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# Dynamics of large herbivores in deserts: kangaroos and caribou

Graeme Caughley and Anne Gunn

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The dynamics of desert plant-herbivore systems are similar whether the deserts are hot or cold, an assertion we support with information on the dynamics of red kangaroos and caribou. The essence of these systems is structural simplicity combined with high year-to-year variation in weather. We argue that such conditions simplify study of the mechanisms underlying changes in rate of increase of herbivores. Except where the herbivore is intrinsically regulated by spacing behaviour, the systems are best summarised by the functional and numerical responses of the herbivores to available forage, coupled with the growth response of the plants. A graphing of rate of increase against density provides little insight even though these systems are density-dependent in the formal sense. We show that long-term aperiodic fluctuations characteristic of such systems are, at least for kangaroos, a mathematical consequence of unpredictable short-term fluctuations in weather. Even when the weather has no time trend there will be marked trends in numbers of herbivores, either up or down, on a time scale of one or two decades. Such trends are intrinsic to the system and do not necessarily reflect special and persistent causes. Similar fluctuations of caribou numbers may be, at least in part, of similar origin.

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Only modest progress has so far been made in divining the causes underlying changes in the population size of vertebrates. Most such attempts have concentrated on establishing correlations between the rate of increase of an animal population and the density of that population, and although these studies have provided useful insights they do not themselves reveal what is driving changes in density. We suspect that what we identify, rightly or wrongly, as a lack of progress, has two causes. First, researchers are making the task too difficult for themselves by studying complex systems, and second they tend to study systems that are fairly stable. The first putative cause is intuitively obvious but the second is not: the causes of stability can be deduced only when the system is perturbed.

We argue that plant-herbivore systems in deserts meet our two preconditions for ease of studying dynamics: they are simple and they are highly labile. As exam-

ples we offer the red kangaroo *Macropus rufus* (Desmarest) to represent hot desert herbivores and caribou *Rangifer tarandus* (Linnaeus) to represent those from cold deserts. We note that such simple systems comprising only a few species of large herbivores are relatively easy to investigate, and that in both climatic zones process studies leading to consonant models of the dynamics of the whole system provide far deeper insights than do those studies of correlation between density and rate of increase which lead largely to single-species predictive models.

## Components of a plant-herbivore system

The main elements of the interaction between a herbivore and the plants that it eats can be summarised as four response functions:

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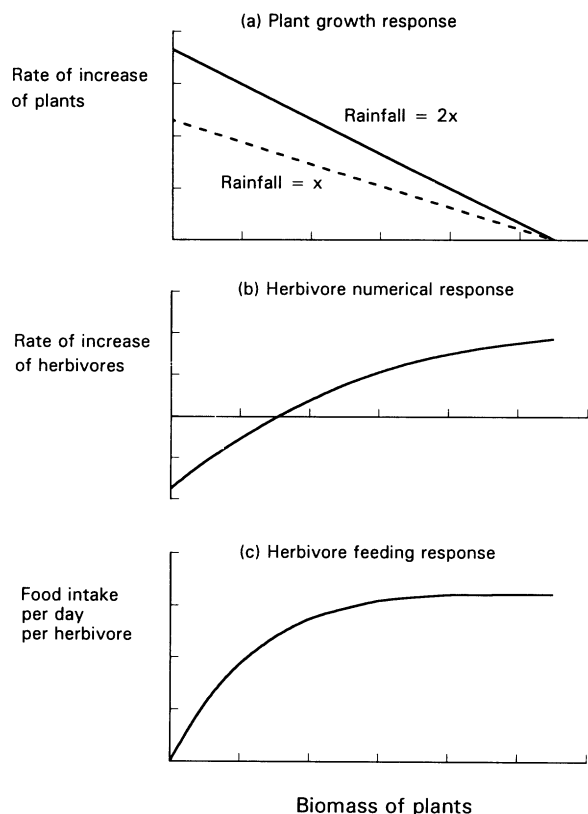


Fig. 1. A possible configuration of response functions of a plant-herbivore system, each of which is graphed against the biomass of available forage per unit area.

- (1) rate of increase of edible plant biomass per unit area as a function of its standing density and such environmental attributes as the temperature of the air and the amount of moisture in the soil (the plant growth response);
- (2) rate of intake of food per herbivore as a function of the standing density of edible vegetation (the herbivore's feeding response, also called the functional response).
- (3) rate of increase of the herbivore population as a function of the standing density of the edible vegetation (the herbivore's numerical response); and
- (4) rate of increase of the herbivore population as a causal function of its own density (the herbivore's intrinsic response).

