



# Optimal harvesting in a two-species model under critical depensation

## The case of optimal harvesting in semi-arid grazing systems

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### Abstract

Ecological systems in general often exhibit the mechanism of critical depensation, i.e. the system may collapse due to decreasing population densities caused by, for example, an increasing predation pressure on the prey that causes both populations to collapse to extinction. In this study a semi-arid predator–prey grazing system is taken as an example and optimal, model based, harvesting rates for the herbivore population are presented that allow survival of both herbivores and grasses during long dry periods without precipitation. Recovery to a maximum sustainable yield is achieved in the next rain season under the assumption of model validity. Optimal control theory is utilized in this example as the principal method of solution. Both analytical and numerical issues of the solution method and obtained solutions are discussed. Survival of the system is possible if the pastoralist is willing to decrease his population considerably once the dry period has set in. The social willingness, necessary to implement these management strategies, can be interpreted in terms of a discount rate in the current value Hamiltonian associated with the dynamical grazing system. The example is worked out in more detail and dynamical solutions for two discount rates are presented.

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### 1. Introduction

Harvesting from two populations of different species has been subject of optimal control theory in ecology for a long time (Clark, 1976). An important question here is how to manage and harvest interdependent populations (Mesterton-Gibbons, 1996). The issue that makes these studies difficult is how to derive strategies to maximize the revenues and sustain the populations since affecting one population may have unforeseen economic and/or ecological consequences for the other (Armsworth and Rougharden,

2001). Clark (1976) assumed two ecologically independent species that experience logistic growth and the harvest rate for each species is proportionally to both its stock level and harvesting effort. This study was extended by Mesterton-Gibbons (1987) who discussed the optimal approach to equilibrium for such a dynamical system.

Several studies have relaxed the original assumptions to meet reality. This however increased the difficulty to derive harvesting strategies. One critical assumption is the dependency of the two populations. Where Clark (1976) and Mesterton-Gibbons (1987) first studied mainly ecologically independent populations, Ragozin and Brown (1985) and Wilen and Brown (1986) investigated harvesting of the predator

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in a predator–prey system. Here, the prey has no market value by virtue of being un-catchable. Chaudhuri (1986, 1988) and Mesterton-Gibbons (1987, 1988) extended this analysis by allowing combined harvesting of both predator and prey.

When populations are subject to mechanisms that increase the likelihood of their extinction with decreasing population size, i.e. the Allee effect, harvesting could have unforeseen consequences. The Allee effect that is responsible for the process of critical depensation, covers such mechanisms that depress the population growth rate at low sizes by, for example, reduced mate availability, reduced anti-predator defence or modification of the environment at low densities (Van de Koppel et al., 1997; Stephens and Sutherland, 1999). Management of renewable resources that have such mechanisms is extensively debated, e.g. (Lande et al., 1994; Meyers et al., 1995; Khan et al., 1997; Shea, 1998; Alvarez, 1998). The majority of these discussions, however, deals with single-species resources. In this study we will attempt to derive and analyze an optimal harvesting strategy in a predator–prey system where the predator is harvested and the prey, essentially, is subject to critical depensation.

Our system is a pastoral grazing system as can be found in arid or semi-arid areas in Africa. In many arid and semi-arid grazing systems, the vegetation may degrade irreversibly due to severe drought or overgrazing (Sinclair and Fryxell, 1985; Schlesinger et al., 1990; Graetz, 1991). Grazing systems essentially gain plant biomass during periods of intense rainfall which can only be observed in short rain seasons. A positive feedback mechanism between water infiltration into the soil and vegetation cover can be observed in the vegetation growth dynamics (Walker et al., 1981; Rietkerk and Van de Koppel, 1997; Rietkerk et al., 1997). However, this positive feedback mechanism carries an essential pitfall, namely that through a decrease of vegetation biomass during long periods of drought and/or overgrazing, infiltration of rainfall into the soil decreases dramatically. The result is that there is less soil water available for plant growth, causing water infiltration to decrease even more rapidly, etc. This decrease in infiltration of rainfall in the soil may indeed be due to erosion and crust formation (Kelly and Walker, 1976). Through this positive feedback mechanism, the effect of critical depensation occurs, meaning that the vegetation biomass collapses once a

critical threshold equilibrium value, say  $P_c$ , has been passed.

