

WILDLIFE RESERVES, POPULATIONS, AND HUNTING OUTCOME WITH SMART WILDLIFE

FRANK JENSEN

Department of Food and Resource Economics, Faculty of Science, University of Copenhagen,
Frederiksberg C, Denmark
E-mail: fje@ifro.ku.dk

JETTE BREDAHL JACOBSEN*

Department of Food and Resource Economics and Center for Macroecology, Evolution and
Climate Change, Faculty of Science, University of Copenhagen, Frederiksberg C, Denmark
E-mail: jbj@ifro.ku.dk

NIELS STRANGE

Department of Food and Resource Economics and Center for Macroecology, Evolution and
Climate Change, Faculty of Science, University of Copenhagen, Frederiksberg C, Denmark
E-mail: nst@ifro.ku.dk

BO JELLESMARK THORSEN

Department of Food and Resource Economics and Center for Macroecology, Evolution and
Climate Change, Faculty of Science, University of Copenhagen, Frederiksberg C, Denmark
E-mail: bjt@ifro.ku.dk

ABSTRACT. We consider a hunting area and a wildlife reserve and answer the question: How does clever migration decision affect the social optimal and the private optimal hunting levels and population stocks? We analyze this in a model allowing for two-way migration between hunting and reserve areas, where the populations' migration decisions depend on both hunting pressure and relative population densities. In the social optimum a pure stress effect on the behavior of smart wildlife exists. This implies that the population level in the wildlife reserve tends to increase and the population level in the hunting area and hunting levels tend to decrease. On the other hand, the effect on stock tends to reduce the population in the wildlife reserve and increase the population in the hunting area and thereby also increase hunting. In the case of the private optimum, open-access is assumed and we find that the same qualitative results arise when comparing a situation with and without stress effects, but of course at a higher level of hunting. We also show that when net social benefits of hunting dominate the net social benefits of populations, wildlife reserves are optimally placed in areas of low carrying capacity and vice versa.

KEY WORDS: Hunting stress, migration behavior, social optimum, open access.

1. Introduction. The simultaneous role of reserves for protecting wildlife populations and biodiversity in the reserve and sustaining hunting or fishing

*Corresponding author. Jette Bredahl Jacobsen, Department of Food and Resource Economics and Center for Macroecology, Evolution and Climate Change, Faculty of Science, University of Copenhagen, Rolighedsvej 23, DK-1958 Frederiksberg C, Denmark, e-mail: jbj@ifro.ku.dk

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outcomes in neighboring communities has long been a focus of conservation policies in both developed and less-developed countries. Resource economists have investigated optimal hunting or harvest levels around the reserves under various assumptions about regulation context, reserve characteristics, density dependent migration rates in and out of reserves, and cost-benefits of population and harvest levels (e.g., Skonhofs et al. [2002], Armstrong and Skonhofs [2006]). With very few exceptions (see Naevdal [2008] and Naevdal et al. [2012]), the behavior of the species in question has been assumed unaffected by the hunting efforts or the direct effect of the size of the harvest. In this paper, we relax this assumption by allowing for hunting to affect directly wildlife behavior and migration rates between reserve and nonreserve areas.

From wildlife ecology research we know that many species are able to adapt and change their behavior in response to predators, including human hunting pressures (e.g., Keuling et al. [2008]). Theoretical models of predator-prey relationships have recognized that sophisticated behavioral interaction among some types of prey and predators is needed for such relationships to be ecologically stable over longer periods of time. Naevdal [2008] contains a survey of ecological literature showing that with respect to wildlife reserve foraging, migration, and population dynamics respond to predatory pressure. Neill [1990] and Miller [2002] illustrate that animals weight the risks of being eaten against the benefits of foraging. Similar behavioral reactions to predation through hunting would appear reasonable. Brown and Kevin [1999] and Heino and Godø [2002] show that fish have substantial capability of learning how to avoid being captured. With respect to hunting, Baskin et al. [2004] estimate the distance that a moose will cover in order to escape hunters. Glushkov [1976] also shows that escape behavior of a moose depends on local hunting pressure. In addition, Laurian et al. [2000] find that human hunting affects habitat selection. More recently, smart and advanced behavioral responses to hunting have been documented empirically for elk (Ciuti et al. [2012]). These behavioral adaptations are not only likely to have significant influence from an evolutionary perspective, but may vary and change during the life of the individual animal in response to exposures and experiences. In the case of elk, Ciuti et al. [2012] find a difference in movement behavior between harvested and surviving animals, both with respect to spatial behavior and in time, including a weekend effect of hunting. Typically, animals with bolder behavioral traits were more frequently harvested. Other studies find that the game's stress levels and mortality of offspring increase with human disturbances (Phillips and Alldredge [2000], Shiverly et al. [2005]). Thus, overall there seems to be evidence that animals respond to predatory pressure.

It is, therefore, relevant to consider how stress effects from hunting can be included in a model for a wildlife reserve. One result of increasing stress may be increased migration out of areas with high hunting pressure, and reduced migration to such areas. It seems likely that accounting for such dynamics will have implications for optimal hunting levels around a reserve and for long-term equilibrium population

levels in and around the reserve itself. We focus on such equilibrium effects of hunting behavior interaction, assuming that behavioral traits are constant over time. We acknowledge that hunting and in particular selective hunting may affect the genetic pool of the population, including behavioral traits. For example, studies on trophy hunting show that it may boost the male population and yield an unnatural high male to female ratio (Naevdal et al. [2012]) or decline the horn size and body mass over time (Coltman et al. [2003]). For fisheries Favro et al. [1979] show that selective pressure caused by harvesting has been so massive that behavioral and physical adaptation has occurred. We leave the analysis of possible genetic drift on behavior for later research. The simultaneous role of reserves for protecting wildlife species and at the same time sustaining hunting or fishing outcomes has been investigated in numerous studies, in particular in the marine resource literature (e.g., Armstrong [2007], Gaines et al. [2010]). Armstrong [2007] reviews the literature on marine management and points to the benefit of reserves as usually being in the form of some density dependent dispersal into the surroundings of the reserve. However, there is little empirical knowledge of the actual dispersal effects. For that reason, it has long been recognized that under certain assumptions about the fishery effort (open-access effort) it will be most profitable to establish marine reserves in areas of high natural productivity (Holland and Brazee [1996]). Through natural dispersion this may increase fishing levels outside the reserve.

