ISSN 1503-299X

WORKING PAPER SERIES

No. 9/2004

CONSERVATION OF WILDLIFE. A BIO-ECONOMIC MODEL OF A WILDLIFE RESERVE UNDER THE PRESSURE OF HABITAT DESTRUCTION AND HARVESTING OUTSIDE THE RESERVE

Claire W. Armstrong
Anders Skonhoft

Department of Economics

Norwegian University of Science and Technology
N-7491 Trondheim, Norway
www.svt.ntnu.no/iso/wp/wp.htm

CONSERVATION OF WILDLIFE.
A BIO-ECONOMIC MODEL OF A WILDLIFE RESERVE UNDER THE PRESSURE OF HABITAT DESTRUCTION AND HARVESTING OUTSIDE THE RESERVE

by

Anders Skonhoft*)
Department of Economics
Norwegian University of Science and Technology
Trondheim, Norway

and

Claire W. Armstrong
Department of Economics
Norwegian College of Fishery Science
University of Tromsø, Norway

Abstract
Biodiversity is today threatened by many factors of which destruction and reduction of habitats are considered most important for terrestrial species. One way to counteract these threats is to establish reserves with restrictions on land-use and exploitation. However, very few reserves can be considered islands, wildlife species roam over large expanses, often via some density dependent dispersal process. As a consequence, habitat destruction, and exploitation, taking place outside will influence the species abundance inside the conservation area. The paper presents a theoretical model for analysing this type of management problem. The model presented allows for both the common symmetric dispersal as well as what is called asymmetric dispersal between reserve and outside area. The main finding is that habitat destruction outside may not necessarily have negative impact upon the species abundance in the reserve. As a consequence, economic forces working in the direction of reducing the surrounding habitat have unclear effects on the species abundance within the protected area. We also find that harvesting outside the reserve may have quite modest effect on the species abundance in the reserve. This underlines the attractiveness of reserves from a conservation viewpoint.

---

*) Corresponding author with e-mail: anders.skonhoft@svt.ntnu.no

We are indebted to The European Commission for support through the BIOECON project, and to participants at the third BIOECON workshop in Montpellier, May, 2003, for useful comments. Thanks also to Ola Flåten, Anne B. Johannesen and two referees for comments on earlier drafts.

1. Introduction

Biodiversity is today threatened by many factors, one of which being over-harvesting, another being destruction and reduction of habitats. The former is generally the most important for aquatic species (Clark 1990) and is often triggered by unclear property rights (Bromley 1991), whereas the latter is considered the most important for terrestrial species (Swanson 1994). One way to counteract these threats is to establish conservation zones, often in the form of national parks, with various restrictions on harvesting, land-use and other types of man-made influences, so that the social benefits of rare and threatened species can at least be kept intact *inside* the reserve[1].

The main motivation behind establishing conservation areas for terrestrial species is somewhat different to that of marine reserves. The central idea here is, at least from an economic point of view, namely to protect spawning stocks or juveniles so they can grow and replenish or recolonise *other* areas and, hence, increase the catch and profitability *outside* the reserves (Conrad 1999, Hannesson 1998, Lauck *et al.*1998, Pezzey, *et al.* 2000, Roberts and Sargant, 2002, Rodwell *et al.*2002, Sanchirico and Wilen 2001 and Sumaila 1998). Just as for marine reserves, however, terrestrial ecological geography seldom corresponds with management geography as the wildlife species frequently roam in and out of the protected areas. As a consequence, while land-use and habitat are kept fixed within a protected area, harvesting can take place when the wildlife is outside the conservation area. In addition, and in contrast to a marine setting, habitat deteriorates and disappears outside. Because of dispersion, there will therefore be a management problem in the sense that land-use changes and harvesting taking place outside the conservation area influences the stock abundance inside the conservation area. This type of management problem, which basically is an externality problem, has been frequently mentioned in the literature (see, e.g., Munasinghe and McNeely 1994, Swanson 1994, Brown 1997). There are, however, few, if any, analyses of this problem in a bio-economic context (but see Skonhoft *et al.* 2002 and Johannesen 2003).

The purpose of this paper is to bridge this gap and, from a theoretical point of view, analyse how habitat changes as well as harvesting taking place *outside* the reserve, spill over to the conservation area. Hence, the focus is different to that of the marine reserve literature, where the effects of reserve implementation upon harvest outside the reserve are the important issue. Few, if any, of these studies, have analysed how harvesting outside spills over to the reserve. There is also no analysis where the effects of habitat changes outside on the species density within the reserve are considered. To facilitate the study, while still capturing the main points, we deal only with two areas, or two patches; a reserve and a neighbouring area, managed by two different agencies and two sub-populations of wildlife. The conservation zone will be of fixed size and land-use is also kept fixed; this is taken as an *institutional* fact[2]. On the other hand, the land-use can change in the neighbouring area as habitat degrades. We

---

[1] The history of establishing conservation zones is old, and today more than 5% of the earth's surface is covered with such areas. These areas, however, serve also other purposes than protection of wildlife and plants, and the International Union for the Conservation of Nature (IUCN) lists seven other kinds of protected areas in addition to parks (see e.g., Dixon and Sherman 1991, Brown 1997).

[2] In other words, we are not analyzing factors affecting the (social) optimal *size* of a conservation area. This is, amongst others, studied in Pezzey *et al.*(2000) in a fishery management context.

abstract from any harvesting taking place in the conservation area (but see Wright 1999), thus also excluding illegal activities such as poaching. We also abstract from any effort to influence the amount of dispersal through fencing, vegetation manipulations, and so forth. For these and other reasons, the following model is relatively simple and general, and intends to be applicable to conservation areas in developing countries as well as in industrialised countries[3].

Introduction of reserves causes changes in inter and intra species composition (Pezzey, *et al.*, 2000). Such stock differences between a reserve and a non-reserve are taken into account in the present study. The model introduced is therefore general in an ecological respect in that it allows for the more common symmetric dispersal between the reserve and the outside area, as well as asymmetric dispersal. Asymmetric dispersal occurs when the relationship between stock size and carrying capacity is not directly comparable between the two areas. Hence dispersal depends on other factors as well. The asymmetric dispersal may result from more advantageous conditions within the reserve, due to habitat preservation (Delong and Lamberson, 1999) or larger fecundity due to greater animal size or age (Pezzey, *et al.*, 2000). Alternatively, the reserve may supply less advantageous conditions, due to greater predatory pressure, competition or cannibalism.

In the next section we formulate the ecological model where the dispersion of wildlife over the two areas depends upon the relative species density and stock specific differences in the two areas. In section 3 it is analysed how habitat changes and harvesting, taking place outside the protected area, influence the species abundance in the protected area. In section 4 we introduce economic motives for the owner of the neighbouring area, and it is studied how these motives translate into pressure on the reserve.