In the current study, we wish to analyze the dynamical behavior of a semi-arid grazing system in more detail and, moreover, we wish to find optimal management strategies for the pastoralists who seek to maximize the revenues of their herd while preventing the system from collapsing, i.e. passing the critical threshold level  $P_c$ . The results obtained can be extended to a general two-species model where the renewable resource is threatened by extinction because of the critical depensation effect.

## 2. A dynamical model for the plant–herbivore relation

Let  $P(t)$  and  $H(t)$  denote the vegetation and herbivore density ( $\text{g}/\text{m}^2$ ), respectively. Plant growth in dry areas is essentially driven by rainfall. Infiltration of water into the upper soil layer depends on the soil type and, moreover, the root density and activities of soil fauna. In mathematical terms the water availability in the soil  $W(t)$  ( $\text{mm}/\text{m}^2$ ) may be expressed as (Van de Koppel and Rietkerk, 2000)

$$\frac{dW(t)}{dt} = \text{PPT} \frac{P(t) + k_1 w_0}{P(t) + k_1} - r_w W(t) - uP(t)W(t) \quad (1)$$

where PPT is the precipitation ( $\text{mm}/\text{d}$ ),  $w_0$  is the fraction of rainfall that infiltrates into bare soil (when  $P(t) = 0$ ),  $k_1$  is a constant determining how quickly water infiltration increases with plant density  $P(t)$ , ( $\text{g}/\text{m}^2$ ),  $r_w$  is the specific loss rate of soil water due to evaporation and percolation ( $1/\text{d}$ ), and  $u$  is an uptake coefficient related to the uptake of water by vegetation ( $\text{m}^2/\text{g}$ ). Note that the first term on the right hand side of (1) includes the earlier discussed positive feedback mechanism between plant availability and soil water availability. Since the time scale on which water availability reaches steady state is small in comparison with the time scale of plant growth, a quasi steady state of the water availability  $W(t)$  may be assumed. Hence, setting  $dW(t)/dt = 0$  determines the water availability  $W^*(P)$  as a function of the vegetation density  $P(t)$  so that

$$W^*(P) = \text{PPT} \frac{P + k_1 w_0}{P + k_1} \frac{1}{uP + r_w} \quad (2)$$

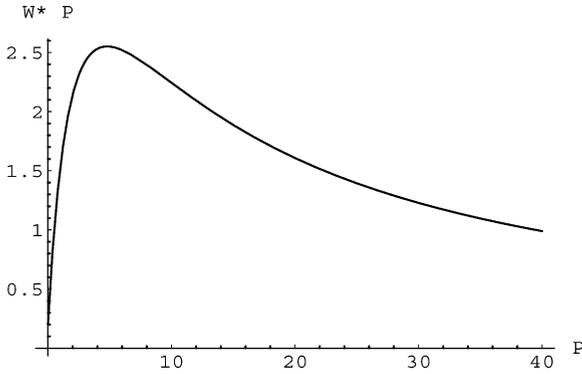


Fig. 1. Soil water availability as a function of vegetation biomass  $P$  in quasi steady-state conditions. Note the sudden decrease in available soil water if  $P$  decreases below the level  $P_m = 4.8$ , the point at which maximum water availability value is obtained.

This water–plant relation is shown in Fig. 1 from which it is clear that below the maximum available soil water  $W_{\max}^*(P)$  the infiltration rate declines sharply meaning that the overland flow of precipitation dominates causing the soil to erode quickly. The vegetation biomass density  $P_m$  corresponding with the maximum available soil water can easily be deduced from (2) as

$$P_m = -k_1 w_0 + \sqrt{\frac{k_1(1 - w_0)(r_w - uk_1 w_0)}{u}} \quad (3)$$

Clearly, the solution depends only on the soil infiltration parameters  $w_0$ ,  $k_1$ ,  $r_w$ , and the specific water uptake  $u$  of the plant.