The marine reserve models (e.g., Armstrong [2007]) allow for dispersal in and out of reserves. However, dispersal (or migration in our terrestrial wildlife model) is usually assumed to depend solely on the population density within the reserves and nonreserves, and not to be sensitive to the fishing or hunting efforts. This may be a reasonable short-run assumption for fish that may be less likely to learn and adapt their behavior to observed fishery activities than higher order animals (in the long run, however, selection pressure may imply changes in species behavior). As a result, increasing migration or dispersal rates tend to undermine the effects of natural reserves on fishery outcomes in neighboring areas. A large density dependent migration effect allows open-access fishery or hunting efforts to slowly drain even the reserve population levels down towards their critical threshold (Flaaten and Mjølhus [2010], Ngoc and Flaaten [2010]). This also holds with asymmetric density dependent migration rates in marine reserves (Armstrong and Skonhoft [2006]). Only few studies consider the effects of reserves on the optimal population size and harvest levels of terrestrial game species. Skonhoft et al. [2002] investigate the optimal hunting of a deer species when hunting is allowed outside reserves and population levels in reserves have social values related to recreation. Their model allows for one-way migration out of reserves, but migration behavior remains exogenous to harvest levels.

As mentioned earlier, Naevdal [2008] and Naevdal et al. [2012] also contribute to wildlife response to hunting pressure and potential stress effects. Naevdal [2008] is particularly relevant to the problem in the current study where we assume

that hunting directly affects wildlife behavior and migration between the hunting area and the wildlife reserve. In Naevdal [2008], migration is derived from an expected utility maximization approach with respect to energy intake and depends on population levels, carrying capacities, and hunting. Naevdal [2008] considers both a case with exogenous and endogenous hunting. In the first case, hunting is constant and in the second case hunting is determined in an open-access model. Thus, a model for endogenous hunting is constructed in a private optimum. A full dynamic simulation model is applied by Naevdal [2008] to solve for the private optimum. We extend the work of Naevdal [2008] by focusing on the question of how clever migration decisions influenced by hunting stress affect both the social and the private optimum hunting level and population stocks. We include a welfare effect of aggregate population stock and harvest and solve for both the social and private optimum. We build and analyze a theoretical dynamic model and simulate the dynamic optimality conditions in the model.

The paper is organized as follows. Section 2 presents the theoretical model, and simulation results are shown in Section 3. Section 4 discusses the main results and potential implications for optimal wildlife reserve and hunting policies.

2. The model. We consider a case of optimal wildlife management in a simple model of two neighboring areas, a wildlife reserve and a hunting area, when migration of game in and out of both areas depends on both relative population densities and hunting pressure in the nonreserve.

2.1. Modeling population dynamics. The population size in the wildlife reserve (labeled with subscript 1) at time t is x_{1t} and the population size in the hunting area (subscript 2) at time t is x_{2t} . We assume that there are two separate populations in the sense that growth is given by two different growth functions, namely $F(x_{1t})$ for the reserve and $G(x_{2t})$ for the hunting area.

Total aggregate harvest from hunting is labeled h_t . We assume that there are n heterogeneous hunters and h_{it} denotes the harvest of hunter i . Therefore, we have that $h_t = \sum_{i=1}^n h_{it}$. In the wildlife reserve there is no hunting. The *net* migration from the reserve to the hunting area is given by $m(h_t, \frac{x_{1t}}{x_{2t}})$. Thus, net migration is the migration from the reserve to the hunting area minus the migration in the opposite direction. If $m(h_t, \frac{x_{1t}}{x_{2t}}) > 0$ there is a net inflow of animals into the hunting area, while $m(h_t, \frac{x_{1t}}{x_{2t}}) < 0$ implies a net migration to the reserve. Note that net migration depends on both harvest and relative population size. Specifically, we assume that $\frac{\partial m}{\partial h_t} < 0$. Thus, the direct effect of increased harvest is a lower net migration from the reserve to the hunting area. This captures a pure stress effect. In addition, it is assumed that $\frac{\partial m}{\partial (\frac{x_{1t}}{x_{2t}})} > 0$, which expresses that an increase in the relative stock size (the population density) in the reserve increases net migration from the reserve to the hunting area.

Based on these assumptions, two resource restrictions may be set up:

$$(1) \quad \dot{x}_{1t} = F(x_{1t}) - m \left(h_t, \frac{x_{1t}}{x_{2t}} \right)$$

$$(2) \quad \dot{x}_{2t} = G(x_{2t}) + m \left(h_t, \frac{x_{1t}}{x_{2t}} \right) - h_t.$$

According to equation (1) the change in population size in the reserve is equal to the natural growth plus/minus the net migration. Likewise, equation (2) describes the change in population size in the hunting area as equal to the natural growth plus/minus net migration but also minus aggregate harvest.

2.2. The hunters and their optimal solution. We consider a situation with n heterogeneous hunters. The gross benefit for hunter i is given by $B_i(h_{it})$ with $B'_i(h_{it}) > 0$ and $B''_i(h_{it}) < 0$. Thus, the hunter has a direct benefit from harvesting, but for simplicity we assume that the hunter has no direct benefit of population size. For hunter i there is also a cost associated with hunting, $c_i(x_{2t}, h_{it})$. We assume that $\frac{\partial c_i}{\partial h_{it}} > 0$, so that a larger harvest implies a larger cost (Clark [1990]). In addition, we assume that $\frac{\partial c_i}{\partial x_{2t}} < 0$ so that a larger population implies a lower cost. This reflects that the larger the stock, the easier a successful hunting outcome is secured, as costs associated with searching for game decrease with increasing population levels. This assumption is common in resource economics, see, e.g. Neher [1990]. In addition, we assume that the second-order derivatives of the cost function are so that the second-order condition is fulfilled.