Fig. 1 shows a possible configuration of the first three response functions, each graphed against the biomass density of edible vegetation. The fourth, which depicts spacing behaviour, has not been identified as a significant influence upon the dynamics of either kangaroos or caribou, but it is listed here for completeness. If these four responses were estimated for a simple plant-herbivore system comprising one species of herbivore and a

restricted suite of food plants, they would in combination predict the reaction of the system to a given change in weather, animal density or plant density. The causality of the change can be tracked because each response function represents something real. However those responses cannot usually be calculated easily because they require their various dependent variables to be estimated across a broad range of edible plant biomass, and that is usually not forthcoming from a relatively stable system. Hence our second dictum that the easiest system to study is one that is subjected to considerable environmental variation, particularly in year-to-year weather, and which therefore fluctuates violently.

## Weather variability and unpredictability

### Australia

We used Menindee at the edge of Kinchega National Park (New South Wales, 32°S, 142°E) as a representative weather station for arid Australia. A hundred years of records were analysed (Robertson et al. 1987). The climate is characterised by high summer temperatures with evaporation greatly exceeding rainfall. Annual rainfall is low at 236 mm but with high variability as indicated by the coefficient of variation between years of 45%. The timing of the rainfall is unpredictable within and between years: the coefficient of serial correlation between rainfall in the same three-month season from one year to the next is only 0.05, and between consecutive twelve-month periods is 0.13.

### The Arctic

We used Sachs Harbour (Northwest Territories, 72°N, 125°W) as a representative station for the western Arctic. Twenty-eight years of weather records were analysed. The climate is cold and dry with temperatures high enough for plant growth only between June and August. High coefficients of variation of weather variables (Table 1) attest to the general unpredictability of the weather. Serial correlation between one year and the next yielded a non-significant 0.26 for snow depth at the end of May and a non-significant -0.21 for degree days above 0°C. However serial correlation between consecutive years is significant at 0.49 for snowfall over the 9 months of winter.

Table 1. Climate and its variability at Sachs Harbour.

	Mean	SD	CV%
Snow cover (mm) last day May	135	118	87
Total snowfall (mm)	684	285	42
Thawing degree days (above 0°C)	430	124	29
Growing degree days (above 5°C)	124	58	47

Table 2. Kangaroo population estimates in 1981, 1984, and 1987 within areas of each state common to all three surveys. Estimates for grey kangaroos are reckoned to be underestimates. Source: Fletcher et al. (1990).

Species	State	1981	1984	1987
Red	Queensland	1 362 000	1 333 000	1 466 000
	New South Wales	3 837 000	1 663 000	2 770 000
	South Australia	1 138 000	745 000	963 000
	Western Australia	1 004 000	1 999 000	2 329 000
Southern grey	Queensland	104 000	55 000	76 000
	New South Wales	876 000	242 000	806 000
	South Australia	198 000	91 000	208 000
	Western Australia	424 000	666 000	652 000
Eastern grey	Queensland	2 468 000	2 040 000	2 863 000
	New South Wales	2 010 000	929 000	1 824 000

## System dynamics

### Weather, kangaroos and plants

The abundance of the red kangaroo, the southern (= western) grey kangaroo *Macropus fuliginosus* (Desmarest) and the eastern grey kangaroo *Macropus giganteus* Shaw have been monitored in most regions of Australia, starting about 1975. The trends have been summarised at continental scale by three publications (Caughley et al. 1983, Grigg et al. 1985 and Fletcher et al. 1990) which serve also as a source of references to the surveys of the individual regions. These surveys show that kangaroos increased over most of Australia throughout the

1970s in response to a decade of above-average rainfall. In the winter of 1982 the rains failed in south-eastern Australia. During the subsequent spring and summer the drought spread out and intensified until broken by widespread rains in March 1983. The three species of kangaroo declined by about 40% across more than a million square kilometres, most of the deaths occurring over the four months of summer at a massive  $r = -1.62$  on a yearly basis (Caughley et al. 1985). The drought did not spread to the western half of the continent and so the kangaroos there were not affected. Subsequently kangaroos built up again during the mid and late 1980s which were years of generally favourable weather. Table 2 lists estimates of abundance from 1981 through 1984 to 1987 for the areas of each state common to the three surveys. It shows that the general trend of high-low-high for the eastern states is not duplicated in Western Australia.

