Ecological Applications, 16(5), 2006, pp. 1959–1966

INTEGRATING ECONOMIC COSTS INTO THE ANALYSIS OF FLEXIBLE CONSERVATION MANAGEMENT STRATEGIES

Martin Drechsler,[1,3] Karin Johst,[1] Frank Wätzold,[2] and Michael I. Westphal[1]

[1]*Department of Ecological Modelling, UFZ Centre for Environmental Research Leipzig-Halle, Permoserstrasse 15, 04318 Leipzig, Germany*
[2]*Department of Economics, UFZ Centre for Environmental Research Leipzig-Halle, Permoserstrasse 15, 04318 Leipzig, Germany*

Abstract. Flexible conservation management, where measures (e.g., mowing of meadows, removing invasive species) are selected in each decision period depending on the current state of the ecological system, is generally perceived as superior to fixed management, where the same measure is applied in each decision period independent of the current state of the system. In past comparisons of fixed and flexible conservation strategies the additional costs that arise only in flexible strategies have usually been ignored. In this paper, we present a framework to integrate costs of flexible management into the evaluation of flexible conservation strategies. Using the example of an endangered butterfly species we demonstrate that the costs of flexible management may reverse the rank order of flexible and fixed conservation strategies, such that fixed strategies may lead to better ecological results than flexible ones for the same financial budget.

Key words: conservation; ecological-economic model; extinction; flexible management; stochastic dynamic programming.

Introduction

Recent research on optimal conservation management has stressed the importance of state-dependent, or flexible, management strategies (e.g., Possingham 1997). The characteristic of state-dependent strategies is that, in each period, the decision about the optimal management strategy is made dependent on the state of the managed ecosystem or population in the current period. In contrast, for state-independent, or fixed, strategies, the optimal management strategy remains the same over all periods.

Flexible management strategies have conservation benefits. Extinction probabilities of Southern Emu-wren (*Stipiturus malachurus intermedius*) are improved by 50–80% over 30 years when the optimal state-dependent management actions are selected (Westphal et al. 2003). In contrast, the best fixed, state-independent sets of strategies are only 30% better than no management. Selecting fire management strategies also benefits from a flexible approach. In Ngarkat Conservation Park, Australia, the optimal fire strategy to maintain community diversity (either "let wildfires burn unhindered," "fight wildfires," or "perform controlled burns") depends on, among other factors, the current state of the park (Richards et al. 1999).

However, it needs to be pointed out that state-dependent management may generate costs that do not exist for fixed management and that if such costs are considered in the development of optimal conservation strategies, flexible conservation management may not always be the better choice. There are two types of costs that are relevant for flexible conservation management: monitoring costs and flexibility costs. Monitoring costs are from monitoring activities in each period that have to be carried out to gain the necessary information about the population state. Flexibility costs may arise if the conservation measures are carried out by landowners who have to change their production activities and are compensated for the costs incurred. A compensation approach is frequently chosen to induce farmers or forest owners to change their production activities to take into account conservation concerns. Programs that compensate landowners for conservation measures exist in many parts of the world (Clough 2000) and are typical for conservation in Europe (Wätzold and Schwerdtner 2005). European programs are mostly directed at farmers to encourage voluntary farming of their land in a conservation-friendly manner. Experience with such programs has shown that it is important for landowners to have planning reliability for their economic activities (Wilson 1997, Höft et al. 2005). As state-dependent management requires short-term decisions, landowners will not only demand compensation for the conservation costs but also for the lost planning reliability and the need to make short-term adjustments to their economic activities.

The purpose of this paper is to provide a formal framework for the integration of economic costs into the analysis of flexible conservation management and to demonstrate that taking into account the costs of flexible management may indeed reverse the rank order of

Manuscript received 18 July 2005; revised 23 December 2005; accepted 16 January 2006. Corresponding Editor: J. M. Marzluff.
[3] E-mail: martin.drechsler@ufz.de

flexible and fixed conservation strategies. For this purpose, we apply the framework to a case study which addresses conservation management of the Large Blue butterfly (*Maculinea teleius*) in Germany (see Plate 1).