Note that we have assumed that hunters are heterogeneous and that they have individual gross benefit and cost functions. Thus, a subscript, i , is included in the cost and benefit functions. In addition, we let the harvest of hunter i , h_{it} , be the control variable. Since hunters are heterogeneous, some of them have a large net benefit (gross benefit minus cost) while others have a low net benefit.

We assume that the hunting activity can be characterized as an open-access problem (see, e.g. Clark [1990]). Under open-access each hunter disregards the resource restrictions, (1) and (2), and maximizes static benefit (e.g., Clark [1990] and Naevdal [2008]). Thus, with net benefit as objective for hunter i , the maximization problem becomes:

$$(3) \quad \text{Max}_{h_{it}} [B_i(h_{it}) - c_i(h_{it}, x_{2t})].$$

The first-order condition is:

$$(4) \quad B'_i(h_{it}) - \frac{\partial c_i}{\partial h_{it}} = 0.$$

Equation (4) states that the marginal net benefit is equal to zero. With open-access (free entry and exit) and heterogeneous hunters, equation (4) holds for the marginal participating hunter. For infra-marginal hunters (hunters with a lower cost and/or higher private benefit) a positive net benefit is generated.

Based on (4) we may consider a situation with and without clever migration. A pure stress effect implies increased migration to the wildlife reserve from the hunting area. The effect of this change in population distribution is a change in population densities. This in turn works to increase migration from reserves to hunting areas (a population effect). Thus, two counteracting forces exist. A pure stress causes smart animals to move out of the hunting area and into the wildlife reserve. However, this migration and hunting itself reduce population densities in the hunting area relative to the wildlife reserve. This means more food and habitat available in the hunting area, which induces migration out of the reserve and to the hunting area. We assume that the pure stress effect dominates the population effect. Thus, the total effect of clever migration is to increase population in the wildlife reserve and decrease population in the hunting area.

2.3. The social planner problem and its optimal solution. The social planner is interested in obtaining the highest possible welfare associated with both the hunting outcome and the population level. Part of this welfare is the individual hunter's net benefit of the hunting activity. Thus, hunter benefits are included in the welfare function. However, the social planner also takes into account the flow of benefits generated by wildlife population levels, e.g., conservation benefits, existence, and recreational values. Willingness to pay studies show that people value larger population sizes (see Adamowicz et al. [1998] and Jacobsen et al. [2012]). In other words, other individuals than hunters may have benefits associated with wildlife populations and these benefits must be included in the welfare function. Formally, the welfare function can be defined as $D(x_{1t}, x_{2t}, \sum_{i=1}^n [B_i(h_{it}) - c_i(h_{it}, x_{2t})])$. Note that the welfare function depends on the outcome of each hunter i as hunters are heterogeneous. In addition, we assume that $\frac{\partial D}{\partial x_{1t}} > 0$ and $\frac{\partial D}{\partial x_{2t}} > 0$. The sign of these derivatives is due to the social planner including a benefit of a large population size.

The social planner is interested in maximizing the discounted welfare for all users and includes the two resource restrictions, (1) and (2), in the maximization problem. Thus, the optimization problem becomes:

$$(5) \quad \text{Max}_{h_{1t}, \dots, h_{nt}} \int_{t=0}^{\infty} D \left(x_{1t}, x_{2t}, \sum_{i=1}^n [B_i(h_{it}) - c_i(h_{it}, x_{2t})] \right) \cdot e^{-\delta t} dt$$

s.t.

$$(6) \quad \dot{x}_{1t} = F(x_{1t}) - m\left(h_t, \frac{x_{1t}}{x_{2t}}\right)$$

$$(7) \quad \dot{x}_{2t} = G(x_{2t}) + m\left(h_t, \frac{x_{1t}}{x_{2t}}\right) - h_t,$$

where δ is the discount rate. In equations (5)–(7), h_{it} for $i = 1, \dots, n$ is the control variable while x_{1t} and x_{2t} are the state variables. Because hunters are heterogeneous, individual hunters' harvests are control variables.

Based on equations (5)–(7) a current-value Hamiltonian may be set up (see Neher [1990]):

$$(8) \quad H = D\left(x_{1t}, x_{2t}, \sum_{i=1}^n [B_i(h_{it}) - c_i(h_{it}, x_{2t})]\right) + \lambda_t \left(F(x_{1t}) - m\left(h_t, \frac{x_{1t}}{x_{2t}}\right)\right) + \mu_t \left(G(x_{2t}) + m\left(h_t, \frac{x_{1t}}{x_{2t}}\right) - h_t\right),$$

where λ_t and μ_t are shadow prices or co-state variables. The shadow prices may be interpreted as the welfare gain of a marginal unit of the resource restrictions. Note that if resource restrictions are not included (open-access) $\lambda_t = 0$ and $\mu_t = 0$.

The optimality conditions of society for hunter i with $\frac{\partial h_t}{\partial h_{it}} = 1$ are:

$$(9) \quad \frac{\partial H}{\partial h_{it}} = \frac{\partial D}{\partial B_i} \frac{\partial B_i}{\partial h_{it}} - \frac{\partial D}{\partial c_i} \frac{\partial c_i}{\partial h_{it}} - \lambda_t \left(\frac{\partial m}{\partial h_t}\right) + \mu_t \left(\frac{\partial m}{\partial h_t} - 1\right) = 0$$

$$(10) \quad \dot{\lambda}_t = \delta \lambda_t - \frac{\partial H}{\partial x_{1t}} = \delta \lambda_t - \frac{\partial D}{\partial x_{1t}} - \lambda_t \left(F'(x_{1t}) - \frac{\partial m}{\partial x_{1t}}\right) - \mu_t \left(\frac{\partial m}{\partial x_{1t}}\right)$$

$$(11) \quad \dot{\mu}_t = \delta \mu_t - \frac{\partial H}{\partial x_{2t}} = \delta \mu_t - \frac{\partial D}{\partial x_{2t}} + \frac{\partial D}{\partial c_i} \frac{\partial c_i}{\partial x_{2t}} + \lambda_t \left(\frac{\partial m}{\partial x_{2t}}\right) - \mu_t \left(G(x_{2t}) + \frac{\partial m}{\partial x_{2t}}\right).$$