Having established an algebraic relation for the available water as a function of plant biomass, the dynamical model for the plant–herbivore relation is straightforward to derive. Assuming that plant biomass grows proportionally to the water availability  $W^*(P)$  at a rate of  $h$  per plant, the rate of increase of the plant density  $(1/P)(dP/dt)$  is  $hW^*(P)$ . Furthermore, define  $m_P$  and  $m_H$  as the natural mortality rates of vegetation and herbivores, respectively. The herbivore population consumes the plant biomass at a rate  $bP(t)$  ( $\text{g}/\text{m}^2 \text{d}$ ) per herbivore  $H(t)$ , thereby increasing its own biomass at a rate  $bgP(t)$  ( $\text{g}/\text{m}^2 \text{d}$ ) per herbivore. Finally, we assume that the pastoralists harvest from their herd (that is grazing in a confined area) with harvest effort  $E(t)$  ( $1/\text{d}$ ) where  $0 < E(t) < E_{\max}$ , so that the complete model reads

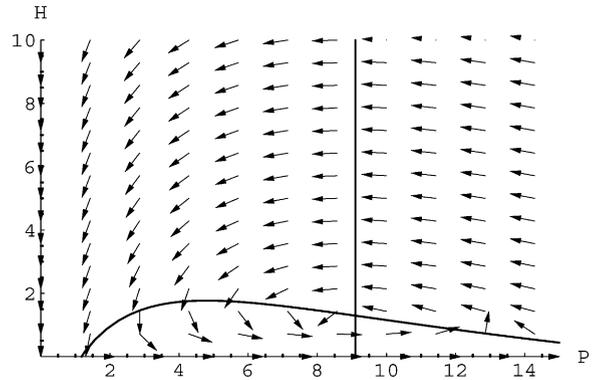


Fig. 2. Phase plot of plant–herbivore balance, driven by a constant precipitation  $\text{PPT} = 6 \text{ mm}/\text{day}$ .

$$\frac{dP(t)}{dt} = hW^*(P)P(t) - m_P P(t) - bP(t)H(t) \quad (4)$$

$$\frac{dH(t)}{dt} = bgP(t)H(t) - m_H H(t) - E(t)H(t) \quad (5)$$

The critical vegetation biomass density  $P_c$  below which infiltration rate is too small for plant growth can be derived setting  $dP(t)/dt = 0$  and solving for  $P(t)$ . This yields the trivial solution  $P(t) = 0$ , and the solution  $W(P) = (m_P + bH(t))/h$ . The last  $P$ -isocline obtains its maximum exactly at the maximum water availability  $P_m$  which is also the critical vegetation density  $P_c$  below which the ecosystem will collapse. If  $P(t)$  is above  $P_c$ , however, there will be no danger and, assuming the harvest rate  $E(t)$  is constant, the system will settle down in an equilibrium on the intersection of the  $P$ -isocline and the  $H$ -isocline for which  $P(t) = (m_h + \bar{E})/bg$ , see also Fig. 2.

Eqs. (4) and (5) comprise a set of coupled differential equations that reflect the underlying mechanisms for the plant–herbivore dynamics. Indeed, the herbivore population draws on the plant population through a coupling term  $bgP(t)H(t)$ . Since  $g > 0$  and  $b > 0$  the transfer of biomass is clearly in one direction. Given the pitfall of extinction of plant biomass once the vegetation density decreases below the critical level  $P_c$ , but also the natural tendency of the pastoralist to increase his herd size (for economic and social reasons) the essential question to answer is: ‘How should the pastoralist harvest his herd in order to have a maximum benefit, given a price  $p_H$  of the renewable resource  $H(t)$  and a (possible) discount rate  $\delta \geq 0$  on the

market value  $p_H E(t)H(t)$ ? Here  $p_H$  is the price per capita harvested animal.

In more exact terminology the pastoralist’s objective is to maximize the goal function

$$J \triangleq \int_0^\infty e^{-\delta\tau} p_H E(\tau)H(\tau) d\tau \tag{6}$$

under the dynamical constraints (4) and (5).

