ECOLOGICAL ECONOMICS 62 (2007) 223–231

available at www.sciencedirect.com

www.elsevier.com/locate/ecolecon

Economic modeling approaches for wildlife and species conservation

Anders Skonhoft

Department of Economics Norwegian University of Science and Technology N-7491 Dragvoll-Trondheim, Norway

ARTICLE INFO

Article history:
Received 3 June 2005
Received in revised form
3 February 2006
Accepted 28 February 2006
Available online 30 June 2006

Keywords:
Modeling
Conservation bioeconomics
Animal species

ABSTRACT

This paper presents modeling approaches for wildlife and species conservation with a special emphasis on large mammals in a developing country setting. In such countries there are frequently conflicts over land use and species conservation, and institutions for managing conflicts are often weak or even lacking. In addition, most of the world species and biodiversity are found in developing countries. Two main issues are discussed. First, we study a situation where the wildlife is valuable, but is considered a pest by the local people living close to the wildlife. Second, we consider models with a discrepancy between management geography and biological geography, and where the species flows between a conservation area with no harvesting and a neighboring area with harvesting and possible habitat degradation.

1. Introduction

Establishment of protected areas, like national parks, has traditionally been recognized as the single most important method for securing conservation of terrestrial animal species. In many developing countries, this practice dates back to the colonial era, and the objective has always been to protect wild animals and natural habitats through strongly restricted wildlife utilization.[1] However, particularly in developing countries, it is well known that this conservation policy has had some adverse effects. Land for establishing the parks has often directly displaced rural communities and curtailed their access to natural resources that traditionally were theirs. Land for cultivation and pasture has been lost, and antipoaching laws have criminalized subsistence hunting. Moreover, local people are often prevented from eliminating 'problem' animals to protect their crops and livestock. If they are bearing the real cost of conservation without obtaining any significant benefits from it, it is easy to understand why a negative attitude against wildlife conservation has emerged among the local people, in sub-Saharan Africa as well as in other places (see among others, Kiss, 1990; Swanson, 1994; Johannesen and Skonhoft, 2005).

Some aspects of this conflict between wildlife utilization and conservation will be discussed in this paper. The paper's focus is on wildlife in the sense of large mammals, and the discussion is primarily related to a sub-Saharan Africa context where the institutions to tackle such conflicts are often weak, or even lacking. Particularly because of rapid human population growth, the basic underlying conflict between wildlife conservation and rural development in these countries, as well as in many other developing countries, is over *land use*. Land-use conflicts frequently translate into land conversion (see, e.g., Swanson, 1994; Schulz and Skonhoft, 1996), but in this paper, land use for conservation is assumed unchanged. In the models to be considered, the setting is therefore that in which a well-defined agency is managing a national park or game reserve of *fixed* size. On the other hand, this is also a setting in which the rural people, agropastoralists and smallholder farmers, are entitled to use the land near the

---

E-mail address: anders.skonhoft@svt.ntnu.no.

[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., IUCN web page).

0921-8009/$ - see front matter © 2006 Elsevier B.V. All rights reserved.
doi:10.1016/j.ecolecon.2006.02.025

park, and where the wildlife exploitation typically takes place in a *myopic*, or *open-access*, manner.

Within this broad framework, I discuss two main issues. I first look at the conflicting interests among the park agency and the local people, where wildlife is considered as valuable as well as a pest and nuisance. The park agency benefits from wildlife through tourism and possible safari hunting, while the local people also hunt wildlife, partly motivated by the need for reducing crop and other agricultural damage. Next, a situation with a discrepancy between management geography and biological geography is considered. The setting is here a protected area with no harvesting, and a surrounding area with harvesting and habitat changes where the species flows between the areas. Both density-dependent and density-independent dispersal are studied. The modeling approach is consistent throughout with bioeconomic models treating the species as biomass, or 'normalized' number of animals. I am therefore not considering models with different stages, or classes, of wild species. The models are formulated in a standard manner with a concave natural growth function and 'well-behaved' utility and profit functions meaning that the important issue of nonconvexity is not touched. Valuation issues are not discussed. Uncertainties of various types (environmental and ecological uncertainty, price fluctuations, etc.) are also swept under the carpet irrespective of their well-known presence.

The paper is organized as follows. In Section 2, the conflict models are presented, and I first look at a static model before touching upon some dynamic considerations. Section 3 contains the migratory models. I start with a situation where the dispersal is assumed to be of the density-dependent type, and then briefly present some results when the dispersal is governed in a density-independent manner. Section 4 concludes the paper.

2. Conflicting views on conservation and species values

In sub-Saharan Africa, where wildlife conservation and establishment of protected areas have taken place at the expense of rural communities, a wild species is often a nuisance, interfering with livestock and crop production (Kiss, 1990). The agricultural damage may take place in a variety of ways; including eating crops and pastures, preying on livestock, rooting, tramping, or pushing away obstructions such as fences. It is therefore a conflict related to wildlife conservation. This conflict is formulated in a two-agent model with a group of local people and a conservation agency. Within this framework, I first look at a situation where harvest is equal to natural growth and its ecological equilibrium. The economic equilibrium is assumed to be of the Nash type.

2.1. *An equilibrium conflict model*

As in Johannesen and Skonhoft (2005), I consider the conflicting interest between an agency managing a protected area and the local people living in the vicinity of this area. The park agency benefits from wildlife through safari hunting and non-consumptive tourism services, such as wildlife viewing. The local people also hunt wildlife, but as the wildlife knows no boundaries and moves freely in and out of the protected area, the game also destroys agricultural crops and competes with livestock when outside the protected area. The wildlife therefore also represents a nuisance for the local people. Hunting by the local people is assumed to be illegal. However, because of just a small funding for policing a large protected area, poaching cannot be prevented by the park manager. Hence, *de jure* and *de facto* property rights differ.