In equation (9) $-\lambda_t \left(\frac{\partial m}{\partial h_t}\right) + \mu_t \left(\frac{\partial m}{\partial h_t} - 1\right)$ corresponds to the net marginal welfare of migration depending on harvest. $\frac{\partial D}{\partial B_i}$ and $\frac{\partial D}{\partial c_{it}}$ are the marginal effects of private benefit and cost on welfare. Thus, equation (9) states that the marginal net welfare of harvest $\left(\frac{\partial D}{\partial B_i} \frac{\partial B_i}{\partial h_{it}} - \frac{\partial D}{\partial c_{it}} \frac{\partial c_i}{\partial h_{it}}\right)$ must equal the net benefit of migration in terms of the dynamic population effects on hunting outcome. We noted above that $\lambda_t = 0$ and $\mu_t = 0$ under open-access. Consequently, from equation (9) we see that λ_t and

μ_t are the welfare gains received by solving a market failure. This market failure arises because individual hunters, contrary to society, do not include the resource restrictions in the maximization problem and, therefore, the market failure can be labeled a stock externality.

Without stress effects equation (9) reduces to an optimality condition for optimal management of renewable resources:

$$(12) \quad \frac{\partial D}{\partial B_i} \frac{\partial B_i}{\partial h_{it}} - \frac{\partial D}{\partial c_i} \frac{\partial c_i}{\partial h_{it}} - \mu_t = 0.$$

Equation (12) is an optimality condition for the exploitation of a renewable resource (see Neher [1990]). It states that the marginal welfare of harvest equals the shadow price of the resource restriction.

Equation (10) may be rewritten as:

$$(13) \quad \frac{\dot{\lambda}_t}{\lambda_t} = \delta - \frac{1}{\lambda_t} \frac{\partial D}{\partial x_{1t}} - \left(F'(x_{1t}) - \frac{\partial m}{\partial x_{1t}} \right) - \frac{\mu_t}{\lambda_t} \left(\frac{\partial m}{\partial x_{1t}} \right).$$

From equation (13) is seen that the change in shadow price ($\frac{\dot{\lambda}_t}{\lambda_t}$) of the stock in the reserve must equal the discount rate (δ) minus the marginal net welfare of net migration to the reserve, $(-F'(x_{1t}) - \frac{\partial m}{\partial x_{1t}}) + \frac{\mu_t}{\lambda_t} (\frac{\partial m}{\partial x_{1t}})$, plus the marginal net welfare of the population $(-\frac{1}{\lambda} \frac{\partial D}{\partial x_{1t}})$.

Similarly, equation (11) may be rewritten as:

$$(14) \quad \frac{\dot{\mu}_t}{\mu_t} = \delta - \frac{1}{\mu_t} \left(\frac{\partial D}{\partial x_{2t}} - \frac{\partial D}{\partial c_i} \frac{\partial c_i}{\partial x_{2t}} \right) + \frac{\lambda_t}{\mu_t} \left(\frac{\partial m}{\partial x_{2t}} \right) - \left(G(x_{2t}) + \frac{\partial m}{\partial x_{2t}} \right).$$

Equation (14) illustrates that the change in shadow price ($\frac{\dot{\mu}_t}{\mu_t}$) of the stock in the hunting area must equal the discount rate minus the net welfare of migration $+\frac{\lambda_t}{\mu_t} (\frac{\partial m}{\partial x_{2t}}) - (G'(x_{2t}) - \frac{\partial m}{\partial x_{2t}})$ plus the marginal net welfare of the population $(-\frac{1}{\mu_t} (\frac{\partial D}{\partial x_{2t}} - \frac{\partial D}{\partial c_i} \frac{\partial c_i}{\partial x_{2t}}))$.

By comparing the social and private optima (9) and (2) we find the well-known result that harvest is larger in the private optimum. The reason is that a social planner includes a resource restriction in the maximization problem and incorporates the value of population levels in the objective function. However, it is more interesting to compare the social planner optimum with and without stress effects as we did for the private optimum. As for the private optimum an assumption in the paper is that clever migration implies that the population in the wildlife reserve increases and the population in the hunting area decreases. Exactly as in the case

of the private optimum, two counteracting forces are present. Stress causes smart animals to move out of the hunting area and into the wildlife reserve, but both this migration and hunting reduce population densities in the hunting area relative to the reserve. By assumption, the first effect dominates the second effect.

3. Simulations. In this section, we present numerical simulations of the private and social optimum. We focus on the implications of stress effects on the two optima and simulate the implications of various carrying capacities across the reserve and nonreserve areas. We base the simulations on generally applicable functional forms of the relations described in Section 2 and on relevant parameter values (see Conrad and Clark [1987]) and solve in discrete time to make it more intuitive (see also Neher [1990]).

One extra assumption is imposed compared to Section 2 in order to simplify the analysis. We assume that the harvest level is determined by a representative hunter who selects aggregate harvest. Thus, $i = n = 1$. Now h_t denotes the harvest of the representative hunter but because $i = n = 1$ h_t is also the aggregate harvest, as in Section 2. In addition, with $i = n = 1$ we can change notation such that $c_i(h_{it}, x_{2t}) = c(h_t, x_{2t})$ and $B_i(h_{it}) = B(h_t)$.