From a social point of view for the pastoralists a large herd of livestock increases the status of the herd owner in the community. From an economic point of view, the herd of livestock is seen as a capital asset. The livestock essentially reflects stored energy that can be used in the long term and, more specifically, during periods of low rainfall when supplies are scarce. Thus, harvesting from the herd is an expenditure to ensure survival and reproduction of the pastoral community. As for all harvesting, however, the question is what is more profitable: To harvest on the short term horizon or to wait for a longer period before harvesting (Clark, 1976)? The value of a capital can be expressed as the present value of future revenues that it is expected to yield. The goal function  $J$  (6), which is to be maximized, expresses these present values of the revenues. Another interpretation of the discount rate  $\delta$  is that it is a measure of the relative preference of present harvesting over future harvesting or the *social willingness* not to harvest now but in the future and to enforce sustainable management policies. Harvesting of livestock now may release the vegetation from grazing due to smaller livestock herds and therefore prevent the vegetation from decreasing below the critical vegetation biomass  $P_c$ .

$$F = \begin{pmatrix} -m_P - bH(t) + d_1 & -bP(t) \\ bgH(t) & -m_H + bgP(t) - E(t) \end{pmatrix}_{(P(t), H(t))=(P_\infty(\bar{E}), H_\infty(\bar{E}))} \tag{7}$$

### 3. Steady-state analysis

In Fig. 2 the isoclines  $dP(t)/dt = 0$  and  $dH(t)/dt = 0$  are presented at a constant harvest level  $E(t) = \bar{E} = E_{msy} = 0.127^1$  for the parameter values PPT = 6,

<sup>1</sup>  $E_{MSY}$  will be explained in the discussion of the maximum sustainable yield for the grazing system.

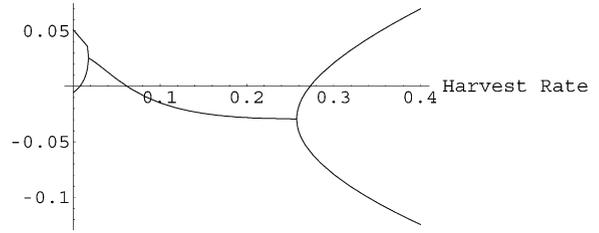


Fig. 3. Real part of the eigenvalues of the Jacoby matrix in the non-trivial equilibrium.

$k_1 = 5, w_0 = 0.02, r_w = 0.1, u = 0.02, m_P = 0.1, m_H = 0.01, b = 0.03, h = 0.01, g = 0.5$ , together with the directions  $(dP(t)/dt, dH(t)/dt)$  induced by the grazing model (4) and (5). The values of these parameter values were obtained from literature values, for example (Rietkerk and Van de Koppel, 1997), and on the basis of ‘educated guessing’ and expertise. Clearly, the isocline  $dH(t)/dt = 0$ , i.e. the constant line  $\bar{P} = m_H + \bar{E}/bg$ , has one point of intersection with the isocline  $dP(t)/dt = 0$  where the system is in a non-trivial equilibrium  $(P_\infty(\bar{E}), H_\infty(\bar{E}))$ . It can also be observed that decreasing the harvest rate  $\bar{E}$  shifts the isocline  $dH(t)/dt = 0$  to the left, thereby increasing the equilibrium population density  $H_\infty$  until the resource capacity of the vegetation passes the threshold value  $P_c$  beyond which the system collapses to the stable equilibrium  $(P_\infty(\bar{E}), H_\infty(\bar{E})) = 0$ . The nature of the non-trivial equilibrium  $(P_\infty(\bar{E}), H_\infty(\bar{E}))$  can be studied further when observing the eigenvalues of the associated Jacoby matrix  $F(P_\infty(\bar{E}), H_\infty(\bar{E}))$  of the dynamic system (4) and (5), i.e.

$$d_1 = \frac{hPPT(k_1^2 r_w w_0 + 2k_1 r_w P(t) + (r_w + k_1 u - k_1 u w_0 P(t)^2))}{(k_1 + P(t)^2(r_w + uP(t)))^2} \tag{8}$$

Fig. 3 presents the real part of the eigenvalues of  $F(P_\infty(\bar{E}), H_\infty(\bar{E}))$  for various harvest rates  $\bar{E}$  and corresponding equilibria  $(P_\infty(\bar{E}), H_\infty(\bar{E}))$ . Clearly, for the case PPT = 6, after substituting the parameter values mentioned in the above, the harvest rate  $\bar{E}$  has

