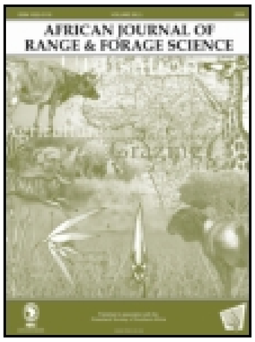

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Modelling the complex dynamics of vegetation, livestock and rainfall in a semiarid rangeland in South Africa

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Predicting the effect of different management strategies on range condition is a challenge for farmers in highly variable environments. A model that explains how the relations between rainfall, livestock and vegetation composition vary over time and interact is needed. Rangeland ecosystems have a hierarchical structure that can be described in terms of vegetation composition, stocking rate and rainfall at the ecosystem level, and the performance of individual animals and plants at the lower level. In this paper, we present mathematical models that incorporate ideas from complex systems theory to integrate several strands of rangeland theory in a hierarchical framework. Compared with observed data from South Africa, the model successfully predicted the relationship between rainfall, vegetation composition and animal numbers over 30 years. Extending model runs over 100 years suggested that initial starting conditions can have a major effect on rangeland dynamics (divergence), and that hysteresis is more likely during a series of low rainfall years. Our model suggests that applying an upper threshold to animal numbers may help to conserve the biodiversity and resilience of grazing systems, whilst maintaining farmers' ability to respond to changing environmental conditions, a management option here termed controlled disequilibrium.

Keywords: catastrophe theory, complexity theory, disequilibrium, hysteresis, moving attractors

Introduction

Rangeland is defined as indigenous vegetation used as grazing or browsing by domestic or wild animals. The arid and semiarid zones of sub-Saharan Africa account for 55% of the subcontinent's area and for 57% of the biomass of domestic ruminants (Sandford 1995). Livestock products from these regions constitute between 14% and 25% of the total value of agricultural production in the subcontinent (Scoones 1995), and multipurpose herds and flocks on extensive rangeland are an effective way of satisfying human needs from marginal resources.

For many decades, concern has been expressed over the sustainability of livestock production from arid rangeland in Africa (Anon. 1923, Acocks 1988), and various conceptual and mathematical models have been developed with the aim of assessing the effects of different management options. Initially, conceptual models describing the interactions between rainfall, changes in plant species composition of vegetation and livestock were used to predict equilibrium stocking rates based on fixed carrying capacity. Overgrazing has frequently been cited as the cause of declining productivity (Acocks 1988, Dean and MacDonald 1994, Milton and Dean 1996), yet where recommended stocking rates have been exceeded, the expected long-term decline in livestock numbers has not always been observed, despite high interannual variability in livestock numbers – for example, on communal rangeland from southern Zimbabwe (Scoones 1993), in the Herschel district of the Eastern Cape (Vetter et al. 1998) or Namaqualand (Hoffman et al. 1999a). The conflicting findings cited above may be a consequence of the complex dynamics of semiarid rangelands.

The terms 'equilibrium', 'non-equilibrium' and 'disequilibrium' are used to describe the dynamics of rangeland systems and must be defined clearly; in this paper the definitions of Illius and O'Connor (2004) are used. Equilibrium would be reached between animal populations and forage production under stable weather conditions. Rainfall variability perturbs the system leading to disequilibrium. Non-equilibrium is the special case where animal population dynamics are linked to the availability of key resources in the dry season and not to wet-season grazing.

Over the past 15 years, the relevance of equilibrium concepts such as carrying capacity, and associated definitions of range degradation, have been questioned in regions dominated by highly variable rainfall. It has been argued that in disequilibrium systems, frequent droughts cause severe episodic mortality in livestock and wild animals and so reduce the long-term impact of herbivores on vegetation (Ellis and Swift 1988, Westoby et al. 1989, Hoffman and Cowling 1990, Behnke and Scoones 1993). Illius and O'Connor (1999), however, have suggested that in spatially heterogeneous landscapes, density-dependent competition may occur in key resource areas that sustain animals during the dry season. Illius and O'Connor (1999) also suggest that stochastic, arid grazing systems behave differently to semiarid systems where density-dependent processes cause the system to tend towards equilibrium, which is never reached because herbage production and animal birth and death rates vary over time. Thus the system is in permanent orbit around a moving attractor. Even under uniform environmental conditions such as irrigated pastures, grassland systems may not attain a steady state as they can exhibit sustained oscillations as many of the interrelations are non-linear (Thornley 1998, Thornley and France 2007). In such systems parameter values and the initial values of the state variables influence the behaviour of the system.

A further element of rangeland theory describes the change in species composition of rangeland vegetation in response to variation in animal numbers and rainfall, as well as the effects of interactions between plants. Early conceptual models were directional, and arranged different vegetation states along a single successional pathway (e.g. Stoddart et al. 1975). Milton et al. (1994), however, suggested that arid rangeland degradation is not the continuous, reversible process envisaged by Stoddart et al. (1975), but proceeds in steps, with successive steps being more difficult to reverse. The first step is the replacement of palatable plants by less palatable species; this may be gradually reversed by strict control of animal numbers and/or grazing season. However, if the range is so severely degraded that vegetation cover is completely lost and the soil is severely eroded, restoration cannot be achieved by grazing management alone.

A related group of models, termed cyclical models (Milton and Hoffman 1994), postulates that both plant and animal populations fluctuate in response to variations in rainfall (Hoffman and Cowling 1990, Hoffman et al. 1990) or interactions between plant species. These factors are assumed to have a greater influence on vegetation composition than the intensity of herbivory (Milton and Hoffman 1994). Stochastic models, such as state and transition models, propose that unpredictable factors such as rainfall or fire can change vegetation from one state to another in terms of species composition (Milton and Hoffman 1994). Transitions are changes in species composition that are not readily reversed. Furthermore, Ward et al. (1998) suggested that the rate of recovery of animal numbers following a drought is an important factor influencing the subsequent rangeland condition and productivity. DeAngelis and Waterhouse (1987) suggested that two mechanisms lead to stability in ecosystems dominated by stochastic variation in abiotic factors such as rainfall. First, as temporal variations in environmental factors vary from place to place, stable equilibrium will be seen over a sufficiently large area (DeAngelis and Waterhouse 1987). These authors concluded that a stable equilibrium state is not a fundamental property of ecosystems but a property that emerges from extrapolation to sufficiently large spatial scales. This scale-dependent stability was observed in South Africa on two occasions during the twentieth century, when the sheep population increased to an asymptotic level of approximately 39 million before decreasing substantially as result of drought, economic factors or government policy (Figure 1). Stability at large (national) spatial scales may mask the variable and complex interplay between climate, management preferences and environmental heterogeneity at smaller spatial scales.

De Angelis and Waterhouse (1987) also proposed that biotic compensatory mechanisms, which operate at smaller spatial scales, can ensure persistence of the system during a very dry year or series of dry years. For example, during dry years animals can adapt to low energy intakes caused by a shortage of forage by a reduction in maintenance energy expenditure (Ledger and Sayers 1977, Burrin et al. 1990). Grazing animals may also adapt by browsing leaves and fruit of woody plants that are not normally eaten when grass is abundant (Illius and O'Connor 1999).

Lockwood and Lockwood (1993) suggested that complexity theory, and specifically catastrophe theory, provides a mathematical framework for the study of discontinuous phenomena, but also generates models that permit continuous dynamics thus unifying the succession and state-and-transition models (Lockwood and Lockwood 1993). Thus there is a need to re-examine the relevance of catastrophe theory and move towards a synthesis of equilibrium and disequilibrium ideas as well as changes in plant species into a new integrated understanding of rangeland dynamics (Gillson and Hoffman 2007).

A hierarchical theory

All ecosystems including rangelands are hierarchical in nature and characterised by many organisational levels, with variables at one level influencing processes at higher and lower levels (Allen and Starr 1982, Wu and Loucks 1995, Archer and Bowman 2002, Richardson et al. 2005, Thornley and France 2007). This concept forms the basis of many mathematical models (Richardson et al. 2005, Thornley and France 2007). Furthermore, processes within different levels operate on widely different temporal and spatial scales that are much larger at a high level of organisation, such as an ecosystem, compared with the lower cellular level (Allen and Starr 1982, O'Neill et al. 1986).

The various theories of rangeland dynamics described above were developed to increase understanding of how the populations and productivity of both of plants and animals vary over time. Modelling of rangeland systems is a critical tool for increasing understanding of how rangeland systems work and how they will respond to interventions. It is essential that model outputs are tested against real data from the systems that they describe, if local variations in climate and vegetation are to be effectively captured. It seems likely that real rangeland systems exhibit elements of stochastically driven, density dependence and phase and transitions under different circumstances or at different levels of the hierarchy. It is this interrelationship that is a key to the integrated model presented here.

The dynamics of different levels of the system must be considered in the development of a new, hierarchical theory that integrates processes at different scales. Two levels of the system that have a major impact on its overall performance are the organism level (bioenergetics of plants and individual animals) and the ecosystem level (population dynamics of vegetation and livestock). These are shown in

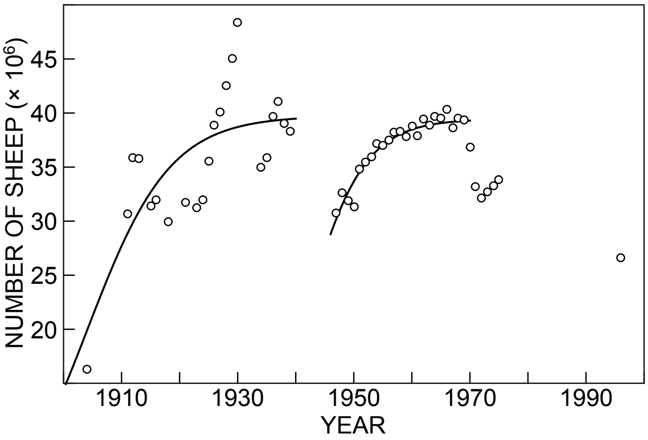

Figure 1: Number of sheep in South Africa for the period 1904–1996. Fitted curves for population growth during two periods: 1904–1939: Y = 39737.4/(1 + Exp(0.563576 − 0.139643X)); 1946–1996: Y = 39633.9/(1 + Exp(6.5876) − 0.167027X)) (data source: MT Hoffman)

Figure 2: Two organisational levels of rangeland systems

System	Components	Time Scale	Processes
Ecosystem	Plant and animal populations	Years	Population dynamics
Organism bioenergetics	Individual animals and plants	Days	Growth Herbivory Milk and fibre production Reproduction Senescence and mortality

Figure 2. The interactions between different levels can lead to complex dynamics of the system as a whole (Ellis 2005).