2. The ecological model

As noted, we consider two areas and two sub-populations of wildlife. Both areas are assumed to be of fixed size, but the land-use can change outside as habitat land can be converted into other uses. The protected area may be owned by the state and managed by a park authority while we assume that the neighbouring area is managed and owned by a single private agent, or by many agents, in sum behaving like a single manager. The owner of the neighbouring area has the right to appropriate the benefits of the fugitive biological resources when it is inside this area, and hence, has the property rights over the wildlife when it leaves the protected area. So while there is no harvesting in the protected area, harvesting takes place outside in the neighbouring area if it is a profitable activity.

We let one stock of wildlife represent the whole game population, though one could also imagine this one stock being an aggregation of the wildlife species present. The dynamics of the two sub-populations are given by

---

[3] One significant difference between conservation areas in developing countries and industrialized countries is the often conflicting views of the rights to these areas. In developing countries, say, in sub-Saharan Africa, the establishment of national parks and game reserves has frequently directly displaced rural communities from the land that traditionally was theirs. Moreover, the local people have generally lost their traditional harvesting rights as anti-poaching laws have turned the old practice of subsistence hunting into a crime. Largely due to these facts, the local people generally have a skeptical outlook on reserves, and see wildlife mostly as a nuisance (see, e.g., Kiss 1990 for an overview, and Skonhoft and Solstad 1998 for an analysis).

$$(1)\ dX_1/dt = F(X_1) - M(X_1,X_2,K_2) = r_1X_1(1 - X_1/K_1) - m(ßX_1/K_1 - X_2/K_2)$$

and

$$(2)\ dX_2/dt = G(X_2,K_2) + M(X_1,X_2,K_2) - h(e,X_2,K_2) = r_2X_2(1 - X_2/K_2) + m(ßX_1/K_1 - X_2/K_2) - \varphi eX_2/K_2$$

where X_1 is the population size in the protected area at a given point of time and X_2 is the population size in the neighbouring area at the same time. F(.) and G(..) are the accompanying logistic natural growth functions, with r_i, i=1,2, defining the maximum specific growth rates and K_i the carrying capacities, inside and outside the protected area, respectively. The carrying capacity depends on the natural environment for the species, assumed to be proportional to the size of the habitat (see e.g., Swallow 1990 and Swanson 1994). Because the land-use in the protected area is kept fixed, the carrying capacity is also fixed here. Outside, the land-use generally changes, and so does the carrying capacity; that is, conversion of habitat land into other uses means a reduction of K_2. The harvesting $h(.) \geq 0$ only takes place outside the protected area. It is specified as a Schäfer function and determined by the harvest effort e, the catchability coefficient φ and the species density X_2/K_2 as the carrying capacity, as mentioned, is assumed to be proportional to the size of the habitat land (Pezzey *et al.* 2000).

In addition to natural growth and harvesting, the two sub populations are interconnected by dispersion as given by the term M(…). Migration and dispersal can be triggered by various factors. There may be species with a distinct and more or less fixed yearly migration pattern, cf. the famous wildebeest population in the Serengeti-Mara ecosystem in Tanzania (see, e.g., Sinclair and Arcese 1995), and there may be density dependent factors present (Skonhoft *et al.* 2002). Here we focus on the latter, and M(…) is assumed to depend on the *relative* stock densities in the two areas, ignoring any other migratory patterns[4]. $m > 0$ is a parameter reflecting the general degree of dispersion; that is topography, size of the areas, type of species, and so forth. Hence, a high dispersion parameter m corresponds to species and a natural environment with large spatial movement. The parameter $ß > 0$ takes care of the fact that the dispersion may be due to, say, different environmental conditions, predator-prey relations and competition within the two sub-populations (again, see Pezzey *at al.* 2000). For equal X_i/K_i, i=1,2, $ß > 1$ results in an outflow from the conservation area and could be expected in a situation where there was greater predatory pressure inside the protected area, for instance due to there being no hunting in the reserve. Hence, if mobile prey species choose, for instance, breeding sites based on their chance for survival and reproductive success (Fretwell and Lucas, 1970), there would be an outflow surpassing that of when the relative densities do not involve ß. On the other hand, when $0<ß<1$, the circumstances outside the reserve are detrimental, creating less potential migration out of the reserve. Hence, as opposed to the simpler sink-source models found in the literature (cf. the sink-source concept of the metapopulation theory, see, e.g., Pulliam 1988), this model incorporates possible intra-

---

[4] In the following we will use the term density for the relationship between the stocks and their respective carrying capacities despite the K's not actually defining area. This relationship nonetheless has the essence of density, in the sense that it describes the degree to which the respective areas are filled to their capacity. Due to the possibility of asymmetric dispersal, $\beta X_1/K_1$ and *not* X_1/K_1 represents the (effective) density in the protected area (see the main text below).

stock or inter-species relations that may result in different concentrations in the two areas; that is, the dispersal may be *asymmetric*. Hence, β is independent of the carrying capacity and functions as density regulating parameter, depending on the conditions in the relevant areas.

In the bio-economic literature a simpler version of this type of dispersion function is used, amongst others, by Huffaker *et al.*(1992) and Bhat *et al.*(1996), to analyse the optimal management of a beaver population in a two patch model (as here) managed by two different agents, where the beaver population is a nuisance (damage on timber stand) and costly to hunt in one of the areas. Sanchirico and Wilen (1999) analyse a more general model of an open access fishery with n-patches. See also Conrad (1999) and Hannesson (1998) for simple density dependent bioeconomic models of marine reserves. Huffaker *et al.*(1992), Bhat *et al.*(1992) and Sanchirico and Wilen (2001) assume symmetric dispersion. Hence, $ß=1$ in their models. Biological aspects of density dependent dispersion growth models are analysed, amongst others, by Hastings (1982), Holt (1985) and Tuck and Possingham(1994). Asymmetric dispersal is described in several works (Delong and Lamberson, 1999, Pezzey *et al.*, 2000), but to our knowledge not modelled earlier.

In the absence of man there is no harvesting, $e=0$, and there is no land-use change taking place in the neighbouring area, thus K_2 is fixed. The isoclines of the system (1) and (2) will then be as in Figure 1, depicted for $\beta>1$. We assume that there are some restrictions on the dispersion so that the marginal dispersion rates are below that of the maximum specific growth rates; that is, $mß/K_1<r_1$ and $m/K_2<r_2$, respectively. The X_1-isocline will then intersect with the X_1-axis at $(K_1 - mß/r_1)>0$. It is a strictly convex function of X_1 and runs through the point $(K_1, ßK_2)$. Above the isocline the natural growth plus dispersion yield a positive growth so that $dX_1/dt>0$, while the population growth is negative below the isocline. The X_2-isocline, on the other hand, is a strictly concave function of X_1. It intersects the X_2-axis at the point $(K_2 - m/r_2)>0$ and runs through the point $(K_1/ß, K_2)$. Below the isocline natural growth plus dispersion add up to positive growth, and hence, dX_2/dt is positive[5].