Now consider how the model is simulated for the social optimum. In discrete form, the first-order conditions from Section 2 can be expressed as (equations (9)–(11) and (6)–(7)):

$$(15) \quad \frac{\Delta D}{\Delta B} \frac{\Delta B}{\Delta h_t} - \frac{\Delta D}{\Delta c} \frac{\Delta c}{\Delta h_t} - \lambda_t \frac{\Delta m}{\Delta h_t} + \mu_t \left(\frac{\Delta m}{\Delta h_t} - 1 \right) = 0.$$

$$(16) \quad \lambda_{t+1} = \lambda_t + \delta \lambda_t - \frac{\Delta D}{\Delta x_{1,t}} - \lambda_t \left(F'(x_{1,t}) - \frac{\Delta m}{\Delta x_{1,t}} \right) - \mu_t \frac{\Delta m}{\Delta x_{1,t}}$$

$$(17) \quad \mu_{t+1} = \mu_t + \delta \mu_t - \frac{\Delta D}{\Delta x_{2,t}} + \frac{\Delta D}{\Delta c} \frac{\Delta c}{\Delta x_{2,t}} + \lambda_t \frac{\Delta m}{\Delta x_{2,t}} - \mu_t \left(G'(x_{2,t}) + \frac{\Delta m}{\Delta x_{2,t}} \right)$$

$$(18) \quad x_{1,t+1} = F(x_{1,t}) - m \left(h_t, \frac{x_{1,t}}{x_{2,t}} \right) + x_{1,t}$$

$$(19) \quad x_{2,t+1} = G(x_{2,t}) + m \left(h_t, \frac{x_{1,t}}{x_{2,t}} \right) - h_t + x_{2,t}$$

where, for example, $x_{1,t+1}$ denotes population 1 at time $t+1$.

From the literature on renewable resources we have that if the terminal time period and the initial values of the control variables are known, we may determine

time paths for the control variable, the state variables, and the co-state variables by forward induction (see, e.g., Neher [1990]). The procedure represents an optimization within a time period given the value of the control variable, the state variables, and the co-state variables at the beginning of the period. We present simulation results for a terminal time period of $t = 150$ (Figure 1 below). But we have also conducted simulations for $t = 2,000$ to ensure that the equation system in equations (15)–(19) converges towards a steady-state equilibrium. With respect to initial starting values ($x_{1,0}$, $x_{2,0}$, h_0, λ_0 , and μ_0) we begin with three observations. First, because we use a discrete time formulation, we have replaced the partial derivative sign with a Δ in equations (15)–(19). Second, in equations (16)–(19) variables for time $t + 1$ (the left-hand side) are a function of variables for time t . In addition, equation (15) only depends on variables for t . Third, equations (15)–(19) represent the first-order conditions from Section 2. Thus, equations (15)–(19) are derived by optimizing a welfare function. If we know $x_{1,0}$, $x_{2,0}$, h_0 , λ_0 , and μ_0 we can calculate $x_{1,1}$, $x_{2,1}$, h_0, λ_1 , and μ_1 (variables for $t = 1$) using equations (15)–(19). Then, the control variable, the state variables, and the co-state variables for $t = 1$ can be used to calculate the variables for $t = 2$ using equations (15)–(19) and so on. This procedure can be repeated to the terminal time period ($t = 150$).

Now the only remaining issue is to find a method for determining starting values for the control variables. It is well-known that the solutions to dynamic systems are sensitive to the selection of starting values (see Neher [1990]). Several methods for selecting starting values exist (see, e.g., Gilli and Schumann [2010]). We choose the best guess method combined with a criterion for the adjustment paths to be reasonable. For a set of $x_{1,0}$, $x_{2,0}$, h_0 , solutions to the equation system (15)–(19) are solved for 10,000 combinations of λ_0 and μ_0 over a set of time steps. Among the values for λ_0 and μ_0 that generate a reasonable path, the path that maximizes the aggregate discounted benefit along the path is chosen.

Now we turn to the private optimum. In discrete form the simulation model is (equations (1), (2) and(4)):

$$(20) \quad B'(h_t) - \frac{\Delta c}{\Delta h_t} = 0$$

$$(21) \quad x_{1,t+1} = F(x_{1,t}) - m \left(h_t, \frac{x_{1,t}}{x_{2,t}} \right) + x_{1,t}$$

$$(22) \quad x_{2,t+1} = G(x_{2,t}) + m \left(h_t, \frac{x_{1,t}}{x_{2,t}} \right) - h_t + x_{2,t}.$$

As for the social optimum, if the starting values for the control variables and stock levels (h_0 , $x_{1,0}$ and $x_{2,0}$) and the terminal time period are known we can find paths for h_t , $x_{1,t}$, and $x_{2,t}$. Again, we set the terminal time period equal to 150 ($t = 150$),

but also here we run simulations for $t = 20,000$ in order to investigate whether the system converges towards steady-state solutions. As for the social optimum, the solution is sensitive to the starting values but we use the same approach to ensure that we find an optimal solution.

When solving the two numerical problems, we used appropriate scaling of the variables to ensure a fine grid in the time step dimension. Scaling implies that all variables and functions are scaled by the same factor in order to secure interior solutions and variability in the functions. 1000 is used as scaling factor.

3.1. Selecting functional forms. In order to simulate the model we need specific functional forms and parameter values. Net migration from the wildlife reserve to the hunting area can be captured by:

$$(23) \quad m_{12} = \frac{ax_{1,t}}{x_{2,t}} - \frac{cx_{2,t}}{x_{1,t}} - \frac{bh_t}{x_{2,t}}.$$

Naevdal [2008] derives a migration function based on the assumption that animals maximize expected utility with respect to energy intake and movement behavior is adapted accordingly to this objective. Though the model applied in this paper is not explicitly based on individual animal behavior and energy uptake, the migration model presented in equation (23) has similar dynamic properties as the model in Naevdal [2008]. The first two terms correspond to the density dependent competition for food resources (for equal carrying capacity in the two areas), and the last term reflects a probability of being killed in the hunting area. For the growth standard logistic functions are assumed (see, e.g., Clark [1990]) and the growth functions may be written as:

$$(24) \quad F(x_{1,t}) = ex_{1,t} \left(1 - \frac{x_{1,t}}{f} \right)$$

$$(25) \quad G(x_{2,t}) = gx_{2,t} \left(1 - \frac{x_{2,t}}{k} \right),$$

where e and g are the intrinsic growth rates and f and k are the carrying capacities. The logistic growth function is a well-known specification in the literature on natural resources (see, e.g., Conrad and Clark [1987] and Naevdal [2008]). We simulate the model for a symmetric case where the intrinsic growth rates and carrying capacities are identical in the two areas in order to focus on the implications of stress effects (see Table 1 for parameter values). In addition, we conduct sensitivity analysis by varying the carrying capacities and we vary f and k with $\pm 10\%$ and $\pm 20\%$ but such that $f + k$ is unchanged.