We use models that simulate two levels of the hierarchical organisation of semiarid rangeland. First, the productivity of individual animals and plants is modelled on a daily basis (the bioenergetics model). Second, the dynamics of the flock of animals and the vegetation are represented on an annual basis (by the population dynamics model). Together they enable us to study how interactions between different levels of the system influence the dynamics of the system as a whole. Each level is an integration of processes at lower levels. The productivities of plants and animals are simulated mechanistically as they are dependent on processes at a lower level. Animal growth and milk production are dependent on forage intake, digestion and the partition of nutrients between maintenance, tissue growth, lactation and gestation. Plant growth is determined by soil moisture and the amount of green leaf. In this model the population dynamics of plants and animals are simulated on a yearly basis. The dynamics of livestock and vegetation depend on animal birth and death rates, the production of plant dry matter and its removal by animals and loss by senescence and decay. In fact, processes at three levels of the system are represented.

The first objective is to look at the interaction between hierarchical levels, specifically the interaction between the productivity of plants and animals in relation to the species composition of the vegetation. A second objective is to examine whether rangeland degradation in terms of the replacement of productive palatable species by unpalatable or poisonous plants can occur in disequilibrium systems. A further objective is to study how the short-term interrelations between the temporal distribution of abiotic factors such as rainfall and biotic factors such as the numbers and liveweights of animals influence animal survival. A final objective is to make the outputs of the model relevant to management recommendations by testing the effect of different management strategies including imposing an upper limit on animal numbers, the use of supplementary food to reduce mortality during a drought and restoring flock size after a drought by purchasing animals.

In the first part of the paper (methods), the four stages in the development of the models are described. In the second part of the paper (results), outputs of the long-term model are compared with data from rangelands in Paulshoek, South Africa.

Methods: models of the dynamics of rangelands

The models are developed in four stages:

1. Stocking-rate models demonstrate the effects of resource limitation in a hypothetical, constant environment on animal numbers or productivity.
2. A short-term dynamic bioenergetics model shows how forage production and its consumption by livestock change over time in relation to rainfall and range condition within years in a semiarid environment and why the system cannot reach equilibrium.
3. A long-term model is developed that models transitions in vegetation composition in relation to variations in rainfall and animal numbers over time. The position of the moving attractor and forage availability depends on guild composition of the vegetation as well as rainfall.
4. The interaction between hierarchical levels of the system is studied by using the short-term model to simulate the effects of changes in botanical composition of the vegetation on forage production, the performance of individual animals and their organs, including the mammary gland.

Resource-limited stocking-rate models

A quantitative approach to predicting population size postulates that the growth of any population must eventually be limited by the availability of resources (Renshaw 1991). In its simplest form, equilibrium population size (carrying capacity) can be modelled as a logistic relationship between animal numbers and parameters if the environment remains constant, Equation 1 (Renshaw 1991). This equation has time as an explicit variable, however, plant (or forage) production is not represented explicitly. Livestock numbers and productivity are related to a specific area or region. Changes in sheep numbers (N) over time (t) may be described by Equation (1):

$$N = A / [1 + \exp(b - ct)] \qquad (1)$$

where A is maximum population that may be carried by the environment, and b and c are parameters.

Much of the variation between areas in carrying capacity is due to rainfall. For example, in South Africa, recommended stocking rates have been related to rainfall (Equation 2) (Hoffman et al. 1999b):

$$Y = 10^{-5} X^{1.4724} \qquad (R^2 = 0.854) \qquad (2)$$

where Y is stocking rate (LSU ha^{-1}) and X is mean annual rainfall (mm).

This approach may be extended to include the relation between stocking rate and animal performance. For example, Jones and Sandland (1974) proposed an empirical model for predicting production per animal (Y_a) and per hectare (Y_h) in relation to stocking rate (Equations 3 and 4) that was used for estimating the carrying capacity of rangeland in South Africa (Tainton, 1981).

$$\begin{aligned} Y_a &= a \\ & \qquad\qquad (X \le X_c) \qquad (3) \\ Y_h &= aX \end{aligned}$$

$$\begin{aligned} Y_a &= a - bX \\ & \qquad\qquad (X > X_c) \qquad (4) \\ Y_h &= aX - bX^2 \end{aligned}$$

where X is stocking rate (animals ha^{-1}), a and b are constants, and X_c is the critical stocking rate below which animal production is unrelated to stocking rate.

Bransby (1984) studied the effect of rainfall on the relation between animal performance and stocking rate for planted pastures during four successive years. Maximum live-weight gain (a) decreased with an increase in annual rainfall probably because the increase in herbage growth led to a decrease in the proportion of leaf and a reduction in digestibility of available forage. However, the rate of decline in live-weight gain with an increasing stocking rate (b) also decreased with increasing rainfall, which reflected the increase in herbage yield.

Because the relation varies with rainfall and between sites, in a further refinement Gillard and Monypenny (1990) suggested that production per animal is related to the product of total rainfall and grazing area per animal (Equation 5). However, this model did not give a close fit to the combined data for several ranches as it did not allow for the effects of soil characteristics and timing of rainfall and ignored any carry-over effects. Equations of the same form were fitted for reproductive and mortality rates. Pasture proxy is effectively a surrogate for the weight of available herbage per animal.

$$\text{Pasture proxy } (P_p) = R \text{ (ha animal}^{-1})$$

where R is annual rainfall (mm) and ha animal^{-1} is the stocking rate.

$$Y_a = a + bP_p - cP_p^2 \qquad (5)$$

Short-term dynamic models of forage and livestock

In contrast to the static models described above, dynamic models have time as a variable within the model; mathematically, dynamic models consist of update equations (differential or difference equations or the solutions to those equations) that show how rainfall patterns and livestock numbers in one year affect the behaviour of the system over several subsequent years. Any change in input and initial values of state variables can cause chaotic behaviour of the system that in the long-term leads to divergence.

We describe models of a communal rangeland at Paulshoek in the arid north-western region of South Africa. The vegetation comprises a large number of plant species that to simplify modelling are aggregated into four guilds or ecologically meaningful groups of species (Todd and Hoffman 1999, Hahn et al. 2005):

(1) woody perennial shrubs palatable to livestock (WP) (e.g. *Tripteris sinuatum*, *Pentzia incana*)
(2) moderately palatable succulent shrubs, primarily in the family Mesembryanthemaceae (Mesembs; ME) (e.g. *Ruschia robusta*, *Leipoldtia schulzii*)
(3) an unpalatable and often poisonous shrub guild dominated by *Galenia africana* (kraalbos; GA)
(4) annuals and geophytes (AG) (e.g. *Leysera tenella*); most of these are assumed to be palatable.

We have developed two separate models of the Paulshoek system that simulate processes that operate at different levels of the hierarchy and on two widely different time scales. First, we use the short-term bioenergetics model of edible forage and individual animals in the Paulshoek pastoral system with a time step of 1 d developed by Richardson and Hahn (2007a). The features of the bioenergetics model that are relevant to the discussion in this paper are briefly described in the following section. A second model, the long-term model, with a time step of one year simulates the population dynamics of plants and livestock and was developed in part by fitting equations to the output of the short-term model (Hahn et al. 2005, Richardson and Hahn 2007b).

A major input to the short-term bioenergetics model is daily rainfall. A soil moisture module partitions daily rainfall between runoff, infiltration and drainage and also simulates the loss of soil moisture by evaporation and transpiration. Forage production by different types of plant is modelled in relation to soil moisture and the present potential for growth. The diet selection submodel is developed from the MIAMH model of Genin and Quiroz (1993). Three factors affect the preference of animals for a guild: relative availability, ease of harvesting, and nutritional quality of each guild (see Appendix).

In the short-term model the rate of growth of edible material, $Fe_{(i)}gr$, of each plant guild is represented by a logistic equation (Equation 6). The maximum potential growth rate of each guild, $Femax_{(i)}$, is related to the number of plants per hectare for that guild, while the fractional growth rate, $\mu fegr_{(i)}$, rate is a function of soil moisture and rate of transpiration.

$$Fe_{(i)}gr = \mu fegr_{(i)}\, Fe_{(i)}\, [1 - (Fe_{(i)}/Femax_{(i)})] \tag{6}$$

The rate of consumption of each guild, $C_{(i)}$, where intake is limited by forage density is simulated by the sigmoid function proposed by Johnson and Parsons (1985) (Equation 7):

$$C_{(i)} = Nha\, A\{(Fe(i)/k_{b(i)})^{qb}/[1 + (Fe(i)/k_{b(i)})^{qb})]\} \tag{7}$$

where *N*ha is the stocking rate (SSU ha^{-1}), *A* the maximum rate of intake by a goat (kg d^{-1}), and $k_{b(i)}$ and *q*b are parameters.

In our model the maximum rate of intake varies with the width of the dental arcade, physiological status of breeding does and may also be limited by the capacity of the digestive system to process foods of low digestibility. Rate of intake is also affected by the density of edible material on individual shrubs and number of shrubs per hectare. The rate of change of forage density for guild $_{(i)}$ is predicted by Equation 8:

$$dFe_{(i)}/dt = Fe_{(i)}gr - C_{(i)} \tag{8}$$

In young animals, their growth potential limits their capacity to utilise energy and consequently their intake. The simulated intake is the smallest of those predicted by the three mechanisms.

