A MODEL OF A RANGELAND GRAZING SYSTEM WITHIN A MANAGEMENT PROCEDURE APPROACH FRAMEWORK

Ecology honours project

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Abstract

A model describing livestock grazing system dynamics was developed and fitted to available data. This study preliminarily explored the use of a formal management procedure (MP) approach to determine appropriate annual offtake in a terrestrial system. This approach has been applied in marine systems with great success, but has never been tried in terrestrial ecosystems. Rangelands and marine systems have in common the fact that there is often an offtake component to them and so stakeholders in those systems need knowledge of optimal harvesting strategies within defined management strategies. Three models were developed that described the growth of female goats in Paulshoek. The first (basic livestock model) depicted the growth of livestock as a logistic equation with an adult survival term and an annual growth term. The second model (rainfall-livestock model) added a rainfall component, with livestock productivity modelled as a function of rainfall. The final version of the model (vegetation-rainfall-livestock model) added a vegetation component that interacted with rainfall and livestock. The rainfall-livestock model provided a statistically significant better fit to the data, followed by the vegetation-rainfall model. The vegetation-rainfall-livestock model provided a reasonable representation of livestock population changes through time, with the largest deviations evident over the period 1975-1980. Results show that environmental factors alone are unable to fully explain observed system dynamics because anthropogenic factors for which no data are available may also play a role. Preliminary exploration with a simple MP suggested that a low offtake rate of 10% provided the highest average annual offtake. Our study has shown that a rangeland stocking system can be reasonably described by a simple model that uses only rainfall data and a rainfall-vegetation-livestock interaction. Rangeland livestock systems would benefit greatly from adopting an MP approach as it would allow stakeholders to make informed decisions on stocking rates and annual offtake.

Introduction

The succulent Karoo is one of the world's most diverse arid ecosystems, with almost 5000 species of plants, 40% of which are endemic (Milton *et al.* 1997). One of the most distinguishing features of this ecosystem is the high proportion of leaf succulents, especially from the Mesembryanthemaceae family (Milton *et al.* 1997), an unusual feature for arid ecosystems. The species richness and the high level of endemism has resulted in the succulent Karoo being recognised as a biodiversity hotspot (Myers *et al.* 2000), the only arid ecosystem to deserve such a distinction.

Namaqualand, where the succulent Karoo is found, is home to over 60,000 people (Hoffman and Rohde 2007) that depend on livestock farming for their livelihood. Conservation of this ecosystem and the use of the land by the local people are often seen as opposing forces and there have been many studies analysing the impacts of livestock production on biodiversity in the succulent Karoo (Todd and Hoffman 1999, Riginos and Hoffman 2003, Benjaminsen *et al.* 2006, Anderson and Hoffman 2007). Some studies (Todd and Hoffman 1999, Riginos and Hoffman 2003) have found that there is a decrease in palatable shrub species with increasing grazing pressure, as well as an increasing dominance of the unpalatable shrub *Galenia africana*. However, a more recent study by Anderson and Hoffman (2007) failed to find a decrease in species richness due to heavy grazing, although it did detect a compositional shift from larger, woody and succulent shrubs to smaller shrubs and perennial herbaceous plants. According to Todd and Hoffman (1999), such a shift can result in increased vulnerability of livestock to drought conditions. This is because although herbaceous plants are usually more palatable than woody plants, they tend to be shallow rooted and thus more vulnerable to drought (Todd and Hoffman 1999) so, in years of bad rainfall, they may be completely absent.

One of the ways of testing the impact of different management decisions is to use models. Models can be powerful analytical tools that allow different hypothetical scenarios to be tested. One important application of models is in studying population dynamics, such as predator-prey interactions and density dependent growth. In addition, models can assist in providing management advice by showing the response of a population to different management strategies. There are two extremes when considering an ecological modelling approach (after Gilman and Hails (1997)). The first is to identify and measure all the factors that affect the population of interest (mechanistic models). Mechanistic models seek to explain the processes occurring in a system by dividing it into its components and analysing the behaviour of the whole system in terms of its individual components and their interactions with one another. At the other end of the spectrum we have empirical models that attempt to describe the patterns by using available data directly to quantify relationships. Statistical population dynamics models estimate population parameters by fitting to available data. The approach used here seeks to broadly capture the major features of the system dynamics without explicitly including all the detailed underlying mechanics

There have been several attempts to model rangeland ecosystem dynamics. Milton *et al.* (1994) developed a conceptual model which predicted that overgrazing can lead to irreversible losses in productivity in arid rangelands. Plant *et al.* (1999) developed a spatial state-and-transition model which depicted the dynamics of a rangeland in Sierra Nevada. Their model analysed rangelands at the scale of individual paddocks and was able to explain the vegetation dynamics of the system. A spatially explicit simulation model representing the life history of five dominant plants in the Karoo was developed by Wiegand *et al.* (1995). They showed that the vegetation dynamics in this system are characterized by "episodic and discontinuous changes" and grazing has a large impact on recruitment.

The models described above have dealt mostly with the interactions among the major plant groups and have not explicitly modelled the effects of herbivores. Rangelands are often used for livestock farming, so being able to predict the effects of grazing is particularly important. The interaction between livestock, vegetation and rainfall in Paulshoek was recently described in two models. First, a short-term mechanistic model that simulated the system was developed (Richardson and Hahn 2007). The vegetation was divided into four guilds (woody perennials; leaf succulents; *G. africana;* and annuals and geophytes) with palatability, response to rain and competition parameters determined for all of them. Second, a long-term model (Hahn *et al.* 2005) was developed using the output of the short-term model to predict the changes in livestock numbers and vegetation cover over time.