The two production activities practised by the conservation agency, non-consumptive tourism and hunting, and illegal hunting by the local people are constrained by wildlife abundance. One stock of wildlife X (measured in biomass, or number of 'normalized' animals) represents the whole game popuzlation. The population dynamics is determined by natural growth $F(X)$, assumed to be density-dependent and of standard logistic type (see below), and the hunting of the park manager y_1, depending on effort use and number of animals $y_1 = y_1(e_1, X)$, and the hunting of the local people y_2, depending on the same factors, $dX/dt = F(X) - y_1(e_1, X) - y_2(e_2, X)$. Therefore, in biological equilibrium where total harvest equals natural growth, we have $F(X) = y_1(e_1, X) + y_2(e_2, X)$, or:

$$X = X(e_1, e_2). \tag{1}$$

Increased hunting effort reduces the stock, $\partial X/\partial e_i < 0$, $i = 1, 2$, and for a given stock level Eq. (1) is hence downward-sloping in the (e_1, e_2) space. The biological equilibrium condition (1) may therefore be considered as an *iso-conservation* line. Lines closer to the origin imply more animals as it represents less harvesting effort.

The park manager obtains income from hunting wildlife, by selling hunting licences, and from non-consumptive tourism. The net benefit of hunting may be expressed as $B_1(e_1, X) = p_1 y_1(e_1, X) - c_1 e_1$ where p_1 is the price of the safari hunting licence and c_1 is the unit cost of organizing the hunting, both assumed to be fixed. $W(X)$, with $W'(X) > 0$, and $W(0) = 0$, represents the benefit from non-consumptive tourism. Therefore, the current profit of the park manager is:

$$\pi = B_1(e_1, X) + W(X). \tag{2}$$

The local people derive utility from hunting wildlife illegally. The poaching benefit may also be written as $B_2(e_2, X) = p_2 y_2(e_2, X) - c_2 e_2$, and where the price p_2 and unit cost c_2 generally differ from those of the park manager. Wildlife is also a nuisance, and the damage cost $D(X)$ depends on the size of the stock. More wildlife means more damage, $D'(X) > 0$ with $D(0) = 0$. Accordingly, the net benefit to the local people is given by:

$$U = B_2(e_2, X) - D(X). \tag{3}$$

In the absence of a unified resource policy, there are several externalities. Just as in standard harvesting models, reciprocal harvesting externalities work through the hunting benefit functions. In addition, there are reciprocal stock externalities related to the stock values: more hunting effort by the park manager, *ceteris paribus*, induces a positive externality on the local people through a reduction in $D(X)$. On the other hand, more hunting effort by the local people induces a negative external effect on the park manager through a reduction in $W(X)$.

The economic problem of the park agency is to determine the profit-maximizing hunting effort under the ecological constraint (1), given the effort of the local people. The necessary condition for a maximum (when having an interior solution) is:

$$\partial B_1(e_1, X)/\partial e_1 + [\partial B_1(e_1, X)/\partial X](\partial X/\partial e_1) + W'(X)(\partial X/\partial e_1) = 0. \quad (4)$$

This represents also the park manager's best-response function, denoted by $e_1 = R_1(e_2)$ in Fig. 1. Along the best-response curve, profit depends on the effort of the local people, $\pi = \pi(e_2)$. In Fig. 1, π^0 and π^1 yield two iso-profit curves, where $\pi^1 > \pi^0$.

The economic problem of the local people is to determine the utility-maximizing harvesting effort e_2, subject to the ecological constraint (1) and the effort of the park manager. The necessary condition for maximum is:

$$\partial B_2(e_2, X)/\partial e_2 + [\partial B_2(e_2, X)/\partial X](\partial X/\partial e_2) - D'(X)(\partial X/\partial e_2) = 0, \quad (5)$$

and is the local people's best-response function, denoted by $e_2 = R_2(e_1)$ in Fig. 1. Along the best-response curve, utility depends on the effort of the park manager, $U = U(e_1)$, and implicit differentiation (the envelope theorem) implies $\mathrm{d}U(e_1)/\mathrm{d}e_1 = (\partial B_2/\partial X - D')(\partial X/\partial e_1)$. Accordingly, greater effort by the park manager reduces the optimal utility of the local people if the marginal harvesting benefit dominates the marginal damage effect; i.e., if $(\partial B_2/\partial X - D') > 0$. Hence, under this condition, the iso-utility curves, U^0 and U^1, in Fig. 1 are such that $U^0 > U^1$. Otherwise, in the 'nuisance' case, when $(\partial B_2/\partial X - D') < 0$, greater effort by the park manager is beneficial because reduced damage dominates the reduced harvesting benefit. This is illustrated by the two iso-utility curves U^3 and U^2. These iso-utility curves bend in the opposite direction to that of U^0 and U^1. The Nash equilibrium is given by the effort levels $e_1^* > 0$ and $e_2^* > 0$ in Fig. 1. In addition, the iso-conservation schedule through the Nash equilibrium $X^* = X(e_1^*, e_2^*)$ yields the stock size.

Within this simple model the degree of species conservation is determined by several forces that work in a relatively complex way. It is also generally not clear how the utility, or welfare, of the local people is influenced. Welfare and conservation may go hand in hand, or in the opposite direction, as the comparative static results in Table 1 shows. The stock value functions are here assumed to be linear; i.e., $W(X) = wX$ and $D(X) = \gamma X$ while the harvesting functions are specified as Schäfer functions $y_1(e_1, X) = \theta_i e_i X$ where θ_i is a productivity ('catchability') coefficient under which $B_i(e_i, X) = p_i \theta_i e_i, - c_i e_i$ $(i = 1,2)$. In addition, the natural growth function is specified logistic, $F(X) = rX(1 - X/H)$ with r as the intrinsic growth rate and H as the species carrying capacity represented by the size of the conservation area expressed in number of animals (or biomass).

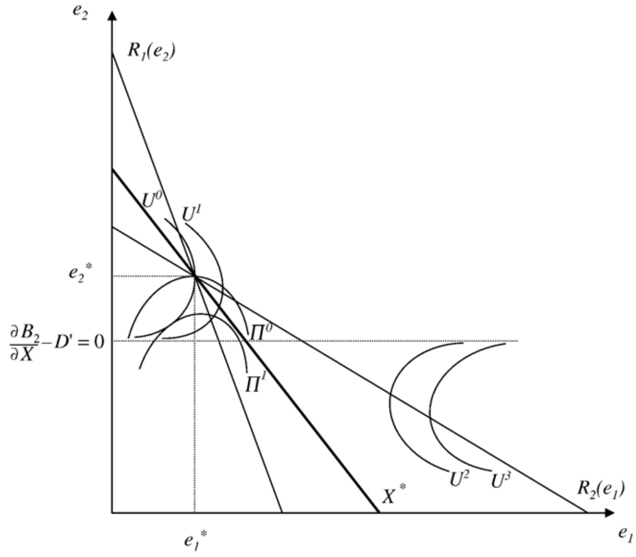

Fig. 1 – The two agent conflict model. The Nash equilibrium.