Given the hierarchical nature of rangeland systems, the output of the short-term bioenergetics model is used to develop the parameters of the long-term model of population dynamics and the ecosystem. The dynamics of the short-term model influence the behaviour of the long-term model. When a sigmoid function was fitted to output of the short-term model, the point of inflection of the forage consumption curve was found to occur at an edible forage density of 20 kg ha^{-1}. This is unrealistic, even though a sigmoid function (Equation 7) was used to predict intake in the short-term model. Consequently, use of the diminishing returns function used to predict forage intake in the long-term model (Hahn et al. 2005) is justified. Richardson et al. (2005) used the short-term model to develop a simplified long-term model of vegetation and livestock that behaved as an equilibrium model when soil moisture is uniform, but when rainfall varies between years it simulates a system at disequilibrium. In that model the vegetation comprised one aggregated species.

Long-term model of the interaction between rainfall, grazing and vegetation guild dynamics

None of the quantitative models mentioned so far have considered the effects of rainfall and herbivory on the species composition of rangeland vegetation; the final element of the integrated model is a long-term model that simulates changes in the populations of different plant species (guilds) in response to rainfall, grazing pressure, plant competition and the interactions between them.

The long-term model (Paulshoek ecosystem model) has a time step of one year that simulates the population dynamics of plants and livestock so that the effects of different management strategies on vegetation changes and livestock production may be studied (Hahn et al. 2005).

The proportion of plants of different types changes in response to the variation between years in the total amount of rain and its distribution within the year (Esler et al. 2006). When heavily utilised, palatable productive perennial plants are replaced by the less-productive annuals and by the perennial unpalatable and toxic shrub *Galenia africana* (Hoffman et al. 1999a). The model assumes that changes in the shrub population and the production of edible forage by shrubs are partially independent of one another. For example, the production of edible forage by WP is a function of both rainfall and WP cover, which is a surrogate for the population of WP plants (Figure 3). Most important, the plant guilds compete with one another for space.

Results: modelling complex behaviour in rangelands of the Succulent Karoo, South Africa

Application of the short-term bioenergetics model

The short-term bioenergetics model of Richardson and Hahn (2007a) was run using recorded rainfall data for 1978 and 1979 and a stocking rate of 0.11 adult goats ha^{-1} at the start of the year. Following rainfall, the rate of forage growth is substantially greater than the rate at which it is removed by grazing (Figure 4). For a large part of the year forage growth is effectively zero while the edible fraction is still removed by grazing. At no time is the system in a stable steady state and any steady states are extremely transient. Consequently, the concepts of catastrophe theory are not applicable to the dynamics of such rangelands within years. An important result of the lack of steady state in this system is the relatively rapid accretion of edible forage for use during periods when no growth takes place (Figure 4). A similar pattern is generated by the model of semiarid

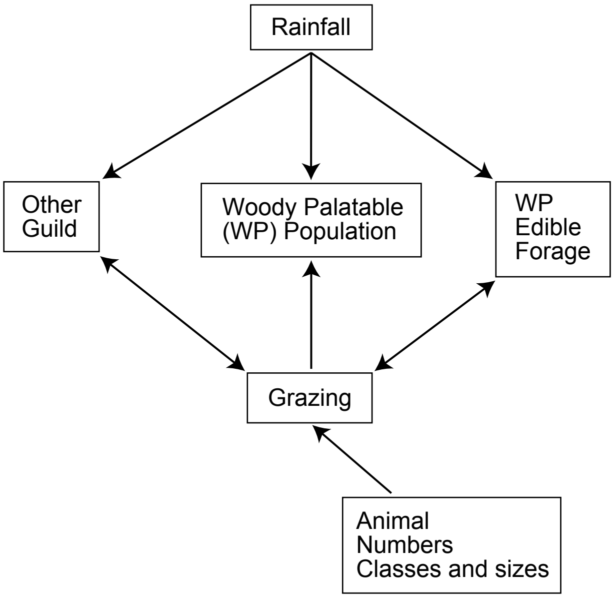

Figure 3: Ecosystem model: structure of the woody perennials component of the vegetation submodel. This submodel simulates both the cover of each guild and forage production. Figure reproduced from Richardson et al. (2004) by permission of the publishers

savanna grazed by cattle described by Richardson et al. (2000). The magnitude of edible forage at the end of the rainy season determines the probability of animals surviving until the start of next season of forage growth and has a major effect on reproductive rates in the following year.

Comparison of model output using the rainfall data for 1978 and 1979 (Figure 4) illustrates the important effect of distribution of rain during the year on forage growth. These were years when the total annual rainfall was similar (106 mm in 1978 and 116 mm in 1979). In 1979, forage growth, although variable, was almost continuous between days 150 and 300. However, for 1978 the model predicted a short period of forage growth at about day 95 followed by a dry period of 120 d. The model simulated leaf senescence in drought deciduous perennials during this time and this would have adversely affected the subsequent growth of that guild. Between days 225 and 330 several periods of relatively slow growth were predicted.

Not only do stochastic variations in the distribution of rainfall affect the productivity of the system, but the values of the state variables also interact with the magnitude and timing of rainfall events. The liveweight of Paulshoek does

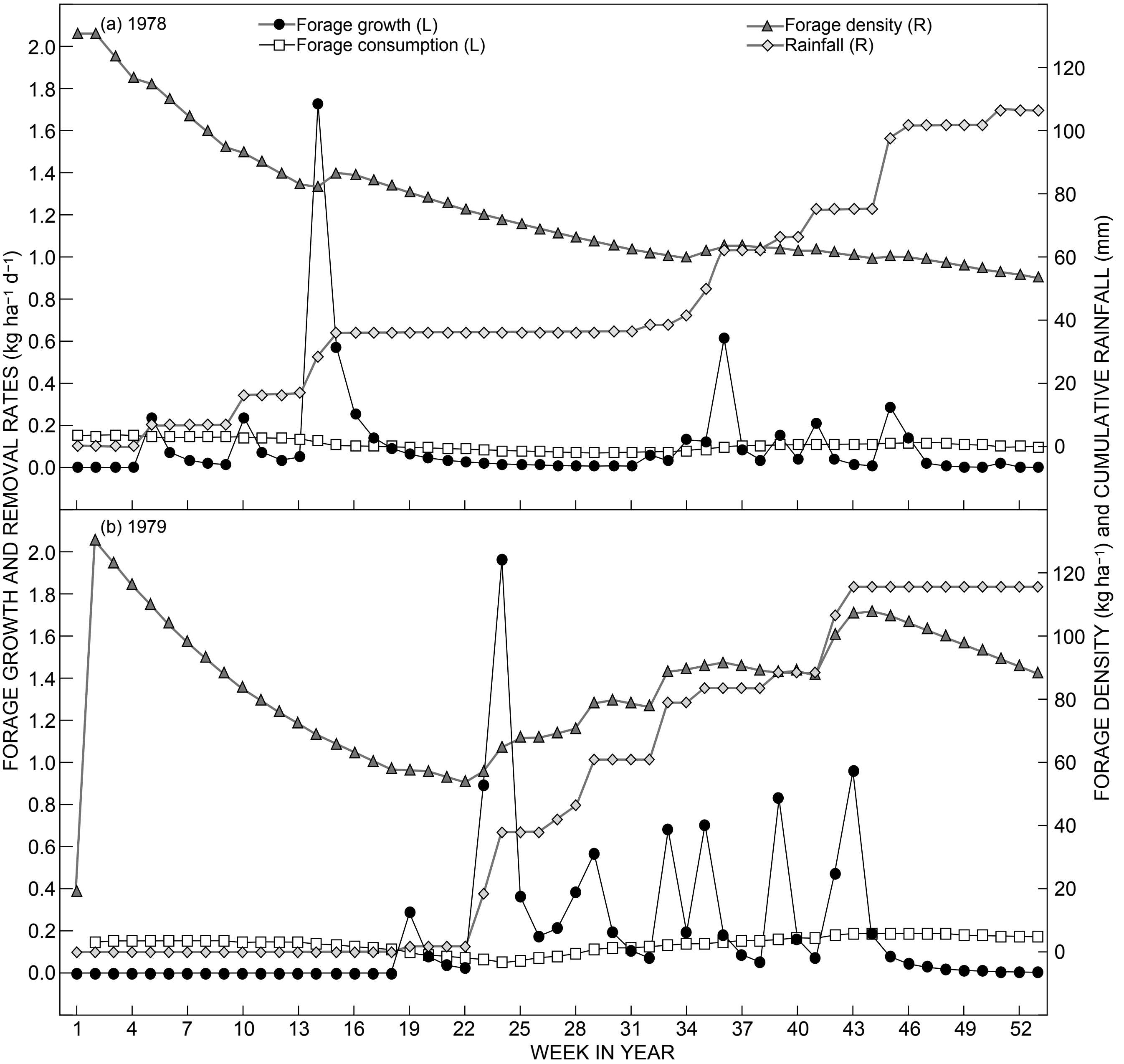

Figure 4: Rates of forage growth and consumption and the density of edible forage predicted by the model of Richardson and Hahn (2007a) together with cumulative rainfall for the Paulshoek rangeland during 1978 (annual rainfall 106 mm) and 1979 (annual rainfall 116 mm). Stocking rate 0.11 adult goats ha^{-1} at the beginning of the year

on January 1 influences their weight and the magnitude of their body reserves of protein and fat at kidding in early July. This in turn affects their milk yields during the first two weeks of lactation and the mortality of their kids during this period. With the rainfall pattern of 1978, the mortality during the first two weeks of single kids of does having an empty body weight (EBW) of 31 kg on January 1 was far greater than of the progeny of does with an EBW of 45 kg on January 1 (Figure 5a). However, when the model was run using the 1979 rainfall data the effect of doe EBW at the beginning of the year was relatively small (Figure 5b). This indicates that interrelations within the system at the level of individual animals are complex.

Modelling the effects of rainfall variability using the long-term population dynamics model

In this section, outputs of the long-term model are compared with data from Paulshoek. The long-term model unifies the disequilibrium dynamics described in stages 1–3 above with the vegetation composition submodel of stage 4.