Management procedures (MP) are a predictive framework that utilise collected data to test different models of population dynamics, according to specified objectives (Butterworth and Punt 1999). These can be, for example, maximizing annual sales or decreasing annual variability in stock to avoiding collapse of the resource (Rademeyer *et al.* 2007). MPs use Operating Models (OM), which are statistical models used to describe population dynamics and predict future behaviour (Rademeyer *et al.* 2007). Several OMs that depict different (plausible) scenarios of population dynamics are often used, in order to account for uncertainties in the model. OMs are assumed to provide a realistic representation of the system dynamics and used to simulation test different management options (Rademeyer *et al.* 2007).

A model that describes the dynamics of the Paulshoek livestock system is already available (Hahn *et al.* 2005), but it is a detailed mechanistic model with a very high level of complexity. The objective of this study was to determine whether that system could be explained with a much simpler model that was fitted to available data. To achieve this we started with a simple logistic equation depicting annual growth of female goats (does) and gradually added complexity to determine what level of detail is needed to explain the observed data. Rangelands are often used for grazing of livestock, with an offtake component (Berzborn 2007) which can be equated to harvesting of fish populations in a marine ecosystem. The second part of this study involved preliminary explorations with an MP approach to determine the best rate of offtake based on a projection of the livestock population 20 years into the future.

Study area

Paulshoek is a village in the Leliefontein rural district of Namaqualand (30°24'S; 18°08'E), in the Northern Cape Province. Most inhabitants depend on livestock farming of goats and sheep. Paulshoek occupies about 20 000 ha and is located on the eastern escarpment of the Kamiesberg, at an altitude of approximately 1000 m above sea level. It has winter rainfall (annual rainfall between 150-250 mm) but very high seasonal and annual variation (CV of MAR is 39%). The land has been under communal tenure since the early 19th century although Paulshoek itself was first settled in the early 1900s. The surrounding lands are privately owned and have much lower stocking rates. This has permitted several studies on the effects of different stocking rates on the vegetation.

The vegetation in Namaqualand forms part of the succulent Karoo biome, with deciduous shrubs, succulent perennials and geophytes forming the major plant groups (Todd and Hoffman 1999). Under heavy grazing, the unpalatable shrub *G. africana* tends to increase in abundance, especially at the expense of the succulents (Todd and Hoffman 1999). Most herds in the region are composed of goats and sheep (Hendricks 2004) and the farmers adopt several herding strategies, but will usually release the herds in the morning and return them to the stockposts in the afternoons (Samuels *et al.* 2007).

Methods

Data

The observed data on rainfall and livestock numbers (Table 1) were obtained from monthly records of livestock numbers in the Paulshoek area, from 1971 to 2000 (Hoffman, unpublished data). Sheep and goats have differing birth and survival rates (Hahn 2005) so, for reasons of simplicity, this study focuses only on goats. From 1971 to 1998, the data consists only of goat and sheep numbers. From 1998 onwards, there is data about the different size classes (kids, weaners, does, castrated males and rams). The number of does was calculated by averaging the ratio of their abundance from 1998-2006 and then multiplying this value by the goat numbers for each year.

Offtake was obtained from the output of the Hahn *et al.* (2005) model. In their model, Hahn *et al.* (2005) had offtake numbers for all livestock, so these were transformed into number of does by multiplying offtake numbers by the ratio of goats/sheep and does/total of goats.

An important observation pertaining to the observed data is that they contained some years (1972, 1975 and 1982) in which the livestock population more than doubled, something which should not be possible even under perfect environmental conditions.

The maximum annual growth rate of does (with no adult or juvenile mortality and maximum reproductive rate) is 55%. Thus, for at least 3 years (1972, 1975 and 1982) the census was not accurate. To account for this inaccuracy, for the three years where growth rate exceeded the maximum possible value, a purchase term was introduced (Richardson, pers. comm.), so that growth rate for that year was 55%.

Model description

Basic livestock model

The basic discrete model used to represent the population dynamics of the adult female goats is:

$$N_{y+1} = N_y S + (N_{y-T+1}) q_f p . S_j . S^{T-1} - H_y \qquad (1)$$

where:

Ny is the number of mature adult females on "counting" day,

S is the post first-year survival rate,

T is the average age at first breeding,

p is the reproductive rate in year y,

q_f is the fraction of kids that are female,

S_j is the annual survival rate of juveniles from when they are born to the end of their first year, and

H_y is the annual offtake in year y.

Table 1: Paulshoek rainfall, livestock and offtake data used in the model (from Hahn *et al.* (2005)). Annual growth rate also included. For some years there is no livestock data (ND) available.

Year	Rainfall (mm)	No. of does	Offtake	Growth rate (%)
1971	200	1050	-667	-
1972	165	2295	188	118.6
1973	134	1563	281	-31.9
1974	218	1363	-183	-12.8
1975	192	2296	224	68.5
1976	335	2513	314	9.5
1977	240	2910	380	15.8
1978	106	2318	377	-20.3
1979	116	892	102	-61.5
1980	190	811	76	-9.1
1981	178	890	-435	9.7
1982	200	1814	124	103.8
1983	276	ND	138	-
1984	109	2020	198	-
1985	199	2029	228	0.4
1986	209	ND	242	-
1987	172	2199	253	-
1988	151	ND	274	-
1989	175	1516	282	-
1990	160	ND	344	-
1991	228.9	1582	359	-
1992	189	ND	339	-
1993	291	ND	365	-
1994	212.3	ND	281	-
1995	263	ND	335	-
1996	375.5	1537	296	-
1997	161.0	1864	254	21.3
1998	61.5	1174	376	-37.0
1999	166	965	18	-17.8
2000	177.3	1312	15	36.0

This model is a discrete growth equation, where *Ny* represents the number of adult females on the counting day. The first term represents the number of mature individuals that survived from the previous year, while the middle term is the growth function.

