Functional Response of Rabbits and Sheep in the Central Tablelands, N.S.W.

F.T. FALKENSTEIN*[1], D. CHOQUENOT° AND P.J. JARMAN*
*UNE, Dept. of Ecosystem Management;
°Agricultural and Veterinary Research Center Orange, Vertebrate Pest Unit.
[1] present address: UNE, Dept. of Agronomy and Soil Science

(1) Food intake rates of sheep and rabbits were compared from an intensive grazing trial in a temperate zone on the central Tablelands of NSW. Animals grazed on pasture composed of annual and perennial grasses interspersed with annual forbs.
(2) Food intake declined progressively over the trial periods for both species, but rabbits were better able to maintain their intake at low pasture biomass. The maximum food intakes of sheep and rabbits during the trial were 64.4 and 35.9 g $kg^{-0.75}$ day^{-1}, respectively.
(3) The two herbivore species were equally capable of reducing the pasture to ungrazeable residues which were centered around O.95 t/ha.
(4) Harvesting efficiencies (i.e. the ability to maintain food intake at low vegetation biomasses) were lower than those reported for arid grazing systems.
(5) The results indicate that rabbit control is necessary at all levels of pasture biomass to maximise the stability and productiveness of sheep grazing systems.

INTRODUCTION AND BACKGROUND

Rabbits and their Impact on Australian Agriculture

The European rabbit (*Oryctolagus cuniculus*) is native to north western Africa, Spain and Portugal but is now found in most of western Europe as far north as southern Scandinavia [NSW 1988a]. Wild-type individuals were introduced into Australia in the mid- to late 1800's, and the species now inhabits an area of some 4.5 million km^2 [Myers *et al.* 1989]. Rabbits spread into the Tablelands of New South Wales towards the end of the last century and rapidly became a major pest [Parer & Libke 1991].

It is estimated that between 7-16 rabbits will consume a quantity of pasture equivalent to that of one sheep [Short 1985, Myers & Poole 1963]. The 'carrying capacity' of a 4500 ha property doubled when rabbits were eradicated, and further research has since shown that 25 to 30 rabbits per hectare can reduce pasture yield by as much as 25 per cent [NSW 1988b]. Sheep production is further jeopardised under conditions of drought if sheep have to compete with another species for the same resource. Determining the degree of competition between sheep and rabbits, under various levels of food availability is therefore very beneficial to the agricultural industry.

The Role of Models in Grazing Management

A model can be defined as "a mathematical representation of populations or systems to assist in description, calculations or predictions" [Recher *et al.* 1986]. The functional responses of rabbits and sheep which this study investigated are essentially models that describe the change in food intake, as pasture biomass declines from high to low. From the shape of both species' response curves, comparisons can be made in terms of (1) maximum or satiated intake rate, (2) grazing efficiency and/or (3) the level of pasture availability at which food intake can no longer be maintained and food becomes limiting.

Using a functional response model, a manager can decide at which level of biomass to maintain their sheep's intake rate. By combining the functional and numerical response in an interactive model [see Caughley 1987 for review], population dynamics of rabbits or sheep can be forecast under given environmental conditions, particularly rainfall.

Environment and Site Description

The experiments were conducted in the central Tablelands of New South Wales at an altitude of 895m (latitude = S 33°19'14.8, longitude = E 149°05'5.8) on the grounds of the Department of Agriculture and Fisheries' Center for Agricultural and Veterinary Research in Orange. Soils are clayey and of basaltic origin with medium to low permeability.

Climate of the area is temperate; average annual temperatures are 17.6°C maximum and 7.0°C minimum with 873.6mm average annual precipitation (data from 1976 to 1993, measured at the department's meteorological station) a small percentage of which may fall as snow. Average monthly rainfall and average daily maximum and minimum temperatures for each month of the year before the study are depicted in Figure 1.

