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Economically optimal management of two deer species competing for food

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ABSTRACT

This paper presents a bioeconomic model to analyze the role of interspecies competition between roe deer (*Capreolus capreolus*) and fallow deer (*Dama dama*) and the implications of the competition on optimal harvesting strategies. Analytical solutions derived from the model suggest that the degree of inter-specie competition is an important factor in the landowner's decision to maintain a given population of both species, as it affects the net marginal benefit from managing the two species. Our numerical results suggest that the effect of inter-species competition on total net economic benefit is small compared to the impact on roe deer population density. Inclusion of trophy values implies reduced harvest of young males, but also reduced harvest of females. Our model also shows that a pulse harvesting regime for the dominant species is economically optimal.

Keywords: stage structured modelling, optimal management, specie competition, bioeconomic

1. Introduction

Game species, especially large grazers are a renewable natural resource of great importance. They provide a wide range of benefits to society including: meat, recreational hunting, aesthetic values, employment, health and nutrition, maintenance of ecosystem balance, and as symbols of religious and other cultural practices (Brandner et al., 1990; McInnes et al., 1992; Andrén and Angelstam, 1993; Bradshaw, 1996; Angelstam et al., 2000; Chardonnet et al., 2002). On the other hand, there are costs associated with wildlife, such as damages to agricultural crops and forestry, dispersal of invasive pests and vehicle collisions (Olausen and Skonhøft, 2011; Chardonnet et al., 2002). The multiple impacts of wildlife on people and ecosystems imply that there is a need for management strategies which take into account the trade-off between the positive and negative impacts of the species.

Ecologists have shown that there exists strong interdependence between different wildlife species (Caughley and Sinclair 1994). Such interactions include, e.g., competition between individuals of different species which utilize common resources that are in short supply, i.e. exploitation competition; or where members of a particular species through their behavior prevent members of the other species from accessing a resource, even if the resource is not in short supply, i.e. interference competition (Birch 1957). Thus, there can potentially be significant economic externalities among wildlife species in a given habitat.

The existence of interdependences among the species needs to be taken into account if the joint system is to be managed to the best of society. However, there is still limited knowledge about the implications of such inter-species interactions for the economically optimal management of wildlife. Most existing studies on wildlife management are based on single species models (see, e.g., Skonhøft et al., 2013; Olausen and Myrsetrud, 2012; Olausen and Skonhøft, 2011; Xu and Boyce, 2010; Collier and Kremenetz, 2007). Bioeconomic models that account for species interdependencies are mostly found in the fishery economics literature (see, e.g., Conrad and Adu-Asamoah, 1986; Flaaten, 1988, 1991; Hannesson, 1983; Chaudhuri, 1986; Chaudhuri, 1987; Finnoff and Tschirhart, 2003). For instance, Conrad and Adu-Asamoah (1986) assess the role of competition among tuna species for the maximum sustainable yield, and find that effectively, it implies a reducing carrying capacity of the species. In terms of wildlife there are a couple of applications, including Tahvonen et al. (2014), Virtala (1992, 1996), Horan et al. (2008) and Moxnes et al. (2001). The methodological approach of these multi-species bioeconomic models varies. Whereas some are based on biomass models (Virtala 1992, 1996; Moxnes et al. 2001; Horan et al., 2008), others apply age-structured modelling (Tahvonen et al, 2014; Finnoff and Tschirhart, 2003). The main criticism against biomass models is that they are unable to account for the role of life history and age structure in optimal management of species. For instance, Virtala (1992, 1996) and Moxnes et al. (2001) use the biomass approach to analyze the interrelationship between a reindeer population and its main winter food, lichen, and the associated implications for optimal harvest and steady-state populations of lichen and reindeer. However, these studies were based on biomass models, thereby ignoring the potential role of more complex life histories including age and sex structure on the harvest and steady state population levels. Tahvonen et al. (2014) analyzed the same issue using an age-structured model and show that life history and age structure can have a considerable impact on the results. Notwithstanding this methodological difference, available

bio-economic multi-species models unequivocally assert that species interdependencies are key factors to consider in wildlife management.

Given this background, this study seeks to extend the literature on the role of species interdependencies in wildlife management, using the roe-fallow deer relationship as a case study. It has been shown that the presence of fallow deer (*Dama dama*) exerts negative effects on the foraging behavior of roe deer (*Capreolus capreolus*), but not vice-versa (Focardi et al., 2006), thus making the fallow deer superior relative to roe deer in terms of competition for food and other resources. This suggests that inter-species competition can be a key factor in the joint management of the two species. Key questions of interest are, e.g.: how large is the impact of inter-species competition on the joint economic value of roe and fallow deer? What are the implications of species competition on optimal harvesting strategies and on populations of the two species? To our best knowledge, these questions have not been addressed in the earlier literature.

The aim of this paper is to examine the impact of interspecies dependence of roe and fallow deer on total net present value of jointly managed species system. The associated impacts on harvesting strategies and densities of the two species are identified. The two species provide different benefits to society, such as meat, recreational hunting and trophies. We examine how the role of species interdependences is affected by the choice of benefits to include in the analysis. To these ends, we develop a numerical stage-structured bio-economic model on the two species. We use data from an estate in south-western Sweden, where multiple species are actively co-managed on a commercial basis.

We contribute to the literature through the development of a biologically relevant empirical stage-structured, bio-economic model of two ungulate species competing for food. This model is used to demonstrate the analytical and numerical consequences of competition among roe and fallow deer and their implications for joint management of the two-species.

Our findings suggest that the effect of interspecies competition on total net economic value of the two species depends on biological and economic factors, such as the relative economic value of the two species involved in combination with the direction of the competition effects. We find that the impact of interspecies competition on total net benefits is small when competition is unilateral and borne by the economically less valuable species, i.e. the roe deer. On the other hand, the effect of competition on population densities is significant. Further, our study reveals that given a delayed impact of competition on recruitment, the optimal harvesting strategy includes pulse harvesting.

The rest of the paper is structured as follows. In section 2, we present the ecological interrelationship between the roe and fallow deer. Section 3 describes the joint population model used in the study. In section 4 we present our bioeconomic model and discuss the analytical solutions proceeding from the model. A description of the data used in the simulations is presented in section 5. Results from the model are presented in section 6. Section 7 presents a discussion of the results and concludes the study.

2. Roe and fallow deer interactions

By their behavioral nature, the roe deer is a relatively solitary species, while the fallow deer is described as sociable with relatively large tolerance for habitats with high population densities (Cederholm, 2012; Calstrom and Nyman, 2005; Kjellander, 2000). In addition, the fallow deer is 3-4 times larger than the roe

deer. Therefore, in a given habitat, the fallow deer often displaces the roe deer from feeding sites and from areas with high fallow population density (Ferretti et al., 2008, 2011). Using a field experiment, Ferretti et al. (2008) observe that the presence of the fallow deer displaces roe deer to distant locations¹ in 83% of cases. Their results further show that 94% of such displacement events occurred while the roe deer was feeding which in most cases results in roe deer being interrupted and ultimately even abandoning the feeding site. Even when the fallow deer showed no sign of aggression towards the roe, the latter moved away in 72% of the cases. This suggests that a high fallow deer density will lead to reduced access to food for roe deer, which will ultimately have negative impact on roe deer recruitment and hence population growth.

The roe deer is known to be highly selective in feed type, preferring herbs and leaves, whereas the fallow is considered as a generalist herbivore with a broad spectrum of feed types, such as grass, leaves and bark (Alm et. al., 2001; Chapman and Chapman, 1975). In a joint habitat, the fallow deer tend to reduce the high quality food resource available to levels which are insufficient to sustain a positive growth rate in the local roe deer population.

Based on the above, it can be concluded that there is a negative and largely unilateral effect of fallow deer on roe deer, whereas the opposite impact of the roe deer on the fallow deer is insignificant. Adding to the inter-species competition, there is of course also intra-species competition within each deer populations, given the competition for food and other resources.

3. Roe and fallow deer joint population model

To account for the interdependences between the two species in an optimal co-management model, we develop a stage-structured population model² where a representative land owner seeks to maximize the net benefits from the management of the species on his/her land. We classify the life cycle of both species into four (4) main stages: fawns, yearlings, adult and senescence based on species specific life history data. The importance of classifying the populations into life stages (age classes) is among other things, to account for the inherent nonlinearities largely attributed to biological and life cycle characteristics which vary with age. Thus, in our stage classification, the roe population at time t is structured as follows: fawns ($yr < 1$), yearling ($1 \leq yr \leq 2$), adult ($2 < yr \leq 7$) and senescence ($yr > 7$); whereas the fallow deer population is structured as: fawns ($yr < 1$), yearling ($1 \leq yr \leq 2$), adult ($2 < yr \leq 11$) and senescence ($yr > 11$). Notice that the stage size for the two species differs, which is mainly due to the biological differences among them i.e., life span, physiological growth rate, reproductive maturation, etc. Further, within stages 2-4, the population is further classified into males and females.

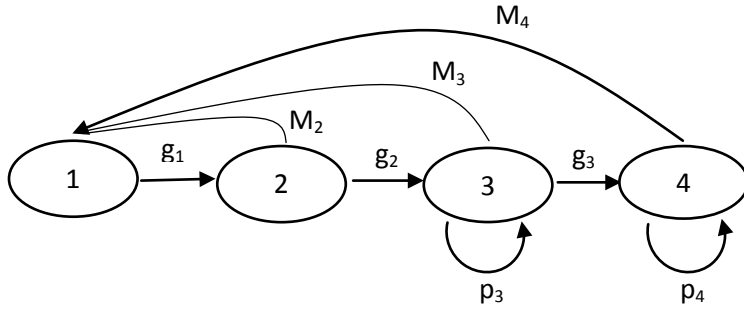
Using a 4-staged-structured projection matrix (Fig. 1), we show the population transition across stages with individuals in stages 2-4 contributing towards recruitment in stage 1 via reproduction (M). Since the

¹ Exceeding 50 meters

² Studies on stage (age) structured modelling has its roots from biology and largely inspired by the works of Leslie (1945) and Lefkovich (1965). Leslie (1945) designed a matrix² based on the mortality and fecundity rates to project population distribution of species based on initial distribution of population in various age groups (Bruce and Shernock, 2002). This laid the foundation for age-structured modelling. The Lefkovich matrix however, though similar to the Leslie matrix, classifies populations into stage classes instead of age groups. This is more useful especially in the case of a species with long life span and inadequate data on their population demographics. Thus, instead of being based on age-specific survival and fecundity rates, the Lefkovich matrix is based on stage specific survival and fecundity rates. This implies that at each time period, individuals can either move to the next stage or remain in the same stage since the stage size is incongruous with time (i.e. stage sizes do not vary directly with time/years)

duration (size) of stages 3 and 4 is incongruous with time moving from year t to $t+1$, some of the surviving individuals (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.

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



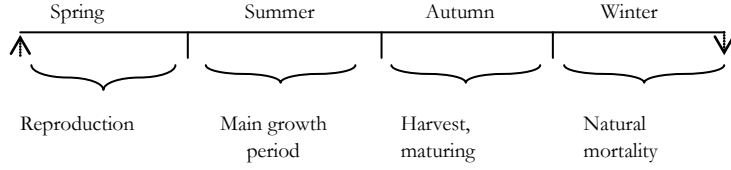
Following the approach of Crouse et al., (1987) and Chaloupka (2002) we estimate these transition probabilities based on the stage specific survival rates and stage duration. Without loss of generality, we assume constant survival and growth rates within each stage. The procedure for estimating these probabilities have been outlined in appendix A.

Population equations

In our two species population model we define R and F for roe and fallow deer, respectively. Each of these species is further classified into three types: c , x and y representing calves (recruits), females and males respectively. This (gender) classification is represented by the index j , where $j = c, x, y$. Also, as indicated earlier, the species are grouped into (4) stages represented by i where $i = 1, 2, 3, 4$. Therefore, the number of roe and fallow deer of type j in stage i at time t can be specified as $R_{j,t}^i$ and $F_{j,t}^i$ respectively.

Further, population size is measured in spring just before calving, while the hunting season (harvest) takes place in autumn (September-October) before mortality, which is assumed to occur in the winter, as mortality in the summer and fall is generally negligible (Olaussen and Skonhott, 2011; Naevdal et al. ,2012; Skonhott et. al, 2013), see Fig. 2. At time t , the number of the roe and fallow deer harvested is given as $HR_{j,t}^i$ and $HF_{j,t}^i$ respectively. To guarantee a sustainable harvest, we impose the restriction that harvests are strictly less than the population, i.e. $0 \leq HR_{j,t}^i < \bar{R}_{j,t}^i$ and $0 \leq HF_{j,t}^i < \bar{F}_{j,t}^i$.