The private harvest benefit function is assumed to be given as:

$$(26) \quad B(h_t) = ph_t^m$$

Equation (26) is a natural simplification of a Cobb-Douglas function. Concerning the costs we assume a function which has been extensively used within fisheries economics:

$$(27) \quad c(h_t, x_{2,t}) = \frac{jh_t}{x_{2,t}}$$

The derivatives of equation (27) are consistent with the assumptions from Section 2.

As mentioned in Section 2, we assume that gross benefit depends on both population levels and private benefit. Conservation benefits and recreational values imply that population levels enter the benefit function. In other words, other users than hunters may have a benefit associated with population levels. Thus, for the social planner we assume the following gross welfare function:

$$(28) \quad D(h_t, x_{1,t}, x_{2,t}) = B(h_t)(x_{1,t} + x_{2,t})^{1-m} - c(h_t, x_{2,t}) = ph_t^m (x_{1,t} + x_{2,t})^{1-m} - \frac{jh_t}{x_{2,t}}$$

Equation (28) is a standard Cobb-Douglas function.

For conducting simulations we need parameter values for the functional forms in equations (23)–(28). In Table 1, we show the assumed parameter values. In addition, we have restated the functional forms in Table 1 in order to facilitate the interpretation of the parameter values.

Two things are worth remarking in connection with the assumed parameter values in Table 1. First, concerning the migration function, the model is simulated with stress effects ($b = 40$) and without stress effects ($b = 0$), but otherwise a symmetric case ($a = c = 50$) with no other reasons to migrate than hunting related stress and differences in populations densities resulting from hunting. Second, we mentioned earlier that we conducted sensitivity analysis with respect to the carrying capacities. In the benchmark case we assume that $e = g = 0.5$ and $f = k = 50$. In the sensitivity analysis the model is simulated for f and k equal to $\pm 10\%$ and $\pm 20\%$ but we change the carrying capacities such that $f + k$ is equal to the same number as in the benchmark case (100). This implies that the following five scenarios are considered:

TABLE 1. The assumed parameter values.

Function	Assumed functional form	Assumed parameter value
Net migration	$m_{12} = \frac{ax_{1,t}}{x_{2,t}} - \frac{cx_{2,t}}{x_{1,t}} - \frac{bh_t}{x_{2,t}}$	$a = c = 50$ and $b = 0$ (no stress effect) $a = c = 50$ and $b = 40$ (stress effects)
Growth functions	$F(x_{1,t}) = ex_{1,t}(1 - \frac{x_{1,t}}{f})$ $G(x_{2,t}) = gx_{2,t}(1 - \frac{x_{2,t}}{k})$	Benchmark case $e = g = 0.5$ $f = k = 50$
Private harvest benefit	$B(h_t) = ph_t^m$	$p = m = 0.5$
Cost function	$c(h_t, x_{2,t}) = \frac{jh_t}{x_{2,t}}$	$j = 2$
Gross welfare function	$D(h_t, x_{1,t}, x_{2,t}) = ph_t^m (x_{1,t} + x_{2,t})^{1-m} - \frac{jh_t}{x_{2,t}}$	$p = m = 0.5$
Discount rate		4%

- (a) $f = 40$ and $k = 60$
- (b) $f = 45$ and $k = 55$
- (c) $f = 50$ and $k = 50$
- (d) $f = 55$ and $k = 45$
- (e) $f = 60$ and $k = 40$.

For all five cases, we evaluate the social benefit functions, the population levels and the harvest.

3.2. Simulation results for the social optimum. Figure 1 illustrates simulation results for the social optimum with stress effects ($b = 40$) and without stress effects ($b = 0$).

In Figure 1, we have shown the optimal path for harvest and population levels and we see that a constant harvest is optimal if we are interested in an interior optimum. If the harvest is slightly above this constant harvest, extinction is optimal in the steady-state equilibrium. On the contrary, the system converges towards $h_t = 0$ if the harvest is slightly below the constant. An adjustment path with a constant harvest level is optimal both with and without stress effects and is a variant of a

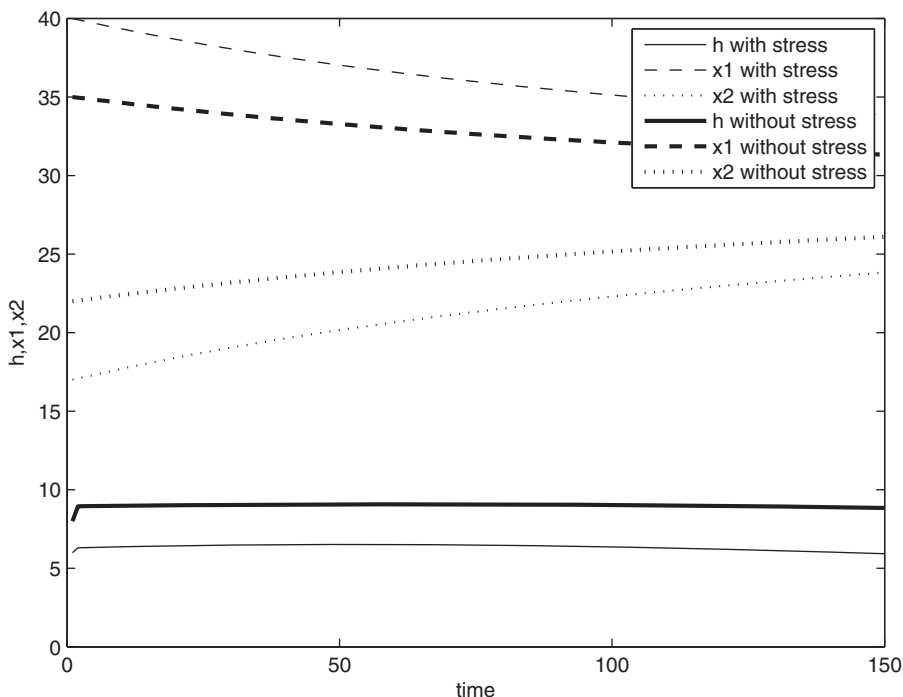


FIGURE 1. Social optimum with and without stress effects.

saddle-point equilibrium (see Clark [1990]). The constant harvest rule requires a specific combination of starting values for the population sizes and shadow prices. For the case with stress effects $x_{1,0} = 40$, $x_{2,0} = 17$, $\lambda_0 = 0.45$, and $\mu_0 = 0.59$ while $x_{1,0} = 35$, $x_{2,0} = 22$, $\lambda_0 = 0.46$, and $\mu_0 = 0.58$ without stress effects. From these values it is clear that the initial shadow prices or co-state variables do not vary much with and without stress effects. The main variation in the starting values is due to population sizes.