Table 1 – The two agent conflict model

	e_1^*	e_2^*	X^*	π^*	U^*
p_1	+	–	–	+	?
w	–	+	+	+	?
γ	–	+	–	–	–
p_2	–	–/+	–/+	–/+	?
c_1	–	+	+	–	?
c_2	+	–	+	+	?
r	?	?	?	?	?
H	?	?	?	?	?

Note: ± implies different sign effects e_2^* and x^* (and π^*). ? implies ambiguous sign effect.
Comparative static results.

Consider first the effect of an increase in the price of safari hunting licences p_1. The relative profitability of consumptive and non-consumptive activities of the park manager is affected, and the price increase results in greater hunting effort, given the effort levels of the local people. This causes an outward shift in $R_1(e_2)$, and hence, $\partial e_i^*/\partial p_1 > 0$ and $\partial e_i^*/\partial p_1 < 0$ It can be shown that the increased effort of the park manager dominates the indirect effect relating to the local people. We therefore find $\partial X^*/\partial p_1 < 0$ and the new economic equilibrium intersects with an iso-conservation schedule further from the origin. The profit of the park manager increases, $\partial \pi^*/\partial p_1 > 0$, while the utility effect for the local people depends on the sign of $(\partial B_2/\partial X - D')$. If the marginal harvesting benefit dominates, then $\partial U^*/\partial p_1 < 0$. In the opposite 'nuisance' case, when $(\partial B_2/\partial X - D') < 0$, we find $\partial U^*/\partial p_1 > 0$, in which case, increased profit for the park manager is associated with improved welfare for the local people.

Increased profitability in non-consumptive tourism through a positive shift in w has the opposite effect of an increase in p_1 as $R_1(e_2)$ shifts downwards. Increased wildlife-induced damage motivates the local people to expend more harvesting effort and $R_2(e_1)$ shifts upwards. Therefore, $\partial e_1^*/\partial \gamma < 0$ and $\partial e_2^*/\partial \gamma > 0$. We also find $\partial X^*/\partial \gamma < 0$. In addition, more nuisance reduces the welfare of the local people. An increase in p_2 increases the net harvesting benefit and motivates the local people to expend greater hunting effort. On the other hand, the increase in p_2 also reduces the value of wildlife damage relative to the value of wildlife meat, which has the opposite effect. Hence, the standard result of the Clark model (Clark, 1991), $\partial e_2^*/\partial p_2 > 0$, only arises if the nuisance is low relative to the harvesting cost. If the nuisance is relatively high, the price increase leads to reduced harvesting effort by the local people and to more wildlife. As shown in Table 1 more productive wildlife conditions through higher intrinsic growth rate r and biological carrying capacity H not necessarily mean more conservation. The welfare effects of the local people are also unclear.

The above analysis demonstrates that wildlife conservation may work directly against the interests of the local people, but the overall picture is far from clear. One important message is that reduced nuisance works beneficial for conservation as well as welfare improving of the local people. Hence, measures taken to reduce nuisance may therefore pay well off. Recently, however, the main approach to wildlife management and conservation has been to include the local people to gain their cooperation and support, which has eventually resulted in so-called integrated conservation and development projects (ICDPs) (see, e.g., Wells and Brandon, 1992). These projects involve varying levels of local participation, ranging from pure benefit sharing, such as transfers from wildlife-related activities, to a more far-reaching design of community based management. In Johannesen and Skonhoft (2005) pure benefit-sharing strategies are analyzed. The general findings here are that while more conservation may be obtained, the effect on the welfare of the local people is ambiguous.

The fact that transfers to the local people may reduce their welfare is obviously a strange result, but can be explained that such transfers take place within a general equilibrium type framework where the harvesting effort of both agents as well as degree of species conservation are influenced by shifting prices and income. If, say, the local people obtain a fixed proportion of the total park income, the relative valuation of the two activities of the park manager (hunting and tourism) is not influenced. The best-response function of the park manager $R_1(e_2)$ stays therefore unchanged. On the other hand, $R_2(e_1)$ shifts inwards because the transfer increases the marginal cost of hunting and reduces the hunting effort. The new Nash equilibrium is thus characterized by more harvesting effort by the park manager and reduced harvesting effort of the local people. The indirect transfer effect, working through increased harvesting effort of the park manager and less harvesting of the local people, may be negative. Therefore, if this indirect effect is strong enough, the net result can be negative. An uncertain, or even negative, welfare effect of the local people is just what is predicted as a possible outcome following the logic of the classic externality paper of Lipsey and Lancaster (1955).

In the above model the local people has been treated as a homogeneous group and hence, any conflicting interests among them have been neglected. Utility maximization is assumed as well. Whether utility maximization is an adequate representation of the behaviour of smallholder farmers living under complex and often harsh conditions can clearly be questioned. Alternatively, assuming poaching to be of the pure open-access type, we may find that the species abundance is determined by the zero-profit (or zero-rent) harvesting condition. This arises given the standard Schäfer harvesting assumption where $B_2(e_2,X)=(p_2\theta_2X-c_2)e_2=0$ (see also above). The degree of conservation is then determined only by the price and cost parameters together with the harvesting productivity of the local people, $X^\infty=c_2/p_2\theta_2$. This zero-rent stock size yields at the same time the iso-conservation line through Eq. (1). Together with the profit maximization condition of the conservation agency (4), or $e_1=R_1(e_2)$, the harvesting effort of the two agents are found. The only factors affecting the welfare of the local people under these assumptions are the prices. The effect of an increased $p_2$will hence lead to less wildlife and damage and higher welfare as there is zero-profit harvesting.

The assumption that the park manager maximizes profit from both park activities may also be questioned. In many protected areas there is no commercial hunting, and hunting activity is simply culling to maintain the ecological system (see, e.g., Starfield and Bleloch, 1986). Therefore, the goal of the park manager is typically to maintain a large and 'sustainable' stock of wildlife while keeping the ecosystem in shape. Under such a management scheme, the best-response function of the conservation agency coincides with the iso-conservation schedule representing the target stock size. Hence, this condition together with the best-response function of the local people determines the harvesting effort of the two agents. We suggest that an interior solution exists for the effort use, we then find that factors improving the harvesting profitability of the local people at the same time will increase welfare as the nuisance is unchanged.

