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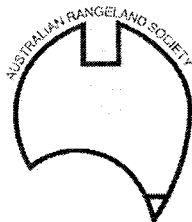
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# THE OUTSIDERS: COMPETITION BETWEEN INTRODUCED HERBIVORES AND DOMESTIC STOCK IN RANGELAND GRAZING SYSTEMS

David Choquenot

Vertebrate Pest Research Unit, NSW Agriculture, Trangie

## ABSTRACT

Introduced herbivores are an important component of rangeland grazing systems. For a variety of reasons: densities of introduced herbivores are usually uncontrolled, their abundance being regulated through interactive plant-herbivore processes. Because of the dominant effect of rainfall on these processes, mechanisms affecting the potential that introduced herbivores have to impact upon the rangelands pasture resource are complex. Despite this, current management of introduced herbivores assumes overly simple relationships between herbivore abundance and pasture availability. It is argued that to develop sensible management options for introduced herbivores, they should be recognised as another component of rangelands grazing systems, and their influence on such systems understood. Examples of how incorporating introduced herbivores into our understanding of grazing system dynamics, helps identify appropriate information and management needs, are given. These examples emphasise the role of competition between introduced and domestic herbivores.

## INTRODUCTION

This paper is about perceptions. The status of introduced herbivores in the rangelands as pests stems from two perceptions:

1. Introduced herbivores do not belong there
2. The presence of introduced herbivores in the rangelands threatens something we value.

The first of these perceptions represents an ideological judgement about which animals belong in which settings. I will not discuss it further. Rather, I will focus on the perception that introduced herbivores in the rangelands threaten something we value and confine my comments to the perception that introduced herbivores reduce agricultural production in the rangelands by competing with stock for feed.

### *Introduced herbivores as competitors with stock*

The current approach to the management of introduced herbivores is based on the perception that they reduce agricultural production through direct competition with domestic stock. Further, current recommended management practices implicitly assume that competition between introduced and domestic herbivores occurs in a "range succession" context. Range succession-style lines of thinking are used to argue that decreasing the abundance of introduced herbivores will increase pasture available to domestic stock, thereby increasing agricultural productivity. This sequence of associations gives rise to the basic philosophy underlying current pest management; "less pests is better". Two related axioms rounding out current approaches to pest control are

- (1) reductions in pest abundance will return a commensurate increase in productivity, and
- (2) that eradication should be the logical endpoint to pest management.

However, environmental fluctuation (primarily unpredictable variation in rainfall) in the rangelands complicates the notion of competition for a common food resource. If variation in the abundance of the food resource has more to do with variation in rainfall than with grazing pressure, competition will be as much a function of prevailing seasonal conditions as the absolute abundance of introduced herbivores.

To determine the magnitude of competition between introduced and domestic herbivores in the rangelands, the grazing system within which they compete

for pasture, and the factors which drive it, must be understood. The rest of this paper discusses what we know about rangeland grazing systems, and what implications the dynamic nature of these systems has for competition between introduced and domestic herbivores.

### *The dynamics of rangelands grazing systems*

The abundance of introduced herbivores will usually vary with seasonal conditions as these affect available vegetation. The abundance of vegetation varies with the rainfall supplied to it, and the demands placed upon it by grazing. Similarly, the number of the herbivores feeding on the vegetation source will vary, often spectacularly, in relation to vegetation abundance. (Fig. 1) When a herbivore is introduced into a new environment, there is an initial eruption in its abundance in response to high vegetation availability, followed by a precipitous crash as the herbivores eat themselves out of house and home. In many real instances this crash is severe enough to lead to extinction of the introduced herbivore. In other instances, such as that shown in Fig. 1, the decline in herbivore abundance eases grazing pressure on the vegetation enough to allow its partial recovery. A series of reciprocal oscillations in vegetation and herbivore abundance follows, leading to a stable equilibrium between plants and animals. At this point, there is no surplus of vegetation, all productivity being consumed in maintaining the population of herbivores. In reality, environments constant enough to lead to some long-term, stable equilibrium between plants and animals probably do not exist. More commonly vegetation and herbivore abundance will continue to oscillate in a reciprocal fashion in response to environmental fluctuation. The amplitude of such oscillations will depend upon the degree of variation in rainfall and the biology of the plants and herbivores comprising the grazing system.

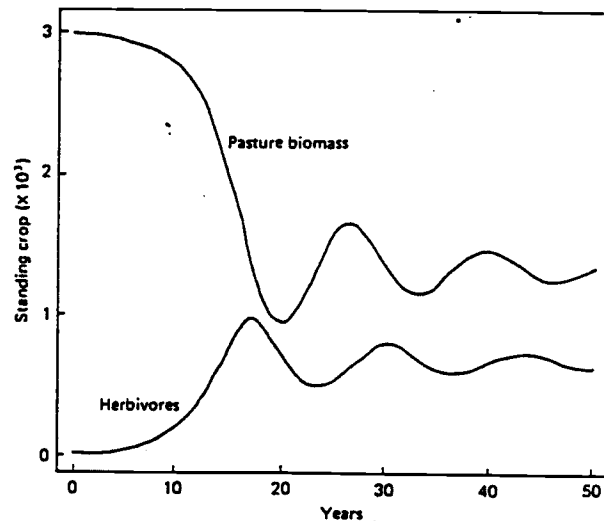


Figure 1. Modelled trend of pasture biomass and animal numbers during an eruption of herbivores (from Caughley 1976).

