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Resource heterogeneity and ungulate population dynamics

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It has been suggested that climatic variation has the effect on the dynamics of arid and semi-arid grazing systems of reducing animal numbers below the level at which they have much impact on vegetation or soils, and that spatial heterogeneity in resource availability serves to buffer herbivores against climatic variation. Modelling was used to test these hypotheses and to examine the interacting effects of temporal and spatial variability in plant production on animal population dynamics and defoliation intensity. The model distinguishes areas of the range that are accessible during wet and dry seasons, and examines the effect of seasonal restrictions in foraging area. It was established that the animal population is in long-term equilibrium with dry-season resources, on which it depends for survival; that dry season resource areas and outlying areas thus operate in a source-sink manner; and that the ratio of these areas determines the strength of consumer-resource coupling outside the dry-season range. A high ratio of dry season to wet season resources may support a sufficiently large animal population to impose non-trivial defoliation impacts on the outlying range. Increasing degrees of variability in primary production on areas used by animals for surviving the dry season increased the annual variation in animal abundance and reduced the mean. By comparison with a stable environment, for which the model predicts virtually stable animal numbers and constant, low defoliation intensity, variation in annual rainfall causes wide fluctuations in animal numbers and defoliation intensity. Under climatic variation, animal numbers can build up enough to impose much higher defoliation intensities than under a constant regime. Periodic intense defoliation is a consequence of climatic variability which is likely to make these environments more, not less, prone to ecological change.

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Ungulates commonly experience considerable seasonal, climatic and spatial variation in resources, especially in arid and semi-arid tropical environments, where such variation is extreme. Alternating wet and dry seasons impose a cycle of plant growth and phenology that results in a cycle of food abundance and quality. Resource limitation occurs during the dry season, when low food quality causes animals to lose weight; their survival then depends on the adequacy of body fat reserves carried over from the growing season (Sinclair 1975, Fryxell 1987). Annual rainfall in semi-arid environments typically has a coefficient of variation greater than 25%, with the result that droughts are common causes of herbivore mortality (Ellis and Swift 1988, Owen-Smith 1990). Ungulate populations are regulated mainly through density-dependent mortality outside the breeding season, with environmental stochasticity often combining with density dependence through a common effect on resources supply (Caughley and Gunn 1993, Sæther 1997). Environmental variability therefore has a fundamental effect on herbivore population dynamics in arid and semi-arid grazing systems.

Spatial variation in semi-arid grazing systems arises from variation in soil characteristics and topography, causing variation in nutrient content and hydrology, such that low-lying areas that receive runoff from up-

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slope have longer growing seasons and may have plant communities, including woody browse, that differ from the more arid land further up the catena. Access to drinking water is an additional spatial variable. As the dry season progresses, surface water sources become depleted and dry up, forcing herbivores to range over areas that are accessible from permanent sources of drinking water, and to abandon outlying areas that are beyond herbivores' foraging radius, regardless of the abundance of food there. This spatial separation of the area over which herbivores can range during the dry season ('dry season range', DSR) and the outlying areas accessible only during the wet season ('wet season range', WSR) is reinforced by the distinctions between the botanical and phenological characteristics of the forage in the two areas.

Spatial separation of range areas accessible during the wet and dry seasons is regarded as having important implications for the dynamics of herbivore populations and their impact on vegetation, for a number of reasons. First, herbivore population size would be expected to be lower under such conditions than would be the case if all the resources present were accessible throughout the year. Second, spatial variability of the type described could buffer seasonal and perhaps climatic variability, by allowing a dry-season refuge to herbivores. This would occur if, by comparison with WSR, DSR was less prone to variability, due to the prolonged period of adequate soil moisture or the presence of deep-rooting woody browse allowing greater seasonal persistence of green plant material. The potentially important role played by spatial and temporal heterogeneity in the dynamics of semi-arid grazing systems was recognised by Scoones (1995), who studied seasonal diet shifts in livestock under communal grazing management in southern Zimbabwe and argued that livestock were dependent on 'key resource' areas during the dry season. Walker et al. (1987) compared ungulate mortality from a two-year drought in four wildlife conservation areas in southern Africa, and concluded that mortality was greater where the establishment of watering points led to reduced spatial heterogeneity of grazing impacts and abolition of reserve stands of lightly grazed grassland. Although this effect is confounded by the higher animal biomass in watered sites, it was argued that spatial patterning of resources acted as a buffer during drought.

Rangeland degradation is one of the central concerns about semi-arid grazing systems: whether animal population densities are sufficient to adversely affect the long-term capacity for primary and secondary production. One view is that plant production in highly variable climates is largely determined by rainfall and is unaffected by animal population density, because intermittent die-offs during extended droughts keep densities below equilibrium (Ellis and Swift 1988, see also Choquenot 1998). This, together with the potential role of key resources in buffering the effects of climatic variation, has led to a re-assessment of range ecology in recent years (e.g. Behnke and Scoones 1993). It was argued that if livestock populations are dominated by density-independent drought mortality, then they are only weakly coupled to vegetation resources, and that such systems are therefore 'non-equilibrial'. In the absence of strong consumer-resource coupling, livestock may not have a long-term negative effect on range resources, and, thus 'The risk of environmental degradation in non-equilibrial environments is limited, as livestock populations rarely reach levels likely to cause irreversible damage' (Scoones 1994). For example, an analysis of long-term trends in livestock population dynamics led Scoones (1992) to argue that, despite the build-up between droughts of high population densities, the absence of directional trends in population size suggested that degradation of the forage resource was not apparent, or at least not affecting the key resource areas.