2.2. *Lack of information and a dynamic framework*

The above analysis is based on an assumption of complete information. Therefore, in the present context, the conservation agency is assumed to know the utility function of the local people and to know that this function is to be maximized, and vice versa. The species natural growth function is also common knowledge. Obviously, there are good reasons to question the complete information assumption, and the above model may be reformulated into a situation where the information is more restricted. In what follows, I assume that the agents just know the species abundance, in addition to own cost and benefit functions. In a restricted information situation, it is generally more appropriate to formulate the model in a time-discrete manner (see, e.g., Weitzman, 2002), and where the stock growth reads:

$$X_{t+1} = X_t + F(X_t) - y_1(e_{1,t}, X_t) - y_2(e_{2,t}, X_t). \tag{6}$$

With incomplete information, we have to be very clear about the timing and sequencing of the information coming up. At time t both agents know the size of the wildlife stock. They harvest, and the harvest is based on the known stock size. When the natural growth is governed by the stock size *before* harvesting, the next period stock size evolves as in Eq. (6).[2] The stock is then assessed by both agents and is known for sure before next year's harvest starts, and so forth. In essence, each agent can therefore not distinguish between population changes due to natural growth and harvesting by the other agent. The agents are assumed to have the same

---

[2] Alternatively, natural growth may be governed by the stock size after harvesting, $F(X_t-y_{1,t}-y_{2,t})$. This formulation is appropriate if reproduction takes place after harvesting. It gives more complex maths, but does not change the qualitative structure of the model.

profit and utility functions as above, but now written as $\pi_t = B_1(e_{1,t}, X_t) + W(X_t)$ and $U_t = B_2(e_{2,t}, X_t) - D(X_t)$. If they base their harvest just on current economic and ecological conditions, and hence are *myopic* (see, e.g., Smith, 1975), profit and utility-maximizing give the first-order conditions $\partial B_1(e_{2,t}, X_t)/\partial e_{1,t} = 0$ and $\partial B_2(e_{2,t}, X)/\partial e_{2,t} = 0$, respectively (when again assuming interior solutions). These conditions yield the effort of both agents as a function of the stock size, and when inserted into Eq. (6) the species growth can be found.

The above solution concept is, however, somewhat unrealistic, as the agents' valuation of the stock does not influence their harvesting decisions. The fact that the species is a pest for the local people while representing a positive stock value for the conservation agency is therefore not taken into account. A simple, yet realistic, way to capture this problem is to assume that own harvesting effect on stock evolvement within the *same* period is anticipated. The benefit functions then read $\pi_t = B_1(e_{1,t}, X_t) + W(X_t - y_{1,t})$ and $U_t = B_2(e_{2,t}, X_t) - D(X_t - y_{2,t})$ with first-order necessary conditions for maximum as:

$$\partial B_1(e_{1,t}, X_t)/\partial e_{1,t} - W'(X_t - y_{1,t})(\partial y_{1,t}/\partial e_{1,t}) = 0 \tag{7}$$

and

$$\partial B_2(e_{2,t}, X_t)/\partial e_{2,t} + D'(X_t - y_{2,t})(\partial y_{2,t}/\partial e_{2,t}) = 0. \tag{8}$$

Condition (7) says that the conservation agency should harvest up to the point where the marginal harvesting profit equalizes the marginal stock value. This clearly implies positive marginal harvesting profit (as above). Condition (8) is parallel but implies negative harvesting profit on the margin. Again, these first-order conditions yield effort as a function of number of animals, $e_{1,t} = e_1(X_t)$ and $e_{2,t} = e_2(X_t)$. Inserted into Eq. (6), I then find $X_{t+1} = X_t + F(X_t) - y_1(e_1(X_1), X_t) - y_2(e_2(X_t), X_t)$, which is a first-order nonlinear difference equation.

Fig. 2 demonstrates the dynamics when using the modified Schäfer harvesting function $y_{i,t} = \theta_i e_{i,t}^a X_t^b$ with $a = b = 0.5$ together with logistic natural growth. The stock growth may then simply be written as:

$$X_{t+1} = X_t + rX_t(1 - X_t/H) - k_1 X_t - k_2 X_t \tag{9}$$

with $k_i > 0$ $(i = 1, 2)$.[3] As seen in the figure, there are no oscillations and the equilibrium is approached monotonically. There are two reasons for this: first, the intrinsic growth rate r for large mammals is small, and, second, harvesting stabilizes (see the classic May (1976) paper). The steady-state stock value can readily be found, and the profit and utility may be calculated as well.

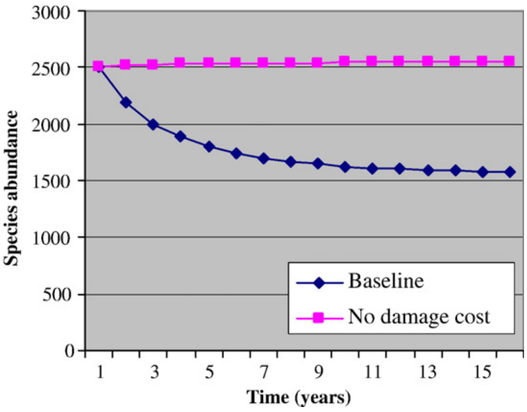

Fig. 2 – Species abundance in number of animals X_t. Myopic, dynamic harvesting model. Baseline; $k_1 = 0.088$ and $k_2 = 0.172$. No damage cost, $k_1 = 0.040$.Other parameter values; $r = 0.45$, $H = 3500$ (number of animals). Initial stock value $X_0 = 2500$ (number of animals).

Also, the degree of species conservation is now determined by several factors, and although the mechanism is different compared to the previous Nash model of strategic interaction, the ecological and economic driving forces are very much the same. Higher damage reduces the steady-state number of animals (see also Fig. 2) while increased profitability in non-consumptive tourism means more conservation. However, in contrast to the previous model, more profitable harvesting by the local people through a higher harvesting price unambiguously leads to fewer animals. The welfare effects on the local people of shifting economic and ecological conditions are also now generally ambiguous. If, say, the price of safari hunting licenses increases, we find the species abundance and hence the nuisance to be reduced in the long term. The harvest of the local people is reduced as well so the old equilibrium is located either to the left- or the right-hand side of the peak value of the natural growth function. However, irrespective of this, the harvest benefit is unclear as the actual outcome hinges on whether reduced offtake or reduced species density dominates the harvest benefit function. Therefore, the welfare effect on the local people is again generally ambiguous as well.