In the Western Division of NSW between 1860 and 1984, sheep numbers erupted then stabilised as expected during a successful herbivore introduction (Fig. 2). The high degree of variation around long-term sheep abundance reflects fluctuations in stocking rates related primarily to rainfall, but also to commodity prices. Wide variation in the abundance of herbivores is a feature of semi-arid rangeland grazing systems, reflecting the influence of unpredictable patterns of rainfall on variation in pasture biomass and herbivore abundance. Extreme variation characterises long-term trends in abundance of native and introduced herbivores in the Australian rangelands. For example, a model simulating 100 year runs of variation in kangaroo and pasture abundance in western NSW (Caughley 1987b) returns a coefficient of variation of 64% in annual average kangaroo abundance. Another example, is the extreme variation in the abundance of three controlled feral pig populations in north-western NSW over four years. (Fig. 3)

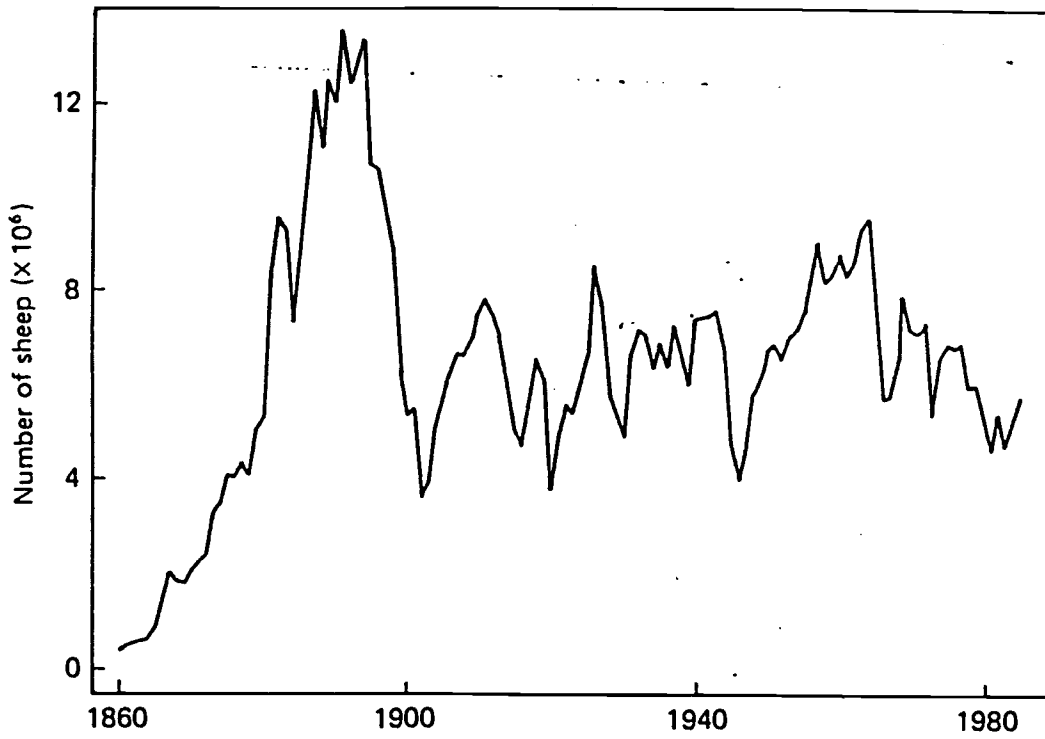


Figure 2. Trend in sheep numbers in the rangelands of NSW between 1860 and 1984 (from Caughley 1987a).