The dependence of rate of increase of kangaroos on environmental conditions determined principally by weather is apparent from the large-scale aerial surveys, but those data do not of themselves map the causal pathways or reveal the strength of interaction between components of the plant-herbivore system. Instead the system must be studied at a scale of finer resolution. We use Kinchega National Park (440 km<sup>2</sup>) and the surrounding sheep stations as an example of an arid Australian plant-herbivore system. Robertson (1987) showed that the plants there respond rapidly to rain. Rate of change of the biomass of forbs and grasses is affected by any fall of rain greater than 15 mm and its ungrazed standing biomass is predictable from the total rainfall over the previous six months. A fall of rain in winter germinated mainly forbs whereas the same precipitation in summer germinated mainly grasses. However, the addition to the biomass is much the same irrespective of calendar month. These findings allowed Robertson (1987) to construct a simplified plant growth response in which species were aggregated and their growth plotted against only rainfall and plant biomass (Fig. 2).

The area hosts four species of large kangaroo (adult

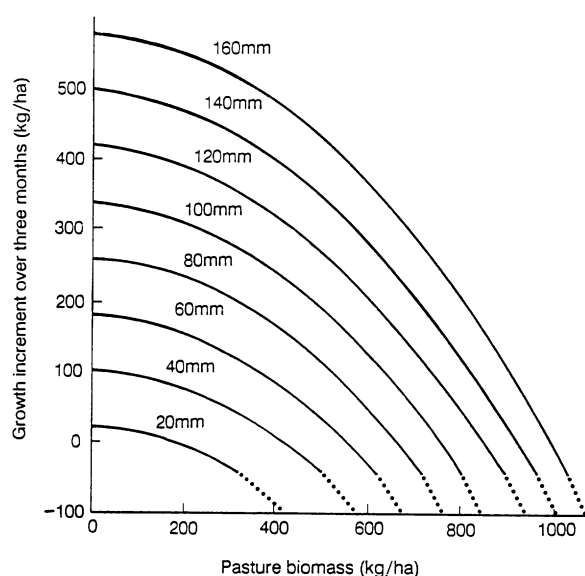


Fig. 2. Plant growth response of grasses and forbs at Menindee, Australia, as a function of their standing biomass at the beginning of a three-month period and the rainfall during that period. The regressions are a tight fit to measured growth and rainfall over 14 three-month periods. Note that the threshold rainfall allowing growth is 15 mm. Source: Robertson (1987).

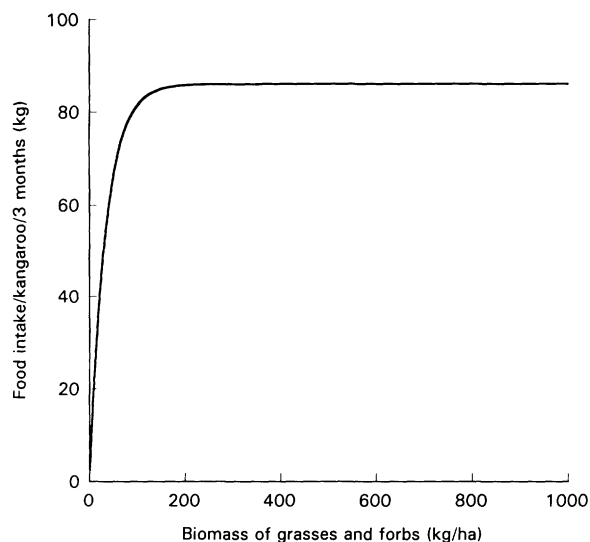


Fig. 3. Herbivore feeding response: fitted food intake in kg dry weight per red kangaroo over three months, as a function of availability of forage. The data are from graze-down experiments. Source: Short (1987).

males about 50 kg and adult females 25 kg for all four species) but only two of these, the red kangaroo and the southern grey kangaroo are common. We limit our discussion of the plant-herbivore system to the red kangaroo and the herb layer that provides its food.

Short (1987) estimated the feeding response of red kangaroos by carefully measuring the rate at which they grazed down vegetation in pens on Kinchega National Park (Fig. 3).