Fig 2. Population cycle



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, which in turn affects its fecundity, and hence the number of offspring. We model recruitment of both species within the framework of the Ricker (1954) type recruitment functions, which takes into account the impact on the number of births from population density. The effect of population density on reproduction varies among the two species. We therefore extend the Ricker recruitment function to incorporate the impact of fallow deer density on roe deer reproduction. The respective recruitment functions are shown in equations (1) and (5).

Thus, recruitment of roe deer at a given time t , is determined by

$$R_{c,t}^1 = \sum_{i>1} R_{x,t}^i \kappa_r^i e^{-\sum_{ij} (\beta_r R_{j,t-1}^i + \mu F_{j,t-1}^i)} \quad (1)$$

where κ_r^i is the fecundity rate (number of offspring per female) of female roe deer in stage i in the absence of inter and intra-species competition; $R_{x,t}^i$ is the number of females in stage i ; $R_{c,t}^1$ is the number of recruits, while β_r and μ measures the degree of intra and inter-species competition respectively. According

to equation (1), fecundity of the roe deer is affected by the factor, $e^{-\sum_{ij} (\beta_r R_{j,t-1}^i + \mu F_{j,t-1}^i)}$, which implies that reproduction of roe deer decreases with population density of both species³. This effect is largely determined by the coefficients, β_r , which denote the degree of resource (food) competition within roe deer population (intra-species competition), and μ which captures the degree of resource competition between the two species (inter-species competition). In other words, the reproduction of the roe deer is not only affected by its own-population density but also by the presence of fallow deer in the same area. This is because, by the assumption of density dependent competition, an increase in fallow deer density will ultimately have negative effects on roe deer fecundity, and consequently, on recruitment. An important point worth mentioning is that the effect of competition (both inter and intra-species) on the recruitment is delayed, due to long gestation periods and seasonal dispersal patterns, rather than instantaneous, thereby accounting for the lag-effect terms ($R_{j,t-1}^i$ and $F_{j,t-1}^i$). Thus, a reduction in population size, through increased harvest in the autumn, implies increased access to food in the winter and spring for the remaining population, thereby making them healthier and thereby increasing reproduction, which subsequently occurs

³ Where $\beta_r, \mu > 0$

in early summer. Thus, a change in population size affects roe and fallow deer reproduction about one year later, which motivates a one year time lag in the model.

Further, even though the recruitment function is largely determined by female population size, see equation (1), we impose a harvest constraint, which ensures that a sufficient size of the male population is available to guarantee sustainable reproduction, see equations (A2)-(A9) in the Appendix.

The yearling population at time $t+1$ is given by the number of fawns that survive after harvest until the next period and expressed as:

$$R_{j,t+1}^2 = 0.5g_{c,r}^1 (R_{c,t}^1 - HR_{c,t}^1), \quad \forall j = x, y \quad (2)$$

where the same sex ratio (0.5) is assumed for fawns when they enter into the yearling stages, with $g_{c,r}^1$ denoting the probability of roe fawns surviving and growing into the yearling stage. Further, the adult (female/male) population abundance is expressed as:

$$R_{j,t+1}^3 = g_{j,r}^2 (R_{j,t}^2 - HR_{x,t}^2) + p_{j,r}^3 (R_{j,t}^3 - HR_{j,t}^3), \quad \forall j = x, y \quad (3)$$

where $g_{j,r}^2$ and $p_{j,r}^3$ are the probabilities of a (female/male) roe deer in stage 2 surviving and moving to the next stage, and the probability of the (female/male) roe deer population in stage 3 surviving and remaining in the same stage, respectively.

Finally, the abundance equation for roe (female/male) senescence populations consist of 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).

$$R_{j,t+1}^4 = g_{j,r}^3 (R_{j,t}^3 - HR_{j,t}^3) + p_{j,r}^4 (R_{j,t}^4 - HR_{j,t}^4), \quad \forall j = x, y \quad (4)$$

The fallow deer, on the other hand is assumed to be affected only by intra-species competition effects on reproduction (β_f) and no inter-species effects, since they are not affected by the presence of the roe. The effect of inter-species competition on fallow deer recruitment is thus assumed to be zero. Thus, the recruitment function for fallow deer is expressed as:

$$F_{c,t}^1 = \sum_{i>1} F_{x,t}^i \kappa_f^i e^{-\sum_j (\beta_f F_{j,t-1}^j)} \quad (5)$$

where κ_f^i is the fecundity rate (number of offspring per female) of female fallow deer in stage i . The corresponding fallow deer abundance equations for equations (2-4) are represented by equations (6-8), where $g_{j,f}^i$ and $p_{j,f}^i$ are the corresponding probabilities.

$$F_{j,t+1}^2 = 0.5g_{c,f}^1 (F_{c,t}^1 - HF_{c,t}^1), \quad \forall j = x, y \quad (6)$$

$$F_{j,t+1}^3 = g_{j,f}^2 (F_{j,t}^2 - HF_{j,t}^2) + p_{j,f}^3 (F_{j,t}^3 - HF_{j,t}^3), \quad \forall j = x, y \quad (7)$$

$$F_{j,t+1}^4 = g_{j,f}^3 (F_{j,t}^3 - HF_{j,t}^3) + p_{j,f}^4 (F_{j,t}^4 - HF_{j,t}^4), \quad \forall j = x, y \quad (8)$$

4. Bioeconomic model

Given these population dynamics, a representative landowner, assumed to be the manager of the deer habitat, aims at maximizing the net present value of the joint management of the species (roe and fallow deer). In our model three main benefits are considered: meat, recreational and trophy benefits. Also, we take into account the cost of supplemental winter feeding, borne by the manager. Thus, the assumed goal of the landowner is to manage the two populations in such a manner that it will yield the maximum net present value of the stream of benefits and costs over time.

In the analytical section, we first present the model taking into account meat and recreational values, then show how the model changes when trophy values are included. The first order conditions are only presented with meat and recreation benefits, but still provide the necessary understanding of the model, as the inclusion of trophy values does not alter the optimal conditions significantly.

Net meat and recreational benefits only

In this section, we examine the simple case where the landowner maximizes the sum of meat and recreational benefits that are derived from hunting less the cost of feeding the animals during the winter season. The meat values and recreational values for both species are expressed as

$$\left[\hat{q}_r \left(\sum_{j=c}^{i=1} w_j^i HR_{j,t}^i \right) + \hat{q}_f \left(\sum_{j=c}^{i=1} \psi_j^i HF_{j,t}^i \right) \right] \text{ and } m \left(\sum_{j=c}^{i=1} HR_{j,t}^i + \sum_{j=c}^{i=1} HF_{j,t}^i \right) \text{ respectively. Where the}$$

terms \hat{q}_r and \hat{q}_f represent the meat price per kg of roe and fallow respectively, assumed to be fixed over time and independent of the level of harvest; while w_j^i and ψ_j^i denote the stage specific slaughter weights of roe and fallow deer respectively. The recreational value per animal shot (m) is assumed to be equal across species, stages and time. Therefore total meat and recreational values associated with harvesting of both species can be represented as

$$V_t = \sum_{j=c}^{i=1} q_r^i HR_{j,t}^i + \sum_{j=c}^{i=1} q_f^i HF_{j,t}^i \quad (9)$$

where $q_r^i = (\hat{q}_r w_j^i + m)$ and $q_f^i = (\hat{q}_f \psi_j^i + m)$ refers to the net economic value per animal for roe and fallow deer, respectively, in stage i . At the same time, the landowner incurs costs by providing supplemental feed⁴ during the winter season when natural food resources become scarce. In our model, the fallow deer is considered to be the only species artificially fed during the winter season. There are three reasons for this: first, grass silage, which is the most common winter food, is not preferred by roe deer because it has

⁴ This is often referred to as artificial feeding mainly due to the fact that food (consisting of grass silage, oats etc.) are provided at artificially created feeding sites, at regular intervals.

generally too low quality in relation to its digestive system. Second, during harsh winters, fallow deer spend almost all their time in big groups around the feeding stations, and the considerably smaller and solitary roe deer have very little access to the food. Third, in south-west Sweden, where these results are applied, fallow deer need artificial feeding to survive most winters. The cost of winter feeding can be specified as:

$$C_t = \sum_{ij} d_j^i (F_{j,t}^i - HF_{j,t}^i) \quad (10)$$

where d_j^i is the cost of feed per fallow deer of type j in stage i .

The decision problem that the manager faces is to maximize the discounted present value of future streams of net benefits (11)

$$\underset{HR_{j,t}^i, HF_{j,t}^i}{Max} \sum_{t=0}^T \rho^t (V_t - C_t) \quad (11)$$

subject to equations the population equations (1-8), and where $\rho = 1/(1+\delta)$ refers to the discount factor which measures the rate of time preference, with $\delta \geq 0$ as the annual rate of discount. The above-mentioned harvest restrictions are also imposed.

Trophy values included

In addition to meat and recreational values, trophy hunting values also constitute an important aspect of hunting. Since trophy hunting is largely associated with shooting mature males, we specify the total trophy values as a linear function of harvest as shown in equation (12), where z_r^i and z_f^i refers to the trophy prices for roe and fallow deer respectively. We assume that trophy hunting occurs only for male roe and fallow deer in the final stages, since matured males produce high quality trophies that most hunters prefer.

$$B_t = z_r^i HR_{y,t}^i + z_f^i HF_{y,t}^i, \forall i = 4 \quad (12)$$

Given the inclusion of trophy values, the associated optimization problem facing the landowner is to maximize

$$\underset{HR_{j,t}^i, HF_{j,t}^i}{Max} \sum_{t=0}^T \rho^t (V_t + B_t - C_t) \quad (13)$$

subject to the constraints as shown in the previous section.

Optimality Conditions

As indicated earlier, only the analytical solutions for the meat and recreational values optimization case are presented and discussed. For brevity, we present in this section the resultant (selected) optimal harvest and stock conditions while the remainder are shown in the appendix (B). This is largely because the first order

conditions (FOC) for the different stages are quite similar (qualitatively) and hence carry similar interpretations. Therefore we present FOCs for the adult cohorts as shown in equations (14)- (18).

$$\begin{aligned} \rho^{-t} L'_{HR_{j,t}^3} &= q_r^3 - \rho \lambda_{j,t+1}^3 p_{j,r}^3 - \rho \lambda_{j,t+1}^4 g_{j,r}^3 \leq 0; \quad 0 \leq HR_{j,t}^3 < \bar{R}_{j,t}^3 \\ \rho^{-t} L'_{HR_{j,t}^3} HR_{j,t}^3 &= 0; \quad t = 0, 1, \dots; j = x, y \end{aligned} \quad (14)$$

$$\begin{aligned} \rho^{-t} L'_{HF_{j,t}^3} &= q_f^3 + d_j^3 - \rho \gamma_{j,t+1}^3 p_{j,f}^3 - \rho \gamma_{j,t+1}^4 g_{j,f}^3 \leq 0; \quad 0 \leq HF_{j,t}^3 < \bar{F}_{j,t}^3 \\ \rho^{-t} L'_{HF_{j,t}^3} HF_{j,t}^3 &= 0; \quad t = 0, 1, \dots; j = x, y; \end{aligned} \quad (15)$$

Equation 14 and 15 represents the optimal harvest conditions for adult (male and female) roe and fallow deer populations respectively. Equation 14 states that adult (male/female) roe deer can be harvested up to the point where the marginal harvest benefit (q_r^3) is at most equal to the marginal user cost $\rho(\lambda_{j,t+1}^3 p_{j,r}^3 + \lambda_{j,t+1}^4 g_{j,r}^3)$ in terms of the reduced adult and senescence populations evaluated at the shadow prices of both populations while taking discounting into account. When this condition holds with equality harvest is positive, while holding with inequality imply zero harvest since the marginal benefit of harvesting will be less than the associated marginal user cost. The optimal harvesting condition for the adult fallow deer population (15) is analogous to the optimal harvest conditions for the roe deer (14) and hence carries similar interpretations except for the inclusion of marginal cost of winter feeding (d_j^3). Thus, an adult fallow deer can be harvested up to the point where by the incremental benefits from one more harvest is at most equal to the marginal user cost $(\rho \gamma_{j,t+1}^3 p_{j,f}^3 + \rho \gamma_{j,t+1}^4 g_{j,f}^3 - d_j^3)$ in terms of the reduced adult and senescence populations evaluated at their shadow prices while taking discounting and cost of winter feeding into account.