Vegetation in yards is representative of pastures in the central Tablelands with predominantly sown grasses and regrown natives to a lesser extent. Cocksfoot (*Dactylis glomerata*), perennial ryegrass (*Lolium perenne* L.) and Yorkshire fog

(*Holcus lanatus* L.) are the three dominant species. Less dominant grasses include Australian bent (*Agrostis australiensis* Mez.), wallaby grass (*Danthonia* sp.), brome (*Bromus* sp.), squirrel tail fescue (*Vulpia bromoides* L.), two *Paspalum* spp. and two species of rush (*Juncus* spp.). Dandelion (*Taraxacum officinale*), ribwort (*Plantago* sp.) and clovers (*Trifolium* spp.) are common. The paddock containing the study sites is usually grazed during the lambing season and was not grazed for at least six months prior to the study.

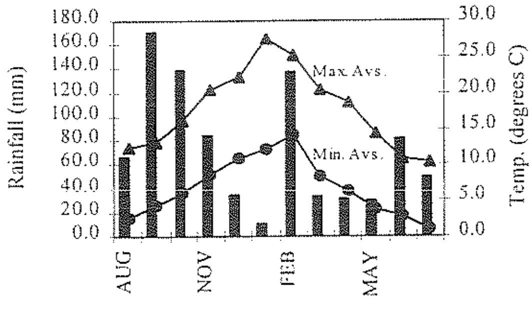

Figure 1 Summary of climatic data (Aug. 1993 to July 1994) from a station near the study sites. The bars depict average monthly rainfall and the lines associate average daily maximum and minimum temperatures for each month.

METHODS

The functional responses of rabbits and sheep were determined in four experiments over periods from 15 to 22 days. The experiments consisted of one grazing trial for sheep (23rd of June to 14th of July 1994) and one for rabbits (29th of June to 14th of July 1994) during winter, which were replicated next to the former yards, just before spring (3rd to 23rd of August 1994).

Daily biomass was estimated using the non-destructive Comparative Yield Analysis (CYA) [Haydock & Shaw 1975]. Daily pasture estimates were smoothed by calculating four-point running averages before any other calculation. The offtakes were converted to food intake rates (g kg$^{-0.75}$day^{-1}) (metabolic). The functional response models assumed to be inverted exponential curves of Ivlev form [Noy-Meir 1975; Short 1985, 1986] and were calculated by least-squares analysis from plots of metabolic food intake against vegetation biomass using GENSTAT. The curve has the form:

$$c = c_s \left\{1 - e^{(-V/V_s)}\right\}$$

where c is the food intake at a given vegetation biomass (V); c_S, the satiated food intake; V_S, the biomass at which a fraction $1\text{-}e^{-1} \approx 0.63$ of the satiated food intake is reached, [Noy-Meir 1975; Short 1985, 1986, 1987] $1/V_S$ (steepness of the curve) is a measure of the harvesting efficiency of a herbivore.

Experimental units consisted of four fenced pastures with only one rabbit and one sheep yard (10m x 10m and 20m x 20m respectively) standing at a time.

Four 6-year-old merino wethers and thirteen experimental rabbits, five of which escaped (maximum number of rabbits at any one time was eight rabbits). It is acknowledged that the rabbits were taken from a drought-affected area with little pasture and were put onto a highly productive paddock with abundant, green pasture. Average weight of the sheep and rabbits at the beginning of trial A and B were 58.8 and 59 kg, 1.36 and 1.48 kg, respectively.

Dieback through trampling was assessed by scoring plant litter (dead plant matter that was not connected to a plant) using the CYA (50 scores each day per yard). Daily biomass estimates were adjusted for trampling.

RESULTS

The decline in pasture biomass and increase in litter during both trials are shown in Figure 2 for sheep and Figure 3 for rabbits.

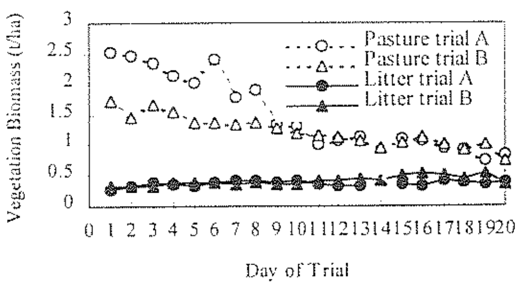

Figure 2 The decline in pasture biomass and increase in biomass of litter over time in sheep yards at trial A and B.