A Framework for Integrating Costs into the Analysis of Flexible Management

Assume a conservation manager has to manage a population over L time periods and wants to maximize the probability of the population surviving these L periods. In each period, the manager selects from a range of conservation measures. Generally, the value of a particular measure for the survival of the population depends on the current population size N (an example for this is provided in the Appendix). Therefore, an optimal flexible management strategy ("flex"), where in each period l the conservation measure is optimally selected depending on the population size in period $l-1$, will be advantageous compared to a fixed strategy ("fix"), where the same measure is applied in all periods. If we denote the cost of a conservation measure m_l as $\mathrm{C}(m_l)$ then this statement may be mathematically expressed as

$$P_L^{(\mathrm{flex})} > P_L^{(\mathrm{fix})} \tag{1}$$

with

$$P_L^{(\mathrm{flex})} = \max_{\{m(N)\}} P_L\left[m_1,\ldots,m_L \middle| \sum_{l=1}^{L} C(m_l) = B\right]$$

$$P_L^{(\mathrm{fix})} = P_L[m_1,\ldots,m_L | C(m_1) = \cdots = C(m_L) = B/L] \tag{2}$$

where P_L is the survival probability of the population over the L periods and the maximum in $P_L^{(\mathrm{flex})}$ is taken over all possible population-size-(N)-dependent strategies $m(N)$ under the constraint that the sum of all $C(m_l)$ is constant and equal to the available conservation budget B. The latter constraint is necessary to make the strategies "economically" comparable. In the following, the term "flexible" strategy always refers to the optimal flexible strategy that maximizes the management objective under the given constraints.

Eqs. 1 and 2 seem to fully cover all relevant ecological and economic aspects of the decision problem, i.e., the costs of conservation measures, the effects on ecological parameters and the effect of these parameters on the conservation target. But management activities may also generate costs that are not yet considered and may substantially affect the inequality in Eq. 2.

First, if the management is made dependent on the size of the population, this size has to be known, which generates monitoring costs. For simplicity, we assume that the monitoring costs are identical for all periods and denote them as M.

Second, it may be that the conservation measures are not carried out by the conservation agency. Rather, the agency may ask landowners on whose land the population is located to carry out the measure and compensate them for their costs. To induce a landowner to carry out conservation measures they have to be compensated for (a) the above-mentioned actual costs $C(m_l)$ of the conservation measures and, in the case of a flexible management strategy, (b) the costs that result from the fact that the landowner is informed only at relatively short notice about the measure to be carried out. Such costs arise because the landowner may need to make short-term adjustments to production activities and because mid- to long-term ability to plan production activities is inhibited (e.g., to make many types of agricultural production activities worthwhile for a farmer, a planning horizon of several years is needed). For these costs the landowner has to be compensated, which creates flexibility cost F. The sum of monitoring and flexibility costs may be denoted as flexible management cost,

$$K = F + M \tag{3}$$

measured per period. With this, Eq. 2 becomes

$$P_L^{(\mathrm{flex})} = \max_{\{m(N)\}} P_L\left[m_1,\ldots,m_L \middle| \sum_{l=1}^{L} C(m_l) = B - KL\right]$$

$$P_L^{(\mathrm{fix})} = P_L[m_1,\ldots,m_L | C(m_1) = \cdots = C(m_L) = B/L]. \tag{4}$$

Because funds are allocated through time, we have to discount future costs. First, we have to take into account interest gained by the conservation agency that spends money in later periods instead of today. Secondly, the costs for conservation measures may also rise in future periods because of a time preference among landowners for receiving a certain amount of money today rather than in the future. We consider discounting by multiplying the costs C and K in each period with a discount factor $\delta^l = (1 + i - \rho)^l$ where i is the interest rate per period, ρ represents the cost increase of conservation measures per period, and l is the number of the period. With this, Eq. 4 becomes

$$P_L^{(\mathrm{flex})} = \max_{\{m(N)\}} P_L\left[m_1,\ldots,m_L \middle| \sum_{l=1}^{L} C(m_l)\delta^{-l} = B - K\sum_{l=1}^{L}\delta^{-1}\right]$$

$$P_L^{(\mathrm{fix})} = P_L\big[m_1,\ldots,m_L | C(m_1)\delta^{-1} = \cdots = C(m_L)\delta^{-1} = B/L\big]. \tag{5}$$

The probability $P_L^{(\mathrm{flex})}$ is not necessarily larger than $P_L^{(\mathrm{fix})}$. Whether $P_L^{(\mathrm{flex})}$ exceeds $P_L^{(\mathrm{fix})}$ depends on the magnitude of K. From Eq. 5, the following statements can be derived:

1) For $K = B/L$ the flexible strategy is not feasible because the entire budget would have to be spent to cover the flexible management costs and nothing would be left to finance the costs $C(m_l)$ of the actual

conservation measures. More generally, there exists a critical magnitude of flexible management costs, $K_{\max}$ ($0 \leq K_{\max} \leq B/L$), such that the flexible strategy is feasible for $K < K_{\max}$ and infeasible for $K \geq K_{\max}$. If $K_{\max} = 0$ there exists no feasible flexible strategy.