The corresponding optimal population equations are also examined as follows (16-18):

$$\begin{aligned} \rho^{-t} L'_{R_{x,t}^3} &= \lambda_{c,t}^1 \kappa_r^3 e^{-\sum_y (\beta_r R_{j,t}^i + \mu F_{j,t}^i)} - \rho \lambda_{c,t+1}^1 \beta_r \sum_{i>1} R_{x,t+1}^i \kappa_r^i e^{-\sum_y (\beta_r R_{j,t}^i + \mu F_{j,t}^i)} + \rho \lambda_{x,t+1}^3 p_{x,r}^3 + \rho \lambda_{x,t+1}^4 g_{x,r}^3 - \lambda_{x,t}^3 \leq 0 \\ \rho^{-t} L'_{R_{x,t}^3} R_{x,t}^3 &= 0; \quad R_{x,t}^3 \geq 0; \quad t = 0, 1, 2, \dots; j = c, x, y \end{aligned} \quad (16)$$

Equation (16) is the optimal stock condition for adult female roe deer. The first term on the right-hand side (r.h.s) of equation (16) is the marginal increase in roe deer recruitment resulting from holding an additional unit of female adult roe deer. It measures the direct positive contribution of holding one more female adult roe deer on roe deer recruitment. Meanwhile the second term (r.h.s) captures the indirect, negative effect of holding an additional adult female roe deer on roe deer recruitment via increasing intra-species competition. The third and fourth terms capture, respectively, the expected contribution of an additional female adult roe deer to female adult roe deer populations in stages 3 and 4. Finally, the fifth term is the shadow value of holding an additional female adult roe deer in time t until the following year ($t+1$). Rewriting equation (16) and holding with equality, we obtain (17) which states that 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 growth of the adult and senescent female stages, evaluated at their respective discounted shadow prices:

$$\lambda_{x,t}^3 = \lambda_{c,t}^1 \kappa_r^3 e^{-\sum_y (\beta_r R_{j,t-1}^i + \mu F_{j,t-1}^i)} - \rho \lambda_{c,t+1}^1 \beta_r \sum_{i>1} R_{x,t+1}^i \kappa_r^i e^{-\sum_y (\beta_r R_{j,t}^i + \mu F_{j,t}^i)} + \rho \lambda_{x,t+1}^3 p_{x,r}^3 + \rho \lambda_{x,t+1}^4 g_{x,r}^3. \quad (17)$$

Examining equation (17) reveals that it is only worthwhile to keep the animal if it's the net value of its contributions to recruitment and population in different stages is positive. The attainment of this is largely dependent on the level of intra- and inter-species competition as evidenced in the first and second terms. To see this, assume a steady state where all the variables are constant across time, i.e. all time subscripts are cancelled. Now we can see that an increased intra-species competition (β_r) will reduce net contribution to recruitment, hence reducing the overall marginal benefit of holding an additional stock until the following year and vice versa. In the same way, an increase in inter-species competition from fallow deer will also reduce the net contribution to recruitment in roe deer and thereby reducing the marginal benefit of holding an additional adult female roe deer.

Compared to equation (17), the corresponding condition for fallow deer, equation (18), entails the effect on roe deer population via the inter-species competition. This additional term captures the negative effect of the presence of fallow deer on roe deer recruitment.

$$\rho^{-1} L_{F_{x,t}^3} = -\rho \lambda_{c,t+1}^1 \mu \sum_{i>1} R_{x,t+1}^i \kappa_r^i e^{-\sum_y (\beta_r R_{j,t}^i + \mu F_{j,t}^i)} + \gamma_{c,t}^1 \kappa_f^3 e^{-\sum_y (\beta_f F_{j,t}^i)} - \rho \gamma_{c,t+1}^1 \beta_f \sum_{i>1} F_{x,t+1}^i \kappa_f^i e^{-\sum_y (\beta_f F_{j,t}^i)} - \gamma_{x,t}^3 - d_x^3 + \rho \gamma_{x,t+1}^3 p_{x,f}^3 + \rho \gamma_{x,t+1}^4 g_{x,f}^3 \leq 0 \quad (18)$$

$$\rho^{-1} L_{F_{x,t}^3} F_{x,t}^3 = 0; F_{x,t}^3 \geq 0 \quad ; t = 0, 1, 2, \dots; \quad j = c, x, y$$

For example, the stock condition (18) states that the number of adult (female) fallow deer should be maintained such that their shadow value ($\gamma_{x,t}^3$) is at least equal to the sum of the value of its net

contribution to fallow deer recruitment $\left(\gamma_{c,t}^1 \kappa_f^3 e^{-\sum_y (\beta_f F_{j,t}^i)} - \rho \gamma_{c,t+1}^1 \beta_f \sum_{i>1} F_{x,t+1}^i \kappa_f^i e^{-\sum_y (\beta_f F_{j,t}^i)} \right)$ and the value of its

contribution to the growth of the adult and senescent stage $\left(\rho \gamma_{x,t+1}^3 p_{x,f}^3 + \rho \gamma_{x,t+1}^4 g_{x,f}^3 \right)$ less the value of its

indirect effect on roe deer recruitment $\left(\rho \lambda_{c,t+1}^1 \mu \sum_{i>1} R_{x,t+1}^i \kappa_r^i e^{-\sum_y (\beta_r R_{j,t}^i + \mu F_{j,t}^i)} \right)$ and cost of winter feeding (d_x^3).

An increase in inter-species competition (μ) also reduces the marginal benefit of keeping an additional adult female fallow deer.

Due to the combination of time dynamics and nonlinearities in the model, it is difficult to obtain in-depth analytical solutions. Thus, as in many earlier studies, insights from the model are better explored through the numerical solutions (cf. Olaussen and Skonhøft, 2011; Tahvonen et al. 2014).

5. Case study and Data

Data and Parameter Specifications

The model is illustrated numerically using empirical data, mainly obtained from the Koberg estate in south-west Sweden. The Koberg estate is a private property, covering approximately 90 km², which provides commercial hunting of wildlife, and where several wildlife species are actively managed in their natural habitat. The dominating wildlife species in the estate are fallow deer and wild boar while small populations of roe deer and moose also occur together with small numbers of red deer and mouflon sheep. Game harvest in the estate is managed by the landowner selling hunting permits for certain occasions or longer periods, to individuals and groups to hunt in restricted areas of the estate during the hunting season. The choice of the Koberg estate⁵ as a study area is motivated by the fact that it provides an example of active commercial co-management of several sympatric game species whereby the landowner faces the problem of maximizing the net returns from the species.

Age classes are classified into four stages, except for male fallow deer where our empirical data suggest that the average male fallow deer lives a maximum of 11 years, implying that they never survive to stage four⁶. Biological (fecundity and survival) data on fallow deer were obtained from a field study carried out at the Koberg estate during 2006 – 2014 (Kjellander, 2014). On the other hand, roe deer fecundity and survival data were based on estimates from the 1.2 km² Bogesund research area, located in east-central Sweden (Kjellander, 2000). Stage-specific slaughter weights are taken as the closest proxy of the edible meat weight from the two deer species. Slaughter weight was assumed to be 70% of dressed weight, obtained from the examination of 1183 and 2712 harvested roe and fallow deer (Cederlund et al., 1991; Andersson et al., 1996). Using data on the survival rate of both species, across the various stages, transition probabilities (g, p) were calculated using equations (A1)–(A2) in appendix A, based on the approach of Crouse et al. (1987) and Chaloupka (2002). All parameter values used in the model are shown in Table 1.

Further, we assume constant inter and intra-species competition (β and μ) across stages and time but differing between species. We calibrate these parameters using existing data from the Koberg and Bogesund to a steady state bioeconomic equilibrium as described in the following. In calibrating intra-species competition effects for each species, we first develop two separate single-species stage structured population models. By using data from the Bogesund research area, where the roe deer has an unharvested carrying capacity of 35 animals/km², we calibrate the intra-species competition (β_r) to be consistent with this being the unharvested steady state. In the case of the fallow deer, a similar model was developed. This was done using empirical data on fallow deer in the Koberg area, showing a harvested carrying capacity equal to 45 fallow deer/km². We calibrate the intra-species competition (β_f) such that it will be consistent with the observed carrying capacity in an optimally harvested steady state. Given the intra-species competition parameters calibrated from the single species models, we proceed to calibrate the inter-species

⁵ The estate is located in the boreonemoral zone consisting of deciduous and mixed coniferous forest which covers 80% of the area, while 15% is agricultural lands (Kjellander et al., 2012; Cederholm, 2012).

⁶ This implies that equation (12) becomes $B_t = z_r^4 HR_{y,t}^4 + z_f^3 HF_{y,t}^3$

competition parameter using the population model described in section 3. Based on empirical data on a six (6) year population and harvest levels of roe and fallow deer from the Koberg estate, we solve the model over a six year period using these harvest and stock data as given, to calibrate the level of inter-species competition (μ) that is consistent with these observations. The results suggest intra-species competition effects among roe and fallow deer to be 0.0004227 and 0.0003445, respectively, thus indicating that the intra-species competition effect among roe deer is slightly higher than among fallow deer. This is related to the fact that fallow deer, as said above, are adapted to high local densities, while the more selectively feeding roe deer has a lower carrying capacity⁷ (Cederholm, 2012; Calström and Nyman, 2005). The inter-species competition effect was calibrated to be 0.00007. This reflects the fact that inter-species competition is lower than intra-species competition, which is normally the case when two species have only partially overlapping diets and habitats, as is relevant here (Dutch, 2011).

We assume constant economic parameters for all stages and over time, which is motivated by our choice to model a small geographical area, where the manager can be assumed to be a price-taker on both in- and output markets. The price, \hat{q}_r and \hat{q}_f , of harvested meat is set at SEK 65 per kg for both roe and fallow deer which corresponds to the price that hunters pay to the Koberg estate when they choose to keep the meat after participating in a hunt. Recreational hunting is an important source of income from the hunting activity in the study area. Data from the estate show that their net revenue⁸ from arranged hunts is about SEK 3,167 per animal shot. 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). 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 oldest male age classes, since the trophies from older males generally become valuable to hunters by their large size and high quality. The baseline scenario also assumes a 3% discount rate as recommended in cost-benefit analysis of public projects (see: Boardman et al, 2011).

We begin the numerical illustration of the model using initial total roe and fallow deer population sizes set at the steady-state level in the economic optimum with the two species. Using the baseline data, we solve the dynamic model above to derive optimal harvest over a 50 year period using the CONOPT solver in the GAMS software. Given the presence of a final time period in the model; greater emphasis is placed on the results and analysis of the short and medium term.

⁷ The intra-species competition parameter is positively related to carrying capacity.

⁸ This is corresponds to the amount paid for hunting (per animal) less the cost of organized hunter (per animal).