3. Discrepancy management geography and biological geography

The traditional way to counteract biodiversity threats and habitat destruction through establishing protected areas may also be challenged more directly by the fugitive nature of the animals. When wildlife moves freely in and out of a conservation area, it may be harvested legally, as well as illegally, outside the area. In addition, habitat land may deteriorate and disappear outside, and this may influence the species flow as well. Because of dispersal and lack of congruency between management geography and ecological geography, it will therefore be a conservation management problem in the sense that land-use changes and harvesting taking place outside the conservation area influence, or spillover to, the

---

[3] With $a = b = 0.5$, the (myopic) first-order condition of the conservation agency and the local people yield $e_{1,t} = e_1(X_t) = [0.5\theta_1(p_1 - w)/c_1]2X_t$ and $e_{2,t} = e_2(X_t) = [0.5\theta_2(p_2 + \gamma)/c_2]^2 X_t$, respectively. Inserted into the stock growth equation gives $X_{t+1} = X_t + F(X_t) - \theta_1\{[0.5\theta_1(p_1 - w)/c_1]^2 X_t\}^{0.5} X_t^{0.5} - \theta_2\{[0.5\theta_2(p_2 + \gamma)/c_2]^2 X_t\}^{0.5} X_t^{0.5}$. With $k_1 = \theta_1[0.5\theta_1(p_1 - w)/c_1]$ and $k_2 = \theta_2[0.5\theta_2(p_2 + \gamma)/c_2]$ this reduces to the main text Eq. (9). Therefore, using this modified Schäfer function makes the harvest of both agents as fixed proportions of the stock size.

species density inside this area. I first look at a situation with dispersal governed by a density-dependent process.

3.1. *Spillover of harvest and land-use changes into the conservation area*

Two areas: a reserve and a neighboring area, with two subpopulations of wildlife managed by two different agents are considered. The protected area is again managed by a conservation agency while the neighboring area is used by a group of local people (e.g., smallholder farmers). By assumption, the conservation zone is of fixed size and land use is also kept fixed. On the other hand, land use may change in the neighboring area, as habitat land can be converted into agricultural land. I abstract from any harvesting taking place in the conservation area, thus also excluding illegal activities such as poaching.

As in Skonhoft and Armstrong (2005), I use a time-continuous model, and the population dynamics are given by (the time subscript is omitted):

$$dX_1/dt = F(X_1) - M(X_1, X_2) \tag{10}$$

and

$$dX_2/dt = G(X_2) + M(X_1, X_2) - y, \tag{11}$$

where X_1 is the protected area subpopulation, X_2 is the neighboring area subpopulation while $F(X_1)$ and $G(X_2)$ are the natural growth functions of the two subpopulations. In addition to natural growth and harvesting, taking place only outside the protected area, the two subpopulations are interconnected by dispersal given by $M(X_1,X_2)$. The dispersal, or migration, depends on the stock *densities* $X_i/H_i(i=1,2)$ in the two areas, for the moment ignoring any other migratory patterns (but see below).

With no hunting (or harvesting), $y=0$, and no land-use change taking place in the neighboring area; that is, for this area, carrying capacity H_2 is fixed and the isoclines of the systems (10) and (11) will typically be as depicted in Fig. 3 with the unique ecological equilibrium, X_1^*. To say something more about the equilibrium, the functional forms have to be specified. Natural growth is again assumed to be logistic (see above), while the dispersal function is specified as $M(X_1,X_2)=m[\beta(X_1/H_1)-(X_2/H_2)]$ with m as a parameter reflecting the general degree of dispersion–that is, topography, size of the areas, type of species, and so forth–and where a large m value corresponds to species and a natural environment with large spatial movement. On the other hand, the parameter $\beta>0$ reflects that the dispersion may be due to, say, different environmental conditions, predator–prey relations and competition within the two subpopulations. For equal X_i/H_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. On the other hand, when $0<\beta<1$, the circumstances outside the reserve are detrimental, creating less potential migration out of the reserve. Therefore, in contrast to the standard density-dependent dispersal models (see, e.g., Conrad, 1999), possible intrastock or interspecies relations that may result in different concentrations in the two areas are incorporated; that is, the dispersal may be *asymmetric* (for more details, see Skonhoft and Armstrong, 2005).

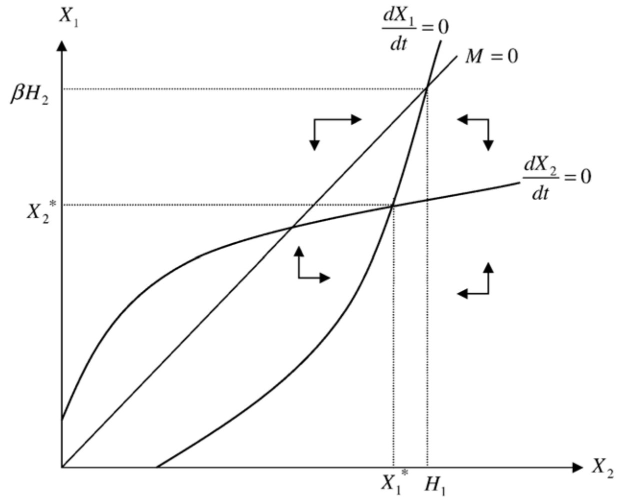

Fig. 3 – Density-dependent dispersal model, $\beta>1$.The isoclines in absence of harvesting.

In the standard case of symmetric dispersal with $\beta=1$ and no harvesting, it can easily be confirmed that both equilibrium stocks will be at their carrying capacities, $X_1^*=H_1>0$ and $X_2^*=H_2>0$, and in equilibrium there are no flow of species between the two areas, $M^*=0$. On the other hand, with $\beta>1$, as depicted in Fig. 3, the result is $X_1^*<H_1$ and $X_2^*>H_2$. The natural growth in the conservation area is then positive while it is negative in the neighboring area. With $0<\beta<1$, $X_1^*<H_1$, $X_2^*<H_2$, and $M^*<0$ will hold. $M=m[\beta(X_1/H_1)-(X_2/H_2)]=0$ represents a straight line from the origin through the point $(H_1,\beta H_2)$ in the figure. Hence, under this line we have $M>0$ making the reserve a source. When $\beta>1$ as in Fig. 3, it is therefore clearly an outflow of species from the conservation area and $M^*>0$ plus positive natural growth adds up to ecological 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.