Several parameters were fixed, based on available information. Average age at first breeding (T) was set to one. Ewes can start breeding before they are one year old, but as this is a discrete model, one year was considered an adequate approximation. N_{y-T+1} is the number of females T years ago. An even sex ratio at birth (q) was assumed. Pregnancy rate (p) was determined by calculating the ratio of kids to ewes in the month of October, from the 1998 to 2006 records. This month is usually when the number of kids is at their highest. Pregnancy rate is an extremely variable term (0.02-1.11 (Hoffman, unpublished data), but the average value (0.6) from 1998-2006 was used in the basic livestock model. Juvenile survival (S_j) was obtained from the output of Hahn *et al* (2005). The average value over the period of 1971-2000 was used. The only parameter to be estimated in the basic livestock model is adult survival (S). It was restricted to values between 0 and 1, to ensure biologically realistic estimates. A summary of the parameter values is given in Table 2.

Table 2: Parameter values used in the model (Hahn *et al.* 2005).

Parameter	Value
Age at first pregnancy (years)	1
Average reproductive rate	0.6
Fraction of kids that are female	0.5
Average annual survival rate of juveniles	0.7
Maximum reproductive rate	1.1
Maximum survival rate of juveniles	0.98

Sensitivity analysis

A sensitivity analysis was conducted to determine what parameters the model is most sensitive to and whether the model results are robust to parameter uncertainty. Two parameters were tested, namely S and S_j. Of the other three parameters, age at first pregnancy and sex ratios are well determined, whereas changing pregnancy rate has the same effect as changing juvenile survival, as they both affect the same term (growth), and hence only juvenile survival was used in the sensitivity analysis. The values were changed by ±5% and the change in the ratio of *N(2000)/N(1971)* i.e. the current depletion level, was evaluated.

Rainfall-livestock model

The basic livestock model sets growth rates to the average value for each time step. However, it is known that rainfall is one of the critical factors affecting livestock because of its effect on vegetation (Hahn *et al.* 2005, Richardson *et al.* 2005). The rainfall-livestock model adds a term (RF_y) which modifies growth based on the amount of rain of each year. The model can be represented as follows:

$$N_{y+1} = N_y S + (N_{y-T+1}) q_f p.RF_y.S_j.S^{T-1} - H_y \qquad (2)$$

with RF determined by:

$$RF_y = (0.01 * e^{(0.03 * R_y)})/(1 + 0.01 * e^{(0.03 * R_y)}) \qquad (3)$$

where:

RF_y is the rainfall effect in year y, and

R_y is the observed rainfall (mm) in year y.

The shape of the *RF* curve was initially tested as a negative exponential curve. However, a sigmoid shaped curve (Figure 1) was found to provide a better representation of the effect of rainfall on livestock. At very low rainfall values, livestock growth will be severely impaired. The response to increasing rainfall decreases as rainfall increases above 180 mm. This relationship between rainfall and livestock is much more realistic than a steady increase in growth rate with increasing rainfall. This model scales the growth rate of livestock according to rainfall. Reproductive rate and juvenile survival are set to the potential values and so growth becomes a function of rainfall (through the *RF* term).

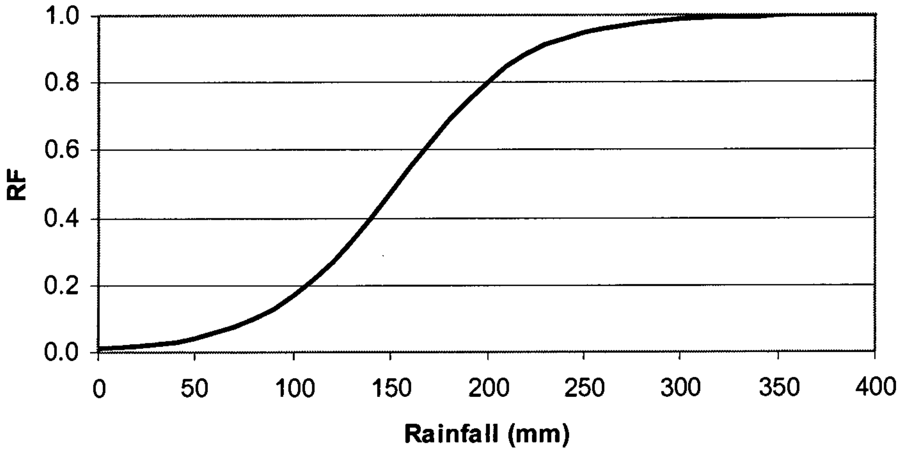

Figure 1: Model formulation of the change in the effect of rainfall on livestock growth (*RF*) with increasing rainfall.

Vegetation-rainfall-livestock model

The next step in the modelling process was to add an explicit vegetation equation. The vegetation term represents the amount foliage left as a proportion of maximum foliage density. Vegetation is affected both by rainfall (through the *RF* term) and by livestock abundance. Livestock growth is now a function of the vegetation instead of rainfall. The two equations developed in this study to represent livestock and vegetation are as follows:

$$N_{y+1} = N_y S + (N_{y-T+1}) q_f p.S_j VF_y .S^{T-1} - H_y \qquad (4)$$

$$Veg_{y+1} = Veg_y + r_{veg} Veg_y \left(1 - \left(\frac{Veg_y}{1}\right)\right) - \frac{\lambda \mathrm{N_y V_y}}{\mathrm{V_h} + V_\mathrm{y}} \qquad (5)$$

with

$$VF_y = 1.01 - 1.3 * \mathrm{e}^{(-3.5*\mathrm{Veg(i)})} \qquad (6)$$

$$rveg_y = 0.8 * RF_y \qquad (7)$$

and

$$RF_y = 1 - 1.15 * e^{(-R_r * 120)} \qquad (8)$$

where:

VF_y is the effect of the vegetation on livestock growth in year y

Veg_y is the vegetation cover in year y,

$rveg_y$ is the growth rate of the vegetation,

λ is the maximum per capita rate of vegetation consumption by the livestock, and

V_h is the level of vegetation cover at which per capita livestock consumption drops by 50% of the maximum.