Table 1. Baseline ecological and economic parameter values

Parameter	Stages(i)				Source	
	1	2	3	4		
κ_r^i	Fecundity rate for (female) roe deer	0	1.23	1.83	1.58	<i>Kjellander (2000)</i>
κ_f^i	Fecundity rate for (female) fallow deer	0	0.89	0.96	0.76	<i>Kjellander (2014)</i>
$g_{i,r}^i$	Probability of (female) roe surviving and moving from stage i to $i+1$	0.72	0.89	0.22	0.74	<i>Authors' calculation</i>
$g_{i,r}^i$	Probability of a (male) roe surviving and moving from stage i to $i+1$	0.85	0.89	0.20	0.72	<i>Authors' calculation</i>
$g_{i,f}^i$	Probability of a (female) fallow surviving and moving from stage i to $i+1$	0.857	0.963	0.095	0.963	<i>Authors' calculation</i>
$g_{i,f}^i$	Probability of a (male) fallow surviving and moving from stage i to $i+1$	0.759	1.00	0.015	*	<i>Authors' calculation</i>
$p_{i,r}^i$	Probability of a (female) roe surviving and staying in stage i	0	0	0.72	0.69	<i>Authors' calculation</i>
$p_{i,r}^i$	Probability of a (male) roe surviving and staying in stage i	0	0	0.73	0.68	<i>Authors' calculation</i>
$p_{i,f}^i$	Probability of a (female) fallow surviving and staying in stage i	0	0	0.868	0.868	<i>Authors' calculation</i>
$p_{i,f}^i$	Probability of a (male) fallow surviving and staying in stage i	0	0	0.711	*	<i>Authors' calculation</i>
w_x^i	Slaughter weight of (female) roe deer (kg/animal)	7.6	7.6	12.1	12.1	<i>Kjellander (2000)</i>
w_y^i	Slaughter weight of (male) roe deer (kg/animal)	7.6	7.6	12.1	12.1	<i>Kjellander (2000)</i>
ψ_x^i	Slaughter weight of (female) fallow deer (kg/animal)	13.2	21.6	26	26	<i>Kjellander (2000)</i>
ψ_y^i	Slaughter weight of (male) fallow deer (kg/animal)	13.9	28.5	49.7	*	<i>Kjellander (2000)</i>
$R_{x,t}^i$	Initial roe (female) population ($t=0$) in stage i	623 ⁹	215	842	0	Calibrated
$R_{y,t}^i$	Initial roe (male) population ($t=0$) in stage i		257	0	0	Calibrated
$F_{x,t}^i$	Initial fallow (female) population ($t=0$) in stage i		551	1689	0	Calibrated
$F_{y,t}^i$	Initial fallow (male) population ($t=0$) in stage i	1123	427	0	*	Calibrated
β_r	Intra-species competition (roe)		0.0004227			Calibrated
β_f	Intra-species competition (fallow)		0.0003445			Calibrated
μ	Inter-species competition		0.00007389			Calibrated
d_x^i	Winter feeding cost (female) fallow deer (SEK)	49.4	71.6	82.3	82.3	Case study area
d_y^i	Winter feeding cost (male) fallow deer (SEK)	51.6	88.2	134.7	*	Case study area
z_r^i	Trophy values/price for roe deer (SEK)	*	*	*	6,000	Case study area
z_f^i	Trophy values/price for fallow deer (SEK)	*	*	18,580	*	Case study area
\hat{q}_r	Meat price (SEK/per kg)-roe deer		65			Case study area
\hat{q}_f	Meat price (SEK /per kg)-fallow deer		65			Case study area
M	Recreational value (SEK/ per animal killed)		3,167			Case study area
δ	Discount rate (% p.a)		3			Boardman et al, (2011)

Nb: male fallow deer is grouped into only 3 stages

6. Results

In what follows, we demonstrate: (i) the effects of inter-species competition on total net benefits and harvest; and (ii) the effects of including trophy values. We also analyze (iii) the efficiency of the Koberg estate in managing the two species; and (iv) the sensitivity of results to assumptions made about discount rate and trophy prices.

A. Effects of species competition on net economic value and harvest

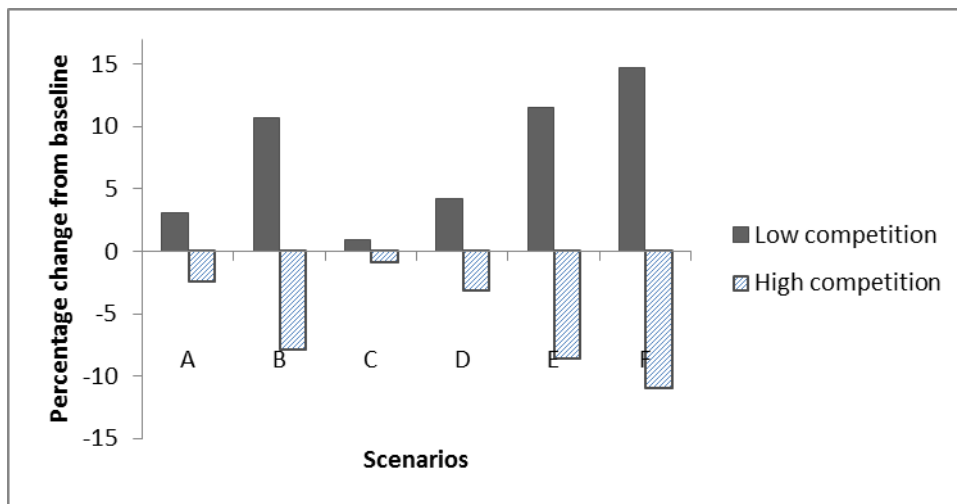
To examine the role of interspecies competition on the net economic value of the jointly managed species we first compare the impact of inter- and intra-species competition on the net present value (INPV). Subsequently, the associated implications for the optimal harvesting strategy and population are investigated.

⁹ This figure refers to total fawn population. Note that in our model we assume a sex ratio of 0.5 for fawns.

The impact of intra and inter-species competition on TNPV

We first investigate the joint impact of assumptions made about inter- and intra-species competition on the total net present value, TNPV, accruing from the simultaneous management of the two species. This is done by comparing the percentage change in the TNPV when inter- and/or intra-species competition parameters are changed. We calculate the TNPV for six scenarios A-F: A. changing intra-species competition of roe deer; B. changing intra-species competition of fallow deer; C. changing inter-species competition only; D. changing intra-species competition of roe and inter-species competition; E. changing intra-species competition of fallow deer and inter-species competition; F. and changing inter and intra-species competition for both species together. In each scenario, the level of competition is either increased (“high competition”) or reduced (“low competition”) by 15% from the baseline value, see Table 1. The resulting TNPVs are then compared with the TNPV calculated based on parameters in Table 1, results are found in Figure 2.

Fig. 2 Effects of changing competition parameters on the total net present value (TNPV).



From Figure 2, we find that an increase in the level of competition reduces TNPV relative to the baseline, and the effect is larger for a change in intra-species competition for fallow deer than for roe deer. The response of TNPV to changes in inter-species competition is small, approximately 1%. Thus, intra-species competition matters more for the TNPV than interspecies competition. This result is particular for the case we study, where interspecies competition is unilateral, and negatively affects the less valuable species, i.e. the roe deer. Further, the results of scenarios D-F suggest that the effect of intra and interspecies competition in the species population is largely additive.

Effects of competition on harvest and population density

In the baseline model, where data from Table 1 are used, pulse harvesting of the fallow deer is optimal, roe deer harvest is constant across time except minor pulses in the harvest of male roe yearlings (see Fig. 3A). Pulse harvesting describes a harvesting regime where harvest levels oscillate within some bounds or levels

over time in steady state, i.e., where harvest is intense at regular intervals, separated by periods of little or zero harvests (Garnache, 2013; Clark, 1990; Naevdal et al., 2012). Uniform¹⁰ harvesting imply that the level of harvest remains at constant level over time, at steady state. According to the results, harvesting of adult female fallow deer exhibit the highest pulse cycle length and oscillate between 0 and 1000 with a three year pulse harvest regime. Thus for every 3rd year, optimal harvest of adult female fallow deer is high and for years in-between, harvest falls to zero. Similar three year cycles is observed for adult male and senescent fallow deer except that in these cases, harvest levels oscillate with lower amplitude and no periods of zero harvest. Harvests of roe deer however are generally uniform, with positive harvest for male yearlings and senescent females.

The outcome of pulse harvesting is not uncommon in the literature on age- and stage-structured population modelling (Walters, 1969; Hannesson, 1975; Clark et al., 1973; Tahvonen et al., 2013). Clark et al. (1973) argue that pulse harvesting is largely the result of the choice of discount rate, and Tahvonen et al. (2013) shows that increasing the discount rate transforms pulse harvesting to converge towards a steady state uniform smooth harvesting regime.

Table 2. Steady state results under different levels of competition

Competition Level	TNPV (SEK million)	Steady State					
		Density (animal/km ²)		Total Population		Total Harvest	
		Roe	Fallow	Roe	Fallow	Roe	Fallow
Baseline	215.86	21.6	36-46	1952	3200-4200	474	619-1800
<i>Changing inter species competition</i>							
Low	217.79	22.6	36-46	2037	3301-4000	500	657-1792
High	213.83	20.4	36-46	1866	3200-3667	446	833-1806
<i>Changing (roe deer) intra- species competition-</i>							
Low	222.46	25.5	36-46	2295	3200-4200	561	633-1788
High	210.66	18.6	36-47	1699	3278-4266	406	622-1796
<i>Changing (fallow deer) intra- species competition</i>							
Low	238.84	20.1	43-55	1822	3884-4970	446	800-1922
High	198.93	22.6	31-40	2031	2800-3600	505	600-1600
<i>Changing (roe deer) intra- species competition and inter species competition</i>							
Low	224.96	26.6	36-46	2396	3200-4200	577	636-1808
High	209.04	17.8	35-38	1606	3200-4200	400	630-1800
<i>Changing (fallow deer) intra- species competition and inter species competition</i>							
Low	240.66	21.3	42-50	1932	3974-5000	482	749-1974
High	197.28	21.3	30-40	1954	3193-3622	468	520-1619
<i>Changing both intra (all) and inter species competition</i>							
Low	247.48	25.4	42-54	2290	4000-5000	542	800-1746
High	192.24	18.7	32-40	1703	2800-3600	412	546-1590

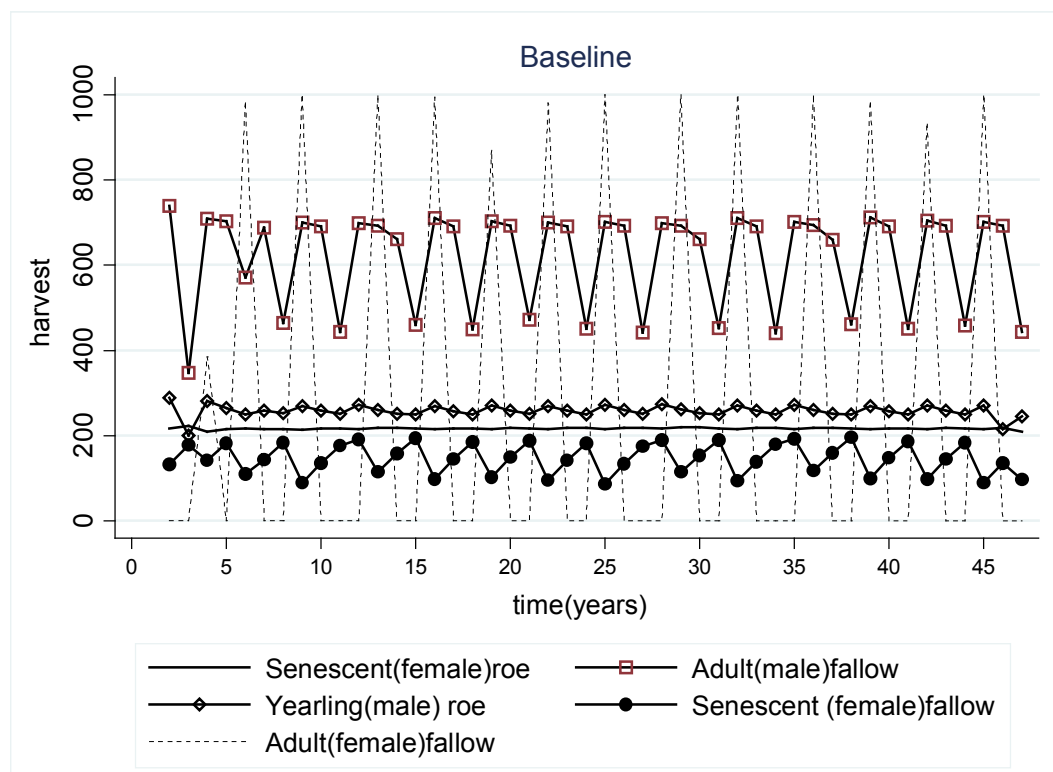
Competition parameters were either increased (High competition) or decreased (Low competition) by 15% from baseline values. The presence of pulse harvesting in fallow deer populations result in steady state density, population and harvest oscillating within a pulse cycle length.

However, in this study, the resulting pulse harvest is not mainly due to the choice of the discount rate, but rather to the lagged competition effects in the recruitment function, see Appendix C. In fact, our results suggest that pulse harvest is robust in relation to a variation in discount rate, see table 5.

¹⁰ Also referred to as continuous, smooth or stationary harvesting

Specifically, we show that assuming an instantaneous effect of competition (both intra- and inter-) on recruitment yields a uniform harvesting regime across the stages (see Fig. C1 and C2 in Appendix C). Similar results are also obtained (see Fig. C3 and C4 in appendix) when we assume an instantaneous intra-species competition but a lagged inter-species competition. This suggests that the pulse harvest regime resulting from this study is mainly attributable to the lagged intra-species competition for fallow deer. In reality, there is no reason to believe there are differences in the time effects of intra and inter-species competition on recruitment. Hence, we conclude that the pulse harvesting is rather a result of the lagging of competition effects as a whole, than just a single competition effect.