The abundance of kangaroos was tracked by aerial surveys. The density of red kangaroos in Kinchega National Park between 1973 and 1984 varied from a low of 10/km<sup>2</sup> to a high of 40/km<sup>2</sup> (Bayliss 1987). That included a population collapse of 45% in the summer of 1982/83 as a drought bit. These data, and measurements of the biomass of the herb layer, allowed construction of a numerical response curve (Fig. 4) for red kangaroos (Bayliss 1987). It is convex upward, thereby imparting an asymmetry to the effect of variation in plant biomass on the dynamics of kangaroo populations. An increase in plant biomass generates an increase in kangaroo numbers whereas a reduction in plant biomass triggers a decline. But for the same absolute variation in plant biomass, a decline in biomass has a much greater effect on the dynamics of the kangaroos than does an increase. The kangaroos decrease much faster than they increase. Thus, a drought can cause a rapid and massive drop in numbers but an equivalent time of plenty must last much longer to produce an increase of the same magnitude.

The structural equations of the red kangaroo grazing system at Menindee can be summarised as follows:

Rainfall (R):

	Mean (mm)	SD
Dec-Feb	62	59
Mar-May	57	47
Jun-Aug	59	34
Sep-Nov	61	44
Annual	236	107

Plant growth response:

$\Delta V = -55.12 - 0.01535V - 0.00056V^2 + 2.5R$ , where  $\Delta V$  = the growth increment to standing biomass in kg/ha over 3 months,  $V$  = the standing biomass in kg/ha at the beginning of those 3 months, and  $R$  = rainfall in mm over those three months. The 2.5 coefficient of  $R$  used here differs from Robertson's (1987) 3.946 for reasons given by Caughley (1987:164).

Feeding response:

$I = 86(1 - e^{-V/34})$ , where  $I$  = intake of food in kg dry weight over 3 months, per red kangaroo, assuming a mean body weight of 35 kg; from Short (1987).

Numerical response:

$r = -1.6 + 2(1 - e^{-0.007V})$ , where  $r$  = exponential rate of increase of red kangaroos on a yearly basis; from Bayliss (1987) as modified by Caughley (1987).

Typical population trends can be built with these equations. Rainfall is simulated as a sequence of random draws from the mean and standard deviation of the seasonal rainfall given above, and the consequent

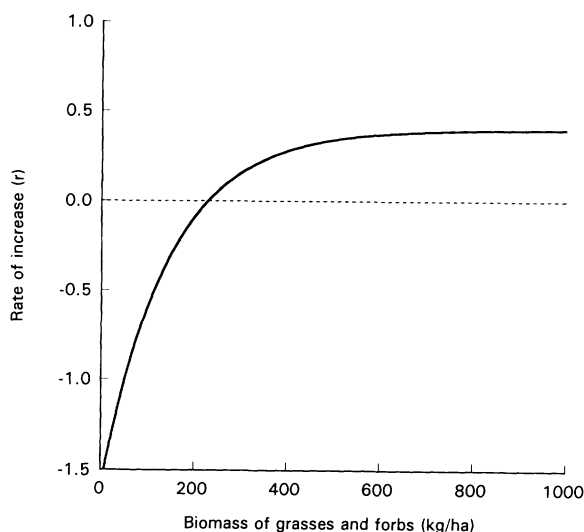


Fig. 4. Herbivore numerical response: fitted exponential rate of increase of red kangaroos as a function of availability of forage. Rate of increase is zero at a little over 200 kg/ha dry weight of forage. The regression was fitted to 10 points, four from increasing populations and six from decreasing populations. Pasture biomass varied between 10 and 1000 kg/ha dry weight. Source: Bayliss (1987).