The figure also indicates that the equilibrium is stable, and what happens outside equilibrium. Hence, starting with 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 subpopulations 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.

The crucial question is how harvesting and habitat degradation, both activities taking place in the neighboring area, may influence species conservation in the protected area. We start with habitat changes when there is no harvest, $y=0$. When the local people use more land for agricultural production and H_2 decreases, both isoclines in Fig. 3 change. In line with intuition, the equilibrium stock size X_2^* outside the reserve decreases. However, the effect on the stock inside the conservation area X_1^* is ambiguous. The reason is that as both H_2 and X_2^* decline, the change of the ratio X_2^*/H_2 is unclear, and hence the effect on the dispersion between the areas becomes ambiguous as well.

More detailed analysis (Skonhoft and Armstrong, 2005) demonstrates that habitat degradation taking place outside the protected area generally represents no problem for species conservation in the protected area following the logic of this model of density-dependent dispersion. If the reserve is more advantageous for the species and $0<\beta<1$, it can be shown that the effect of habitat destruction outside means fewer animals and less conservation within the reserve, but all the time we have $X_1^*>H_1$. 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. In the standard symmetric dispersal models found in the literature with $\beta=1$, more land for agricultural use and habitat destruction outside the reserve has no effect whatsoever upon the stock in the reserve.

When $y>0$ and harvesting takes place with no changes in the land use and H_2 is fixed, the X_2-isocline in Fig. 3 shifts down compared to the nonharvesting case. The X_1-isocline is unaffected. As a result, the stocks in both areas decrease either species flow into or out of the conservation area. Not surprisingly, harvesting outside the protected area therefore translates unambiguously into a lower species density in the protected area. The degree of harvesting spillover is, however, closely related to the exploitation scheme of local people in the outer area. Different schemes may be analyzed, but open-access only is considered here.

When again applying the standard Schäfer harvesting function $y=\theta e X_2$ and the open-access zero-profit assumption (cf. also Section 2), the number of species in the neighboring area becomes $X_2^\infty=c/p\theta$. Inserted into Eq. (10) in equilibrium when $F(X_1)=r_1X_1(1-X_1/H_1)$, the protected area subpopulation stock size reads $X_1^\infty=\frac{H_1}{2r_1}\left[\left(r_1-\frac{m\beta}{H_1}\right)+\sqrt{\left(r_1-\frac{m\beta}{H_1}\right)^2+\frac{4r_1mc}{p\theta H_1H_2}}\right.$. Therefore, while the open-access stock size outside the reserve is unaffected by the dispersal asymmetry (as well as the other biological parameters) due to the standard Schäfer harvesting function assumption, it is observed that a higher β means a smaller open-access stock in the reserve. Hence, $\beta>1$, implying detrimental conditions within the reserve, reduces the stock size compared with the standard models in which $\beta=1$. The reason is that a higher β, for a fixed density in the outer area, means more dispersal. In a next step, this translates into a higher natural growth through the equilibrium condition $F(X^1)=M(X^1,X^2)$, and hence, a smaller stock abundance. Habitat degradation unambiguously means more animals as the species density in the outer area increases and the flow out of the reserve decreases. On the contrary, more intensive harvesting in the outer area due to a higher price, or a lower effort cost, works in the direction of less conservation. Therefore, in contrast to the Nash equilibrium model of Section 2, the price effect is unambiguous. A high harvesting price may very well also drive the species density in the reserve below the maximum sustainable yield level, X_1^{msy}. This typically takes place if the natural environment at the same time is characterized by large spatial movement so that m is high. The intuitive reasoning saying that it is more difficult to conserve highly fugitive species holds irrespective of the outer area management practice. In reality, however, the dispersal may be influenced by fencing and other management measures taken by the conservation agency. An extension of the above model may be to introduce such control measures.

3.2. *Density-independent dispersal.*

While the norm has been to focus on some form of density-dependent dispersal between a conservation area and neighboring areas, we often find that the dispersal is not of this type. The dispersal, or movement, may take place cyclically over the year, and the famous wildebeest migration in the Serengeti–Mara ecosystem is an example of such pattern (Sinclair and Arcese, 1995). Among others, reindeer migration and moose dispersal are typically seasonal as well (e.g., Skonhoft and Olaussen, 2005). I proceed to look at a simple model with dispersal of this type, where the ecological conditions are such that a fixed fraction of the conservation area subpopulation *temporarily* migrates out while there is no migration of the other subpopulation. Again, a reserve without harvesting is considered, also neglecting possible poaching, while hunting takes place outside.

This problem is studied by using a time-discrete model. When the harvesting (or hunting) *fraction* in the outer area at time t is h_t and α is the dispersal fraction, assumed constant over time, and migration (and harvesting) takes place after natural growth, the population dynamics of the conservation area subpopulation writes:

$$X_{1,t+1}=X_{1,t}+F(X_{1,t})-\alpha(X_{1,t}+F(X_{1,t}))h_t. \tag{12}$$

With no dispersal, the equilibrium population size will therefore simply be at its carrying capacity. For the subpopulation staying in the outer area all the time, the population dynamics is:

$$X_{2,t+1}=X_{2,t}+G(X_{2,t})-(X_{2,t}+G(X_{2,t}))h_t. \tag{13}$$

Therefore, the assumption is that the outer area harvesters are not able to select between the two subpopulations. The conservation area subpopulation number of animals hunted is $\alpha(X_{1,t}+F(X_{1,t}))h_t$ while $(X_{2,t}+G(X_{2,t}))h_t$ is for the outer area. Total harvest in number of animals (or biomass) year t is accordingly $y_t=[\alpha(X_{1,t}+F(X_{1,t}))+(X_{2,t}+G(X_2,t))]h_t$. In contrast to the previous model, there is no ecological interaction between the two subpopulations as there are no density-dependent processes (e.g., mortality) during the subpopulation 1 migration period.