Fig 3. Steady state harvest levels from baseline model



Age classes with zero steady state harvest levels are omitted from the graph

Further, we find that a higher degree of inter-species competition is associated with a reduction in steady state roe deer density and harvest relative to the baseline. Also, the results show that changes in intra-species competition among roe deer affect population density, while fallow deer intra-species competition affects not only the fallow deer population but also exerts a spillover effects on the roe deer population due to inter-species competition, see Table 2. For instance, a 15% reduction in intra-species competition in roe deer increases roe deer density by 8% (from 21.6 animals/km² in the baseline scenario to 25.5 animals/km²). A similar reduction in intra-species competition among fallow deer does not only boost

fallow deer density from the baseline level of between¹¹ 36-46 animals/km² to 43-55 animals/km², but also reduce roe deer density to 20.1 animals/km² from the baseline.

To sum up, we observe that even though the effect of interspecies competition on total net economic benefits is marginal, its effect on roe deer populations is very significant.

B. Introducing trophy values

In this section we examine the effects of the inclusion of trophy values on the net economic benefits accruing to the landowner, and on steady state population and harvests. Results suggest that the inclusion of trophy hunting enhances both economic and ecological benefits. The inclusion of trophy values increases the TNPV by more than twice from SEK 215.1 million (baseline) to SEK 527.2 million (Table 3), and fallow deer densities at steady state increase from 36-46 animals/km² in the baseline to 40-53 animals/km². Roe deer densities at steady state however, remain unaffected. The increased population is explained by the landowner having economic incentives to conserve the male animals (especially fallow deer since they produce bigger trophies than roe deer) until they are fully matured to produce high quality trophies, rather than to harvest them for meat values when they are young. This is confirmed by the reduction in the steady state harvest levels under trophy hunting relative to the baseline model.

Table 3. Steady state results with the inclusion of trophy values

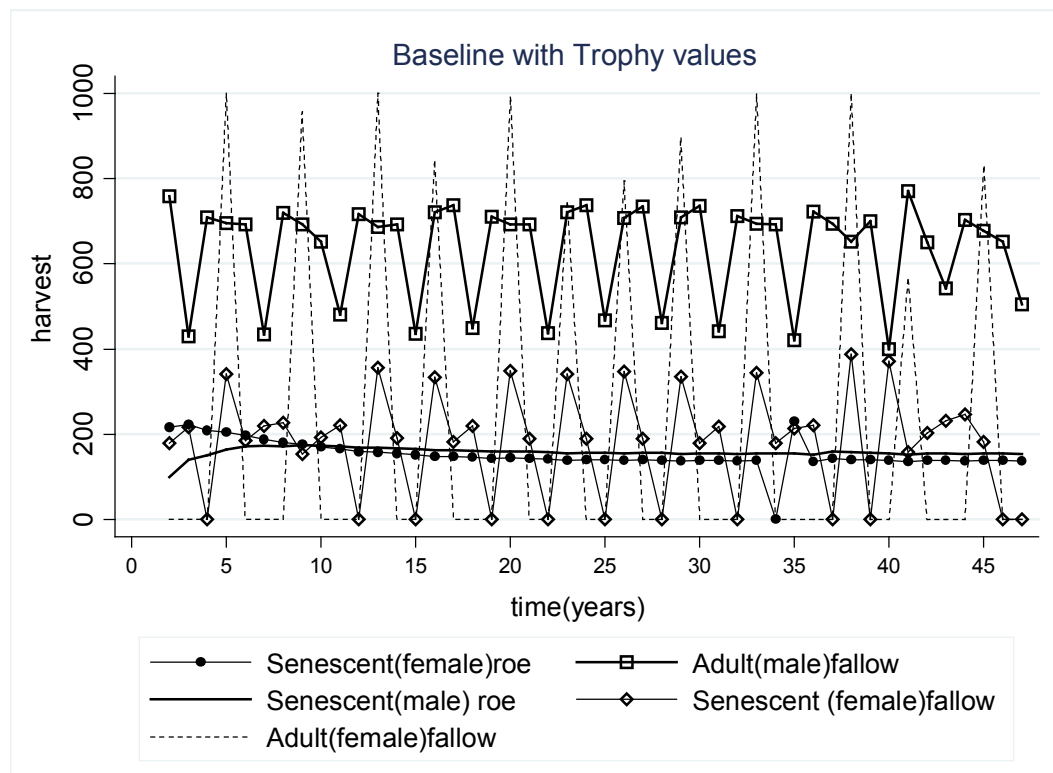
Competition Level	TNPV (SEK million)	Steady State					
		Density (animal/km ²)		Total Population		Total Harvest	
		Roe	Fallow	Roe	Fallow	Roe	Fallow
Baseline	215.86	21.6	36-46	1952	3200-4200	474	619-1800
Including trophy values	527.93	21.5	40-53	1889	3600-4800	303	436-1809

The presence of pulse harvest in fallow deer population management results in a steady state density, population and harvest oscillating between bounds.

Further, there are noticeable changes in the harvesting patterns when trophy values are included, see Fig. 4A. For instance, the baseline model (with no trophy hunting) prescribe a steady state harvest of male and female roe deer in stages 2 (yearling) and 4 (senescent), respectively. However, with the inclusion of trophy values, the results indicate that whereas it remain optimal to harvest female roe deer in stages 4 (senescent), it is now more beneficial to conserve the male cohorts to survive into stage 4. The intuition again is that the landowner conserves male roe deer until they are fully matured to produce high quality trophies. On the other hand, the fallow deer stages harvested remain unaffected by the inclusion of trophy values, except for the fact that the pulse cycle length for female fallow deer in stage 4 (senescent) increases significantly after accounting for trophy values. The reason for this increase in pulse cycle length is that even though trophy hunting provides an incentive for the landowner to boost male stocks, at the same time it implies reducing female harvest since females are required for producing more males (and females). The reduction in female harvest, with a view of boosting recruitment of male population, will over time build up female numbers which requires high harvest levels to maintain the population at a sustainable level to support future recruitment and vice versa. Thus, one can deduce that trophy hunting induces low female harvest when population size is low and high harvest when population size is high.

¹¹ Notice that the range in steady density for fallow deer is a result of the pulse harvesting regime with results in oscillating population levels at steady state.

Fig 4. Steady state harvest levels with the inclusion of trophy values



Age classes with zero steady state harvest levels are omitted from the graphs

Further, we conduct sensitivity analysis of the effects of inter-species competition on total economic value when trophy hunting is accounted for. Results here are similar to the outcome in section 6A, but of a higher magnitude. Specifically we find that a 15% rise in the degree of inter-specie competition is associated with a 1.5% fall in total net present value of the two species, while a fall in inter-specie competition of the same magnitude is associated with a 3% increase in net economic returns. Thus, the effect of inter-specie competition is relatively higher when trophy values are considered compared to the baseline model.

C. Empirical Application of the Model: the Koberg Estate case

We test the empirical relevance of our model by fitting the initial population data to actual data at the Koberg estate and compare the model outcome with the optimal (bioeconomic) management scenario, as estimated in the previous sections. This will help us to evaluate how far the current management practice at the estate is from the economically optimal one. It will also allow us to identify measures that could be implemented to increase the estate's TNPV. Achieving this objective requires fitting our model to an initial population representative of the current population levels in the estate. To obtain a representative measure of current population level¹², we use a 5 year population average, estimated to be 3526 (38 animals/ km²) and 238 (3 animals/ km²) for fallow and roe deer, respectively. Again, since the key control variable in the model is harvest, we impose a harvest constraint that mimics the current harvest regime in the Koberg

¹² i.e. initial population at time t=0

estate: by setting harvest to fluctuate between the highest and minimum harvest levels (i.e. share of population harvested) at the estate based on the 5 year data obtained. We estimate the Koberg model with and without trophy values, and compare the results herein with the results of the bioeconomic optimum. Results from both models, with and without trophy hunting, estimated for the Koberg estate reveal that current management practice at the Koberg gives 82% and 93% of the total maximum TNPV with and without trophy values, respectively (Table 4).

Table 4. *Comparison of steady state results under different management regimes*

Model	TNPV (SEK million)	Steady State					
		Density (animal/km ²)		Total Population		Total Harvest	
		Roe	Fallow	Roe	Fallow	Roe	Fallow
Baseline	215.86	21.6	36-46	1952	3200-4200	474	619-1800
Baseline with trophy hunting	527.93	21.5	40-53	1889	3600-4800	303	436-1809
Study area	178.05	25	41-46	2306	3802-4160	394	800-1200
Study area with trophy hunting	492.83	21	45-50	1872	4167-4470	294	800-1300

The steady state population density in Koberg exceeds the levels in the bioeconomic optimum. For example, the Koberg steady state density for roe and fallow deer is estimated to be 25 and 41-46 animals/km² respectively, compared to the optimal outcome of 21.5 and 36-46 respectively. The steady state harvest at Koberg is also lower than when the species are optimally managed. Thus, the results herein suggest that the Koberg estate is doing appreciably well in managing roe and fallow deer, as their deviation from the optimal path is small. In addition, our model does not take into account possible recreational values that can be attributed to the population numbers, i.e. attributed to the possibilities to spot, rather than shoot, deer.

D. Effect of discount rate and trophy values on optimal management

The bioeconomic outcome of joint management of the two deer species is not only governed by ecological factors but also, the prevailing economic conditions. Economic theory suggests that, at a high discount rate, the present value of current consumption is higher than future consumption and vice versa. Hence, economic agents prefer maximizing present consumption at the expense of future consumption whenever interest/discount rate is rising. In the same vein, natural resource models assert that increasing discount rate (high degree of impatience) implies maximizing short run benefits via increased harvest in the initial period, but with a declining population and harvest in the long run (Tahvonen et al., 2014). To this end, we examine the response of steady state population and harvest levels, and their associated net revenues in relation to changes in the discount rate using the baseline model (Table. 5).

Table 5. *Effects of discount rate on optimal steady state.*

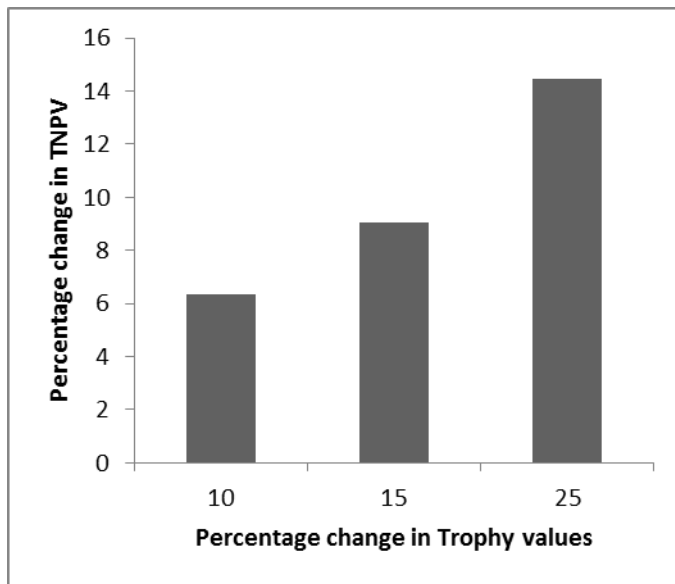
Discount rate per annum (%)	TNPV (SEK million)	Steady State					
		Density (animal/km ²)		Total Population		Total Harvest	
		Roe	Fallow	Roe	Fallow	Roe	Fallow
0	464.36	21.4	38-48	1925	3384-3864	479	642-1809
3	215.86	21.6	36-46	1952	3200-4200	474	619-1800
5	147.01	21.3	35-46	1856	3101-3578	445	636-1773
8	95.55	17-19	34-44	1600-1800	3000-4000	355-641	600-1774

The presence of pulse harvesting result in steady state density, population and harvest oscillating around bounds. TNPV = total present value of net benefits

Our results show that with a rise in discount rate, harvest levels increase in the short run before stabilizing towards long run levels that are lower for higher discount rates. Population density for roe and fallow deer in a zero discount regime is estimated to be 21.4 and 38-48 animals/km² respectively (Table 5). However, roe and fallow deer population density decline to 17-19 and 33-44 animals/km² respectively, with an 8% discount rate. This confirms earlier assertion that higher discount rates are associated with lower steady state population. Interestingly, we see traces of pulse harvesting in roe deer populations at the 8% discount rate. As expected, the results show that greater total net present value (TNPV) is accrued when discount rates are lower and vice versa.