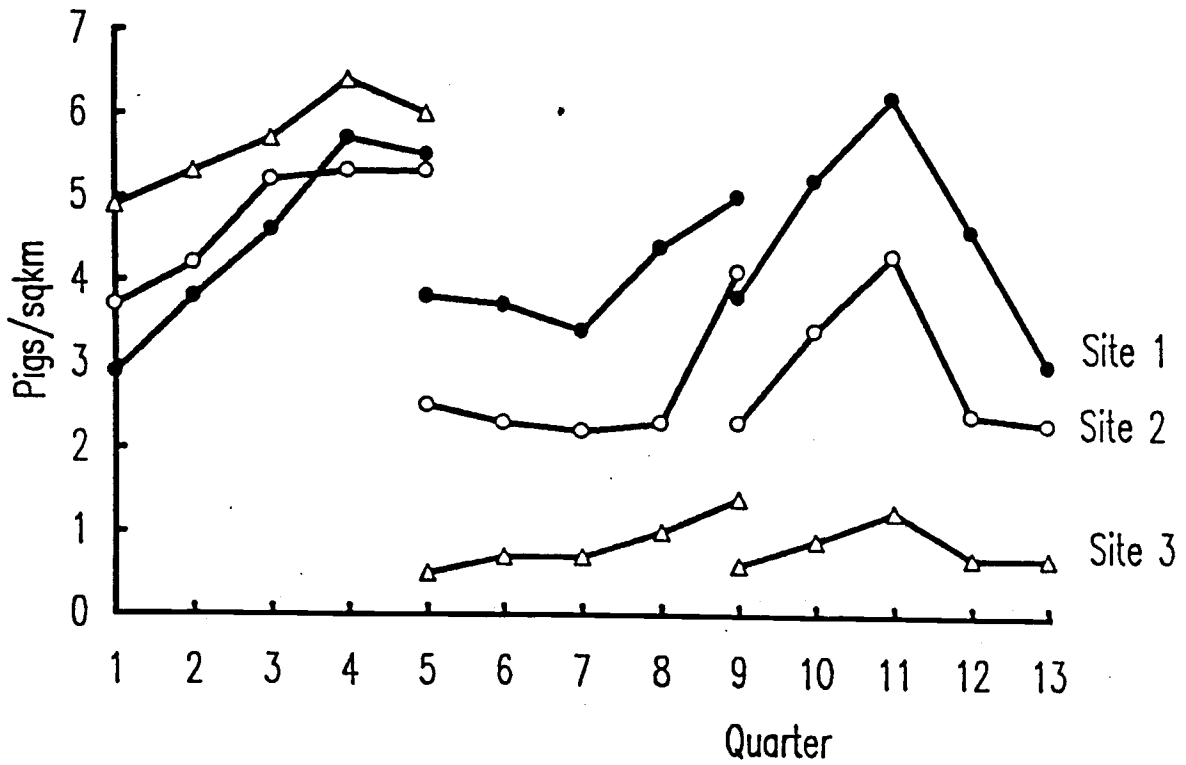


Figure 3. Variation in the abundance of three controlled feral pig populations in north-western NSW (Choquenot unpubl. data).

How do herbivore populations, introduced or otherwise, persist under conditions of such extreme rainfall variation? Caughley (1976) identified three negative feed back loops which define the nature of interaction between plants and herbivores in grazing systems:

1. **Parabolic Plant Productivity**

Plant growth is essentially logistic. For given levels of rainfall, plant growth will ultimately be limited by available space, leading to a density-dependent feed back loop where productivity is parabolically related to standing biomass (Fig. 4a). Parabolic plant productivity has the effect of placing an upper limit on pasture productivity when rainfall is abundant and grazing pressure light.

