PART VI

TAMMAR GRAZING AND THE PYROSERE ON MIDDLE ISLAND

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INTRODUCTION

The effects of grazing upon the course of secondary succession in Australian plant communities following fire have, according to Leigh and Holdgate (1979), been little-studied. The few cited by Leigh and Holdgate, including their own, have been undertaken in stands of vegetation that either include a significant component of alien annuals or are subject to grazing by introduced mammals or both. The absence of alien mammals and rarity of alien plants on Middle Island, largest island in the Recherche Archipelago, render it an exceptionally suitable site for the observation of the effects of grazing by indigenous mammals upon pyroseres in natural Australian plant communities.

As an adjunct to long-term observations of plant succession on Middle Island following the extensive, very hot 1972-1973 fire (Hopkins et al, Part VI, this volume) we carried out a brief investigation concerning the influence of grazing by herbivores on plant community development. The aims of the investigation were twofold: to enumerate the species of plants subjected to heavy grazing during the early stage of the pyrosere and to determine the importance of the grazed species in the diets of the herbivores.

The area chosen for the study was a completely burned stand of Melaleuca globifera forest on the southeast side of the granite outcrop west of Lake Hillary. This site, twenty months after the fire, was largely covered with a variety of shrubs and vines to a height of 50 cm (cf. Hopkins et. al., Part V, this volume). In terms of density, cover and biomass the most important of these were Anthocercis genistoides, Muehlenbeckia adpressa, Kennedia nigricans and Alyogyne hakeaefolia, all four of which were rare or absent from the island before the fire.

METHODS

The methods of investigation can be regarded as three stages, two undertaken on Middle Island in November 1974, and the third in the Zoology Department of the University of Western Australia, in Nedlands, subsequent to the field work.

During random traverses walked through the study area, a list of consistently heavily-grazed species was compiled. Samples of these species sufficiently large to be analyzed for water and nutrient composition were collected for subsequent analysis at the Zoology Department.

Trapping the putative grazers, the Tammar Wallaby (Macropus eugenii), and transporting them to the Zoology Department was the second stage of the investigation. The Tammar, a small, herbivorous, macropod marsupial, is the largest mammal recorded on the island, where it exists in low to moderate densities. Its preferred habitat on Garden Island and other places where it has been studied (Storr 1965, Kelsall 1965, Kinnear 1970, Bakker 1973) is a shrub community with a dense

canopy from 2 to 4 meters in height. The dense canopy provides protection from ~~aerial~~ avian predators, and below the canopy the Tammars prefer areas with little or no ground cover so that there is extensive visibility between the stems of the shrubs. During the night they move from these resting places to forage on low shrubs, forbs and grasses in nearby areas. Tammars were caught in circular net traps which were placed in the study area and nearby at the edge of a dense Leucopogon revolutus shrub community. The traps were baited with small pieces of bread flavoured with anise oil.

Stage three ~~was~~ comprised ~~of~~ physiological tests and laboratory analyses. Immediately after an animal's capture a bloodsample was taken, and upon ~~its~~ its arrival at the laboratory urine and faecal samples were collected. Total bodywater of ~~its~~ each captured animal was determined by the injection-of-tritiated-water technique described by Bakker and Bradshaw (1978). Plant water content was determined by drying the samples ~~its~~ at 105 C to constant weight, and nitrogen determinations were made using the Kjeldahl method (----------). The diet of the Tammars was inferred from visual observations of grazing animals and by signs of overgrazing on the vegetation. These observations were substantiated by the identification of pieces of epidermis in Tammar faecal pellets, following earlier work by Storr (1964), on Quokkas.

RESULTS

Three of the four most important species in the study area, Anthocercis genistoides, Kennedia nigricans and Muehlenbeckia adpressa, showed signs of heavy grazing. The following three ~~A fourth~~, much less common species, Rulingia cygnorum, were also heavily grazed. Petrophile linearis and

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one of the latter, the abundant _Alyogyne hakeaefolia_, was second only ~~to~~ _Kennedia nigricans_ in crude protein content. ~~and~~ The lowest crude protein content was _Muehlenbeckia adpressa_, one of the heavily grazed species. Apparently, the Tammars preferred a low nitrogen, relatively low water content species ~~to~~, _Anthocercis genistoides_, to some ~~of~~ higher nitrogen and higher water content species.

In some more disturbed regeneration plots *Acacia cyclops* was also grazed [illegible]

Table 1 gives the water content and crude protein percentages of the three most important species together with two other, control species that did not seem to form part of the Tammars' diet.