Finally, since trophy values constitute an important factor in harvest, we analyze the effects of changes in trophy values on optimal harvest, population and net benefits. An implicit assumption in this study is that the landowner is a price taker¹³, in terms of trophy values and prices; therefore the essence of this sensitivity analysis is to analyze elasticity of net revenues to changes in trophy prices. The results show that increasing trophy values exert a positive impact on net revenues, albeit being fairly inelastic. A 10% increase in trophy values can boost TNPV by 6.3% from SEK 527.93 to 578.7 million, while a 25% increase in trophy prices is associated with a 14.4% in TNPV (Fig. 5). The impact on harvest patterns however is not so obvious. The results herein suggest that a trophy price is a key factor and determinant of the net revenue accruing to the landowner.

Fig. 5. Effects of changing trophy values on TNPV



¹³ This was validated by the game keeper in the study area, who indicated that the trophy prices administered in the Koberg estate is set according to prevailing prices in other game estates in Europe.

7. Discussions and conclusion

The main goal of this paper is to analyze and demonstrate empirically, the role of ecological interdependencies among two deer species, in optimal management of the species. To this end, we develop a stage-structured population model for the optimal management of roe and fallow deer in the presence of intra- and interspecies competition. The contribution of this paper to existing literature is enviable: it demonstrates analytically and numerically, the effects and implications of inter-species competition on total net economic value and harvesting strategies of two deer species—roe and fallow deer.

Analytical solutions from the model suggest that the landowner's decision to maintain a given population of both species depends to some extent on the degree of competition within and among the two species. This is because it remains worthwhile to conserve one more animal until a future time t if its marginal benefits measured by its net contribution to recruitment and the current population, is positive. However, since strong competition has negative effects on recruitment, it implies that high levels of competition reduce the marginal benefits attributable to conserving one more unit of both species population from harvest. This result suggests that the degree of species competition is a key factor to consider in the landowners harvest decisions.

Simulating the bioeconomic model over a 50 year period, our numerical results illustrates the predictions of the theoretical model. These are summarized as follows:

Our results suggest that total net economic value from the management of the two species is more sensitive to the level of intraspecies competition than interspecies competition, since we find a small impact of interspecies competition on total economic benefits of the two species. However, this result is only valid in this particular case where interspecies competition is unilateral and affects the relatively less valuable species, in this case, the roe deer. Thus, the real impact of interspecies competition depends on the underlying ecological and economic conditions characterizing the species concerned. That is, one would expect the impact of inter-species competition to be higher if a unilateral negative effect of interspecies competition is borne by the economically more valuable species. However, contrary to that, the impact of interspecies competition on the population density of the affected species – the roe deer – is large, implying that ecological effects related to roe deer population size, can be large.

Also, our stage-structured joint population model predicts a pulse harvesting regime, especially for fallow deer, when the effect of competition on recruitment is lagged rather than instantaneous. Pulse harvesting has been the subject of debate in the literature especially in age- and stage-structured modelling, and several reasons for pulse harvesting have been identified, such as the level of the discount rate (Tahvonen et al., 2013). However, sensitivity analysis undertaken in this study suggest that the pulse harvesting regime derived from our model is robust to the choice of the discount rate, and is largely attributed to the lag effects of competition on recruitment. Therefore, when such lagged competition effects are present, landowners should consider pulse harvests, in particular if the wildlife species in question is relatively stationary, implying that the landowner can reap the benefits of his harvesting strategy. This result is robust for assumptions on trophy prices.

Further, comparing the current management regime for roe and fallow deer at the Koberg estate in Sweden, to the optimal management regime studied here shows that the current management practice at the estate though sub-optimal, is relatively close to the economically optimal level. Our results suggest that the estate is doing appreciably well as the deviations in total economic value and population densities from the economically optimal levels is relatively low. Average annual economic loss is estimated to be between 6.7% and 17.5% depending on whether trophy values are accounted for or not.

A limitation of this paper however, is that the present model does not account for all the cost and benefits associated with the management of the two species in the estate; hence results on the total economic values should be interpreted with caution. For example, aesthetic values associated with people observing the animals in the estate were not included in the present study, mainly due to data unavailability. Also, costs such as browsing damages to agriculture crops and forestry are not accounted for in the present study, due to similar reasons. This provides an interesting avenue for future research into the issue by incorporating these omitted benefits and cost.

Finally, our results indicate that economic conditions such as the choice of discount rate and trophy prices are important considerations for optimal management of commercially valuable wildlife species. This confirms the results of Moxnes et al. (2001), Rantamäki-Lahtinen (2008), Elofsson et al (2012) and Tahvonen et al (2014). In conclusion, findings from this paper demonstrates empirically the importance of accounting for species competition in the management of wildlife species with strong ecological interdependences.

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Appendix A: Estimating Transition Probabilities

Given constant survival and growth rates in each stage, for a representative stage i , there are individuals who have stayed in the stage for 1, 2, 3, ..., n_i years. By setting the share of individuals alive in the first cohort of stage i at time t , to unity (1) and the probability of those individuals surviving in $t+1$ to ϕ^i , then the probability of surviving until the n^{th} year can be expressed as $(\phi^i)^{n_i}$ (Crouse et al., 1987).

Further, by assuming a stationary population and stable age distribution within stages¹⁴, the survival of individuals within stage i becomes $\phi^i, (\phi^i)^2, (\phi^i)^3, \dots, (\phi^i)^{n_i-1}$. The idea is that for every additional year ($t+1$), the oldest cohort in stage i migrate to stage $i+1$ while younger cohorts remain in the same stage until the following year. This process continues iteratively. Therefore, the probability of surviving and moving from stage i to stage $i+1$ is computed as

$$g^i = \left(\frac{\phi^{i n_i - 1}}{1 + (\phi^i) + (\phi^i)^2 + \dots + (\phi^i)^{n_i - 1}} \right) \phi^i = \gamma^i \phi^i \quad (\text{A1})$$

where $\gamma^i = \left(\frac{\phi^{i n_i - 1}}{1 + (\phi^i) + (\phi^i)^2 + \dots + (\phi^i)^{n_i - 1}} \right)$ is stage-specific transition probability (i.e the probability of growing(moving) into the next stage).

On the other hand, the probability of surviving and staying in the stage i is also expressed as

$$p^i = \left(\frac{1 + (\phi^i) + (\phi^i)^2 + \dots + (\phi^i)^{n_i - 2}}{1 + (\phi^i) + (\phi^i)^2 + \dots + (\phi^i)^{n_i - 1}} \right) \phi^i = (1 - \gamma^i) \phi^i \quad (\text{A2})$$

Note that in stages 1 and 2, $p^1 = p^2 = 0$, since all surviving individuals migrate into the next stage ($\gamma^1 = \gamma^2 = 1$).

Table A1. Survival data on Fallow and Roe deer

Parameter	States				Source	
	1	2	3	3		
$\phi_{1,r}^i$	Natural survival of (female) roe deer	0.72	0.89	0.94	0.74	<i>Kjellander (2000)</i>
$\phi_{2,r}^i$	Natural survival of (male) roe deer	0.85	0.89	0.93	0.72	<i>Kjellander (2000)</i>
$\phi_{1,f}^i$	Natural survival of (female) fallow deer	0.857	0.963	0.963	0.963	<i>Kjellander (2014)</i>
$\phi_{2,f}^i$	Natural survival of (male) fallow deer	0.759	1.00	0.726	*	<i>Kjellander (2014)</i>

¹⁴ i.e ruling out dispersal out of or immigration into the particular area.

Appendix B. Optimization Problem and optimal 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 (1-8). Let $\lambda_{j,t}^i$ and $\gamma_{j,t}^i$ denote the Lagrange multipliers for constraints (1)-(4) and (5-8) respectively. Thus the resulting Lagrangian optimization problem (see: Conrad, 2010) is expressed as:

$$L = \sum_{t=0} \rho^t \left\{ \begin{aligned} & \left[q_r^i \left(\sum_{j=c}^{i=1} HR_{j,t}^i \right) + q_f^i \left(\sum_{j=c}^{i=1} HF_{j,t}^i \right) \right] - \left[\sum_{j=c}^{i=1} d_j^i (F_{j,t}^i - HF_{j,t}^i) \right] \\ & + \lambda_{c,t}^1 \left[\sum_{i>1} R_{x,t}^i \kappa_r^i e^{-\sum_{j'} (\beta_r R_{j,t}^{j'} + \mu F_{j,t}^{j'})} - R_{c,t}^1 \right] \\ & + \rho \sum_{j=x} \lambda_{j,t+1}^2 \left[0.5 g_{c,r}^1 (R_{c,t}^1 - HR_{c,t}^1) - R_{j,t+1}^2 \right] \\ & + \rho \sum_{\substack{i=3 \\ j=x}} \lambda_{j,t+1}^i \left[g_{j,r}^{i-1} (R_{j,t}^{i-1} - HR_{j,t}^{i-1}) + p_{j,r}^i (R_{j,t}^i - HR_{j,t}^i) - R_{j,t+1}^i \right] \\ & + \gamma_{c,t}^1 \left[\sum_{i>1} F_{x,t}^i \kappa_f^i e^{-\sum_{j'} (\beta_f F_{j,t}^{j'})} - F_{c,t}^1 \right] + \rho \sum_{j=x} \gamma_{j,t+1}^2 \left[0.5 g_{c,f}^1 (F_{c,t}^1 - HF_{c,t}^1) - F_{j,t+1}^2 \right] \\ & + \rho \sum_{\substack{i=3 \\ j=x}} \gamma_{j,t+1}^i \left[g_{j,f}^{i-1} (F_{j,t}^{i-1} - HF_{j,t}^{i-1}) + p_{j,f}^i (F_{j,t}^i - HF_{j,t}^i) - F_{j,t+1}^i \right] \end{aligned} \right\} \quad (A1)$$

The Kuhn-Tucker first order conditions for the above optimization problem including the slack conditions are:

$$\rho^{-t} L'_{HR_{c,t}^1} = q_r^1 - 0.5 \rho \left(\sum_{j=x} \lambda_{j,t+1}^2 \right) g_{c,r}^1 \leq 0; \quad 0 \leq HR_{c,t}^1 < \bar{R}_{c,t}^1; \quad (A2)$$

$$\rho^{-t} L'_{HR_{c,t}^1} HR_{c,t}^1 = 0; \quad t = 0, 1, \dots; \quad j = x, y$$

$$\rho^{-t} L'_{HR_{j,t}^2} = q_r^2 - \rho \lambda_{j,t+1}^3 g_{j,r}^2 \leq 0; \quad 0 \leq HR_{j,t}^2 < \bar{R}_{j,t}^2; \quad (A3)$$

$$\rho^{-t} L'_{HR_{j,t}^2} HR_{j,t}^2 = 0; \quad t = 0, 1, \dots; \quad j = x, y$$

$$\rho^{-t} L'_{HR_{j,t}^3} = q_r^3 - \rho \lambda_{j,t+1}^3 p_{j,r}^3 - \rho \lambda_{j,t+1}^4 g_{j,r}^3 \leq 0; \quad 0 \leq HR_{j,t}^3 < \bar{R}_{j,t}^3; \quad (A4)$$

$$\rho^{-t} L'_{HR_{j,t}^3} HR_{j,t}^3 = 0; \quad t = 0, 1, \dots; \quad j = x, y$$

$$\begin{aligned}\rho^{-t}L'_{HR_{j,t}^4} &= q_r^4 - \rho\lambda_{j,t+1}^4 p_{j,r}^4 \leq 0; \quad 0 \leq HR_{j,t}^4 < \bar{R}_{j,t}^4 \\ \rho^{-t}L'_{HR_{j,t}^4} HR_{j,t}^4 &= 0; \quad t=0,1,\dots; j=x,y\end{aligned}\tag{A5}$$

$$\begin{aligned}\rho^{-t}L'_{HF_{c,t}^1} &= q_f^1 + d_j^1 - 0.5\rho\left(\sum_{j=1} \gamma_{j,t+1}^2\right) \mathbf{g}_{c,f}^1 \leq 0; \quad 0 \leq HF_{c,t}^1 < \bar{F}_{c,t}^1 \\ \rho^{-t}L'_{HF_{c,t}^1} HF_{c,t}^1 &= 0; \quad t=0,1,\dots; j=x,y\end{aligned}\tag{A6}$$