2) On the feasible interval [0, $K_{\max}$) the performance of the flexible strategy strictly monotonically decreases with increasing K, as less money can be spent for the conservation measures.

3) Because of the statement in (2), and depending on the problem, there may or may not be a break-even point K_c with $0 < K_c < K_{\max}$, such that the flexible strategy outperforms the fixed one on the interval [0, K_c) and is outperformed on the interval (K_c, $K_{\max}$). For $K = K_c$ both strategies show equal performance.

To complete the mathematical considerations, according to Eq. 5, the maximum feasible flexible management cost, $K_{\max}$, is the difference between $B/\Sigma\delta^{-l}$ and the cost of the cheapest conservation measure (or zero if this difference is negative):

$$K_{\max} = \max\left[\frac{B}{\sum_{l=1}^{L}\delta^{-l}} - \min_{\Delta r} C(\Delta r), 0\right] \tag{6}$$

(note that for $\delta = 1$ we have $\Sigma\delta^{-l} = L$, and so the fraction in Eq. 6 is the budget available per period). If a break-even point K_c exists it is given by

$$P_L^{(\text{flex})} = P_L^{(\text{fix})}. \tag{7}$$

To conclude, if all economic constraints are considered, flexible conservation management is not necessarily feasible. If it is feasible, it may or may not be the optimal type of conservation management, which depends on the economic constraints as well. Before implementing a flexible conservation strategy, its various costs and benefits must be taken into account thoroughly. In the next section, we do so for the case study of butterfly conservation in Germany.

Dynamic Conservation Management of the Large Blue Butterfly in Germany

The Large Blue butterfly (*Maculinea teleius*) is an endangered species protected by the European Union Habitats Directive (Council Directive 92/43/EEC). It inhabits open grasslands that are usually found in the form of grazed or mowed meadows in Germany. The butterfly mainly depends on two resources: oviposition sites on great burnet (*Sanguisorba officinalis*) plants, and ants of the species *Myrmica scabrinodis*. On the *Sanguisorba* plants, the eggs develop into larvae, which fall onto the ground. The ants mistake these larvae with their own larvae and carry them into their nests. There the larvae feed on the ant brood, pupate, and overwinter (Thomas 1984, Thomas and Settele 2004).

Management is needed to keep meadow vegetation appropriate for the butterfly. If the vegetation on the meadow gets too high, the *Sanguisorba* is out-competed by other plant species and the ants disappear because the microclimate becomes unsuitable for them. In this study, we consider a meadow with a typical type of economic land use in Germany (mowing twice a year for cattle fodder production: once at the end of May and a second time in mid-July). This type of management is detrimental to the butterfly, as the second cut falls exactly in the eclosion period where the butterflies disperse and deposit their eggs. Drechsler et al. (2005) investigated various alternative mowing regimes in a region east of the town of Landau in the Rhine Valley in terms of their effect on the butterfly population and their ability to achieve butterfly conservation at lowest costs. The effects of these mowing regimes on the survival of the butterfly population in the region were determined by a simulation model that followed the life cycle of the butterflies and, in particular, considered the impacts of mowing on the mortality of eggs and larvae feeding on the plants.

To induce farmers to adopt a more butterfly-friendly mowing regime than the conventional one, they must be compensated for the costs incurred. Such compensation payments are typical for conservation in agricultural landscapes in Europe (e.g., Hanley et al. 1998, Hampicke and Roth 2001, Kleijn et al. 2001). The additional costs generated by the alternative mowing regimes were determined in an agro-economic cost assessment (Bergmann 2004).

We modified the study of Drechsler et al. (2005) by considering flexible, population-state-dependent, mowing regimes. We use the costs for the different mowing regimes and the same parameters for the simulation model. However, for simplicity, we consider a single meadow of size 1 ha (aspects of regional butterfly dynamics are discussed in Drechsler et al. 2005) and a subset of the mowing regimes considered in Drechsler et al. (2005). Seven possible fixed mowing regimes are considered: meadows are mowed once every second year in the first week of July (denoted as week 1), the second week of July (week 2), and so on, to the third week of August (week 7). Earlier weeks are excluded as they are critical breeding times for meadow birds; later weeks have identical ecological and economic effects to week 7. Not mowing at all is not a feasible mowing regime as, even after a few years, this leads to an unacceptable degradation of the meadow in terms of both ecological (Johst et al. 2006) and economic (Bergmann 2004) quality. With a flexible mowing regime, every two years the conservation manager decides whether to mow in week 1, 2, 3, 4, 5, 6, or 7. Thus, in this case study the period length is two years. We consider $L = 20$ periods which corresponds to a time horizon of 40 years.