As rainfall varies widely between years, livestock numbers and forage production vary over time unless the size of the

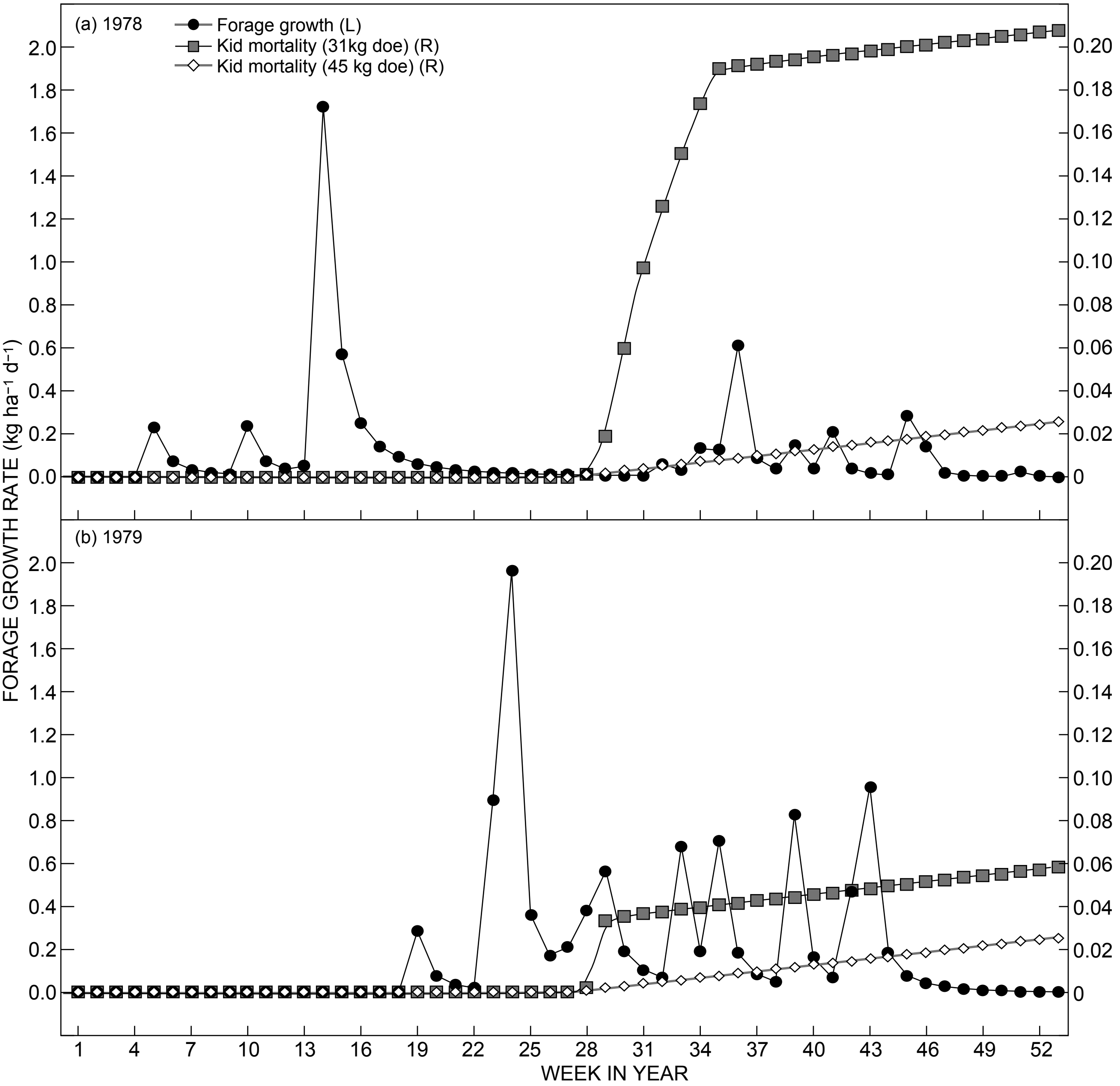

Figure 5: Kid mortality and forage growth rates predicted by the model of Richardson and Hahn (2007a) for the Paulshoek rangeland during two years 1978 (Annual rainfall 106 mm) and 1979 (Annual rainfall 116 mm).

animal population is deliberately controlled. The ecological level model for Paulshoek is run using 36 years of recorded rainfall data and the management strategy simulated involves sale or slaughter of half the kids (almost all the males) before they are one-year old and does are culled before they are eight-years old. The model predicts varying stock numbers that closely match the real stock numbers observed at Paulshoek until 1999 as reported by Richardson et al. (2005). Results for an additional seven years are presented in Figure 6 together with the previous data. Following the very low rainfall in 1998 (61 mm), stock numbers recorded in 1999 were substantially higher than those predicted by the model (Figure 6). The possible reasons for this discrepancy include the provision of supplementary food provided by the South African government, access to alternative range or stock purchases to replace animals that died.

If the model is run with stock numbers in 1999 set at the observed value, livestock numbers predicted by the model track the observed numbers remarkably well until 2003 when the recorded decline in population is far greater than that predicted by the model. This decline was almost certainly the result of very cold weather (see Appendix).

The model is run using a 200-year set (set 3) of simulated rainfall having the same mean and variability as the data recorded at Springbok, the nearest town (Figure 7a), but the temporal distribution of rain is different from the sets used by Richardson et al. (2005). This in turn led to different patterns of change over time in the populations of animals and plants. Livestock numbers vary over the whole period (Figure 7b), severe population crashes are associated with low rainfall and high livestock numbers, for example year 24 followed a year of low rainfall (130 mm) and a very high number of animals (7 539).Total perennial cover and the percentage cover of each plant guild also vary (Figure 7b and c). A transition occurred involving the severe decline in percentage cover of all guilds between years 44 and 62 that was associated with several years of below-average rainfall and many years of high stock numbers that precede the sudden decrease in population in year 52. The gradual recovery in the cover of all guilds from year 84 onwards is associated with five years of relatively high rainfall and a relatively low livestock population. Another transition occurs after year 177 when *Galenia* replaces WP as the most plentiful guild. The predicted density of annuals varies widely between years in response to rainfall (Figure 7d).

With this rainfall sequence, the solution trajectory indicates a transition as the attractor moves into a different region where total perennial cover remains less than 20% between years 57 and 83 (Figure 8). This is 80 years earlier than in the simulation reported by Richardson et al. (2005) using their second set of rainfall data. During this time livestock numbers do not increase above 3 000 head even during years of relatively high rainfall such as years 63 and 73. This is a consequence of the consistently low levels of forage production associated with the low cover of perennial plants. When driven by this rainfall sequence, the system exhibits disequilibrium and a transition, a form of complex dynamics.

Modelling the effects of management intervention using the long-term model

One management option in semiarid rangelands is to allow animal numbers to vary over time, but to impose an upper

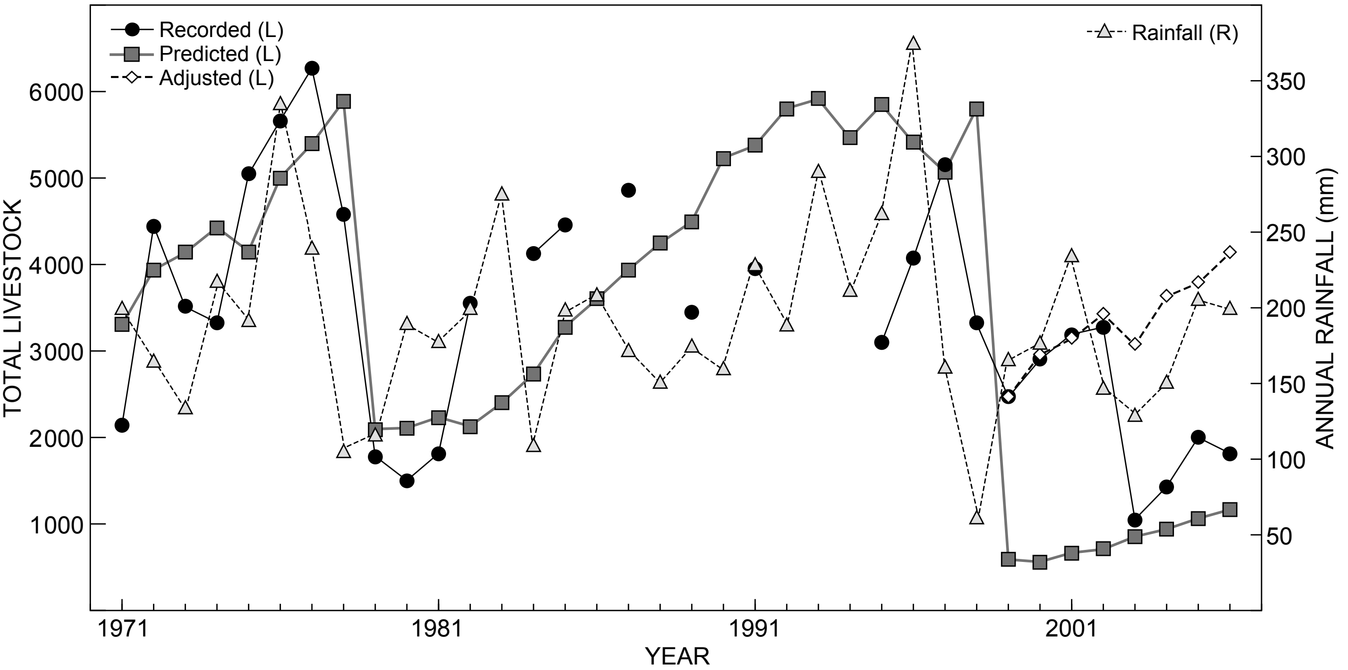

Figure 6: Recorded rainfall and small-stock numbers for Paulshoek, compared with ecosystem model predictions of stock numbers. For the adjusted prediction, stock numbers in 1999 were set at the observed value