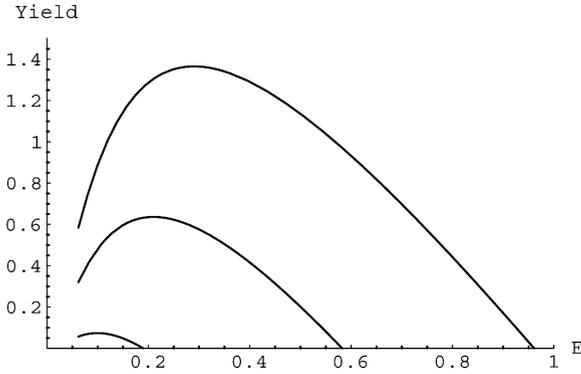


Fig. 4. Yield as a function of the (constant) harvest rate  $\bar{E}$  for three precipitation levels, namely PPT = 15 (top), PPT = 10 (middle), and PPT = 5 (bottom).

to be in the range  $0.062 \leq \bar{E} \leq 0.27$  for the system to be asymptotically stable, i.e. with both eigenvalues smaller than zero. In addition, a harvest rate  $\bar{E} < 0.062$  causes the system to collapse, i.e. the grazing pressure is too high for these cases causing too high a decrease in infiltration of water into the soil.

In Fig. 4 the maximum sustainable yield  $p_H \bar{E} H_\infty$  corresponding with various constant harvest rates  $\bar{E}$  is presented. The effort level  $\bar{E}_{max}$  corresponding to the maximum sustainable yield (MSY) can be observed clearly for the three constant precipitation levels. As the precipitation level decreases, so does the maximum sustainable harvest rate and, in case of PPT = 5, maximum sustainable yield almost leads to extinction of the resource. Extinction occurs at a level  $E_{min}$  below which the harvest rate is too low to survive since the associated grazing pressure is too high – a pitfall in which both the herbivore and plant population density collapses.

#### 4. Dynamic optimization

##### 4.1. Analysis

When assuming a dynamic harvest rate  $E(t)$ , the analysis becomes more complex and needs more elaborate calculations. A current value Hamiltonian  $H$  (Clark, 1976) associated with the discounted pastoralist' yield (6) is defined as

$$H \triangleq -p_H E(t)H(t) + \mu_P(t)\{hW^*(P)P(t) - m_P P(t) - bP(t)H(t)\} + \mu_H(t)\{bgP(t)H(t) - m_H H(t) - E(t)H(t)\} \tag{9}$$

$$H \triangleq \sigma(t)E(t) + \mu_P(t)\{hW^*(P)P(t) - m_P P(t) - bP(t)H(t)\} + \mu_H(t)\{bgP(t)H(t) - m_H H(t)\} \tag{10}$$

where  $\mu_P(t)$  and  $\mu_H(t)$  are the current-value co-states associated with the current value Hamiltonian  $H$ , i.e.

$$\frac{d\mu_P(t)}{dt} = \delta\mu_P(t) - \frac{dH}{dP} \tag{11}$$

$$\frac{d\mu_H(t)}{dt} = \delta\mu_H(t) - \frac{dH}{dH} \tag{12}$$

and  $\sigma(t)$  is the switching function, i.e.

$$\sigma(t) = \frac{dH}{dE} = -(p_H + \mu_H)H(t) \tag{13}$$

Pontryagin's minimum principle, see e.g. (Kirk, 1970), requires that the switching function  $\sigma(t)$  vanishes along a singular arc so that, assuming the non-trivial case  $H(t) \neq 0$

$$\mu_H(t) = -p_H \tag{14}$$

On a compact interval  $[t_1, t_2]$  for which  $\sigma(t) = 0$  differentiation of the switching function allows solution of the second co-state  $\mu_P(t)$ , yielding

$$\mu_P(t) = \frac{p_H(m_H + \delta - bgP(t))}{bP(t)} \tag{15}$$

The current value co-states (14) and (15), together with the current value Hamiltonian  $H$  determine the locus of singular arcs in the  $P$ - $H$  state-space. It is possible to continue differentiating the switching function  $\sigma(t)$  repeatedly, (Bryson and Ho, 1975; Bryson, 1999). Using the values of the co-states as determined in the above, together with the constraint  $d^3\sigma(t)/dt^3 = 0$ , one can determine the optimal harvest rate explicitly as a function of the states  $P(t)$  and  $H(t)$ . The complexity of the obtained expression, however, is beyond the scope of this discussion and therefore not included. Instead, we will follow a more comprehensible route to a solution of the optimal control problem.