The objective of the following analysis is to compare flexible and fixed mowing regimes with regard to their effect on the survival of the butterfly population for several budgets. For simplicity, we assume that the interest rate i for saved budgets and the discount rate ρ

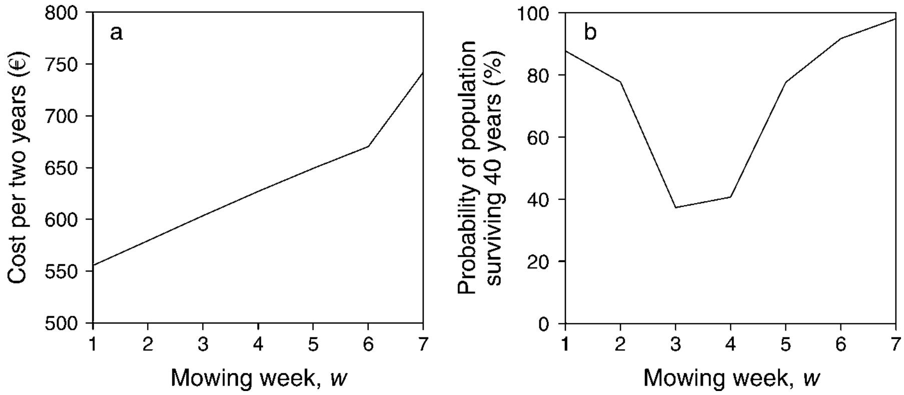

FIG. 1. (a) Costs (in euros) and (b) ecological effects (probability of population survival) of the seven fixed mowing regimes, $w = 1 \ldots 7$.

for the costs of mowing are equal, so the total discount rate δ introduced in the previous section is one. We identify measure m_l of Eq. 4 with the mowing week w_l selected in period l where $w_l \in \{1, \ldots, 7\}$ and apply Eq. 4 with $L = 20$:

$$P_{20}^{(\mathrm{flex})} = \max_{\{w(N)\}} P_{20}\left[w_1, \ldots, w_{20} \middle| \sum_{l=1}^{20} C(w_l) = B - 20K\right]$$

$$P_{20}^{(\mathrm{fix})} = P_{20}[w_1, \ldots, w_{20} | C(w_1) = \cdots = C(w_{20}) = B/20]. \tag{8}$$

Eq. 8 can now be used to compare fixed and flexible mowing regimes. We start with the first fixed mowing regime, mowing always in week 1, $w_1 = \cdots = w_L = 1$, and determine its ecological effect, $P_{20}^{(\mathrm{fix})}$ and the required budget $B = 20C(w_l)$. Then we insert this budget into Eq. 8 for the flexible mowing regime and calculate $P_{20}^{(\mathrm{flex})}$ as a function of K. Comparison of $P_{20}^{(\mathrm{flex})}$ and $P_{20}^{(\mathrm{fix})}$ allows us to determine which strategy is better for given K and, where applicable, the break-even point K_c (Eq. 7). The same analysis is carried out for the remaining six fixed mowing regimes.

RESULTS

The costs ($C(w)$, $w = 1, \ldots, 7$) and their ecological effects vary for the seven fixed mowing regimes (Fig. 1). Costs increase approximately linearly with increasing date of the cut. Ecological effect (probability of population survival) is relatively high for early mowing weeks, then drops to low values and increases again at later weeks. The poor performance of mowing weeks 2–5 is because these are the critical weeks during which the butterflies deposit their eggs and larvae are feeding on the plants. As a consequence, mowing in weeks 2, 3, 4, or 5 is not optimal because a higher ecological benefit can be achieved at lower costs by mowing in week 1. A real trade-off exists among weeks 1, 6, and 7, because mowing late leads to a higher ecological benefit but also to higher costs.

The budget required for a particular fixed mowing regime is given by its cost per period (Fig. 1a) multiplied by the number of periods ($L = 20$). The corresponding maximum flexible management cost per period ($K_{\max}$) beyond which flexible mowing is infeasible follows from Eq. 6 and is given in Table 1. As expected, for the lowest budget of €11 108 we have $K = 0$, because the cheapest measure (mow in week 1) is applied in every period, so any deviation from that fixed mowing regime will exceed the budget. For the remaining six budget levels (B) and under the constraint $0 < K < K_{\max}(B)$, the (optimal) flexible mowing regime and the resulting ecological effect can be determined as a function of K using stochastic dynamic programming (e.g, Clark 1990, Dixit and Pindyck 1994, Richards et al. 1999, Westphal et al. 2003, Costello and Polasky 2004, Drechsler and Wätzold 2004). The basic idea of (stochastic) dynamic programming is to determine the optimal decision (that maximizes the target variable) in the penultimate period as a function of the system state in that period. Then, under the assumption that in the penultimate period the optimal decision will be taken, the optimal decision in the preceding period is determined as a function of the system state. In that way, one moves backward in time until the first period is reached. With increasing K, the

TABLE 1. The budgets (for 40 years; B), maximum flexible management costs per period $K_{\max}$ (Eq. 6), and break-even (h_c) and maximum ($h_{\max}$) feasible monitoring cost per hour for the seven fixed mowing regimes.