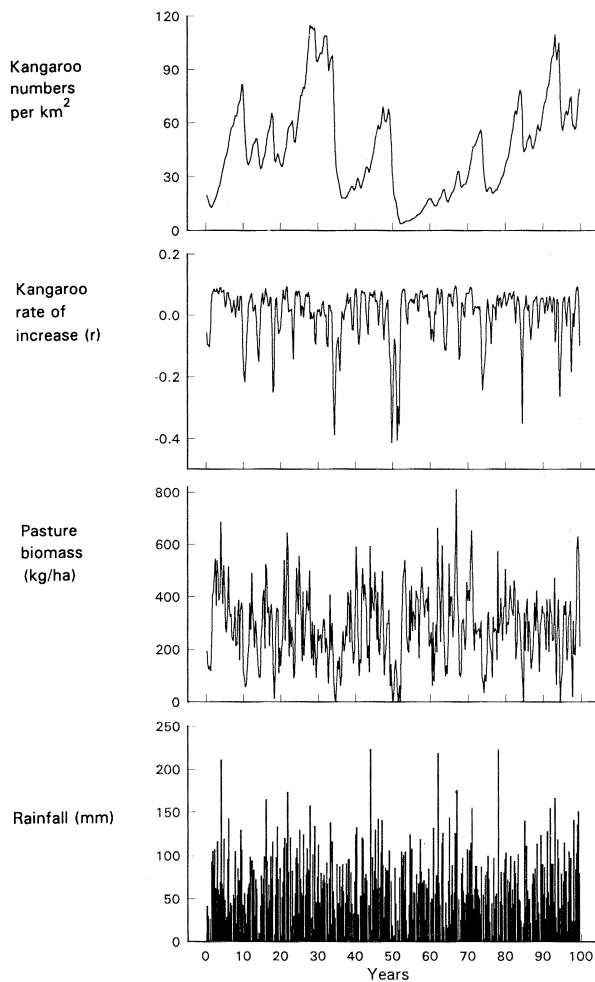


Fig. 5. The bottom histogram shows modelled three-monthly rainfall drawn from the Menindee climate. The next graph up is the biomass of grasses and forbs that would be generated by that rainfall and reduced by the grazing of kangaroos. Above that is rate of increase of kangaroos, on a three-monthly basis, as it reacts to plant biomass; and the top graph is the trend of red kangaroo numbers generated by the run of rates of increase directly below it.

changes in vegetation biomass and kangaroo numbers can be calculated accordingly. Initial conditions are not highly influential: the system remembers previous plant biomass for only 3 years but the memory of kangaroo density can linger for 10 years.

Fig. 5 shows typical time trends in plants and kangaroos as generated by the equations describing the unpredictable rainfall and the responses to it of the plants and herbivores. The rainfall of this region takes the form of high-amplitude, high-frequency fluctuations. The herb layer, whether grazed or ungrazed, generates a similar trace of high-amplitude, high-frequency fluctuations as it reacts speedily to the rainfall or the lack

thereof. The fluctuations are paralleled by similar but more constrained fluctuations in the kangaroos' rate of increase as the population reacts dynamically to variations in food supply. Those rates are truncated above, reflecting that there are physiological constraints on maximum rate of increase but considerably less so on rate of decrease. The trend of kangaroo density differs from the other three, comprising fluctuations of high amplitude but of low frequency. Perhaps that might have been predictable from first principles. Present den-

