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Control and adaptation strategies for invasive species with different life history

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Abstract

The issue of timing and scope of policies to manage invasive species has achieved considerable attention in the economic literature. Whereas many earlier studies compare prevention and control for a single invading species, we focus instead on the optimal balance of adaptation and control when an invasive species competes for scarce resources with a resident species. In particular, we focus on the role that species' life history, i.e. the degree of evolutionary specialization in survival or reproduction, plays for the choice of strategy. A numerical age-structured optimization model is used for the analysis. Results show that life history is an important factor for the trade-off between direct control of the invader and adaptation of harvesting strategies for the resident species. Life history is also crucial for the trade-off between early and delayed control of the invader. When a direct control technology is not available, there are larger economic losses with a resident species specialized in survival, whereas if such technologies are available, the larger losses occur with a resident species specialized in reproduction.

Key words:

Invasive species, life history, control, harvest, adaptation, costs

1. Introduction

Invasive species, i.e. species that are introduced into a natural environment where they are not normally found, can give rise to large economic damage due to their impact on native species, wildlife habitats, forest and agriculture productivity, and recreation (Pimentel et al., 2005; Gren et al., 2009). Estimates of damage cost indicate that they can correspond 5-10% of GDP (Gren et al., 2009). In principle, there are three ways of controlling damage of invasive species; prevention, control and adaptation measures. Prevention efforts inhibit the entrance of species into new regions, control measures regulate the size and spread of the invader, and adaptation measures affect the damage caused by the invader through adjustments of economic activities at the site such as, e.g., the management of native species already present in the habitat (see e.g. Perrings 2005 and Finnoff et al., 2005 for definitions of the different types of measures). Existing international instruments for biodiversity conservation are mainly focused on prevention of unwanted introductions, while providing little guidance regarding the issue of control or adaptation (Secretariat of the Convention on Biological Diversity, 2001). However, these prevention measures sometimes fail to stop the entrance of invasive species, and the associated establishment and growth are determined by the interaction with resident species. The implication of this interaction for optimal choice of control and adaptations strategies has, to the best of our knowledge, not been analyzed in the economic literature (see Gren 2008 for a review). The purpose of this paper is to examine how optimal control and adaptation policies depend on the economic and biological characteristics of invading and resident species. To this end, we use a two-population discrete dynamic model with an invasive species, which compete for scarce resources with a commercially valuable harvested resident species

A vast majority of the economic studies on invasive species focus on the trade-off between prevention and control measures, and abstract from the interaction with the resident species. Because of the stochastic impact of prevention measures on the invader, the impact of prevention is typically modeled as random, while control is assumed to exert a known impact on the invader population (Olson and Roy, 2005; Kim et al., 2006; Leung et al., 2002; Finnoff et

al., 2007). Within this type of framework, Olson and Roy (2005) use a static stochastic model to examine how the trade-off between prevention and control depends on the economic and biological characteristics of a single invader, such as initial invasion size, invader growth rate, and the probability distribution of introductions. Kim et al. (2006) assume that discovery of the invader occurs with a delay, and show that it is economically efficient to spend more on prevention before than after the discovery of the invader. After discovery, prevention can still be more important than control if the invader population is small enough, but when the population increases, prevention is no longer optimal. Total expenditures on prevention and control are shown to decrease with the population of the invader, and increase with the invader population growth rate and the carrying capacity of the invaded ecosystem.

The consideration of uncertainty in invader growth, in particular when entering a new ecosystem, is recognized by Leung et al. (2002). They use stochastic dynamic programming model to identify the optimal combination of prevention and control, and derive associated acceptable invasion risk. Finnoff et al. (2007) argue that national and regional managers frequently implement policies when invaders have arrived and show that this can be explained by risk aversion if the effect of control on invader population is certain whereas the effect of prevention is not. The importance of recognizing uncertainty in the spread of an introduced invader is supported by ecological literature, where it is argued that the efficacy of control is dependent on the progress stage of the invasion (e.g. Grice, 2009). It is, e.g., suggested that control strategies should exploit times when the invasive species population is low. It is also emphasized that ability of the invasive species to compete with resident species and survive in the new habitat is increasingly more important compared to biological dispersal ability (MacArthur and Wilson, 1967). Therefore, the focus in this article is on the role that life history of invasive and commercial resident species plays for the economic damage of invasions actually occurring, while we abstract from the role that life history can have for species' dispersal. Developing a bio-economic model, we analyze how the trade-off between control and adaptation depends on invasive and resident species life history and on technologies for control and adaptation. In our

view, this paper contributes to the literature on control and adaptation through *i*) the inclusion of an interaction between invading and resident species, *ii*) the use of an age-structured model, which allows for analysis of the role of the age of the invader at the time of arrival as well the role of age for the optimal control and harvesting decisions, and *iii*) modeling of alternative species types that differ only in terms of life history, which allows for the analysis of life history for the above trade-off.

The main results of this paper show that life history is an important factor for the trade-off between direct control of the invader and adaptation of harvesting strategies for the resident species. Life history is also crucial for the trade-off between early and delayed control of the invader. When a direct control technology is not available there are larger economic losses with a resident species specialized in survival, whereas if such technologies are available, the larger losses occur with a resident species specialized in reproduction.

The paper is organized as follows; the bio-economic model is presented in Section 2, and data for the empirical are given in Section 3. Next, the results are presented and the paper ends with a brief summary and discussion in Section 5.

2. Bio-economic model

The bio-economic model builds on Elofsson et al., (2012) and adds the possibility of adaptation measures. In order to analyze the role of invading and resident species life history, we then classify species into two types, *A* and *B*, corresponding to iteroparous species of type I and III, respectively. The classification is based on the observation that species have a limited amount of

energy available, which must be allocated between fecundity and survival, thereby defining their life history strategy. The type *A* life history is found among species that spend large efforts to protect to their relatively few offspring, thereby increasing the probability of survival of the young, such as e.g. mammals (Deevey, 1947; Polis and Farley, 1980). The type *B* life history is found among species that produce high numbers of young at a cost of low juvenile survival. This type of life history is common among e.g. fish, insects, marine invertebrates, and plants. The two species types have the following characteristics (cf. Lack 1954; Williams, 1966; Pianka and Parker, 1975):

- Type *A* species has, as a juvenile, a high survival rate which falls as age increases. Reproduction is low for all mature age classes.
- Type *B*, juvenile survival is low but the survival rate increases with age. Reproduction is high for reproductive age classes and increases with age.

Following Elofsson et al. (2012) we assume there are two species populations, one resident and one invader, each associated with a life history j , with $j=A,B$. A stock transition relationship describes the development of the populations over time. The fraction of individuals of cohort a surviving until the following year is denoted $\alpha^{a+1,j}$. The number of individuals of the two species in a habitat is assumed to affect survival and offspring production due to competition for limiting resources. Survival and offspring production of the species from one year to another is therefore assumed to be determined by a factor $e^{-\sum (\beta^{aj} R_t^{aj} + \mu^{aj} I_t^{aj})}$, which is decreasing in the number of residents and invaders. The coefficients β^{aj} and μ^{aj} indicate, respectively, the carrying capacity of the habitat with regard to the species own population, and the degree of competition for scarce resources such as food or space between the two species.