The livestock equation is similar to that of the rainfall-livestock model, except that a vegetation function is used instead of the rainfall function (Figure 2). The vegetation equation is a discrete logistic growth equation, where the last term represents the rate at which livestock eat the vegetation (based on the formulation in Mori and Butterworth 2004). This model adds another estimated parameter, λ. V_h was set at 0.1. Consumption rates of livestock remain high even when fodder is reduced to very low levels, as the herds are moved to the locations where fodder is still available

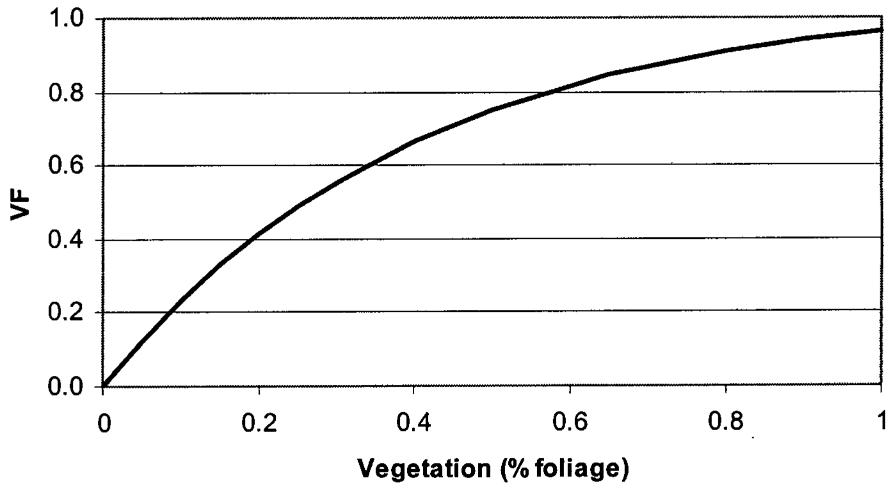

Figure 2: Effect of vegetation cover on livestock growth function (*VF*).

Management procedure

Preliminary simulations using a management procedure approach were attempted using the vegetation-rainfall-livestock model as the OM, assuming for current purposes that the coupled rainfall-vegetation-livestock equations provide an adequate representation of the system's dynamics. Simulated rainfall data was created, with the same mean and standard deviation as the dataset from 1971-2000 (mean=195mm, standard deviation=66.3mm). This dataset contained 100 sets of 20 years of rainfall data and was used to project the livestock population from 2000 to 2020. Starting values of *Nmod* and *Veg* were obtained by setting these to the final values from the vegetation-rainfall-livestock model. The same parameter values were used as those used in the vegetation-rainfall-livestock model and the survival rate parameter was set to the best fit value obtained. 20-yr projected trends in the livestock population under three constant offtake rates (10%, 15% and 20%) were then evaluated with two main objectives in mind. Having the highest annual offtake possible and preventing livestock population numbers from dropping to zero. The projected livestock populations were presented as probability envelopes. These give a better representation of the uncertainty in the model than point estimates (such as median).

Model fitting procedure

The coding was done in AD Model Builder (ADMB) (AD Model Builder^{TM}, Otter Research, Ltd.). ADMB is a program that performs nonlinear minimisation with a computational speed that is likely to be unmatched by any other software currently available. In addition, it has useful features such as imposing boundaries on parameters (akin to a prior in Bayesian estimation) and performing parameter estimation in several steps.

The livestock counts are assumed to be log-normally distributed indices of the total numbers of adult goats such that:

$$I_y = \hat{I}_y e^{\varepsilon^S{}_y} \qquad \text{or} \qquad \varepsilon_y = \ln(I_y) - \ln(\hat{I}_y) \qquad (9)$$

where:

I_y is the observed count (expressed in terms of females only) for year y,

$\hat{I}_y$ is the corresponding model estimated value, as given by Equation (1), and

ε_y from $N(0,(\sigma^s{}_y)^2)$.

The negative of the log likelihood function (after removal of constants) is computed as:

$$-\ln L = n\ln(\sigma) + \frac{n}{2} \qquad (10)$$

with

$$\sigma = \sqrt{\left[\sum_{y=1}^{n}(\ln I_y - \ln \hat{I}_y)^2\right] \Big/ n} \qquad (11)$$

where:

n is the number of years for which there are data.

Model selection

Akaike's Information Criterion (AIC)

In order to choose between different models, Akaike's Information Criterion (AIC) was used (Burnham and Anderson 1998). The choice between two models is dependent on the fit of the model (sigma) and the number of parameters that the model is estimating. Thus, complex models have to provide a significantly better fit than simpler models in order to be preferred.

$$AIC = n\log(\sigma^2) + 2K \qquad (12)$$

Where:

n: sample size,

σ: Estimate of sigma, and

K: number of estimated parameters.

Results

All three models had similar trends in the fit to the data (Figures 3-5). The rainfall-livestock model gave a statistically significant better fit to the data (L=135.966) than the vegetation-rainfall-livestock model (L=141.982), while the vegetation-rainfall-livestock model gave a significantly better fit than the basic livestock model (L=147.305). Although rainfall is a very important factor affecting livestock population numbers, it is clearly not the only one. In the period of 1971-1990 livestock populations seem to track the rainfall fairly well. However in the period of 1991-1996, when rainfall was unusually high, livestock numbers remained relatively constant. Possible reasons for this are explained in the discussion section. The fit of the Hahn *et al.* (2005) model (Figure 6) was considerably different from the three models developed here. Their detailed mechanistic model was better able to track the livestock population numbers for the period of 1971-1990, especially the extreme changes from 1975-1980, but could not capture the variation in the last 10 years effectively. Preliminary trials with the vegetation-rainfall-livestock model could not appropriately describe the interaction between vegetation and livestock. The best fit of the model was always when the consumption rate parameter (λ) was estimated to be very low, so that livestock had a minimal effect on vegetation. If this parameter was set to be higher, it invariably resulted in the vegetation term being reduced to zero, followed by the livestock population crashing. Thus, vegetation was unaffected by livestock density, although livestock numbers still depended on vegetation cover.

