

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

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**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 analyzing 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.

**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<sup>1</sup>.

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 recolonize *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; however, see Skonhøft et al. [2002] and Johannesen [2003].

The purpose of this paper is to bridge this gap and, from a theoretical point of view, analyze 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 analyzed 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 neighboring 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<sup>2</sup>. On the other hand, the land use can change in the neighboring area as habitat degrades. We abstract from any harvesting taking place in the conservation area, 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 industrialized countries<sup>3</sup>.

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 analyzed 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 neighboring 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 neighboring 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 neighboring 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 neighboring 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

$$(1) \quad \begin{aligned} \frac{dX_1}{dt} &= F(X_1) - M(X_1, X_2, K_2) \\ &= r_1 X_1 \left(1 - \frac{X_1}{K_1}\right) - m \left(\beta \frac{X_1}{K_1} - \frac{X_2}{K_2}\right) \end{aligned}$$

and

$$(2) \quad \begin{aligned} \frac{dX_2}{dt} &= G(X_2, K_2) + M(X_1, X_2, K_2) - h(e, X_2, K_2) \\ &= r_2 X_2 \left(1 - \frac{X_2}{K_2}\right) + m \left(\beta \frac{X_1}{K_1} - \frac{X_2}{K_2}\right) - \varphi \frac{e X_2}{K_2} \end{aligned}$$

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 neighboring area at the same time.  $F(\cdot)$  and  $G(\cdot)$  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  $h(\cdot) \geq 0$  only takes place outside the protected area. It is specified as a Schäfer function

and determined by the harvest effort  $e$ , the catchability coefficient  $\varphi$  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  $M(\dots)$ . 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 (Skonhofs et al. [2002]). Here we focus on the latter, and  $M(\dots)$  is assumed to depend on the relative stock densities in the two areas, ignoring any other migratory patterns<sup>4</sup>.  $m > 0$  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  $\beta > 0$  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 et al. [2000]). For equal  $X_i/K_i$ ,  $i = 1, 2$ ,  $\beta > 1$  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  $\beta$ . On the other hand, when  $0 < \beta < 1$ , 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-stock or inter-species relations that may result in different concentrations in the two areas; that is, the dispersal may be *asymmetric*. Hence,  $\beta$  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

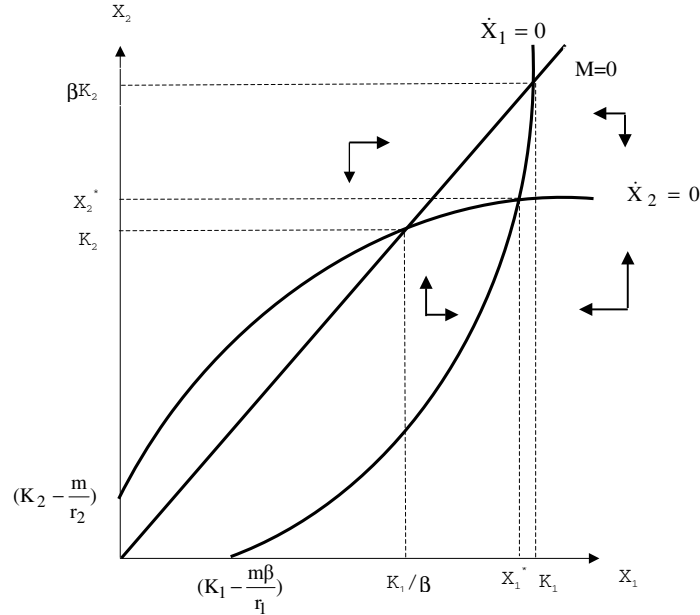


FIGURE 1. The  $X_1$ -isocline and  $X_2$ -isocline in absence of harvesting,  $\beta > 1$ .

Bhat et al. [1996], to analyze 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] analyze 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,  $\beta = 1$  in their models. Biological aspects of density dependent dispersion growth models are analyzed, 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 modeled earlier.

In the absence of man, there is no harvesting,  $e = 0$ , and there is no land use change taking place in the neighboring 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,  $m\beta/K_1 < r_1$  and  $m/K_2 < r_2$ , respectively. The  $X_1$ -isocline will then intersect with the  $X_1$ -axis at  $(K_1 - m\beta/r_1) > 0$ . It is a strictly convex function of  $X_1$  and runs through the point  $(K_1, \beta K_2)$ . 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  $(K_1/\beta, K_2)$ . Below the isocline natural growth plus dispersion add up to positive growth, and hence,  $dX_2/dt$  is positive<sup>5</sup>.