The number of individuals in cohort $a+1$ of the resident species, $R_{t+1}^{a+1,j}$, counted before the reproductive season, is defined by:

$$R_{t+1}^{a+1,j} = R_t^{aj} \alpha^{a+1,j} e^{-\sum_a (\beta^{aj} R_t^{aj} + \mu^{aj} I_t^{aj})} - H_t^{aj} \quad \forall j = A, B, \quad \forall a = 0, 1, \dots, \bar{a}$$

where

$$H_t^{aj} = 0 \quad \forall a < \underline{h}, \quad (1)$$

$$H_t^{aj} \geq 0 \quad \forall \underline{h} \leq a \leq \bar{a} \text{ and}$$

$$R_0^{aj} = \bar{R}_0^{aj}$$

where R_t^{aj} and I_t^{aj} denote the number of individuals of resident and invader species, respectively, belonging to cohort a at time t and H_t^{aj} is the harvest of the resident species at time t . It is assumed that only individuals above age \underline{h} are captured. The number of individuals in different cohorts of the resident species at time $t=0$ is given by \bar{R}_0^{aj} .

Individuals of the resident species are assumed to reach maturity at the age of \underline{a} , and continue to reproduce until they die at an age of \bar{a} . Resident species recruitment is assumed to be determined by:

$$R_t^{0j} = \sum_{a \geq \underline{a}}^{\bar{a}} \left[R_t^{aj} \alpha^{0j} e^{-\sum_a (\beta^{0j} R_t^{aj} + \mu^{0j} I_t^{aj})} m^{aj} e^{-\sum_a (\beta^{aj} R_t^{aj} + \mu^{aj} I_t^{aj})} \right] \quad \forall j = A, B, \quad (2)$$

where $m^{aj} e^{-\sum_a (\beta^{aj} R_t^{aj} + \mu^{aj} I_t^{aj})}$ is the gross number of offspring produced and $\alpha^{0j} e^{-\sum_a (\beta^{0j} R_t^{aj} + \mu^{0j} I_t^{aj})}$ is the survival rate in the same year, with both terms being affected by inter- and intra-species competition.

Stock dynamics of the invading species are defined by:

$$I_{t+1}^{a+1,j} = I_t^{aj} \alpha^{a+1,j} e^{-\sum_a (\beta^{aj} I_t^{aj} + \mu^{aj} R_t^{aj})} + \bar{V}_t^{aj} - W_t^{aj} \quad \forall j = A, B, \text{ and } \forall a = 0, 1, \dots, \bar{a}$$

where

$$W_t^{aj} = 0 \quad \forall a < \underline{g},$$

$$W_t^{aj} \geq 0 \quad \forall \underline{g} \leq a \leq \bar{a} \text{ and}$$
(3)

where \bar{V}_t^{aj} , with $\bar{V}_t^{aj} \geq 0$, is the number of individuals of cohort a of the invading species entering the habitat in time period t , and W_t^{aj} is the number of invaders subject to control in the same time period. It is assumed that no individual below age \underline{g} is captured.

Invader recruitment is analogous to that of the resident:

$$I_t^{0j} = \sum_{a \geq \underline{a}} \left[I_t^{aj} \alpha^{0j} e^{-\sum_i (\beta^{0j} I_t^{aj} + \mu^{0j} R_t^{aj})} m^{aj} e^{-\sum_a (\beta^{aj} I_t^{aj} + \mu^{aj} R_t^{aj})} \right] \quad \forall j = A, B$$
(4)

It is assumed that there is a sole manager of the habitat, whose objective is to maximize the net present value from joint management of the two species. The manager is assumed to be a price-taker in all markets. Revenues from harvests of the resident species, TR_t^j , are:

$$TR_t^j = p^j \sum_{a \geq \underline{h}} w^{aj} H_t^{aj} \quad ,$$
(5)

where p^j is the price per kilo, w^{aj} is the age-specific weight of the resident species and H_t^{aj} is the catch of cohort a . The total harvesting cost, TCR , is:

$$TCR_t^j = \eta^j \left(\sum_{a \geq h} w^{aj} R_t^{aj} \right)^{\gamma^j} \left(\sum_{a \geq h} w^{aj} H_t^{aj} \right)^{\delta^j}, \quad (6)$$

where γ^j is the stock elasticity, δ^j the output elasticity and η^j a calibration parameter (cf. Danielsson et al. [1997], Sandberg [2006]).

Following Olson and Roy (2005), the total cost for control of the invader is assumed to depend on the magnitude of control as well as on the stock of the invader, and is defined by:

$$TCI_t^j = \psi^j \left(\sum_{a \geq h} w^{aj} I_t^{aj} \right)^{\theta^j} \left(\sum_{a \geq h} w^{aj} W_t^{aj} \right)^{\tau^j}, \quad (7)$$

where ψ^j and θ^j are the stock and output elasticities, and τ^j is a calibration parameter.

Profits in a given time period, π_t , are defined by:

$$\pi_t = TR_t^j - TCR_t^j - TCI_t^j, \quad (8)$$

and the total net present value, $TNPV$, is given by:

$$TNPV = \sum_{t=1}^T \rho_t \pi_t, \quad (9)$$

where $\rho_t = (1/(1+r))^t$ is the discount factor with r as the annual discount rate. The manager of the two-population system is assumed to choose harvests and control in order to maximize (9) given (1)-(8). Setting up the Lagrangian function and solving for the Kuhn-Tucker first order

conditions (see Appendix), gives the following equations for the development of H_t^{aj} , W_t^{aj} , R_t^{aj} and I_t^{aj} along the optimal path:

$$\begin{aligned}\rho^{-t} L'_{H^{aj}} &= TR_t^{j'} - TCR_t^{j'} - \rho \lambda_{t+1}^{a+1,j} \leq 0, \\ \rho^{-t} L'_{H^{aj}} H_t^{aj} &= 0, \quad 0 \leq H_t^{aj}, \quad t = 0, 1, \dots, \quad \text{and } a = \underline{h}, \dots, \bar{a}\end{aligned}\tag{10}$$

$$\begin{aligned}\rho^{-t} L'_{R_t^{aj}} &= -TCR_t^{j'} + \rho \lambda_{t+1}^{a+1,j} R_{t+1}^{a+1,j'} - \lambda_t^{aj} + \lambda_t^{0j} R_t^{0j'} - \rho \sum_{i=0}^{\bar{i}} \omega_{t+1}^{a+1,j} I_{t+1}^{a+1,j'} - \omega_t^{0j} I_t^{0j'} \leq 0, \\ \rho^{-t} L'_{R_t^{aj}} R_t^{aj} &= 0, \quad R_t^{aj} \geq 0, \quad t = 0, 1, \dots, \quad \text{and } a = 1, \dots, \bar{a} - 1\end{aligned}\tag{11}$$

