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## **Integrating economic costs into the analysis of flexible conservation management strategies**

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## **Abstract**

Flexible conservation management, where measures are selected in each decision period and depending on the current state of the ecological system, are 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 these “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

## 1 Introduction

Recent research on optimal conservation management has stressed the importance of state-dependent, or flexible, management strategies. 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 preceding period. In contrast, for state-independent, or fixed, strategies, the optimal management strategy remains the same over all periods.

There are several studies that demonstrate the advantages of flexible management strategies. For example, Westphal et al. (2003) analyse various management strategies to conserve the Southern Emu-wren (*Stipiturus malachurus intermedius*). They find that the extinction probability over 30 years for the optimal state-dependent management actions is 50-80% better than no management, whereas the best fixed, state-independent sets of strategies are only 30% better than no management. Another example is Richards et al. (1999) who analyse the problem of optimal fire management to maintain community diversity in Ngarkat Conservation Park, Australia. Their results show that the optimal choice between the strategies “let wildfires burn unhindered”, “fight wildfires”, or “perform controlled burns” depends – among other factors – on the current state of the park.

However, it needs to be pointed out that state-dependent management may lead to 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: (i) monitoring costs and (ii) flexibility costs.

(i) If management decisions in each period depend on the state of the managed ecosystem or population costly *monitoring activities* in each period have to be carried out to gain the necessary information about that state. (ii) *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. Programmes 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 programmes are mostly directed at farmers to induce them on a voluntary basis to farm their land in a conservation-friendly manner.

Experience with such programmes has shown that it is important for landowners to have planning reliability for their economic activities (cf. 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. We refer to costs arising from lost planning reliability and short-term adjustments as flexibility costs.

The purpose of this paper is to provide a formal framework for the integration of economic costs into the analysis of flexible conservation management (Section 2) and to demonstrate that taking into account the costs of flexible management may indeed reverse the rank order of 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 (Section 3). In a final section, the results of the paper are summarised and discussed.

## 2 A framework for integrating costs into the analysis of flexible management

In this section we present a framework that integrates costs into the analysis of flexible conservation management in a conceptual, formal manner. Assume a conservation manager has to manage a population over  $L$  time periods and wants to maximise the probability of the population surviving these  $L$  periods. In each period s/he can select 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 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  $C(m_l)$  then this statement may be mathematically expressed as

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

with

$$P_L^{(\text{flex})} = \max_{\{m(N)\}} P_L \left( m_1, \dots, m_L \mid \sum_{l=1}^L C(m_l) = B \right) \tag{2}$$

$$P_L^{(\text{fix})} = P_L (m_1, \dots, m_L \mid C(m_1) = \dots = C(m_L) = B/L)$$

where  $P_L$  is the survival probability of the population over the  $L$  periods and the maximum in  $P_L^{(\text{flex})}$  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 maximises the management objective under the given constraints.

At first sight, 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. The management activities, however, 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  $M$ .

Secondly, it may be that the conservation measures are not carried out by the conservation agency but that the agency asks landowners on whose land the population is located to do this and compensates them for the costs incurred. To induce a landowner to carry out conservation measures s/he has 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 his or her production activities and because his or her 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

$$P_L^{(\text{flex})} = \max_{\{m(N)\}} P_L \left( m_1, \dots, m_L \mid \sum_{l=1}^L C(m_l) = B - KL \right) \tag{4}$$

$$P_L^{(\text{fix})} = P_L (m_1, \dots, m_L \mid C(m_1) = \dots = C(m_L) = B/L)$$