Figure 1 about here

For the given restrictions on dispersion when $e=0$, there will be a unique, positive interior equilibrium, X_1^* and X_2^*, and as Figure 1 indicates, which also can be confirmed analytically, the equilibrium will be stable. If $ß=1$, both equilibrium stocks will be at their carrying capacities, $X_1^*=K_1$ and $X_2^*=K_2$ and in equilibrium there is no flow of species between the two areas, $M^*=0$. If $ß>1$, as depicted in Figure 1, the result is $X_1^*<K_1$ and $X_2^*>K_2$. The natural equilibrium growth in the conservation area is then positive while it is negative in the neighbouring area. On the other hand, when $0<ß<1$, $X_1^*>K_1$, $X_2^*<K_2$, $M^*<0$ will hold. From equations (1) and (2) and Figure 1 we also see that combinations of X_1 and X_2 giving $M=0$ can be represented by a straight line from the origin through the points $(K_1/ß,K_2)$ and $(K_1, \beta K_2)$. Hence, under this line we have $M>0$, making the reserve a source, while above this line $M<0$, making the reserve a sink. When $ß>1$ as in Figure 1, we therefore clearly have that

---

[5] The X_1-isocline of equation (1) may be expressed as $X_2=K_2X_1[\beta/K_1-(r_1/m)(1-X_1/K_1)]$ and has generally two roots; $X_1=0$, and $X_1=K_1-m\beta/r_1$. If the X_2-isocline of (2) is expressed in a similar manner (when $e=0$), it may be recognized that if the above mentioned dispersal restrictions are violated and we have $mß/K_1>r_1$ and $m/K_2>r_2$, there will be no intersection of the isoclines for positive X-values. The model yields then no meaningful ecological equilibrium (see also the main text below). The same type of restrictions are assumed tacitly also in Sanchirico and Wilen (2001).

positive natural growth in the conservation area plus outflow of species $M^* = m(\beta X_1^*/K_1 - X_2^*/K_2) > 0$ adds up to equilibrium. At the same time, the equilibrium stock size in the surrounding area is too large to support positive natural growth, meaning that mortality dominates recruiting, and is balanced by the inflow.

From Figure 1 it is also clear what happens outside equilibrium. Hence, starting with, say, a small X_1 and large X_2, X_1 grows while X_2 initially decreases, before it eventually starts growing as well. During the transitional phase where both sub-populations grow, the dispersal may change sign with inflow into the conservation area being replaced by outflow; that is, the conservation area changes from being a sink to being a source. The same shift in dispersal may happen when starting with a small X_2 as well as a small X_1. In what follows, however, we will only study what happens when we have ecological equilibrium.

3. The effects of habitat destruction and exploitation

Having seen the basic mechanisms determining the equilibrium stock sizes in absence of man, we proceed to analyse how harvesting and habitat degradation, both activities taking place in the neighbouring area, translate into conservation and stock changes in the protected area. In a first step, these changes are studied without taking account of the underlying economic motives guiding the behaviour of the owner (or owners) of the neighbouring area. Hence, at this stage, the consequences for the conservation area are studied for a *given* harvesting effort, and a *given* habitat degradation.

3.1 Habitat destruction

We start to analyse the case when $e = 0$, so there are only land-use changes. When more land is made up for agricultural production or activities completely unrelated to the biosphere (e.g., residences and factories) in the neighbouring area, the habitat shrinks and consequently, the carrying capacity K_2 decreases. The X_2-isocline will then shift down accompanied by a rotation in a clockwise manner, while the X_1-isocline rotates clockwise around its intersection point with the X_1-axis. It seems difficult to show generally what happens to the equilibrium stock size X_2^* outside the reserve, but it is possible to show that it decreases, at least as long as β is 'small'[6]. On the other hand, the effect of habitat changes upon the stock inside the conservation area, X_1^*, will generally be ambiguous. The reason is that as both K_2 and X_2^* decline, the change of the ratio X_2^*/K_2 is unclear, and hence, the effect on the dispersion between the areas is unclear as well. In the following we study this in detail.

Analytically, the long-run stock effects can be found by taking the total differential of equations (1) and (2) when $dX_1/dt = dX_2/dt = 0$ together with $e = 0$. For the population in the conservation area, we obtain

$$(3)\quad \partial X_1^*/\partial K_2 = (1/N)(mr_2X_2/K_2^2)(1 - X_2/K_2),$$

where $N = \{[r_1 - (2r_1/K_1)X_1 - m\beta/K_1][r_2 - (2r_2/K_2)X_2 - m/K_2] - (m\beta/K_1)(m/K_2)\} > 0$ is positive because the X_1-isocline intersects the X_2-isocline from below (cf. Figure 1). We therefore

---

[6] The effect of habitat change upon the stock size outside the reserve is $\partial X_2^*/\partial K_2 = -(1/N)(X_2/K_2^2)[(r_1 - 2r_1X_1/K_1 - m\beta/K_1)r_2X_2 - mr_1(2X_1/K_1 - 1)]$ where $N > 0$ (see the main text below). After some small rearrangements it follows that $\partial X_2^*/\partial K_2 > 0$ if $(K_1 - 2X_1) < (m\beta r_2X_2)/(r_1r_2X_2 + mr_1)$. Utilising the fact that $1 < X_1/K_1 < 1/\beta$ if $\beta < 1$ and $1/\beta < X_1/K_1 < 1$ if $\beta > 1$, we first find that $\partial X_2^*/\partial K_2 > 0$ holds for all $\beta < 1$. We next cheque the case of $X_1/K_1 = 1/\beta$ when $\beta > 1$. It then follows that $\partial X_2^*/\partial K_2 > 0$ holds at least for all $\beta \leq 2$.

have $\partial X_1^*/\partial K_2 > 0$ only as long the equilibrium stock size in the neighbouring area is below its carrying capacity, $X_2^* < K_2$, or equivalently, if $X_1^* > K_1$. As demonstrated above, this will be the result when $0 < ß < 1$ and there is an inflow of species into the protected area. Thus, when the reserve has mitigating characteristics due to, say, advantageous living conditions, a lower carrying capacity outside decreases the reserve stock as the inflow will decline when K_2 is reduced. This also implies that the species density outside the protected area decreases; that is, $\partial(X_2^*/K_2)/\partial K_2 > 0$. However, all the time we will have $X_1^* > K_1$. On the other hand, $\partial X_1^*/\partial K_2 < 0$ if $ß > 1$ as the outflow declines when K_2 shrinks. This time the density outside the protected area increases, $\partial(X_2^*/K_2)/\partial K_2 < 0$. In the case when $ß = 1$, no changes take place in the conservation area, $\partial X_1^*/\partial K_2 = 0$. Consequently, the species density outside also stays unchanged, $\partial(X_2^*/K_2)/\partial K_2 = 0$.