Illius and O'Connor (1999) reviewed the non-equilibrium viewpoint, and attempted a synthesis of the ecological phenomena. For the purposes of the present work, the following predictions were made. **P1**: Despite the apparent lack of equilibrium under climatic variation, animal numbers are likely to be regulated in a density-dependent manner by the limited forage available in 'key resource' areas. 'Key resource' can thus be interpreted by analogy to the key factor (sensu Varley and Gradwell 1960): given that the key factor determining animal population size is survival over the season of plant dormancy, key resources are those whose supply determines the size of the key factor. **P2**: The existence of strong equilibrial consumer-resource coupling over a limited part of the system might indeed imply that the animal population is virtually uncoupled from resources elsewhere in the system. Spatially and temporally, the whole system appears to be heterogeneous in the strength of the forces tending to equilibrium, these diminishing with distance from watering and key resource areas and during the wet season. It was also argued that (**P3**) WSR would be more heavily utilised by animal populations sustained by key resource areas than would apply in the absence of key resources, and that uncoupling of the animal population from vegetation could actually carry an increased risk of degradation. Lastly, (**P4**) grazing systems prone to climatic variability might actually be more at risk of extreme herbivore impacts, because droughts may impose more intense and localised defoliation on vegetation than would occur in a system at or near equilibrium.

The purpose of the present paper is to examine some of these predictions by modelling a spatially and climatically varying grazing system. The specific purpose was to examine the relative effects of variability in plant production in WSR and DSR and of varying the accessibility of the whole range area during the dry season on animal population dynamics and defoliation intensity.

The model

The model needs to account for the effect of rainfall on plant production, and the functional and numerical response of the animal population. Defoliation of grass plants is only expected to be of adverse physiological significance to the plant if live tissue is removed (Ash and McIvor 1998), requiring live and dead tissue be distinguished in the model. Because an important component of animals' response to seasonality is the use of body reserves (Sinclair 1975), the model addresses the physiological processes of energy metabolism, such that reproduction and mortality are functions of the state of fat reserves. The animal component of the model is a simplification of that described in detail by Illius and Gordon (1998). In other respects the model is an elaboration of that of Fryxell et al. (1988), who developed a model distinguishing discrete vegetation types that are fed on for only part of each annual cycle by migratory ungulates.

To keep things simple, *potential* primary production in the two range areas was assumed to be equal, given equal rainfall, and there were assumed to be no differences in the digestibility of live and dead vegetation between each area. The purpose of this was to be able to ascribe results to differences in the variability of primary production, unobscured by the differences in productivity, length of the respective growing seasons and plant nutrient contents that probably occur in reality. The designation of two areas of range (DSR and WSR) each as separate homogeneous units is a considerable simplification. In reality, a gradient of accessibility is likely to exist, and resource richness, animal ranging behaviour and utilisation of range is likely to be heterogeneous at smaller spatial scales than applies in the simple distinction examined here. Furthermore, the assumption to be applied in the model is that there is no feedback of herbivory on primary productivity: i.e., defoliation does not affect regrowth potential. The purpose of these simplifications is to clarify fundamental relationships, free of the complexity of fine-scale heterogeneities and the necessity for assumptions about the sensitivity of vegetation to herbivory.

The model uses a daily iteration interval. Table 1 summarises the model's variables and parameters.

Plant production

Semi-arid rangeland is taken to be a water-limited system, for which a simple relation between rainfall and plant growth is appropriate. Le Houérou et al. (1988) show that, over a period of years, annual above-ground primary production is linearly related to annual rainfall by a coefficient representing rain use efficiency, r (kg ha^{-1} mm^{-1}). Accordingly, the daily change in live and dead vegetation biomass, $\mathrm{d}V_{l,i}/\mathrm{d}t$ and $\mathrm{d}V_{d,i}/\mathrm{d}t$ on range type i, is a function of growth, herbivory and decomposition, and is given by

$$\frac{\mathrm{d}V_{l,i}}{\mathrm{d}t} = \frac{rR}{g}(1 + s_i x) - qV_{l,i} - \frac{NI_{l,i}}{a_i}$$

$$\frac{\mathrm{d}V_{d,i}}{\mathrm{d}t} = qV_{l,i} - (n_1 + n_2)V_{d,i} - \frac{NI_{d,i}}{a_i} \qquad (1)$$

$$V_i = V_{l,i} + V_{d,i}$$

where g is the length of the growing season (d); R is mean annual rainfall (mm); s_i is the cv of annual rainfall (= standard deviation/mean); x is a normally distributed random variable with mean = 0 and SD = 1; q is a rate constant controlling senescence of live tissue to dead (d^{-1}); n_1 and n_2 are, respectively, fractional rates of tissue loss to detritivores and decomposition (d^{-1}); N is the number of animals; I is their per capita daily intake and a_i is the area of range type i. Invertebrate herbivory is assumed to occur mostly by termites, and invertebrate consumption of green tissue is ignored.

With a new value of x drawn each year, the term $(1 + s_i x)$ simulates annual variation in rainfall, which is therefore directly equivalent to annual variation in primary production. Note that the same value of x, the random variable, was applied annually to both WSR and DSR, such that a drought in any one year occurred throughout the entire area, with the relative severity of drought on each area being determined by setting the cv of annual rainfall, s_i, to the desired value for each range type. Note also from eqn. 1 that the cv of primary production equals the cv of rainfall, and the terms are therefore interchangeable.