Another approach to solving the optimal harvesting problem is to calculate the solution to a finite horizon

optimal control problem numerically using, for example, a gradient search method or, alternatively, a direct optimization method. In the following section we will follow this route and obtain numerical results for two interesting cases with different discount rates  $\delta$ .

4.2. Numerical solution

The pitfall of a vegetation collapse due to overgrazing becomes much more severe in case there is no precipitation. The grazing model then reduces

$$\frac{dP}{dt} = -m_P P(t) - bP(t)H(t) \tag{16}$$

$$\frac{dH}{dt} = b g P(t) H(t) - m_H H(t) - E(t) \tag{17}$$

Of course, management of the grazing system should prevent it from falling into the pitfall of critical depensation as long as possible although, of course, the pitfall will be reached with certainty if the dry period lasts for too long. Since the rainfall intensity may be guessed for the coming rain season one could progress as follows:

Make a guess (based on past experience and statistical records) for the rainfall in the coming season ( $PPT_{exp}$ ) and, given the optimal harvesting rate of the past rain season at  $t = t_0$  and associated optimal equilibrium ( $P(E_{M_{sy}}), H(E_{M_{sy}})$ ), apply a harvest rate  $E(t)$  that guarantees  $P(t_2) > P_c$  where  $t = t_2$  marks the beginning of the new rain season. In addition, we require the recovery of the plant population to the expected new equilibrium ( $P(t_2), H(t_2)$ ) to be swiftly so that optimal harvesting may be performed quickly during the new rain season.

Since both  $t_0$  and  $t_2$ , as well as  $P = P_c$  for the expected rainfall in the new season are known, the problem can be formulated as

$$\begin{aligned} & \max_{E(t) \in \mathbb{E}_{adm}} J(t_2) \\ & = \int_{t_0}^{t_2} \exp(-\delta(t - t_0)) p_H q E(t) H(t) dt \end{aligned} \tag{18}$$

starting from  $(P(t_0), H(t_0))$ , which is known, and recovering to the new (expected) equilibrium  $(P(t_2), H(t_2))$  as quickly as possible. Here,  $\mathbb{E}_{adm}$  represents the set of admissible harvesting rates which are all continuous functions for which  $\forall t : 0 < E(t) < E_{max} = 0.5$ .

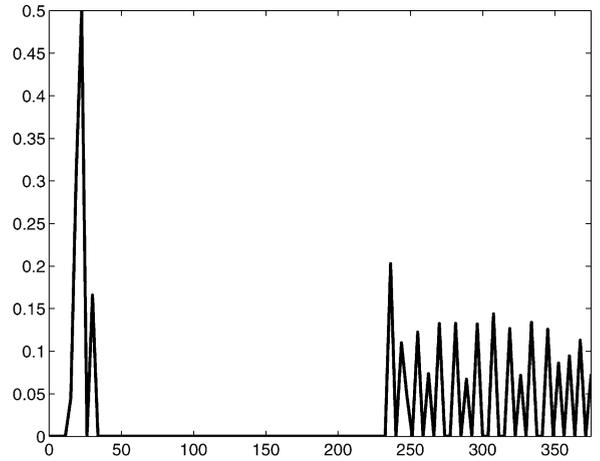


Fig. 5. Optimal harvest rates for a discount rate  $\delta = 0\%$ .

The above optimization problem was solved numerically starting at maximum sustainable yield equilibrium corresponding with a rainfall PPT = 10 until  $t = 10$  days, a dry period of 5 months, and a return equilibrium  $(P(375), H(375))$  corresponding with a maximum sustainable yield for a rainfall PPT = 6. The optimization was *dynamic*, meaning that the harvesting rate  $E(t)$  was explicitly assumed to be time dependent. The harvesting rates were calculated for two discount rates, namely  $\delta = 0\%$  and  $\delta = 3\%$ . The results of the numerical optimization are presented in Figs. 5–8. Clearly, the optimal solution anticipates immediately on the expected dry season by *increasing* the herbivore population just before the dry season start, thereby gaining as much biomass as possible, after which a high harvesting rate is applied to yield biomass just after the dry period sets in. The system is now in ‘survival mode’ meaning that a minimum number of cattle is maintained as to release the grazing pressure as much as possible. Furthermore, note that the plant population recovers just before the critical vegetation density (a constant dashed line in the figure) is reached. Once the rainfall starts again in the new rain season, the harvesting rate remains at zero as to recover both the herbivore and plant population as quickly as possible to the new equilibrium  $(P(t_2), H(t_2))$ . After the 5 months dry period a return to a maximum sustainable yield is maintained after an initial ‘overshoot’ which is clearly visible and the new equilibrium corresponds to the maximum sustainable