As just mentioned, we have $\partial X_1^*/\partial K_2 < 0$ when $ß > 1$ and $X_1^* < K_1$. It can also be demonstrated that $\partial X_1^*/\partial m < 0$ holds in this case. Hence, the combination of a well intact habitat in the neighbouring area, K_2 is large, and high spatial movement, m is large, may give a small stock size in the conservation area. It is straightforward to say something more about this case as the species density in the neighbouring area X_2^*/K_2 approaches 1 when K_2 becomes large (this holds when we have $0 < ß < 1$ as well). Substitution of $X_2^*/K_2 = 1$ into equation (1) (when $dX_1/dt = 0$) gives

$$(4)\ X_1^* = (K_1/2r_1)\{[r_1 - (mß/K_1)] + [(r_1 - (mß/K_1))^2 + (4r_1 m/K_1)]^{1/2}\}.$$

When $ß > 1$, equation (4) therefore expresses the lowest possible equilibrium stock size in the reserve in absence of harvesting. All parameters of the model except r_2 and K_2 influence the outcome, and calculations demonstrate that $\partial X_1^*/\partial m < 0$ (as already indicated), $\partial X_1^*/\partial ß < 0$, $\partial X_1^*/\partial r_1 > 0$ and $\partial X_1^*/\partial K_1 > 0$ hold. From equation (4) the condition for $X_1^* < X_1^{msy} = K_1/2$ can also be found, which yields $m(ß - 2) > K_1/2$ after some small rearrangements. Hence, a highly asymmetric dispersion, $ß > 2$, is therefore a necessary condition for a stock size below X_1^{msy} when there is no harvesting outside. This implies that only if the reserve for some reason is severely detrimental for species survival, will the aggregate stock be below its maximum sustainable yield level.

Summing up, we have found that habitat degradation taking place outside the protected area represents no problem for the species abundance in the protected area and hence, the degree of conservation, according to our model of asymmetric density dependent dispersion. This occurs since the equilibrium stock in the protected area all the time either will be over its carrying capacity, or increase as a result of habitat destruction. If the reserve is more advantageous for the species and $0 < \beta < 1$, the effect of habitat destruction outside means less conservation within the reserve, but all the time we have $X_1^* > K_1$. On the other hand, if the reserve is less advantageous for the species wellbeing with $\beta > 1$, habitat destruction outside means more conservation within the reserve as the dispersal out of the reserve then decreases. In the symmetric dispersal models found in the literature with $\beta = 1$, habitat destruction outside the reserve has no effect whatsoever upon the stock in the reserve. The above discussion assumes that conservation is preoccupied with preserving stocks against the threat of extinction. However, conservation may include the securing of specific stock levels. In that case it is not sufficient to solely focus on the stock in the reserve, but rather verify the developments for the sum of the two sub-stocks. The details of such an analysis is left out of the present exposition, but it follows directly from above that the sum will decrease as a result of habitat destruction when $0<\beta<1$ while the outcome is ambiguous when $\beta>1$ and species flow out of the reserve making $M^* >0$.

3.2 Harvesting

When $e>0$ and harvesting takes place with no changes in the land-use and K_2 is fixed, the X_2-isocline in Figure 1 shifts down compared to the non-harvesting case. The X_1-isocline is unaffected. As a result, the stocks in both areas decrease. This happens when either species flow into or out of the conservation area. Harvesting outside the protected area translates therefore unambiguously into a lower equilibrium stock size in the protected area. Analytically the effect can again be found by taking the total differential of equations (1) and (2) when $dX_1/dt = dX_2/dt = 0$. The result is

(5) $\partial X_1^*/\partial e = -(1/R)mqX_2/K_2^2 < 0$

where the determinant R is slightly different from the non-harvesting case, $R=\{[r_1 - (2r_1/K_1)X_1 - m\beta/K_1][r_2 - (2r_2/K_2)X_2 - m/K_2 - qe/K_2] - (m\beta/K_1)(m/K_2)\}$. $R>0$ because the X_1-isocline intersects with the X_2-isocline from below, also when $e>0$.

The effect on the dispersion between the two areas may also be found, and this reads

(6) $\partial M^*/\partial e = (1/R)(qmr_1X_2/K_1K_2^2)(2X_1 - K_1)$.

In absence of harvesting and $0<\beta<1$, we found $X_1^*>K_1$ together with a flow of species into the conservation area, $M^*<0$. Introduction of harvesting effort then clearly yields $\partial M^*/\partial e>0$, and, hence, decreased inflow. As we also have $F(X_1^*) = M^* <0$, the natural growth $F(X_1^*)$ becomes less negative as well, and X_1^* approaches K_1. For even more effort, X_1^* becomes eventually lower than that of K_1. The natural growth is thus positive, and we have $F(X_1^*) = M^* >0$ and species flow out of the reserve. During the course of increased harvesting effort, the reserve may therefore *change* from being a sink to being a source[7]. Moreover, when being positive, M^* increases all the time as long as we have $X_1^* <K_1/2 = X_1^{msy}$. If eventually reaching a stock size below that of X_1^{msy} when e becomes large, we therefore also have that there must exist a maximum degree of dispersion out of the reserve, taking place at $X_1^* = X_1^{msy}$. See Figure 2, panel a. This may happen if the natural environment for dispersion is high, and hence, m is large, cf. equation (7) below[8].

Figure 2 about here

If, on the contrary, we had $F(X_1^*) = M^* >0$ and $X_1^*<K_1$ when $\beta>1$ together with $e=0$, species will always flow out of the conservation area when harvesting effort is introduced. Moreover, if initially $X_1^* >K_1/2$, condition (6) again tells us that M^* increases when e shifts up. If eventually reaching a stock size below that of $K_1/2=X_1^{msy}$ when e becomes large, we therefore also now find that there must exist a maximum degree of dispersion out of the reserve. See Figure 2, panel b.

---

[7] This outcome may also easily be realised when redrawing Figure 1 for $0<\beta<1$ and introducing harvesting effort e shifting the X_2-isocline downwards.

[8] This issue is clearly of interest also in the case of *marine* reserves, since we observe a positive effort level that maximises migration out of the reserve.

As already seen, the X_2-isocline shifts down compared to the non-harvesting case. However, it can be shown that it always yields a positive X_2 when $X_1 > 0$, irrespective of the amount of harvesting effort introduced[9]. Consequently, X_2^*, as well as X_1^*, will be positive for all finite values of e. When e approaches infinity, the X_2-isocline approaches the X_1-axis, and X_2^* approaches zero. In sharp contrast to the standard one patch model, the effort must therefore approach infinity to totally deplete the stock. This is due to the protective effect of the closed area. Hence, even if the stock outside the reserve is depleted, or close to being depleted, the stock in the protected area will be kept intact. From equation (1) (when $dX_1/dt = 0$) it namely follows that X_1^* approaches

(7) $X_1^* = (K_1 - m\beta/r_1) > 0$

when X_2 approaches zero, and hence, e approaches infinity. This condition yields a positive X_1^* due to the given restrictions on dispersion (cf. section 2). Consequently, even for very high harvesting pressure the stock in the protected area may still be positive. This underlines the attractiveness of reserves from a conservation viewpoint. As seen, the critical low level of conservation is positively related to the size of the carrying capacity K_1. A high intrinsic growth rate r_1 works in the same direction while a higher dispersion parameter m together with a higher value of ß has opposite effects. Again the condition for $X_1^* < X_1^{msy} = K_1/2$ may be found, which now reads $m\beta/r_1 > K_1/2$. This condition is therefore met in all cases in Figure 2.