Animals

The animal population is assumed to be cattle with a mature body mass of 400 kg, and is structured into age classes, but no distinction is made between the sexes. Each age class is assigned a mean body mass, and assumed to have a maximum permissible body fat mass. In each age class, the mean body fat mass and the numbers of animals are state variables. Progression of juveniles through age classes is performed annually, at the end of the dry season. The three juvenile and one adult age classes considered here, representing animals aged > 1, 1–2, 2–3, and > 3 years old, respectively, were included to account for differential susceptibility to starvation (Clutton-Brock et al. 1997). The other changes in animal numbers, due to births, B, and

Table 1a. State variables, inputs and parameters of the vegetation model.

		Wet season value	Dry season value	Reference or basis of assumption
Vegetation state variables				
$V_{l,i}$, $V_{d,I}$	Biomass of live or dead vegetation in area *i* (kg/ha)			
Inputs and parameters				
g	Growing season length (d)	183		Half a year
R	Mean annual rainfall (mm)	600	0	Average for semi-arid rangeland
s	cv of annual rainfall			
a_I	Area (ha) of WSR or DSR			
r	Rain use efficiency (kg ha^{-1} yr^{-1})	4	0	Le Houérou et al. (1988)
q	Rate of senescence of live tissue (d^{-1})	0.03		Busque, J. and Herrero, M. unpubl.
n_1	Dead tissue loss to detritivores (d^{-1})	0.00245	0.00245	Dunham (1990)
n_2	Decomposition rate (d^{-1})	0.004	0	Kinyamario and Imbamba (1992)

b. State variables, inputs and parameters of the animal model.

		Wet season value	Dry season value	Reference or basis of assumption
Animal state variables				
N_j	Number of animals in age class *j*			
W_j	Body mass (kg)			
F_j	Fat mass (kg)			
Inputs and parameters				
A	Mature mass (kg)	400		Cattle
$F_{m,j}$	Maximum fat mass for each age-class (kg)	$0.3A$		Ledger (1968) for adults; younger age classes assumed to be $0.15A$, $0.2A$, $0.25A$.
k	Intrinsic rate of increase	0.8		Adult male:female sex ratio of 1:4; all females have one offspring each year if fat reserves are sufficient
l	length of birth season (yr)	0.25		Half the growing season
b, c	Parameters controlling effect of body reserves on reproductive rate	$b = 15$ $c = 0.3$		50% of adults will breed when $F/F_{\max,4} = 0.3$ and 95% will breed when $F/F_{\max,4} = 0.5$
σ	Standard deviation of body fat	$0.125\ F_{\max,j}$		Ledger (1968)
β	*V* at which intake is half its maximum value (kg/ha)	400		O'Reagain (1994)
d_l, d_d	Digestibility of live, dead vegetation	0.7, 0.4		Gives diet digestibility over the range observed by O'Reagain and Owen-Smith (1996)

mortality, M, were calculated daily. Assuming that only adults (age class 4) breed,

$$B = \frac{N_4 k}{l\left[1 + e^{-b\left(\frac{F}{F_{\max,4}} - c\right)}\right]} \tag{2}$$

where k is the annual intrinsic rate of increase and l is the length of the birth season (in fractions of a year). The term in square brackets reduces birth rate as a function of current body condition: $F/F_{\max,4}$ is the ratio of fat reserves to the maximum fat mass for the breeding age class, and b and c are parameters controlling the effect of body reserves on reproductive rate.

Mortality occurs due to the exhaustion of body reserves during periods of under-nutrition. Mean body fat, F_j, in each age class is obtained daily from the calculated energy balance (below), and is assumed to be normally distributed with standard deviation σ. Mortality occurs in the proportion of animals in the tail of this distribution that projects below zero.

The daily change in fat reserves is the difference between energy intake, I_j and expenditure, E_j (MJ/d):

$$\frac{dF_j}{dt} = \frac{(I_j - E_j)}{m} \tag{3}$$

where m is a metabolic coefficient for the conversion between energy and fat, such that $m = 39.3$ MJ net energy/kg for $I < E$ (catabolism) and $m = 54.6$ for $I > E$ (anabolism) (Blaxter 1989).

Daily energy expenditure, including resting metabolism and an allowance for activity and reproduction is taken to be $0.4 W_j A^{-0.27}$ MJ/d (Taylor et al. 1981), where A is the mature mass and W_j is the nominal mass of each age class. Expressed in this way, the model allows any size of animal to be considered.

Daily food intake is a saturating function of plant biomass on whichever part of the range is being grazed, and is given by

$$I_j = I_{\max,j} \frac{V_i}{\beta + V_i} \quad \text{if } F_j + \frac{(I_j - E_j)}{m} < F_{m,j}$$

$$I_j = m(F_{m,j} - F_j) + E_j \quad \text{else} \tag{4}$$

The condition applies a metabolic constraint on intake such that maximum fat reserves for each age class ($F_{\max,j}$) is not exceeded. β is the value of V at which I is half its maximum value, and was estimated from the data of O'Reagain (1994) to be in the range 320–411 kg/ha for cattle grazing tropical swards.