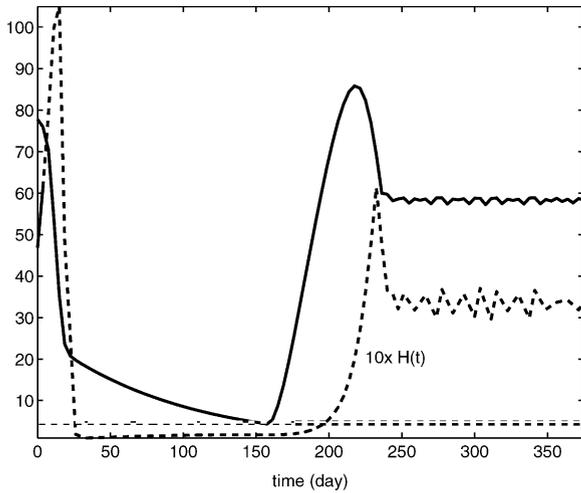


Fig. 6. Optimal state trajectories for herbivores  $H(t)$  and plants  $P(t)$  for a period of 375 days and  $\delta = 0\%$ . The dry period starts after 10 days of maximum sustainable yield at a precipitation level  $PPT = 10$ , i.e. the end of the previous rain season.

yield at a constant rainfall  $PPT = 6$  mm/day. Indeed, the herbivore population is very small at the end of the dry season but just enough to recover optimally to the new equilibrium. Other solutions found with different lengths of dry periods showed qualitatively the same behavior, i.e. harvesting of the herbivores to very small population sizes after which a ‘bang’ of no harvesting ensured maximum growth of the population once the dry season is over. The plant level at day 160, when the new rain season starts, is very low indeed

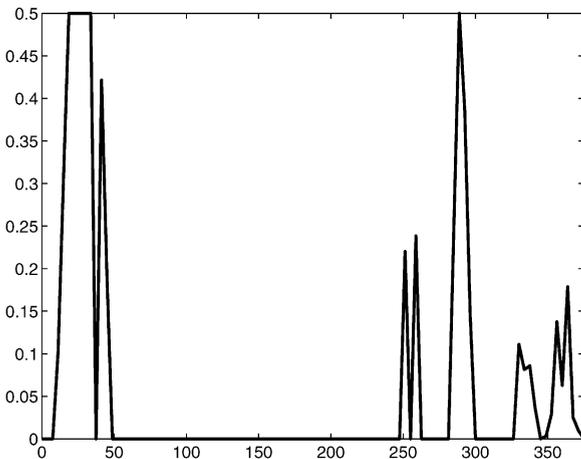


Fig. 7. Optimal harvest rates for a discount rate  $\delta = 3\%$ .

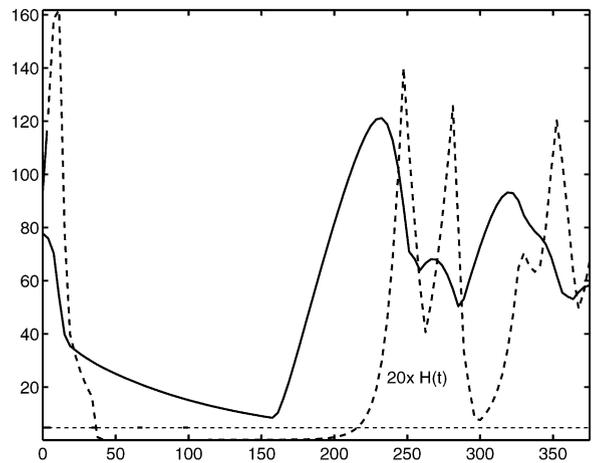


Fig. 8. Optimal state trajectories for herbivores  $H(t)$  and plants  $P(t)$  for a period of 375 days and  $\delta = 3\%$ . The dry period starts after 10 days at a precipitation level  $PPT = 10$ , i.e. the end of the previous rain season.

and for a practical calculation one should consider to increase this level, thereby allowing a safety margin for the optimization.