$$\begin{aligned}\rho^{-t}L'_{HF_{j,t}^2} &= q_f^2 + d_j^2 - \rho\gamma_{j,t+1}^3 \mathbf{g}_{j,f}^2 \leq 0; \quad 0 \leq HF_{j,t}^2 < \bar{F}_{j,t}^2 \\ \rho^{-t}L'_{HF_{j,t}^2} HF_{j,t}^2 &= 0; \quad t=0,1,\dots; j=x,y\end{aligned}\tag{A7}$$

$$\begin{aligned}\rho^{-t}L'_{HF_{j,t}^3} &= q_f^3 + d_j^2 - \rho\gamma_{j,t+1}^3 p_{j,f}^3 - \rho\gamma_{j,t+1}^4 \mathbf{g}_{j,f}^3 \leq 0; \quad 0 \leq HF_{j,t}^3 < \bar{F}_{j,t}^3 \\ \rho^{-t}L'_{HF_{j,t}^3} HF_{j,t}^3 &= 0; \quad t=0,1,\dots; j=x,y; \quad \mathbf{g}_{j,f}^3 = 0 \quad \forall j=y; \quad \mathbf{g}_{j,f}^3 \neq 0 \quad \forall j=x\end{aligned}\tag{A8}$$

$$\begin{aligned}\rho^{-t}L'_{HF_{j,t}^4} &= q_f^4 + d_j^4 - \rho\gamma_{j,t+1}^4 p_{j,f}^4 \leq 0; \quad 0 \leq HF_{j,t}^4 < \bar{F}_{j,t}^4 \\ \rho^{-t}L'_{HF_{j,t}^4} HF_{j,t}^4 &= 0; \quad t=0,1,\dots; j=x\end{aligned}\tag{A9}$$

$$\begin{aligned}\rho^{-t}L'_{R_{c,t}^1} &= -\rho\lambda_{c,t+1}^1 \beta \sum_{i>1} R_{x,t+1}^i \kappa_r^i e^{-\sum_{ij}(\beta_r R_{j,t}^i + \mu F_{j,t}^i)} - \lambda_{c,t}^1 + 0.5\rho\left(\sum_{j=x} \lambda_{j,t+1}^2\right) \mathbf{g}_{c,r}^1 \leq 0 \\ \rho^{-t}L'_{R_{c,t}^1} R_{c,t}^1 &= 0; \quad R_{j,t}^1 \geq 0; \quad t=0,1,2,\dots; j=c,x,y\end{aligned}\tag{A10}$$

$$\begin{aligned}\rho^{-t}L'_{R_{x,t}^2} &= \lambda_{c,t}^1 \kappa_r^2 e^{-\sum_{ij}(\beta_r R_{j,t-1}^i + \mu F_{j,t-1}^i)} - \rho\lambda_{c,t+1}^1 \beta \sum_{i>1} R_{x,t+1}^i \kappa_r^i e^{-\sum_{ij}(\beta_r R_{j,t}^i + \mu F_{j,t}^i)} - \lambda_{x,t}^2 + \rho\lambda_{x,t+1}^3 \mathbf{g}_{x,r}^2 \leq 0 \\ \rho^{-t}L'_{R_{x,t}^2} R_{x,t}^2 &= 0; \quad R_{x,t}^2 \geq 0; \quad t=0,1,2,\dots; j=c,x,y\end{aligned}\tag{A11}$$

$$\begin{aligned}\rho^{-t}L'_{R_{y,t}^2} &= -\rho\lambda_{c,t+1}^1 \beta_r \sum_{i>1} R_{x,t+1}^i \kappa_r^i e^{-\sum_{ij}(\beta_r R_{j,t}^i + \mu F_{j,t}^i)} - \lambda_{y,t}^2 + \rho\lambda_{y,t+1}^3 \mathbf{g}_{y,r}^2 \leq 0 \\ \rho^{-t}L'_{R_{y,t}^2} R_{y,t}^2 &= 0; \quad R_{y,t}^2 \geq 0; \quad t=0,1,2,\dots; j=c,x,y\end{aligned}\tag{A12}$$

$$\begin{aligned}\rho^{-t}L'_{R_{x,t}^3} &= \lambda_{c,t}^1 \kappa_r^3 e^{-\sum_{ij}(\beta_r R_{j,t-1}^i + \mu F_{j,t-1}^i)} - \rho\lambda_{c,t+1}^1 \beta_r \sum_{i>1} R_{x,t+1}^i \kappa_r^i e^{-\sum_{ij}(\beta_r R_{j,t}^i + \mu F_{j,t}^i)} + \rho\lambda_{x,t+1}^3 p_{1,r}^3 - \lambda_{x,t}^3 + \rho\lambda_{x,t+1}^4 \mathbf{g}_{x,r}^3 \leq 0 \\ \rho^{-t}L'_{R_{x,t}^3} R_{x,t}^3 &= 0; \quad R_{x,t}^3 \geq 0; \quad t=0,1,2,\dots; j=c,x,y\end{aligned}\tag{A13}$$

$$\rho^{-t} L'_{R_{y,t}^3} = -\rho \lambda_{c,t+1}^1 \beta_r \sum_{i>1} R_{x,t+1}^i \kappa_r^i e^{-\sum_y (\beta_r R_{j,t}^i + \mu F_{j,t}^i)} + \rho \lambda_{y,t+1}^3 p_{y,r}^3 - \lambda_{y,t}^3 + \rho \lambda_{y,t+1}^4 \mathbf{g}_{y,r}^3 \leq 0 \quad (\text{A14})$$

$$\rho^{-t} L'_{R_{y,t}^3} R_{y,t}^2 = 0; R_{y,t}^2 \geq 0; t = 0, 1, 2, \dots; j = c, x, y$$

$$\rho^{-t} L'_{R_{x,t}^4} = \lambda_{c,t}^1 \kappa_r^4 e^{-\sum_y (\beta_r R_{j,t}^i + \mu F_{j,t}^i)} - \rho \lambda_{c,t+1}^1 \beta_r \sum_{i>1} R_{x,t+1}^i \kappa_r^i e^{-\sum_y (\beta_r R_{j,t}^i + \mu F_{j,t}^i)} + \rho \lambda_{x,t+1}^4 p_{x,r}^4 - \lambda_{x,t}^4 \leq 0 \quad (\text{A15})$$

$$\rho^{-t} L'_{R_{x,t}^4} R_{x,t}^3 = 0; R_{x,t}^3 \geq 0; t = 0, 1, 2, \dots; j = c, x, y$$

$$\rho^{-t} L'_{R_{y,t}^4} = -\rho \lambda_{c,t+1}^1 \beta_r \sum_{i>1} R_{x,t+1}^i \kappa_r^i e^{-\sum_y (\beta_r R_{j,t}^i + \mu F_{j,t}^i)} + \rho \lambda_{y,t+1}^4 p_{y,r}^4 - \lambda_{y,t}^4 \leq 0 \quad (\text{A16})$$

$$\rho^{-t} L'_{R_{y,t}^4} R_{y,t}^4 = 0; R_{y,t}^4 \geq 0; t = 0, 1, 2, \dots; j = c, x, y$$

$$\rho^{-t} L'_{F_{c,t}^1} = -\rho \lambda_{c,t+1}^1 \mu \sum_{i>1} R_{x,t+1}^i \kappa_f^i e^{-\sum_y (\beta_r R_{j,t}^i + \mu F_{j,t}^i)} - d_c^1 - \rho \gamma_{c,t+1}^1 \beta_f \sum_{i>1} F_{x,t}^i \kappa_f^i e^{-\sum_y (\beta_f F_{j,t}^i)} - \gamma_{c,t}^1 + 0.5 \rho \left(\sum_{j=x} \gamma_{j,t+1}^2 \right) \mathbf{g}_{0,f}^1 \leq 0 \quad (\text{A17})$$

$$\rho^{-t} L'_{F_{c,t}^1} F_{c,t}^1 = 0; F_{c,t}^1 \geq 0; t = 0, 1, 2, \dots; j = c, x, y$$

$$\rho^{-t} L'_{F_{x,t}^2} = -\rho \lambda_{c,t+1}^1 \mu \sum_{i>1} R_{x,t+1}^i \kappa_r^i e^{-\sum_y (\beta_r R_{j,t}^i + \mu F_{j,t}^i)} + \gamma_{c,t}^1 \kappa_f^2 e^{-\sum_y (\beta_f F_{j,t}^i)} - \rho \gamma_{c,t+1}^1 \beta_f \sum_{i>1} F_{x,t+1}^i \kappa_f^i e^{-\sum_y (\beta_f F_{j,t}^i)} - \gamma_{x,t}^2 - d_x^2 + \rho \gamma_{x,t+1}^3 \mathbf{g}_{x,f}^2 \leq 0 \quad (\text{A18})$$

$$\rho^{-t} L'_{F_{x,t}^2} F_{x,t}^2 = 0; F_{x,t}^2 \geq 0; t = 0, 1, 2, \dots; j = c, x, y$$

$$\rho^{-t} L'_{F_{y,t}^2} = -\rho \lambda_{c,t+1}^1 \mu \sum_{i>1} R_{x,t+1}^i \kappa_r^i e^{-\sum_y (\beta_r R_{j,t}^i + \mu F_{j,t}^i)} - \rho \gamma_{c,t+1}^1 \beta_f \sum_{i>1} F_{x,t+1}^i \kappa_f^i e^{-\sum_y (\beta_f F_{j,t}^i)} - \gamma_{y,t}^2 - d_y^2 + \rho \gamma_{y,t+1}^3 \mathbf{g}_{y,f}^2 \leq 0 \quad (\text{A19})$$

$$\rho^{-t} L'_{F_{y,t}^2} F_{y,t}^2 = 0; F_{y,t}^2 \geq 0; t = 0, 1, 2, \dots; j = c, x, y$$

$$\rho^{-t} L'_{F_{x,t}^3} = -\rho \lambda_{c,t+1}^1 \mu \sum_{i>1} R_{x,t+1}^i \kappa_r^i e^{-\sum_y (\beta_r R_{j,t}^i + \mu F_{j,t}^i)} + \gamma_{c,t}^1 \kappa_f^3 e^{-\sum_y (\beta_f F_{j,t}^i)} - \rho \gamma_{c,t+1}^1 \beta_f \sum_{i>1} F_{x,t+1}^i \kappa_f^i e^{-\sum_y (\beta_f F_{j,t}^i)} - \gamma_{x,t}^3 - d_x^3 + \rho \gamma_{x,t+1}^4 p_{x,f}^3 + \rho \gamma_{x,t+1}^4 \mathbf{g}_{x,f}^3 \leq 0 \quad (\text{A20})$$

$$\rho^{-t} L'_{F_{x,t}^3} F_{x,t}^3 = 0; F_{x,t}^3 \geq 0; t = 0, 1, 2, \dots; j = c, x, y$$

$$\rho^{-t} L'_{F_{y,t}^3} = -\rho \lambda_{c,t+1}^1 \mu \sum_{i>1} R_{x,t+1}^i \kappa_r^i e^{-\sum_y (\beta_r R_{j,t}^i + \mu F_{j,t}^i)} - \rho \gamma_{c,t+1}^1 \beta_f \sum_{i>1} F_{x,t+1}^i \kappa_f^i e^{-\sum_y (\beta_f F_{j,t}^i)} - \gamma_{y,t}^3 - d_y^3 + \rho \gamma_{y,t+1}^4 p_{y,f}^3 + \rho \gamma_{y,t+1}^4 \mathbf{g}_{y,f}^3 \leq 0 \quad (\text{A21})$$

$$\rho^{-t} L'_{F_{y,t}^3} F_{y,t}^3 = 0; F_{y,t}^3 \geq 0; t = 0, 1, 2, \dots; j = c, x, y$$

$$\rho^{-t} L'_{F_{x,t}^4} = -\rho \lambda_{c,t+1}^1 \mu \sum_{i>1} R_{x,t+1}^i \kappa_r^i e^{-\sum_y (\beta_r R_{j,t}^i + \mu F_{j,t}^i)} + \gamma_{c,t}^1 \kappa_f^4 e^{-\sum_y (\beta_f F_{j,t}^i)} - \rho \gamma_{c,t+1}^1 \beta_f \sum_{i>1} F_{x,t+1}^i \kappa_f^i e^{-\sum_y (\beta_f F_{j,t}^i)} - \gamma_{x,t}^4 - d_x^4 + \rho \gamma_{x,t+1}^4 p_{x,f}^4 \leq 0 \quad (\text{A22})$$

$$\rho^{-t} L'_{F_{x,t}^4} F_{x,t}^4 = 0; F_{x,t}^4 \geq 0; t = 0, 1, 2, \dots; j = c, x, y$$