Asymptotic intake when metabolic constraints do not apply is defined by the digestive constraint: the maximum daily throughput of plant material. This is related to animal size and food digestibility (d, proportion). For grass, the following expression for maximum daily Net Energy intake (MJ/d) has been derived, using the model of Illius and Gordon (1992, 1998):

$$I_{\max,j} = 0.034\, e^{3.57d} A^{(0.077\, e^{d} + 0.73)} u_g$$

$$\text{where } u_g = \left(\frac{W_j}{A}\right)^{0.75} \tag{5}$$

Diet and range selection

It is well known that cattle select green material and avoid dead. For example, Chacon and Stobbs (1976) compared diet composition during progressive defoliation of tropical swards, and their data show that the proportion of green leaf in the diet, G_d, is related to its proportion in the sward by

$$G_d = G_s^{0.2} \tag{6}$$

The standard error of the exponent was 0.032, $r^2 = 0.62$. This expression was used to describe diet selection in the model. Diet digestibility, d, is then calculated from the proportion of live and dead leaf in the diet, and from the digestibility of these components. Under conditions where animals have access to both range types in any given season (see below), then the area selected each day was that giving the highest daily energy intake rate, as calculated above.

Simulation procedure

Simulations were run for ten replicates of each of 105 continuous years, discarding results from the first five years to get rid of effects of the starting values of the state variables. Initial conditions were for $V_{l,1} = V_{d,1} = V_{l,2} = V_{d,2} = 500$ kg/ha and $N = 1.25 a_{\mathrm{DSR}}$. Each replicate was seeded with a particular value for the generation of replicate strings of pseudo-random numbers to simulate annual variation in rainfall. Annual records were collected at the end of the dry season of the total number of animals, and of plant growth and consumption in each range area.

The analysis of animal abundance was carried out on the natural logarithm of animal numbers ($\log_e(N)$), averaged over the last 100 years of each run, and its standard deviation ($\mathrm{SD}[\log_e(N)]$) was used to analyse the variability of abundance in each run (Gaston and McArdle 1994). Analysis of variance was carried out using the ten series of pseudo-random numbers as blocks. In cases where both series were analysed together in an unbalanced design, REML (in Genstat 5.3.2; Genstat 5 Committee, 1993) was used with replicate as a random effect.

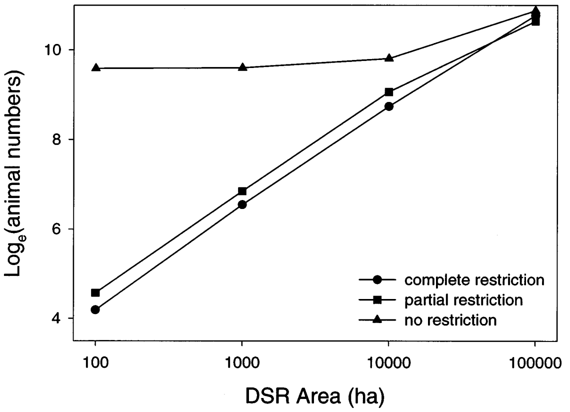

Fig. 1. Model results from Series 1: Mean animal abundance in response to increasing area of DSR, with WSR area held at 100000 ha, and with either no, partial or complete restriction in the seasonal accessibility of range areas. The data points are means of ten replicate 100-year runs at each of four levels of variability in DSR primary production (cv = 0, 0.1, 0.2, 0.3).

Experiments

The assumptions to be examined by the model are that seasonal segregation of foraging areas and the relative sizes and variability of each area affect plant-animal dynamics. To this end, the areas of DSR and WSR were varied independently in two series of experiments. In Series 1, DSR was varied from 100 to 100000 ha while keeping WSR at 100000 ha. In Series 2, WSR was varied from 1000 to 100000 ha, while keeping DSR at 1000 ha. Throughout, the annual cv of primary production on WSR was kept at 0.3, and the cv on DSR was varied from 0 to 0.3, to assess the effect of variability of DSR plant production. In each case, the effect of seasonal range restriction was examined by allowing the herbivore population to have access to: (1) the whole area throughout the year ('no restriction'); or (2) the whole area in the wet season but only DSR during the dry season ('partial restriction'); or (3) only WSR in the wet season and only DSR during the dry season ('complete restriction'). Defoliation intensity in each range area was assessed by determining, for each year, the consumption of green vegetation as a proportion of primary production.

The model was also run with no annual variation in rainfall on either range type.

Results

Mean herbivore population size

Model predictions of mean herbivore numbers were significantly affected by range restriction, range area and variability treatments ($p < 0.001$).

The effect of reducing the area of DSR while holding WSR at 100 000 ha was to reduce animal numbers in cases where partial or complete seasonal restriction in range use applied, but not otherwise (Series 1, Fig. 1). The same relationship between animal population size and DSR area was apparent when the area of WSR was increased while holding DSR at 1000 ha (Series 2, Fig. 2). Without any restriction in seasonal range use, animal numbers increased as WSR area was increased (Fig. 2a). In contrast, seasonal range restriction largely prevented animal population size from increasing in response to increasing WSR (Fig. 2b, c).

Fig. 2 also illustrates the negative effect on animal numbers of increasing the variability of DSR primary production while holding the WSR cv at 0.3. The back-transformed mean population size at cv = 0.3 was generally less than half the value at cv = 0. This effect was less for the unrestricted range treatment than in the