$$\begin{aligned}\rho^{-t} L'_{W_t^{aj}} &= -TCI_t^{j'} - \rho \varpi_{t+1}^{a+1,j} \leq 0, \\ \rho^{-t} L'_{W_t^{aj}} W_t^{aj} &= 0, \quad 0 \leq W_t^{aj}, \quad t = 0, 1, \dots, \quad \text{and } a = \underline{g}, \dots, \bar{a}\end{aligned}\tag{12}$$

$$\begin{aligned}\rho^{-t} L'_{I_t^{aj}} &= -TCI_t^{j'} + \rho \sum_{a=0}^{\bar{a}} \lambda_{t+1}^{a+1,j} R_{t+1}^{a+1,j'} + \lambda_t^{0j} R_t^{0j'} + \rho \varpi_{t+1}^{a+1,j} I_{t+1}^{a+1,j'} - \varpi_t^{aj} + \varpi_t^{0j} I_t^{0j'} \leq 0 \\ \rho^{-t} L'_{I_t^{aj}} I_t^{aj} &= 0, \quad I_t^{aj} \geq 0, \quad t = 0, 1, \dots, \quad \text{and } i = 1, \dots, \bar{i} - 1\end{aligned}\tag{13}$$

Equation (10) shows that the optimal harvest of an age cohort at time t is determined by the marginal net benefit of harvesting in current period and the marginal user cost, $\rho \lambda_{t+1}^{a+1,j}$. Similarly, equation (11) shows that the resident population is determined by the marginal increase in harvesting cost, the discounted marginal value of the age cohort at time $t+1$, the marginal value of one individual of the cohort at time t , the marginal value of the direct and indirect impact on recruitment, and discounted marginal value of the impacts on survival and recruitment of the invader. Noting the one-to-one relationship between R_t^{aj} and $H_{t-1}^{a-1,j}$, see equation (1), the two last term in equation (11) indicate the additional marginal cost of harvesting at time $t-1$ in the presence of an invasion, due to the increased growth of the invader. The increased growth of the invader will, in turn, reduce growth of the resident population and thereby increase harvesting costs through the stock term in the cost function.

Equation (12) demonstrates that optimal control of the invader is determined by marginal control cost and the negative marginal user value of the invader. Given the one-to-one relationship between control and invader population, equations (12) and (13) show that the marginal user cost of control is jointly determined by the negative increase in control cost owing to the stock effect, the marginal value of the positive impact on resident species survival and reproduction and the negative marginal value of the positive impact on invader species survival and reproduction, divided by the marginal survival of the invader. Therefore, control is higher if the marginal stock effect on control costs is low, there is high competition with the resident species and the own density dependence is low, where the latter occurs when the invader population is small. The remaining first order conditions are included in the Appendix.

3. Data

Data used for the population model are generic data from Järemo and Bengtsson (2011) which illustrate the typical life history of type *A* and *B* species. Both species have a life span of six years, which implies that we have six age cohorts, with $a=0, \dots, 5$. Survival data illustrate the characteristics of the different species types, described above. Hence, a type *B* species has a higher reproduction than type *A*, but a lower juvenile survival. Reproduction parameters are calibrated such that both species have the same finite rate of increase at a stable age distribution and density independence. In the absence of competition between species, the age of highest reproductive value¹ is three for a type *A* organism and five for a type *B*. The age specific intra- and inter-species competition effects, β^{aj} and μ^{aj} , are subjectively set to 0.00001 for all age classes and species. The age-specific weight is assumed to increase linearly with age and is normalized to 1 for 5-year olds of both species. All parameter values that characterize the life histories of the different species types are given in Table 1.

¹ The age with the highest expected reproduction of an individual from their current age onward, given that they have survived to their current age.

TABLE 1. Model Data.

	Age					
	0	1	2	3	4	5
Age specific survival (α^{aA}), sp. A ^a	0.80	0.70	0.50	0.32	0.22	0.14
Age specific survival (α^{aB}), sp. B ^a	0.10	0.30	0.50	0.60	0.70	0.80
Fecundity (m^{aA}), sp. A ^a	0	0	4	4	4	5
Fecundity (m^{aB}), sp. B ^a	0	0	20	40	80	150
Intra- and interspecies competition (β^{ak} and μ^{ak})	0.00001					
Weight at age (w^{aj}), sp. A and B	0.0	0.2	0.4	0.6	0.8	1.0
Number of individuals at $t=0$ (\bar{R}_0^{aA}), sp. A	2239	1497	716	65	0	0
Number of individuals at $t=0$ (\bar{R}_0^{aB}), sp. B	2894	831	397	227	152	16

We assign the identical economic parameters to both species types. The price of harvest, p^j in eq. (5) is normalized to one. Harvest and control technologies are assumed to be similar. It is presumed that only individuals of age 2 or older can be harvested or controlled, respectively. The size of stock elasticity in equations (6) and (7) depends on whether we have group-living or solitary species, i.e. for group-living species a stock elasticity less than minus one can generally be expected (Bjørndal, 1987, 1988). We assign the value -1 to γ^j and θ^j , thereby assuming that the species are relatively uniformly dispersed over the habitat. Output elasticity is determined by the size of scale economies in harvesting and control. Here, the output elasticities τ^j and δ^j are both assumed to be equal to one, implying that we have linear cost functions. Diseconomies of scale would be associated with an output elasticity would be larger than one, whereas under economies of scale it would be smaller than one. The parameters η^j and ψ^j are arbitrarily set to 1. The initial vector \bar{R}_0^{aj} is set as the steady-state stock in the economic profit-maximizing equilibrium with harvest in the absence of invaders and the discount rate r is set to 3 percent, as suggested by e.g. Boardman et al. (2011) to be in concordance with values used for cost-benefit analysis of public projects.

In the following, optimal harvests are simulated over 50 years. Simulations show that when direct control is included then steady state conditions, with positive levels of harvest, control and

populations of both species which last over a longer time, are found for most invasions given the level of propagule pressure assumed here. This contrasts with the situation where harvest adaptation is the only available management measure, i.e. when $W_t^{aj} = 0$. In that case, steady state conditions have not been achieved in simulations. With the resident species initially at the economic equilibrium, steady state condition prevail, approximately, between year 15 and 35, thereafter the resident species is completely harvested when time approaches T .