Above we mentioned that the constant harvest rule requires a specific combination of $x_{1,0}$, $x_{2,0}$, λ_0 , and μ_0 and this combination must be very precise. In fact, it must be correct on an indefinite number of decimals. If this is not the case, the system converges towards extinction or $h_t = 0$. Of course it is impossible to reach such a precision in numerical simulations and therefore a constant harvest cannot be illustrated unless the terminal time period is small. Therefore, we chose $t = 150$. To see if the population levels converge towards a steady-state equilibrium, we have run simulations using $t = 2000$, and the steady-state values for populations reported below are for this terminal time period. Note, also, that both with and without stress effects the total population size ($x_{1,t} + x_{2,t}$) is approximately constant

TABLE 2. Social benefit for varying carrying capacities.

	$f = 60$ $k = 40$	$f = 55$ $k = 45$	$f = 50$ $k = 50$	$f = 45$ $k = 55$	$f = 40$ $k = 60$
Discounted social benefit, 10^3	1.0765	1.1371	1.1978	1.3670	1.3894
H	4	5	6	7	8
$x_{1,0}$	46	42	40	36	33
$x_{2,0}$	12	15	17	21	24
x_1 in equilibrium	36	34	32	30	29
x_2 in equilibrium	21	23	25	26	28

along the adjustment path. A constant total population is required for the constant harvest rule. From Figure 1 we see that h_t is largest when there is no stress effect of hunting (6 with and 8 without stress effects). The steady-state value of $x_{1,t}$ is higher (32 with and 30 without stress effects) and the steady-state value of $x_{12,t}$ is lower (25 with and 28 without stress effects) without stress effects. Thus, the pure stress effect dominates the population effect in steady-state as assumed in Section 2.

In the above, we have assumed that the carrying capacity in the two areas are identical. Often a situation arises where spatial variation of habitat quality causes the carrying capacities between areas to differ. A question that now arises is where to locate the wildlife reserve and the hunting area. To analyze this, we conducted sensitivity analysis of the social optimum with respect to the carrying capacities. The sensitivity analysis is carried out for the case with stress effects ($b = 40$). In the original analysis $f = k = 50$. Now f and k are varied so that the sum of carrying capacities is the same as in the benchmark case. The results are shown in Table 2.

We start by noting that the discounted benefit in Table 2 is found for $t = 150$ in order to be consistent with Figure 1, and irrespective of the carrying capacities a constant harvest rule is optimal if we want an interior solution. With respect to time paths for $x_{1,t}$ and $x_{2,t}$ the system also converges towards a steady-state equilibrium. This result is found for $t = 150$ and as expected $x_{1,t}$ decreases and $x_{2,t}$ increases with increasing k in steady-state. However, along the entire time paths $x_{1,t}$ and $x_{2,t}$ vary such that the total population is unchanged. This reflects the role of population levels in the social benefits function. In addition, we note that the constant harvest level increases with increasing k as $x_{2,t}$ and the growth in $x_{2,t}$ increase.

From Table 2 is also seen that the discounted social benefit increases with increasing k . Thus, within the simulated model the hunting area should be placed where the carrying capacity is high. This result reflects that hunting levels increase with k while the total population is constant. In addition, the effect on costs of an increasing k is ambiguous because both h and $x_{2,t}$ increases. However, the conclusion

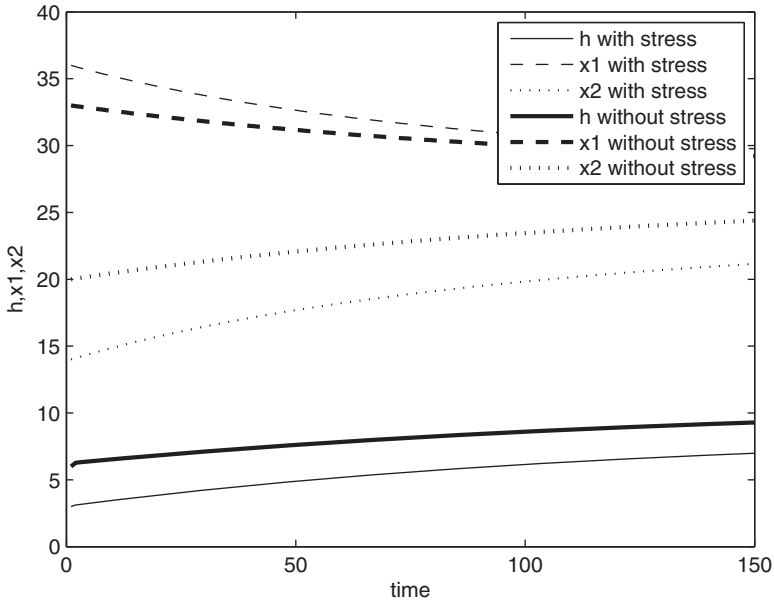


FIGURE 2. Private optimum with and without stress effects.

that the hunting area should be placed where the carrying capacity is high depends on the assumed functional forms and parameter values.

3.3. Simulation results for the private optimum. Turning to the private optimum, the results of the simulations with stress effects ($b = 40$) and without stress effects ($b = 0$) are shown in Figure 2.