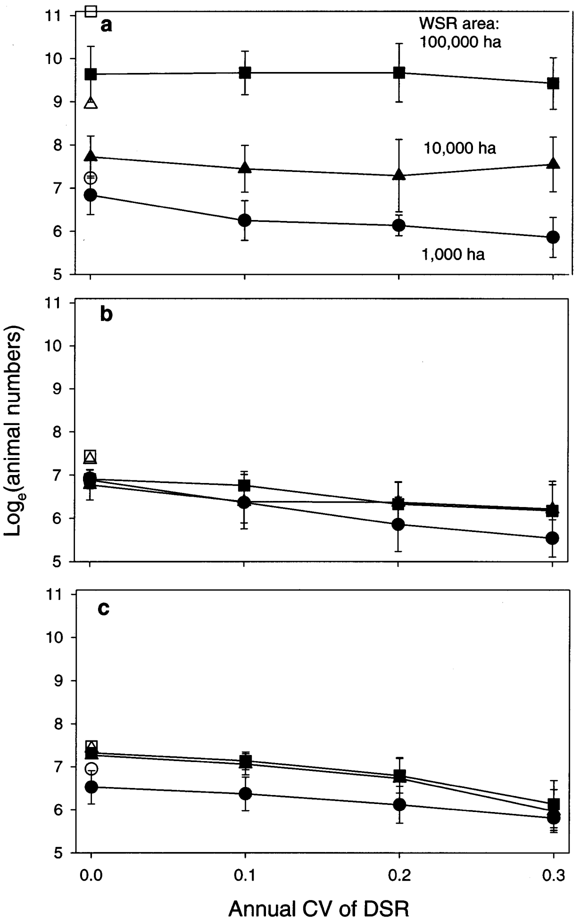

Fig. 2. Model results from Series 2: Mean animal abundance in response to increasing variability of primary production in DSR and with WSR area of 1000 ha (●), 10000 ha (▲), or 100000 ha (■). Three degrees of seasonal range restriction are compared: none (a); partial (b) and full (c). DSR range area was 1000 ha, and WSR cv of primary production was 0.3 throughout. The error bars show the SD of the ten replicates of each treatment combination. Open symbols show log$_e$ (N) predicted by the model when it was run without climatic variation.

Table 2. Annual variation in animal numbers, expressed as the standard deviation of $\log_e$ (animal numbers). The results are taken from Series 2 runs of the model.

Seasonal range restriction	Variability of primary production on WSR	Variability of primary production on DSR	WSR area (ha)		
			1000	10 000	100 000
None	0	0	0.20	0.21	0.30
	0.3	0	0.98	1.80	1.93
	0.3	0.1	1.67	1.84	1.86
	0.3	0.2	1.79	2.00	1.89
	0.3	0.3	1.85	1.81	2.18
Partial	0	0	0.04	0.03	0.04
	0.3	0	0.41	1.03	0.93
	0.3	0.1	1.20	1.45	1.12
	0.3	0.2	1.71	1.54	1.58
	0.3	0.3	1.87	1.66	1.73
Complete	0	0	0.04	0.04	0.04
	0.3	0	1.0	0.44	0.41
	0.3	0.1	1.22	0.82	0.76
	0.3	0.2	1.59	1.21	1.17
	0.3	0.3	1.81	1.85	1.83
Standard error of difference 0.212, 315 df					

scenarios in which range accessibility was subject to some degree of seasonal restriction ($P < 0.001$; Series 2, Fig. 2). Mean animal numbers were greater when the model was run without any climatic variation (open symbols in Fig. 2) than when variation was included.

The combined results from Series 1 and Series 2 can be summarised by the following regressions, which have highly significant main effects of DSR and WSR area and DSR variability, with no significant interaction ($r^2 = 0.96$):

$$\log_e(N) = \text{intercept} + 0.95 \log_e(a_{\mathrm{DSR}}) + 0.06 \log_e(a_{\mathrm{WSR}})$$

(partial range restriction)

where intercept $= -0.28, -0.67, -0.93, -1.16$, respectively, for DSR cv $= 0, 0.1, 0.2, 0.3$;

$$\log_e(N) = \text{intercept} + 0.88 \log_e(a_{\mathrm{DSR}}) + 0.10 \log_e(a_{\mathrm{WSR}})$$

(complete range restriction)

where intercept $= -0.10, -0.25, -0.58, -1.08$, respectively, for DSR cv $= 0, 0.1, 0.2, 0.3$.

These regressions show that animal numbers are closely dependent on the area of DSR when some degree of range restriction applies, and that a small positive effect of WSR area is also present.

Temporal variability in herbivore numbers

Table 2 shows the inter-annual variability in animal numbers, as assessed by SD[$\log_e(N)$], for each treatment, including values obtained when the model was run without any climatic variability. Annual variability in animal numbers was minimal when climatic variation was excluded, being almost entirely attributable to the dampening of oscillations arising from the initial values at the start of each run. Comparing the effect on SD[$\log_e(N)$] of constant and variable environmental conditions clearly shows that annual variation in rainfall provokes large variation in animal numbers, as expected. SD[$\log_e(N)$] increased significantly with increasing variability of DSR ($P < 0.001$). As variability in primary production increased from cv $= 0$ to cv $= 0.3$, SD[$\log_e(N)$] increased from 1.57 to 1.95 ($t_{315} = 3.1$) without range restriction, from 0.79 to 1.75 ($t_{315} = 7.8$) with partial restriction and from 0.62 to 1.83 ($t_{315} = 9.9$) with complete range restriction. Most of the difference between the three range restriction scenarios is due to the differences in $\log_e(N)$, as can be seen from the scenarios' similar values of SD[$\log_e(N)$] at a WSR area of 1000, when they all had similar $\log_e(N)$ for any given cv of primary production on DSR. SD[$\log_e(N)$] was unaffected by the area of WSR available ($F_{2,315} = 0.15$).