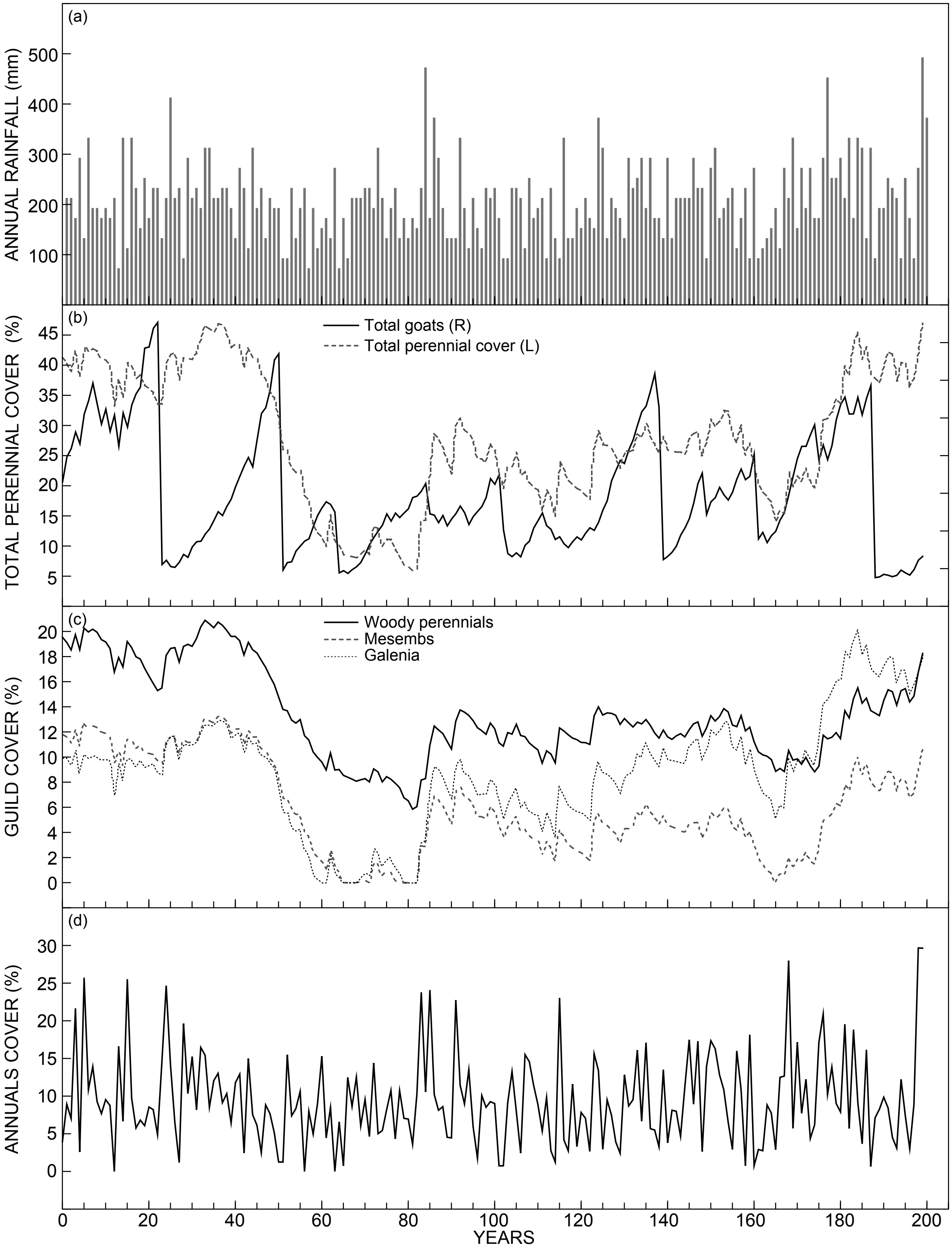

Figure 7: Long-term ecological level model for Paulshoek using rainfall set 3: predicted variation over 200 years (a) in annual rainfall, (b) total goat numbers and total perennial cover, (c) in percentage cover of each perennial guild and (d) in percentage cover of annuals. Notice that after a series of low rainfall years (44–62) with high stocking rates, the system collapses and both perennial cover and goat numbers are low

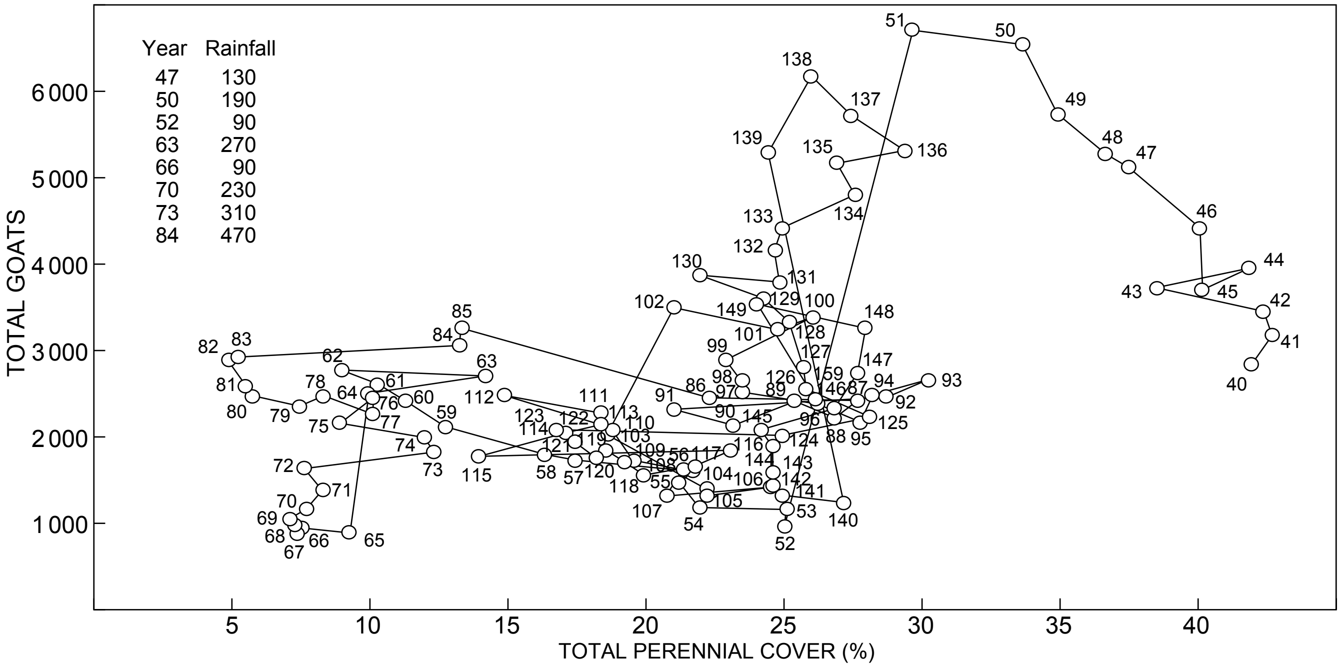

Figure 8: Long-term model: solution trajectory showing predicted changes over time in the relation between goat numbers and total perennial cover using rainfall set 3. Where the moving attractor is depends on the condition of the range

limit so that livestock productivity and rangeland condition may be maintained. When using the same rainfall data as before, if the number of adult animals is not allowed to exceed 1 500 head, the variability of the goat population is substantially reduced and so is the variation in cover of the different plant guilds (Figure 9). This is a smaller upper limit to the adult animal population than used by Richardson et al. (2005). However, even with the smaller upper limit, total goat numbers drop below 2 000 head more frequently than in the previous study. The total number of animals frequently exceeds 1 500 as a result of the birth and survival of kids to weaning. Throughout the period WP remains the most plentiful guild. This type of management may be described as controlled disequilibrium.

The effects of rainfall can be explored by running the model again with yet another rainfall sequence (set 4) but having the same mean and variability as in the previous simulations. One such run (Figure 10), when animal numbers are allowed to vary without restriction, predicts that the cover of all guilds except *Galenia* remains higher and varies to a lesser extent than with the first sequence shown in Figure 7. The cover of *Galenia* declines rapidly from year 190. Guild cover changes are not only due to stocking rate but are contingent on the temporal pattern of rainfall and animal numbers. This supports our thesis that the interrelations between vegetation, rainfall and animal number are complex.

With this rainfall sequence, limiting stock numbers to a maximum of 1 500 adults prevents a severe decline in WP cover (Figure 11). Furthermore, the livestock population only varies between 2 216 and 2 978 as a result of the availability of forage due to the consistent abundant cover of productive palatable species. Ellis and Swift (1988) postulated that the condition of the grazing system at a specific time may be determined more by the chance temporal distribution of rainfall than by the interaction of livestock and vegetation. However, the results presented in Figures 7, 9, 10 and 11 suggest that vegetation condition is determined by the interactions of livestock, vegetation and the random distribution of rainfall over time.

Another management intervention is to ensure that after a drought, the size of the flock is not less than a specific number of animals. This would be achieved by means of either supplementary feeding or the purchase of replacement stock. If the number of animals is not allowed to fall below 1 000 head, the fluctuation in the animal population is less than when the minimum size of the flock is allowed to fall to 100 head. This is because animal numbers do not rise as high after a drought when the minimum size of the flock is 1 000 head as they do when the minimum flock is only 100 animals. This is a consequence of the decrease in WP cover and increase in *Galenia* when a larger number of animals are kept during and after a drought (Figure 12).

The interaction between different levels of the system

The short-term model was used to simulate the behaviour of the vegetation and individual animals grazing range in either standard or degraded condition in years of average or low rainfall. Total perennial cover and the percentage cover and plant populations for each perennial guild vary with rangeland condition (Table 1) and reflect changes at the ecosystem level. Two successive years, 1977 and 1978, having annual rainfall of 230 and 106 mm, respectively, are simulated. The stocking rate is 0.1 does ha^{-1} and the does give birth to single kids.