4. Results

The above model describes a system with two types of decision variables, harvest of the resident species and direct control of the invader. Given that both resident and invasive species can have one out of two different life history types, there are four different possible combinations of resident and invading species types. Furthermore, the invasions can be made by individuals belonging to six different age classes. Thus, there are a large number of different possible invasion scenarios. Below, results are calculated for invasions of ten individuals of a given age and type in each time period in each scenario. The calculations are made using GAMS (Brooke et al. [1998]). In the following, we *(i)* investigate the role of direct control technologies for the economic vulnerability of resident species of different type, *(ii)* compare the scope and timing of control and harvest adaptation, *(iii)* investigate the trade-off between harvest adaptation and direct control, and *(iv)* examine the balance between early and delayed control for invaders of different type and age.

4.1 The role of direct control possibilities for economic damages

In order to investigate the economic implications of a direct control technology being available, we compare the *TNPV* for the case where *(i)* adaptation of harvests of the resident species is the only means available to manage the invader and *(ii)* both adaptation of harvests and direct control of the invader are possible. Results are shown in figure 1. The figure reveals that in the

absence of the direct control technology, there is larger economic damage when the invader is of type *B* or the resident is of type *A*, *ceteris paribus*. With chosen data, the possibility to control invaders directly will substantially improve the *TNPV*. Moreover, when the control option is included, residents of type *A* become economically more robust with regard to invasions compared to type *B*, while the situation is reversed when control is not included. Type *B* remains the more damaging species whether control is included or not. The large positive impact of the control option on a resident type *A* is explained by the high cost for harvest adaptation for this type of species when control is not possible, in combination with the small impact of harvest adaptation on invader population growth due to the comparatively low reproduction of the harvested age-classes. Thus, large adaptation costs are saved when the control option is available. Adding to the effect is that in equilibrium, a larger biomass is harvested for a type *A*, implying that there is a larger value to be spared when applying control.

For a type *B* invader, the relative difference between invaders of different age with regard to the economic damage caused is altered when control is available. Without control, a type *B* age 4 is the most damaging, which is explained by its high remaining life-time reproduction. However, when direct control is possible, a type *B* species age 5 causes the largest economic damage. The explanation is that direct control is effective when directed towards 4-year olds² given their high remaining life-time reproduction. Control of age-class 4 is also the optimal strategy when this is the age of the invader at the time of introduction. However, when the invading age-class is 5 years old, then it is less efficient to wait until the juveniles produced reach age-class 4, given the relatively large growth of the invader population in the meantime. When invaders are age 5 at the time of introduction, only about 1/3 of the direct control is directed towards 4-years olds, while the rest of the control is directed towards 5-year olds. Consequently, with a 5-year old invader, control is less efficient. Moreover, control costs are larger than with a 4-year old invader per individual controlled, given the higher weight of 5-year old individuals. Together, this implies

² Age class 4 is targeted by control when the invader is age-class 3 to 5.

that the control technology is more efficient when the invader is 4 years old, explaining the reversal of the outcome between these age-classes.

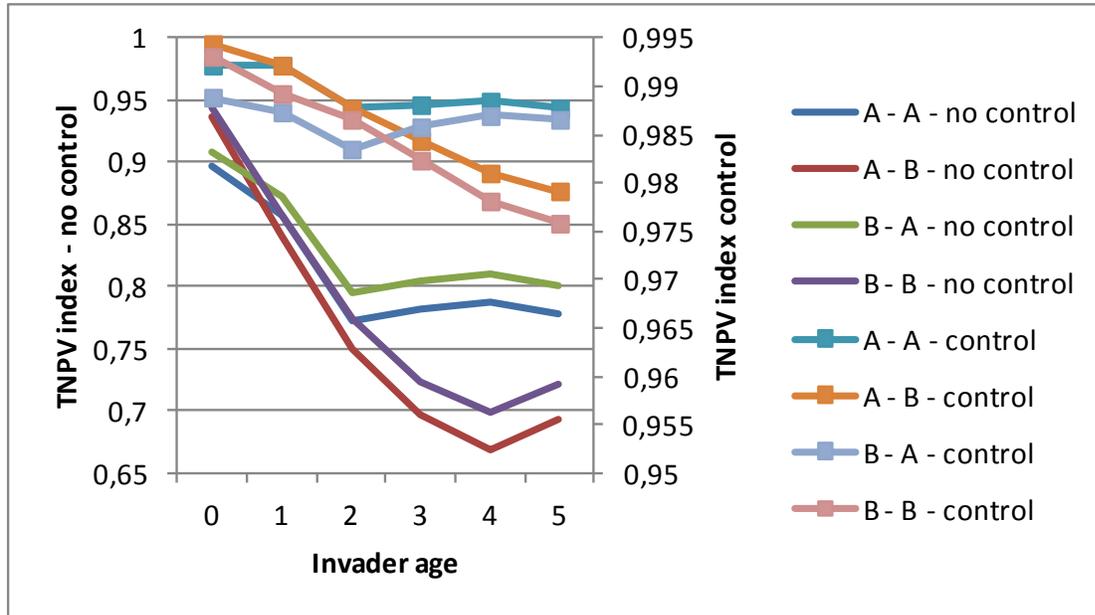


FIGURE 1. *TNPV* of harvest under different invasions. Data series display “resident species type - invasive species type – control option availability”. The vertical axis shows the *TNPV* in the invasion scenario divided by *TNPV* in the case with no invasion. The primary and secondary vertical axis indicates scenarios when a control technology is unavailable and available, respectively.

4.2 Scope and timing of management

The scope and timing of control differs substantially between invasion scenarios. With a type A invader, only age class 2 is controlled if the invader is between zero and two years old at the time of invasion. This is explained by the high damaging potential of age-class 2, see Figure 1, given that this age-class causes the most rapid growth of invader population, in combination with the restriction on control of age-classes below 2, and the lower cost per individual controlled for younger individuals due to their lower biomass. For invaders age class 0-2, control is increasing

over the first years, reaching a stable level after 10-15 years, cf. Figure 2. Low control in the first years is explained by the high control cost because of the small stock of the invader.

For older age classes, control of age class 2 is combined with control of the invading age class. This illustrates the trade-off between immediate control of invading individuals and control directed towards the most damaging age-class as well as the role of control cost where, as mentioned above, control cost is related to weight. Total numbers controlled is increasing over the first years, reaching a stable level after approximately 10 years.

When there is a type *B* invader, control efforts are directed towards age class 3 and 4 when the invader is of age 3 or below. When the invader is age 4, control is focused on this age class only, whereas if the invader is age 5, control efforts are directed towards age classes 4 and 5. A stable level of total control is achieved after 9-20 years, where the adjustment path increases with age.

A comparison of the timing of control and harvest reveals that the presence of an invasion implies that harvests will, in the first few time periods, be higher than without an invasion, because it is anticipated that the future stock of the resident will be lower and hence harvesting costs higher, cf. Figure 2. In the medium term, harvests will be lower than in the no-invasion case.