Defoliation intensity

Fig. 3 shows examples of the frequency distribution of annual defoliation intensity (the proportion of plant growth consumed when green) under the three range restriction scenarios. The data are from Series 2 with WSR area = DSR area = 1000 ha and with DSR production cv $= 0$ and 0.3. In these cases, there was little difference between range restriction scenarios in animal numbers, and so the main differences are between scenarios themselves. The negative effect of DSR variability on animal numbers only tended to reduce defoliation intensity slightly, as shown by the slightly higher frequencies of low defoliation intensities (see also

Fig. 4). It is not surprising that complete seasonal restriction in range use caused the only major divergence in defoliation intensities between range areas, because DSR was inaccessible when most green material was present (Fig. 3c). In this case, concentration of the animal population on WSR during the growing season produced more intense defoliation than occurred under the less restrictive scenarios.

Defoliation intensity recorded when the model was run without any climatic variation is given in Table 3. Note that these values were virtually constant, having a cv in the range 0 to 0.01, in contrast to the range of intensities observed when the model was run with climatic variation (Fig. 3).

Defoliation intensity is obviously a function of the animal population density supported by the system. To separate the effects of animal numbers from effects of the degree of range restriction and DSR variability, the arithmetic mean animal density (i.e. N/[DSR area + WSR area]) was used as an independent variable. This estimate of animal density was chosen because it reflects more closely than does $\log_e(N)$ the wide variability in animal numbers which is the cause of the spread of defoliation intensities. A new dependent variable was derived to express the average severity of defoliation over each 100-year run. This was the proportion of years in which defoliation intensity exceeded some arbitrary threshold, chosen to be 0.3. This is plotted against animal density in Fig. 4, for each range restriction scenario. Without any restriction in seasonal range use (Fig. 4a), defoliation intensity of WSR exceeded 0.3 in about 0.15 of all years, or roughly every 6–7 years, compared with every 3–6 years for DSR, depending on the variability of production there. This applied regardless of WSR area. Under partial range restriction (Fig. 4b), defoliation intensity of DSR only exceeded 0.3 in about 1 year in ten, and then only at low DSR cv. WSR was generally less severely defoli-

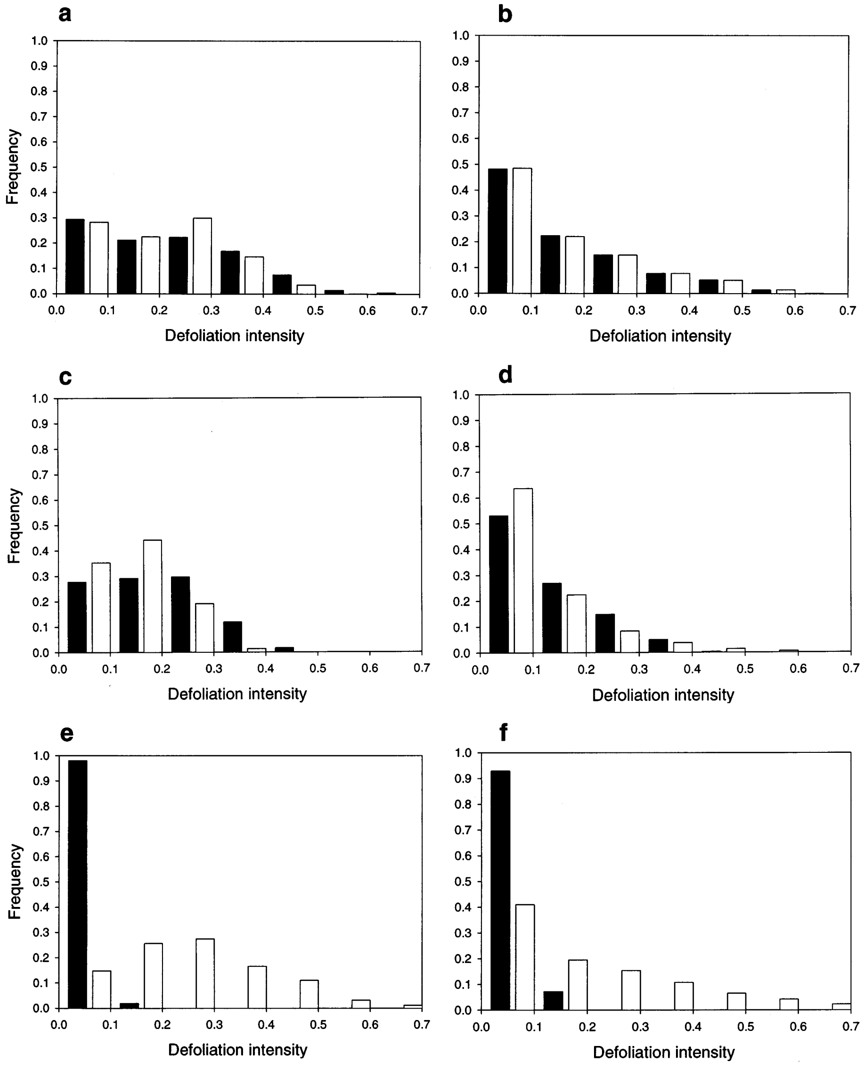

Fig. 3. Frequency distributions of annual defoliation intensity for DSR (black) and WSR (open) under the three degrees of seasonal range restriction: none (a, b); partial (c, d) and full (e, f) and when the cv of primary production on DSR was either 0 (a, c, e) or 0.3 (b, d, f). DSR and WSR areas were each 1000 ha, and WSR cv of primary production was 0.3 throughout (Series 2).

