1} R^i_{x,t+1}\kappa^i_r \exp\left(-\sum_{ij}\left(\beta_r R^i_{j,t} + \mu F^i_{j,t}\right)\right)\\ &\quad + \rho\lambda^3_{x,t+1} p^3_{1,r} - \lambda^3_{x,t} + \rho\lambda^4_{x,t+1} g^3_{x,r} + \varpi^3_{x,t} \le 0; R^3_{x,t} \ge 0; t = 0, 1, \ldots, T; j = c, x, y,\end{aligned} \tag{A12}$$

$$\begin{aligned}\rho^{-t} L'_{R^3_{y,t}} &= -\rho\lambda^1_{c,t+1}\beta_r \sum_{i>1} R^i_{x,t+1}\kappa^i_r \exp\left(-\sum_{ij}\left(\beta_r R^i_{j,t} + \mu F^i_{j,t}\right)\right)\\ &\quad + \rho\lambda^3_{y,t+1} p^3_{y,r} - \lambda^3_{y,t} + \rho\lambda^4_{y,t+1} g^3_{y,r} + \varpi^3_{y,t} \le 0; R^2_{y,t} \ge 0; t = 0, 1, \ldots, T; j = c, x, y,\end{aligned} \tag{A13}$$

$$\begin{aligned}\rho^{-t}L'_{R^4_{x,t}} &= \lambda^1_{c,t}\kappa^4_r \exp\left(-\sum_{ij}\left(\beta_r R^i_{j,t-1}+\mu F^i_{j,t-1}\right)\right)\\ &\quad -\rho\lambda^1_{c,t+1}\beta_r\sum_{1>1}R^i_{x,t+1}\kappa^i_r\exp\left(-\sum_{ij}\left(\beta_r R^i_{j,t}+\mu F^i_{j,t}\right)\right)\\ &\quad +\rho\lambda^4_{x,t+1}p^4_{x,r}-\lambda^4_{x,t}\le 0;\ R^3_{x,t}\ge 0;\ t=0,1,\dots,T;\ j=c,x,y,\end{aligned} \tag{A14}$$

$$\begin{aligned}\rho^{-t}L'_{R^4_{y,t}} &= -\rho\lambda^1_{c,t+1}\beta_r\sum_{i>1}R^i_{x,t+1}\kappa^i_r\exp\left(-\sum_{ij}\left(\beta_r R^i_{j,t}+\mu F^i_{j,t}\right)\right)\\ &\quad +\rho\lambda^4_{y,t+1}p^4_{y,r}-\lambda^4_{y,t}+\varpi^4_{y,t}\le 0;\ R^4_{y,t}\ge 0;\ t=0,1,\dots,T;\ j=c,x,y,\end{aligned} \tag{A15}$$

$$\begin{aligned}\rho^{-t}L'_{F^1_{c,t}} &= -\rho\lambda^1_{c,t+1}\mu\sum_{i>1}R^i_{x,t+1}\kappa^i_r\exp\left(-\sum_{ij}\left(\beta_r R^i_{j,t}+\mu F^i_{j,t}\right)\right)-d^1_c\\ &\quad -\rho\gamma^1_{c,t+1}\beta_f\sum_{i>1}F^i_{x,t}\kappa^i_f\exp\left(-\sum_{ij}\beta_f F^i_{j,t}\right)-\gamma^1_{c,t}+0.5\rho\left(\sum_{j=x}\gamma^2_{j,t+1}\right)g^1_{0,f}+\theta^1_{c,t}\le 0;\\ &\quad F^1_{c,t}\ge 0;\ t=0,1,\dots,T;\ j=c,x,y,\end{aligned} \tag{A16}$$