3.3 The simultaneous effect of harvesting and habitat destruction

So far we have studied the effects of changes in harvesting effort and carrying capacity separately. It is however clear that both effort and carrying capacity may change simultaneously in habitats connected to natural reserves, and the effects upon the reserve stock size may be expected to vary depending on the migrational characteristics. This is illustrated in Figure 3.

Figure 3 about here

We see from the figure (panel b) that for ß >1 there is a trade-off between increased harvesting effort and habitat degrading outside the reserve. That is, a given stock size or level of conservation in the reserve may be maintained with increased effort and reduced carrying capacity outside. Furthermore, for an increased stock size in the reserve, a given carrying capacity outside the reserve implies lower effort. When 0 <ß <1 (panel a) there is no such trade-off, as reduced carrying capacity outside means less protection in the conservation area. In this case an increased stock size in the reserve, for a given effort level, is accompanied by a higher carrying capacity.

4. On the optimal exploitation of the neighbouring area

The consequences for the species density in the conservation area have been analysed for given changes in harvesting and habitat destruction. In what follows, however, we will

---

[9] A simple way to realise this is to rewrite the X_2-isocline as $r_2X_2(1 - X_2/K_2) = (m/K_2 + qe/K_2) X_2 - (m\beta/K_1)X_1$, and study the intersection between the LHS and RHS of this equation for various values of X_1 and e.

introduce economic motives for a single owner of the neighbouring area and analyse how these motives influence harvesting and land-use, and hence, translate into species density in the protected area. The justification for studying a single owner situation is either that one owner manages the land outside the reserve, or that many owners co-operatively manage hunting and land-use. For land-based resources such a management, as a stylized fact scheme, fits probably better to reality than so-called open access exploitation (but see Swanson 1994). All the time it will, for simplicity, be assumed that profit maximisation in ecological equilibrium ('sustainable rent') is steering the land-use and harvesting policy. Compared to scenarios of present-value maximisation, what happens outside the various steady-states is therefore neglected, and the rate of return on alternative assets (the rate of discount) is also disregarded (see, e.g., Munro and Scott 1985).

The current net benefit is given by

(8) $\pi = Q(A) + J(X_2) + B(X_2,K_2)e$,

where the first term $Q(A)$ gives the net benefit of land-use from alternative activities, say, agricultural production with A as the amount of land allocated to this activity. The second term $J(X_2)$ yields the non-consumption benefits of the wild species, and can represent various types of values; direct use-value in the form of eco-tourism benefit, or indirect value as it can capture ecosystem functions, etc. (see, e.g., Freeman (1993) for an overview). The third term $B(X_2,K_2)e$ gives the harvesting benefit as the owner of the neighbouring area appropriates the benefits of the wildlife when it is outside the protected area, assumed to be linear in effort use under the present assumption of a Schäfer harvesting function[10].

If the total land is fixed as T, and aK_2 is the size of habitat land and hence, $1/a$ is the fixed coefficient transforming habitat land into potential biological productivity (cf. section 2), the land-use constraint reads $A \leq (T - aK_2)$. We assume that $Q(0) = 0$ and $Q' > 0$ while the marginal benefit may be either decreasing or constant, $Q'' \leq 0$. $Q'' = 0$, implies that land from an alternative point of view is homogeneous, and is in accordance with the assumption of homogeneous habitat land reflected by the fixed coefficient a. The non-consumptive benefit function $J(X_2)$ is assumed to have the properties $J(0) = 0$, $J' > 0$ and $J'' \leq 0$. Under the Schäfer harvesting function assumption, the harvesting profit reads $B(X_2,K_2)e = (p\varphi X_2/K_2 - c)e$. p is the harvest price, assumed to be fixed and unaffected by the harvesting and the stock density, and c is the unit effort cost, also assumed to be fixed. A smaller size of habitat, for a given stock size, therefore means a higher unit profit, as it becomes easier to catch the species.

The optimal equilibrium land-use and harvesting policy for the owner of the neighbouring area is found by maximising the net-benefit function (8), subject to the ecological constraints (1) $dX_1/dt = 0$ and (2) $dX_2/dt = 0$. On reduced form, these constraints may be represented as $X_1 = V(K_2,e)$ and $X_2 = W(K_2,e)$, respectively. The sign of $\partial V/\partial K_2 = V_K$ is negative or positive depending on whether species flow out of or in to the conservation area (cf. section 3.1), while the harvesting effect all the time is negative, $V_e < 0$. Moreover, $W_e < 0$ and we assume that $W_K > 0$ always hold (cf. also footnote 6).

---

[10] No investment costs for converting wilderness land into cultivated land are included. The land-use is also tacitly assumed to be reversible.

The Lagrangian of this problem is $L = Q(T - aK_2) + J(X_2) + B(X_2,K_2)e + \lambda[W(K_2,e) - X_2]$, where $\lambda > 0$ is the shadow price of the wildlife sub-population X_2. Notice that the constraint $X_1 = V(K_2,e)$ is not directly included in the optimisation problem as X_1 follows recursively when the other variables are found. The economic reason is the presence of a *unidirectional* externality working from the outside area to the reserve.

The first order conditions for a maximum are

(9) $\partial L/\partial K_2 = -Q'a + eB_K + \lambda W_K = 0$,

(10) $\partial L/\partial e = B + \lambda W_e \leq 0$

and

(11) $\partial L/\partial X_2 = J' + eB_X - \lambda = 0$

when there always is land-use in the domain (0,T), with or without harvesting. Equation (9) is the equilibrium land-use condition with $Q'a$ as the marginal benefit of agricultural land while $(eB_K + \lambda W_K)$ gives the marginal benefit of the habitat. Condition (11), on the other hand, represents the (economic) equilibrium condition of keeping species where $(J' + eB_X)$ represents the marginal benefit while λ represents the marginal opportunity cost of doing so.

4.1 Zero harvest

When we in a first stage assume that harvesting does not take place because there is no market, or a very thin market, for meat and/or trophies, and the harvesting price is non-existent or low, the above first order conditions reduce to

(9') $-Q'a + \lambda W_K = 0$

(11') $J' - \lambda = 0$.

These two conditions together with the reduced form ecological equilibrium condition $X_2 = W(K_2,0)$ then determine the shadow price λ^*, the equilibrium stock size X_2^* and the carrying capacity K_2^* and hence, the land-use. In a next step, X_1^* is found through $X_1^* = V(K_2^*,0)$. It can easily be confirmed that higher marginal benefit of agricultural production (or other economic activities), implies more land allocated to agriculture and reduced biological productivity, i.e., K_2^* decreases when Q' shifts up. Hence, also X_2^* decreases. A positive shift in the marginal non-consumptive value of the species J' gives the opposite results. These results are as expected.