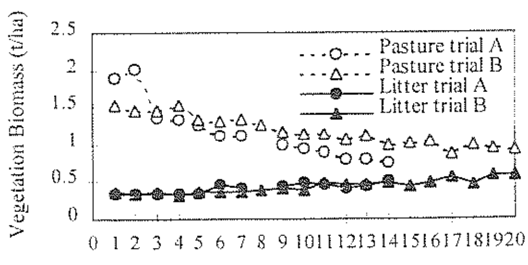

Figure 3 The decline in pasture biomass and increase in biomass of litter over time in rabbit pens at trial A and B.

Approximate rates of litter increase were derived from tests of regression. Test outcomes were:

for sheep (trial A) $F_{1,\,18} = 1.42$; $P=0.25$,
$y=0.0019x + 0.3456$, $R^2=0.08$
(trial B) $F_{1,\,19} = 21.06$; $P<0.001$,
$y=0.0080x + 0.3269$, $R^2=0.54$

for rabbits (trial A) $F_{1,\ 13} = 31.08$; $P<0.001$,

$y=0.0081x + 0.3270$, $R^2=0.50$

(trial B) $F_{1,\ 19} = 95.64$; $P<0.001$,

$y=0.0121x + 0.3058$, $R^2=0.84$

The rates of litter increase, attributed to trampling and used to adjust daily intake of animals were given by the slopes of the above functions. All four slopes were accepted despite a very weak relation of the function in the first sheep yard.

Functional Responses

Data points and fitted model for the animals' food intake expressed on a metabolic weight basis are presented in Figure 4.

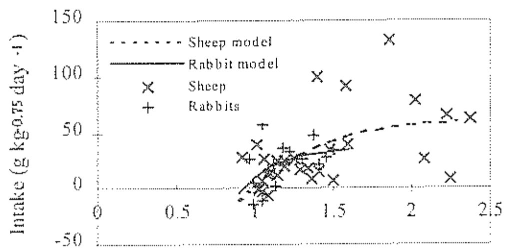

Figure 4 Functional response models for sheep and rabbits. Food intake rates are expressed as a function of metabolic weight (g $kg^{-0.75}day^{-1}$). The function of the curves are

$y=64.4\ \{1-e^{-(V-0.98)/0.474}\}$ for sheep, and

$y=35.9\ \{1-e^{-(V-0.925)/0.221}\}$ for rabbits.

It was not possible to fit the desired curve for the rabbit data of the first trial. The outcome was a 'negative' inverted exponential curve, decreasing with increasing biomass. Hence, the functional response curve for rabbits above was the result from data of trial B alone.

From the functions $y=64.4\ \{1-e^{-(V-0.98)/0.474}\}$ for sheep and $y=35.9\ \{1-e^{-(V-0.925)/0.221}\}$ for rabbits, the first numbers (64.4 g $kg^{-0.75}day^{-1}$ and 35.9 g $kg^{-0.75}day^{-1}$) are the exponential curves' asymptotes representing theoretical maximum metabolic food intake rates for rabbits and sheep. That for sheep was almost twice the amount for rabbits. If intake is expressed as maximum average intake rate per animal per day, these values convert to 1323.7 for sheep and 46.7 g $animal^{-1}day^{-1}$ for rabbits. The second number in these functions (0.98 t/ha and 0.925 t/ha) are the curves' intercepts with the x-axis and represent pasture residuum, being greater for sheep than rabbits. The third numbers (0.474 t/ha and 0.221 t/ha) are inversely related to the harvesting efficiencies of the animals and also represent, after adding the ungrazeable residue, the biomasses at which the herbivores' metabolic intake rates are depressed to 63% of maximum intake rates.

DISCUSSION

The functional response curve for sheep reported in this paper is similar to those produced from graze-down trials on chenopod shrubland in arid grazing systems [Short 1985] (see Figure 5). The major difference between these responses lies in the ungrazeable residue. One explanation for this may be found in the physical character and patchiness of pasture species, for example the presence of a continuous leaf canopy at low biomass may hinder grasping of vegetation by a herbivore [Leigh & Mulham 1966]. On the contrary, the same level of biomass represented by widely separated plants, may aid the grasping of vegetation [Short 1985].