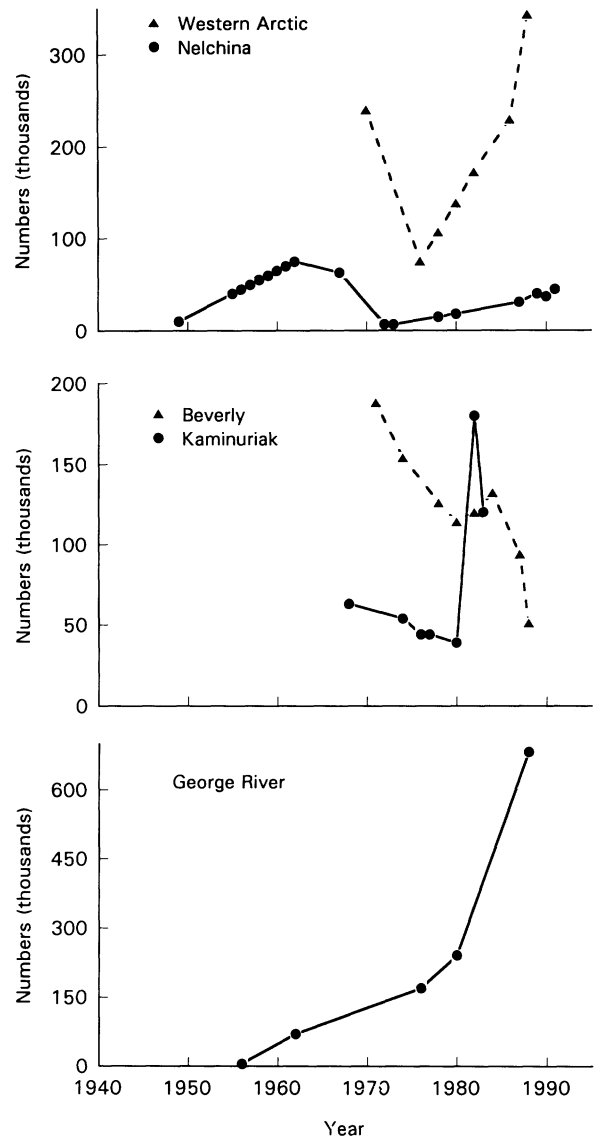


Fig. 6. Trends of Canadian and Alaskan caribou herds. The estimates are from Messier et al. (1988) for George River, Heard and Calef (1986) for Kaminuriak, Heard and Jackson (1989) for Beverly, and Van Ballenberghe (1985), Lieb et al. (1988) and J. D. Woolington (pers. comm.) for the Nelchina herd.

sity is an integration of past rates of increase, not of present conditions. Density is thus smoothed and lagged with respect to environmental conditions.

### Weather, caribou and plants

Data on fluctuations in the numbers of arctic herbivores is piecemeal. Aerial surveys of Pearly caribou (*Rangifer tarandus pearyi*) record marked fluctuations of density on the High Arctic Islands and on Banks Island (Miller 1991). Caribou have declined on Banks Island from 11000 in 1973 to 900 in 1991 ( $r = -0.14$  on an annual basis). They suffered at least two substantial die-offs in the mid-1970s. In contrast, during the 1970s and 1980s, the numbers of caribou on the neighbouring island of Victoria increased after a decline in the 1920s which followed a period of high numbers: the rates of increase and decrease were unmeasured (Miller 1991). Caribou numbers on the High Arctic Islands slumped by 40–60% in the winter of 1973–74 after unusually heavy snowfall and icing prevented the caribou from feeding. The subsequent trends of the caribou numbers varied between the different High Arctic islands (Miller 1991). Meldgaard (1986) traces a similar picture of wide fluctuations in the numbers of caribou over many decades on Greenland: the sequence of peak and trough tended to repeat over 30–50 years and were asynchronous among areas.

Although often lacking the rigour of a designed census, the reports of changing abundance of caribou from arctic mainland areas are remarkably consistent. They tell of short-term fluctuations in density and wider swings over the longer term. The George River herd of woodland caribou (*R. t. tarandus*) of eastern Canada was large in the 1880s but declined sharply thereafter until the 1920s (Fig. 6). The herd increased between 1954 and 1984 at an annual rate of  $r = 0.14$  but began to decline again in the late 1980s (Messier et al. 1988). The barren-ground caribou herds (*R. t. groenlandicus*) of the Northwest Territories, such as the Kaminuriak, Beverly and Bathurst, have fluctuated in a similar manner (summarised in Hall 1989). The Kaminuriak herd was reputedly 100000 strong in the 1940s but had by the early 1970s declined to an estimated 63000. The decline continued through the 1970s. A reversal of fortune was apparent by the early 1980s, the herd increasing through the 1980s to an estimated size of 180000 (Fig. 6). The Nelchina herd of Alaska grew rapidly from a trough in the 1930s to about 90000 in 1964 (Van Ballenberghe 1985). Subsequently it declined to 8000 in 1972–73 and then increased to 31000 in 1987 (Lieb et al. 1989). The Western Arctic caribou herd dropped from 240000 in the early 1970s to 75000 in 1976 before recovering to 343000 in 1988 (Machina 1992). Examples of fluctuations in numbers of caribou or reindeer not exposed to predation are to be found in Skogland's (1985) review of the population dynamics of wild Norwegian reindeer and in Leader-Williams (1988). The overriding impres-

sion from these accounts is that the caribou is a species with highly labile population dynamics.

The numerical response of caribou to available forage has not been measured, but circumstantial evidence points to a strong relationship between the flush of spring growth and the condition, lactation, fecundity and calf survival of the caribou (Thomas 1982, White 1983, Parker et al. 1990). The onset of the availability of new plant growth is dependent on the unpredictable timing of the snow melt.