Land-use conversion triggered by improved profitability in agricultural production therefore works in the direction of more wildlife and more conservation in the protected area if it serves as a source and species flow out, $M^* > 0$. This result is the opposite of Schulz and Skonhoft (1996) who in a somewhat different setting, find that improved profitability in agriculture always represents a threat to species conservation. On the other hand, if the protected area serves as a sink, $M^* < 0$, a higher opportunity cost of the surrounding habitat land reduces the species abundance here as well as in the conservation area as the inflow declines.

4.2 Positive harvesting

When harvesting is a profitable activity and e >0, the first order condition (10) will also hold as an equation. Hence, equations (9) – (11) together with $X_2 = W(K_2, e)$ then determine X_2^*, K_2^*, e^* and the shadow price in this case. In a next step, as above, the stock size in the protected area follows through $X_1^* = V(K_2^*, e^*)$. The comparative static results are now more complex than in the non-harvesting case, and numerical experiments demonstrate that the off-take price has unclear effects on the species abundance and land-use in the neighbouring area. The effect on the degree of conservation is also unclear. An increased harvest price may also increase the effort use while more land is allocated to habitat, K_2^* rises, at the same time. Table 1 demonstrates the effects where the harvest price – marginal agricultural benefit ratio shifts. For these shifts the species abundance in the conservation zone (last column) decreases all the time, also when $\beta > 1$, meaning that the 'harvesting effect' outbalances the 'habitat effect' (cf. also Figure 3, panel b).

Table 1 about here

The reason for these ambiguous results is that an increased p for a given land-use, motivates for more harvesting and stock depletion according to the standard harvesting model (Clark 1990). On the other hand, an increased p makes habitat investments more attractive as the marginal benefit ratio of the two competing activities harvesting and agricultural production p/Q' increases. Hence, an increased p has a two-sided effect on land-use and species abundance, thus when there is dispersion, more habitat and species can go hand in hand with more harvesting.

5. Concluding remarks

One way to counteract destruction and reduction of habitats is to establish conservation zones with restrictions on harvesting and land-use. However, very few reserves can be considered islands because wildlife species move around. As a consequence, habitat destruction and exploitation, taking place outside influences the species abundance inside the conservation area as well. The paper presents a theoretical model for analysing this type of management problem where two sub-populations, in the reserve and in a neighbouring area, are linked together through a density dependent dispersal process. Reserves cause change in inter and intra species composition, and such stock differences between a reserve and a surrounding non-reserve are taken into account in the present analysis as it is opened up for what is said to be an asymmetric dispersal. All the time it is studied what happens in ecological equilibrium.

The main finding is that habitat destruction outside does not necessarily yield a negative impact upon the long-term species abundance in the reserve. It is shown that the critical factor for what happens is whether the wildlife flows from the reserve to the outside area or the opposite; that is, whether the conservation zone serves as a source or sink. When the reserve is a source, habitat reduction outside gives a higher long-term population size inside the protected area. The reason being, that a smaller surrounding habitat increases the species density outside and hence reduces the dispersion out of the reserve. Consequently, economic forces working in the direction of reducing the surrounding habitat through increased profitability in, say, agriculture, give *ceteris paribus* a higher species abundance in the conservation zone. In real life there are many examples that the species density has increased within a protected area while the outer area has been less useless for the same species. One example is reported by Vistnes *et al*. (2004) who find that building of roads and power lines in south-central Norway during the last years has increased the density of wild reindeer in its core area (the reserve) while the density has decreased in the areas affected by the encroachment.

The effect of harvesting outside the reserve always yields a smaller stock within the reserve. When conditions are more attractive to the species outside the reserve than inside, increased effort increases the flow out of the reserve. In the opposite case, i.e. when conditions are more attractive within the reserve, the reserve will at low effort levels function as a sink. As effort increases, migration into the reserve will decrease, until finally the reserve will become a source. However, moderate harvesting pressure, changing the reserve from sink to source, may not represent a problem from a conservation point of view, as long as the conservation effect within the reserve still is strong.

Generally we have shown that, if taking place, harvesting and harvesting profitability outside the reserve have unclear effects on the species abundance in the reserve. If the surrounding area is managed by a single owner maximising profit in ecological equilibrium , we find that this unclear effect is a result of to the fact that the direct harvesting effect due to the traditional Clark-model may be counterbalanced by investment in habitat being profitable in the surrounding area. And when there are unclear stock as well as land-use effects in the surrounding area, the conservation effect in the reserve may also be unclear.

ooo00ooo

References

Bhat, M., R. Huffaker and S. Lenhart 1996: Controlling transboundary wildlife damage: modeling under alternative management scenarios. *Ecological Modelling* 92, 215-224

Bromley, D. 1991: *Environment and Economy. Property Rights and Public Policy.* Blackwell, Oxford

Brown, G. 1997: Management of wildlife and habitat in developing countries. Pp. 555-573 in P. Dasgupta and K. G. Mäler (eds.): *The Environment and Emerging Developing Issues* (Vol. 2). Clarendon Press, Oxford

Clark, C. 1990: *Mathematical Bioeconomics* (2th. ed.). Wiley Interscience, New York

Conrad, J. 1999: The bioeconomics of marine sanctuaries. *Journal of Bioeconomics* 1, 205-217

Delong, A. K. and R. H. Lamberson, 1999: A habitat based model for the distribution of forest interior nesting birds in a fragmented landscape. *Natural Resource Modeling* 12, 129-146

Dixon, J. and P. Sherman 1990: *Economics and Protected Areas. A New Look at Benefit and Costs*. Island Press, Washington D.C.

Freeman, A. M. 1993: Nonuse values in natural resource damage assessment. Pp. 264-303 in R. Kopp and V. K. Smith: *Valuing Natural Assets*. Resources for the Future, Washington D.C.

Fretwell, S.D. and H.L. Lucas 1970: On territorial behavior and other factors influencing habitat distribution of birds. *Acta Biotheoretica* 19, 16-36

Hannesson, R. 1998: Marine reserves: what would they accomplish? *Marine Resource Economics* 13, 159-170

Hastings, A. 1982: The dynamics of a single species in a spatially varying environment: The stabilising role of high dispersion rates. *Journal of Mathematical Biology* 16, 49-55

Holt, R. 1985: Population dynamics in two-patch environments: Some anomalous consequences of an optimal habitat distribution. *Theoretical Population Biology* 28, 181-208

Huffaker, R. M. Bhat and S. Lenhart 1992: Optimal trapping strategies for diffusing nuisance-beaver populations. *Natural Resource Modeling* 6, 71-97

Johannesen, A. B. 2003: Wildlife conservation, human welfare and the failure of protected areas. *Working Paper* Department of Economics NTNU, Trondheim

Kiss, A. (eds.) 1990: *Living with Wildlife.* The World Bank, Washington D.C.