The model was not very robust to a change in parameter values. For either *S* or *Sj*, a decrease of 5% led to the population crashing to 0. Looking at an increase of 5% in parameter values revealed that the model was much more sensitive to *S* than to *Sj*. In both cases, however, an increase of 5% caused population numbers to go above any historical records.

None of the three models had any severe biases in the estimation of livestock population numbers (Figures 7-9). However, a common trend to all models was the underestimation of high population numbers and the overestimation of low population numbers. This is not an unexpected trend however, as the model tries to capture the trend in data, resulting in a tendency to "prefer" an average value between several high and low numbers.

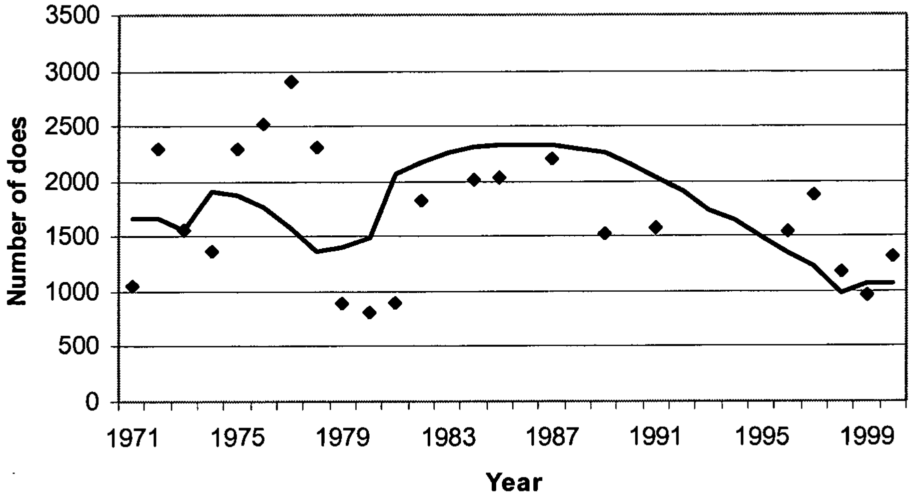

Figure 3: Basic livestock model prediction of doe population (black line). Observed values indicated by dots.

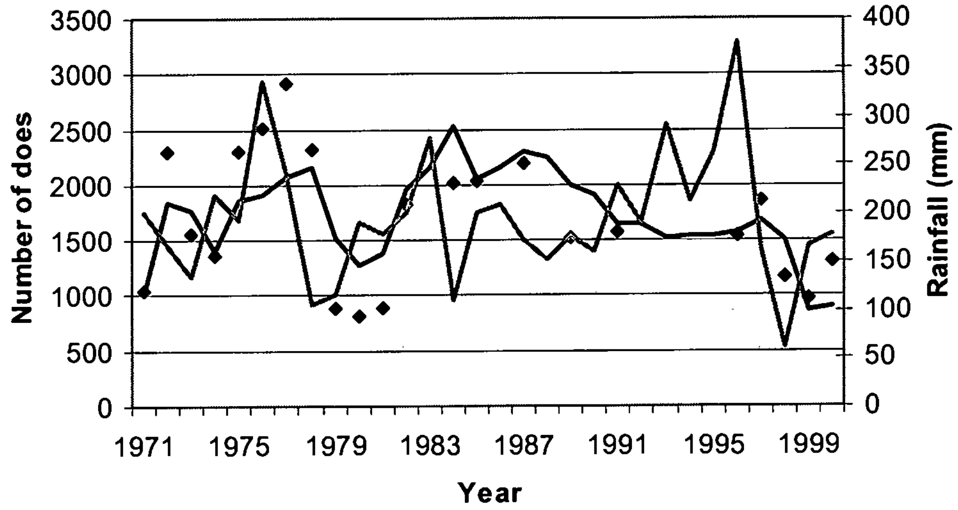

Figure 4: Rainfall-livestock model prediction of doe population (black line). Annual rainfall indicated as a grey line, observed values for does indicated by dots

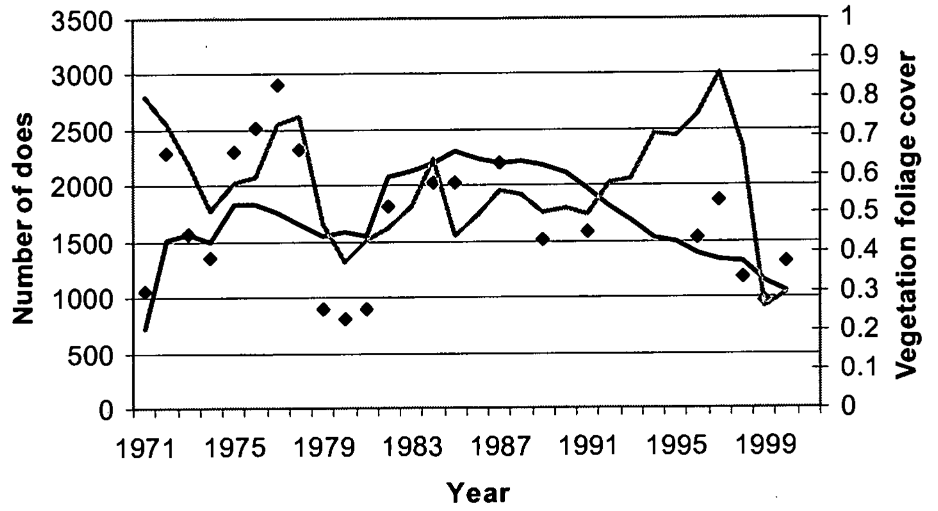

Figure 5: Vegetation-rainfall-livestock model prediction of doe population (black line). Proportion of remaining vegetation foliage cover indicated as a grey line, observed values for does indicated by dots.