The amount of forage available to an individual animal in winter is determined by how much remains from the previous growing season (absolute food supply) and how much of that is close enough to the surface of the snow for the animal to find and uncover it (relative food supply). Thus, a food shortage may be absolute, but more commonly it is a shortage only relative to the animal's ability to find and use it. The timing of snow melt and thus the initiation of plant growth varies between years: the coefficient of variation for snow depth at the end of May is 87%. Arctic plants initiate their growth under snow cover during the initial phases of snow melt (Svoboda 1977). Their annual cycle of growth has a relatively fixed duration so variation in the length of the growing season has less effect on standing crop of green forage than does the warmth of the season as measured in degree days above 5°C. But this is highly variable with a coefficient of variation of 47% (Table 1).

White et al. (1981) estimated the feeding response (rate of intake per animal per day as a function of available forage density) for three sex-age classes of reindeer in wet sedge meadows in summer. A similar analysis, utilising much of the same data, is given in Skogland (1984: Fig. 23). These provide the same measure as was estimated subsequently for kangaroos (Short 1987). The relationship for caribou may or may not differ substantially according to whether the diet is mainly lichens, or dead grass in winter, or mainly forbs and grasses. Arctic island caribou feed while on the move on smaller and scattered plants along beach ridges. They are therefore likely to have a feeding response curve that rises steeply and plateaus at relatively low plant density.

### Discussion

The most striking comparison between the hot desert and cold desert plant-herbivore systems is not the differences but the similarities. The weather of both habitats, particularly those components of climate that determine plant growth, vary prodigiously from year to year. The growth and decline of populations of the large herbivores is eerily alike: swings of high amplitude and of aperiodic low frequency. In both cases a high proportion of the variation in the herbivores' rate of increase is clearly a reflection of extremes of weather, unpredict-

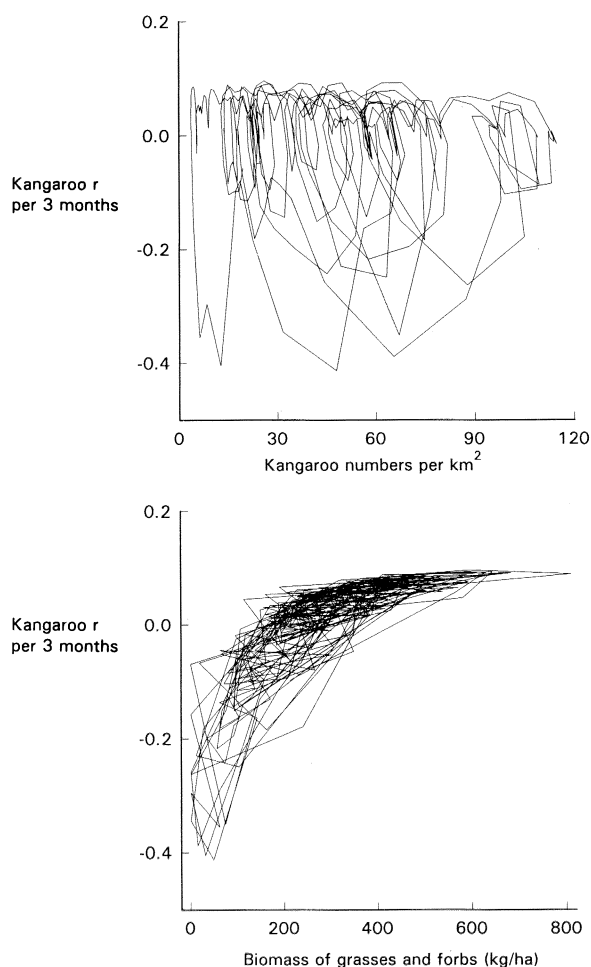


Fig. 7. Modelled rate of increase of red kangaroos, on a three monthly basis, taken from Fig. 5. The trends are graphed first against kangaroo density and then against the biomass density of grasses and forbs, showing that in this system the latter is a tighter predictor of herbivore rate of increase.

able in their timing and variable in their duration. A drought affects a kangaroo in much the same way as a period of excessive snow cover affects a caribou. Both reduce the supply of available forage. A fall of rain boosts the food supply of a kangaroo much as a warm summer stimulates the growth of forage needed by a caribou. The essence of the similarity is that both plant-herbivore systems face unpredictable weather.