$$\begin{aligned}\rho^{-t}L'_{F^2_{x,t}} &= -\rho\lambda^1_{c,t+1}\mu\sum_{i>1}R^i_{x,t+1}\kappa^i_r\exp\left(-\sum_{ij}\left(\beta_r R^i_{j,t}+\mu F^i_{j,t}\right)\right)+\gamma^1_{c,t}\kappa^2_f\\ &\quad \times\exp\left(-\sum_{ij}\beta_f F^i_{j,t-1}\right)-\rho\gamma^1_{c,t+1}\beta_f\sum_{i>1}F^i_{x,t+1}\kappa^i_f\exp\left(-\sum_{ij}\beta_f F^i_{j,t}\right)-\gamma^2_{x,t}-d^2_x\\ &\quad +\rho\gamma^3_{x,t+1}g^2_{x,f}+\theta^1_{x,t}\le 0;\ F^2_{x,t}\ge 0;\ t=0,1,\dots,T;\ j=c,x,y,\end{aligned} \tag{A17}$$

$$\begin{aligned}\rho^{-t}L'_{F^2_{y,t}} &= -\rho\lambda^1_{c,t+1}\mu\sum_{i>1}R^i_{x,t+1}\kappa^i_r\exp\left(-\sum_{ij}\left(\beta_r R^i_{j,t}+\mu F^i_{j,t}\right)\right)-\rho\gamma^1_{c,t+1}\beta_f\sum_{i>1}F^i_{x,t+1}\kappa^i_f\\ &\quad -\gamma^2_{y,t}-d^2_y+\rho\gamma^3_{y,t+1}g^2_{y,f}+\theta^2_{x,t}\le 0;\ F^2_{y,t}\ge 0;\ t=0,1,\dots,T;\ j=c,x,y,\end{aligned} \tag{A18}$$

$$\begin{aligned}\rho^{-t}L'_{F^3_{x,t}} &= -\rho\lambda^1_{c,t+1}\mu\sum_{i>1}R^i_{x,t+1}\kappa^i_r\exp\left(-\sum_{ij}\left(\beta_r R^i_{j,t}+\mu F^i_{j,t}\right)\right)+\gamma^1_{c,t}\kappa^3_f\\ &\quad \times\exp\left(-\sum_{ij}\beta_f F^i_{j,t-1}\right)-\rho\gamma^1_{c,t+1}\beta_f\sum_{i>1}F^i_{x,t+1}\kappa^i_f\exp\left(-\sum_{ij}\beta_f F^i_{j,t}\right)-\gamma^3_{x,t}-d^3_x\\ &\quad +\rho\gamma^3_{x,t+1}p^3_{x,f}+\rho\gamma^4_{x,t+1}g^3_{x,f}+\theta^3_{x,t}\le 0;\ F^3_{x,t}\ge 0;\ t=0,1,\dots,T;\ j=c,x,y,\end{aligned} \tag{A19}$$

$$\begin{aligned}\rho^{-t}L'_{F^3_{y,t}} &= -\rho\lambda^1_{c,t+1}\mu\sum_{i>1}R^i_{x,t+1}\kappa^i_r\exp\left(-\sum_{ij}\left(\beta_r R^i_{j,t}+\mu F^i_{j,t}\right)\right)\\ &\quad -\rho\gamma^1_{c,t+1}\beta_f\sum_{i>1}F^i_{x,t}\kappa^i_f\exp\left(-\sum_{ij}\beta_f F^i_{j,t-1}\right)-\gamma^3_{y,t}-d^3_y+\rho\gamma^3_{y,t+1}p^3_{y,f}\\ &\quad +\rho\gamma^4_{y,t+1}g^3_{y,f}+\theta^3_{y,t}\le 0;\ F^3_{y,t}\ge 0;\ t=0,1,\dots,T;\ j=c,x,y,\end{aligned} \tag{A20}$$