Being confronted with the problem of intertemporal allocation of funds, we have to discount future costs. First, we have to take into account that if the conservation agency spends money in later periods instead of today this money generates interest. 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,  $\rho$  represents the cost increase of conservation measures per period, and  $l$  is the number of the period. With this, eq. (4) becomes

$$P_L^{(\text{flex})} = \max_{\{m(N)\}} P_L \left( m_1, \dots, m_L \mid \sum_{l=1}^L C(m_l) \delta^{-l} = B - K \sum_{l=1}^L \delta^{-l} \right) \quad (5)$$

$$P_L^{(\text{fix})} = P_L \left( m_1, \dots, m_L \mid C(m_1) \delta^{-1} = \dots = C(m_L) \delta^{-L} = B/L \right)$$

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

1. For  $K=B/L$  the flexible strategy is infeasible, 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 (3), 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  $B/\sum \delta^l$  and the cost of the cheapest conservation measure (or zero if this difference is negative):

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

(note that for  $\delta=1$  we have  $\sum \delta^l=L$ , 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

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

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 will carry out such an analysis for the case study of butterfly conservation management in Germany.

### 3 Dynamic conservation management of the Large Blue butterfly in Germany

The Large Blue butterfly (*Maculinea teleius*) is an endangered butterfly species protected by the European Union Habitats Directive (Council Directive 92/43/EEC). It inhabits open grasslands which are usually found in the form of grazed or mowed meadows in Germany. The butterfly mainly depends on two resources: Great Burnet (*Sanguisorba officinalis*) plants to deposit its eggs on and ants of the species *Myrmica scabrinodis* which adopt the butterfly larvae when they have fallen off the *Sanguisorba* flowerheads and carry them into their nests. Here the butterfly larvae feed on the ant brood, pupate and overwinter (Thomas and Settele 2004, Thomas et al. 2004).

If the vegetation on the meadow gets too high, the *Sanguisorba* is out-competed by other plant species and the ants disappear too, because the microclimate becomes unsuitable for them. So to maintain the suitability of the meadow for the butterfly, the vegetation of the meadow has to be kept low by some form of management.

In this study we consider a meadow with a typical type of economic land-use in Europe: mowing for cattle fodder production. Conventionally, in Germany meadows are mowed twice a year: 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 ecological effects of these mowing regimes, i.e. the survival of the butterfly population in the region, were determined by an ecological simulation model that follows the life cycle of the butterflies and, in particular, considers 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).

In Drechsler et al. (2005) the mowing regimes were considered in a “fixed manner” in that on a particular meadow the same mowing regime (e.g. “mow every second year at the end of June”) was applied throughout the time horizon of the simulation. As can be seen, these mowing regimes are dynamic in a way (in one year there is a cut, in the following year there is no cut, etc.), but the decision to mow or not to mow is not made dependent on the current state of the butterfly population.

In this analysis we modify the study of Drechsler et al. (2005) by considering flexible, population-state-dependent mowing regimes. We use the same data, in particular the same costs for the different mowing regimes and the same parameters for the ecological 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),..., or 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 as 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. *subm.*) and economic (Bergmann 2004) quality.

With a flexible mowing regime, every two years the conservation manager decides whether to mow in week 1, week 2, ..., or week 7. Thus, in this case study the period length is 2 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  $\rho$  for the costs of mowing are equal, so the total discount rate  $\delta$  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  $w_l \in \{1, \dots, 7\}$  and apply eq. (4) with  $L=20$ :

$$P_{20}^{(\text{flex})} = \max_{\{w^{(N)}\}} P_{20} \left( w_1, \dots, w_{20} \mid \sum_{l=1}^{20} C(w_l) = B - 20K \right) \quad (8)$$

$$P_{20}^{(\text{fix})} = P_{20} (w_1, \dots, w_{20} \mid C(w_1) = \dots = C(w_{20}) = B/20)$$

Equation (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:  $w_1 = \dots = w_L = 1$  and determine its ecological effect,  $P_{20}^{(\text{fix})}$  and the required budget  $B = 20C(w_1)$ . Then we insert this budget into eq. (8) for the flexible mowing regime and calculate  $P_{20}^{(\text{flex})}$  as a function of  $K$ . Comparison of  $P_{20}^{(\text{flex})}$  and  $P_{20}^{(\text{fix})}$  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.