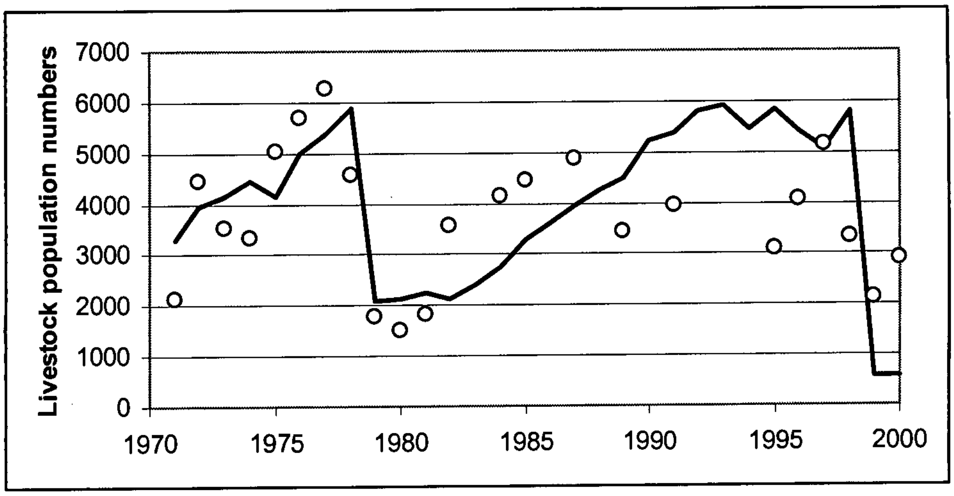

Figure 6: Plot of livestock numbers (white dots) and the Hahn *et al.* (2005) model prediction (black line). Livestock number included all goats and sheep in Paulshoek (from Hahn *et al.* 2005).

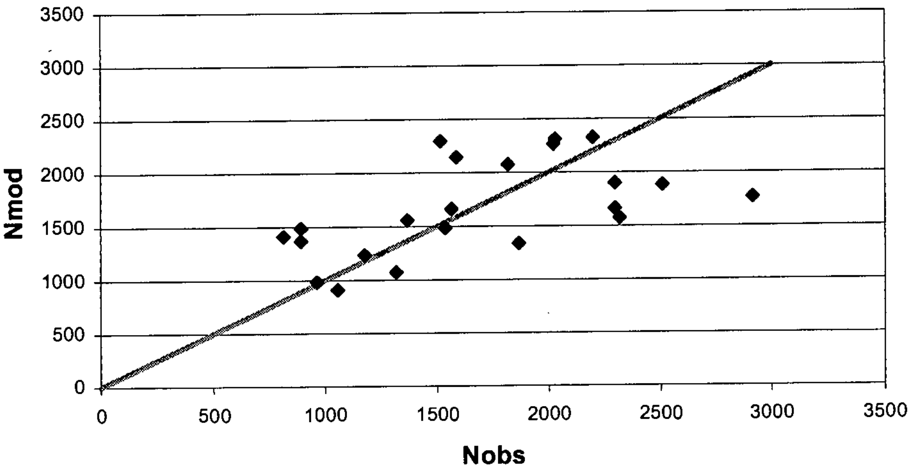

Figure 7: Plot of the modelled versus the observed livestock values for the basic livestock model.

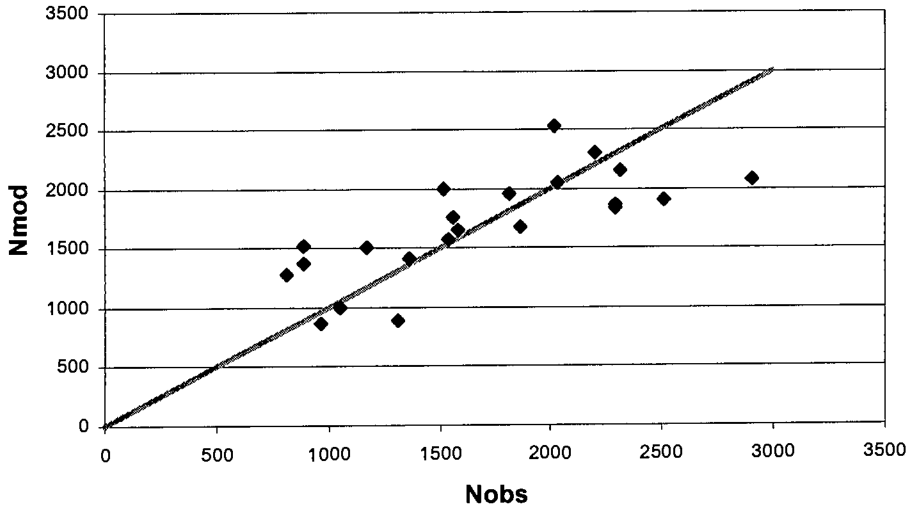

Figure 8: Plot of the modelled versus the observed livestock values for the rainfall-livestock model.

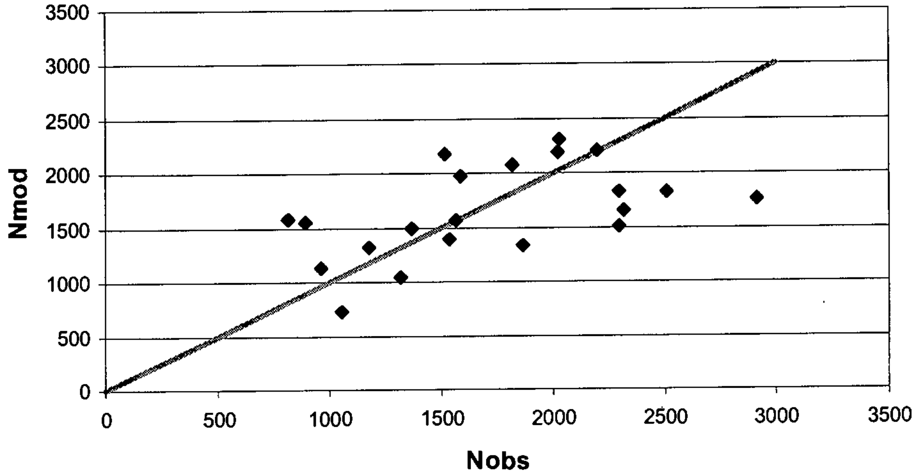

Figure 9: Plot of the modelled versus the observed livestock values for the vegetation-rainfall-livestock model.