Fixed mowing regime	B (€)	$K_{\max}$ (€)	h_c (€)	$h_{\max}$ (€)
Week 1	11 108	0	0	0
Week 2	11 587	24	0	0
Week 3	12 070	48	0	0
Week 4	12 538	72	0	3
Week 5	12 984	94	0	6
Week 6	13 403	115	7	9
Week 7	14 842	187	11	18

Note: Costs are in euros (€).

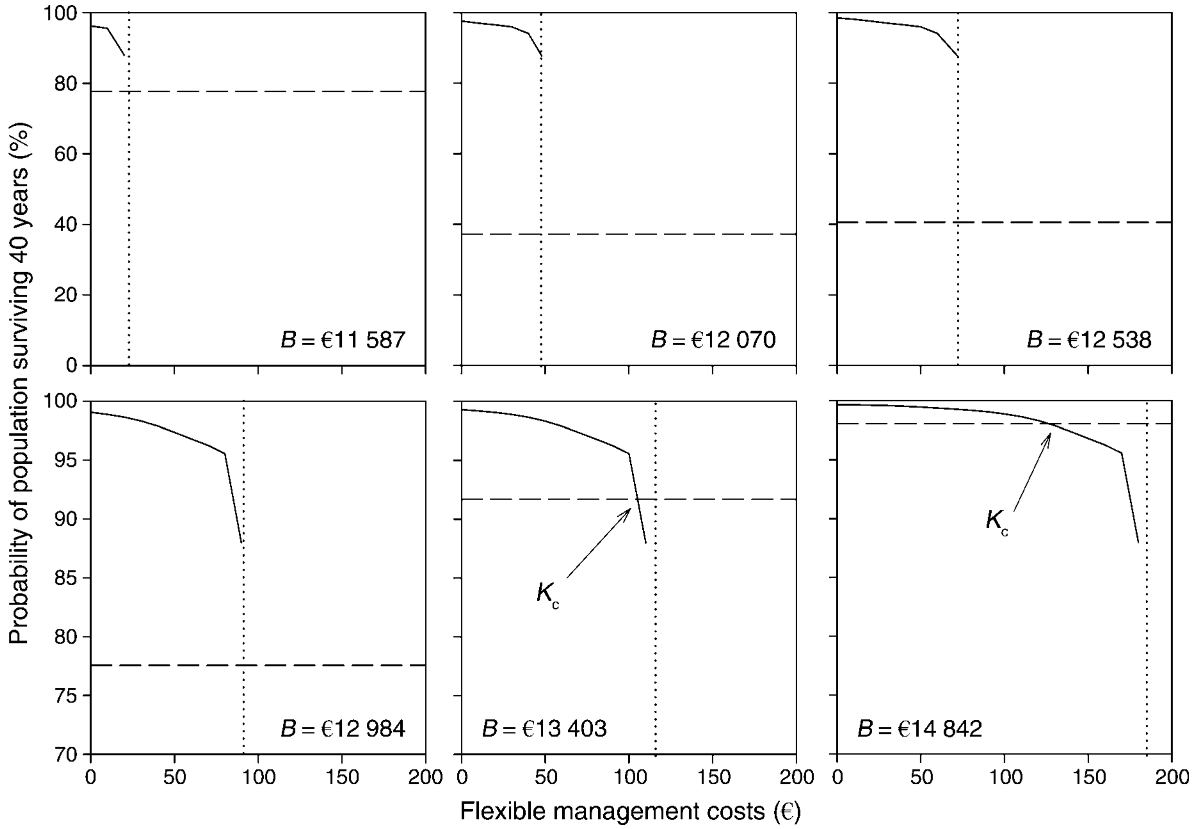

FIG. 2. Ecological benefit (population survival shown as solid line) for six different budget levels, B (corresponding to weeks 2–7; Table 1) as a function of the flexible management costs K. Dashed lines mark the ecological benefit obtained by the fixed mowing regime (cf. Fig. 1). Dotted lines mark the maximum flexible management costs, $K_{\max}$. Feasible flexible mowing regimes exist only for $K < K_{\max}$. At the break-even point K_c, flexible and fixed mowing have the same performance (cf. Eq. 7). Costs are in euros.

relative advantage of flexible mowing decreases until K reaches its maximum value $K_{\max}$, beyond which flexible mowing becomes infeasible (Fig. 2). For the four lowest budget levels in Fig. 2, no break-even point exists (cf. Eq. 7), i.e., flexible mowing is either infeasible (if $K \geq K_{\max}$) or it outperforms fixed mowing (if $K < K_{\max}$). For larger budgets, however, a break-even point $K_c < K_{\max}$ exists, such that for median flexible management costs $K_c < K < K_{\max}$ fixed mowing outperforms flexible mowing. For the highest budget level of €14 842, the break-even point is about $K_c = €130$.