The major difference is a more predictable seasonality for the caribou than for the red kangaroo. Time lags between a change in forage availability and a change in birth rate are also different, being in the region of 6 months for caribou and 3 months for red kangaroos. Time lags between a change in forage availability and a change in rate of mortality are likely to be short in both systems.

Populations of both red kangaroos and caribou appear to be buffeted, and occasionally hammered, by changes in the availability of food mediated entirely by capricious weather. But for kangaroos certainly, and for caribou probably, appearances are deceptive. The kangaroos were not completely at the mercy of the weather. Instead, the system is centripetal with negative feedback loops pushing the system back toward an equilibrium as the environmental variations pushed it away (Caughley 1987). One feedback loop is entirely within the vegetation: rate of increase of biomass declines as the standing crop increases. Fig. 2 shows this loop. The second loop links density of kangaroos to density of edible vegetation through grazing pressure: more forage results in more kangaroos which leads to less forage and thence to fewer kangaroos. A potential third feedback loop linking rate of increase of kangaroos directly to kangaroo density through some form of spacing behaviour was not found. Thus, kangaroos appear to be regulated extrinsically by their influence upon their own food supply but they are not regulated intrinsically by some direct social effect of density upon their ability to survive and reproduce. We suspect that similar mechanisms affect changes in caribou density.

Caribou are subject to predation by wolves and by people whereas kangaroos in the study cited above are preyed upon only by people. It was possible to separate the effect of that hunting, and also the effect of competition from sheep, from the effect of other influences upon the dynamics of the plant-herbivore system. Those analyses (Caughley 1987) suggested that although competition from sheep and predation by people had a marked effect on mean kangaroo density, it had little or no effect upon variations in rate of increase. Hence the major fluctuations observed, and duplicated by a modelling of the system, are not likely to be by-products of predation or of competition between species.

One of the more important findings on the ecology of the plant-kangaroo grazing system is that the short-term fluctuation of weather and plant density generate longer term fluctuations in kangaroo density, on a scale of decades rather than of years. Hence no special reason need be sought for a long period of increase or a long decline, such effects being intrinsic to the system and to be expected as a product of the fluctuating weather. We note that similar rises and declines in caribou populations are almost invariably discussed in terms of special causes, the most frequently advanced being hunting, competition with other species and predation by wolves (see for example Leader-Williams 1988: Fig. 1.8).

There is a debate of long standing on the effect of predation on the dynamics of caribou and other large herbivores (for example see recent reviews by Skogland 1991, Boutin 1992). Caribou numbers fluctuate whether there are predators or not, as do the populations of many other large herbivores (e.g. Clutton-Brock et al. 1991, Fryxell et al. 1991). It is not our intention to enter this debate: instead we agree with the suggestion of



reviewers such as Boutin (1992) that further advances in understanding the effects of predators on herbivore population dynamics are unlikely until an experimental approach is adopted. We take that further by suggesting that the relationship between the dynamics of the herbivores and their food supplies need to be elucidated before attempting to determine the added effect of predation.

In this paper we have viewed herbivores as one half of an interacting system, the other half being the plant community upon which they depend. That contrasts with the usual approach in which the dynamics of the herbivore are presented in the context of a single-species model and correlations are sought between population parameters and animal density. We consider that approach useful only where numbers are regulated intrinsically (self-regulated) through spacing behaviour. Otherwise it tends to obscure rather than illuminate causal mechanisms of regulation where that regulation is powered by feedback between plant density and animal density. With such extrinsic regulation the density of forage strongly influences the rate of increase of the animals and the density of the animals strongly influences the rate of increase of the plants.

Fig. 7 makes the point that in such density-dependent systems it is available forage rather than herbivore density upon which herbivore rate of increase is causally dependent. It gives the data of Fig. 5 presented in another way, showing that despite stochastic fluctuation the tightest relationship is with vegetation density rather than animal density.

We have stressed in this paper that long-term aperiodic fluctuations in kangaroos can be generated by short-term fluctuations in weather. We ask whether some of the reported fluctuations in caribou and reindeer numbers might not also reflect that mechanism. Such trends are essentially a mathematical artefact of year-to-year fluctuations in weather. Marked trends in the numbers of the large desert herbivores, on a time scale of decades rather than of years, are to be expected even when the weather has no time trend. That effect is probably intrinsic to desert systems and does not necessarily require a postulated mechanism couched in terms of special and persistent causes to explain it.

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