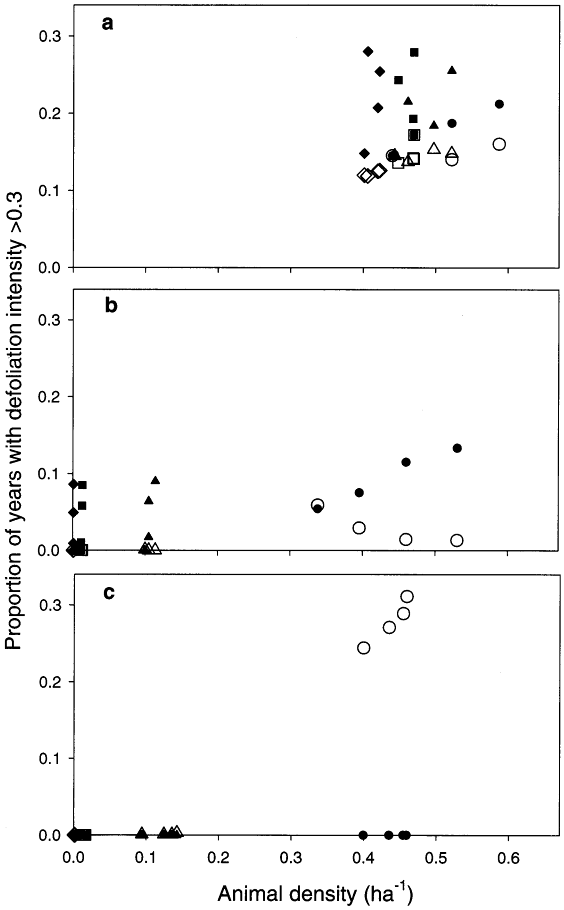

Fig. 4. The proportion of years in which defoliation intensity on WSR (open symbols) or DSR (closed symbols) exceeded 0.3 in relation to mean animal density, for each degree of seasonal range restriction: (a) none; (b) partial; and (c) full. In each case WSR area was 100000 ha and DSR area was 100 ha (diamonds), 1000 ha (squares), 10000 ha (triangles), or 100000 ha (circles) (Data from Series 1). Each point is derived from ten replicate runs of 100 years at either 0, 0.1, 0.2 or 0.3 cv in DSR primary production.

ated. With complete seasonal segregation of range use (Fig. 4c), DSR was never defoliated above the threshold intensity, because animals did not have access to it during the growing season. On the other hand, WSR incurred a defoliation intensity of more than 0.3 with an annual frequency of about 0.2–0.3 when the area of DSR and WSR were both 100000 ha. At lower areas of DSR, animal density was never sufficient to result in defoliation intensity being higher than the threshold value of 0.3.

Discussion

Semi-arid grazing systems appear to vary widely in the propensity to respond to herbivore pressure by exhibiting species change, soil erosion and loss of productive potential, although there is some doubt about whether 'degradation' feeds through to reduced secondary production (Illius and O'Connor 1999). In attempting to delineate the factors likely to predispose systems to degradation, Illius and O'Connor (1999) identified, along with soil characteristics, the relative area and variability of WSR and key resource areas, referred to here as DSR. The simulations carried out here were designed to test the hypotheses that temporal and landscape heterogeneity are determinants of herbivore impact, and that climatic variability may intensify episodes of impact in a manner which may provoke ecological change.

The results show clearly that animal population size and vegetation defoliation intensity are affected by the relative size and variability of key resource areas and outlying areas (DSR and WSR, respectively). Herbivore numbers are reduced as plant production on DSR becomes more variable, due to the increased temporal variability in animal numbers. There was greater sensitivity of animal numbers to increasing variability in primary production if some degree of range restriction was applied, due to a decrease in spatial buffering of climatic variability (compare declines in $\log_e(N)$ with increasing DSR cv in Fig. 2b and c with virtually no decline in Fig. 2a). The negative effect of variability on mean animal population size is to be expected (e.g. Burgman et al. 1993) because of the asymmetry in the positive and negative responses of population size to good and bad environmental conditions. In other words, population decline in bad years can greatly exceed the capacity of the population to grow in good years.

Table 3. Mean annual defoliation intensity under constant environmental conditions. Uniformly low SD were recorded: from 0 to 0.0023

Seasonal range restriction	Range type	WSR area (ha)		
		1000	10 000	100 000
None	DSR	0.23	0.25	0.28
	WSR	0.23	0.23	0.22
Partial	DSR	0.18	0.11	0.10
	WSR	0.15	0.04	0.004
Complete	DSR	0.07	0.09	0.09
	WSR	0.27	0.04	0.005

The results support the simple deduction that defoliation intensity of WSR will be greater if key resource areas are present than if they were absent, because they play the dominant role in supporting the animal population. Provided that animals show some degree of seasonal segregation of range use, population size is a function of DSR area (**P1**; Fig. 1), and this translates directly into the intensity of defoliation (**P3**; Fig. 4). It is the resources available during the dry season that, as Sinclair (1975) argued, determine how rapidly animals exhaust their body fat reserves. Therefore it is the supply of these resources that regulates the size of the animal population and with which the animal population is in long-term equilibrium (**P1**). Accordingly, Illius and O'Connor (1999) argued that key resource and outlying areas must operate in a source-sink manner, with key resource areas maintaining, by definition, a higher level of herbivory in outlying areas than these could support on their own. Uncoupled herbivory in outlying areas will therefore be more severe than would occur if the animal population was coupled to them. A similar conclusion was drawn by Oksanen (1990) in her model of heterogeneous habitat complexes, but without temporal variation. She showed that migration of herbivores from high-quality habitat allows 'spillover exploitation' of poor habitat that would otherwise not support herbivores, and that the degree of such exploitation is positively related to the proportion of the area consisting of high-quality habitat, as in our present model. The model of Fryxell et al. (1988), some of whose results anticipate those of our model, also showed that seasonal migration between wet and dry season range can lead to increased herbivore numbers. However, the main disparity in their model between co-existent ungulate populations with either resident or migratory strategies was due to escape from predators resident in DSR.