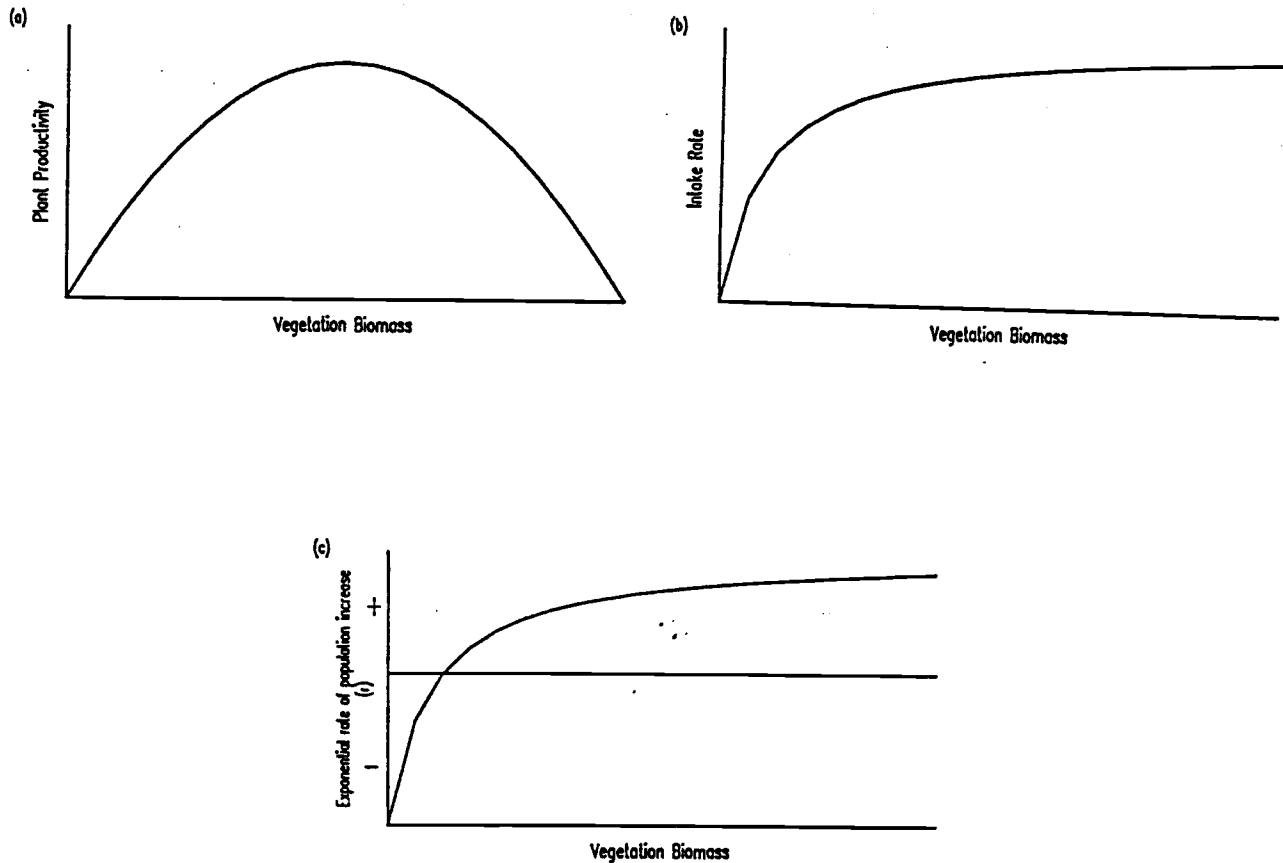
2. **The Functional Response**

The intake rate of a herbivore is a function of available vegetation. Intake rate is suppressed at low vegetation biomass through the herbivores inability to find and/or consume available vegetation. Intake rate increases to a maximum or saturated rate as vegetation becomes more available. Beyond the point where intake rate becomes saturated, further increases in vegetation biomass will not improve intake rate (Fig. 4b). The functional response has the effect of lowering the intake rate of each herbivore as pasture becomes progressively harder to find, and placing an upper limit on intake rate when vegetation is abundant.

3. **The Numerical Response**

The exponential rate of increase in herbivore abundance is a function of available food. Rate of increase will be negative at low vegetation biomass, increasing to a genetically set maximum rate of increase (the intrinsic rate of increase) at progressively higher vegetation availability (Fig. 4c). The numerical response has the effect of decreasing herbivore abundance at an increasing rate as vegetation becomes scarcer, and placing an upper limit on the maximum rate of increase in herbivore abundance when vegetation is abundant.

Under certain biological conditions of vegetation and herbivore population dynamics, these three functions can provide enough stability in a grazing system to allow the plants and herbivores to persist in the face of extreme environmental variation. For example, in estimating the processes involved in the regulation of a red kangaroo population grazing chenopod shrubland pastures, Caughley (1987b) found that the three feedback loops enabled the grazing system to persist in the face of extreme rainfall variation. Persistence in this case means that neither pasture nor kangaroos went into terminal decline, or unrealistic infinite phases of growth. Although variation in pasture biomass was primarily driven by rainfall, grazing by kangaroos "tended to clip the tops off the peaks of pasture production and deepen the troughs". That is, kangaroos, via the functional and numerical responses, tended to suppress further pasture growth when production was high and drive pasture biomass to lower levels during droughts. The potential for competition between kangaroos and sheep is not a function of absolute kangaroo abundance, but of their abundance in relation to available pasture. In the same fashion, pasture off-take by introduced herbivores will be a product of their abundance and their rate of intake, both of which will vary according to available pasture. Estimates of introduced herbivore abundance in the absence of information on available pasture biomass tell us nothing about the potential for competition with domestic stock.



**Figure 4.** (a) Parabolic plant productivity indicating how vegetation productivity varies as a function of vegetation biomass, (b) the functional response relating intake rate of a herbivore to available vegetation, (c) the numerical response relating the exponential rate of herbivore increase ( $r$ ) to vegetation biomass.

#### ***Competition between introduced and domestic herbivores***

Competition for food between herbivores occurs when an individual suppresses the rate of food intake of another, and/or affects its ability to select an adequately nutritious diet. Competition can be intra- or interspecific and can take the form of a suppression of food intake rate through direct interference with another grazing animal, or more commonly, through reduction of pasture biomass to levels where intake rate declines, or diet selection is inhibited. Competition between introduced and domestic herbivores may or may not be commercially significant, depending upon the value of the reduction in productivity involved. Some examples illustrating these points follow:

#### ***Rabbits and sheep in the semi-arid rangelands***

Despite the lack of unequivocal data, rabbits continue to be blamed for reducing wool production in the rangelands through competition with sheep. The perception is that rabbits consume pasture which, in their absence, could be used to grow wool. Williams (1991) analysed two unpublished studies conducted specifically to measure the effect of rabbits on wool production. In one study conducted in far western NSW by D.H. Wood of CSIRO, intensive rabbit control led to no increase in the weight of clean fleece produced by sheep (Table 1). In the other trial, conducted in the central tablelands of NSW by J.D. Croft of NSW Agriculture, only extremely high densities of rabbits (equivalent to 50 rabbits/ha) had any measurable effect on wool production. Such high rabbit densities are unknown under rangelands conditions.