This population model may be applied for studying dynamic as well as equilibrium harvesting. To begin with, I briefly summarize some dynamic features. Suppose first that harvesting takes place with a fixed harvesting fraction through time, $h_t=h$. Such harvesting may be due to some type of 'routinized' behavior among the local people, and because of weak institutions and the uncontrolled nature of the hunting, the harvesting fraction is likely to be high. When the harvesting is fixed in this manner, Eqs. (12) and (13) will be two independent first-order nonlinear difference equations. Therefore, there will be no economic interaction among the two subpopulations, and the protected area subpopulation stock dynamics (as well as the outside subpopulation dynamics) will be very much the same as that found in the discrete time conflict model (Section 2.2 above). The steady-state will hence typically be approached without oscillations. When $X_{1,t+1}=X_{1,t}$, the conservation area subpopulation Eq. (12) yields $F(X_1)=(\alpha h/(1-\alpha h))X_1$. Not surprisingly, a higher harvesting fraction and a higher dispersal fraction thus spillover to a smaller equilibrium number of animals when the natural growth function is of the standard logistic type—that is, just as in the above density-dependent dispersal model.

On the other hand, if the outside area harvesting takes place in a myopic profit-maximizing manner, it will generally be an economic interdependency between the two subpopulations. As already noted, the stock size when the harvest takes place, consisting of the outside area stationary subpopulation and the conservation area migratory subpopulation, is $\tilde{X}_t=\alpha(X_{1,t}+F(X_{1,t}))+(X_{2,t}+G(X_{2,t}))$. When again using the modified Schäfer harvesting function $y_1=\theta e_t^a \tilde{X}_t^b$ (with $0<a<1$ and $b>0$), myopic profit-maximizing makes harvesting an increasing function of the stock size, $y_t=y(\tilde{X}_t)$ (see also Section 2.2). Therefore, the harvesting fraction is linked to both subpopulations as well, $h_t=y_t(\tilde{X}_t)/X_t$.[4] Inserted into the population dynamics (12) and (13), the result is two interconnected first-order nonlinear difference equations. Under the assumption of logistic natural growth, I also now find the steady-states to be approached monotonically for all realistic parameter values, and again harvesting works in a stabilizing manner.

Equilibrium harvesting is then considered. When $X_{i,t+1}=X_{i,t}=X_i (i=1,2)$ and $h_t=h$, with $0<h\leq 1$, combination of Eqs. (12) and (13) yields:

$$F(X_1)/\alpha(X_1+F(X_1)) = G(X_2)/(X_2+G(X_2)). \tag{14}$$

With logistic natural growth $F(X_1)=r_1X_1(1-X_1/H_1)$ and $G(X_2)=r_2X_2(1-X_2/H_2)$, and assuming the whole conservation area subpopulation subject to dispersal out of the conservation area so that $\alpha=1$, Eq. (14) can be written as $X_2=H_2(1-r_1/r_2)+(H_2r_1/H_1r_2)X_1$ after some few rearrangements. When also assuming the same maximum specific growth rates for both subpopulations, $r_1=r_2=r$, it reduces to $X_2=(H_2/H_1)X_1$. Therefore, for the given functional forms and parameter values, it is a fixed ratio between the equilibrium number of animals in the conservation area and the surrounding area for *all* harvesting levels $0<h\leq 1$.

It is now possible to establish a simple link between the outside harvesting and the reserve species abundance. In ecological equilibrium, natural growth equalizes number of animals removed of each subpopulation, and total harvest is $y=F(X_1)+G(X_2)$. Inserting for the natural growth functions and the fixed stock relationship $X_2=(H_2/H_1)X_1$ yields:

$$y(X_1) = rX_1(1-X_1/H_1) + r(H_2/H_1)X_1(1-X_1/H_1). \tag{15}$$

This relationship represents the equilibrium harvesting spillover from the exploitation area to the conservation area and is defined for all $X_1>0$ that ensures a positive X_2 through Eq. (14).[5] In the present case of $\alpha=1$, this holds for all $X_2>0$. Fig. 4 illustrates the reserve subpopulation natural growth function, and harvest. The difference between these functions yields the outer area natural growth, and harvest.

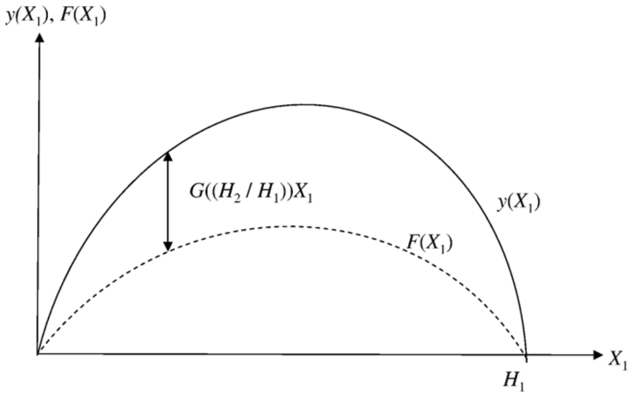

Fig. 4 – Density-independent dispersal model. Total harvest $y(X_1)$ (solid line) and protected area natural growth function $F(X_1)$ (dotted line).

Just as in the standard one-patch harvesting model, a given amount of animals removed may be sustained with a small as well a large degree of conservation while the maximum number of animals harvested coincides with the protected area maximum sustainable-yield stock, $X_1^{msy}=H_1/2$. Different exploitation schemes may also be analyzed in the light of the sustainable-yield function (15). First, it can be shown that the goal of maximizing outer area equilibrium harvesting profit gives a protected stock size above that of X_1^{msy}. This result follows intuitive reasoning, as there are stock dependent costs but no rate of discount involved. However, maximizing profit lacks realism due to weak institutions, and, again, open-access harvesting may fit reality better. The population size when harvest takes place, $\tilde{X}=\alpha(X_1+F(X_1))+(X_2+G(X_2))$, may now be written as $\tilde{X}=(1+H_1/H_2)(X_1+rX_1(1-X_1/H_1))$, when $\alpha=1$ and inserting for $F(X_1)$ and $G(X_2)$ and using $X_2=(H_2/H_1)X_1$. Therefore, with the standard Schäfer harvesting function, zero-profit harvesting $\pi=(p\theta\tilde{X}-c)e=0$ gives $X_1^{\infty}=\frac{H_1}{2r}\left[(1+r)-\sqrt{(1+r)^2-\frac{4rc}{p\theta(H_1+H_2)}}\right]$. X_1^{∞} can be located either to the right- or the left-hand side of the peak value of the yield function (15). A high price–cost ratio drives the solution to the left and below that of X_1^{msy} and was found in the density-dependent dispersal model as well. A small outer area habitat area works in the opposite direction. This result is also just as in the density-dependent dispersal model, albeit with different mechanisms now.