To determine if the butterfly population can, and should, be managed in a flexible manner we have to estimate the actual monitoring and flexibility costs K (Eq. 3). Monitoring costs are mainly determined by the number of hours required to count the butterflies during their eclosion period. To cover the entire eclosion period, the meadow has to be visited three times (one visit per week) and each visit will require about 2.5 hours (J. Settele, *personal communication*). This leads to monitoring costs of $3 \times 2.5h$ where h is the cost per hour of sampling.

Flexibility costs arise, because mowing in different weeks affects to a different extent the quality of silage harvested from the meadows. With later mowing dates, the quality of silage decreases and silage harvested in week 7 cannot be used in cattle nutrition due to its low quality. The resulting costs of required additional cattle fodder and disposal of worthless grass are already included in the costs C. What is not included there, however, is that the purchase of additional fodder and the disposal of grass have to be reorganized every year depending on the prescribed mowing week. We estimate the compensation necessary for these additional management activities to be around €50.

In total, the costs of flexible management are $K = €50 + (3 \times 2.5h)$. Analogous to the quantities K_c and $K_{\max}$, we introduce a break-even cost and a maximum cost per hour, $h_c = (K_c - €50)/7.5$ and $h_{\max} = \max(0,(K_{\max} - €50)/7.5)$. Flexible mowing is infeasible for $h \geq h_{\max}$, feasible and outperforming fixed mowing for $h < h_c$ and feasible but outperformed by fixed mowing for $h_c < h < h_{\max}$ (Table 1).

PLATE 1. *Maculinea teleius* nectaring on its larval foodplant *Sanguisorba officinalis*. Photo credit: Josef Settele.

Hourly rates for simple work in Germany are around $h = €15$ which means that for all but the highest budget level, $h > h_{\max}$ and flexible mowing is infeasible. For the highest budget level we have $h_c < h < h_{\max}$, which means that a flexible mowing strategy is feasible but underperforms state-independent mowing.

DISCUSSION

Recent research has emphasized the benefits of flexible, state-dependent conservation management compared to fixed, non-state-dependent management. The purpose of this paper is to point out that state-dependent management may lead to costs that do not exist for fixed management and that, if such costs are taken into account, flexible conservation management may not always be better than state-independent management. For this purpose, we discussed in a conceptual, formal manner how the analysis of flexible conservation management has to be changed to integrate the costs of flexible management which were identified as monitoring (to assess the state of the population) and flexibility costs (to pay landowners for carrying out measures on short notice). These costs very much depend on the management problem. We further showed in a case study related to the conservation of the Large Blue butterfly in Germany that the costs of flexible management may indeed have an influence on the choice of the optimal management strategy, such that fixed management becomes better than flexible management. On a more general level, the choice between fixed and flexible management may be influenced by other aspects, as well, that are briefly discussed below.

In addition to assessing the current state of the population, monitoring may also be needed in order to ensure that the landowners comply with the requirements of the scheme (legal compliance, cf. Wätzold and Schwerdtner 2005) and to evaluate whether the predicted ecological effects of the management scheme actually appear (cf. Kleijn et al. 2001). Monitoring for these two purposes is probably not identical to monitoring for flexible management. However, we can expect that there is some overlap that reduces the costs of monitoring required for flexible management. Furthermore, the costs of monitoring are not fixed over time. There might be innovations where more cost-effective ways of assessing the state of the population are leading to decreasing monitoring costs. Models can be particularly useful to optimize the allocation of monitoring efforts (e.g., Field et al. 2004, Gerber et al. 2005) or to complement field observations (Hauser et al. 2006). Both aspects—overlapping monitoring costs and innovations—increase the attractiveness of flexible management compared to fixed management.