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  $\beta = 1$ , 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  $\beta > 1$ , 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 neighboring area. On the other hand, when  $0 < \beta < 1$ ,  $X_1^* > K_1$ ,  $X_2^* < K_2$ ,  $M^* < 0$  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  $(K_1/\beta, K_2)$  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  $\beta > 1$  as in Figure 1, we therefore clearly have that 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 analyze how harvesting and habitat degradation, both activities taking place in the neighboring 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 behavior of the owner (or owners) of the neighboring 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 analyze 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 neighboring 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  $\beta$  is ‘small’<sup>6</sup>. 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

$$(3) \quad \frac{\partial X_1^*}{\partial K_2} = \left(\frac{1}{N}\right) \left(\frac{mr_2 X_2}{K_2^2}\right) \left(1 - \frac{X_2}{K_2}\right),$$

where  $N = \{[r_1 - (2r_1/K_1)X_1 - (m\beta/K_1)][r_2 - (2r_2/K_2)X_2 - (m/K_2)]\}$  is



positive because the  $X_1$ -isocline intersects the  $X_2$ -isocline from below, cf. Figure 1. We therefore have  $\partial X_1^*/\partial K_2 > 0$  only as long the equilibrium stock size in the neighboring 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  $0 < \beta < 1$  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  $\beta > 1$  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  $\beta = 1$ , 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  $\beta > 1$  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 neighboring 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 neighboring area  $X_2^*/K_2$  approaches 1 when  $K_2$  becomes large (this holds when we have  $0 < \beta < 1$  as well). Substitution of  $X_2^*/K_2 = 1$  into equation (1) (when  $dX_1/dt = 0$ ) gives

$$(4) \quad X_1^* = \left(\frac{K_1}{2r_1}\right) \left\{ \left[ r_1 - \left(\frac{m\beta}{K_1}\right) \right] + \left[ \left( r_1 - \left(\frac{m\beta}{K_1}\right) \right)^2 + \left(\frac{4r_1m}{K_1}\right) \right]^{1/2} \right\}.$$

When  $\beta > 1$ , 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,  $\partial X_1^*/\partial \beta < 0$ ,  $\partial X_1^*/\partial r_1 > 0$  and  $\partial X_1^*/\partial K_1 > 0$  hold. From equation (4) the condition for  $X_1^* < X_1^{\text{msy}} = K_1/2$  can also be found, which yields  $m(\beta - 2) > K_1/2$  after some small rearrangements. Hence, a highly asymmetric dispersion,  $\beta > 2$ , is therefore a necessary condition for a stock size below  $X_1^{\text{msy}}$  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 well being 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

$$(5) \quad \frac{\partial X_1^*}{\partial e} = -\left(\frac{1}{R}\right) \frac{mqX_2}{K_2^2} < 0$$

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

$$(6) \quad \frac{\partial M^*}{\partial e} = \left(\frac{1}{R}\right) \left(\frac{qmr_1X_2}{K_1K_2^2}\right) (2X_1 - K_1).$$

In the 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<sup>7</sup>. Moreover, when being positive,  $M^*$  increases all the time as long as we have  $X_1^* < K_1/2 = X_1^{\text{msy}}$ . If eventually reaching a stock size below that of  $X_1^{\text{msy}}$  when  $e$  becomes large, we therefore also have that there must exist a maximum degree of dispersion out of the reserve, taking place at  $X_1^* = X_1^{\text{msy}}$ . 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<sup>8</sup>.

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  $K_1/2 = X_1^{\text{msy}}$  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.

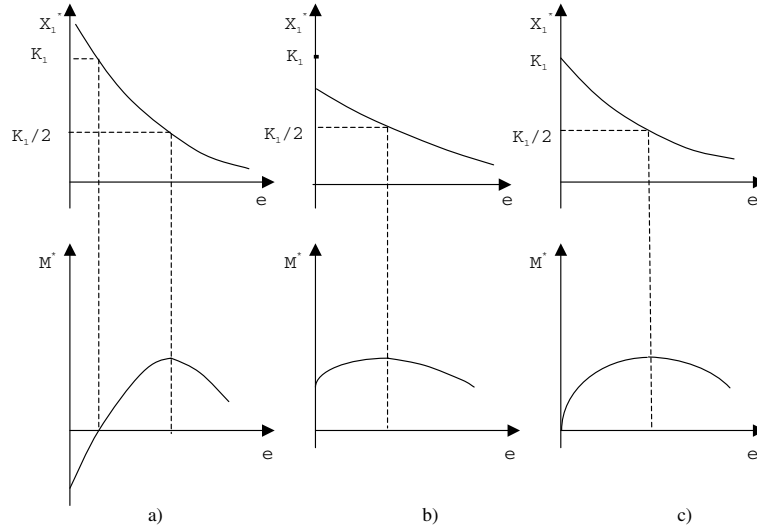


FIGURE 2. The size of the protected stock  $X_1^*$  and dispersal  $M^*$  depending on harvesting effort. Panel a)  $0 < \beta < 1$ , panel b)  $\beta > 1$ , panel c)  $\beta = 1$ .