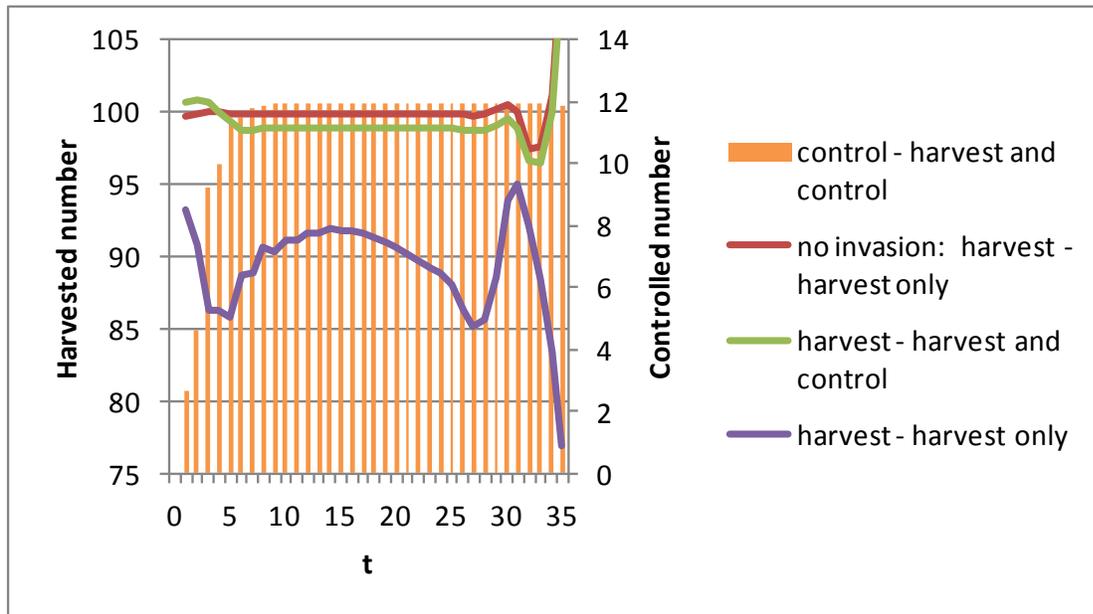


FIGURE 2. Control of invader type A age 2 with a resident B , and harvest of the resident. The data series are indicated by “management strategy – available management strategies”. Harvest in the case with no invasion is included for reference. The primary vertical axis shows the number of resident harvested and the secondary vertical axis the number of invaders controlled.

If there is no possibility to exert direct control towards the invader, harvest adaptation will be used to “crowd-out” the invader, see Figure 2. Over the first five time period, harvests are reduced in order to increase the resident population. This leads to “crowding-out” of the invader and lower harvesting costs in the medium term. Therefore, harvests can again be increased in the medium term, even though they are not as high as in the no-invasion scenario.

4.3 The trade-off between adaptation and control

In principle, the trade-off between harvest adaptation and control is determined by (i) the variation in impact of control of different age classes, where larger variation between age classes implies that direct control is favored over adaptation, and (ii) the costs of control versus harvest

adaptation, where the strategy with lower cost is optimally favored over the other. With the given model, direct control is more efficient with an invading type *B* species given the larger variation in reproduction between age classes. As shown in Elofsson et al. (2012), adaptation is generally more efficient with a resident type *B* species due to the high reproduction of the marginally harvested age class 4, in combination with the modest cost for abstaining from harvesting this age class.

Some harvest adaptation is always optimal, given the construction of the model. However, with equal parameters in the harvest and control cost functions such as assumed above, harvests are little adapted in the medium and long term if there is a possibility to directly and selectively control the invader. In order to investigate conditions when harvest adaptation becomes a significant tool to the policymaker, we examine the role of control cost function parameters for this choice. It seems reasonable that control costs could be higher compared to harvesting costs, given that the invaders behavior might not be equally well known and technologies for control might not be well established. This implies that the cost level ψ^j and the output elasticity could be higher, while there are no obvious expectations to put on the stock elasticity.

Results show that management strategies are insensitive to assumptions about the calibration parameter ψ^j as well as to stock elasticity in the control cost function. This confirms results in Elofsson et al. (2012) regarding the role of the corresponding parameters in the harvesting cost function. If, however, the output elasticity of the control cost function is high, implying rapidly increasing marginal cost of control, harvest adaptation can be included to a significant extent in optimum. We here chose to measure harvest adaptation through the impact on the resident species population. In Figure 3 below, the increase in the resident population, motivated by the crowding-out effect that it has on the invader, is shown when the output elasticity of the control cost function is three times as large as in the reference case. The figure suggests that harvest adaptation can be of importance in an optimal policy, in particular with a resident type *B* and an

invader type *A* age 2. This is also the scenario with largest economic damages, cf. Figure 1. In scenarios where both resident and invasive species are of type *A*, harvest adaptation is of little importance, even with a high output elasticity of control cost.

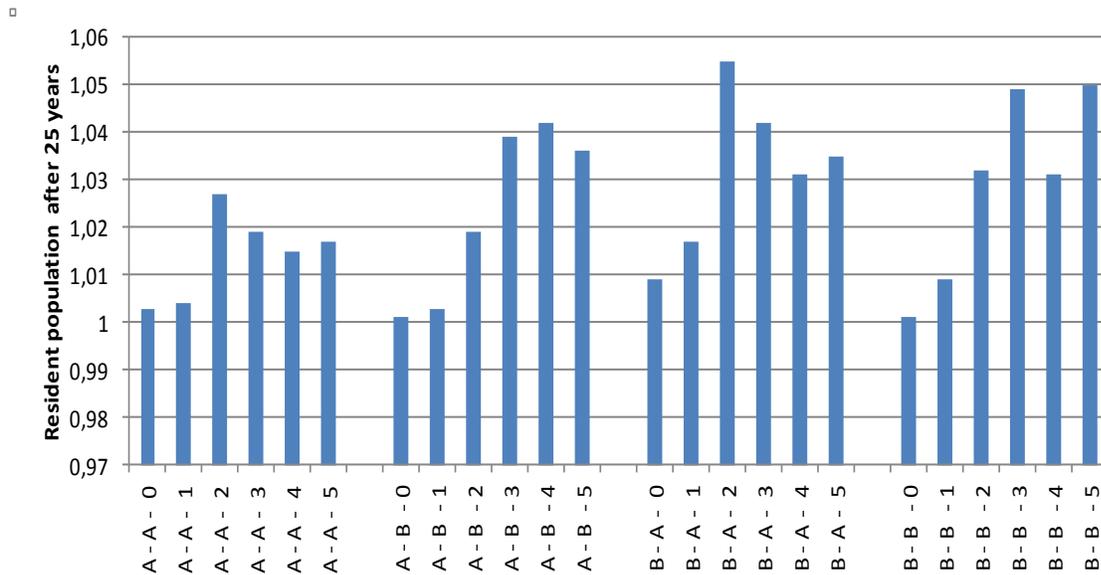


FIGURE 3. Harvest adaptation. Increase in resident species population after 25 years when the output elasticity of the control cost function equals 3. The vertical axis shows total population number in the relevant scenario divided by reference scenario.