Flexible management has the advantage that management measures can be quickly adapted to improved information about their effects on ecosystems. The importance of learning in the face of uncertainty about the impact of human action on ecosystems has been emphasized in the ecological literature on adaptive management (Shea et al. 2002). A similar argument has been made in the economic literature (Arrow and Fisher 1974). Arrow and Fisher argued that if uncertainty and irreversibility surround the impact of human action on ecosystems, postponing the action provides a benefit (a quasi-option value) because improved information of the impact allows better founded decisions to be made at later stages. For conservation problems with a high risk of irreversibility (e.g., extinction of species) the quasi-option value supports the case for state-dependent management. With flexible strategies mistaken management measures can be remedied much earlier than with fixed management strategies reducing the risk of unwanted consequences persisting for all time.

In our analysis, we assumed that the conservation agency knows the conservation costs, and payments to land users equal these costs. However, in practice landowners are often better informed about their conservation costs than the agency. If payments are based on cost compensation land users have an incentive to overstate conservation costs in order to receive higher payments (Innes et al. 1998, Smith and Shogren 2002). This, in turn, will result in less conservation for a given budget. In order to avoid this, the agency has an interest to obtain information about conservation costs. Here flexible management may have an advantage, if it is possible to gather information about costs from the landowners' behavior. The agency can observe the response of the landowners to payment offers for management measures, and if those measures are employed again in later periods it can modify the payments or measures accordingly (e.g., an oversubscription of a voluntary payment scheme indicates that payments could be lowered).

There may be political arguments in favor of state independent management strategies. With flexible management, pressure groups may use the necessity to decide on the management measure after each period as an opportunity for lobbying activities. This may lead to high political decision making costs (cf. Birner and Wittmer 2004). Furthermore, in the context of the debate on the quasi-option value Miller and Lad (1984) pointed out that flexible decisions may entail political costs if changing one's mind is viewed as weakness on the part of a decision maker.

Our results were obtained by integrating ecological and economic knowledge. Recently, such an approach has been increasingly applied in the development of biodiversity management recommendations. For example, the optimal selection and design of reserve sites has been the domain of ecology (Margules et al. 1988). But as Ando et al. (1998) have shown, cost savings of up to 80% could be achieved by integrating economic costs (i.e., land prices) into traditional selection algorithms based on ecological value for reserve sites. Another example of combining ecology and economics is the research by Skonhoft et al. (2002) who integrate conservation, tourism and hunting values in their analysis of various management strategies for a mountain ungulate, the Chamois (*Rupicapra rupicapra*) in the French Alps. Their findings illustrate that research that takes into account many values may lead to different optimal management guidelines than research that focuses only on conservation value. Our findings also demonstrate that better management recommendations may be achieved when ecological and economic knowledge is taken into account in an integrated manner (cf. Wätzold et al. 2006).

Acknowledgments

We are grateful for the helpful comments of two anonymous reviewers.

Literature Cited

Ando, A., J. Camm, S. Polasky, and A. Solow. 1998. Species distributions, land values and efficient conservation. Science **279**:2126–2128.

Arrow, K. J., and A. C. Fisher. 1974. Environmental preservation, uncertainty, and irreversibility. Quarterly Journal of Economics **88**:312–319.

Bergmann, H. 2004. Berechnung von Kosten für Maßnahmen zum Schutz von gefährdeten *Maculinea*-Arten. UFZ-Diskussionspapier 2/2004. ⟨http://www.ufz.de/index.php?de=2301⟩

Birner, R., and H. Wittmer. 2004. On the "efficient boundaries of the state": the contribution of transaction costs economics to the analysis of decentralization and devolution in natural resource management. Environment and Planning C: Government and Policy **22**:667–685.

Clark, C. W. 1990. Mathematical bio-economics (optimal management of renewable resources). John Wiley and Sons, New York, New York, USA.

Clough, P. 2000. Encouraging private biodiversity. Incentives for biodiversity conservation on private land. Treasury Working Paper 00/25, Wellington, New Zealand.

Costello, C., and A. Polasky. 2004. Dynamic reserve site selection. Resource and Energy Economics **26**:157–174.

Dixit, A. K., and R. S. Pindyck. 1994. Investment under uncertainty. Princeton University Press, Princeton, New Jersey, USA.

Drechsler, M., and F. Wätzold. 2004. A decision model for the efficient management of a conservation fund over time. Animal Biodiversity and Conservation **27**(1):283–285.

Drechsler, M., F. Wätzold, K. Johst, H. Bergman, and J. Settele. 2005. A model-based approach for designing cost-effective compensation payments for conservation of endangered species in real landscapes. UFZ discussion papers 2/2005, Leipzig, Germany. ⟨http://www.ufz.de/index.php?de=2301⟩

Field, S. A., A. J. Tyre, K. H. Thorn, P. J. O'Connor, and H. P. Possingham. 2004. Improving the efficiency of wildlife monitoring by estimating detectability: a case study of foxes (*Vulpes vulpes*) on the Eyre Peninsula, South Australia. Wildlife Research **32**(3):253–258.