Property	Year	Kg fleece/head	
		Rabbits	No rabbits
Calinday	1988	2.8	2.8
"	1988-89	4.7	4.9
Tero	1988	2.6	2.2
"	1988-89	4.3	4.2

Table 1. Average fleece weight (kg/hd) for sheep run on paddocks following intensive rabbit control and no control, on two properties in western NSW. (Data is from an experiment by D.H. Wood reported in Williams, 1991).

Williams (1991) suggested that the two experiments failed to indicate any apparent competition between rabbits and sheep because good seasonal conditions prevailed throughout the course of the experiments. He pointed out that the functional response of rabbits and sheep estimated by Short (1985) indicated both species maintained maximum pasture intake rates down to a pasture biomass of around 250kg/ha (Fig. 5). Above this level, competition cannot, by definition, occur. If both experiments occurred while pasture was abundant enough to ensure unrestricted grazing for all herbivores, no effect of rabbits on fleece growth would be expected. Hence, while pasture biomass remains above 250kg/ha, rabbits cannot affect wool growth and management will be of questionable value. However, what happens when biomass falls below this threshold is far from clear.

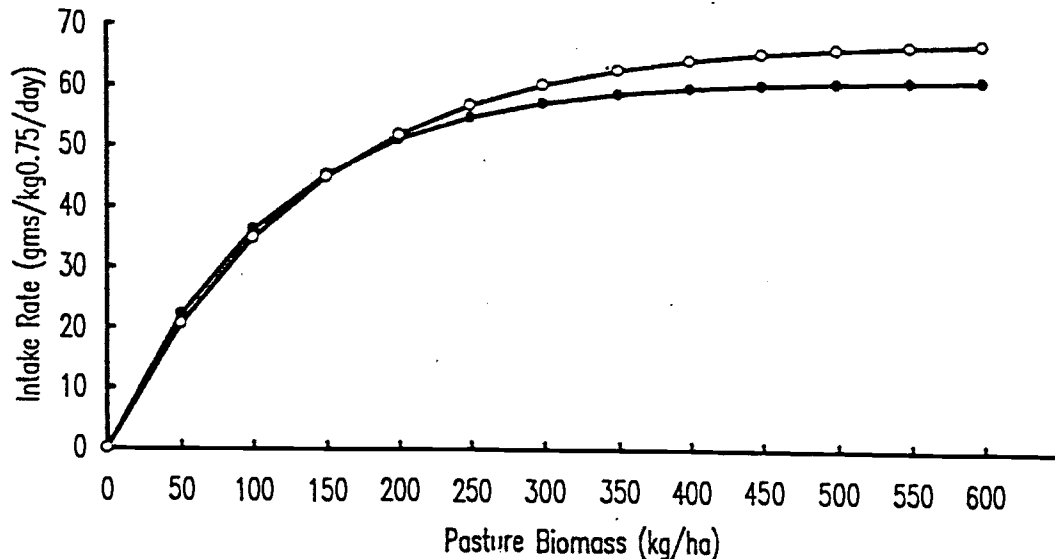


Figure 5. The functional response of sheep (●) and rabbits (○) grazing chenopod shrubland pasture (after Short 1985).

A simulation model can be used to demonstrate that under rainfall fluctuations which could be expected over 50 years in the far west of NSW, the biomass of pasture on a grazing lease set stocked with 0.3 sheep/ha and grazed by uncontrolled densities of kangaroos, will be below 250kg/ha for about 45% of the time (Fig. 6). This suggests that while most of the time pasture biomass in this part of the rangelands will be high enough to preclude competition between rabbits and sheep, the potential for competition exists over a significant proportion of time.