Lauck, T., C. Clark, M. Mangel and G. Munro 1998: Implementing the precautionary principle in fisheries management through marine reserves. *Ecological Applications* 8 (Supplement), s.72-s.78

Munasinghe, M. and J. McNeely 1994: *Protected Area Economics and Policy. Linking Conservation and Sustainable Development*. The World Bank, Washington D.C.

Munro, G. and A. Scott 1985: The economics of fishery management. Pp.623-676 in A. Kneese and J. Sweeney: *Handbook of Natural Resource and Energy Economics* (Vol II). North Holland, Amsterdam

Pezzey, J.C.V., C.M. Roberts and B.T. Urdal 2000: A simple bioeconomic model of a marine reserve. *Ecological Economics* 33, 77–91

Pulliam, H.R. 1988: Sources, sinks, and population regulation. *The American Naturalist* 132, 652-661

Roberts, C.M., and H. Sargant 2002: Fishery benefits of fully protected marine reserve: Why habitat and behavior are important. *Natural Resource Modelling* 15(4), 487-507.

Rodwell, L.D., E.B. Barbier, C.M. Roberts and T.R. McClanahan 2002: A model of tropical marine reserve-fishery linkages. *Natural Resource Modelling* 15(4), 453-485.

Sanchirico, J.N. and J.E. Wilen 1999: Bioeconomics of spatial exploitation in a patchy environment. *Journal of Environment Economics and Management* 37, 129-150

Sanchirico, J.N. and J.E. Wilen 2001: A Bioeconomic Model of Marine Reserve Creation. *Journal of Environmental Economics and Management*, 42, 257-276

Schulz, C.E. and A. Skonhoft 1996: Wildlife, management and land-use conflicts. *Environment and Development Economics* 1, 265-280

Sinclair, A. and P. Arcese (eds.) 1995: *Serengeti II.* University of Chicago Press, Chicago

Skonhoft, A. and J. Solstad 1998: The political economy of wildlife exploitation. *Land Economics* 74, 16-31

Skonhoft, A., N. Yoccoz and N.C. Stenseth 2002: Management of chamois (Ruicapra rupicapra) moving between a protected core area and a hunting area. *Ecological Applications* 12, 1199-1211

Sumaila, U.R. 1998. Protected marine reserves as fisheries management tools: a bioeconomic analysis. *Fisheries Research* 37,.287-296

Swallow, S. 1990: Depletion of the environmental basis for renewable resources. The economics of interdependent renewable and non-renewable resources. *Journal of Environmental Economics and Management* 19, 281-296

Swanson, T. 1994: The economics of extinction revisited and revised. *Oxford Economic Papers* 46, 800-82

Tuck, G.N. and H. Possingham 1994: Optimal harvesting strategies for a metapopulation. *Bulletin Math. Biology* 56, 107-127

Vistnes, I, C. Nellemann, P. Jordhoy and O. Strand 2004: Effects of infrastructure on migration and range use of wild reindeer. *Journal of Wildlife Management* 68, 101-108

Wright, R.G. 1999: Wildlife management in the national parks: questions in search of answers. *Ecological Applications* 9, 30-36

Figure 1. The X_1-isocline and X_2-isocline in absence of harvesting, $\beta > 1$.

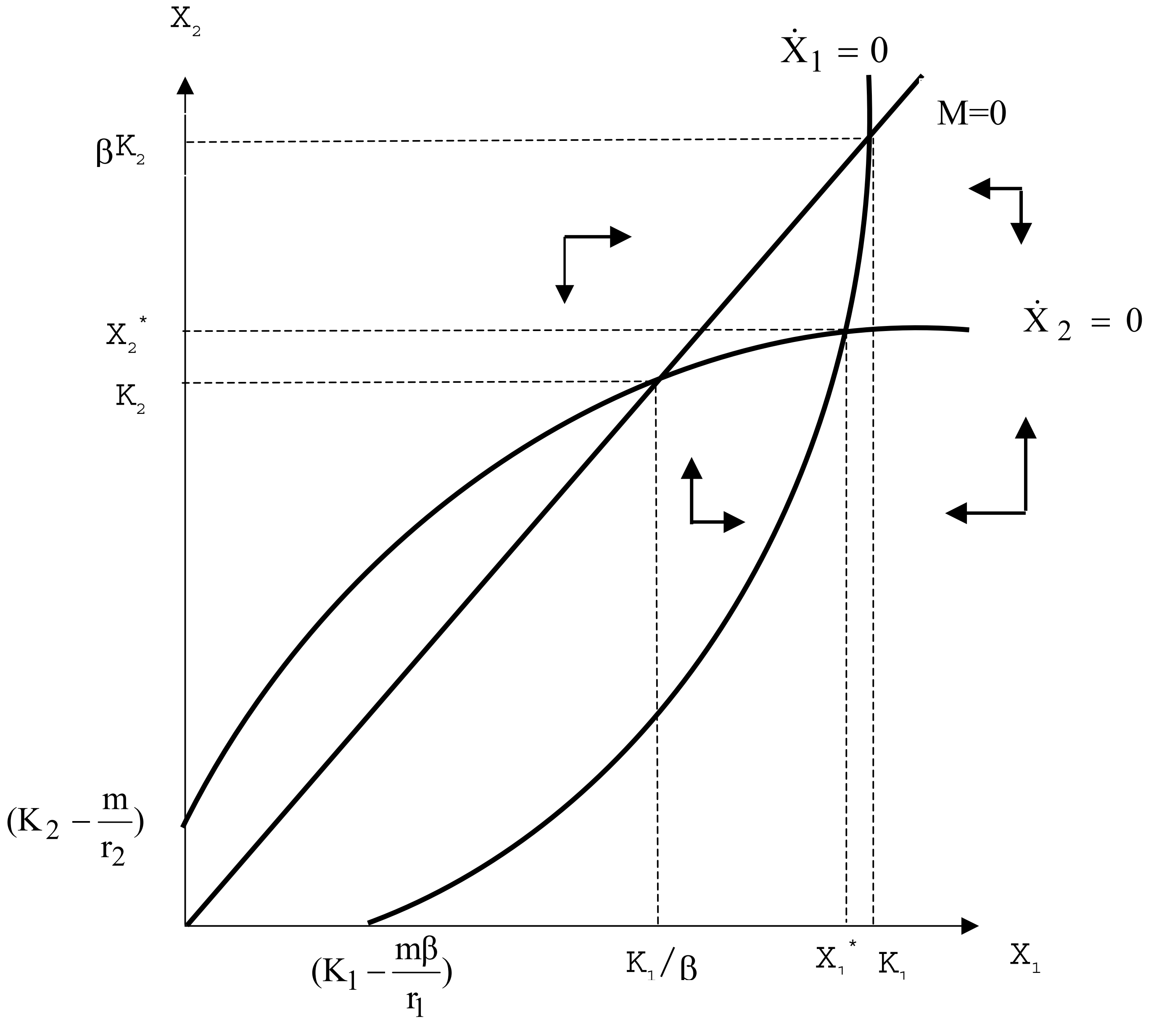

Figure 2. The size of the protected stock X_1^* and dispersal M^* depending on harvesting effort. Panel a) $0<\beta<1$, panel b) $\beta>1$, panel c) $\beta=1$.