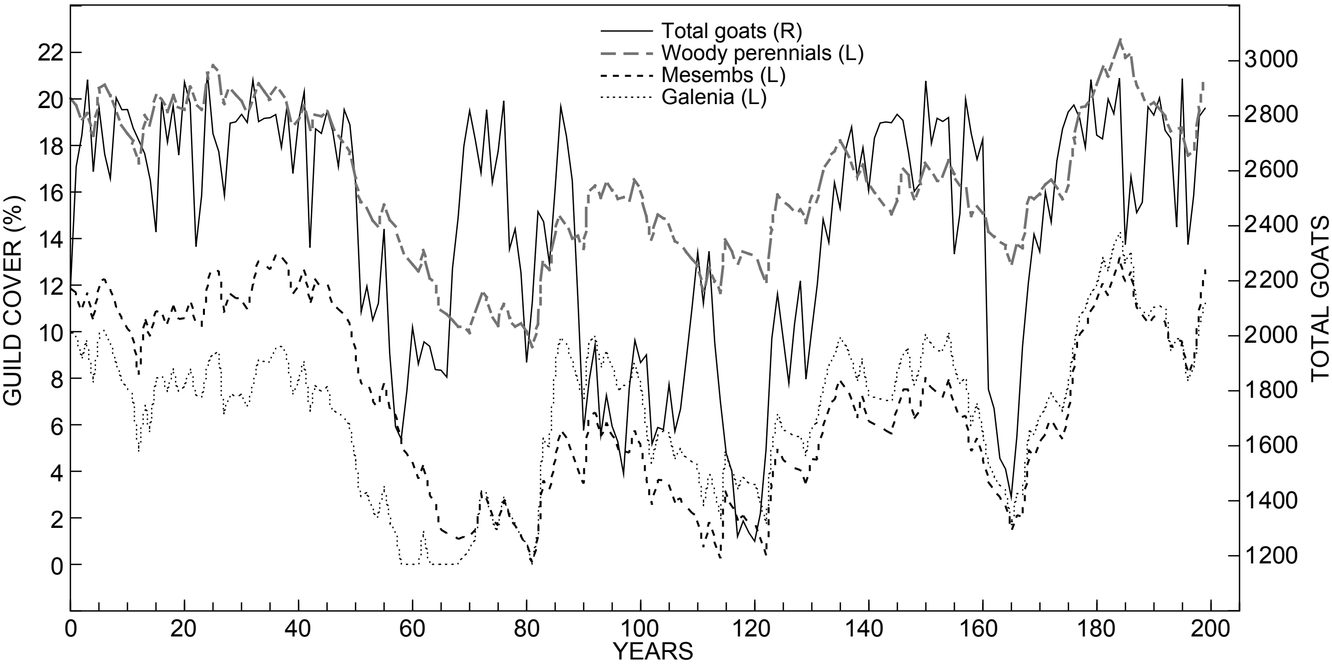

Figure 9: Variation in plant guild cover and number of goats when allowed to vary between years but are limited to a maximum of 1 500 adults (does and yearlings) using rainfall set 3. Mean number of goats (adults + kids) over this period is 2 378 animals

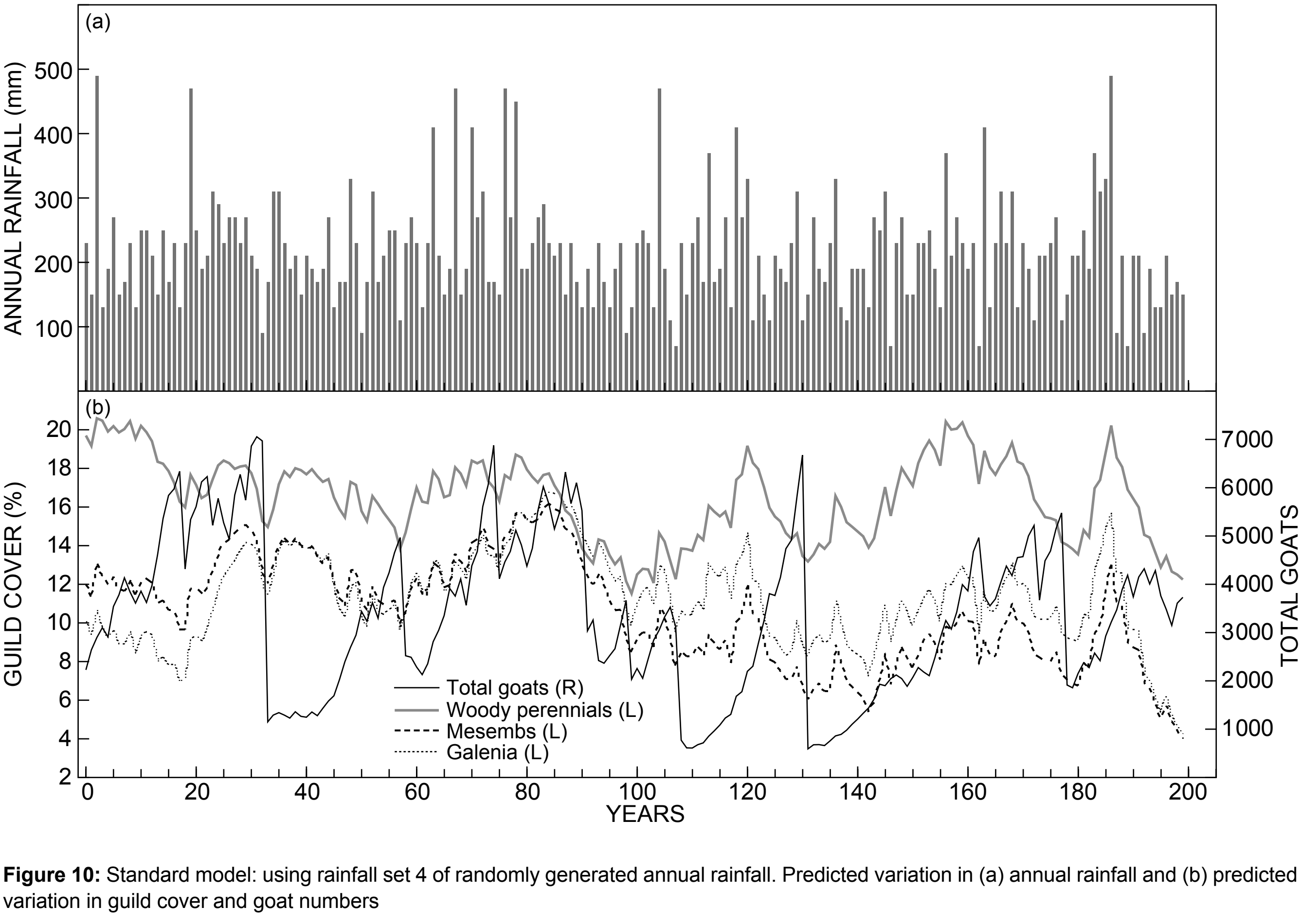

Figure 10: Standard model: using rainfall set 4 of randomly generated annual rainfall. Predicted variation in (a) annual rainfall and (b) predicted variation in guild cover and goat numbers

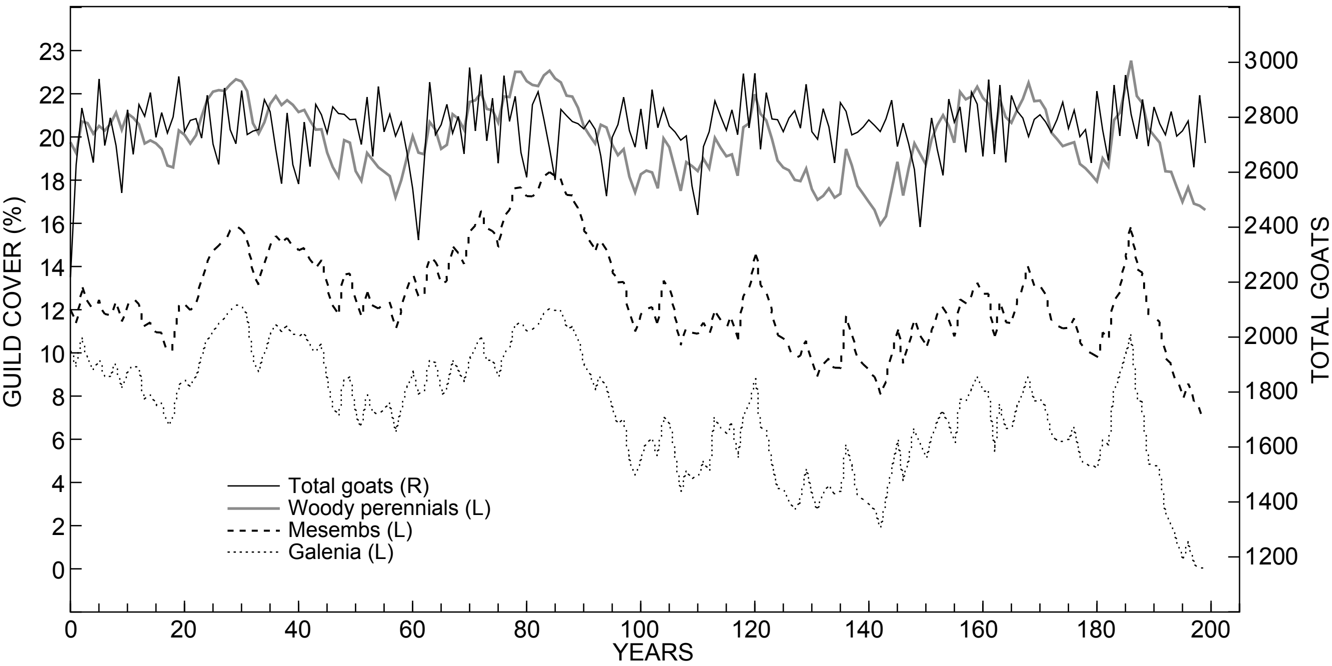

Figure 11: Paulshoek ecosystem model: variation in guild cover and goat numbers using rainfall set 4 of randomly generated annual rainfall and seasonality data. Adult goats limited to a maximum of 1 500 head

As total perennial cover decreases when the rangeland becomes degraded, the yield of edible material by annuals increases. The density of edible forage produced by annuals on degraded range is greater than that of WP except at the start of the growing season during both years (Figure 13). Edible WP density only decreases below that of annuals during the second half of 1978 and is the result of grazing by the goats. Liveweights of both does and kids are unaffected by range condition in 1977 because of the high yield of annuals on degraded range as a result of adequate rainfall during that year (Figure 14, Table 2). However, during 1978, low rainfall leads to a very low yield of forage by annuals and low intakes of woody perennials and annuals on degraded range that causes a substantial reduction in predicted doe liveweight compared with animals grazing range in standard condition. The milk yield of does and growth of their kids on degraded range in 1978 is reduced so severely that only 26.6% survive until they are 70 days old (Figure 14, Table 2). The death of these kids enables 89% of their dams to survive as liveweight losses are reduced. There is no decrease in the survival rates of does and kids due to undernutrition in a year of adequate rainfall (1977) irrespective of range condition and in a low rainfall year (1978) only on degraded range is survival reduced.