The results in Figure 2 are illustrated for $t = 150$ in order to be consistent with the simulations of the social optimum. However, by using $t = 2,000$ it can be shown that both with $b = 40$ and $b = 0$, h_t , $x_{1,t}$, and $x_{2,t}$ converge towards steady-state for the selected starting values. The steady-state values with stress effects are $x_{1,t} = 28$, $x_{2,t} = 23$, and $h_t = 9$ while the values are $x_{1,t} = 27$, $x_{2,t} = 25$, and $h_t = 10$ without stress effects. Thus, $x_{1,t}$ is higher while h_t and $x_{2,t}$ are lower with stress effects in steady-state. This result implies that the pure stress effect dominates the population effect, as assumed in Section 2. We also obtain that $x_{1,0} = 36$ and $x_{2,0} = 14$ with stress effects and $x_{1,0} = 33$ and $x_{2,0} = 20$ without stress effects (Figure 2). That $x_{1,0}$ is lower and $x_{2,0}$ is higher without stress effects is intuitively clear. Stress effects imply increased migration to the wildlife reserve and increased migration out of the hunting area due to harvest pressure. Because the initial values are not the same in the social and private optimum, it does not make sense to compare the steady-state values of harvest and population levels.

4. Concluding discussion. In this paper, we consider the hunting activities of private hunters under open-access and the optimal policy of a social planner, when hunting pressure directly affects migration patterns between hunting areas and wildlife reserves. We build a theoretical model and simulate results for likely dynamics of an animal population. Furthermore, it is assumed that the social welfare function includes population related benefits and hunting outcomes, whereas the private hunters only derive benefit from hunting outcomes. We assume that the population inside the wildlife reserve will increase and the population in the hunting area will decrease when hunting related stress effects on migration patterns are included. Simulations confirm this assumption. Furthermore, the simulation shows that in both cases total population is unchanged with stress effects.

The effect of population density differences on migration is a well-known result from related studies on fisheries and marine reserves (see Armstrong [2007], Armstrong and Skonftoft [2006], Flaaten and Mjølhus [2010]). Here, it is found that the reserve population level may approach a critical level due to the drainage effect. However, in this paper we find that when stress effects cause smart wildlife to adapt their migration patterns across reserve and hunting areas, the population level in the wildlife reserve can be larger. However, stress effects will reduce the drainage effect, which suggests that for wildlife with smart reactions to hunting pressures, wildlife reserves have a better chance of supporting preservation.

The simulations are expanded to evaluate how optimal social net benefits respond to the level of carrying capacities in a wildlife reserve and a hunting area. By evaluating the discounted net social welfare, we show that for our choices of functional forms and parameters the hunting areas are from a social planner perspective better placed in areas with high carrying capacity. This is true when social hunter benefits are dominated by a harvest effect, and when the hunter costs component is low.

Our results have relevance for several discussions on wildlife management and also have practical implications for the optimal spatial allocation of hunting areas and reserves. The more realistic modeling of wildlife's behavioral response to hunting pressures shows that population levels in the wildlife reserve can be higher in the private equilibrium, resulting in the private equilibrium being more beneficial to society than in the absence of the behavioral response. It is straightforward to bring this observation into a discussion of the likelihood of natural reserves preventing extinction of wildlife with migratory tendencies. In the absence of a response to hunting pressures, as is commonly assumed in the literature (e.g., Skonftoft et al. [2002], Armstrong and Skonftoft [2006]), it is possible to drive down a population very much, even with hunting only allowed outside the reserve. Because of density dependent migration, these hunting activities can slowly drain the reserve perhaps below survival thresholds. With the behavioral response assumed here, this effect is less likely to occur as relative hunting pressures may push remaining wildlife into the reserve. Such effects could be part of the explanation for the uneven distributions

of deer populations in the landscape as found in Denmark (Kanstrup et al. [2009]). Studies find a relatively high degree of individual behavioral plasticity and response to hunting pressures, with resulting higher survival probabilities (Ciuti et al. [2012]). The conclusions in this paper are based on general assumptions of the functional forms and parameters. Further research must be invested in analyzing and perhaps parameterize this for real empirical cases.

Finally, our results are also of relevance for public owners of forest and nature lands who should decide which land parcels should be leased out to hunters. As an example, spatial separation of reserves and hunting areas is an explicit part of hunting policies in the Danish state owned forests (constituting more than 25% of the Danish forest area). Furthermore, it is often stated in hunting contracts what the hunting pressure (measured in numbers of hunting days and harvest) can be, and this pressure is usually much lower than for hunting in a privately owned forest. The hunting reserves on public land provide opportunities for the public to meet and enjoy wildlife, and neighboring hunters in private forests benefit from migration (m_{12}) from state owned reserves.

4.1. Caveats, limitations, and possible extensions. We have made several simplifying assumptions in our model, which deserve a short discussion. First, our model does not include negative aspects of wildlife populations such as traffic risks or browsing damage. Such aspects are included in Skonhøft and Olaussen [2005], Wam and Hofstad [2007], Nævdal [2008], and Olaussen and Skonhøft [2011]. Secondly, in our model we assume that migration is only driven by density differentials and hunting pressures. Thus, we neglect that species' migration patterns and habits can be inherent in and even crucial to their breeding, propagation or seasonal behavior. Thirdly, extensions of the presented model could allow for detailed modeling of hunting (Skonhøft and Olaussen [2005]). Further research could attempt to separate hunting effort from hunting outcome and let the former drive migration, because the wildlife is more likely to sense the hunting activity. In Nævdal [2008] and in the present paper an objective probability of dying is assumed, but a number of studies prove that hunting and related disturbances affect wildlife behavior within and outside reserves (Benoist et al. [2013]). These results suggest that stress induced migration should be considered in harvest management. Fourth, model extensions could allow for hunters to choose the optimal mix of hunting approaches. These may differ in disturbance effects and effect on migration and this brings more detailed results useful for the design of hunting policies. Finally, there is a risk of illegal hunting in the wildlife reserve. The larger population densities in the reserve may create an incentive for illegal hunting in this area. This holds particularly for low-income countries where (illegal) hunting is part of subsistence activities (Nielsen et al. [2014]). With illegal hunting it is necessary to have a control policy to reduce incentives for such activities.

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