Next, the question is how harvest adaptation affects the control strategy. We look at the scenario with the largest harvest adaptation when $\theta^j = 3$, i.e. with a resident *B* and invading *A* age 2. Figure 4 shows the optimal development of the resident population and of control of the invader. The results illustrate that with rapidly increasing marginal costs of control, harvest are reduced such that the resident population increases in the medium term in order to crowd out the invader. The higher control costs imply that control is reduced over the first 15 years. Thereafter, control is larger than in the reference case for the next 25 years. The larger control is explained by falling control costs because of the more rapid increase in the stock of the invader over the first 15 years, in combination with larger marginal benefit of control under a larger invader stock as

the marginal impact of the invader on survival and reproduction is increasing in the invader stock. A paradoxical consequence of the higher output elasticity is that the total number of individuals controlled after 35-40 years only slightly exceeds the numbers controlled in the reference scenario, but the invader population is more than eight times as large.

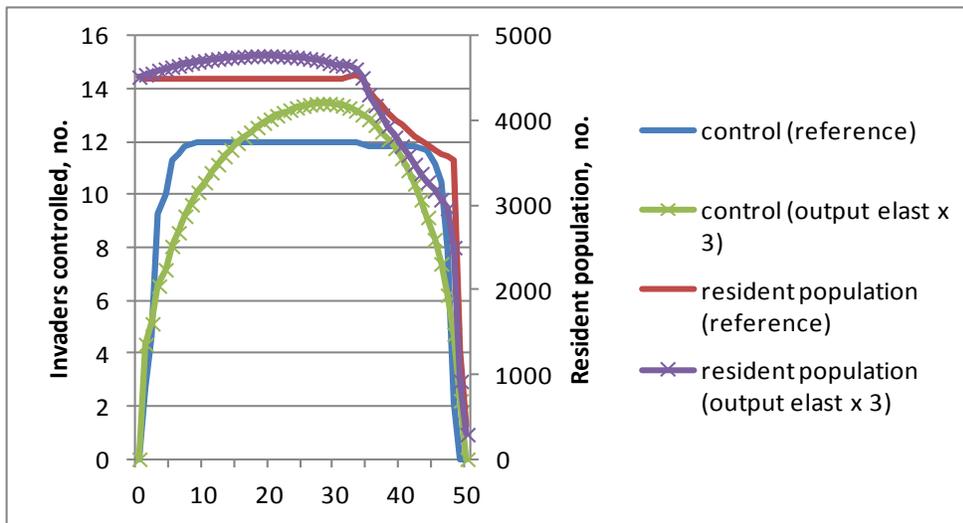


FIGURE 4. Harvest adaptation and control in a scenario with a type *B* resident and invader type *A* age 2. Comparison of reference scenario and a scenario where $\theta^j = 3$.

4.4 Early or delayed control

Next we investigate the balance between efforts to control the invader at an early stage and efforts to control the invader when it is already established. Control at an early stage, namely at the time of introduction, can be approximated by control of the invading age class³. Control when the invader is established can be approximated by control of all other age-classes. The cost

³ In almost all scenarios, control of the invading age class never exceeds 10 individuals, i.e. the number of individuals entering the ecosystem. The single exception is with an invading type *B* age 4, where steady state control is 10-12 individuals.

of control of a particular age class \hat{a} , $CI_t^{\hat{a}j}$, is calculated as the total cost of control, weighted by the biomass-share of that particular age class, i.e.

$CI_t^{\hat{a}j} = \psi^j \left(\sum_{a \geq \underline{h}} w^{aj} I_t^{aj} \right)^{\theta^j} \left(\sum_{a \geq \underline{h}} w^{aj} W_t^{aj} \right)^{\tau^j} (w^{\hat{a}j} W_t^{\hat{a}j}) / \left(\sum_{a \neq \hat{a}} w^{aj} W_t^{aj} \right)$. The net present value of this cost then constitutes the aggregate cost for controlling that particular age class.

The relative costs of efforts spent on early control of invading and delayed control of other age classes are shown in Figure 5 below. The balance between early and delayed control is determined by the relative costs of controlling different age classes, which is determined by age-specific weight. Also, early control is favored if future damages or the costs of delayed control are large. Future damages are large if the invader population grows rapidly in number, and future control costs are large if the invader increases rapidly in weight with age.

Early control of the invading age class is the only type of control if the invader is a type *A* age 2 or a type *B* age 4, independently of the resident species type, see Figure 5. In both cases, these age-classes cause large economic damage given that invader population grows rapidly in numbers. Thus, early control prevents large future damages.

Relatively larger costs are optimally incurred for early control of the invading age class if the resident is of type *A* than if it is of type *B*. This is explained by the larger long term damage of an additional invader individual when there is a resident *A*, given the lower reproduction of type *A* and hence the slower recovery of the resident stock, once it is harmed by competition of an invader.

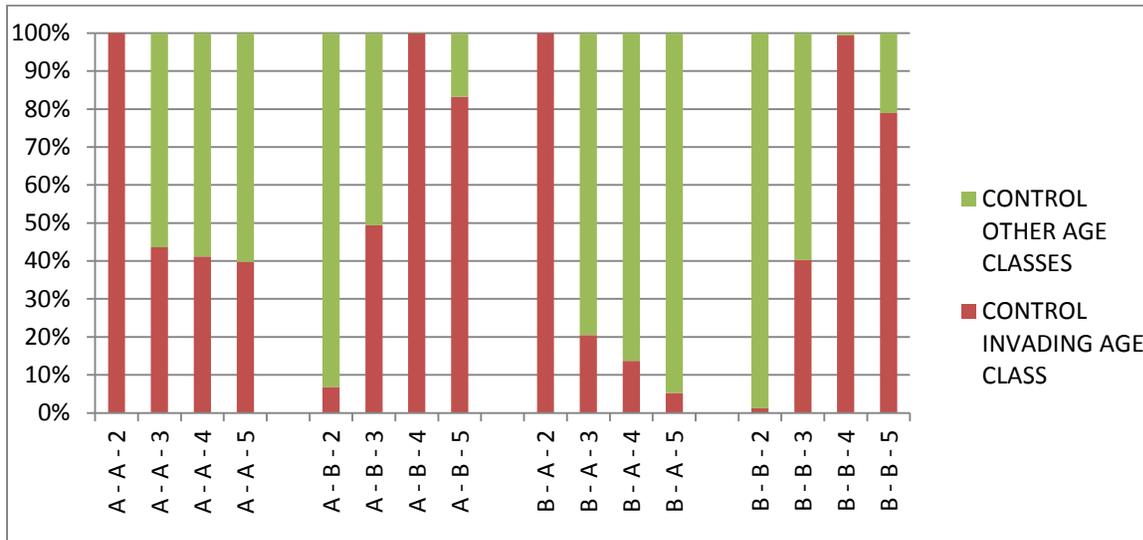


FIGURE 5. Optimal discounted relative costs for control of different age classes when control costs are determined by the biomass controlled. Results are indicated by “resident species type – invader species type – invader age”.