To start with the results for the seven fixed mowing regimes, Figure 1 shows their costs ( $C(w)$  ( $w=1 \dots 7$ )) and their ecological effects. The costs increase approximately linearly with increasing date of the cut. The 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 median mowing weeks is easily explained by the fact that 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 between weeks 1, 6 and 7, because here a higher ecological benefit comes only at higher costs.

The budget 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 ( $K_{\text{max}}$ ) beyond which flexible mowing is infeasible follows from

eq. (6). For the seven fixed mowing regimes, the budgets and maximum flexible management costs are shown in Table 1.

As expected, for the lowest budget of €1,108 we have  $K=0$ , because this budget corresponds to applying the cheapest measure (mow in week 1) 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  $K$ .

The standard method for solving such optimisation problems is 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 maximises the target variable) in the ultimate period as a function of the system state in that period. Then, under the assumption that in the ultimate period the optimal decision will be taken, the optimal decision in the penultimate period is determined as a function of the system state. In that way one moves backwards in time until the first period is reached. For details, see the references given.

The result of the analysis is shown in Figure 2. As discussed in the previous section, flexible mowing outperforms fixed mowing if the flexible management cost is zero,  $K=0$ . With increasing  $K$  the relative advantage of flexible mowing decreases until  $K$  reaches its maximum value  $K_{\max}$  beyond which flexible mowing becomes infeasible.

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 €4,842, the break-even point is about  $K_c \approx €130$ .

Having evaluated the relative performance of flexible mowing as a function of the budget and the flexibility costs, the question is now whether in a concrete case the butterfly population can – and if it can, should – be managed in a flexible manner.

For this 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 2-3 hours (Settele, oral communication).

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 re-organised every year depending on the prescribed mowing week. We estimate the compensation necessary for these additional management activities to be around €0.

With this,  $K = \text{€}0 + 3 \times 2.5h$  where  $h$  is the cost per hour of sampling. Analogous to the quantities  $K_c$  and  $K_{\max}$ , we introduce a break-even cost and a maximum cost per hour,  $h_c = (K_c - \text{€}0)/8$  and  $h_{\max} = \max(0, (K_{\max} - \text{€}0)/7.5)$ . 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  $h_c < h < h_{\max}$ . The numerical values for  $h_c$  and  $h_{\max}$  are given in Table 2.

Hourly rates for simple work in Germany are around  $h = \text{€}15$  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. Our results thus show that if the objective is to maximise an ecological goal at a given budget it is crucial to include the costs of state-dependent conservation in determining optimal conservation strategies as it may reverse the rank-order between state-independent and state-dependent conservation strategies.

#### 4 Summary and discussion

Recent research has emphasised 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 and flexibility costs. Furthermore, we 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.

Whether a flexible or a fixed management strategy is the better option depends on the magnitude of monitoring and flexibility costs. These costs are specific for each conservation problem. However, it is of interest for the comparison of flexible and fixed strategies to briefly discuss two general considerations related to monitoring costs. (1) In addition to implementing a flexible management scheme monitoring may also be needed in order to monitor whether 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 which reduces the costs of monitoring required for flexible management. (2) The costs of monitoring are not fixed over time. There might be innovations where more cost-effective monitoring schemes are developed leading to decreasing monitoring costs (an example for the order Lepidoptera is Nowicki et al., in press).

Both aspects – overlapping monitoring costs and innovations– increase the attractiveness of flexible management compared to fixed management. Similar general conclusions have been derived by Shea et al. (2002) for adaptive management where monitoring is not used to make measures dependent on the current state of the managed system but to learn about the functioning of the system (e.g. uncertain population parameters) in order to adapt conservation management in the medium term.

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 ecology-driven selection algorithms for reserve sites. Another example of combining ecology and economics is the research by Skonhøft 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.

The cited research and this paper 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. *subm.*). We conclude that such an approach should be more often applied in future research.