If the discount rate  $\delta$  is increased slightly, the consequences are quite dramatic for the optimal harvesting rates. Note from Figs. 7 and 8 that the harvesting rates are indeed much more aggressive, meaning that the grazing pressure is released because of a decrease in herbivore population. This decrease is so high that the plant population stays well above the critical vegetation level in the dry season beyond which collapse of the system would occur. Also, the growth of vegetation is much more profound in case of a positive discount rate because of a substantial lower grazing pressure. As said before, one could interpret this behavior in the ‘social willingness’ of the pastoralist to decrease his stock level (meaning less status in the local community!) at a profit of certainty of survival until the next rain season has been reached.

## 5. Conclusion

In this paper, we derive and analyze optimal harvesting strategies in a predator–prey system where the predator is subjected to critical depensation. This specific problem has hardly been addressed in the literature, while the assumption of critical depensation is

certainly a realistic assumption that is often encountered in dynamical behavior of populations in ecosystems. Hence, it is difficult to make a comparison of our results with other studies.

We have proposed a model and have calculated optimal control strategies (assuming a discounted profit for the pastoralist as the goal function) for a pastoral grazing system where there is a risk that the vegetation degrades due to overgrazing and long periods of drought. A static equilibrium analysis showed that maximum sustainable yield can be obtained without an ecosystem-collapse, meaning that both the plant and herbivore population stays well above the critical depensation level ( $P_c$ ,  $H(P_c)$ ) which is exactly the point of intersection of the  $P$ -isocline and  $H$ -isocline.

Extension of the equilibrium analysis, using a constant harvest rate  $\bar{E}$ , to a dynamical optimization study demonstrates that dynamic input profiles can be obtained. These dynamic input profiles, essentially, drive the system to a ‘survival mode’ where the herbivore population is harvested to a minimal size so that the system survives until the new rain season. This optimal harvesting strategy also includes an initial increase of the herbivore population in order to maximize the revenues and to arrive, essentially, at a plant density just above the critical level once the new rain season has started. After this initial increased harvesting effort a period of no harvesting ensures a quick return to a maximum sustainable yield equilibrium, given the assumed constant rainfall  $PPT = 6$ .

Of course, the calculated optimal control policies in this study are debatable since they highly depend on the quality of the model structure, including parameter estimates, as well as the prediction of the start and intensity of the new rain season which are uncertain variables. Qualitatively, however, it was found that the optimal control strategies are similar for a range of realistic parameter values.

An interesting possibility to increase the chance of survival of the ecosystem in the current model setting is to increase the discount rate on the current value capital of the herd. The use of the discount rate for such a purpose is rather unusual since the discount rate affects the plant population *indirectly* via the increase/decrease of grazing pressure, imposed by a herd of cattle on the pastures. It was found that a discount rate of 3% already influences the dynamical behavior substantially and leads to higher vegetation densities,

lower herbivore densities, and a higher safety margin with regard to the critical vegetation level beyond which extinction occurs. Of course, the price that has to be paid for this is a smaller profit in comparison with less aggressive policies causing higher grazing pressures. Indeed, the manager needs to balance his desire for a high ‘social status’ in the community with the laws of survival and sustainable management.

#### List of symbols

$b$	consumption rate of plants to herbivores (gP/(gH d))
$g$	rate of increase of herbivore biomass due to consumption of plant biomass (gH/(gP d))
$h$	rate of increase of plant density due to precipitation (1/mm d)
$m_H$	natural mortality rate of herbivores (1/d)
$m_p$	natural mortality rate of plants (1/d)
$r_w$	the specific loss rate of soil water due to evaporation and percolation (1/d)
$u$	uptake coefficient related to the uptake of water by vegetation (m <sup>2</sup> /g d)
$E$	harvesting effort (1/d)
$H(t)$	herbivore density (g/m <sup>2</sup> )
$P(t)$	vegetation density (g/m <sup>2</sup> )
PPT	precipitation (mm/d)
$W^*(P)$	water availability (as a function of plant density) (mm/m <sup>2</sup> )

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