4. Concluding remarks

This article has presented modeling approaches for wildlife and species conservation with a special emphasis on large mammals, in a developing country context, and with special

---

[4] An exception occurs when $y_t=\theta e_t^a \tilde{X}_t^b$ with $a=b=0.5$. In this case it can be shown that myopic profit maximizing yields a fixed harvesting fraction though time; that is, just as in the above harvesting scheme of 'routinized' harvesting behavior (see also Section 2.2).

[5] Armstrong and Skonhoft (2006) introduce this function as the Induced Sustainable Yield Function (ISYF) in a density-dependent dispersal model.

reference to sub-Saharan Africa. In these countries there are frequently conflicts over land use and species conservation, and the institutions to tackle such conflicts are often weak or lacking. Two main issues have been discussed; conservation conflicts, and cases with discrepancy between management geography and ecological geography because of the fugitive nature of the wildlife. The modeling approach has all throughout been bioeconomic models with wildlife as biomass, or 'normalized' number of animals, where the economy and the ecology interact through harvesting but also through land-use changes. Within this framework, it has been demonstrated that wildlife conservation can work directly against the interests of the local people, while wildlife damage reduction typically improves the degree of conservation as well as the living conditions of the local people. The dispersal models have shown how, and to what extent, harvesting and habitat deterioration from outside areas may spillover to a conservation area.

The strength of stylized natural resource models, as presented here, is to clarify some fundamental principles of wildlife conservation problems. Within this framework, it is reasonable simple to understand the driving forces, and straightforward explanations can readily be given when contra intuitive results come up. The policy implications are often fairly simple to understand as well. In more complex, and hence more realistic models the driving forces are often progressively more difficult to understand and the policy implications are harder to grasp. However, in some instances, we need such models to better understand and explain the actual problem. Abandoning the standard biomass assumption may be such an extension, and the modeling insight can increase when species demography is introduced, see, e.g., Skonhoft et al. (2002) for an application where, among others, trophy hunting and migration are studied. To move behind the simplified assumption of a concave and well-behaved natural growth function may also bring additional understanding in certain cases. Some recent papers (see, e.g., Dasgupta and Mäler, 2003) have demonstrated important new insights from this type of modeling. Including uncertainties of various types, related to the environment and ecology, but also to economic variables, is yet another extension. In cases with small and threatened wildlife populations, uncertainty is especially important to take into account (Lande et al., 2003). All these extensions of stylized natural resource models point in the direction that more integrated ecological–economic modeling approaches for conservation and biodiversity management in many cases may pay well off. Wätzold et al. (in press) discusses such integration.

To better understand and explain the actual conservation and management problem, the economic part of the bioeconomic analysis needs also some reshaping. For example, the ideal, but unrealistic, world of complete information needs to be challenged more frequently. In the present exposition this problem has just been touched upon. However, in situations with more agents and where important information influencing harvesting and conservation is private, the presence of asymmetric information needs to be taken more fully into account for a fuller understanding of the real problem. From a regulation perspective, the distinction between private and common knowledge seems to be equally important (e.g., Weitzman, 2002).

Acknowledgments

Thanks to Claire Armstrong and Anne B. Johannesen for fruitful collaborations during the last few years. Parts of this collaboration are materialized in this paper. Thanks also to three reviewers for constructive comments. I am responsible for any mistakes that may remain.

REFERENCES

Armstrong, C., Skonhoft, A., 2006. Marine reserves. A bioeconomic model with asymmetric density dependent migration. Ecological Economics 57, 466–476.

Clark, C., 1991. Mathematical Bioeconomics, 2th ed. John Wiley, New York.

Conrad, J., 1999. The bioeconomics of marine sanctuaries. Journal of Bioeconomics 1, 205–217.

Dasgupta, P., Mäler, K., 2003. The economics of non-convex ecosystems: introduction. Environmental and Resource Economics 26, 499–525.

Johannesen, A., Skonhoft, A., 2005. Tourism, poaching and wildlife conservation: what can integrated conservation and development projects accomplish? Resource and Energy Economics 27, 208–226.

Kiss, A. (Ed.), 1990. Living with Wildlife. The World Bank, Washington.

Lande, R., Engen, S., Saether, B.E., 2003. Stochastic Population Dynamics in Ecology and Conservation. Oxford U.P, Oxford.

Lipsey, R.G., Lancaster, K., 1955. The general theory of second best. The Review of Economic Studies 24, 11–32.

May, R., 1976. Simple mathematical models with very complicated dynamics. Nature 261, 459–467.

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

Sinclair, A.R.E., Arcese, P., 1995. Serengeti II. Chicago U.P., Chicago.

Skonhoft, A., Armstrong, C., 2005. Conservation of wildlife. A bioeconomic model of a wildlife reserve under the pressure of habitat destruction and harvesting outside the reserve. Natural Resource Modeling 18, 69–90.

Skonhoft, A., Olaussen, J.O., 2005. Managing a migratory species that is both a value and a pest. Land Economics 81, 34–50.

Skonhoft, A., Yoccoz, N., Stenseth, N., 2002. Management of chamois (*Rupicapra rupicapra*) moving between a protected core area and a hunting area. Ecological Applications 12, 199–1211.

Smith, V., 1975. The primitive hunter culture, Pleistocene extinction, and the rise of agriculture. Journal of Political Economy 83, 727–755.

Starfield, A.M., Bleloch, A.L., 1986. Building Models for Conservation and Wildlife Management. Macmillan, New York.

Swanson, T.M., 1994. The economics of extinction revisited and revised. Oxford Economic Papers 46, 800–821.

Wätzold, F, and others, in press. Ecological–economic modeling for biodiversity management: potential, pitfalls, and prospects. Conservation Biology XX.

Wells, M., Brandon, K., 1992. People and Parks: Linking Protected Area Management and Local Communities. World Bank, New York.

Weitzman, M., 2002. Landing fees vs. harvest quotas with uncertain fish stock. Journal of Environmental Economics and Management 43, 325–338.