Discussion

Predicting the effect of different management strategies on range condition is a major challenge for farmers in highly variable environments like semiarid rangelands. Our models simulate not only the interrelations between livestock, forage and rainfall in both the short and long term, but also how rainfall patterns and herbivory cause changes in the species composition of vegetation (Hahn et al. 1999, 2005, Richardson et al. 2005). The models were specifically designed to simulate communally managed rangeland at Paulshoek in the Succulent Karoo, South Africa. Our dynamic models combine elements of density-dependent resource limitation and disequilibrium (stochasticity) and the impact of grazing on botanical composition of the vegetation, thus unifying key elements of rangeland theory. When tested against observed data, the long-term ecosystem model effectively predicted the complex behaviour of the Paulshoek rangeland and demonstrated the significance of rainfall patterns for vegetation composition and animal numbers. An original aspect of our model is that it simulates livestock dynamics in a system where animal numbers are not strictly controlled, but can also simulate different approaches to limiting the variation in stocking rates. Different upper and lower limits to animal numbers for similar environments may reflect the different objectives of stockowners (Hoffman et al. 1999b) indicating the interplay between resource availability and management choice.

We show that rangeland systems exhibit complex dynamics as the interrelations between rainfall, vegetation and livestock are affected by changes in the species composition of the vegetation. Together the models capture several key elements of previously competing or alternative theories of rangeland dynamics and, in addition, they consider changes in plant guilds. Firstly, the short-term bioenergetics model illustrates that within years the system is far from equilibrium and that its complex behaviour depends on the contingency of stochastic events (rainfall) and determinism (current forage availability, and the body reserves of animals) as proposed by Nicolis and Prigogine (1989), and shown in Figures 4 and 5. Furthermore, forage

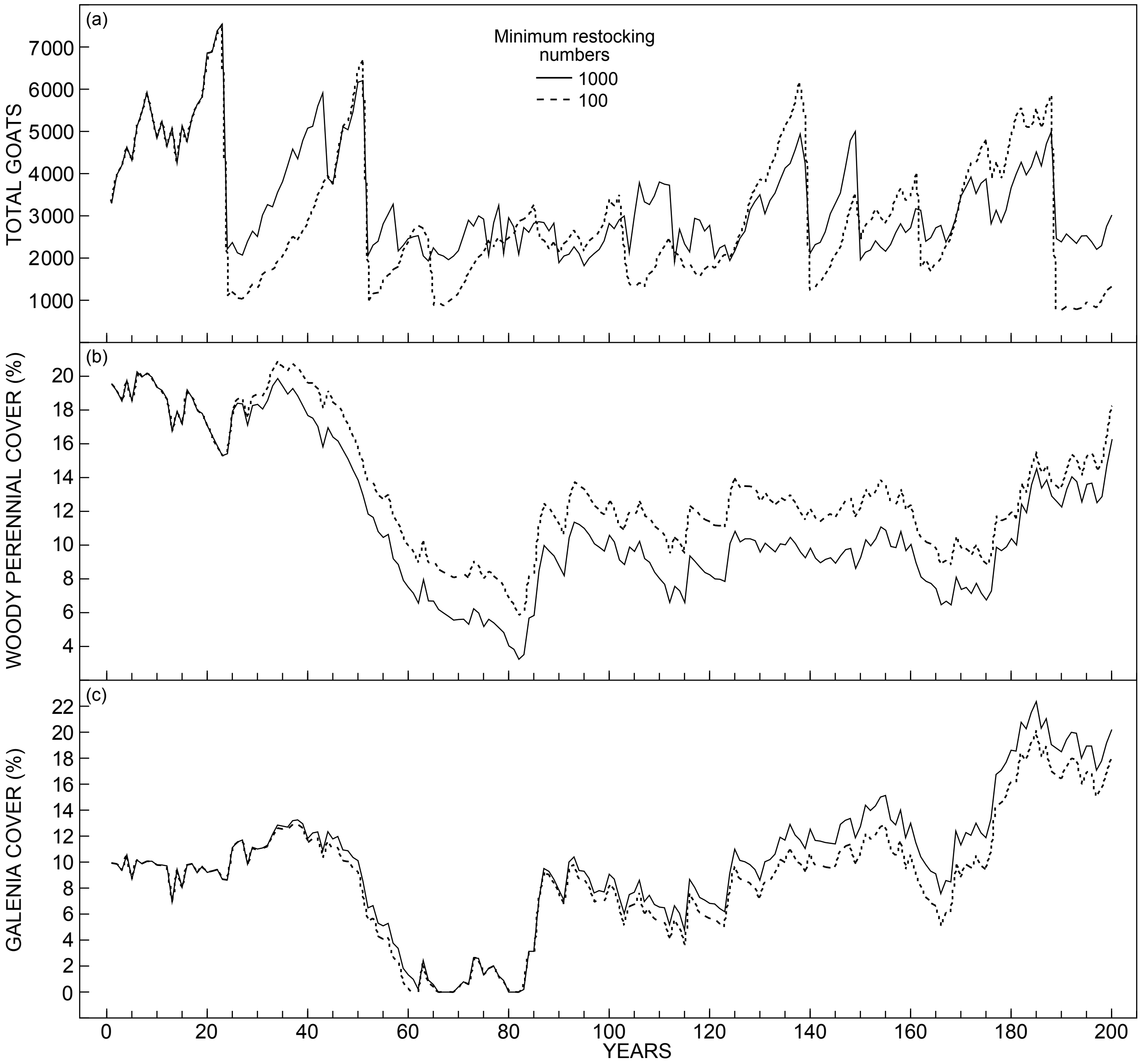

Figure 12: Effects over 200 years of imposing two minimum restocking rates after a major decrease in animal numbers on (a) the total number of goats, (b) percentage cover of woody perennials and (c) percentage cover of *Galenia*, using rainfall set 3

availability is influenced by interactions between vegetation guild composition and stochastic variation in rainfall (Figure 13). This in turn influences food intake, growth, milk yield and survival of individual animals. Complex behaviour at this level has been shown to impact on livestock survival and reproductive rates that are a major component of the long-term population dynamics model (Hahn et al. 2005) (Figures 7, 9, 10 and 11). These interactions between different hierarchical levels of the system also lead to complex dynamics (Ellis 2005).

Higgins et al. (2007) point out that while grass production varies stochastically with rainfall, the relation between

Table 1: Percentage cover and number of plants per hectare of each perennial plant guild for rangeland in either standard or degraded condition

Vegetation condition	Woody perennials	Mesembs	*Galenia*	Total perennials
Standard				
Cover (%)	20	12	10	42
Plants ha^{-1}	5631	1576	100	
Degraded				
Cover (%)	6	6	18	30
Plants ha^{-1}	1689	788	180	

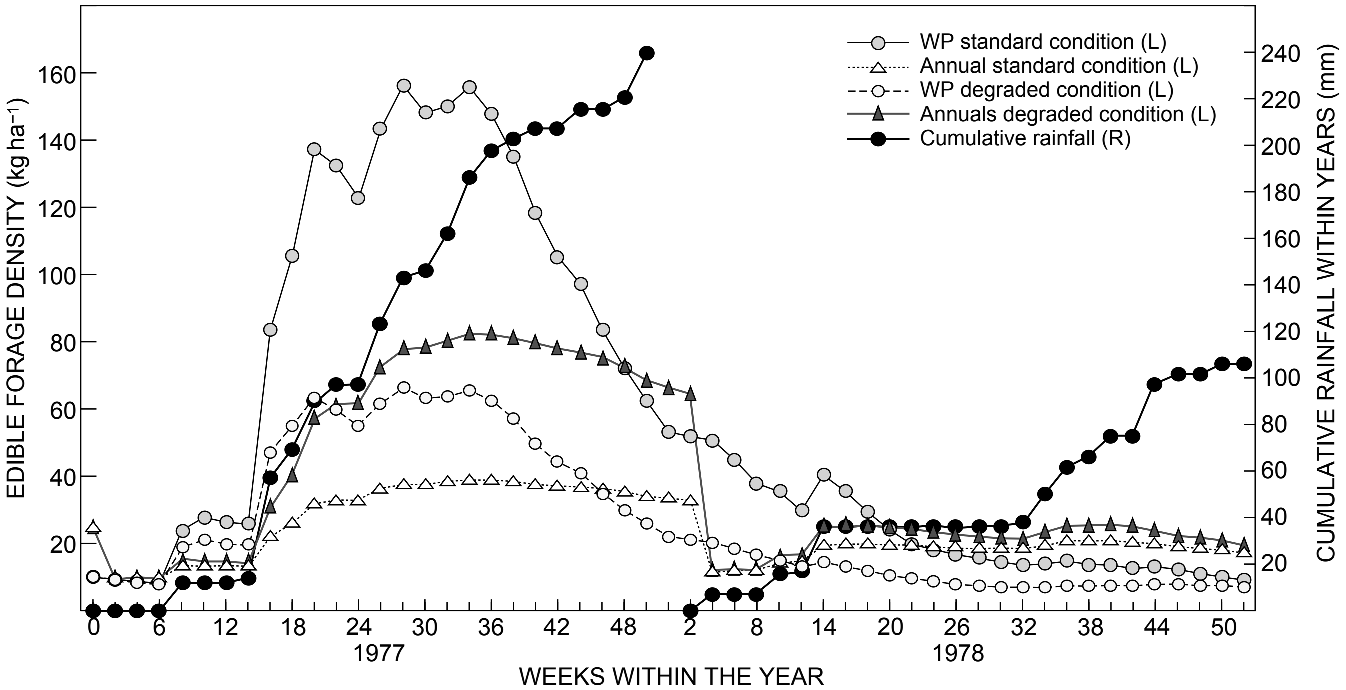

Figure 13: Effect of vegetation condition (standard or degraded) and annual rainfall on edible forage density of for woody perennials (WP) and annuals when stocked at 0.1 does and single kids per hectare