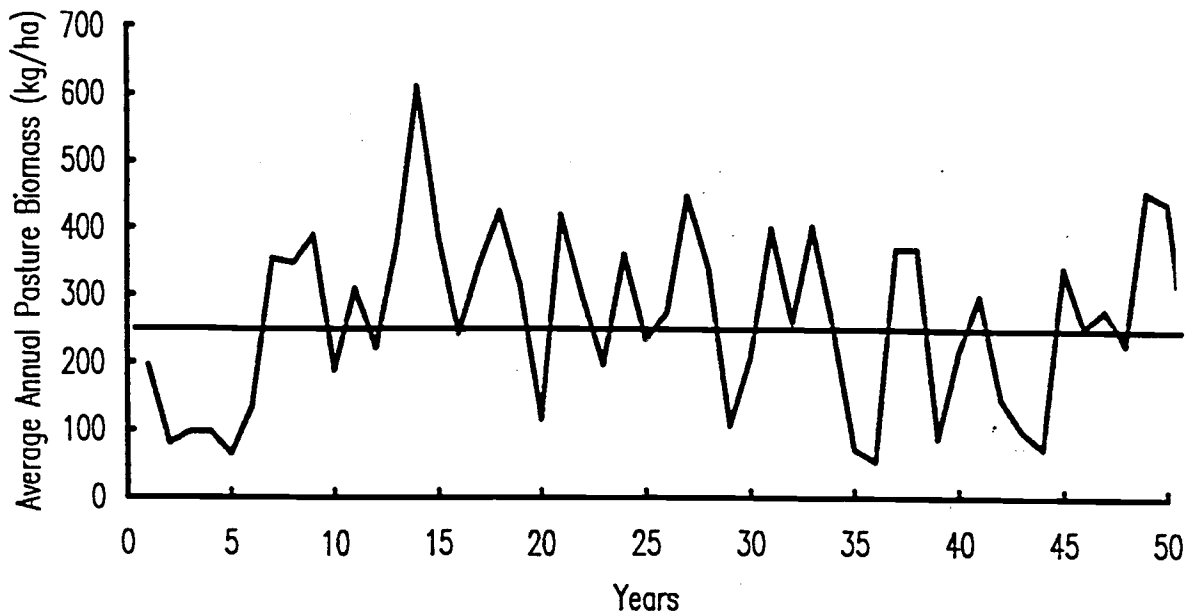


Figure 6. Modelled variation in biomass for a shrubland pasture in western NSW grazed by sheep set stocked at 0.3 sheep/ha and uncontrolled numbers of kangaroos. The straight line indicates pasture biomass of 250kg/ha, below which competition between rabbits and sheep can occur.

Is the competition between rabbits and sheep which occurs at levels of pasture biomass below 250kg/ha commercially significant? Because rabbits are obviously much smaller than sheep and intake rate scales to the metabolic body weight of grazing animals, actual levels of competition between sheep and rabbits will be largely limited by rabbit abundance. To explore potential levels of competition between rabbits and sheep further, the simulated grazing system described above was extended to include rabbits at different densities. The percentage of pasture available per head of sheep which would be consumed by rabbits "stocked" at densities of 2, 5, 7 and 10/ha, as well as a system where rabbit abundance varied according to seasonal conditions, was estimated quarterly. These simulated grazing systems were again run over 50 years for each level of rabbit density, and the results from 5 runs averaged (Table 2).

Rabbits/ha	Quarters < Maint.	% Available pasture/sheep consumed by rabbits				
		Average	SD	CV%	Maximum	Minimum
2	13.6	1.69	0.11	6.51	3.71	0.77
5	11.0	4.15	0.22	5.30	9.87	1.91
7	10.2	5.80	0.31	5.34	12.66	2.72
10	12.0	8.32	0.49	5.89	18.77	3.59
Variable*	14.0	1.14	0.13	11.4	5.16	0.14

\* Rabbit density was varied according to the numerical response:  $r = -2.7 + 3.97(1 - e^{-0.0045V})$  Where  $r$  is the exponential rate of population increase and  $V$  is the prevailing pasture biomass. The response is based on a maximum annual exponential rate of decrease of 2.7 (Robertson & Armstrong cited in Short, 1987), and increase of 1.27 (calculated from body weight as described by Caughley & Krebs, 1983).

Table 2. Summary of a series of simulations examining variation in the percentage of pasture available to sheep which is consumed by rabbits at different densities. The simulations use stochastic rainfall input to drive a grazing system comprising uncontrolled numbers of kangaroos and sheep set stocked at 0.3 sheep/ha. All statistics given are quarterly averages across 5 runs of 50 years each, except Quarters < Maint which gives the average number of quarters (out of 200) where pasture biomass was insufficient to maintain the sheep flock (Choquenot in prep.).



While the percentage of pasture available to sheep that was consumed by rabbits increased with rabbit density, average absolute impact on available pasture was low (<10% available pasture consumed). According to these simulations, competition from rabbits appears to have a only minor effect on average levels of pasture available to sheep or on the frequency with which available pasture fell below that required for flock maintenance. Although data relating long-term variation in pasture biomass to wool production in the rangelands are unavailable, it seems unlikely that the levels of pasture potentially consumed by rabbits would cause commercially significant decreases in wool production. Estimates of rabbit density given by Wood *et al.* (1987) for 17 rangelands locations range from 0.02 to 3.75 rabbits/ha (presumably estimates of 0 rabbits/ha were not included), with an average of 1.54 rabbits/ha<sup>1</sup>. At such densities the impact of rabbits on wool production through competition for pasture would likely be commercially insignificant. Coincidence of high rabbit density and low pasture biomass may elevate the degree of competition between rabbits and sheep to commercially significant levels at particular times. However, densities of rabbits decline rapidly in droughts, suggesting significant competition with sheep would only occur over the short-term.