The results in Figure 5 are calculated assuming that control costs are determined by controlled biomass. An alternative approach would be to assume that control costs are determined by the number of individuals controlled. In order to investigate whether such an assumption would have a significant impact on the balance between early and delayed control, we calculate control costs assuming that all individuals in the invader population have the same weight. This implies that control costs are independent of invader age, and thus only determined by the number of individuals. The results from these calculations are shown in Figure 6. Under such a scenario one would generally expect that older age classes will be controlled to a higher degree than shown in Figure 5, because the cost of controlling older individuals is comparatively lower. This will hold provided that, in the reference scenario, (i) there are older age classes which can be controlled and (ii) the control cost reduction is sufficient to motivate a change of strategy, given the difference in damage done to the resident species. This damage is determined by reproduction and survival of the individual controlled as well as the size of resident and invader stocks.

From Figure 6 one can find that with equal weight per individual, 0.5 weight units, there are, as can be expected, relatively more resources devoted to early control for all invading age classes 3-5 when the resident is type *A*, given the relatively spoken lower cost for controlling these age classes, compared to the case in Figure 5. With a type *A* resident, there are, however, also more resources devoted to early control of type *B* invaders age 2. The invader population in present in the habitat has a higher biomass in the steady state⁴ compared to the situation depicted in Figure 5, which makes control less costly overall, wherefore total control is larger. The higher biomass is explained by juveniles constituting a large share of the population and they now have a relatively spoken higher weight per individual. Given the increase in total control, all individuals age 3 are controlled and therefore, more control is directed towards invaders age 2.

With a resident *B* and an invading *A*, fewer resources are devoted to early control for all invading age classes but age class 5, which is explained by the lower control cost for older age classes. With a resident *B* and an invading *B*, more resources are devoted to early control if the invader is age class 3 or 5, and less if it is age class 2 or 4. For invasions of age class 2 and 4, relatively more resources are allocated to the control of older, more damaging age classes. For invaders of age class 5, the age class is subject to more control as it is highly damaging. For invasions of age class 3, the large share of resources spent on control of the invading age class is, again, explained by the fact that the whole age class 4 is already subject to control. In this scenario equal weight implies that, compared to the reference scenario, control of the invading age class is first reduced in the initial time periods. The manager knows that it will now be less expensive to control age class 4, compared to the reference scenario depicted in Figure 5. Therefore, he or she initially postpones control of 3-year old individuals until they are 4 years old, thereby saving on control costs. Thereafter periods, control is increased above levels in the reference scenario for a number of time periods, because control costs are lower with equal weight as soon as there are enough

⁴ Given that juveniles constitute a large share of the population and now have a higher weight.

juveniles in the population. The invader population stabilizes at a somewhat lower level, compared to the reference scenario.

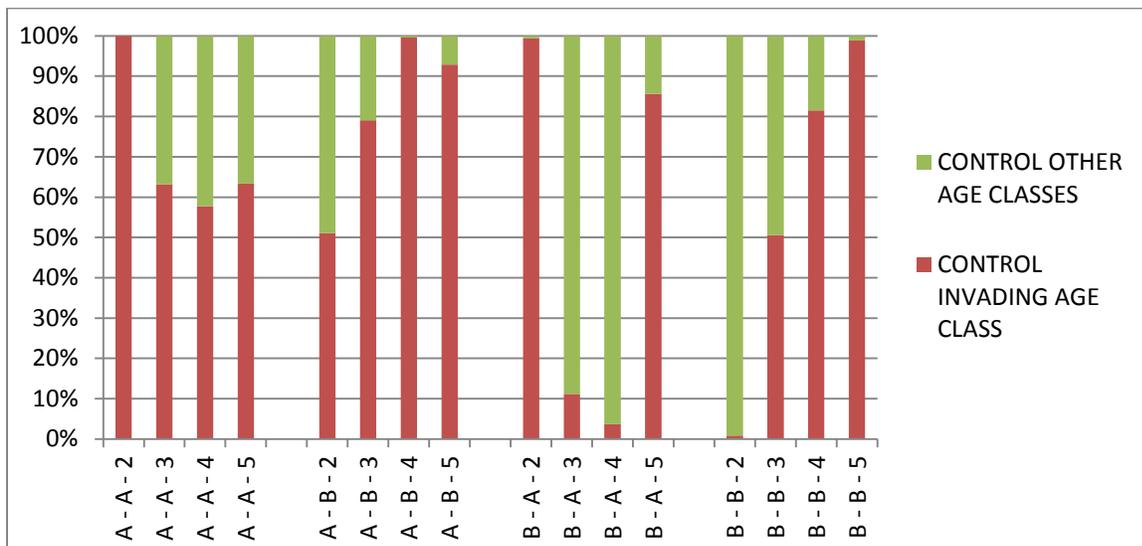


FIGURE 6. Optimal discounted relative costs for control of different age classes when control costs are determined by the number of individuals controlled. Results are indicated by “resident species type – invader species type – invader age”.

5. Summary and discussion

Using a model of optimal co-management of one resident and one invading species, we attempt to examine the balance between harvest adaptation and direct control. We also investigate the trade-off between early and delayed control of invaders once they have entered a new habitat. Both issues are investigated with a focus on species life history and invader age for the trade-offs made. Assuming similar cost functions for harvest of the resident and control of the invader, as well as similar functions describing the development of the two populations, allows us to isolate the role of life history for the choice of management strategy.

The analysis shows that the marginal user cost of the resident species is determined by density of the species, given the role that density has for harvesting cost, survival and reproduction, and by the development of the stock of the invasive species, given the competition between the two for scarce resources such as food or space. Correspondingly, the marginal user cost of the invader is determined by sensitivity of control cost to invader density as well as by density dependence of invader growth and the degree of competition between the two species.

Certain species are, through evolution, specialized in survival rather than reproduction. Results from numerical simulations suggest that this type of species is more economically vulnerable to invasions if harvest adaptation is the only available management tool, compared to species which have specialized in reproduction. However, the situation is reversed if direct and selective control of the invader is possible. In that case, species specialized in reproduction rather than survival, become the most vulnerable type. The reversal of outcome is caused by the inefficiency of harvest adaptation as a tool to manage invaders when the resident species cannot, with the help of harvesting strategy choices, be made to rapidly change its grow rate, such as is the case for species specialized in survival.