Only 7 animals were captured. All of them, 2 adult males, 4 adult females and 1 juvenile male, appeared to be in good condition. The average weight of the females was 3.75 ± 0.03 kg, and of the adult males, 5.53 ± 0.08 kg. The total bodywater content was 74.7 ± 1.04 % per animal. The mean volume of urine collected per 24 hours was 177.6 mls. *Anthocercis genistoides*, *Kennedia nigricans* and *Muehlenbeckia adpressa* comprised the bulk of the Tammars' diet. Faecal swabs analyzed for *Salmonella* gave negative results.

DISCUSSION

Although the effects of the Tammars' selective grazing on the growth, abundance and distribution of plant species are diverse and complex our observations suggest some trends and implications. The most important impact of the selective grazing is its influence upon the rate and nature of plant succession following burning, an impact impossible to quantify without long-term studies involving the use of fenced exclosures as control plots. It was obvious, however, that the rates of spread and of projective foliage cover increase of the two vines or lianas, *K. nigricans* and *M. adpressa*, were reduced by grazing. *A. genistoides* was kept pruned by the grazing to a small, compact shrub. The grazing pressure upon these species probably increases significantly during the dry season, when there is less active plant

Table 2.

Water and crude protein content (%) of some selected plants on Middle Island collected in November 1973. Protein content is expressed as % dry weight.

	% protein	% water
Anthocercis genistoides	8.9	73.7
Kennedya nigricans	14.0	72.0
Alyogyne hakeaefolia	10.8	79.7
Anthocercis viscosa	8.3	79.4
Ehrhlenbeckia adpressa	7.8	81.8

Table 2

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¶ An indirect effect of grazing upon pioneer species was the great reduction in their reproductive capacity. Although a large proportion of the affected plants survived the grazing many did so in stunted form with production of few flowers, as a result seed production would also be reduced and the next generation of these species could be expected to be smaller.

Our hypothesis that selective grazing of pioneer species facilitates the return of the climax community and influences the course of succession in not only the contemporary generation but also future generations is supported by the work of Leigh and Holdgate (1979) on the Southern Tablelands of New South Wales and Taylor and Weston (unpublished) near Perth, as well as by our observations on Middle Island.

growth and when the rock pools and other nonsaline sources of water have dried up. Indicative of this dry-season increase in grazing pressure is the fact that in May 1977 ring-barked Pimelea shrubs were found. Yet, Carpobrotus, a genus heavily utilized, presumably for its water content, by mammal herbivores in other places (e.g. Bald Island (Hopkins pers. comm.) and Rottnest Island (Storr 1964.)) was not grazed on Middle Island. and East Wallaby Island (Kinnear 1970),

The dominants of the climax community, Melaleuca globifera and Leucopogon revolutus, not only were avoided by the grazing Tammars but were benefited by the grazing. Where the pioneer community of clambering, intertangled vines was opened up by the grazing, the initially slower-growing Melaleuca and Leucopogon seedlings grow vigorously, while their counterparts under denser mats suffer a much higher rate of mortality. ~~It appears that selective grazing of pioneer species facilitates the return of the climax community.~~

Taken as a whole, the data seem to show that the animals caught were in good condition as a result of availability of high quality food and sufficient water, both in the plants and as free water in rockpools. This conclusion was supported by the low total bodywater figure, which is inversely related to animal condition (Main and Bakker 1979).

In November 1974 the Tammars in the study area did not seem to graze selectively ~~graze~~ for either water or nitrogen. With regard to water, this is hardly surprising since free water was still available. An explanation for the lack of selective grazing for nitrogen is not so ~~easily found~~. readily apparent. However, studies by Kelsall (1965)

and Kinnear (1970) indicate that Tammars are capable of existing (without ill effects) upon very low nitrogen levels. ~~Animals~~ The nitrogen levels in the plants grazed, and tested, were sufficiently high and similar to be unimportant in respect to the Tammars' food selection activities ~~consequently, other attributes of the species must have been important in the selection process.~~ All were well above the 6.9% figure given by Kinnear (1970) for Mirbelia ramulosa, a species heavily grazed by East Wallabi Island Tammars, collected in Summer (February). ~~Consequently~~ other attributes of the Middle Island species must have been important in their process of food selection or avoidance by the Tammars. The two most likely such sets of attributes are other nutrients (and mixes of nutrients) and chemical unpalatability. Westoby's theoretical discussion of the importance of ~~an~~ optimum mixes of nutrients in diets of large generalist herbivores (Westoby 1974) may be relevant to the Tammar situation on Middle Island. On the other hand, unpalatability could be a more important factor in the selection and avoidance process. For example, the bitter, external sticky covering on the leaves of Anthocercis viscosa may deter Tammars from eating them. It may be that, as Cates and Orians (1975) and Otte (1975) have postulated, early successional plants will be more palatable to generalist

[illegible] than later successional stages. Such a dichotomy could explain the avoidance of *Melaleuca globifera* and *Leucopogon revolutus* seedlings in favour of the vines, lianas and *Anthocercis genistoides*, but it would not ~~apply~~ explain avoidance ~~of~~ of *Alyogyne hakeaefolia*.