## Appendix

The basic idea behind the concept of flexible conservation management is that the value of a given conservation measure for the survival of a population depends on its current state, in particular, its size. In this section we provide an example where this can be proven mathematically. Consider a small exponentially growing population where density-dependent regulation is not effective but extinction due to demographic stochasticity is likely. The dynamics of such a population can be described by a Master equation (e.g. Goel and Richter-Dyn 1974.) with birth and death rates  $\lambda_n$  and  $\mu_n$  which depend on the current population size  $n$  via

$$\begin{aligned}\lambda_n &= n(\gamma + r)/2 \\ \mu_n &= n(\gamma - r)/2\end{aligned}\tag{A1}$$

Here  $r$  is the growth rate of the population and  $\gamma$  ( $\gamma > r$ ) measures the strength of demographic stochasticity (precisely, the variance of population growth due to demographic variation which is modelled as random walk). The model in eq. (A1) has been derived from the models analysed in Wissel and Stöcker (1991) and Drechsler and Wissel (1998).

The expected life-time of a population that currently has the size  $N$ , with birth and death rates given by eq. (A1) is

$$T = \sum_{n=1}^N \sum_{i=n}^{\infty} \frac{1}{\mu_i} \prod_{j=n}^{i-1} \frac{\lambda_j}{\mu_j}\tag{A2}$$

(Goel and Richter-Dyn 1974). The probability of the population surviving a certain time period  $t$  can be approximated by

$$P_t \approx \exp\left(-\frac{t}{T}\right)\tag{A3}$$

(Drechsler and Wissel 1998; Grimm and Wissel 2004) We now assume that some conservation measures increase the population growth rate  $r$  and we are interested in how such an increase affects the survival probability of the population  $P_t$ . For this we define the marginal value  $v(r)$  of an increase in  $r$  with regard to the survival probability  $P_t$  as the derivative  $v(r)=dP_t/dr$  which in first approximation, i.e. for sufficiently small  $t/T$ , is given by

$$v(r) = \frac{dP_t}{dr} = \frac{dP_t}{dT} \frac{dT}{dr} \approx \frac{t}{T^2} \frac{dT}{dr} \quad (\text{A4})$$

The question is now how the marginal value  $v(r)$  depends on the current population size  $N$ . Using  $\lambda_n/\mu_n = (\gamma+r)/(\gamma-r)$ ,  $d(\lambda_n/\mu_n)/dr = 2\gamma/(\gamma-r)^2$ , and

$$\sum_{i=n}^{\infty} \frac{1}{\mu_i} \prod_{j=n}^{i-1} \frac{\lambda_j}{\mu_j} = \sum_{i=0}^{\infty} \frac{2}{(i+n)(\gamma-r)} \left( \frac{\gamma+r}{\gamma-r} \right)^i \quad (\text{A5})$$

we obtain through algebra

$$v(r) = \frac{t}{T^2} \frac{dT}{dr} \approx t \cdot \left[ \frac{1}{2f} + \frac{\gamma}{R-r} \frac{g}{f^2} \right] \quad \text{with} \quad (\text{A6})$$

$$f = \sum_{n=1}^N \sum_{i=0}^{\infty} \frac{1}{i+n} \left( \frac{\gamma+r}{\gamma-r} \right)^i \quad \text{and} \quad g = \sum_{n=1}^N \sum_{i=0}^{\infty} \frac{i+1}{i+n+1} \left( \frac{\gamma+r}{\gamma-r} \right)^i$$

One can immediately see that  $f$  monotonically increases with  $N$ , such that  $1/f$  decreases with  $N$ . The fraction  $g/f^2$  is less easy to analyse. A systematic numerical analysis, however, reveals that regardless of  $\gamma$  and  $r$ ,  $g/f^2$  monotonically decreases with  $N$ . We conclude that  $v(r)$  monotonically decreases with  $N$ . In other words, the larger the population size, the less effective an increase in  $r$ . If density-dependence is included in the considerations, the dependence of  $v(r)$  on  $N$  is more complicated (close to the carrying capacity it can be expected to be rather small, or even negative if intra-specific competition in the population is of scramble type) but we can conclude that  $v(r)$  is indeed a function of population size  $N$ .