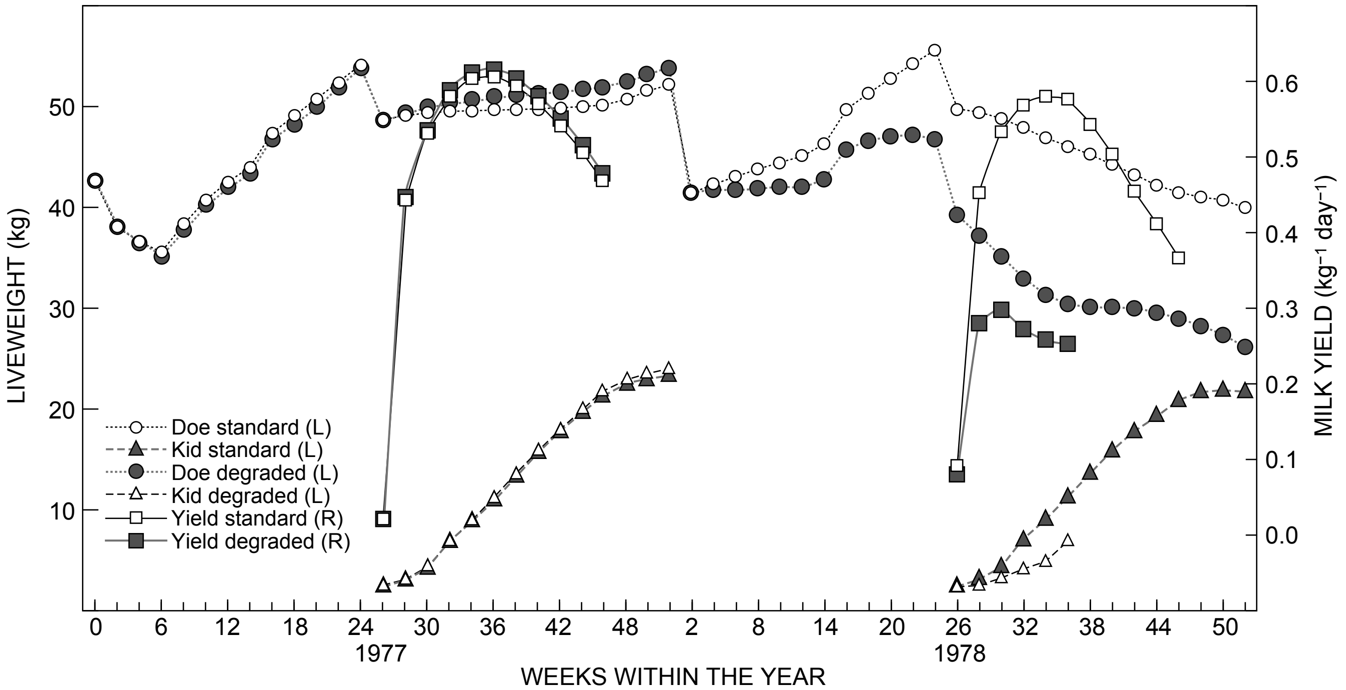

Figure 14: Effect of vegetation condition (standard or degraded) and annual rainfall on the liveweights of does and kids and the milk yield of suckling does when stocked at 0.1 does and single kids per hectare

animal production and grass availability and composition depends on deterministic processes such as forage intake and the partition of energy between different processes in the animal. The long-term model incorporates ideas from phase and transition models (Westoby et al. 1989) in order to describe feedbacks between rainfall, vegetation composition and grazing pressure. The population dynamics component of this model is the first to predict changes in

Table 2: Effect of rangeland condition and rainfall on the quantities of dry matter (DM) eaten by a doe and her kid and on the survival rates of does and kids

Year	Rangeland condition			
	Standard		Degraded	
	1977	1978	1977	1979
Annual rainfall (mm)	239.5	106.0	239.5	106.0
Woody perennials DM eaten (kg y^{-1})	427.9	421.1	286.4	192.1
Annuals DM eaten (kg y^{-1})	53.2	37.4	216.5	127.9
Mesembs DM eaten (kg y^{-1})	21.6	47.9	9.6	24.3
Galenia DM eaten (kg y^{-1})	1.1	2.4	3.1	8.4
Doe survival rate (%)	94.9	94.9	94.9	89.0
Kid survival rate (%)	92.4	92.4	92.4	26.6

the abundance of ecologically meaningful plant guilds in response to changing rainfall and animal numbers, enabling transitions from woody palatable to toxic unpalatable *Galenia* and annual dominated systems to be predicted.

Outputs from the long-term model describe a rainfall-driven system that exhibits both disequilibrium and transition (Figure 8) leading to a form of complex dynamics. The rangeland system at Paulshoek modelled here also demonstrates some of the complex behaviour described by catastrophe theory as suggested by Lockwood and Lockwood (1993): modality (distinct states), hysteresis (processes associated with changes that are not readily reversible), and divergence (relatively small changes in initial conditions can result in dramatically different outcomes over time). However, since the relation between forage density and livestock cannot reach a steady state on either time scale catastrophe theory in the mathematical sense is not applicable.

The present work indicates that the interrelations between rainfall, herbivores and present species composition of the rangeland determine whether the condition of the range will improve or deteriorate.

Outputs from the long-term model indicate that the same management strategy can have radically different effects on range condition, depending on rainfall sequence. Most notably, range vegetation is more likely to switch from palatable woody perennials to unpalatable shrubs and annuals if there is a series of low rainfall years (Figures 10 and 12). Furthermore, the relationship between vegetation, animal numbers and rainfall is hysteretic, in that the recovery of palatable vegetation may be very slow once a transition to less palatable species has occurred.

Outputs from the long-term model suggest that transitions to vegetation dominated by unpalatable shrubs and annuals are less likely to occur when animal numbers are restricted to an appropriate upper limit (Figure 13). This type of management, termed controlled disequilibrium, thus conserves the resilience and variability of the rangeland ecosystem, yet protects it from potentially long-term shifts towards unpalatable and annual plants. In terms of biodiversity conservation, this type of management appears beneficial in preserving plant diversity. A specific upper limit to animal numbers (0.1 adult goats ha^{-1}) has been shown to maximise mean annual output in the long term over 100 years (Richardson et al. 2007). A further reduction to 0.075 adults ha^{-1} leads to a marginal decrease in long-term average output and enables degraded rangeland to recover. Thus, this form of management has the potential to reconcile the ability of farmers to respond to favourable environmental conditions, while preserving plant species diversity during drought periods.

However, even stocking as light as 0.075 adults ha^{-1} (13.3 ha $goat^{-1}$) may not always prevent a substantial decrease in plant cover (Figure 11). This means that the assertion of Higgins et al. (2007) that low stocking rates prevent degradation of vegetation even under conditions of variable rainfall may not be true for all ecosystems. Furthermore, output from the long-term model predicted that stocking constantly at the recommended rate would lead to degradation of the Paulshoek range (Richardson et al. 2005). However, the integrated model does not simulate short-term management decisions by farmers in response to drought or above-average rainfall such as supplementary feeding, and buying or selling animals. On the other hand, increasing the minimum flock size following a drought leads to a deterioration in range condition indicated by a decrease in woody perennial cover and a small increase in *Galenia*. This is accompanied by a reduction in the variability of livestock numbers.

Conclusions

The integrated model described here explains how animal numbers in a semiarid rangeland track environmental conditions over time. Rainfall and forage vary over time and form a moving attractor towards which animal numbers tend. The long-term model predicts the feedback between vegetation composition, rainfall and stock density, and describes transitions in vegetation composition that can occur, especially when high grazing pressure coincides with a series of low rainfall years.

Outputs from the long-term model suggest that transitions from woody palatable plants to unpalatable shrubs and annuals are most probable under conditions of heavy grazing, and are less likely when animal numbers are kept within an appropriate upper limit. This type of management, here termed controlled disequilibrium, might provide a way of maintaining rangeland resilience and diversity whilst allowing farmers to adapt to changing environmental conditions.

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Appendix: Supplementary information for the short-term bioenergetics model

Three factors affect the preference of animals for a guild: relative availability, ease of harvesting, and nutritional quality of each guild. Availability of a guild is the edible material of that guild expressed as a fraction of total edible material. Ease of harvesting is a function of the amount of edible material eaten in an average bite, which in turn is influenced by the breadth of a doe's dental arcade (mm). The latter related to mature weight and the highest weight yet attained by an animal (peak weight) as arcade breadth does not decrease if the animal loses weight. The equation for sheep (Taylor et al. 1987) is used in the absence of data for goats. For the shrubs average bite size is estimated from the amount of edible material on an individual plant using the sigmoidal response described by Johnson and Parsons (1985) and from number of plants ha^{-1} as a fraction of the maximum potential number of plants ha^{-1} of that guild. The majority of species in guild WP are deciduous and the dead leaves are scattered on the ground. Both dead WP (DeWP) and annuals are assumed to be uniformly spread over the range. Since 0.75 of the aboveground biomass of annuals is assumed to be edible (expert consensus) and the plants are relatively small, the effect of plant numbers is ignored. The rate at which animals harvest these two forages is a function of the edible biomass of each. As *Galenia* is toxic, the fraction of GA in the diet selected by adults does not exceed a maximum value, which is assumed to be 0.15 (MT Hoffman unpublished data).

Metabolisable energy intake is partitioned between maintenance, accretion/depletion of body protein and fat, conceptus growth and milk production. Reproductive and survival rates are simulated in relation to predicted liveweight and liveweight changes for the different age classes of livestock. The short-term model allows for the simulation of different genotypes as the user may specify mature liveweight and lactability, which is an index of genetic potential for milk production adjusted for mature liveweight (Taylor et al. 1986). The values used for these parameters are apparently appropriate as the liveweights of single and twin kids born to does of different sizes predicted by the model agree with data from the Paulshoek flock.

The effects of temperature on the survival of low birth-weight kids and adults in poor condition could be readily simulated. However, this would require the prediction of the probability of severe low temperature events for each day during the appropriate months. The variation in temperature is stochastic to an even greater extent than that of rainfall. Richardson and Hahn (2007) found that including the effect of temperature on the growth of Annuals and Geophytes (AG) leads to a small reduction in the biomass and consumption of AG. Consequently, the amount of Woody Perennials (WP) eaten increased but WP biomass was almost unaffected. The effect on animal performance was negligible. For these reasons the effects of temperature are not specifically represented.

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