Management Procedure preliminary results

The OM predicts that the highest average annual offtake will occur under a catch rate of 10% (Table 3). The probability envelopes (Figure 8) show that the population will very likely increase and probably double in 20 years. The high standard deviation under this offtake rate is a result of this constant increase in population numbers. At an intermediate offtake (15%) the probability envelopes show (Figure 9) that the population is very likely to decrease, although the most likely scenario is that it remains stable, at 80% of the 2000 population. Under the highest offtake rate (20%) livestock population is predicted to decrease by at least 60% (Figure 10), leading to the smallest offtake of all three scenarios.

Table 3: Average annual offtake under different harvest rates. Standard deviations are indicated.

Harvest rate	Average annual offtake
10%	127±39.4
15%	114±10.8
20%	97±35.4

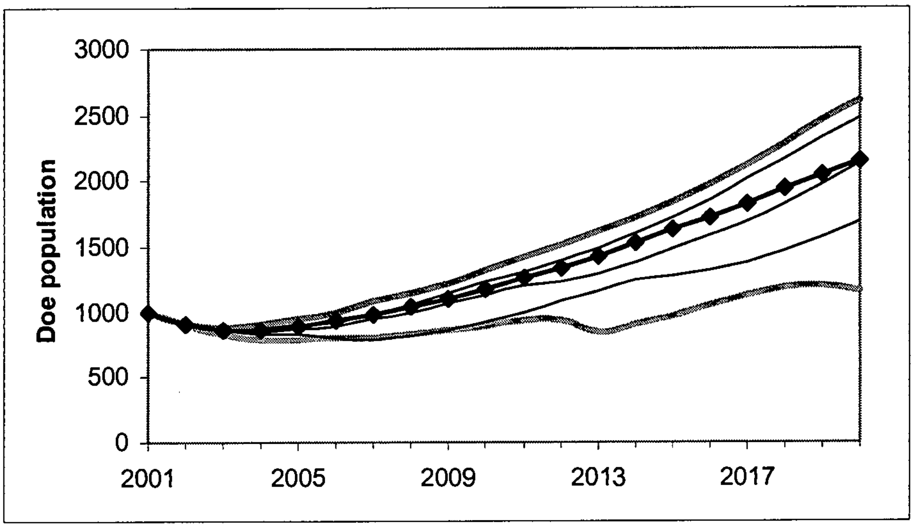

Figure 8: Projection of the doe population under a constant harvest rate of 10%. Three individual trajectories are shown, with a black dotted line indicating the median and the thick grey lines showing the 90% probability envelopes.

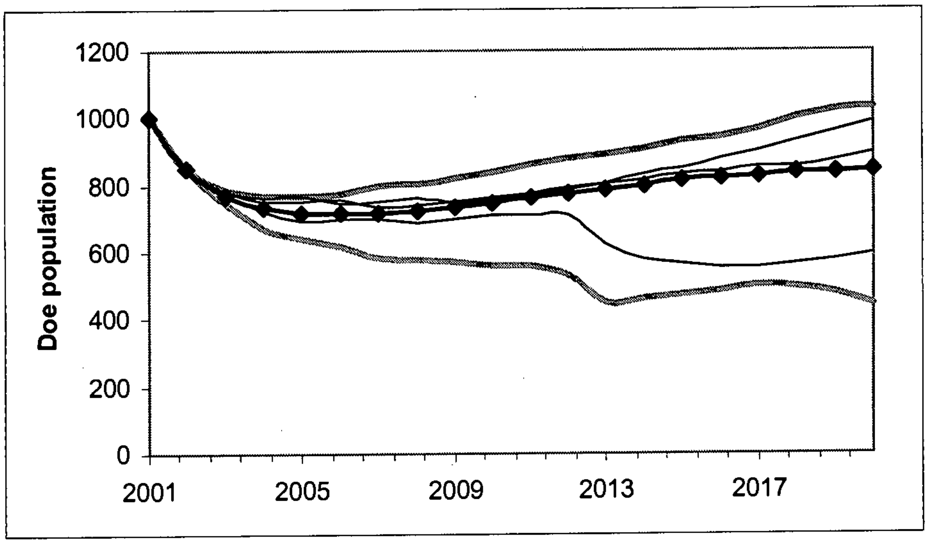

Figure 9: Projection of the doe population under a constant harvest rate of 15%. Three individual trajectories are shown, with a black dotted line indicating the median and the thick grey lines showing the 90% probability envelopes.

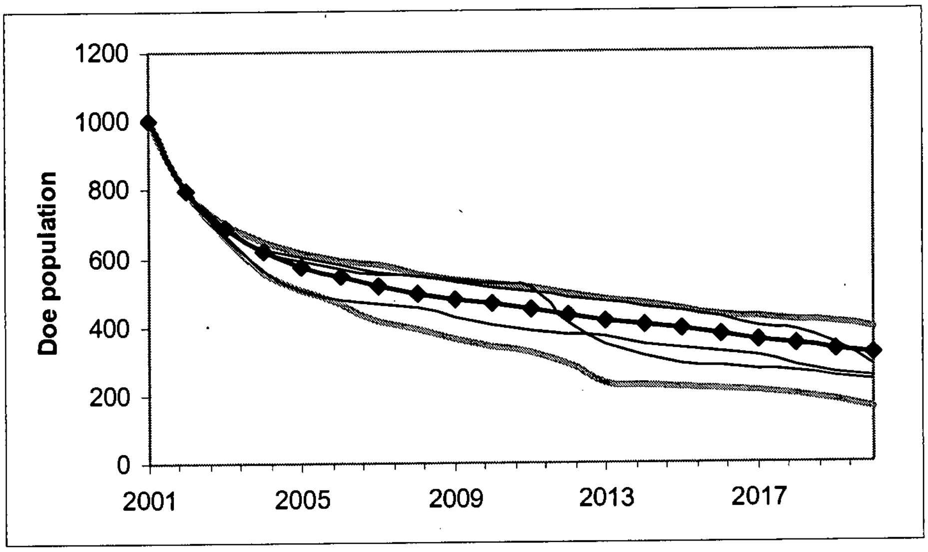

Figure 10: Projection of the doe population under a constant harvest rate of 20%. Three individual trajectories are shown, with a black dotted line indicating the median and the thick grey lines showing the 90% probability envelopes.