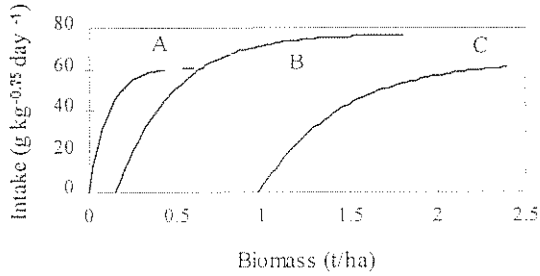

Figure 5 A comparison of functional responses of sheep grazing chenopod shrubland (arid) and improved pastures (temperate) expressed as a function of metabolic weight. (A): Short [1985], (B): Leigh & Mulham [1966], (C): this paper.

In arid grazing systems, grasses are most likely of a tussocky nature, and occur in clumps or clusters [Robertson *et al.* 1987]. Vegetation in the studies by Short [1985] and Leigh & Mulham [1966] consisted, besides forbs and grasses, of shrubs which did not occur in this study. Hence, the ungrazeable residue in this study, centered around 1t/ha, is merely a reflection of differences in character of available vegetation and also due to experimental errors, rather than the grazing ability of sheep.

The residue in rabbit pens was in quantity very similar to that in sheep yards and differed almost as much as the residues of Short's [1985] graze-down trials for rabbits and sheep (see Figures 5 and 6).

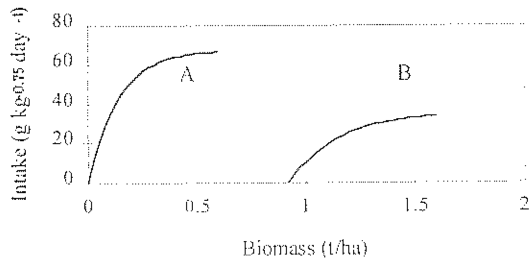

Figure 6 A comparison of functional responses of rabbits grazing chenopod shrubland (arid) and improved pasture (temperate) expressed as a function of metabolic weight. (A): Short [1985], (B): this paper.

A difference in residue between rabbits and sheep in this study was found in its quality and makeup. Whereas sheep contributed almost nothing to the uprooting of species, rabbits were found to actively dig for some species and thus not only destroyed many plants but also made others unavailable by burying these under diggings. The consequences may be that a grazing system under drought conditions could be significantly changed over the years if rabbits are in abundance. Vegetation changes in sheep rangelands of Australia since settlement are extensively documented by Robertson *et al.* [1987].

Maximum food intake for sheep and rabbits has an approximate ratio of 28:1 (1323.7 : 46.7 g animal^{-1}day^{-1}) assuming adult body weights of 59 and 1.48 kg respectively. This suggests that 28 rabbits eat approximately the same amount of food as one merino sheep. Compared to studies by Short [1985] who estimated a ratio of 1:16 (1.25 and 57.5kg adult body weight) or Myers & Poole's [1963] subjective estimate of a ratio of 1:7-10, the ratio in this study appears to be much overestimated. This becomes more apparent when one compares the satiated food intake on a metabolic weight basis which in this study are 64.4 and 35.9 g kg$^{-0.75}$ day^{-1} for sheep and rabbits respectively.

Being eutherians, both herbivores should exhibit similar metabolic intake rates, as was the case in Short's [1985] study with values of 61.1 for sheep and 67.7 g kg$^{-0.75}$ day^{-1} for rabbits. Considering the above, and assuming equal metabolic intake for sheep and rabbits in this study, one may conclude that the underestimates for intake of rabbits are within a factor of 0.56. If the maximum intake rate of rabbits in this study is corrected for this factor, a calculated intake of 83.39g animal^{-1}day^{-1} would thus result in a new ratio of 1:16 which is equal to that in Short's [1985] study. The calculated absolute intake rate of rabbits compares with 76 ± 4.05 g animal^{-1}day^{-1} (calculated from metabolic intake for a weight of 1.48kg) found by Cooke [1982] in a laboratory study.