¶ The effects of large areas of high quality food on the population density ~~ability~~ of the Tammars is impossible to quantify without a regular census programme. One would expect, that under normal circumstances, there would be no more than ~~only a~~ small increases in Tammar numbers. Since only one young is produced per year and since at least two years are required to attain reproductive maturity, Tammar populations ~~they~~ are slow to respond ~~to~~ demographically ~~to~~ to increases in food supplies. Hopkins *et al.* (part V, this volume) shows that by the [illegible] or fourth year after a fire the pioneer plant species are being replaced rapidly by other species. Consequently, ~~[illegible]~~ the length of time during which there are large healthy populations of pioneer plant species ~~[illegible]~~ following an isolated major fire is too brief for the Tammar populations to show a dramatic increase ~~in~~ demographic response. ~~A population response to an increase in pioneer or colonizing species populations has been observed, however, among Tammar Wallabies on Barrow Island, where densities of both pioneer plants and wallabies are greater [illegible]. Here wallaby populations are denser on those parts of the island with regularly graded roads, where, as a consequence, more pioneer or colonizing species are growing.~~

2) Bakker, H.R. and Bradshaw, S.D. 1978. Plasma antiuretic hormone levles in Tammar Wallabies (Macropus eugenii) as measured by a toad bioassay. Journ. of Endocrinology 76: 167-168.

(3) Cates, R.G. and Orians, G.H. 1975. Successional status and the palatability of plants to generalized herbivores. Ecology 56: 410-418.

(10) Otte, D. 1975. Plant preference and plant succession: a consideration of evolution of plant preference in Schistocerca. Oecologia 18: 129-144.

Westoby, M. 1974. An analysis of diet selection by large generalist herbivores. Amer. Natur. 108: 290-304.

Leigh, J.H. and Holgate, M.D. 1979. The responses of the understorey of forests and woodlands of the Southern Tablelands to grazing and burning. Aust. ~~Forest~~ Journ. of Ecol. 4: 25-45.

(6) Kalsall, J.R. 1965. Insular Variability in the Tammar (Protemodon eugenii) of Western Australia. Ph.D. thesis. U.W.A.

(7) Kinnear, J.E. 1970. Nitrogen Metabolism of Macropods with special reference to the tammar (Macropus eugenii). Ph.D. Thesis U

(1) Storr, G.M. 1964. Studies on marsupial nutrition IV. Diet of the Quokka (, Setonix brachyurus (Quoy & Gaimard), on Rottnest Island, Western Australia. Aust. Journ. Biol. Sci. 17: 469-481.

(2) Storr, G.M. 1965. The physiography, vegetation and vertebrate fauna of the Wallaby Group, Houtman ~~and~~ Abrolhos ~~Islands~~. Journ. Proceed. Roy. Soc. W. A. 48: 1-14.

(1) Walker, E.R. 1973. The Hormonal Control of [illegible] and Electrolyte Metabolism of the Yabby (Cherax [illegible]). Ph.D. Thesis. U.W.A.

(4) Hopkins, ... [illegible] ...

(5) Hopkins, ... Part V... [illegible] ...

(9) Main, A.R. and Walker, E.R. 1973. Adaptation of crayfish [illegible] to aridity. In A. Frost (ed.) Ecological Biogeography in Australia (in [illegible]).

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(1) alker, E.R. 1973. The Hormonal Control of [illegible] and Electrolyte Metabolism of the Kowari (Sminthopsis crassicaudata). Ph.D. Thesis. U.W.A.

(4) Hopkins, ... [illegible] ...

(5) Hopkins, ... [illegible] ...

(9) [illegible], A. ... [illegible] ...

Main A.R. & Bakker H.R. (1981) Adaptations of macrop marsupials to aridity. In 'Ecological Biogeograph Australia' (Ed A Keast) pp 1489-519 CJunk-Hetta