Only a small positive contribution of variation in WSR area to variation in animal population size is revealed by the regression summaries of model results for scenarios with some degree of seasonal separation of range use. This effect must result from a dampening in the annual variation in body reserves at the end of the wet season, which carry over from WSR to DSR. It can therefore be concluded that, in spatially heterogeneous systems, ungulate population size is regulated largely by dry-season resources, and that the population is largely, but not wholly, uncoupled from wet-season resources. WSR might therefore be classified as a non-equilibrium area of the system if it is both inaccessible during the dry season and if it is considerably greater than DSR area (**P2**).

High ratios of DSR:WSR supported animal populations which were sufficient to result in quite high defoliation intensities of WSR. An extreme case of this effect would occur if animals were maintained on supplementary food over the dry season. Then, their numbers would tend to become completely uncoupled from range resources, and defoliation intensity of WSR would be a function of the numbers maintained. Uncoupling of animal and plant populations has been shown, in theory, to increase the risk of catastrophic impacts of herbivory (Rietkerk and van de Koppel 1997). The more general case is that, where there are substantial and dependable forage resources available to the animal population during the dry season, when population size is regulated by the availability of these resources (Sæther 1997), the effect is to reduce the coupling of the population to resources available elsewhere in the system, with the result that defoliation intensity there can be much higher than would otherwise occur.

Illius and O'Connor (1999) argued that droughts could focus the effects of herbivory because they result in low primary production relative to animal population size, and hence demand (**P4**). The effect of this was evident in the data collected from the model: analysis of annual defoliation intensity showed that annual rainfall and animal numbers each explained about 25% of variation. However, the severe defoliation intensity at the onset of serious droughts caused sufficient animal mortality by the end of the season, when results were recorded, to obscure the predominant effects of animal numbers. Thus, about 70% of variation in defoliation intensity was accounted for by the previous season's mean animal numbers, reflecting the higher numbers present before a drought-induced population crash. Current season's rainfall typically accounted for a further 10–15% of variation. The argument that droughts focus herbivore impact is upheld, therefore, but a more general conclusion is that systems with highly variable animal numbers show a wide range of annual defoliation intensity (see Fig. 3). This is primarily a direct consequence of fluctuations in animal density, with high animal numbers and low rainfall provoking transient but extreme peaks in defoliation intensity. Accordingly, drought potentiates the impact of high herbivore density (Hodgkinson 1995, O'Connor 1995).

By comparison with a stable environment, for which the model predicts virtually stable animal numbers and constant, low defoliation intensity, variation in annual rainfall causes wide fluctuations in animal numbers. Under climatic variation, animal numbers can build up high enough to impose much higher defoliation intensities than under a constant regime (compare Figs 3 and 4 with Table 3). Note that the average densities predicted by the model are not much different from those observed by Scoones (1992) in southern Zimbabwe: he observed densities between 0.15 and 0.55 and between 0.2 and 0.6 animals/ha in areas with about 550 and 800 mm mean annual rainfall, respectively. But what intensity of defoliation is likely to have ecological consequences? It cannot be assumed that grazing animals have an equal effect on all grass species present. On the contrary, animals defoliate grass species selectively, with the result that herbivore impacts are unequal across species. For example, O'Reagain and Rau (1995) showed that only when 80–100% of preferred and intermediate grass species had been defoliated by cattle or sheep were the least-preferred grass species grazed. Brown and Stuth (1993) argued that cattle selectivity was the most important factor resulting in change in community composition, which was due to differences in the degree of defoliation of more- and less-preferred grass species. Ash and McIvor (1998) used cattle to apply 'low', 'medium' and 'high' defoliation intensities of 0.13, 0.22 and 0.42, respectively, for eight weeks during the early wet season, and found that selective grazing by the cattle subjected *Themeda triandra* to defoliation intensities of 0.39, 0.6 and 0.73, respectively. The medium and high treatments were sufficient to reduce regrowth in the following year, and two years after this single period of grazing the frequency of *Themeda* was lower and the frequencies of annual grasses and forbs were higher as a result of the high defoliation treatment. Their data show, therefore, that an average defoliation intensity of 0.3 is sufficient to have an impact on the preferred species, which bears the brunt of defoliation.

Although fine-scale spatial heterogeneity of defoliation impacts has been ignored in the present model, it is evident that they do occur, and may be important agents of ecological change. Patch grazing occurs where green regrowth of defoliated plants presents higher nutrient density to animals than surrounding vegetation, encouraging re-grazing (Mott 1987, Hobbs and Swift 1988). Although the precise origin of these patches is seldom documented, patch grazing is associated with altered species composition, changes in soil conditions and lower primary production (MacDonald 1978, Fuls 1992).

This study has shown that climatic variability, which causes annual variation in primary production and fluctuations in animal population size, both increases the range of annual defoliation intensities and produces periodic intense defoliation episodes. Coupled with spatial localisation of herbivore impacts, due to seasonal ranging behaviour and selection at the level of plant species and patches, this is likely to make these environments more, not less, prone to ecological change.

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