$$\rho^{-t} L'_{F_{y,t}^4} = -\rho \lambda_{c,t+1}^1 \mu \sum_{i>1} R_{x,t+1}^i \kappa_r^i e^{-\sum_y (\beta_r R_{j,t+1}^i + \mu F_{j,t}^i)} - \rho \gamma_{c,t+1}^1 \beta_f \sum_{i>1} F_{x,t}^i \kappa_f^i e^{-\sum_y (\beta_f F_{j,t}^i)} - \gamma_{y,t}^4 - d_y^4 + \rho \gamma_{y,t+1}^4 p_{y,f}^4 \leq 0 \quad (\text{A23})$$

$$\rho^{-t} L'_{F_{y,t}^4} F_{y,t}^4 = 0; F_{y,t}^4 \geq 0; t = 0, 1, 2, \dots; j = c, x, y$$

$$\rho^t L'_{\lambda_{c,t}^1} = \sum_{i>1} R_{x,t}^i \kappa_r^i e^{-\sum_y (\beta_r R_{j,t-1}^i + \mu F_{j,t-1}^i)} - R_{c,t}^1 = 0 \quad (\text{A24})$$

$$\rho^t L'_{\rho \sum_{j=x} \lambda_{j,t+1}^2} = 0.5 g_{c,r}^1 (R_{c,t}^1 - HR_{c,t}^1) - R_{j,t+1}^2 = 0 \quad (\text{A25})$$

$$\rho^t L'_{\rho \sum_{j=x} \lambda_{j,t+1}^i} = g_{j,r}^{i-1} (R_{j,t}^{i-1} - HR_{j,t}^{i-1}) + p_{j,r}^i (R_{j,t}^i - HR_{j,t}^i) - R_{j,t+1}^i = 0 \quad (\text{A26})$$

$$\rho^t L'_{\gamma_{c,t}^1} = \sum_{i>1} F_{x,t}^i \kappa_f^i e^{-\sum_y (\beta_f F_{j,t-1}^i)} - F_{c,t}^1 = 0 \quad (\text{A27})$$

$$\rho^t L'_{\rho \sum_{j=x} \gamma_{j,t+1}^2} = 0.5 g_{c,f}^1 (F_{c,t}^1 - HF_{c,t}^1) - F_{j,t+1}^2 = 0 \quad (\text{A28})$$

$$\rho^t L'_{\rho \sum_{j=x} \gamma_{j,t+1}^i} = g_{j,f}^{i-1} (F_{j,t}^{i-1} - HF_{j,t}^{i-1}) + p_{j,f}^i (F_{j,t}^i - HF_{j,t}^i) - F_{j,t+1}^i = 0 \quad (\text{A29})$$

Appendix C.

Fig C1. Steady state harvest under instantaneous competition effects on recruitment (IC)-Baseline

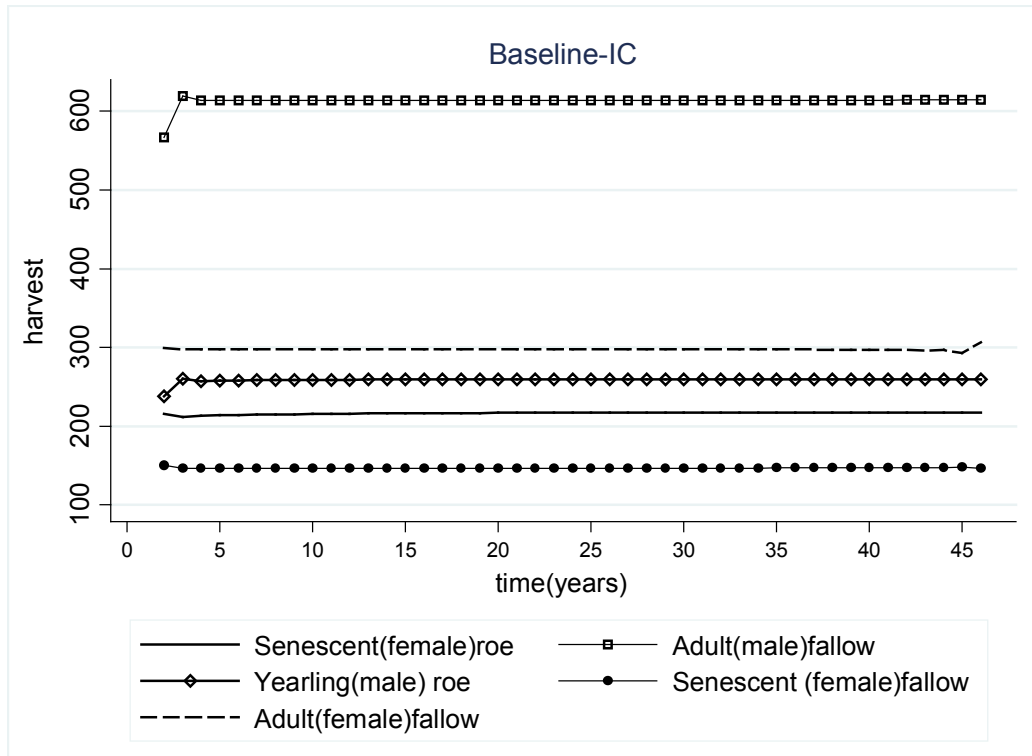


Fig C2. Steady state harvest under instantaneous competition effects on recruitment (IC)-Baseline with trophy values.

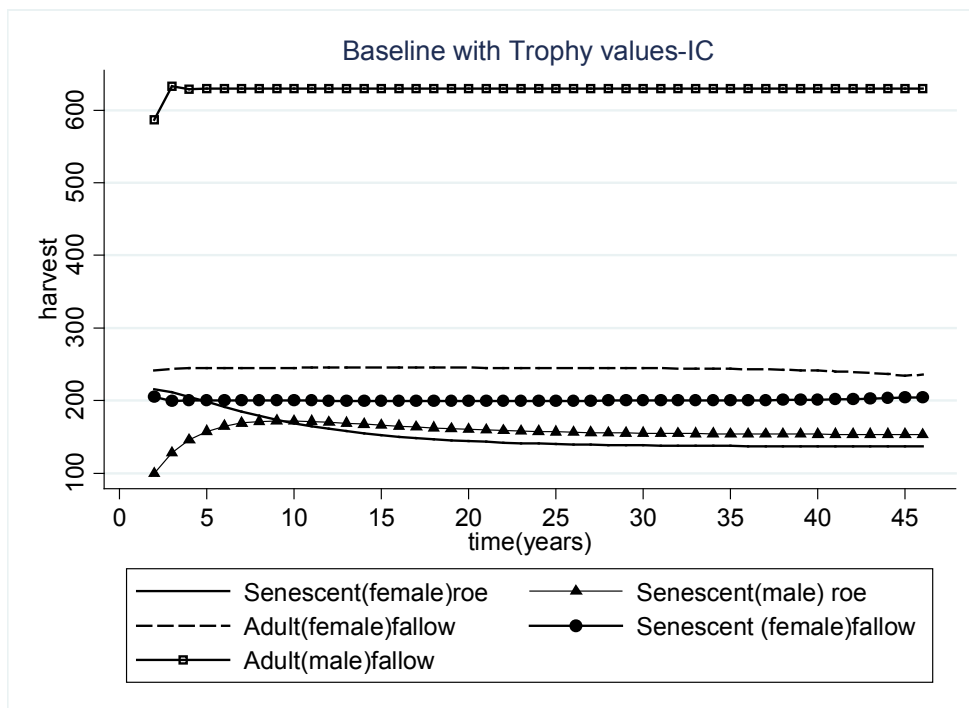


Fig C3. Steady state harvest under instantaneous intra-species competition and lagged inter-species effects on recruitment (ICC)-Baseline

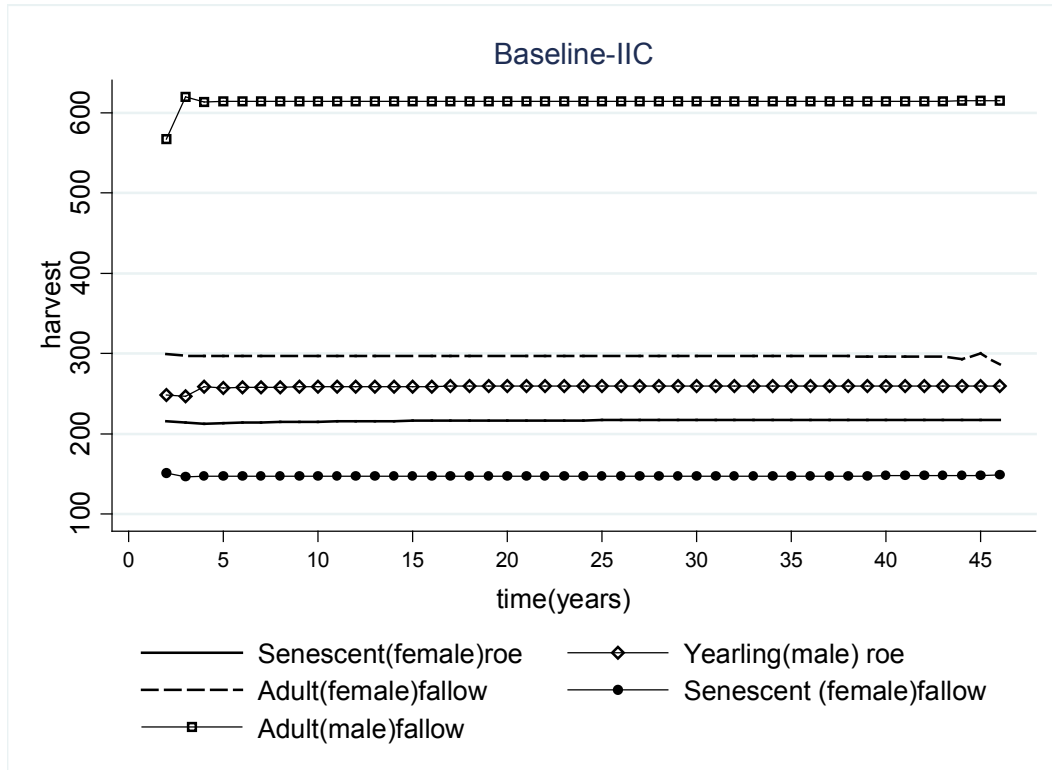
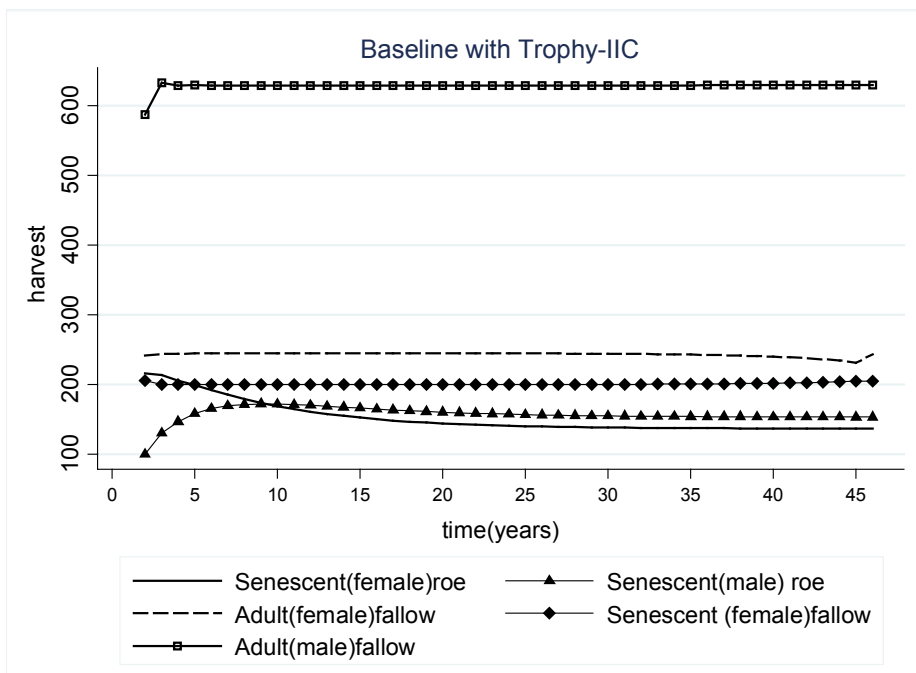


Fig C4. Steady state harvest under instantaneous intra-species competition and lagged inter-species effects on recruitment (ICC)-Baseline with trophy





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