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## Tables

Table 1: The budgets (for 40 years) and maximum flexible management costs per period  $K_{\max}$  (eq. 6) for the seven fixed mowing regimes

Fixed mowing regime	$B$ (€)	$K_{\max}$ (€)
Week 1	11108	0
Week 2	11587	24
Week 3	12070	48
Week 4	12538	72
Week 5	12984	94
Week 6	13403	115
Week 7	14842	187

Table 2: The break-even and maximum feasible monitoring cost per hour for the seven fixed mowing regimes.

Fixed mowing regime	$h_c$ (€)	$h_{\max}$ (€)
Week 1	0	0
Week 2	0	0
Week 3	0	0
Week 4	0	3
Week 5	0	6
Week 6	7	9
Week 7	10	18

## Figure captions

Figure 1: Costs (a) and ecological effects (probability of population survival) (b) of the seven fixed mowing regimes,  $w=1\dots 7$ .

Figure 2: Ecological benefit (population survival) for six different budget levels (corresponding to weeks 2-7, Table 1) as a function of the flexible management costs  $K$  (solid lines). The dashed line marks the ecological benefit obtained by the fixed mowing regime (cf. Fig. 1). The dotted lines mark the maximum flexible management costs,  $K_{\max}$ . Feasible flexible mowing regimes exist only for  $K < K_{\max}$ .

## Figures

Figure 1

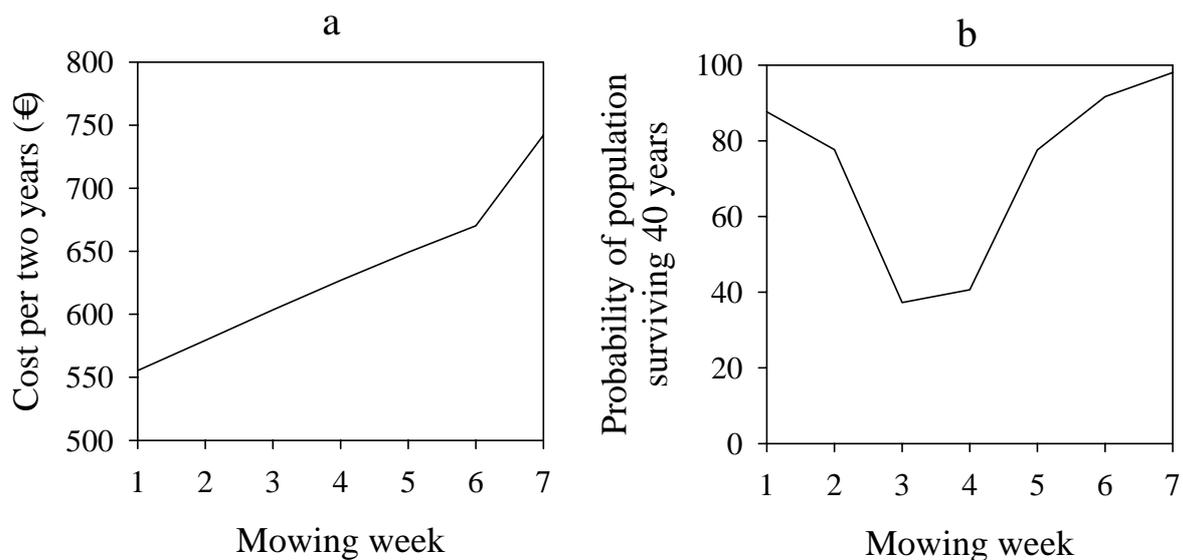


Figure 2