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<sup>9</sup>. 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 follows that  $X_1^*$  approaches

$$(7) \quad X_1^* = \left( K_1 - \frac{m\beta}{r_1} \right) > 0$$

when  $X_2$  approaches zero, and hence,  $e$  approaches infinity. This condition yields a positive  $X_1^*$  due to the given restrictions on dispersion,

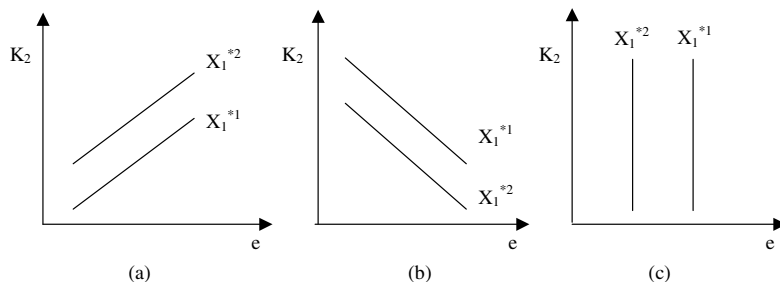


FIGURE 3. The size of the protected stock  $X_1^*$  under simultaneous changes in carrying capacity and harvesting,  $X_1^{*2} > X_1^{*1}$ . Panel a)  $0 < \beta < 1$ , panel b)  $\beta > 1$ , panel c)  $\beta = 1$ .

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  $\beta$  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.

We see from the figure (panel b) that for  $\beta > 1$  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  $0 < \beta < 1$  (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 neighboring area.** The consequences for the species density in the conservation area have been analyzed for given changes in harvesting and habitat destruction. In what follows, however, we will introduce economic motives for a single owner of the neighboring area and analyze 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 maximization in ecological equilibrium, ‘sustainable rent,’ is steering the land use and harvesting policy. Compared to scenarios of present-value maximization, 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

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

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 neighboring 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<sup>10</sup>.

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 neighboring area is found by maximizing 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 endnote 6.

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 optimization 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

$$(9) \quad \frac{\partial L}{\partial K_2} = -Q'a + eB_K + \lambda W_K = 0,$$

$$(10) \quad \frac{\partial L}{\partial e} = B + \lambda W_e \leq 0$$

and

$$(11) \quad \frac{\partial L}{\partial X_2} = J' + eB_X - \lambda = 0$$

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  $\lambda$  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

$$\begin{aligned} (9') \quad & -Q'a + \lambda W_K = 0 \\ (11') \quad & J' - \lambda = 0. \end{aligned}$$

These two conditions together with the reduced form ecological equilibrium condition  $X_2 = W(K_2, 0)$  then determine the shadow price  $\lambda^*$ , 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 Skonhøft [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 neighboring 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. 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  $\beta$ .

	$\beta = 0.5$				$\beta = 1.0$				$\beta = 2.0$			
$p/q$	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

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:  $j/q = 1$ ,  $c/q = 2$ .

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 analyzing this type of management problem where two sub-populations, in the reserve and in a neighboring 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 useful 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 maximizing profit in ecological equilibrium, we find that this unclear effect is a result of 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.

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#### ENDNOTES

1. The history of establishing conservation zones is old, and today more than 5 percent 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.

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 Skonhøft and Solstad [1998] for an analysis.

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).

5. The  $X_1$ -isocline of equation (1) may be expressed as  $X_2 = K_2 X_1 [\beta/K_1 - (r_1/m)(1 - X_1/K_1)]$  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  $m\beta/K_1 > r_1$  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].

6. The effect of habitat change upon the stock size outside the reserve is  $\partial X_2^*/\partial K_2 = -(1/N)(X_2/K_2^2)[(r_1 - 2r_1 X_1/K_1 - m\beta/K_1)r_2 X_2 - mr_1(2X_1/K_1 - 1)]$  where  $N > 0$  (see the main text below). After some small rearrangements it follows that  $\partial X_2^*/\partial K_2 > 0$  if  $(K_1 - 2X_1) < (m\beta r_2 X_2)/(r_1 r_2 X_2 + mr_1)$ . Utilizing 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 check 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  $\beta \leq 2$ .

7. This outcome may also easily be realized 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 maximizes migration out of the reserve.

9. A simple way to realize this is to rewrite the  $X_2$ -isocline as  $r_2 X_2(1 - X_2/K_2) = (m/K_2 + qe/K_2)X_2 - (m\beta/K_1)X_1$ , and study the intersection between the LHS and RHS of this equation for various values of  $X_1$  and  $e$ .

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

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