The perception that continual suppression of rabbit abundance to increase wool production represents an economically sensible management strategy, is questionable on the results of the simulation modelling presented here. However, the experiment of Wood described by Williams (1991) should be repeated under a range of pasture biomass conditions and using a range of rabbit densities in order to test the predictions of these simulations. The low level of competition for pasture between rabbits and sheep is a function of the smaller body size of rabbits and their propensity to decline rapidly in abundance in periods of food shortage. Would a larger more robust herbivore such as feral goats impact more significantly on wool production than do rabbits? Few useful data are available to judge the likely effect of competition between goats and sheep. However, what information is around suggests the potential for competition is higher for goats than for rabbits. Recent surveys have indicated that while the abundance of all wild herbivores has declined markedly through the recent drought in western NSW, preliminary estimates of the exponential rate of decrease in goat abundance ( $a=1.33$ ) has been substantially less than that estimated for feral pigs ( $a=2.24$ ) or red kangaroos ( $a=1.60$ ). This has led in some areas to densities of goats in excess of red kangaroo abundance. It is likely that goats have a slower rate of decline because their diets include a significantly higher browse content than either rabbits or kangaroos. This ability means goats will be able to maintain higher levels of abundance in relation to available pasture. Information on the functional and numerical response of goats in the semi-arid rangelands is required if the significance of their competition with sheep is to be ascertained, and sensible decisions about their management made.

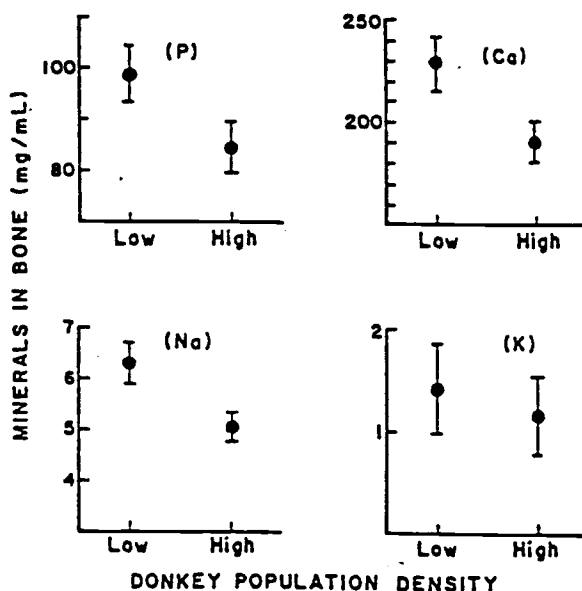
#### *Feral donkeys in northern Australia*

The other form of competition between herbivores involves modification of vegetation composition by one herbivore which reduces the quality of food available to another. In this instance, it is not prevailing pasture biomass alone which influences the degree of competition between the herbivores, but also the degree of dietary overlap at varying levels of pasture availability. Freeland & Choquenot (1990) and Choquenot (1991) describe the dynamics of feral donkey populations occurring in the tropical tallgrass savannas of northern Australia. At high densities, the size of these populations becomes limited by the inability of females to successfully rear their young. High juvenile mortality is directly related to inadequate mineral reserves (primarily calcium, phosphorous and potassium), which inhibit successful lactation and weaning of offspring (Fig. 7). Females in high density populations consume a species poor diet which is low in nitrogen and mineral nutrients, and high in crude fibre. These females are unable to extract adequate nutrients from their diet

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<sup>1</sup>An extreme estimate of 29 rabbits/ha obtained using a different survey technique was excluded from these calculations.

because of its high fibre content (Fig. 8). Indeed, the high fibre content of their diet may lead to accelerated depletion mineral reserves of females by increasing salivary secretion and gastrointestinal irritation. In contrast, female donkeys from populations which have been reduced below densities where dietary quality is limiting, consume a species rich, low fibre diet. These females are in better nutritional condition than their counterparts at high population density and successfully rear almost three times as many offspring, leading to an exponential rate of population increase of  $r=0.21$  (Choquet 1990). It is likely high donkey densities lead to a decline in the overall quality of forage available to other herbivores as well as themselves, while lower donkey densities may increase the quality of available forage.



**Figure 7.** Concentrations of minerals in the caudal vertebrae of female donkeys from growing populations (low density) and populations at carrying capacity (high density). Values are averages with associated 95% confidence intervals (from Freeland & Choquet 1990).