$$\begin{aligned}\rho^{-t}L'_{F^4_{x,t}} &= -\rho\lambda^1_{c,t+1}\mu\sum_{i>1}R^i_{x,t+1}\kappa^i_r\exp\left(-\sum_{ij}\left(\beta_r R^i_{j,t}+\mu F^i_{j,t}\right)\right)+\gamma^1_{c,t}\kappa^4_f\exp\left(-\sum_{ij}\beta_f F^i_{j,t}\right)\\ &\quad-\rho\gamma^1_{c,t+1}\beta_f\sum_{i>1}F^i_{x,t}\kappa^i_f\exp\left(-\sum_{ij}\beta_f F^i_{j,t}\right)-\gamma^4_{x,t}-d^4_x+\rho\gamma^4_{x,t+1}p^4_{x,f}+\theta^4_{x,t}\le 0\\ &\quad\rho^{-t}L'_{F^4_{x,t}}F^4_{x,t}=0;\ F^4_{x,t}\ge 0;\ t=0,1,\ldots..,T;\ j=c,x,y,\end{aligned}\tag{A21}$$

$$\begin{aligned}\rho^{-t}L'_{F^4_{y,t}} &= -\rho\lambda^1_{c,t+1}\mu\sum_{i>1}R^i_{x,t+1}\kappa^i_r\exp\left(-\sum_{ij}\left(\beta_r R^i_{j,t}+\mu F^i_{j,t}\right)\right)\\ &\quad-\rho\gamma^1_{c,t+1}\beta_f\sum_{i>1}F^i_{x,t}\kappa^i_f\exp\left(-\sum_{ij}\beta_f F^i_{j,t-1}\right)-\gamma^4_{y,t}-d^4_y+\rho\gamma^4_{y,t+1}p^4_{y,f}+\theta^4_{y,t}\le 0;\\ &\quad F^4_{y,t}\ge 0;\ t=0,1,\ldots,T;\ j=c,x,y,\end{aligned}\tag{A22}$$

$$\rho^t L'_{\lambda^1_{c,t}} = \sum_{i>1}R^i_{x,t}\kappa^i_r\exp\left(-\sum_{ij}\left(\beta_r R^i_{j,t}+\mu F^i_{j,t}\right)\right)-R^1_{c,t}=0,\tag{A23}$$

$$\rho^t L'_{\rho\lambda^2_{j,t+1}} = 0.5g^1_{c,r}\left(R^1_{c,t}-HR^1_{c,t}\right)-R^2_{j,t+1}=0,\tag{A24}$$

$$\rho^t L'_{\rho\lambda^i_{j,t+1}} = g^{i-1}_{j,r}\left(R^{i-1}_{j,t}-HR^{i-1}_{j,t}\right)+p^i_{j,r}\left(R^i_{j,t}-HR^i_{j,t}\right)-R^i_{j,t+1}=0\quad\forall i>2,\tag{A25}$$

$$\rho^t L'_{\gamma^1_{c,t}} = \sum_i F^i_{x,t}\kappa^i_f\exp\left(-\sum_{ij}\beta_f F^i_{j,t-1}\right)-F^1_{c,t}=0,\tag{A26}$$

$$\rho^t L'_{\rho\gamma^2_{j,t+1}} = 0.5g^1_{c,f}\left(F^1_{c,t}-HF^1_{c,t}\right)-F^2_{j,t+1}=0,\tag{A27}$$

$$\rho^t L'_{\rho\gamma^i_{j,t+1}} = g^{i-1}_{j,f}\left(F^{i-1}_{j,t}-HF^{i-1}_{j,t}\right)+p^i_{j,f}\left(F^i_{j,t}-HF^i_{j,t}\right)-F^i_{j,t+1}=0\quad\forall i>2.\tag{A28}$$

APPENDIX B

TABLE B1 Harvest variation in OPTIMAL scenario in steady state with all harvest benefits included

Data Compared to Reference Set of Parameters in Table 1	Fallow Deer	Roe Deer
Reference set of parameters	633	185
$\mu = 0$	633	206–891
$\mu = 0$, no time lag for interspecific competition	633	354
$\mu = 0.000228$	638	43–116
$\mu = 0.000228$, no time lag for interspecific competition	633	66
Discount rate 9%	633	146–317
Discount rate 9%, no time lag for interspecific competition	633	191