Results also show that although direct control is initially costly when the invader population is small and hence individuals are hard to find in the habitat, control rapidly increases and a steady state with constant control, harvest and populations appears within a limited number of years. This outcome differs from the case where only harvest adaptation is possible, as in that case steady states seem unlikely to arise. If the output elasticity of control is high enough, solutions which include both control and harvest adaptation can be optimal. An exception is when both resident and invader species are specialized in survival. In that case harvest adaptation seems little relevant as a tool to reduce economics damages from invasions.

The choice between early control of the invader at the time of invasion and delayed control in later time periods is determined by differences in costs and effects of controlling different age

classes. Relatively larger costs are optimally devoted to early control if the resident is of type A. This is mainly explained by a slower recovery of the resident stock, once it is harmed by an invader.

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Appendix

The manager of the two-population system is assumed to choose harvests of the resident species and control of the invader in order to maximize (9) given (1)-(8). Let λ_t^{aj} denote the Lagrange multipliers for the constraints (1) and (2) and ϖ_t^{aj} the Lagrange multipliers for the constraints (3) and (4). The Lagrangian function is then:

$$L = \sum_{t=1}^T \left\{ \begin{aligned} & \rho^t \left[TR_t^j(H_t^{aj}) - TCR_t^j(R_t^{aj}, H_t^{aj}) - TCI_t^j(I_t^{aj}, W_t^{aj}) \right] + \\ & \rho \sum_{a=0}^{\bar{a}} \lambda_{t+1}^{a+1,j} \left(R_{t+1}^{a+1,j}(R_t^{aj}, I_t^{aj}, H_t^{aj}) - R_{t+1}^{a+1,j} \right) + \\ & \lambda_t^{0j} \left\{ R_t^{0j}(R_t^{aj}, I_t^{aj}) - R_t^{0j} \right\} + \\ & \rho \sum_{a=0}^{\bar{a}} \varpi_{t+1}^{a+1,j} \left(I_{t+1}^{a+1,j}(I_t^{aj}, R_t^{aj}, W_t^{aj}) - I_{t+1}^{a+1,j} \right) + \\ & \varpi_t^{0j} \left\{ I_t^{0j}(I_t^{aj}, R_t^{aj}) - I_t^{0j} \right\} \end{aligned} \right\} \quad (A1)$$

The first order conditions for this maximization problem, including the complementary slackness conditions, are:

$$\begin{aligned} \rho^{-t} L'_{H_t^{aj}} &= TR_t^{j'} - TCR_t^{j'} - \rho \lambda_{t+1}^{a+1,j} \leq 0, \\ \rho^{-t} L'_{H_t^{aj}} H_t^{aj} &= 0, \quad 0 \leq H_t^{aj}, \quad t = 0, 1, \dots, \text{ and } a = \underline{h}, \dots, \bar{a} \end{aligned} \quad (A2)$$

$$\begin{aligned} \rho^{-t} L'_{W_t^{aj}} &= -TCI_t^{j'} - \rho \varpi_{t+1}^{a+1,j} \leq 0, \\ \rho^{-t} L'_{W_t^{aj}} W_t^{aj} &= 0, \quad 0 \leq W_t^{aj}, \quad t = 0, 1, \dots, \text{ and } a = \underline{g}, \dots, \bar{a} \end{aligned} \quad (A3)$$

$$\begin{aligned} \rho^{-t} L'_{R_t^{aj}} &= -TCR_t^{j'} + \rho \lambda_{t+1}^{a+1,j} R_{t+1}^{a+1,j'} - \lambda_t^{aj} + \lambda_t^{0j} R_t^{0j'} - \rho \sum_{i=0}^{\bar{i}} \omega_{t+1}^{a+1,j} I_{t+1}^{a+1,j'} - \omega_t^{0j} I_t^{0j'} \leq 0, \\ \rho^{-t} L'_{R_t^{aj}} R_t^{aj} &= 0, \quad R_t^{aj} \geq 0, \quad t = 0, 1, \dots, \text{ and } a = 1, \dots, \bar{a} - 1 \end{aligned} \quad (A4)$$

$$\rho^{-t} L'_{R_t^{0j}} = \rho \left[\lambda_{t+1}^{1j} R_{t+1}^{1j'} + \sum_{a=0}^{\bar{a}} \lambda_{t+1}^{a+1,j} R_{t+1}^{a+1,j'} \right] + \lambda_t^{0j} \left\{ R_t^{0j'} + 1 \right\} + \rho \sum_{a=0}^{\bar{a}} \left[\varpi_{t+1}^{a+1,j} I_{t+1}^{a+1,j'} \right] + \varpi_t^{0j} I_t^{0j'} \leq 0,$$

$$\rho^{-t} L'_{R_t^{0j}} R_t^{0j} = 0, R_t^{0j} \geq 0, t = 0, 1, \dots$$

(A5)

$$\rho^{-t} L_{I_t^{aj}} = -TCI_t^{j'} + \rho \sum_{a=0}^{\bar{a}} \lambda_{t+1}^{a+1,j} R_{t+1}^{a+1,j'} + \lambda_t^{0j} R_t^{0j'} + \rho I_{t+1}^{a+1,j'} - \varpi_t^{aj} + \varpi_t^{0j} I_t^{0j'} \leq 0$$

$$\rho^{-t} L_{I_t^{aj}} I_t^{aj} = 0, I_t^{aj} \geq 0, t = 0, 1, \dots, \text{ and } i = 1, \dots, \bar{i} - 1$$

(A6)

$$\rho^{-t} L_{I_t^{0j}} = \rho \sum_{a=0}^{\bar{a}} \lambda_{t+1}^{a+1,j} R_{t+1}^{a+1,j'} + \lambda_t^{0j} R_t^{0j'} + \rho \varpi_{t+1}^{a+1,j} I_{t+1}^{a+1,j'} + \varpi_t^{0j} \left(I_t^{0j'} - 1 \right) \leq 0,$$

$$\rho^{-t} L_{I_t^{0j}} I_t^{0j} = 0, I_t^{0j} \geq 0, t = 0, 1, \dots,$$

(A7)

$$\rho^{-t} \frac{\partial L}{\partial (\rho \lambda_{t+1}^{a+1,j})} = R_{t+1}^{a+1,j} \left(R_t^{aj}, I_t^{aj}, H_t^{aj} \right) - R_{t+1}^{a+1,j} = 0$$

(A8)

$$\frac{\partial L}{\partial \lambda_t^{0j}} = R_t^{0j} \left(R_t^{aj}, I_t^{aj} \right) - R_t^{0j} = 0$$

(A9)

$$\frac{\partial L}{\partial (\rho \varpi_{t+1}^{a+1,j})} = I_{t+1}^{a+1,j} \left(I_t^{aj}, R_t^{aj}, W_t^{aj} \right) - I_{t+1}^{a+1,j} = 0$$

(A10)

$$\frac{\partial L}{\partial \varpi_t^{0j}} = I_t^{0j} \left(I_t^{aj}, R_t^{aj} \right) - I_t^{0j} = 0$$

(A11)



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