Underestimations in rabbit's satiated metabolic intake rate and subsequent absolute intake rate could have resulted from (a) sampling error (i.e. high variation in data and/or the failure to account for rabbits' intake from biomass below ground), (b) lack of data in the higher range of biomasses (see Figure 4 and 6) which could have had a strong influence on the process of model fitting; also by calculating a three-point running average, the first 3 points were excluded from the model fitting, and/or (c) the fact that the experimental rabbits were taken from a drought stricken environment and their subsequent failure to adjust to abundant green pasture and/or confinement.

The most likely cause of underestimations of rabbit's satiated metabolic intake rate is the component of vegetation biomass the rabbits obtained from below-ground (roots). As rabbits were observed to actively dig for roots and this study only measured above-ground vegetation intake, it is probable that this missing component showed up as underestimations in daily intakes and all subsequent calculations. This component was not measured because prior to the study it was believed to be not significant, and also not measured by Short [1985] in his graze-down trials.

Grazing efficiencies, i.e. the extent to which a herbivore can find and harvest food to meet its requirement at low food densities, as represented by the steepness of the functional responses before satiated food intake is reached, appear mathematically to be larger in rabbits. Whereas in this study the grazing efficiency of rabbits was approximately twice that of sheep, this relation was reversed in Short's [1985] study (see Table 1). That grazing efficiencies of sheep in semi-arid zones are generally larger than those of sheep grazing in temperate areas is suggested by Leigh *et al.* [1968]. Leigh *et al.* [1968] maintain that this difference is due to a difference in structure between semi-arid pasture and pasture of higher rainfall areas, as already mentioned above.

Table 1 Comparison of grazing efficiencies ($1/V_s$) in sheep and rabbits in semi-arid pastures and pastures of temperate climates with higher rainfall.

Species (climate)	Grazing efficiency (ha/t)	Source
Sheep (semi-arid)	9.01	Short [1985]
Sheep (semi-arid)	3.08	Leigh & Mulham [1966]
Sheep (temperate)	2.11	This study
Sheep (temperate - higher rainfall areas)	1 - 3	Arnold & Dudzinski [1967a, b] Allden & Whittaker [1970] [reviewed by Short 1985]
Rabbits (semi- arid)	7.25	Short [1985]
Rabbits (temperate)	4.52	This study

Efficiency of rabbits was also lower in this study than that reported by Short [1985] for semi-arid Australia, which is analogous to sheep. However, it is questionable that a larger efficiency can be expected for rabbits in temperate regions. The factors which led to an underestimation of rabbits' satiated intake rate may have also influenced the shape of the curve, leaving questionable results for rabbits' grazing efficiency.

An indication of whether the rate of increase of a herbivore is constrained by the amount of food available to it can be obtained by comparing food availabilities typical in the field to that herbivore's functional response. If the biomass of food is below the satiated food intake, it is likely that the species is food limited [Noy-Meir 1975]. The food intakes of sheep and rabbits in the central Tablelands, are depressed to 63% of satiated intake rate at vegetation biomasses of 1.45 and 1.15 t/ha respectively.

CONCLUSIONS AND RECOMMENDATIONS

Harvesting efficiencies of both species were lower than those reported for arid grazing systems. According to the functional response determined in this study, the maximum food intake (from above-ground vegetation) is 1323.7 and 46.7 g dry weight in sheep and rabbits respectively. Rabbits are able to maintain food intake at a lower biomass than sheep and are therefore better able to compete and reproduce than sheep under conditions approaching drought or overstocking.

The results of this study highlight the need for on-going rabbit control in sheep grazing systems to maximise their long-term stability and productiveness. There is no apparent threshold of pasture biomass above which competition by rabbits for food becomes unimportant to sheep production. While food availability is greater in high biomass pastures, these same conditions may stimulate rabbit fecundity and consequently increase rabbit numbers and competition.

It is possible that the functional response of herbivores to a changing food supply should incorporate a further dimension; that of pasture nutrient content.

ACKNOWLEDGMENTS

There are many people we would like to acknowledge and thank for their assistance, advice and encouragement in particular Steve Ottaway, John Druhan, Brian Lukins, Alan Horspool, Joel Rooskov, Ashley Radburn, Helen Nicols, Kate Phillips and Russel Harlen.