Discussion

Several models that attempt to explain the dynamics of rangeland systems have been developed, ranging from conceptual (Milton *et al.* 1994), to spatially explicit, state-and-transition models (Plant *et al.* 1999), to mechanistic models (Hahn *et al.* 2005). The aim of the model developed in this study was to explain the variation in livestock numbers with the fewest parameters necessary by fitting our model to the recorded livestock population data. The three models of increasing complexity that were developed were able to provide a reasonable representation of observed changes in goat numbers over most of the time period for which data were available. However, in the period of 1975-1980, the models were unable to capture the rapid increase followed by a steep decline of the population. The population increases of 1972, 1979 and 1982 could not have been achieved even under perfect environmental conditions. This could have been caused by animal purchases, which happen in years of high mortality (Richardson and Hahn 2007). Unfortunately, these records are not available and so we are unable to correctly model the changes that occur in those years. Another reason for the unrealistically large changes in population numbers may have to do with the quality of the census data. There could have been a change in the scope of the census, so that more stockposts were included in the later years.

Livestock population numbers in the communal farms of the Namaqualand region are highly dependent on the amount of available fodder (vegetation cover), which in turn is related to annual rainfall (Hahn *et al.* 2005, Richardson *et al.* 2005). However, several anthropogenic factors affect this relationship. A carrying capacity for the region has been defined by the Department of Agriculture meaning that livestock herders are encouraged to keep their herds below a certain number (Benjaminsen *et al.* 2006), regardless of veldt condition or rainfall. In addition, as previously stated, livestock purchases following years of high mortality allow for unrealistically high growth rates. In summary, the Paulshoek herding system is subject to several forces that alter the expected dynamics of the livestock populations. Baker and Hoffman (2006) for example, found that social reasons were often as important as ecological ones in motivating herders to move stockposts. These anthropogenic effects make it extremely difficult to model the behaviour of the livestock population with respect to environmental factors (rainfall, vegetation) only.

The effect of grazers on vegetation in arid ecosystems is a contentious issue. The original equilibrium concept theory (Dyksterhuis 1949) that range condition varies along a continuum of reversible states has been strongly contested. Many authors consider that the carrying capacity concept cannot be applied in arid ecosystems and that changes in vegetation are mostly a response to rainfall (Friedel 1991, Lockwood and Lockwood 1993). However, recent studies (Fernandez-Gimenez and Allen-Diaz 1999, Hahn *et al.* 2005, Richardson *et al.* 2005) have shown that rangeland ecosystem dynamics are complex and that vegetation responds both to rainfall as well as stocking rates. Under this framework, the way that the vegetation-rainfall-livestock model depicts the relationship between vegetation and livestock can be described as a possible scenario. The effect of livestock on vegetation is far from contentious with some studies arguing for (Todd and Hoffman 1999) and others against (Benjaminsen *et al.* 2006, Allsopp *et al.* 2007).

The vegetation-rainfall-livestock model developed in this study was an attempt to describe the dynamics of a rangeland system using a methodology that has been widely used in marine systems. This very simple model was able to explain a reasonable amount of the variation present in the data. However, the vegetation component could be represented in such a way as to make grazing detrimental to it. One way to improve the vegetation-rainfall-model could be to examine other shapes of relationship curves. For the rainfall model a sigmoid relationship between increasing rainfall and livestock growth provided a better fit to the model than a negative exponential curve. It is possible that the relationship between either rainfall and vegetation or vegetation and rainfall could be better explained by using a different curve. Another factor to take into account is the meaning of the vegetation component. It was defined as the proportion of maximum foliage present. However, it could have had a different interpretation, such as the density of individuals. This would have resulted in completely different effects of grazing. If the vegetation component is perceived as the amount of foliage left, then grazing will cause high "mortality" as it effectively reduces the availability of foliage. In addition, plants will have very high growth rate, as it will reflect the growth of new leaves. A vegetation component that considered individual plants would mean that mortality would be lower, but also that growth rates (recruitment) would also be much slower

Management Procedure

The MP analysis revealed that the best harvesting scenario, in terms of annual offtake was with the lowest offtake rate (10%). This was due to the fact that the population increased under this scenario, whereas for the other two scenarios, it either remained stable at slightly lower than present levels (H=15%) or decreased considerably (at H=20%). There are several aspects that limit the application of the MP with confidence. First, the offtake scenarios that were tested were very simple. A constant rate of offtake does not allow for population recovery if the rate is too high, or for population growth curbing, if it is too low. Ideally we would have an offtake rate that was dynamically adjusted as the population numbers varied, so as to keep the population within certain limits, while ensuring a reasonable offtake. Second, the vegetation-rainfall-livestock model was not very robust to errors in parameter estimation, which decreases the confidence in its predictions. Finally, the recommended offtake rate of 10% predicted that the livestock population would increase for the 20 year period, to levels well above present. However, such high stocking rates would probably cause a severe reduction in available fodder. This is something that the model could not capture, but any management recommendations would have to take into account this limitation.

This study attempted to develop a simple model that explained livestock population numbers in an arid rangeland in an MP framework. We succeeded in our first objective as the models that included a rainfall component provided a good representation of the livestock population changes over the period for which data was available. The use of an MP approach in a terrestrial system is something that had not been tried before. Rangeland livestock systems would benefit from such an approach as it would allow stakeholders to make informed decisions on stocking rates taking into account their management objectives.

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