The tropical savannas of Australia's northern rangelands are fundamentally different from semi-arid western NSW. In northern Australia the monsoon initiates an annual flush of high quality pasture at the beginning of each wet season. While this flush of pasture is in excess of what can be consumed by herbivores, high growth rates of grasses last only over the first 8 - 10 weeks of the wet season (Mott et al. 1985). Nitrogen and phosphorous contents of green material fall from 2.0% and 0.15% at the start of this growth phase to 1.0% and 0.08% respectively at its end. Hence, grazing systems in this region undergo a tight regular annual cycle of boom and bust. The boom occurs irrespective of prevailing grazing pressure. The bust on the other-hand varies in its relative severity according to the grazing pressure being exerted, its effect on donkeys being mediated through density dependent intra-specific competition for the more nutritious forage species as the dry season progresses. The degree of competition between feral donkeys and cattle (inter-specific competition) will ultimately depend upon the magnitude of their shared preference for forage species during the late dry season when forage availability is lowest. Whether interspecific competition is commercially important to beef producers, and whether donkey control significantly increases beef production is unknown. While rabbits and sheep share preference for more nutritious plants in the semi-arid rangelands, sheep by virtue of their greater body size are able to tolerate decreasing dietary quality through forced consumption of less palatable species into droughts.

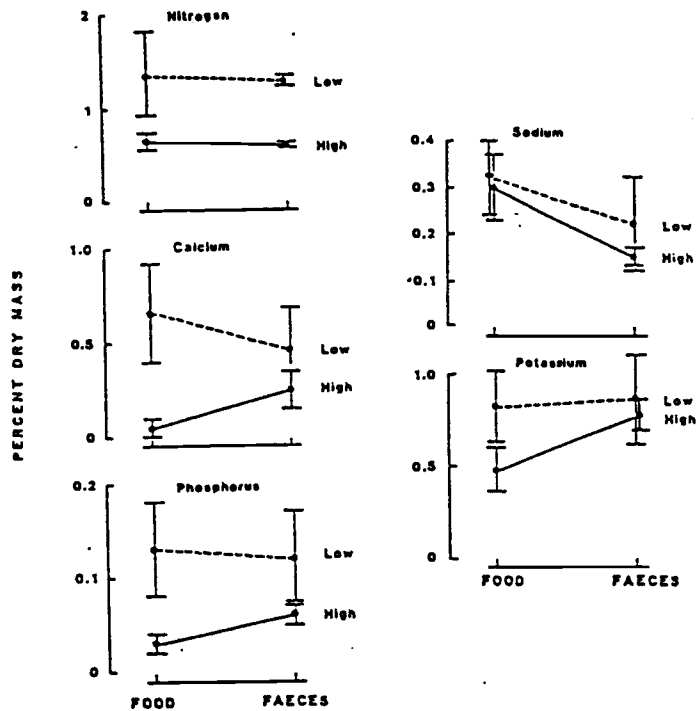


Figure 8. Concentrations of nitrogen, calcium, phosphorous, sodium and potassium in the food and faeces of female donkeys from growing populations (low density) and populations at carrying capacity (high density). Values are averages with associated 95% confidence intervals.

#### *Implications for changing grazing management*

"Introduced herbivores eat grass that I could use to grow more wool/meat; therefore they are pests". Hopefully the discussion so far has laid this overly simplistic notion open to serious question. Competition for pasture resources in rangelands environments involves a series of complex interactions between grazers and the vegetation they live on, made less comprehensible by the vagaries of rainfall.

Historically, management of introduced herbivores in the rangelands has focussed on maximising the number of individuals killed or removed. Typically the motivation for control is a perceived increase in the abundance of the pest species, and the associated perception that the pasture resource is under some threat. The success or failure of such a control program is assessed in terms of the numbers of animals found dead, or the amount of poison or ammunition used. This approach implicitly ignores the real purpose of such management, increasing agricultural productivity and/or sustainability by increasing pasture biomass and quality. Changes in these factors will represent more useful criteria for initiating pest control and assessing a program's success. Ultimately, the success or failure of a management program will depend on whether real pest impacts on productivity and/or pasture biomass and composition are effectively reduced or not. In a commercial setting such as an agricultural production system, this will involve equating the costs of pest control with the measurable benefits of control in terms of increased productivity. In public good settings (environmental protection or sustainable development situations), measures of increased productivity should be replaced with some definable and measurable slowing or reversal in degradation trends. Change in the direction or degree of degradation trends might be assessed in terms of rates of species or individuals lost to an ecosystem, rate of change in vegetation cover, rate of soil loss or increased water quality. In all circumstances costs and benefits of management should be measured over a time-scale appropriate to changes in the specific measure of management success and our ability to measure such changes.

Control of introduced herbivores should be viewed as another component of grazing pressure management, for enhanced agricultural production, better land protection, or more efficient native species conservation. An understanding of the grazing systems which introduced herbivore populations are a part, not just the dynamics of herbivore population itself, is essential in making rational management decisions. This information can be obtained by undertaking experimental manipulations of introduced herbivore density, and measuring appropriate responses in terms of increased agricultural production or reduced rates of land degradation.

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