Gerber, L. R., M. Beger, M. A. McCarthy, and H. P. Possingham. 2005. A theory for optimal monitoring of marine reserves. Ecology Letters **8**:829–837.

Hampicke, U., and D. Roth. 2000. Costs of land use for conservation in Central Europe and future agricultural policy. International Journal of Agricultural Resources, Governance and Ecology **1**:95–108.

Hanley, N., H. Kirkpatrick, I. Simpson, and D. Oglethorpe. 1998. Principles for the provision of public goods from agriculture: modelling moorland conservation in Scotland. Land Economics **74**:102–113.

Hauser, C. E., A. R. Pople, and H. P. Possingham. 2006. Should managed populations be monitored every year? Ecological Applications **16**:000–000.

Höft, A., W. Wichtmann, and S. Jörns. 2005. Akzeptanz extensiver Bewirtschaftung ertragsschwacher Ackerstandorte bei Landnutzern. Pages 103–114 *in* U. Hampicke, B. Litterski, and W. Wichtmann, editors. Ackerlandschaften: Nachhaltigkeit und Naturschutz auf ertragsschwachen Standorten. Springer, Berlin, Germany.

Innes, R., S. Polasky, and J. Tschirhart. 1998. Takings, compensation and endangered species protection on private lands. Journal of Economic Perspectives **12**(3):35–52.

Johst, K., M. Drechsler, J. A. Thomas, and J. Settele. 2006. Influence of mowing on the persistence of two endangered Large Blue (*Maculinea*) butterfly species. Journal of Applied Ecology **43**:333–342.

Kleijn, D., F. Berendse, R. Smit, and N. Gilissen. 2001. Agri-environment schemes do not effectively protect biodiversity in Dutch agricultural landscapes. Nature **413**:723–725.

Margules, C. R., A. O. Nicholls, and R. L. Pressey. 1988. Selecting networks of reserves to maximise biological diversity. Biological Conservation **43**:63–76.

Miller, J. R., and F. Lad. 1984. Flexibility, learning and irreversibility in environmental decisions: a Bayesian approach. Journal of Environmental Economics and Management **11**:161–172.

Possingham, H. P. 1997. State-dependent decision analysis for conservation biology. Pages 298–304 *in* S. T. A. Pickett, R. S. Ostfeld, M. Shachak, and G. E. Likens, editors. The ecological basis of conservation: heterogeneity, ecosystems and biodiversity. Chapman and Hall, New York, New York, USA.

Richards, S. A., H. P. Possingham, and J. Tizard. 1999. Optimal fire management for maintaining community diversity. Ecological Applications **9**:880–892.

Shea, K., H. P. Possingham, W. W. Murdoch, and R. Roush. 2002. Active adaptive management in insect pest and weed control: intervention with a plan for learning. Ecological Applications **12**(3):927–936.

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

Smith, R., and J. Shogren. 2002. Voluntary incentive design for endangered species protection. Journal of Environmental Economics and Management **43**:169–187.

Thomas, J. A. 1984. The behaviour and habitat requirements of *Maculinea nausithous* (the Dusky Large Blue butterfly) and *M. teleius* (the Scarce Large Blue) in France. Biological Conservation **28**:325–347.

Thomas, J. A., and J. Settele. 2004. Butterfly mimics of ants. Nature **432**:283–284.

Wätzold, F., and M. Drechsler. 2005. Spatially uniform versus spatially heterogeneous compensation payments for biodiversity-enhancing land-use measures. Environmental and Resource Economics **31**:73–93.

Wätzold, F., M. Drechsler, C. W. Armstrong, S. Baumgärtner, V. Grimm, A. Huth, C. Perrings, H. P. Possingham, J. F. Shogren, A. Skonhoft, J. Verboom-Vasiljev, and C. Wissel. 2006. Ecological-economic modelling for biodiversity management: potential, pitfalls, and prospects. Conservation Biology **20**:1034–1041.

Wätzold, F., and K. Schwerdtner. 2005. Why be wasteful when preserving a valuable resource? A review article on the cost-effectiveness of European biodiversity conservation policy. Biological Conservation **123**:327–338.

Westphal, M. I., M. Pickett, W. M. Getz, and H. P. Possingham. 2003. The use of stochastic dynamic programming in optimal landscape reconstruction for metapopulations. Ecological Applications **13**(2):543–555.

Wilson, G. 1997. Factors influencing farmer participation in the Environmentally Sensitive Areas Scheme. Journal of Environmental Management **50**:67–93.

APPENDIX

A simple model showing the state-dependent effect of conservation measures on population survival (*Ecological Archives* A016-067-A1).