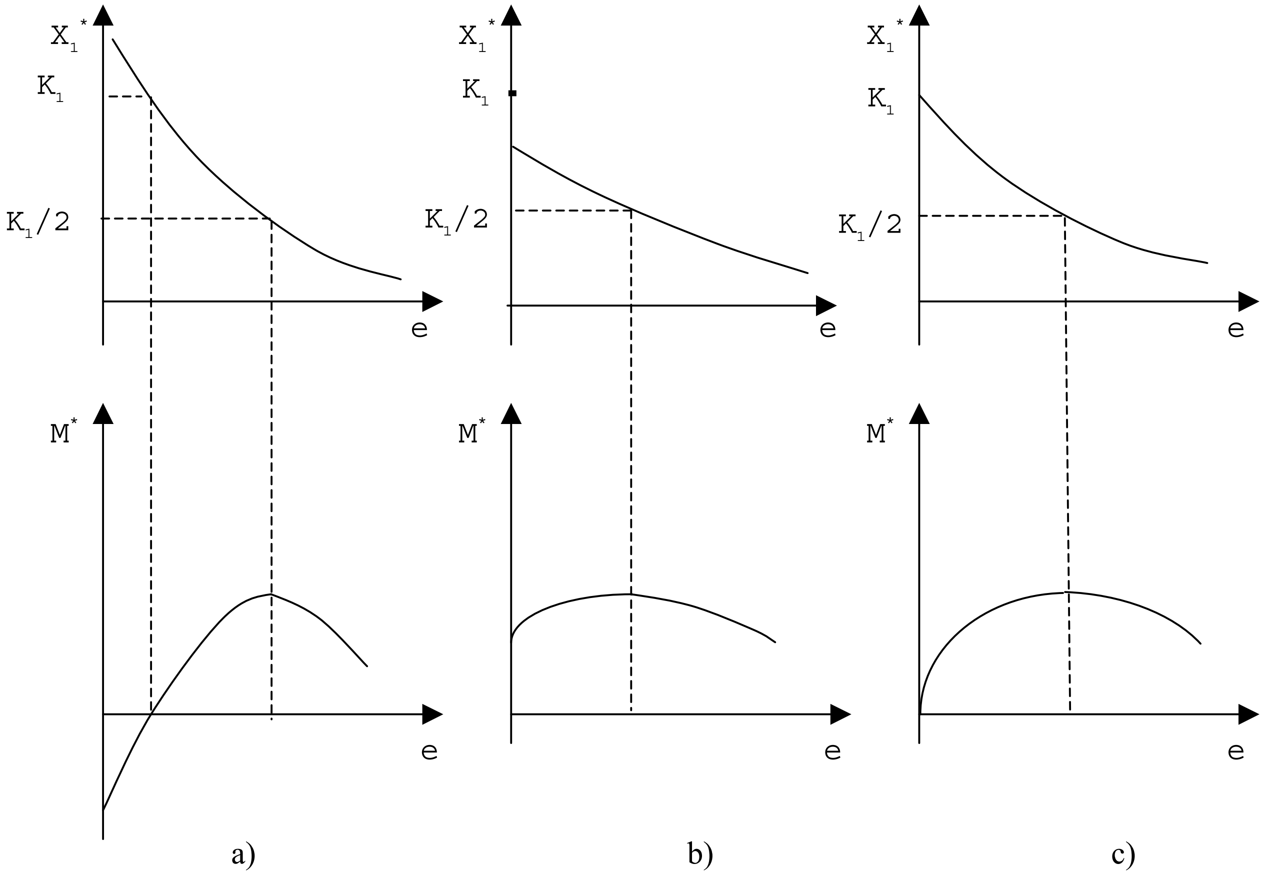

Figure 3. The size of the protected stock X_1^* under simultaneous changes in carrying capacity and harvesting, $X_1^{*2} > X_1^{*1}$. Panel a) $0<\beta<1$, panel b) $\beta>1$, panel c) $\beta=1$.

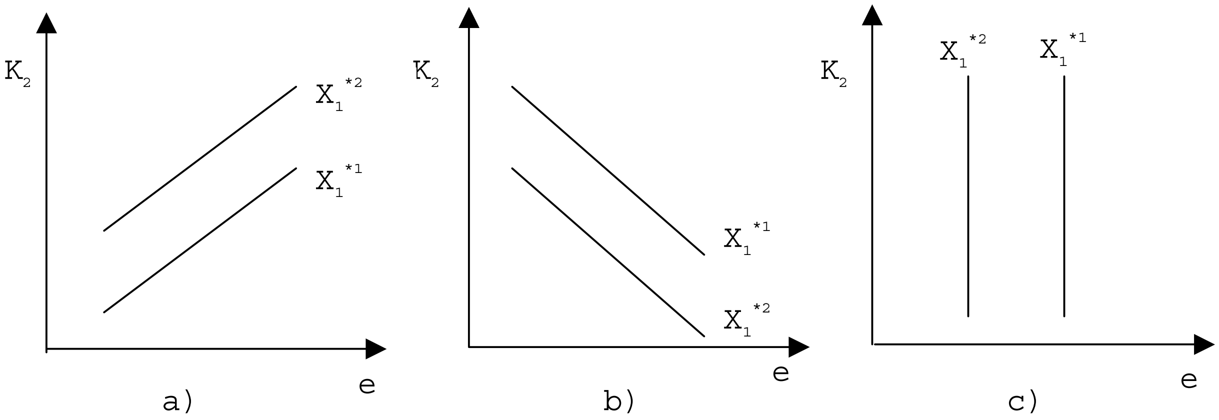

Table 1. Stock sizes X_1^* and X_2^*, habitat land K_2^* and harvesting effort e^* depending on relative harvesting benefit $p/Q' = p/q$ and β.

	β=0.5				β=1.0				β=2.0			
p/q	2	4	6	8	2	4	6	8	2	4	6	8
e^*	0	0	30	50	0	40	70	110	20	60	80	120
K_2^*	40	40	40	60	70	70	120	330	60	60	100	310
X_2^*	21	21	17	23	70	52	75	191	86	61	88	230
X_1^*	1010	1010	967	949	1000	907	863	843	844	713	663	610

Table note: Net benefit function (8) when the marginal benefit of agricultural production is fixed, $Q(A) = qA$ and the non-consumption benefit function is specified as $J(X_2) = jX_2^{0.5}$. Profit per unit value agricultural land, $\pi/q = (T - aK_2) + (j/q)X_2^{0.5} + [(p/q)(\varphi X_2/K_2) - (c/q)]e$. Parameter values; $K_1 = 1000$, $r_1 = r_2 = 0.30$, $T = 1000$, $a = 0.5$. Relative prices; $j/q = 1$, $c/q = 2$.