LIST OF REFERENCES

Allden, W.G. & Whittaker, I.A.M. 1970, 'The determinants of herbage intake by grazing sheep: the interrelationship of factors influencing herbage intake and availability', *Australian Journal of Agricultural Research*, vol. 21, pp. 755-66.

Arnold, G.W. & Dudzinski, M.L. 1967a, 'Studies on the diet of the grazing animal. II. The effect of physiological status in ewes and pasture availability on herbage intake', *Australian Journal of Agricultural Research*, vol. 18, pp. 349-59.

Arnold, G.W. & Dudzinski, M.L. 1967b, 'Studies on the diet of the grazing animal. III. The effect of pasture species and pasture structure on the herbage intake of sheep', *Australian Journal of Agricultural Research*, vol. 18, pp. 657-66.

Caughley, G. 1987, 'Ecological relationships', in *Kangaroos*, eds G. Caughley, N. Shepherd & J. Short, Cambridge University Press, London, pp. 159-87.

Cooke, B.D. 1982, 'Reduction of food intake and other physiological responses to a restriction of drinking water in captive wild rabbits, *Oryctolagus cuniculus* (L.)', *Australian Wildlife Research*, vol. 9, pp. 247-52.

Haydock, K.P. & Shaw, N.H. 1975, 'The comparative yield method for estimating dry matter yield of pasture', *Australian Journal of Experimental Agriculture and Animal Husbandry*, vol. 15, pp. 663-70.

Leigh, J.H. & Mulham, W.E. 1966, 'Selection of diet by sheep grazing semi-arid pastures on the Riverine Plain. I. A bladder saltbush (*Atriplex vesicaria*) - cotton bush (*Kochia aphylla*) community', *Australian Journal of Experimental Agriculture and Animal Husbandry*, vol. 6, pp. 460-7.

Leigh, J.H., Wilson, A.D. & Mulham, W.E. 1968, 'A study of merino sheep grazing a cotton bush (*Kochia aphylla*) - grassland (*Stipa variabilis - Danthonia caespitosa*) community on the Riverine Plain', *Australian Journal of Agricultural Research*, vol. 19, pp. 947-61.

Myers, K. & Poole, W.E. 1963, 'A study of the biology of the wild rabbit *Oryctolagus cuniculus* (L.) in confined populations: IV. the effects of rabbit grazing on sown pastures', *Journal of Ecology*, vol. 51, pp. 435-51.

Myers, P., Parer, I. & Richardson, B.J. 1989, 'Leporidae', in *Fauna of Australia*, vol. 1B, eds D.W. Walton & B.J. Richardson, Australian Government Printing Service, Canberra, pp. 917-31.

Noy-Meir, I. 1975, 'Stability of grazing systems: an application of predator-prey graphs', *Journal of Ecology*, vol. 63, pp. 459-81.

NSW 1988a, *Vertebrate Pest Control Manual*. Department of Agriculture New South Wales. Division of Animal Health.

NSW 1988b, *Effective Rabbit Control*, Agfact A9.0.11. Department of Agriculture New South Wales.

Parer, I. & Libke, J.A. 1991, 'Biology of the wild rabbit. *Oryctolagus cuniculus* (L.), in the south. Tablelands of New South Wales', *Wildlife Research*, vol. 18(3), pp. 327-41.

Recher, H.F., Lunney, D. & Dunn, I. (eds) 1986, *A Natural Legacy: Ecology in Australia*, Maxwell Macmillan Publishing Australia, Sydney.

Robertson, G., Short, J. & Wellard, G. 1987, 'The environment of the Australian sheep rangelands', in *Kangaroos*, eds G. Caughley, N. Shepherd & J. Short. Cambridge University Press, London, pp. 14-34.

Short, J. 1985, 'The functional response of kangaroos, sheep and rabbits in an arid grazing system', *Journal of Applied Ecology*, vol. 22, pp. 435-47.

Short, J. 1986, 'The effect of pasture availability on food intake, species selection and grazing behaviour of kangaroos', *Journal of Applied Ecology*, vol. 23, pp. 559-71.

Short, J. 1987, 'Factors affecting food intake of rangelands herbivores', in *Kangaroos*, eds G. Caughley, N. Shepherd & J. Short, Cambridge University Press, London, pp. 84-99.